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Ecological drivers of songbird stopover behaviour during autumn migration in eastern New Brunswick

Andrew T. Beauchamp, *The University of Western Ontario*

Supervisor: Morbey, Yolanda E., *The University of Western Ontario*
Joint Supervisor: Guglielmo, Christopher G., *The University of Western Ontario*
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Abstract

As songbirds migrate, they must periodically stop to rebuild the energy needed for flight. Individual traits, local habitat characteristics, and the surrounding landscape can affect stopover refuelling and movement, yet the relative importance of endogenous and exogenous factors and the interrelation between refuelling and movement is less well understood owing to the challenge of measuring these aspects concurrently in free-living songbirds. I applied physiological profiling and habitat assessment together with radio telemetry and radar technologies to evaluate key ecological drivers of stopover performance in songbirds. In my first research chapter, I evaluated how refuelling and diel activity patterns differed among five species, testing the hypothesis that refuelling intensity facilitates longer migration. Greater refuelling was associated with longer migration distances after accounting for the negative relationship between refuelling rate and the species-specific onset time of diurnal activity. In my second research chapter, I combined site-level measurements of invertebrate and migrant abundance with measures of refuelling and behaviour at coastal and inland stopover sites to assess how local habitat, landscape, and individual traits affect stopover performance. Songbird abundance was positively associated with invertebrate abundance, likely resulting from the earlier departure of birds experiencing poor refuelling at arrival. Behaviour and refuelling did not differ between coastal and inland stopover sites. In my third research chapter, resource augmentation was used to experimentally test if food availability affects refuelling and movement differently in the age and morph classes of the White-throated Sparrows (*Zonotrichia albicollis*). White-striped birds had greater refuelling when resources were augmented, but stopover behaviour did not differ according to treatment. In my final research chapter, I used radar and acoustic monitoring to test if visual and auditory information from volant migrants acts as a cue for departure, and whether sensitivity to these cues differs by age. Departure behaviour was not influenced by the passage of migrants nor by the number of night flight calls, but occurred earlier when wind conditions were more energetically favourable. Together, these studies provide insights into the relationships between refuelling, movement behaviour, and the environment that further our understanding of the migratory stopover behaviour of songbirds.

Keywords

Stopover Refuelling, Stopover Duration, Metabolite Profiling, Radio Telemetry, Radar, Acoustic Recording, Coastal landscape, Activity patterns, Departure Timing, Social Cues.

Summary for Lay Audience

As songbirds migrate between nesting and wintering areas, they must stop to rest and rebuild the energy needed for flight. Individual traits, such as which species it is or whether it is a young or old migrant, as well as external factors such as food availability and the suitability of conditions to migrate, can influence how long migrants spend at a stopover site. Due to the challenge of measuring these aspects in wild songbirds, whether individual traits or external factors have a greater impact on behaviour and refuelling, and how refuelling may influence behaviour is unclear. To further our understanding of songbird migration, I combined measurements of local food availability and bird abundance with measurements of individual refuelling and behaviour. I first looked at how refuelling and daily activity patterns differed among five study species. As anticipated, species that migrated longer distances were active earlier, refuelled faster, and remained for a shorter amount of time at a stopover site. I next looked at how food availability, the number of birds using a site, and individual traits such as age influenced refuelling and behaviour at coastal and inland stopover sites. More birds were captured at sites when more food was available, and migrants that experienced poor refuelling shortly after arrival were quick to leave a site. Behaviour and refuelling did not differ between coastal and inland stopover sites, suggesting that birds can use each region equally well during migration. I then built on this study by experimentally testing the effect of food availability on the refuelling and behaviour of White-throated Sparrows. Birds of the white-striped plumage morph refuelled better when food was provided, but stopover behaviour did not differ. Lastly, I used radar and acoustic recorders to test if birds were more likely to leave when other birds were passing by. Departure was not influenced the passage of migrants, but occurred earlier when wind conditions were more favourable. Together, these studies provide insights into the relationships between refuelling, movement behaviour, and the environment that further our understanding of the migratory stopover behaviour of songbirds.

Co-Authorship Statement

This dissertation contains modified versions of manuscripts that are under preparation for peer review and publication, for which I am the lead author. Abstracts for all publications have been incorporated into the general introduction, and the main body of the manuscripts have been incorporated into the data chapters. For all chapters, I conceptualised the study, collected and analysed the data, and wrote the manuscripts. Chapters 2, 3, 4, and 5 will be co-authored with Y.E. Morbey, C.G. Guglielmo, and P.D Taylor. Funding for this research was provided by Y.E. Morbey, C.G. Guglielmo, and P.D Taylor with addition support from Dr. Greg Mitchell of Environment and Climate Change Canada. All co-authors provided advice and guidance on study design, data analysis, and feedback during the preparation of the manuscript. In Chapter 5, acoustic and radar data collected as part of a regional avian migration monitoring project associated with wind energy development were provided by Taylor, P.D., with preliminary processing of radar and acoustic data conducted by project technicians H. Mann and J. Walker.

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"If I have seen further, it is by standing on the shoulders of giants."

- Sir Isaac Newton

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This research was conducted within the territories of the Mi’kmaq, Maliseet, and Passamaquoddy peoples. As a Canadian of European ancestry, I respect and recognize Indigenous Peoples of North America as contemporary stewards of the lands and affirm my responsibility of relationship building with Indigenous Peoples, knowledges, and ways of being.

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List of Abbreviations and Symbols

ADT	Atlantic daylight savings time
AHY	After hatch year
AIC	Akaike information criterion
AICc	Akaike information criterion - corrected for small sample size
ARU	Audio recorder unit
AUP	Animal use protocol
BUTY	β-OH-butyrate, β-Hydroxybutyrate, β-Hydroxybutyric acid
CFI	Community Forest International Whaelghinbran Property study site
CPUE	Catch-per-unit effort
dB	Decibel
eResI	Estimated resource abundance index
GAMs	Generalised additive model
HR	Hazard ratio
HY	Hatch year
kHz	Kilohertz
MAF	Mapleton Acadian Forest Nature Preserve study site
MPT	Mary's Point
NCEP/DOE	National Centre for Environmental Prediction/Department of Energy
NEFA	Non-esterified fatty acids
NFC	Night flight call
PC	Principal component
Radar	Radio detection and ranging
ResI	Resource abundance index
RI	Refuelling index
TRIG	Triacylglycerol, triglyceride
VLDL	Very-low-density lipoproteins
WAT	Waterside study site

Chapter 1

1 General Introduction

Spatiotemporal heterogeneity in biotic and abiotic conditions can increase the number of ecological niches present in a region, but this heterogeneity often necessitates specialized adaptations for organisms to persist in these dynamic environments. When patterns of spatiotemporal environmental variability are consistent and predictable, specialised behaviours may evolve that shape the life-history strategy of organisms in these environments. For much of the Earth, seasonal changes in surface insolation resulting from the axial tilt of our planet yields an annual rhythm of environmental change. In temperate regions, this can transform landscapes from icy and barren to verdant and flourishing, and drive pronounced changes in the availability of water in tropical regions. Overcoming such global-scale changes can require animals to move across a global scale, supported by a complex suite of adaptations that carry them away from their place of origin and back again. For many organisms, this type of movement, seasonal migration, is fundamental to their existence on this planet.

1.1 Birds: champions of migration

Among all taxa in which migration can be observed, few if any, can match the richness, diversity, and global ubiquity of migration as seen in birds. Approximately one-fifth of the over 10,000 bird species found around the globe are migratory (Kirby et al. 2008), encompassing an estimated 50 billion individuals (Berthold 2001) from species as diverse as the Ruby-throated Hummingbird (*Archilochus colubris*, Weidensaul et al. 2020) to the Gentoo Penguin (*Pygoscelis papua*, Martínez et al. 2020). Many bird species conduct seasonal to-and-fro journeys between breeding and non-breeding areas, which can range in scale from several hundred kilometers in short distance migrants like the Song Sparrow (*Melospiza melodia*, Davis and Arcese 1999) to the several thousand-kilometer migrations that bring Arctic Terns (*Sterna paradisae*) annually from pole to pole and back (Egevang et al. 2010). For species that breed in polar regions and in the temperate zone, seasonal latitudinal migration enables individuals to capitalise on the bountiful resources available during the productive summer months while avoiding the harsh winter conditions of the non-breeding season, and is the predominant life history strategy among avifauna in these regions (Newton and Dale 1996). In tropical and equatorial regions, migration can also occur across altitudinal gradients in response to variation in precipitation, food availability, and predation (Boyle 2008, Boyle et al. 2010).

Many songbirds, which are oscine birds of the taxonomic order Passeriformes, exhibit a migratory life history strategy. These often small-bodied birds are capable of Herculean feats of movement, with many species migrating thousands of kilometers between breeding and non-breeding areas twice annually. These journeys are not without peril however, and over half of the annual mortality of a species can occur during the migratory period in songbirds (Sillett and Holmes 2002) and other migratory bird groups (Lok et al. 2015, Paxton et al. 2017). To survive the journey and arrive in a timely manner, songbirds and other migratory species exhibit a suite of specialised physical, physiological, and behavioural traits that are tailored by the challenges faced by a species in its environment (Dingle and Drake 2007). In a world where the effects of human-induced climate warming are no longer theory, and where habitat alteration, degradation, and loss continue to plague ecosystems across the globe, understanding the ecology of migratory animals will be key to forecasting and mitigating the impacts of ongoing and future change. To do so will require a robust understanding of how migratory performance is shaped by both the individual and environment.

Songbird species migrate using flight powered by the flapping of their wings, which reduces the total energy required to travel a given distance in exchange for higher instantaneous rates of energy demand relative to other terrestrial modes of locomotion. Relative to similar non-migratory species, migratory species tend to have more streamlined bodies, slender skulls, and more pointed wings (Winkler and Leisler 2005, Dingle 2014) which can enhance flight efficiency by reducing aerodynamic drag. Dynamic changes to the alimentary tract size (McWilliams et al. 1999, McWilliams and Karasov 2014) can facilitate the rapid uptake of energy during periods of feeding between flights. This energy is stored primarily in the form of fat, maximising the caloric density and total energy carried for the additional body mass. Additional energy and supplementary metabolic products can also be provided through catabolism of muscle and digestive organ proteins during flight (Jenni and Jenni-Eiermann 1998, Groom et al. 2019), providing an additional supplemental boost to overall flight efficiency by reducing muscle mass which a now lean individual otherwise no longer requires (Pennycuick 2008).

Avian migrants exhibit numerous behaviours during migratory periods that complement their physical and physiological adaptations. Day length, which provides a consistent and reliable environmental cue for date, entrains the endogenous circannual cycles of migratory behaviour (Gwinner 1996) that are shaped by evolution to ensure the commencement or completion of migration occurs around the seasonally appropriate date. Famed for their sensing and use of the geomagnetic field (Wiltschko and Wiltschko 1972), songbirds can also integrate cues from celestial bodies (Emlen and Emlen 1966, Able 1989, Schmidt-Koenig 1990) to orient and navigate across the long distances travelled during migration. Many songbirds in the Nearctic-Neotropical realm alter their daily activity patterns during migration by conducting migratory flight primarily at night (Berthold 1996), although migratory flight may continue into the daylight hours if birds are unable to land (e.g. Diehl et al. 2003, Adamík et al. 2016). Reduced air turbulence (Schmaljohann et al. 2006), lowered thermoregulatory costs (Bairlein 1985), and decreased predation risk at night are thought to favour this behaviour. Flying by night also maximises the daylight hours available to forage for songbirds that primarily rely on vision to obtain food. Diet breadth and foraging intensity are also altered during the migratory period (Gifford and Odum 1965), likely to facilitate the rapid acquisition of the energy needed to power bouts of migratory flight.

In addition to dietary niche, fine-scale habitat preferences of a species can also differ during migration (reviewed by Petit 2000), although coarse-scale habitat and climatic associations are generally preserved among seasons (Nakazawa et al. 2004, Zurell et al. 2018, Illán et al. 2022). The relaxation of habitat use patterns may allow bird species to exploit the unpredictable environments encountered enroute (Morse 1971) where more preferred habitat types may be limited (Moore et al. 1990). Intra and inter-specific associations often change during the migratory period. Species that are largely solitary in the breeding season may form flocks numbering in the hundreds to thousands. As habitat and dietary preferences are also relaxed, species that do not typically co-occur at the fine scale during the breeding season can also be seen sharing habitat during migration. These changes in social behaviour and niche characteristics contribute to the large mixed-species flocks often observed during the migratory period. Migrating with other con- and hetero-specific migrants can in turn further influence foraging behaviour (Smith et al. 1999), individual predation risk (Cresswell 1994), navigation (Wakefield et al. 2019), and may yield increased flight efficiency if flights are conducted in formation (e.g. Weimerskirch et al. 2001).

1.2 Migratory stopover

Despite the array of behavioural and physiological adaptations that underlie their tremendous capacity for locomotion, most bird species do not complete their migratory journeys in a single flight. Instead, migration is completed as a series of flights punctuated by periods of time spent relatively stationary in patches of habitat encountered enroute, termed stopovers. For most songbirds, carrying sufficient energy to fly non-stop to the migratory destination is either not possible or may impose constraints on mobility that can decrease predator escape flight performance (Lima 1986, Lind et al. 1999, Burns and Ydenberg 2002). Stopovers between bouts of long-distance flight are then necessary to acquire the energy needed to complete the remaining migratory journey. These energy stores are rebuilt during periods of intensive foraging while on stopover, in a process commonly referred to as refuelling. Refuelling is one of the primary activities that occurs during migratory stopovers, but other behaviours such as recovering, resting, waiting for nightfall or favourable weather conditions, information gathering, and social interaction may also shape migratory stopover events (reviewed by Linscott and Senner 2021, Schmaljohann et al. 2022).

Songbirds generally spend more time and energy at stopover sites than in flight along the migratory route (Dolnik and Blyumental 1967, Hedenström and Alerstam 1997, Wikelski et al. 2003, Schmaljohann et al. 2012), primarily due to the slower rate at which energy is accumulated relative to the rate it is expended during migratory flight (Alerstam and Lindström 1990, Hedenström and Alerstam 1997, Alerstam 2011). As a result, variation in stopover duration can play a critical role in defining the overall speed and duration of migration, and prolonged stopover can affect arrival timing at end destinations (Tøttrup et al. 2012). Earlier arrival to breeding areas can be positively associated with individual reproductive success (Aebischer et al. 1996, Norris et al. 2004, Smith and Moore 2005), but arrival timing can also have population level impacts if arrival is not synchronised with environmental conditions on the breeding area (Both et al. 2006, Saino et al. 2011). Maintaining a rapid speed of migration through shorter stopover bouts can also reduce the time exposed to risks encountered enroute, including predators, diseases, and inclement weather events. Reducing the time spent in migration may also alleviate time constraints on other parts of the annual cycle, which may be of greater importance for species with longer migration distances. Correspondingly, these species tend to have faster migration speeds (La Sorte et al. 2013, Schmaljohann 2019), although whether these differences are driven by differences in refuelling and stopover duration remains largely uncertain.

1.2.1 Refuelling and stopover duration

Given that refuelling is one of the primary activities occurring during stopover, it is perhaps unsurprising that migrants captured with greater fuel stores tend to depart sooner from a stopover site (e.g. Goymann et al. 2010, Cohen et al. 2014, Deppe et al. 2015, Dossman et al. 2016). However, departure fuel load is difficult to measure, and this expectation is not universally supported among studies of songbird stopover (Ellegren 1991, Dierschke and Delingat 2001, Salewski and Schaub 2007, Tsvey et al. 2007, Morbey et al. 2018). In addition, departure decisions may be more nuanced. Models of optimal migration theory, derived from patch-selection and optimal foraging theory, have posited that departure decisions should be based on current fuel stores and refuelling conditions (Alerstam and Lindström 1990). Under models of optimal stopover duration (i.e., the marginal value theorem), migrants should depart from stopover when the instantaneous speed of refuelling drops below what is expected elsewhere across the migration route. Given that flight range increases with fuel load at decelerating rate, migrants should depart for a flight once the rate at which flight distance is gained drops to below what may be expected at a subsequent site. The covariates affecting departure fuel load depend on the migration strategy of an individual. For migrants that attempt to minimise time (i.e. maximise the speed or pace of migration) the departure fuel load should be sensitive to post-arrival settling time and the rate of fuel deposition expected across the migratory journey, with greater departure fuel loads when refuelling rates are higher. Expectations of refuelling conditions across the migratory route may be instinctual or based on experience of previous migrations, or may be updated by the conditions experienced at each stopover site (so called “global variation”) (Houston 1998). Global variation may itself be further informed by the distance travelled between consecutive sites, or represent an expectation of future stopover sites formed across multiple previous stopover locations (Weber 1999). The global variation rule tends to fit observed stopover behaviour better when predictions of the time-minimising optimal stopover duration model are tested (reviewed by Alerstam 2011), and many migratory bird species likely follow this strategy given the benefits associated with maintaining a high migration speed. As an alternative stopover refuelling strategy, migrants may opt to minimise the energy expended across the migratory journey by departing at the fuel load which minimises the cost of transport or to minimise the risk of predation which may be body mass dependent (Alerstam and Lindström 1990). Departure fuel loads under such a refuelling strategy should be invariant to the fuel deposition rate experienced at a stopover site.

Under both time and energy-minimising migration strategies, faster refuelling is predicted to reduce the length of time needed to obtain the “appropriate” departure fuel load, leading to a shorter stopover duration. Observations of positive correlations between departure fuel load, refuelling rate, and stopover duration (Carpenter et al. 1983, Lindström and Alerstam 1992, Schmaljohann and Dierschke 2005, Schmaljohann et al. 2013) provide support for the importance of refuelling rate in departure decisions, however, under variable or poor refuelling conditions, migrants may opt to abandon the stopover site early (Kuenzi et al. 1991, Ottich and Dierschke 2003, Schmaljohann and Dierschke 2005, Schaub et al. 2008). Schmaljohann and Eikenaar (2017) found that Northern Wheatears (*Oenanthe oenanthe*) experiencing mass loss or with low fuel deposition rates had a higher probability of leaving Helgoland Island than those with intermediate rates of fuel deposition. Similar patterns were observed among multiple

European Passerine species by Schaub et al. (2008), suggesting that migrants may follow a general behavioural rule where intermediate refuelling rates remained at a stopover site the longest.

1.2.2 How is refuelling shaped by the individual and environment?

Just as migration is a phenomenon shaped by multiple levels of biological organisation, the refuelling performance of songbirds during migratory stopover can be influenced by multiple interrelated factors across biological levels. At the organism level, measured refuelling rate can differ among and within individuals due to underlying physiology (Karasov and Pinshow 2000, McCabe and Guglielmo 2019). Variation in refuelling rate also can be attributed to the ability of migrants to find and obtain the resources needed to refuel in the stopover environment. Foraging ability can vary among individuals (Heise and Moore 2003), and the social status of a migrant may influence the outcome of competition for resources (Arizaga et al. 2011). Fundamentally, food must be available in sufficient quantities for migrants to refuel, and positive associations between the local availability of food and refuelling rate of migrants have been found previously (Schaub and Jenni 2000, Smith et al. 2007a). Other studies report conflicting evidence for a relationship between local food abundance and refuelling rate (Cerasale and Guglielmo 2010, Macdade et al. 2011). Refuelling rate can also be affected by the density of migrants using a site (Moore and Yong 1991, Kelly et al. 2002, Ottich and Dierschke 2003, Cohen et al. 2022), with greater densities leading to poorer refuelling rates. These effects are unlikely to be mutually exclusive, as migrants concentrated in the same patch may divide local resources through scramble or interference competition, leading to lower refuelling rates (Moore and Yong 1991, Moore et al. 2003, Arizaga et al. 2011). Disentangling these effects can be challenging, as local variation in resource availability and competition may mask underlying differences in refuelling based on individual characteristics (Hoh et al. 2018).

In addition to individual and habitat-scale factors, the broader landscape-scale context of a stopover site may further drive patterns of stopover refuelling and behaviour in songbirds. Along ecological barriers, such as waterbodies or deserts, migrants can accumulate in adjacent habitat patches due to limitations on the amount of habitat available in preparation to cross the adjoining barrier (Buler and Dawson 2014, Lafleur et al. 2016, Cohen et al. 2017). Similar constraints on habitat availability may lead to the accumulation of migrants in fragments of habitat patches embedded within inhospitable terrain, such as oases in desert landscapes (Bairlein 1985, Biebach 1985) or on islands. These landscape scale processes have the potential to affect refuelling via local-level competition for resources among migrants constrained to using these locations (Shochat et al. 2002, McCabe et al. 2019, Cohen et al. 2022). For example, Cohen et al. (2022) found negative density-dependent refuelling in songbird migrants using coastal stopover sites in a fragmented and urbanised landscape. Refuelling was poorer in smaller, more isolated patches, where the concentration of migrants was greater per-unit area; a pattern consistent with the non-ideal distribution of migrants limited in their knowledge of potential surrounding habitat.

Much of what we understand about songbird stopover in coastal habitats comes from regions where transit of an adjoining ecological barrier is required (Moore and Kerlinger 1987, Moore et al. 1990, Moore and Yong 1991, Yong et al. 1998, Åkesson and Hedenström 2000, Smith et al. 2007a, Macdade et al. 2011, Smith 2013, Schmaljohann et al. 2013, Dossman et al. 2016, Morbey et al. 2018, Hoh et al. 2018, Beauchamp et al. 2020). The importance of these areas as stopover habitats, and high abundance and turnover of migrants in these locations (Schmaljohann and Eikenaar 2017) may have contributed to the focus on understanding bird behaviour at these locations. These same factors may have contributed to the establishment of bird observatories in these regions, potentially reinforcing the tendency for research to occur at these locations and further shaping our understanding of stopover ecology to these areas. As a result, relatively few studies have assessed migratory refuelling and associated behaviour along coastlines either aligned with the direction of migratory travel or in situations where direct transit of the adjacent ecological barrier is not required. In these contexts, migrant ecology at coastal sites may better reflect the influence of the habitat features separately from any specialised behaviours associated with preparation for or recovery from crossing an ecological barrier.

1.2.3 Birds blown by the wind

Meteorological conditions can also govern stopover departure decisions in songbird migrants (Liechti 2006). The effect of wind conditions on songbird departure behaviour has been repeatedly observed (Åkesson and Hedenström 2000, Dossman et al. 2016, Morbey et al. 2018, Beauchamp et al. 2020, but see Bolus et al. 2017). Wind conditions affect the ground speed of a flying bird, and can significantly alter the energy used and time required to travel a given distance (Liechti 2006). Winds not parallel to the intended direction of travel can also result in directional drift and large-scale displacements that may require later correction (Shamoun-Baranes et al. 2017). Strong or highly turbulent wind conditions may also disrupt the capacity of migrants to maintain controlled flight. In addition to wind, weather conditions such as precipitation, cloud cover, atmospheric pressure, and temperature can also influence the departure behaviour in songbirds (Schaub et al. 2004, Liu and Swanson 2015, Berchtold et al. 2017, Panuccio et al. 2019, Packmor et al. 2020), although these effects can be less consistent (Packmor et al. 2020) or correlated with wind conditions (Beauchamp et al. 2020).

1.2.4 Gutsy young migrants

Migration represents a tremendous challenge for all migrants, but this challenge is likely greatest for young birds during their first migration. There are often only a few months available for a songbird to develop from an altricial nestling to a migration-capable adult and, while adult size and mass is generally reached, marked differences persist between hatch-year aged first-time migrants and after hatch year aged birds during the fall migration. Young birds typically have lower quality feathers that are less ridged and provide poorer insulation, and shorter flight feather lengths result in smaller and more rounded wings relative to adults (Arizaga et al. 2011, Saino et al. 2017, Deakin 2023). During fall migration, differences in the maturation of the skeletal (Wiley and Piper 1992), muscular (Guglielmo et al. 2002), and digestive systems (Graber and Graber 1962) may place hatch-year birds at an energetic disadvantage, although these effects may diminish later in the migration season (Pyle 1997). For example, McCabe and Guglielmo (2019) found young Swainson’s Thrush (*Catharus ustulatus*) and White-throated Sparrows (*Zonotrichia albicollis*) had larger digestive organs and a correspondingly higher basal metabolic rates compared to adults. Migratory birds also adjust decisions based on experience gained during previous migrations (Ketterson and Nolan 1985), and a lack of experience may reduce the capacity of younger birds to meet the contingencies of migration as effectively as adults. Prior to the start of migration, young birds typically forage as proficiently as adults in breeding areas (Wheelwright and Templeton 2003, Heise and Moore 2003), but unfamiliar habitats and novel food items encountered during stopover may contribute to poorer foraging in young birds (Gochfeld and Burger 1984, Wunderle 1991). Lower dominance or social status relative to adults may also reduce access to food for young (Wunderle 1991, Moore et al. 2003). Young birds can be less selective of energetically supportive wind conditions, both at the time of departure (Morbey et al. 2018) and during flight (Mitchell et al. 2015), leading to less energetically efficient migratory flight.

Despite these intrinsic physical and behavioural differences between age classes, evidence that age classes differ in stopover behaviour is inconsistent among studies. In line with purported behavioural differences in foraging ability or social dominance, young birds can have lower refuelling rates than adults during stopover (Woodrey 2000, Moore et al. 2003), although other studies have not detected this pattern (Morris et al. 1996, Jones et al. 2002, Brown et al. 2014). This discrepancy may suggest that age differences are moderated by extrinsic factors such as resource availability, which may alleviate the challenge of finding food or may reduce the competition for the resources available (Arizaga et al. 2011). Similarly, young birds often remain at stopover locations longer than older birds (Ellegren 1991, Morris et al. 1996, Rguibi-Idrissi et al. 2003, Mills et al. 2011, Collet and Heim 2022), but other studies have not observed difference stopover durations between age classes (Morris 1996, Woodrey and Moore 1997). Whether these age differences in stopover duration are associated with underlying differences in refuelling performance remains uncertain, as often the information on refuelling performance and stopover duration at the individual level is not available.

1.3 Studying migration from individual to flock

1.3.1 Fuelling for flight

Measuring refuelling rate during migratory stopover has historically relied on morphometric data collected from captured individuals. Individuals captured multiple times across a stopover bout can be used to directly measure rates of fuel deposition via changes in body mass or through visual assessment of subcutaneous fat deposits. Recapturing individuals can be challenging however, often requiring datasets collected as part of long-term banding efforts (e.g. de Zwaan et al. 2022). There is the potential for measures of refuelling based on recapture to be influenced by repeated capture stress or the higher probability of recapturing individuals that remain longer at stopover sites. An improvement to this technique has been to “recapture” birds using automated balances baited with food items (Dänhardt and Lindström 2001, Bayly 2006), however, this technique alters the availability of food at a stopover site. Refuelling rate can also be estimated for species or groups at the site level using regression between inter-individual capture mass and capture time, with the slope of the relationship representing an average refuelling rate of migrants using that location (e.g. Dunn 2000, Smith et al. 2007a).

Measurement of plasma metabolite concentrations can provide insight into the physiological state of birds and is a powerful tool for both field and lab-based ornithologists interested in bridging the gap between physiology and behaviour. For questions related to the dynamics of energy deposition and use, two metabolites have seen widespread use owing to their direct and clear relation to fat use and deposition: triglyceride and β-OH butyrate. Triglyceride (triacylglycerol), an ester composed of three fatty acids and glycerol “backbone”, is a key molecule facilitating vertebrate fat transport and storage. In birds, triglycerides present in ingested foods are absorbed in the intestine by passive diffusion via enterocytes, and packaged into portomicrons that pass through the hepatic portal system and into the circulatory system for use and storage (Guglielmo 2018, Oketch et al. 2023). In the liver, fatty acids synthesised *de novo* from carbohydrates and amino acid precursors are esterified to produce triglyceride, which is packaged into very-low-density lipoproteins (VLDL) for passage through the circulatory system. Cellular uptake occurs following hydrolysis of plasma VLDL to non-esterified fatty acids

(NEFA) by membrane bound lipoprotein lipase. Following protein mediated passage through the cellular membrane, NEFAs can either be combined with coenzyme-A for use by the mitochondria in energy production or re-incorporated into triglyceride for intercellular storage. For the use of fats stored in adipocytes, hydrolysis of triglyceride to NEFA by intracellular hormone sensitive lipase occurs prior to NEFA re-entering circulation. Concentrations of triglyceride in blood plasma become elevated during periods of feeding when fats are being stored for future use, and elevated concentrations are positively correlated with increases in total mass (Jenni-Eiermann and Jenni 1994, Cerasale and Guglielmo 2006, Smith et al. 2007b, Anteau and Afton 2008) in bird species.

The ketone body β-OH-butyrate (β-Hydroxybutyrate, β-Hydroxybutyric acid) is synthesised from the partial β-oxidation of free fatty acids in the liver during gluconeogenesis. Together with other ketone bodies, butyrate released by the liver acts as a circulating fuel source which can be absorbed and converted to acetyl-CoA for energy production in mitochondria during periods when energy intake is insufficient to meet energy demands. Critically, ketone bodies can cross the blood-brain barrier, providing energy where NEFAs released by adipose tissues cannot. Regulation of ketogenesis through various physiological mechanisms limits production when in a fed state (Grabacka et al. 2016), resulting in low plasma concentrations of β-OH-butyrate during fat deposition. As such, plasma concentrations of β-OH-butyrate show a negative correlation with increases in total body mass (Jenni-Eiermann and Jenni 1994, Smith et al. 2007b, Anteau and Afton 2008).

1.3.2 Songbirds on the move

As animals with a high capacity for movement, sophisticated methods can be required to quantify the movement behaviour of songbirds. Direct observations and methods such as mark-recapture or resighting have been used to measure behaviour and estimate stopover duration (e.g. Rappole and Warner 1976), but collecting movement data with these techniques can be intensive and limited in temporal and spatial scope. Developments in tracking technologies and associated analytical techniques have provided solutions to these challenges, yielding novel methods to answer questions about individual level behaviour in this “Golden Age of bio-logging” (McKinnon and Love 2018). Trade-offs between power requirement, battery life, and relative tag mass typically prohibit the use of global position system (GPS) transmitters on small-bodied birds, and lighter GPS and light-level geo-loggers require recovery to obtain the movement data. For studying songbird behaviour during migratory stopover, radio transmitters currently offer the best balance of size, cost, and precision.

Radio tags emit a signal detectable by a receiver tuned to the same frequency. Tracking individuals is accomplished by homing into the tagged individual based on strength of the received signal. Historically, tracking multiple animals required switching among different tag frequencies. The development of tags that emit encoded radio pulses allowed for the unique identification of multiple radio tags on the same frequency, providing the opportunity for larger study sample sizes and common frequency automated receiver networks. The Motus Wildlife Tracking System (henceforth: Motus) (Taylor et al. 2017) epitomizes the application of this technology, allowing tagged animals to be tracked across hemispheres using a network of collaborator-run receiver stations. Each station consists of a tower with multiple antennae that record the time and signal strength of each detection in addition to other detection variables, with reception of signals from flying animals occurring up to 15 km away in the absence of obstructions.

In addition to inter-station movements, automated radio telemetry systems like Motus can be used to evaluate behaviour at the local scale using the data from a local station. The high rate of radio signals emitted by tags provides a method to “recapture” an animal at a high temporal frequency, allowing for local presence to be determined at the sub-minute resolution. This technique has been employed previously to determine stopover departure time and to estimate stopover duration (e.g. Dossman et al. 2016, Morbey et al. 2018). Data on the onset and end of diel activity can also be obtained from patterns of variability in received signal strength between consecutive detections (Morbey et al. 2018). When temporal variability in signal strength is low, tagged animals are likely stationary, and this is typically observed at night when songbird migrants are presumed to be sleeping. When active, changes in position and orientation relative to the receiver antennae, together with variation in the amount of obstruction, yield high levels of temporal variability in signal strength. When plotted over time, the transition between active and inactive states creates a characteristic pattern that can be used to determine the timing of changes between states of activity and inactivity (Morbey et al. 2018, 2020; Beauchamp et al. 2020, Morales et al. 2022).

1.3.3 Counting migrants on land and above

Assessing the density or relative abundance of migrants at a stopover site can be accomplished using standardised observation protocols or using effort-corrected mist netting (e.g. Dunn et al. 1997, Buler and Moore 2011). Both techniques can be used to derive comparable estimates of relative abundance (Wang and Finch 2002), particularly during migration when species-habitat associations are relaxed and birds are active while foraging (Yong and Moore 1993). Transect or point surveys can be used to assess migrant abundance or density over greater areas with relatively lower effort, but may be biased towards more detectable species and may obscure localised spatial variability in migrant abundance. Conversely, mist netting can be biased towards species that use understory or low-level habitat, but can reduce issues with detectability and observer bias. Quantifying the passage of migrants overhead can represent a greater technical challenge. Visual counts of migrants silhouetted against the Lunar disk (Scott 1881) or using video or thermal imaging technology (Gauthreaux Jr and Livingston 2006, Bridge et al. 2024) can be used to quantify the passage of migrants, but the application of radar has provided revolutionary insights into broad and local scale activity and movement of migrants (Nisbet and Drury 1969, Richardson 1978, Buler and Dawson 2014). Radar, standing for radio detection and ranging, uses the time between the emission and return of a radio wave reflected off an object to estimate the distance between the object and the radar transmitter. Birds have been detected by radar since the early application of this technology in military applications (Lack and Varley 1945). In certain configurations, radar units have the sensitivity to detect discrete flying targets, and these technologies have been applied to quantify local passage of migrants in the air space surrounding the radar unit (Peckford and Taylor 2008). In addition to visual or radar observation, acoustic monitoring for night flight calls (NFCs) and other nocturnal vocalisations made by migratory songbirds can be used to quantify the passage of migrants over a location.

Advances in acoustic recording technology and the development of computer models for identifying recorded NFCs down to the species level have alleviated much of the burden associated with quantifying migrant passage using recordings of vocalisations (e.g. Larkin et al. 2002, Gillings and Scott 2021).

1.4 Regional Context: songbird migration through New Brunswick, Canada

1.4.1 Forest songbirds in Canada

Songbirds are a vital part of Canadian forest ecosystems, yet the majority of species are migratory, spending their non-breeding season in the south. During the summer breeding season, these species help to regulate insect populations (Monteagudo et al. 2023), disperse plant seeds (Holthuijzen and Sharik 1985), and provide other ecosystem services that that are crucial to the maintenance of healthy forest ecosystems (reviewed by Whelan et al. 2008). Like numerous taxa in the global biodiversity crisis of the Anthropocene, recent evidence suggests that songbird species found across the forests of Canada are in decline (Rosenberg et al. 2019), with group-specific and regional declines observed among early successional forest species, Neotropical migrants, and species in the eastern forests (Sauer et al. 2013). Breeding habitat loss and degradation associated with silvicultural and forestry practices has likely contributed to the decline of forest bird species in the Maritime provinces of Canada (Betts et al. 2022). Understanding the ecology of migratory forest songbirds in these regions will increase our general understanding of songbird migration in Canada, and will also contribute to the development of conservation and management strategies aimed at mitigation of ongoing and future threats and challenges faced by these species.

1.4.2 Coastal New Brunswick

In this dissertation, I studied the migratory stopover ecology of forest dwelling songbirds using coastal and inland study sites in eastern New Brunswick, Canada. The study region (Figure 1-1) is characterised by rolling topography interspersed with river valleys and low-elevation mountains (e.g., Caledonia Mountain, ~ 400 meters above sea level), and is within the territories of the Mi’kmaq, Maliseet, and Passamaquoddy peoples. Forests have been the predominant landcover of this region post-glaciation, dominated primarily by northern adapted tree species of the genera *Picea, Abies, Larix, Pinus, Acer,* and *Betula* (Zelazny 2007). This region also borders the Bay of Fundy, and coastal habitat ranges from high cliffs to flat marshlands and mudflats resulting from the highest tidal range in the world. Following the arrival of European colonists, substantial modification of landscape occurred as forests were cleared to harvest timber and in preparation for settlement and agriculture. Earthen dykes were created in coastal marshlands to control tidal flooding and make the habitat available for agriculture. Since around 1940, the percentage of land area devoted to agriculture has substantially diminished in the province, but the historical and present importance of logging and suppression of fire regimes has resulted in changes to composition of the forest towards faster growing softwood species (Zelazny 2007). In the current era, forestry practices (Betts 2005, Betts et al. 2022) and changes to moisture and temperature regimes related to climate change (Albert et al. 2023) continue to threaten the forest of eastern New Brunswick, reducing the quantity and quality of the habitat available for forest songbirds. Wind energy generation is also rapidly growing in the province, both increasing the direct risk of mortality from collisions with turbines and associated energy infrastructure (Rioux et al. 2013, Loss et al. 2015) and further contributing to loss of habitat for forest birds (McDonald et al. 2009, Zimmerling et al. 2013).

1.4.3 Songbird migration in New Brunswick

The province of New Brunswick is home to over 150 species of bird (Stewart et al. 2015), with many other species from a wide range of avian taxa passing through the province during spring and fall migration. Isotopic evidence suggests that autumn songbird migrants in the region represent a mix of individuals from within the Canadian maritime provinces and from further north in the provinces of Newfoundland and Labrador, and Quebec (Dunn et al. 2006, 2023). Much of what is known about songbird ecology in New Brunswick pertains to the breeding season (e.g. Betts 2005, Haché et al. 2016, Ward 2020), often with emphasis on how forestry practices in the province effect habitat use and behaviour, and relatively few studies have been dedicated to assessing migration ecology of forest dwelling songbird species, particularly on mainland locations.

Radar studies using weather surveillance and short-range marine radar occurring across the Atlantic provinces have shown that the movement of migrants is generally occurs parallel to the continental coastline and in regionally consistent “broad front” patterns (Richardson 1972, 1978). Variation in the regional movement behaviour can occur at sites adjacent to ecological barriers, such as the Gulf of Maine, that must be crossed or circumnavigated (Peckford and Taylor 2008, Thurber 2010). The number of birds migrating is also generally greatest with supportive winds and favourable weather conditions (Drury and Keith 1962, Richardson 1978) for a given date within the migratory period.

Much of the recent songbird migration research in the province has occurred on Kent Island, located on the border of New Brunswick and the neighboring state of Maine and centered on a relatively isolated breeding population of Savannah Sparrows (*Passerculus sandwichensis*) (Mitchell et al. 2012, 2015; Woodworth et al. 2016). This system has provided novel insights about aspects of migration ecology such as differential migration timing (Woodworth et al. 2016), carry over effects between breeding and migration (Mitchell et al. 2011, 2012), post-departure movement behaviour (Mitchell et al. 2015), in addition to numerous studies on breeding behaviour, dispersal, and ontogeny (e.g. Wheelwright et al. 1992, Wheelwright and Mauck 1998, Wheelwright and Templeton 2003). Similar breeding and regional movement studies have been conducted on passerine aerial insectivores elsewhere in the province of New Brunswick (e.g. Imlay et al. 2020), though the behaviour of these species may be difficult to extrapolate to other songbirds due to the fly and forage migration strategy used by these species. Studies of songbird migratory departure and regional movement behaviour have also occurred in Nova Scotia and at sites along the coast of Maine. Autumn migrants in southern Nova Scotia are faced with the choice between cross the Gulf of Maine or circumnavigation of this barrier (Woodworth et al. 2014, 2015; Brown and Taylor 2015, 2017; Cormier and Taylor 2019), representing a separate regional context than the province of New Brunswick. Studies of fall migratory movement behaviour in Maine and further abroad in Rhode Island also tend to be located primarily in coastal and island habitats (Morris and Glasgow 2001, Smith and McWilliams 2010, Smetzer et al. 2017, McCabe et al. 2019), which may concentrate migrants the habitat patches available

(McCabe and Olsen 2015) and lead to poorer body condition in migrants using these sites (McCabe et al. 2019).

Despite the historic losses and ongoing threats to forest songbird habitat in New Brunswick, forests cover over 80% of the province (Martin 2003) and the total amount of forest cover in the region has remained relative stable since 1985 (Betts et al. 2022). This relatively high degree of forest cover provides an opportunity to evaluate the migratory stopover ecology of forest songbirds in a largely forested landscape, which may both limit the aggregation of species into available habitat patches and better reflect the landscapes present in the evolutionary history of these species. Most songbird migrants transiting through the coastal regions of eastern New Brunswick during autumn migration are unlikely to be readying for a prolonged overwater crossing, providing an opportunity to assess the effect of proximity to the coast on refuelling and behaviour independent from any barrier-crossing specific behaviours. Given the relatively early position of eastern New Brunswick along the migratory journey of many songbird species, differences between young and old migrants may be greatest during stopovers in this region (Wheelwright and Templeton 2003), and less selective loss of poorer performing young birds may have occurred prior to migrants reaching this area (Sergio et al. 2014). Together, these characteristics of the study regions provide an excellent opportunity to evaluate migratory stopover behaviour North American songbird species in a more natural landscape, and to test how individual traits and environmental conditions influence the migratory behaviour of forest songbirds.

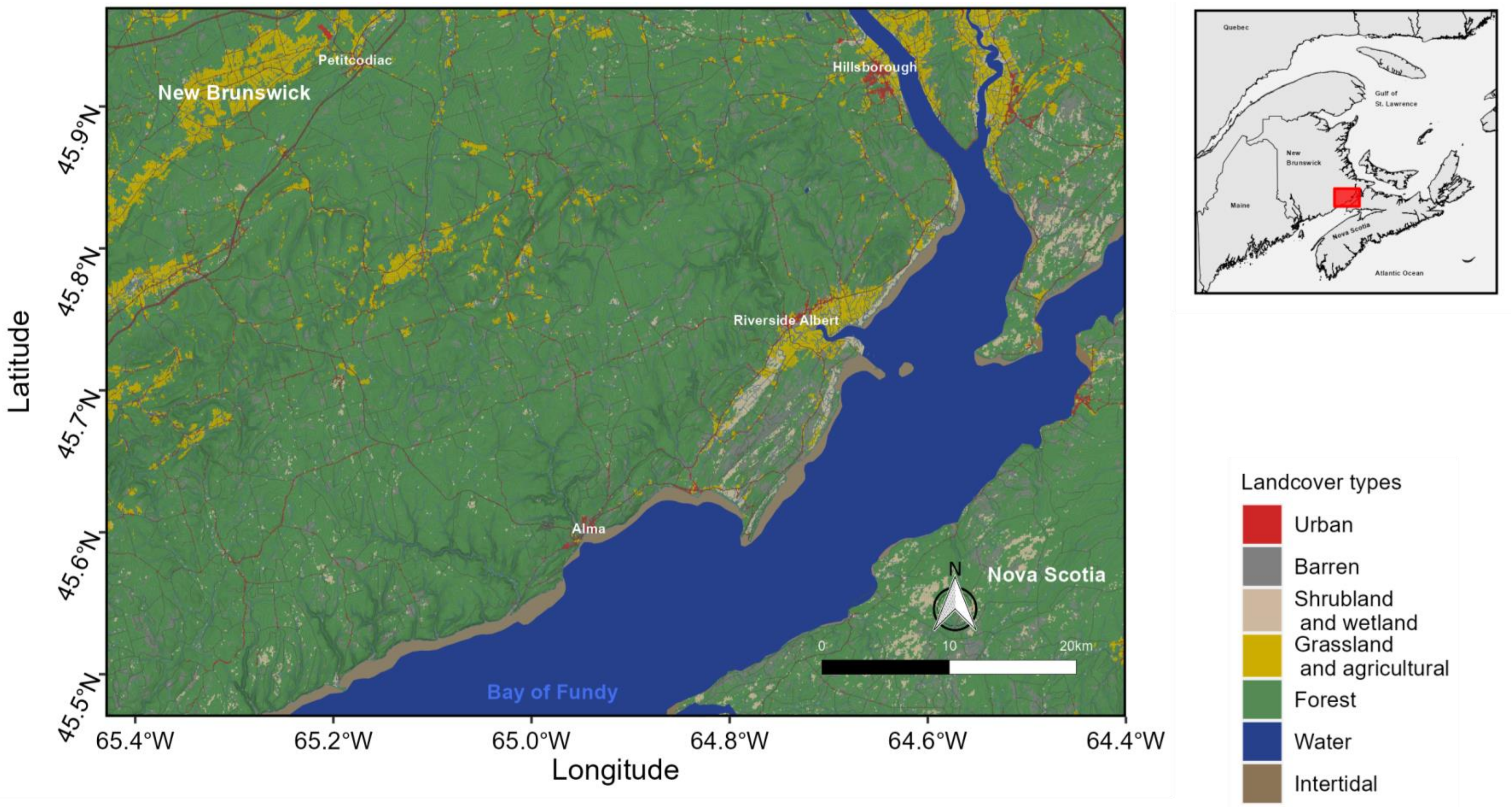


Figure 1-1 Study region, with 2021 landcover classification in eastern New Brunswick, Canada. Also indicated are roadways, watercourses, and topography at intervals of 10 meters. Landcover type “forest” includes coniferous, broadleaf, mixedwood and undifferentiated forest. Raster landcover classification data adapted from (Agriculture and Agri-food Canada 2023), vector data from (DMTI Spatial Inc. 2014a, b, c, 2017a, b, c, 2021).

1.5 Dissertation structure

My dissertation addresses the interactive effects of environmental characteristics and individual traits on the migratory stopover ecology of migratory forest songbirds in the Nearctic-Neotropical realm. While we broadly understand the process of migration, migratory strategies, and the key ecological factors that can influence the process of songbird migration, previous studies have often focused on a limited number of ecological factors and migratory phenotypes in specific contexts which may limit our understanding of the dynamic relationships that shape the migratory behaviour of songbirds. I aimed to address gaps in our knowledge by extending the scope of the ecological factors considered in the context of a relatively undisturbed landscape absent of major barriers to movement, while also providing information about the migration of forest songbird in the understudied region of eastern New Brunswick. The four research chapters focus on the testing the following questions concerning key ecological interactions:

> Chapter 2: How does stopover refuelling rate and stopover behaviour differ according to the migration distance of a species?
>
> Chapter 3: How do key environmental and individual characteristics shape refuelling rate and behaviour at coastal and inland stopover sites?
>
> Chapter 4: How does variation in food availability affect class-specific refuelling and behaviour?
>
> Chapter 5: How do social and environmental conditions affect migratory departure timing?

Chapter 2 was a comparative study of stopover ecology to test the hypothesis of an association between refueling intensity and migration distance. To do so, I applied plasma metabolite profiling and radio telemetry to measure refuelling and diel activity timing, respectively in five songbird species during autumn migratory stopover. I also evaluated how interspecific differences in the onset timing of diel activity affect the assessment of refuelling based on metabolite profiling, which has a known sensitivity to time of day thought to be related to the start time of feeding. Among the species studied, greater instantaneous refuelling rate was associated with longer migration distance, and this effect was significant after accounting for the negative relationship between refuelling rate and the species-specific onset time of diel activity. Longer distance migrants also had shorter stopover duration. The onset, end, and duration of diel activity differed among study species, with greater migration distance and visual acuity associated with the earlier onset of activity. Activity duration also decreased for each day of year at roughly the same rate as the seasonal decrease in daylength. These results show how the faster migration of long-distance migrants can be facilitated by faster instantaneous refuelling, and illustrate how an earlier migration date may promote greater refuelling through longer periods of diurnal activity. This study also suggests that variation in the onset timing of diel activity is important to consider when making assessments of refuelling based on metabolites.

Chapter 3 was an observational study focused on the ecological drivers of refueling intensity and stopover behaviour between inland and coastal sites. I combined site-level measurements of invertebrate and migrant abundance with individual-level measures of refuelling and behaviour, and found little difference in refuelling and behaviour of migratory songbirds between coastal and inland stopover sites in a habitat-rich coastal region where crossing the adjoining waterbody is not necessary to progress migration. Instead, songbirds appeared to use stopover sites in accordance with invertebrate abundance, moderated by earlier departure of birds experiencing poor refuelling on arrival. Across three autumn migrations, I collected 290 plasma samples and deployed 137 radio tags on five migratory songbird species at two coastal and two inland sites in eastern New Brunswick. Local invertebrate abundance was positively associated with the abundance of migratory songbirds at stopover sites, but individual-level refuelling measured using plasma metabolite analysis did not vary according to local invertebrate abundance or the abundance of migrants at the stopover site. After accounting for energetic condition at capture, radio telemetry indicated that poorer refuelling birds had a greater hazard for departure. Together, these results suggest that greater invertebrate abundance enables more individuals to refuel at a stopover site without suffering declines in refuelling rate, and that this pattern is driven by departure of individuals experiencing poorer refuelling conditions on arrival. Refuelling rate and stopover duration were also independent of age class, but younger hatch-year birds moved greater distances during stopover. My study illustrates the complex interplay between the refuelling and behaviour during stopover, and suggest that the large landscape context may play an important role governing stopover behaviour in migratory songbirds.

Chapter 4 used an experimental approach to address the hypothesis that food availability affects individual stopover ecology. Here, I combined physiological profiling and radio telemetry with experimental resource manipulation to test how variation in food availability and class-based differences in foraging proficiency, competitive ability, and social dominance shape stopover refuelling performance and movement behaviour in wild free-living White-throated sparrows (*Zonotrichia albicollis*) during autumn migration. In addition to behavioural and physiological differences related to age class, this species also exhibits genetically determined plumage morphs that differ in dominance and competitive abilities, providing an additional axis along which to test the hypothesis that patterns of class-specific refuelling and behaviour are moderated by local resource availability. When local food availability was augmented, birds of the more competitive white-striped plumage morph had greater refuelling rates than less competitive tan-striped birds, but local movement and stopover duration did not differ between plumage morphs or by food treatment. Age classes did not differ in refuelling rate, local movement behaviour, or stopover duration. Instead, stopover duration was primarily influenced by exogenous factors, decreasing with greater tailwind assistance and capture date. These results illustrate how resource availability can moderate the impact of behavioural differences on refuelling, but that these dynamics have little impact on behaviour in the context of autumn migratory stopover in New Brunswick.

In **Chapter 5**, I tested the hypothesis that visual and auditory social information act as cues for within-night departure in White-throated Sparrows (*Zonotrichia albicollis*), Hermit Thrush (*Catharus guttatus*), and Swainson’s Thrush (*Catharus ustulatus*) during autumn migration. To do so, I used a novel combination of data from an automated radio telemetry system, short-range marine radar units, and acoustic recorders in a survival analysis framework to evaluate how the hazard for migratory departure within the departure night of an individual varied by the overhead passage of migrants and the number of night flight calls recorded. I also tested for the effect of local wind conditions on departure timing to contrast the influence of social and environmental cues on departure timing, and evaluated whether sensitivity to social and environmental cues differed between age classes. Stopover departure hazard was not influenced by the passage of migrants overhead nor the number of night flight calls recorded. Instead, departure hazard increased with more energetically favourable wind conditions, indicating earlier departure on nights more suitable for migratory flight. My findings suggest that social information available from passing migrants is not a dominant cue used to time migratory departure in my study system.

Synthesis of the primary findings from my research chapters is provided in **Chapter 6**, along with discussion of how these findings further our understanding of songbird stopover ecology. I end the chapter by providing some perspectives for future research.

1.6 References

Able, K. P. (1989). Skylight polarization patterns and the orientation of migratory birds. Journal of Experimental Biology 141:241–256.

Adamík, P., T. Emmenegger, M. Briedis, L. Gustafsson, I. Henshaw, M. Krist, T. Laaksonen, F. Liechti, P. Procházka, V. Salewski, and S. Hahn (2016). Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. Scientific Reports 6:21560.

Aebischer, A., N. Perrin, M. Krieg, J. Studer, and D. R. Meyer (1996). The role of territory choice, mate choice and arrival date on breeding success in the Savi's Warbler *Locustella luscinioides*. Journal of Avian Biology 27:143–152.

Agriculture and Agri-food Canada (2023). Annual Crop Inventory 2021 - Pre-packaged GeoTIF files. [Online.] Available at https://agriculture.canada.ca/atlas/data_donnees/annualCropInventory/data_donnees/tif/2021/.

Åkesson, S., and A. Hedenström (2000). Wind selectivity of migratory flight departures in birds. Behavioral Ecology and Sociobiology 47:140–144.

Albert, C., A. R. Taylor, T. Logan, and L. D'Orangeville (2023). The Acadian Forest of New Brunswick in the 21st century: what shifting heat and water balance imply for future stand dynamics and management. Environmental Reviews 31:690–707.

Alerstam, T. (2011). Optimal bird migration revisited. Journal of Ornithology 152:5–23.

Alerstam, T., and Å. Lindström (1990). Optimal bird migration: the relative importance of time, energy, and safety. In Bird Migration. Springer-Verlag, New-York, NY, USA, pp. 331–351.

Anteau, M. J., and A. D. Afton (2008). Using plasma-lipid metabolites to index changes in lipid reserves of free-living Lesser Scaup (*Aythya affinis*). The Auk 125:354–357.

Arizaga, J., H. Schmaljohann, and F. Bairlein (2011). Stopover behaviour and dominance: a case study of the Northern Wheatear *Oenanthe oenanthe*. Ardea 99:157–165.

Bairlein, F. (1985). Body weights and fat deposition of Palaearctic passerine migrants in the central Sahara. Oecologia 66:141–146.

Bayly, N. J. (2006). Optimality in avian migratory fuelling behaviour: a study of a trans-Saharan migrant. Animal Behaviour 71:173–182.

Beauchamp, A. T., C. G. Guglielmo, and Y. E. Morbey (2020). Stopover refuelling, movement and departure decisions in the White-throated Sparrow: The influence of intrinsic and extrinsic factors during spring migration. Journal of Animal Ecology 89:2553–2566.

Berchtold, A., I. Nightingale, C. Vandermeer, and S. A. MacDougall-Shackleton (2017). Experimental temperature manipulations alter songbird autumnal nocturnal migratory restlessness. Animal Migration 4:1–7.

Berthold, P. (1996). Control of Bird Migration. Springer Science & Business Media.

Berthold, P. (2001). Bird migration: a general survey. Oxford University Press, Oxford, UK.

Betts, M. G. (2005). Independent effects of habitat amount and fragmentation on songbirds in a forest mosaic.

Betts, M. G., Z. Yang, A. S. Hadley, A. C. Smith, J. S. Rousseau, J. M. Northrup, J. J. Nocera, N. Gorelick, and B. D. Gerber (2022). Forest degradation drives widespread avian habitat and population declines. Nature Ecology & Evolution 6:709–719.

Biebach, H. (1985). Sahara stopover in migratory flycatchers: fat and food affect the time program. Experientia 41:695–697.

Bolus, R. T., R. H. Diehl, F. R. Moore, J. L. Deppe, M. P. Ward, J. Smolinsky, and T. J. Zenzal (2017). Swainson’s Thrushes do not show strong wind selectivity prior to crossing the Gulf of Mexico. Scientific Reports 7:14280.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser (2006). Climate change and population declines in a long-distance migratory bird. Nature 441:81–84.

Boyle, W. A. (2008). Can variation in risk of nest predation explain altitudinal migration in tropical birds? Oecologia 155:397–403.

Boyle, W. A., D. R. Norris, and C. G. Guglielmo (2010). Storms drive altitudinal migration in a tropical bird. Proceedings of the Royal Society B: Biological Sciences 277:2511–2519.

Brown, J. M., B. J. McCabe, L. V. Kennedy, and C. G. Guglielmo (2014). Genetically-based behavioural morph affects stopover refuelling performance in White-throated Sparrows *Zonotrichia albicollis*. Journal of Avian Biology 45:522–527.

Brown, J. M., and P. D. Taylor (2015). Adult and hatch-year Blackpoll Warblers exhibit radically different regional-scale movements during post-fledging dispersal. Biology Letters 11:20150593.

Brown, J. M., and P. D. Taylor (2017). Migratory Blackpoll Warblers (*Setophaga striata*) make regional-scale movements that are not oriented toward their migratory goal during fall. Movement Ecology 5:15.

Buler, J. J., and D. K. Dawson (2014). Radar analysis of fall bird migration stopover sites in the northeastern U.S. The Condor 116:357–370.

Buler, J. J., and F. R. Moore (2011). Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. Journal of Ornithology 152:101–112.

Burns, J. G., and R. C. Ydenberg (2002). The effects of wing loading and gender on the escape flights of Least Sandpipers (*Calidris minutilla*) and Western Sandpipers (*Calidris mauri*). Behavioral Ecology and Sociobiology 52:128–136.

Carpenter, F. L., D. C. Paton, and M. A. Hixon (1983). Weight gain and adjustment of feeding territory size in migrant hummingbirds. Proceedings of the National Academy of Sciences 80:7259–7263.

Cerasale, D. J., and C. G. Guglielmo (2006). Dietary effects on prediction of body mass changes in birds by plasma metabolites. The Auk 123:836–846.

Cerasale, D. J., and C. G. Guglielmo (2010). An integrative assessment of the effects of tamarisk on stopover ecology of a long-distance migrant along the San Pedro river, Arizona. The Auk 127:636–646.

Cohen, E. B., W. C. Barrow, J. J. Buler, J. L. Deppe, A. Farnsworth, P. P. Marra, S. R. McWilliams, D. W. Mehlman, R. R. Wilson, M. S. Woodrey, and F. R. Moore (2017). How do en route events around the Gulf of Mexico influence migratory landbird populations? The Condor 119:327–343.

Cohen, E. B., J. M. Lafleur, and F. R. Moore (2022). Density dependent refueling of migratory songbirds during stopover within an urbanizing coastal landscape. Frontiers in Ecology and Evolution 10.

Cohen, E. B., F. R. Moore, and R. A. Fischer (2014). Fuel stores, time of spring, and movement behavior influence stopover duration of Red-eyed Vireo *Vireo olivaceus*. Journal of Ornithology 155:785–792.

Collet, L., and W. Heim (2022). Differences in stopover duration and body mass change among *Emberiza* buntings during autumn migration in the Russian Far East. Journal of Ornithology 163:779–789.

Cormier, D. A., and P. D. Taylor (2019). Contrasting patterns of post-fledging movements of two sympatric warbler species with different life-history strategies. Journal of Avian Biology 50.

Cresswell, W. (1994). Flocking is an effective anti-predation strategy in Redshanks, *Tringa totanus*. Animal Behaviour 47:433–442.

Dänhardt, J., and Å. Lindström (2001). Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Animal Behaviour 62:235–243.

Davis, A., and P. Arcese (1999). An examination of migration in Song Sparrows using banding recovery data. North American Bird Bander 24:124–128.

Deakin, J. (2023). Differential migration timing and the form and function of avian wings. [Online.] Available at https://ir.lib.uwo.ca/etd/9779.

Deppe, J. L., M. P. Ward, R. T. Bolus, R. H. Diehl, A. Celis-Murillo, T. J. Zenzal, F. R. Moore, T. J. Benson, J. A. Smolinsky, L. N. Schofield, D. A. Enstrom, et al. (2015). Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. Proceedings of the National Academy of Sciences 112:E6331–E6338.

Diehl, R. H., R. P. Larkin, J. E. Black, and F. R. Moore (2003). Radar observations of bird migration over the Great Lakes. The Auk 120:278–290.

Dierschke, V., and J. Delingat (2001). Stopover behaviour and departure decision of Northern Wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535–545.

Dingle, H. (2014). Migration: The Biology of Life on the Move. Oxford University Press, Oxford, UK.

Dingle, H., and V. A. Drake (2007). What is migration? BioScience 57:113–121.

DMTI Spatial Inc. (2014a). National Water (WAT). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2014b). Hydrography - Regions (HYR). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2014c). Route File (RTE). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017a). Water Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017b). Major Roads Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017c). Contour Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2021). Administrative Area Region. [computer file]. Markham, Ontario, Canada.

Dolnik, V. R., and T. I. Blyumental (1967). Autumnal premigratory and migratory periods in the Chaffinch (*Fringilla coelebs coelebs*) and some other temperate-zone passerine birds. The Condor 69:435–468.

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. Behavioral Ecology 27:567–574.

Drury, W. H., and J. A. Keith (1962). Radar studies of songbird migration in coastal New England. Ibis 104:449–489.

Dunn, E. H. (2000). Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. The Auk 117:12–21.

Dunn, E. H., D. J. T. Hussell, and R. J. Adams (1997). Monitoring songbird population change with autumn mist netting. The Journal of Wildlife Management 61:389–396.

Dunn, E. H., K. J. Kardynal, K. M. Covino, S. R. Morris, R. L. Holberton, and K. A. Hobson (2023). Feather isotopes (δ^2H_f) and morphometrics reveal population-specific migration patterns of the Blackpoll Warbler (*Setophaga striata*). Avian Conservation and Ecology 18.

Dunn, E., K. Hobson, L. Wassenaar, D. Hussell, and M. Allen (2006). Identification of summer origins of songbirds migrating through southern Canada in autumn. Avian Conservation and Ecology 1.

Egevang, C., I. J. Stenhouse, R. A. Phillips, A. Petersen, J. W. Fox, and J. R. D. Silk (2010). Tracking of Arctic Terns *Sterna paradisaea* reveals longest animal migration. Proceedings of the National Academy of Sciences 107:2078–2081.

Ellegren, H. (1991). Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. Ornis Scandinavica (Scandinavian Journal of Ornithology) 22:340–348.

Emlen, S. T., and J. T. Emlen (1966). A technique for recording migratory orientation of captive birds. The Auk 83:361–367.

Gauthreaux Jr, S. A., and J. W. Livingston (2006). Monitoring bird migration with a fixed-beam radar and a thermal-imaging camera. Journal of Field Ornithology 77:319–328.

Gifford, C. E., and E. P. Odum (1965). Bioenergetics of lipid deposition in the Bobolink, a trans-equatorial migrant. The Condor 67:383–403.

Gillings, S., and C. Scott (2021). Nocturnal flight calling behaviour of thrushes in relation to artificial light at night. Ibis 163:1379–1393.

Gochfeld, M., and J. Burger (1984). Age differences in foraging behavior of the American Robin (*Turdus migratorius*). Behaviour 88:227–239.

Goymann, W., F. Spina, A. Ferri, and L. Fusani (2010). Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. Biology Letters 6:478–481.

Grabacka, M., M. Pierzchalska, M. Dean, and K. Reiss (2016). Regulation of ketone body metabolism and the role of PPARα. International Journal of Molecular Sciences 17:2093.

Graber, R. R., and J. W. Graber (1962). Weight characteristics of birds killed in nocturnal migration. The Wilson Bulletin 74:74–88.

Groom, D. J. E., J. E. Deakin, M. C. Lauzau, and A. R. Gerson (2019). The role of humidity and metabolic status on lean mass catabolism in migratory Swainson's Thrushes (*Catharus ustulatus*). Proceedings of the Royal Society B: Biological Sciences 286:20190859.

Guglielmo, C. G. (2018). Obese super athletes: fat-fueled migration in birds and bats. Journal of Experimental Biology 221.

Guglielmo, C. G., N. H. Haunerland, P. W. Hochachka, and T. D. Williams (2002). Seasonal dynamics of flight muscle fatty acid binding protein and catabolic enzymes in a migratory shorebird. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 282:R1405–R1413.

Gwinner, E. (1996). Circadian and circannual programmes in avian migration. Journal of Experimental Biology 199:39–48.

Haché, S., R. Cameron, M.-A. Villard, E. M. Bayne, and D. A. MacLean (2016). Demographic response of a neotropical migrant songbird to forest management and climate change scenarios. Forest Ecology and Management 359:309–320.

Hedenström, A., and T. Alerstam (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Heise, C. D., and F. R. Moore (2003). Age-related differences in foraging efficiency, molt, and fat deposition of Gray Catbirds prior to autumn migration. The Condor 105:496–504.

Hoh, C. M., S. S. Pagano, and C. J. Norment (2018). Spatial variation in White-throated Sparrow (*Zonotrichia albicollis*) refueling rate near a migratory barrier. The Wilson Journal of Ornithology 130:891–901.

Holthuijzen, A. M. A., and T. L. Sharik (1985). The avian seed dispersal system of eastern red cedar (*Juniperus virginiana*). Canadian Journal of Botany 63:1508–1515.

Houston, A. I. (1998). Models of optimal avian migration: state, time and predation. Journal of Avian Biology 29:395–404.

Illán, J. G., G. Wang, D. T. King, and F. L. Cunningham (2022). Seasonal variation and tracking of climate niche of a migratory bird. Global Ecology and Conservation 37:e02155.

Imlay, T., S. Saldanha, and P. Taylor (2020). The fall migratory movements of Bank Swallows, *Riparia riparia*: fly-and-forage migration? Avian Conservation and Ecology 15.

Jenni, L., and S. Jenni-Eiermann (1998). Fuel supply and metabolic constraints in migrating birds. Journal of Avian Biology 29:521–528.

Jenni-Eiermann, S., and L. Jenni (1994). Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the Garden Warbler. The Auk 111:888–899.

Jones, J., C. M. Francis, M. Drew, S. Fuller, and M. W. S. Ng (2002). Age-related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. The Condor 104:49–58.

Karasov, W. H., and B. Pinshow (2000). Test for physiological limitation to nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological and Biochemical Zoology 73:335–343.

Kelly, J. F., L. S. DeLay, D. M. Finch, and C. Blem (2002). Density-dependent mass gain by Wilson's Warblers during stopover. The Auk 119:210–213.

Ketterson, E. D., and V. Nolan (1985). Intraspecific variation in avian migration: evolutionary and regulatory aspects. In: Rankin MA, editor. Migration: Mechanisms and Adaptive Significance. University of Texas Press, Port Aransas, Texas.

Kirby, J. S., A. J. Stattersfield, S. H. M. Butchart, M. I. Evans, R. F. A. Grimmett, V. R. Jones, J. O&#39, Sullivan, G. M. Tucker, and I. Newton (2008). Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Conservation International 18:S49–S73.

Kuenzi, A. J., F. R. Moore, and T. R. Simons (1991). Stopover of Neotropical landbird migrants on East Ship Island following trans-gulf migration. The Condor 93:869–883.

La Sorte, F. A., D. Fink, W. M. Hochachka, J. P. DeLong, and S. Kelling (2013). Population-level scaling of avian migration speed with body size and migration distance for powered fliers. Ecology 94:1839–1847.

Lack, D., and G. C. Varley (1945). Detection of birds by radar. Nature 156:446–446.

Lafleur, J. M., J. J. Buler, and F. R. Moore (2016). Geographic position and landscape composition explain regional patterns of migrating landbird distributions during spring stopover along the northern coast of the Gulf of Mexico. Landscape Ecology 31:1697–1709.

Larkin, R. P., W. R. Evans, and R. H. Diehl (2002). Nocturnal flight calls of Dickcissels and Doppler radar echoes over south Texas in spring. Journal of Field Ornithology 73:2–8.

Liechti, F. (2006). Birds: blowin' by the wind? Journal of Ornithology 147:202–211.

Lima, S. L. (1986). Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology 67:377–385.

Lind, J., T. Fransson, S. Jakobsson, and C. Kullberg (1999). Reduced take-off ability in Robins (*Erithacus rubecula*) due to migratory fuel load. Behavioral Ecology and Sociobiology 46:65–70.

Lindström, A., and T. Alerstam (1992). Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. The American Naturalist 140:477–491.

Linscott, J. A., and N. R. Senner (2021). Beyond refueling: Investigating the diversity of functions of migratory stopover events. Ornithological Applications. https://doi.org/10.1093/ornithapp/duaa074

Liu, M., and D. L. Swanson (2015). Stopover duration, movement patterns and temporary home ranges of fall migrant Yellow-rumped Warblers *Setophaga coronata* in native and anthropogenic woodlands of the Northern Prairie region, USA. Journal of Avian Biology 46:452–461.

Lok, T., O. Overdijk, and T. Piersma (2015). The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. Biology Letters 11:20140944.

Loss, S. R., T. Will, and P. P. Marra (2015). Direct mortality of birds from anthropogenic causes. Annual Review of Ecology, Evolution, and Systematics 46:99–120.

Macdade, L. S., P. G. Rodewald, and K. A. Hatch (2011). Contribution of emergent aquatic insects to refueling in spring migrant songbirds. The Auk 128:127–137.

Martin, G. (2003). Management of New Brunswick's crown forest. Department of Natural Resources.

Martínez, I., D. Christie, F. Jutglar, E. Garcia, and C. J. Sharpe (2020). Gentoo Penguin (*Pygoscelis papua*), version 1.0. Birds of the World. https://doi.org/10.2173/bow.genpen1.01species_shared.bow.project_name

McCabe, B. J., and C. G. Guglielmo (2019). Migration takes extra guts for juvenile songbirds: energetics and digestive physiology during the first journey. Frontiers in Ecology and Evolution 7.

McCabe, J. D., A. J. Leppold, R. L. Holberton, and B. J. Olsen (2019). Coastal songbird condition on migratory stopover varies by geographical location and bird age. The Auk. https://doi.org/10.1093/auk/ukz025

McCabe, J. D., and B. J. Olsen (2015). Landscape-scale habitat availability, and not local geography, predicts migratory landbird stopover across the Gulf of Maine. Journal of Avian Biology 46:395–405.

McDonald, R. I., J. Fargione, J. Kiesecker, W. M. Miller, and J. Powell (2009). Energy sprawl or energy efficiency: climate policy impacts on natural habitat for the United States of America. PLOS ONE 4:e6802.

McKinnon, E. A., and O. P. Love (2018). Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. The Auk 135:834–856.

McWilliams, S. R., E. Caviedes-Vidal, and W. H. Karasov (1999). Digestive adjustments in Cedar Waxwings to high feeding rate. Journal of Experimental Zoology 283:394–407.

McWilliams, S. R., and W. H. Karasov (2014). Spare capacity and phenotypic flexibility in the digestive system of a migratory bird: defining the limits of animal design. Proceedings of the Royal Society B: Biological Sciences 281:20140308.

Mills, A. M., B. G. Thurber, S. A. Mackenzie, and P. D. Taylor (2011). Passerines use nocturnal flights for landscape-scale movements during migration stopover. The Condor 113:597–607.

Mitchell, G. W., C. G. Guglielmo, N. T. Wheelwright, C. R. Freeman-Gallant, and D. R. Norris (2011). Early life events carry over to influence pre-migratory condition in a free-living songbird. PLoS ONE 6:e28838.

Mitchell, G. W., A. E. M. Newman, M. Wikelski, and D. Ryan Norris (2012). Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. Journal of Animal Ecology 81:1024–1033.

Mitchell, G. W., B. K. Woodworth, P. D. Taylor, and D. R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Movement Ecology 3:19.

Monteagudo, N., J. M. R. Benayas, E. Andivia, and S. Rebollo (2023). Avian regulation of crop and forest pests, a meta-analysis. Pest Management Science 79:2380–2389.

Moore, F. R., and P. Kerlinger (1987). Stopover and fat deposition by North American wood-warblers (*Parulinae*) following spring migration over the Gulf of Mexico. Oecologia 74:47–54.

Moore, F. R., P. Kerlinger, and T. R. Simons (1990). Stopover on a Gulf Coast barrier island by spring trans-gulf migrants. The Wilson Bulletin 102:487–500.

Moore, F. R., S. Mabey, and M. Woodrey (2003). Priority access to food in migratory birds: age, sex and motivational asymmetries. In Avian Migration (P. D. P. Berthold, P. D. E. Gwinner and E. Sonnenschein, Editors). Springer-Verlag, New-York, NY, USA, pp. 281–292.

Moore, F. R., and W. Yong (1991). Evidence of food-based competition among passerine migrants during stopover. Behavioral Ecology and Sociobiology 28:85–90.

Morales, A., B. Frei, G. W. Mitchell, C. Bégin-Marchand, and K. H. Elliott (2022). Reduced diurnal activity and increased stopover duration by molting Swainson’s Thrushes. Ornithology 139:ukab083.

Morbey, Y. E., A. T. Beauchamp, S. J. Bonner, and G. W. Mitchell (2020). Evening locomotor activity during stopover differs on pre-departure and departure days in free-living songbirds. Journal of Avian Biology 51.

Morbey, Y. E., C. G. Guglielmo, P. D. Taylor, I. Maggini, J. Deakin, S. A. Mackenzie, J. M. Brown, L. Zhao, and D. Stephens (2018). Evaluation of sex differences in the stopover behavior and post departure movements of wood-warblers. Behavioral Ecology 29:117–127.

Morris, S. R. (1996). Mass Loss and Probability of Stopover by Migrant Warblers during Spring and Fall Migration (Pérdida de Masa Corporal y Probabilidad de Recaptura en Lugares de Parada por Parte de Aves Durante la Migración en la Primavera y el Otoño). Journal of Field Ornithology 67:456–462.

Morris, S. R., and J. L. Glasgow (2001). Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. The Wilson Bulletin 113:202–210.

Morris, S. R., D. W. Holmes, and M. E. Richmond (1996). A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. The Condor: Ornithological Applications 98:395–409.

Morse, D. H. (1971). The insectivorous bird as an adaptive strategy. Annual Review of Ecology and Systematics 2:177–200.

Nakazawa, Y., A. T. Peterson, E. Martínez-Meyer, and A. G. Navarro-Sigüenza (2004). Seasonal niches of Nearctic-Neotropical migratory birds: implications for the evolution of migration. The Auk 121:610–618.

Newton, I., and L. C. Dale (1996). Bird migration at different latitudes in eastern North America. The Auk 113:626–635.

Nisbet, I. C. T., and W. H. Drury (1969). A migration wave observed by moon-watching and at banding stations. Bird-Banding 40:243–252.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:59–64.

Oketch, E. O., S. S. Wickramasuriya, S. Oh, J. S. Choi, and J. M. Heo (2023). Physiology of lipid digestion and absorption in poultry: An updated review on the supplementation of exogenous emulsifiers in broiler diets. Journal of Animal Physiology and Animal Nutrition 107:1429–1443.

Ottich, I., and V. Dierschke (2003). Exploitation of resources modulates stopover behaviour of passerine migrants. Journal für Ornithologie 144:307–316.

Packmor, F., T. Klinner, B. K. Woodworth, C. Eikenaar, and H. Schmaljohann (2020). Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? Movement Ecology 8:6.

Panuccio, M., G. Dell’Omo, G. Bogliani, C. Catoni, and N. Sapir (2019). Migrating birds avoid flying through fog and low clouds. International Journal of Biometeorology 63:231–239.

Paxton, E. H., S. L. Durst, M. K. Sogge, T. J. Koronkiewicz, and K. L. Paxton (2017). Survivorship across the annual cycle of a migratory passerine, the Willow Flycatcher. Journal of Avian Biology 48:1126–1131.

Peckford, M. L., and P. D. Taylor (2008). Within night correlations between radar and ground counts of migrating songbirds. Journal of Field Ornithology 79:207–214.

Pennycuick, C. J. (2008). Modelling the Flying Bird. Academic Press, London, UK.

Petit, D. R. (2000). Habitat use by landbirds along Nearctic-Neotropical migration routes: implications for conservation of stopover habitats. 20:15–33.

Pyle, P. (1997). Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA, USA.

Rappole, J. H., and D. W. Warner (1976). Relationships between behavior, physiology and weather in avian transients at a migration stopover site. Oecologia 26:193–212.

Rguibi-Idrissi, H., R. Julliard, and F. Bairlein (2003). Variation in the stopover duration of Reed Warblers *Acrocephalus scirpaceus* in Morocco: effects of season, age and site. Ibis 145:650–656.

Richardson, W. J. (1972). Autumn migration and weather in eastern Canada: a radar study. American Birds. American Birds 26:10–16.

Richardson, W. J. (1978). Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272.

Rioux, S., J.-P. Savard, and A. Gerick (2013). Avian mortalities due to transmission line collisions: a review of current estimates and field methods with an emphasis on applications to the Canadian electric network. Avian Conservation and Ecology 8.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra (2019). Decline of the North American avifauna. Science 366:120–124.

Saino, N., R. Ambrosini, D. Rubolini, J. von Hardenberg, A. Provenzale, K. Hüppop, O. Hüppop, A. Lehikoinen, E. Lehikoinen, K. Rainio, M. Romano, and L. Sokolov (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proceedings of the Royal Society B: Biological Sciences 278:835–842.

Saino, N., D. Rubolini, R. Ambrosini, A. Romano, M. Parolini, L. Canova, M. Corti, and A. Costanzo (2017). Sex- and age-dependent morphology and selection on wing shape in the Barn Swallow *Hirundo rustica*. Journal of Avian Biology 48:1441–1450.

Salewski, V., and M. Schaub (2007). Stopover duration of Palearctic passerine migrants in the western Sahara – independent of fat stores? Ibis 149:223–236.

Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski (2013). The North American Breeding Bird Survey 1966–2011: summary analysis and species accounts. North American Fauna 79:1–32.

Schaub, M., and L. Jenni (2000). Fuel deposition of three passerine bird species along the migration route. Oecologia 122:306–317.

Schaub, M., L. Jenni, and F. Bairlein (2008). Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19:657–666.

Schaub, M., F. Liechti, and L. Jenni (2004). Departure of migrating European Robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. Animal Behaviour 67:229–237.

Schmaljohann, H. (2019). The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: a cross-continental analysis. Movement Ecology 7:25.

Schmaljohann, H., and V. Dierschke (2005). Optimal bird migration and predation risk: a field experiment with Northern Wheatears *Oenanthe oenanthe*. Journal of Animal Ecology 74:131–138.

Schmaljohann, H., and C. Eikenaar (2017). How do energy stores and changes in these affect departure decisions by migratory birds? A critical view on stopover ecology studies and some future perspectives. Journal of Comparative Physiology A 203:411–429.

Schmaljohann, H., C. Eikenaar, and N. Sapir (2022). Understanding the ecological and evolutionary function of stopover in migrating birds. Biological Reviews 97:1231–1252.

Schmaljohann, H., J. W. Fox, and F. Bairlein (2012). Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. Animal Behaviour 84:623–640.

Schmaljohann, H., F. Korner-Nievergelt, B. Naef-Daenzer, R. Nagel, I. Maggini, M. Bulte, and F. Bairlein (2013). Stopover optimization in a long-distance migrant: the role of fuel load and nocturnal take-off time in Alaskan Northern Wheatears (*Oenanthe oenanthe*). Frontiers in Zoology 10:26.

Schmaljohann, H., F. Liechti, and B. Bruderer (2006). Songbird migration across the Sahara: the non-stop hypothesis rejected! Proceedings of the Royal Society B: Biological Sciences 274:735–739.

Schmidt-Koenig, K. (1990). The sun compass. Experientia 46:336–342.

Scott, W. E. D. (1881). Some observations on the migration of birds. Bulletin of the Nuttall Ornithological Club 6:97–100.

Sergio, F., A. Tanferna, R. De Stephanis, L. L. Jiménez, J. Blas, G. Tavecchia, D. Preatoni, and F. Hiraldo (2014). Individual improvements and selective mortality shape lifelong migratory performance. Nature 515:410–413.

Shamoun-Baranes, J., F. Liechti, and W. M. G. Vansteelant (2017). Atmospheric conditions create freeways, detours and tailbacks for migrating birds. Journal of Comparative Physiology A 203:509–529.

Shochat, E., Z. Abramsky, B. Pinshow, and M. E. A. Whitehouse (2002). Density-dependent habitat selection in migratory passerines during stopover: what causes the deviation from IFD? Evolutionary Ecology 16:469–488.

Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Smetzer, J. R., D. I. King, and P. D. Taylor (2017). Fall migratory departure decisions and routes of Blackpoll Warblers *Setophaga striata* and Red-eyed Vireos *Vireo olivaceus* at a coastal barrier in the Gulf of Maine. Journal of Avian Biology 48:1451–1461.

Smith, J. W., C. W. Benkman, and K. Coffey (1999). The use and misuse of public information by foraging Red Crossbills. Behavioral Ecology 10:54–62.

Smith, R. J., and F. R. Moore (2005). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231–239.

Smith, R. J., F. R. Moore, and C. A. May (2007a). Stopover habitat along the shoreline of northern Lake Huron, Michigan: emergent aquatic insects as a food resource for spring migrating landbirds. The Auk 124:107–121.

Smith, S. B. (2013). A physiological assessment of seasonal differences in spring and autumn migration stopover at Braddock Bay, Lake Ontario. The Condor 115:273–279.

Smith, S. B., and S. R. McWilliams (2010). Patterns of fuel use and storage in migrating passerines in relation to fruit resources at autumn stopover sites. The Auk 127:108–118.

Smith, S. B., S. R. McWilliams, and C. G. Guglielmo (2007b). Effect of diet composition on plasma metabolite profiles in a migratory songbird. The Condor 109:48–58.

Stewart, R. L. M., K. A. Bredin, A. R. Couturier, A. G. Horn, D. Lepage, S. Makepeace, P. D. Taylor, M.-A. Villard, and R. M. Whittam (Editors) (2015). Second Atlas of Breeding Birds of the Maritime Provinces. Bird Studies Canada, Environment Canada, Natural History Society of Prince Edward Island, Nature New Brunswick, New Brunswick Department of Natural Resources, Nova Scotia Bird Society, Nova Scotia Department of Natural Resources, and Prince Edward Island Department of Agriculture and Forestry, Sackville.

Taylor, P. D., T. Crewe, S. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. Francis, C. Guglielmo, D. Hamilton, R. Holberton, et al. (2017). The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:8.

Thurber, B. G. (2010). Daily flight timing and movement strategies of migrant landbirds: importance of local wind patterns.

Tøttrup, A. P., R. H. G. Klaassen, M. W. Kristensen, R. Strandberg, Y. Vardanis, Å. Lindström, C. Rahbek, T. Alerstam, and K. Thorup (2012). Drought in Africa caused delayed arrival of European songbirds. Science 338:1307–1307.

Tsvey, A., V. N. Bulyuk, and V. Kosarev (2007). Influence of body condition and weather on departures of first-year European Robins, *Erithacus rubecula*, from an autumn migratory stopover site. Behavioral Ecology and Sociobiology 61:1665–1674.

Wakefield, E. D., R. W. Furness, J. V. Lane, J. W. E. Jeglinski, and S. J. Pinder (2019). Immature gannets follow adults in commuting flocks providing a potential mechanism for social learning. Journal of Avian Biology 50.

Wang, Y., and D. M. Finch (2002). Consistency of mist netting and point counts in assessing landbird species richness and relative abundance during migration. The Condor 104:59–72.

Ward, C. R. E. (2020). Breeding home range and habitat use of a rare high-elevation songbird in industrial forests of New Brunswick.

Weber, T. P. (1999). Blissful ignorance? Departure rules for migrants in a spatially heterogeneous environment. Journal of Theoretical Biology 199:415–424.

Weidensaul, S., T. R. Robinson, R. R. Sargent, M. B. Sargent, and T. J. Zenzal (2020). Ruby-throated Hummingbird (*Archilochus colubris*), version 1.0. Birds of the World. https://doi.org/10.2173/bow.rthhum.01species_shared.bow.project_name

Weimerskirch, H., J. Martin, Y. Clerquin, P. Alexandre, and S. Jiraskova (2001). Energy saving in flight formation. Nature 413:697–698.

Wheelwright, N. T., and R. A. Mauck (1998). Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah Sparrows. Ecology 79:755–767.

Wheelwright, N. T., C. B. Schultz, and P. J. Hodum (1992). Polygyny and male parental care in Savannah Sparrows: effects on female fitness. Behavioral Ecology and Sociobiology 31:279–289.

Wheelwright, N. T., and J. J. Templeton (2003). Development of foraging skills and the transition to independence in juvenile Savannah Sparrows. The Condor 105:279–287.

Whelan, C. J., D. G. Wenny, and R. J. Marquis (2008). Ecosystem services provided by birds. Annals of the New York Academy of Sciences 1134:25–60.

Wikelski, M., E. M. Tarlow, A. Raim, R. H. Diehl, R. P. Larkin, and G. H. Visser (2003). Avian metabolism: costs of migration in free-flying songbirds. Nature 423:704–704.

Wiley, R. H., and W. H. Piper (1992). Timing of cranial pneumatization in White-Throated Sparrows. The Condor 94:336–343.

Wiltschko, W., and R. Wiltschko (1972). Magnetic compass of European Robins. Science 176:62–64.

Winkler, H., and B. Leisler (2005). To be a migrant: ecomorphological burdens and chances. In Birds of two worlds (R. Greenberg and P. Marra, Editors). Johns Hopkins University Press., Baltimore, MD, USA.

Woodrey, M. (2000). Age-dependent aspects of stopover biology of passerine migrants. Studies in Avian Biology 20:43–52.

Woodrey, M., and F. Moore (1997). Age-dependent stopover of fall landbird migrants along the northern coast of The Gulf of Mexico. The Auk 114:695–707.

Woodworth, B. K., C. M. Francis, and P. D. Taylor (2014). Inland flights of young Red-eyed Vireos *Vireo olivaceus* in relation to survival and habitat in a coastal stopover landscape. Journal of Avian Biology 45:387–395.

Woodworth, B. K., G. W. Mitchell, D. R. Norris, C. M. Francis, and P. D. Taylor (2015). Patterns and correlates of songbird movements at an ecological barrier during autumn migration assessed using landscape- and regional-scale automated radiotelemetry. Ibis 157:326–339.

Woodworth, B. K., A. E. M. Newman, S. P. Turbek, B. C. Dossman, K. A. Hobson, L. I. Wassenaar, G. W. Mitchell, N. T. Wheelwright, and D. R. Norris (2016). Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. Oecologia 181:413–422.

Wunderle, J. M. (1991). Age-specific foraging proficiency in birds. Current Ornithology 8:273–324.

Yong, W., D. Finch, F. R. Moore, And, and J. Kelly (1998). Stopover ecology and habitat use of migratory Wilson’s Warblers. The Auk 115:829–842.

Yong, W., and F. R. Moore (1993). Relation between migratory activity and energetic condition among thrushes (*Turdinae*) Following passage across the Gulf of Mexico. The Condor 95:934–943.

Zelazny, V. F. (2007). Chapter 4: From Glacial Wilderness to a Home for Humanity. In Our Landscape Heritage: The Story of Ecological Land Classification in New Brunswick. Government of New Brunswick, pp. 39–50.

Zimmerling, J., A. Pomeroy, M. d’Entremont, and C. Francis (2013). Canadian estimate of bird mortality due to collisions and direct habitat loss associated with wind turbine developments. Avian Conservation and Ecology 8.

Zurell, D., L. Gallien, C. H. Graham, and N. E. Zimmermann (2018). Do long-distance migratory birds track their niche through seasons? Journal of Biogeography 45:1459–1468.

de Zwaan, D. R., A. Huang, Q. McCallum, K. Owen, M. Lamont, and W. Easton (2022). Mass gain and stopover dynamics among migrating songbirds are linked to seasonal, environmental, and life-history effects. Ornithology 139:ukac027.

Chapter 2

2 The early bird gets the triacylglycerol: covariation of refuelling rate with migration distance and diel activity timing in five songbird species during autumn stopover.

2.1 Introduction

Migrating quickly between breeding and non-breeding areas can yield survival and reproductive benefits for seasonally migrating bird species. Reducing the time spent migrating can decrease exposure time to biotic and abiotic hazards encountered along the migratory path, and may alleviate time constraints that influence subsequent events in the annual cycle (Gow et al. 2019). Theoretical modelling also suggests that rapid migration can contribute to earlier arrival to breeding or non-breeding areas among long distance migrants (Morbey and Hedenström 2020), contributing to enhanced mating opportunities and priority access to high quality territories relative to later arriving conspecifics (Price 1981, Møller et al. 2009). One of the greatest factors governing the overall speed and duration of migration is the total time required to acquire the energy needed to power migratory flight (Lindström et al. 2019), accrued primarily during inter-flight stopover bouts where energy stores are replenished (Hedenström and Alerstam 1997). To facilitate rapid refuelling during the migratory period, birds can increase the amount of food consumed relative to non-migratory periods (e.g. Gifford and Odum 1965, Kvist and Lindström 2000), with associated seasonal changes in alimentary and hepatic systems facilitating the assimilation of nutrients from the greater volume of food consumed (Bairlein 1985, Dykstra and Karasov 1992, McWilliams et al. 1999, Karasov and Pinshow 2000). Patterns of diel activity can also be altered to allocate more time to feeding (Kvist and Lindström 2000), enhancing total daily fuel deposition. These within-species behavioural and physiological changes act to increase both the instantaneous rate of energy intake during stopover and the amount of time dedicated to refuelling.

Greater fuel deposition rate can reduce the time needed to accumulate energy, reducing stopover duration and facilitating the faster migration speeds of longer distance migrants (Ellegren 1993, La Sorte et al. 2013, Schmaljohann 2019, Morbey and

Hedenström 2020) in conjunction with a lower frequency of prolonged stopovers or greater flight speeds. Evidence for the relationship between stopover refuelling rate and migration distance can be found in studies conducted on the subspecies of the Northern Wheatear (*Oenanthe oenanthe*), with the longer distance migrant *O. o. leucorhoa* foraging more intensively during stopover in the wild (Dierschke and Delingat 2001), and gaining mass faster when fed *ad libitum* in captivity (Corman et al. 2014) relative to the shorter distance migrant *O. o. oenanthe*. Using banding recapture data, De Zwaan et al. (2022) found that wood-warbler (Parulidae) and sparrow (Passerelidae) species with longer migration distances tended to have greater refuelling rates and shorter stopover durations. Other interspecific datasets on fuel deposition rates show that larger bird species tend to refuel more slowly than smaller bird species, and that mass gain rates do not differ among taxonomic orders after accounting for inter-order differences in body size (reviewed by Lindström 2003). Migration distance is largely independent of body size in songbirds, and body mass did not affect migration speed when evaluated in passerine species (Schmaljohann 2019).

Interspecific differences in daily fuel deposition can arise from both differences in instantaneous refuelling rate and the daily time allocated for refuelling. Estimates of daily refuelling rate can be made directly by measuring mass change, either at the individual level using repeated measurement (e.g. Schaub and Jenni 2000) or by applying regression techniques to mass measurements made in a group of individuals across a period of time which may include intervals of both feeding and non-feeding (e.g. Smith et al. 2007). Quantifying differences in the instantaneous rate of refuelling using these techniques may be confounded by variation in the proportion of time spent feeding, which is often difficult to assess in free living birds. Information on the instantaneous refuelling state of an individual can also be obtained from a single capture event by measuring the concentrations of triacylglycerol (triglyceride) and the ketone body β-OH butyrate in the blood plasma (Jenni-Eiermann and Jenni 1994, Guglielmo et al. 2005, Zajac et al. 2006). These metabolites are strongly associated with fat deposition and fat catabolism respectively, and have opposing relationships with changes in body mass over time (Jenni-Eiermann and Jenni 1994). Plasma triglyceride concentrations rise when birds are feeding, and decrease during periods of low energy intake while β-OH butyrate concentrations rise as fat stores are metabolized. However, plasma metabolite concentrations respond rapidly to changes in feeding status (Zajac et al. 2006), requiring methodological considerations for their use in gauging refuelling. Samples must be collected quickly (< 20 minutes) after capture so that the metabolite profile best reflects the pre-capture state. Furthermore, the turnover of the plasma metabolite profile from the nocturnal fasting state following the onset of diurnal feeding can yield a positive relationship between metabolite concentration and time of day (Jenni and Jenni-Eiermann 1996, Brown et al. 2014). This dynamic may pose a confound to interspecific comparative studies where the onset of diurnal feeding may differ among species, with earlier awakening and onset of feeding leading to higher measured refuelling rates for a given time relative to sunrise. As a result, inferences regarding whether species differ in their instantaneous rate of refuelling may be limited without additional information on the onset diurnal activity.

While interspecific difference in diel activity timing during the migratory period has been observed in songbirds (Morbey et al. 2018), it remains uncertain how these differences are associated with migration strategy or morphological characteristics of the species. As prolonging the fuelling period during migratory stopover can enhance daily fuel deposition rate (Kvist and Lindström 2000), the earlier onset and late cessation of activity may form part of the strategy used by species with longer migration distances to achieve greater migration speeds via short stopover duration. Variation in diel activity timing may also result from differences in visual acuity, which is associated with eye size and positively correlated to body size in passerines (Kiltie 2000, Thomas et al. 2002). Evidence that diel activity schedule varies according to visual acuity can be found in the timing of dawn chorus during the breeding season, with larger eye size (Thomas et al. 2002, Berg et al. 2006) and greater retinal thickness (McNeil et al. 2005) correlating with the earlier start of dawn chorus, presumably because these species are better able to detect predators under low light conditions. Whether a similar pattern exists in activity timing during migratory stopover is uncertain. As primarily visual foragers, the ability of songbirds to forage effectively is reduced under low-light levels (Kacelnik 1979), and engaging in conspicuous activities such as foraging may also become riskier when the capacity to detect predators is compromised. Species with better low-light visual acuity may be able to detect prey and predators under low light conditions, enabling them to commence activity earlier in the morning and remain active later into the evening.

Establishing the individual-level onset and end of activity in wild songbirds is now possible through recent advances in automated radio telemetry, transmitter miniaturization, and analytical techniques. By employing automated radio receivers at fixed locations, the variation in received signal strength generated by the locomotor activity of tagged individuals can be used to delineate stationary periods from periods of activity. The abrupt change in signal strength variation between diurnal foraging and nocturnal roosting can be used to determine the onset or end of activity (Morbey et al. 2018), and this technique has been used to characterise the changes in locomotory behaviour of songbirds between departure and non-departure nights (Morbey et al. 2020) and among individuals (Beauchamp et al. 2020, Morales et al. 2022).

In this study, I combined plasma metabolite profiling and radio telemetry to better understand how instantaneous refuelling rate, diel activity patterns, and stopover duration vary in relation to migration distances. To ensure that the measured refuelling rate and stopover behaviour of migrants would reflect primarily endogenous differences among species. Birds were sampled within the same spatiotemporal scope to limit any bias arising from exogenous factors. Furthermore, by studying stopover refuelling in a landscape with abundant habitat and a low degree of fragmentation, I aimed to minimise any confounding density-dependent or habitat selection effects on refuelling that can arise when the availability of stopover habitat is constrained (Cohen et al. 2022). Under the proximate ecological hypothesis that refuelling intensity facilitates longer migration, I expected that instantaneous refuelling rate would increase with migration distance and would be greater when the onset of activity was earlier for a given time of day since sunrise. I also expected that stopover duration would decrease with increasing migration distance, reflecting the lower time required by long distance migrants to obtain fuel loads adequate for departure. Regarding diel activity patterns, I predicted longer distance migrants would have an earlier onset, later end, and overall greater duration of diurnal activity after accounting for daylength, as this would enable the rapid accumulation of energy during migratory stopover.

2.2 Methods

Research was conducted at four sites in eastern New Brunswick, Canada (Figure 2-1). Data collection occurred over three autumn migratory seasons: 13 September to 28 October 2019, 6 September to 28 October 2020, and 28 August to 24 October 2021. Two sites were located coastally near Waterside (45°37’30.4” N 64°47'30.47"W) (WAT) and Mary’s Point (45°43'28.07"N 64°40'31.16"W) (MPT). The other two sites were located approximately 25 km inland at the Mapleton Acadian Forest Nature Preserve (45°49'19.94"N 65° 3'33.49"W) (MAF) and the Community Forest International Whaelghinbran Property (45°44'4.88"N 65°18'2.41"W) (CFI). Study sites were sampled on a four-day rotation, using five to eight mist nets to passively capture birds. Netting commenced one hour after local sunrise to minimise the time-of-day effect associated with metabolite profiling (Guglielmo et al. 2005) and ceased seven hours after local sunrise. Birds were banded with U.S. Fish and Wildlife Service/Canadian Wildlife Service aluminum leg bands. Data collection was conducted under the banding permit 10911C issued by Environment and Climate Change Canada to ATB, with approval by the University of Western Ontario’s Animal Care Committee (AUP # 2017-160).

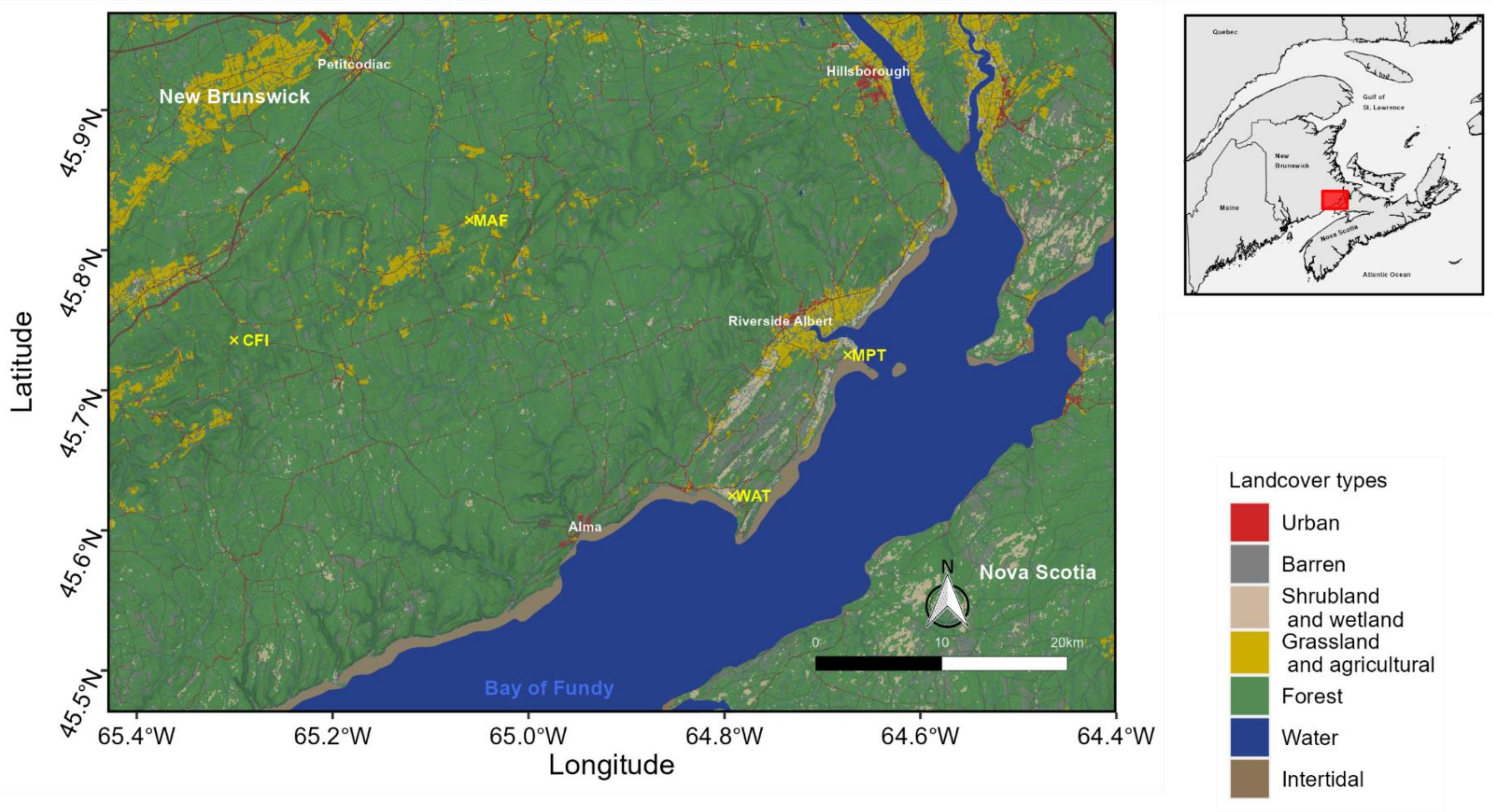


Figure 2-1. Location of study sites and 2021 landcover classification in eastern New Brunswick, Canada. Also indicated are roadways, watercourses, and topography at intervals of 10 meters. Sites labels; CFI = Community Forest International Whaelghinbran Property; MAF = Mapleton Acadian Forest Nature Preserve; WAT = Waterside; MPT = Mary's Point. Raster landcover classification data adapted from (Agriculture and Agri-food Canada 2023), vector data from (DMTI Spatial Inc. 2014a, b, c, 2017a, b, c, 2021)

2.2.1 Plasma metabolite profiling and movement

Plasma metabolite profiling was used to measure refuelling (Jenni-Eiermann and Jenni 1994, Guglielmo et al. 2005, Hoh et al. 2018, Beauchamp et al. 2020) in White-throated Sparrow (*Zonotrichia albicollis*), Swainson's Thrush (*Catharus ustulatus*), Hermit Thrush (*Catharus guttatus*), Yellow-rumped Warbler (*Setophaga coronata*) and Blackpoll Warbler (*Setophaga striata*). These species were selected because they represent a mixture of taxonomic families and both long and short-distance migrants, and they were sufficiently abundant at the study sites. Nets were continuously monitored where possible or checked every eight to ten minutes, and a digital stopwatch was used to record the time elapsed between the last check of a net and the completion of blood collection from a captured bird (bleed time). Following collection, blood samples were centrifuged at 2000 *g* for 10 min to separate plasma, which was transferred into cryogenic tubes and stored in a liquid nitrogen dry shipper (Taylor-Wharton CX 100).

Plasma concentrations of β-OH butyrate, glycerol, and triglyceride (mmol·L^{-1}) were measured using colorimetric assays (R Biopharm: 10907979035, SIGMA: Trinder reagent A and B) following Guglielmo et al. (2005). Birds ingesting enough food to deposit fat have elevated plasma triglyceride concentration, whereas birds unable to ingest sufficient quantities of food to deposit fat will have elevated plasma β-OH butyrate concentration (Guglielmo et al. 2005). Plasma concentrations of triglyceride (correcting for free glycerol) and β-OH butyrate were $\log_{10}(x + 1)$ transformed, and principal component analysis was applied to create a refuelling index (RI) (Guglielmo et al. 2005). Samples with a bleed time greater than 20 minutes were omitted from this analysis, due to the rapid turnover of these metabolites from feeding to fasting following capture (Zajac et al. 2006). Granivorous species sampled in 2020 were also omitted from this dataset, as resource manipulations targeting granivorous species occurred in 2020 as part of chapter 4.

Following blood collection, digitally encoded radio transmitters (model NTQB2-1 and NTQB2-2, Lotek Wireless, www.lotekwirelss.ca) were used to measure diel activity patterns, stopover duration, and post departure flight bearing using automated radio telemetry. Radio tags weighed approximately 0.29 – 0.35 g and were affixed to the bird using a leg-loop harness constructed of elastic thread (Rappole and Tipton 1991), with pulse intervals ranging from 6.10 s to 12.5 s depending on the model used.

2.2.2 Estimation of migration distance

Migration distance was estimated at the species level as the great circle distance between the centroids of the breeding and non-breeding range (La Sorte et al. 2013) determined using the function and *st_centroid* and *st_distance* from the package "sf" (Pebesma 2018). Range map polygons were obtained from eBird Status and Trends Data Products, using data from the year 2021 (Fink et al. 2022) (Figure 2-2). I elected to use the entire breeding and non-breeding area in the calculation of range centroids for the estimation of migration distance to avoid introducing biases from restricting the breeding or non-breeding area. As such, estimates of migration distance represent an average linear migration distance for each species.

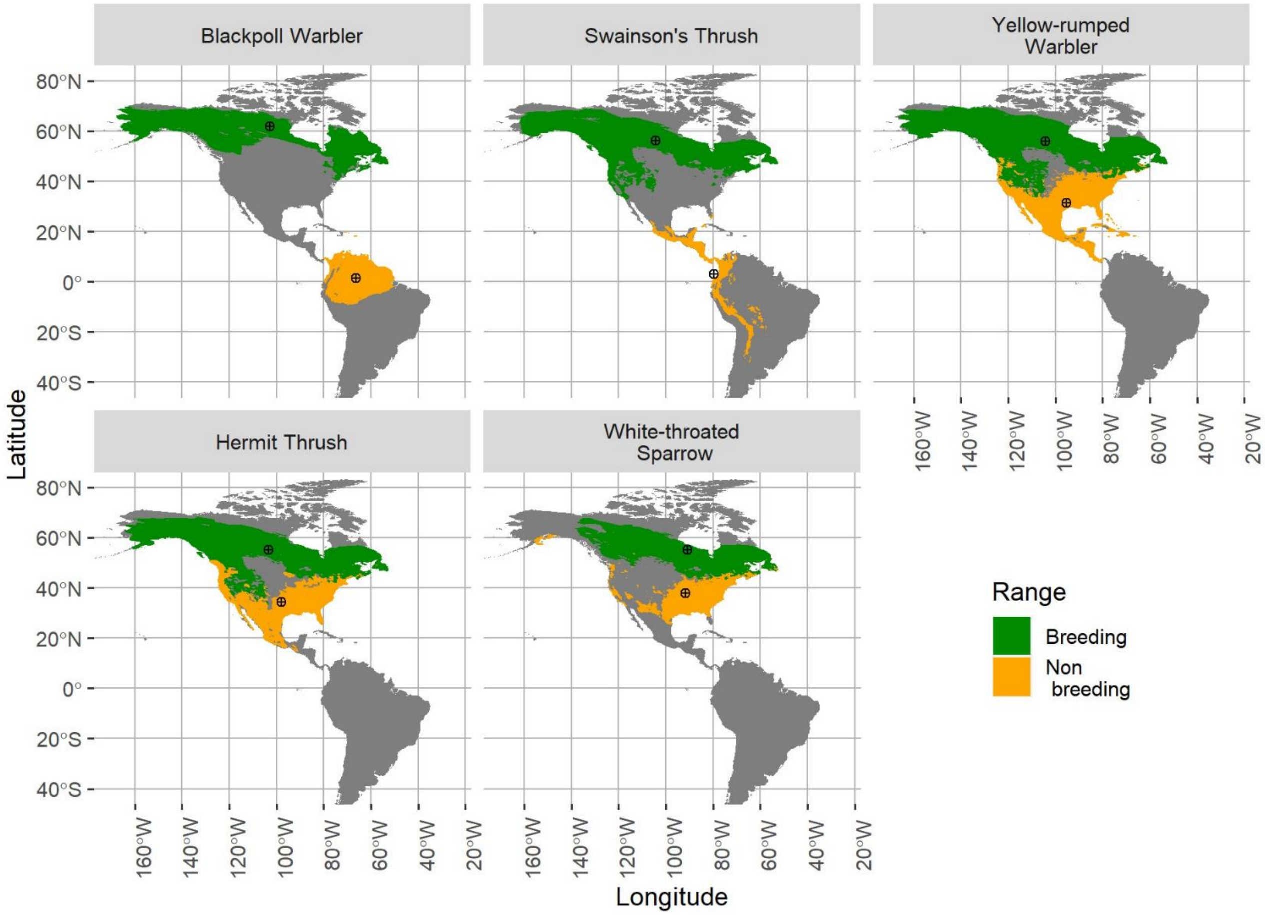


Figure 2-2. Breeding and non-breeding ranges and centroids of five migratory songbird species. Data from the Cornell Lab of Ornithology (Fink et al. 2022). Estimated migration distances: Blackpoll Warbler = 7,400 km; Swainson’s Thrush = 6,317 km; Yellow-rumped Warbler = 2,834 km; Hermit Thrush = 2,347 km; White-throated Sparrow = 1,926 km. This material uses data from the eBird Status and Trends Project at the Cornell Lab of Ornithology, eBird.org. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the Cornell Lab of Ornithology.

2.2.3 Measuring the onset and end of activity

The onset of activity during stopover was determined using changepoint analysis, excluding capture and departure days (Morbey et al. 2018, Beauchamp et al. 2020). This method uses characteristic changes in signal strength variation between consecutive detections to delineate the timepoint when a tagged birds becomes active in the morning (i.e., foraging) and quiescent in the evening (i.e., roosting). Changepoints in signal variation were determined using the package “changepoint” (Killick and Eckley 2014), for detections occurring between midnight and 10:00 ADT for the onset of activity, and between 10:00 ADT and midnight for the end of activity. Signal attenuation by habitat characteristics and individual position relative to the receiver can reduce detection probability of birds on the ground (Crewe et al. 2019), yielding periods where there are no detections recorded. Prior to changepoint analysis, individuals with numerous gaps in their recorded signals were identified and removed by plotting the received signals across the stopover duration, and periods with fewer than 800 detections were omitted to filter out periods and individuals with poor signal coverage. Changepoint analysis was conducted on the square-root of the absolute value of the difference between a detection’s signal strength, and the previous detection’s signal strength (diff.abs). Conceptually, consecutive detections from stationary birds should have relatively consistent signal strength, resulting in a diff.abs value with a mean and variance near zero. Active birds will have diff.abs values with a greater positive mean, and high variance. This measure is stronger than the use of signal strength alone, as variation in signal strength and signal variance resulting from the distance between a tagged individual and the receiver station is controlled. Prior to changepoint analysis, diff.abs values derived from consecutive detections greater than 30 seconds apart were removed, to minimise the impact of high values resulting from prolonged periods without detections. The function cpt.meanvar was used to determine a single changepoint within these periods, with an asymptotic penalty with a value of 0.001 and minimum segment length of 20 (the number of observations between changes). This function determines where a change in the mean and variance of the diff.abs data occurs, using a theoretical type I error of 0.001 specified by the penalty term. For the onset of activity, the timestamp of the signal following the changepoint was used, as this more accurately reflects the onset of activity. Post filtering included removal of changepoints where the change in mean and variance of diff.abs was counter to expectation (e.g., greater variance *prior* to the onset of daily activity).

2.2.4 Determining stopover duration and departure bearing

Stopover duration and post-departure movement bearing was measured using the Motus Wildlife Tracking System (Motus; Taylor et al. 2017). Detections of radio signals from tagged individuals on the receiver located at each site was used to determine that a bird was still at the capture site. Stopover duration was calculated as the number of days between tagging and departure + 1, providing the minimum length of stopover. Post-departure detections were processed following (Birds Canada 2022) to remove likely false-detections, and the bearing between the capture site and the next detection on the Motus array was averaged across all individuals using the package “circular” (Agostinelli and Lund 2022) to provide the average post-departure flight bearing in all birds.

2.2.5 Analysis of diel activity timing, duration, and first capture date

The onset and end of activity were standardised by taking the difference between the changepoint time and local sunrise and sunset time respectively, obtained using the package “maptools” (Bivand and Lewin-Koh 2021). As such, these activity metrics represent relative differences in activity patterns relative to sunrise and sunset independent of the local time of each event. The duration of diurnal activity was calculated as the difference between the time of activity onset and end, using days where measurements of both metrics were available. Measurements from individual capture and departure days were omitted due to the potential for changes in behaviour resulting from capture stress or in preparation for migratory departure (Morbey et al. 2020). Changepoints from six birds with stopover durations exceeding 30 days were also omitted from the analysis.

Separate linear mixed-effect models were used to test for differences in the onset of activity, end of activity, and duration of diurnal activity between species, with individual included as random intercepts to account for repeated measures of activity timing across multiple days of an individual’s stopover. Day of year was included in the analysis of activity duration to account for decreasing daylength with date. A separate one-way analysis of variance was conducted using the first capture date of each tagged individual to test for species-level differences in passage date. Following this, separate planned linear contrasts were used to test competing explanations for the differences between species in activity timing and following the methods outlined in Schad et al. (2020), using the function *glht* in package “multcomp” (Hothorn et al. 2008). In the first analysis, the ordering of activity measures by species-level migration distance was tested to see if activity patterns relate to migration strategy. The second analysis tested if the ordering of activity measures was related to differences in low-light visual acuity, using the average tarsus length (mm) of each species as a proxy for eye size (Kiltie 2000, Thomas et al. 2002). A separate linear contrast was also used to test if passage date differed according to migration distance.

2.2.6 Analysis of stopover refuelling rate

Linear mixed effect regression was used to test for a relationship between the instantaneous rate of refuelling during stopover and migration distance. Both capture time relative to local sunrise and the interval between capture and completion of blood sampling (bleed time) were included in the model to control for the effect of these covariates on measured refuelling rate (Jenni and Jenni-Eiermann 1996, Zajac et al. 2006). To control for interspecific differences in the daily onset of feeding, species-level estimates of the onset of activity relative to sunrise were included in the analysis of refuelling. These estimates were obtained from the analysis of activity onset timing using the function *emmeans* from the package “emmeans” (Lenth 2023). Finally, species was included as a random intercept term to account for interspecific variation in refuelling not captured by migration distance and activity onset. Analyses were conducted in R version 4.1.2 (R Core Team 2022). In all analyses, models were fit using maximum likelihood and continuous independent variables were scaled and centred prior to analysis. Scaled model residuals were visualised using the function *simulateResiduals* in R package “DHARMa” (Hartig 2022) to verify model assumptions were met.

2.2.7 Analysis of stopover duration

To test for the relationship between stopover duration and migration distance, Cox semi-parametric hazard regression was applied in a proportional hazard modelling framework using the function *coxph* in package “survival” (Therneau 2023). In this framework, covariates that increase hazard for migratory departure can be viewed as decreasing stopover duration. Prior to analysis, the total migration distance of each species (km)was divided by 1000 to aid in the interpretation of parameter estimates. In addition to migration distance, capture day of year, and a time varying covariate of nocturnal tailwind assistance and crosswind was included in the analysis. Day of year was included to account for increasing departure hazard later in the migratory season (e.g. Beauchamp et al. 2020, Packmor et al. 2020). Tailwind and crosswind were included as songbirds tend to migrate using energetically favourable tailwinds (Liechti 2006, Mitchell et al. 2015, Morbey et al. 2018), and avoid migrating in crosswinds to minimise lateral drift during flight (Packmor et al. 2020).

To include tailwind and crosswind as a time-varying covariates, each bird was assigned a tailwind and crosswind value for each day it was at risk of departure. Local wind data for each date was obtained from the NCEP/DOE Reanalysis 2 data set (http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis2.html) which provides meteorological data four times each day at 2.5° x 2.5° spatial resolution. Wind speed in $m \cdot s^{-1}$ in the easterly and northerly direction was extracted using the “RNCEP” package (Kemp et al. 2012), and interpolated for an individual’s stopover site using the function *NCEP.interpol* with the option for linear interpolation. Wind was interpolated for ground level for 21:00 ADT. Tailwind was estimated as $V_w \cdot \cos(\beta)$, where V_w is wind speed ($m \cdot s^{-1}$) and β is the difference between wind direction and the average post-departure flight bearing of 225°. Crosswind was estimated perpendicular to the average post-departure flight bearing. The proportional hazard assumption was assessed by visualising the sum of scaled Schoenfeld residuals across time (Grambsch and Therneau 1994) using function *cox.zph*.

2.3 Results

2.3.1 Activity timing and duration

The onset of diurnal activity was analysed using 734 changepoints from 102 birds of five species after post-filtering 141 changepoints and removing an additional 12 as outliers (six earlier than sunrise and six later than 60 minutes post sunrise). Median onset time of activity was 28.7 minutes prior to local sunrise across all species (range: 58.4 to 1.1 minutes prior to sunrise; Table 2-1). The onset of activity differed among species ($F_{4, 114.6} = 31.90$, $p < 0.01$, Figure 2-3), and separate linear contrasts showed that onset time was earlier in longer distance migrants ($\beta = -4.70 \pm 1.52$ SE, $z = -3.1$, $p < 0.01$) and earlier in larger bodied species ($\beta = -14.35 \pm 1.70$ SE, $z = -8.4$, $p < 0.001$).

The end of activity was analysed using 661 changepoints from 96 birds of five species after post-filtering 106 changepoints and removing an additional 18 outliers (four earlier than 35 minutes prior to sunset and 14 later than 60 minutes post-sunset). Median end time of activity was 18.2 minutes following local sunset (range: -25.4 to + 57.0 minutes relative to sunset) The end of activity differed among species ($F_{4, 81.4} = 15.03$, $p < 0.01$), and these differences were unrelated to species level migration distance or body mass (both $p > 0.5$).

Activity duration was calculated for 587 days, using data from 94 individuals that had at least one day where both the onset and end of activity were determined. The median duration of activity was 12.6 hours (range: 10.5 to + 14.3 hours). Total activity span differed significantly among species ($F_{4, 83.6} = 20.88$, $p < 0.01$), but there was only marginal evidence that total activity duration increased linearly with greater migration distance ($\beta = 0.14 \pm 0.07$ SE, $t_{83.2} = -1.91$, $p = 0.05$). Activity span also decreased approximately 3 minutes for each day of year ($\beta = -0.05 \pm$ SE 0.001, $t_{145.08} = -29.81$, $p < 0.01$, Figure 2-4).

Among tagged individuals with information on activity duration, first capture date significantly differed by species ($F_{4,89} = 7.39$, $p < 0.01$), however, a linear contrast of species by migration distance indicated that differences among species in first capture timing were not associated with migration distance ($p > 0.5$).

Table 2-1. Sample size and summary statistics by study species.

	Onset of activity (minutes since sunrise)			End of activity (minutes since sunset)			Duration of activity (hours)			First capture day of year		Stopover duration (days)	
Species (Estimated migration distance)	Birds	Change-points	Median (min, max)	Birds	Change-points	Median (min, max)	Birds	Stopover days	Median (min, max)	Birds	Median (min, max)	Birds	Median (min, max)
Blackpoll Warbler 7,400 km	5	20	-18.6 (-33.5, -3.9)	3	22	14.1 (-3.7, 35.0)	3	18	11.2 (10.5, 12.6)	3	270 (266, 293)	26	7 (1, 23)
Swainson’s Thrush 6,317 km	22	150	-32.5 (-56.1, -18.0)	21	128	24.3 (1.7, 40.5)	21	117	13.5 (12.1, 14.3)	21	256 (240, 284)	37	10 (1, 23)
Yellow-rumped Warbler 2,834 km	6	26	-13.0 (-20.6, -1.1)	4	20	5.9 (-25.4, 22.3)	5	20	12.3 (11.2, 13.0)	5	262 (260, 276)	31	5 (1, 22)
Hermit Thrush 2,347 km	15	121	-31.3 (-51.9, -3.6)	15	115	20.1 (-24.4, 57.0)	13	97	12.2 (10.9, 13.7)	13	284 (248,292)	29	11 (1, 29)
White-throated Sparrow 1,926 km	54	417	-27.2 (-58.4, -3.8)	53	376	16.1 (-23.3, 54.1)	52	335	12.5 (10.6, 14.1)	52	268 (252, 292)	118	11 (1, 30)

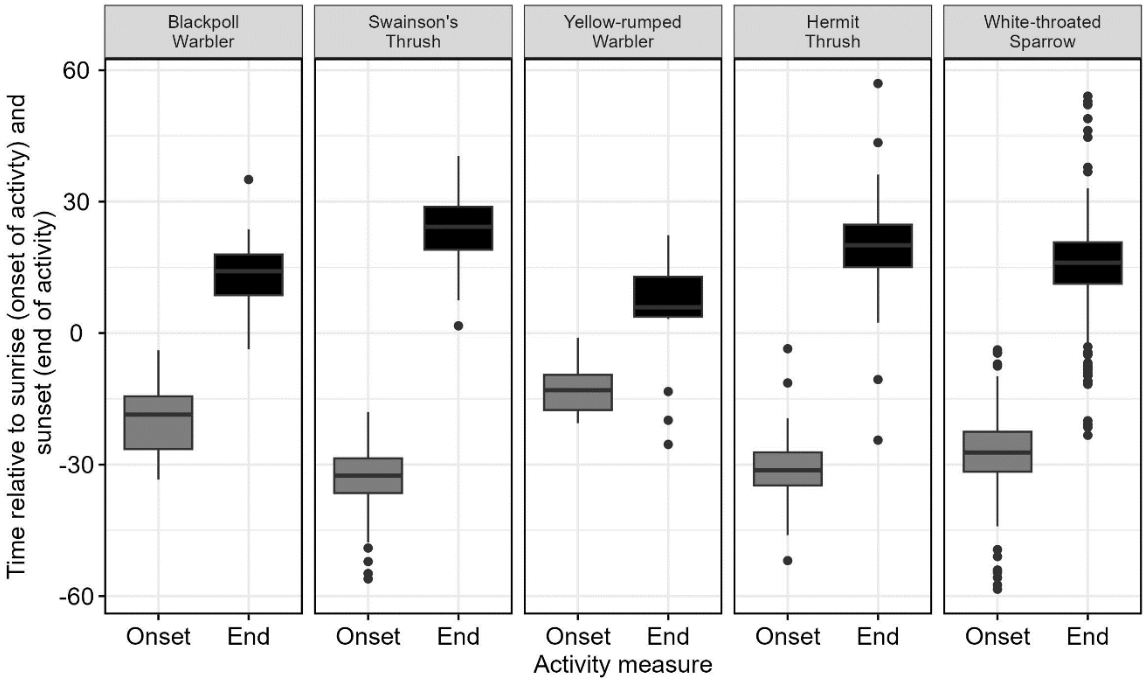


Figure 2-3. The onset and end of diel activity relative to either sunrise (onset) or sunset (end) for five migratory songbird species radio-tagged in eastern New Brunswick during autumn migration in 2019, 2020 and 2021. Species panels are ordered by migration distance in descending order from the left of the plot.

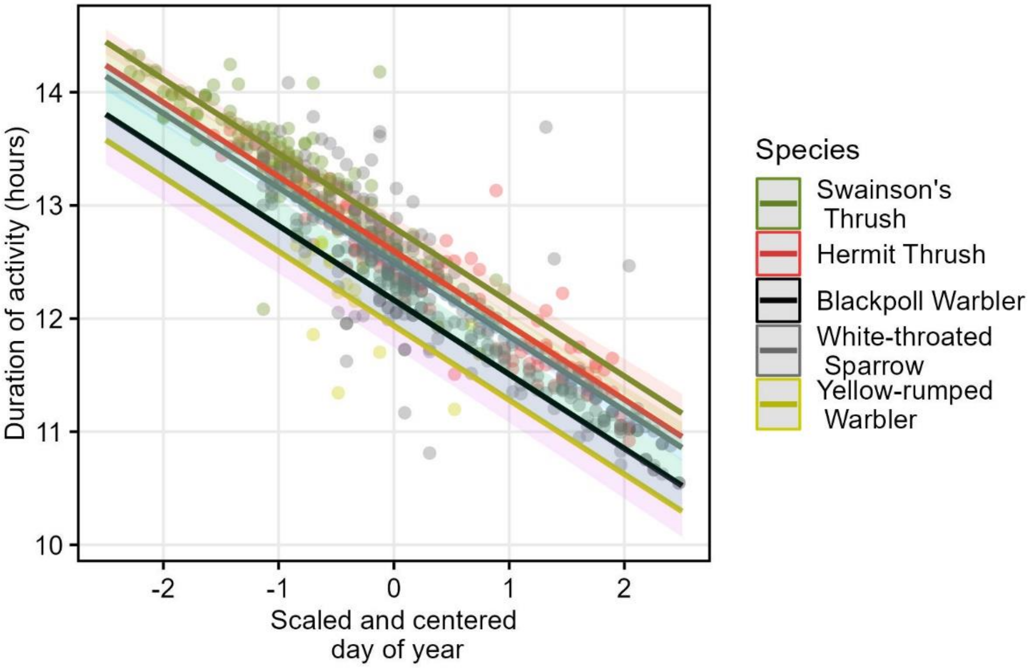


Figure 2-4. Diurnal activity durations by day of year for 100 individuals of five migratory songbird species radio-tagged in eastern New Brunswick during autumn migratory stopover in 2019, 2020 and 2021. Also shown are the raw data points and 95% confidence intervals.

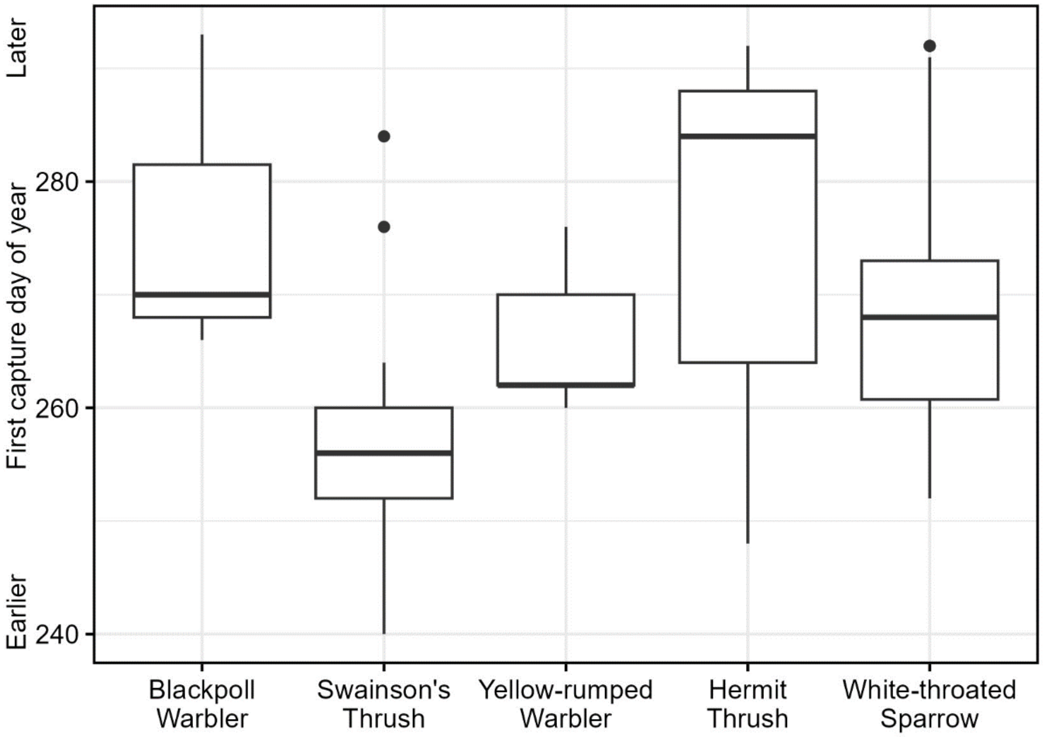


Figure 2-5. First capture dates for 100 songbirds of five species capture during autumn stopover in eastern New Brunswick. Species are ordered by migration distance in descending order from the left of the plot. Passage date significantly differed by species ($F_{4,89} = 7.39$, $p < 0.01$), but was not associated with species-level migration distance ($p > 0.5$). For reference, day 244 ~ 1 September.

2.3.2 Stopover refuelling rate

Data on plasma triglyceride and β-OH butyrate concentrations were available from 269 birds. Triglyceride and β-OH butyrate concentrations were negatively correlated ($R^2 = -0.36$, $p < 0.01$), and the first principal component accounted for 68.4% of the variation in the dataset with $\log_{10}$([triglyceride]+1) loading positively into PC1 (0.71) and $\log_{10}$([β-OH butyrate] +1) loading negatively (-0.71). Sample sizes by species and summary statistics on metabolite concentrations and refuelling rate index can be found in Table 2-2.

After back-scaling coefficients to original units, greater stopover refuelling rate was positively associated with longer migration distance (km) among the species examined ($\beta = 0.0001$ ± SE 0.00003, $t_{8.3} = 4.43$, $p < 0.01$, Figure **2-6**), indicating that species had a 0.1 unit greater refuelling rate index value for every additional 1000 km of migration distance. Furthermore, refuelling rate significantly decreased with each minute later onset of activity ($\beta = -0.06$ ± SE 0.01, $t_{9.4} = -5.36$, $p < 0.01$, Figure 2-7), indicating species with a later onset of activity relative to sunrise (more positive) had lower a refuelling rate index for a given time of day relative to sunrise. Finally, stopover refuelling rate increased with each minute elapsed since sunrise ($\beta = 0.003$ ± SE 0.0006, $t_{267.0} = 4.12$, $p < 0.01$) and decreased with each second of bleed time ($\beta = -0.0009$ ± SE 0.0002, $t_{268.3} = -4.35$, $p < 0.01$, Table 2-3).

Table 2-2. Sample sizes by species for birds included in the analysis of refuelling rate. Also shown are the mean ± SE of triglyceride concentrations, β-OH Butyrate concentrations, and refuelling rate index values.

Species	Sample size	Mean ± SE triglyceride (mmol•L^{-1})	Mean ± SE β-OH Butyrate (mmol•L^{-1})	Mean ± SE Refuelling index
Blackpoll Warbler *Setophaga striata*	33	2.71 ± 0.2	1.14 ± 0.07	0.18 ± 0.03
Swainson's Thrush *Catharus ustulatus*	42	2.65 ± 0.21	0.45 ± 0.05	0.93 ± 0.14
White-throated Sparrow *Zonotrichia albicollis*	88	2.33 ± 0.22	1.56 ± 0.08	-0.46 ± -0.05
Hermit Thrush *Catharus guttatus*	68	2.24 ± 0.16	0.67 ± 0.06	0.44 ± 0.05
Yellow-rumped Warbler *Setophaga coronata*	38	1.58 ± 0.22	1.6 ± 0.11	-0.9 ± -0.15

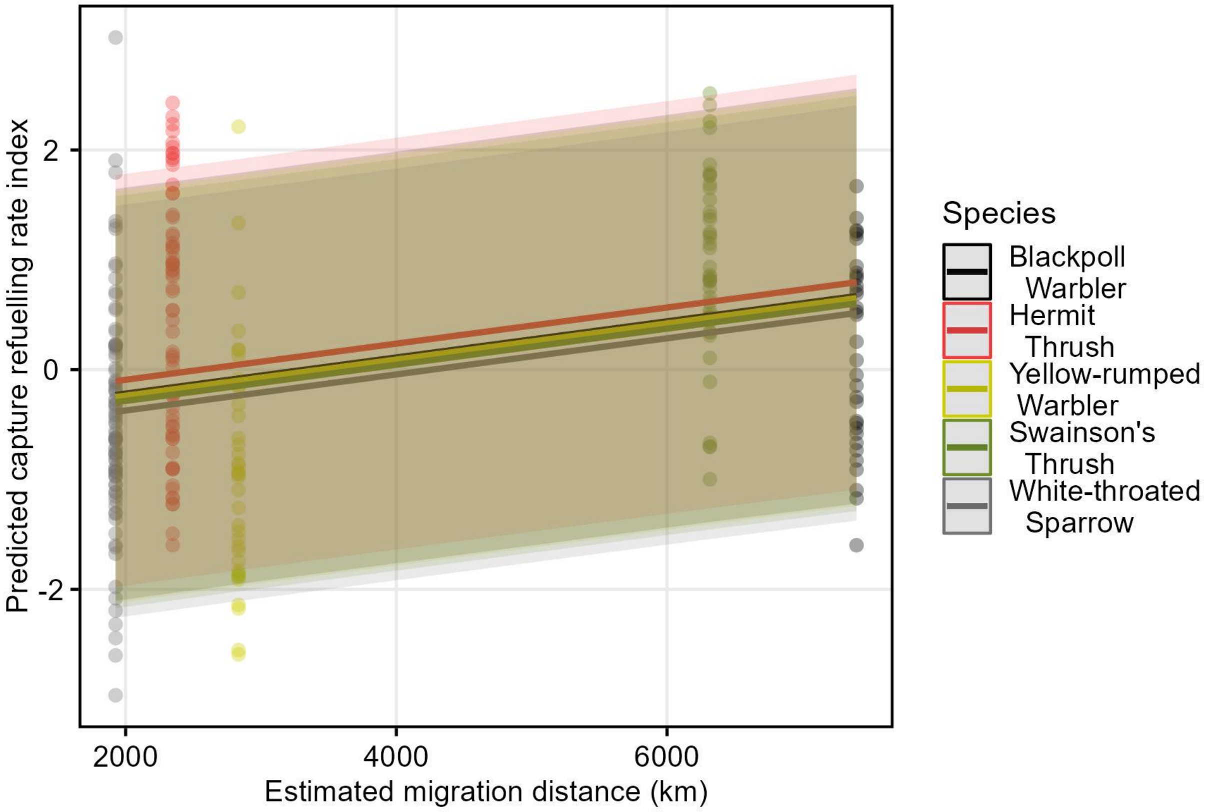


Figure 2-6. Predicted refuelling rate by estimated migration distance for five species of songbird sampled during autumn stopover in eastern New Brunswick, Canada. Migration distance was estimated at the species level as the distance between breeding and non-breeding range centroids. Also shown are the raw data points and 95% prediction intervals.

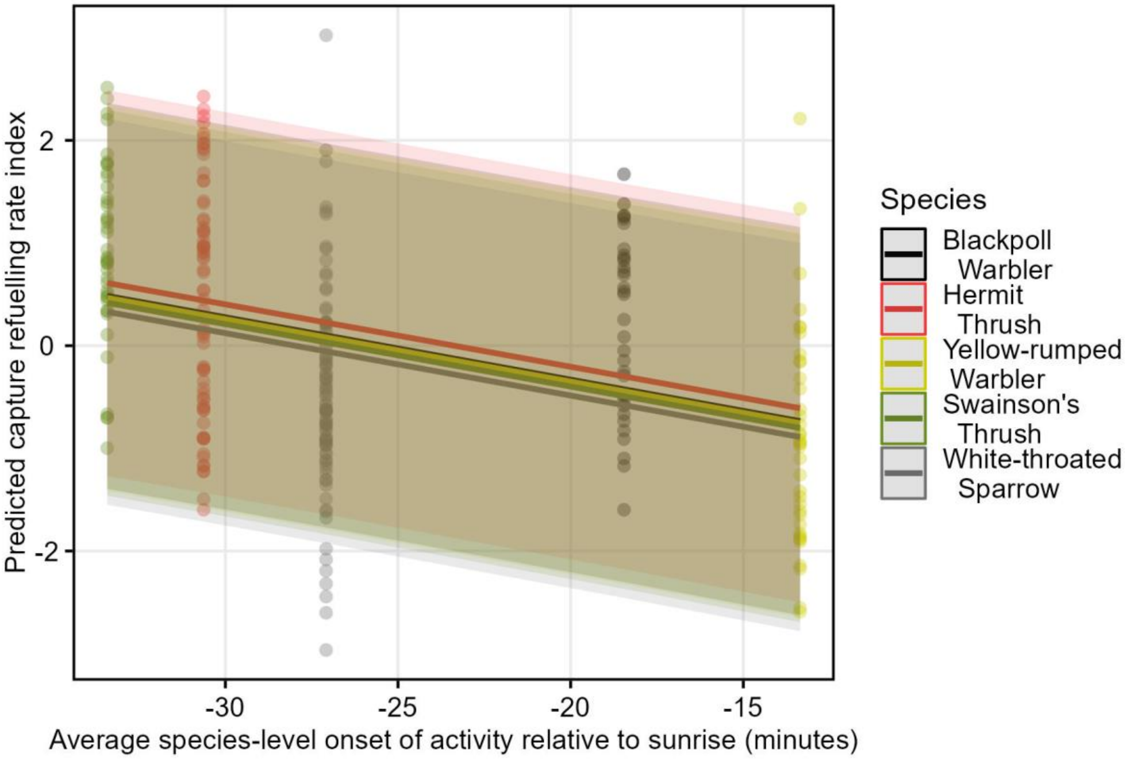


Figure 2-7. Refuelling rate by the onset of diel activity relative to sunrise for five species of songbird sampled during autumn stopover in eastern New Brunswick, Canada. The onset of diel activity was estimated at the species level as the marginal mean from a mixed-effect analysis of activity onset timing using data from 108 radio tagged birds. Also shown are the raw data points and 95% prediction intervals.

Table 2-3. Parameter estimates for the analysis of the capture refuelling rate of 269 individuals of five songbird species captured during autumn migratory stopover in eastern New Brunswick. Shown are the fixed effects and random effects and model marginal and conditional R^2. Activity onset and migration distance are both species-level estimates.

Fixed effects

Parameter	Estimate	Standard error	Degree of freedom	t-value	Pr (>|t|)
Intercept	0.009	0.08	5.6	0.10	> 0.5
Bleed time (seconds)	**-0.0009**	**0.0002**	**268.3**	**-4.35**	**< 0.01**
Capture time (minutes)	**0.003**	**0.0006**	**267.0**	**4.12**	**< 0.01**
Activity onset (minutes relative to sunrise)	**-0.06**	**0.01**	**9.4**	**-5.36**	**< 0.01**
Migration distance (km)	**0.0001**	**0.00004**	**8.3**	**4.43**	**< 0.01**

Random effects

Group	Variance	Model Marginal R^2	Model Conditional R^2
Species	0.01	0.33	0.34

2.3.3 Stopover duration

Stopover duration was determined for 252 birds across all study sites and years, representing 177 unique nights across 2019, 2020, and 2021. Eleven birds were removed from the dataset as outliers with stopover durations greater than 30 days (six Hermit Thrush and five White-throated Sparrows), leaving a total of 241 birds in the analysis. Median stopover duration was 10 days (range = 1 to 30 days), with species-specific values available in Table 2-1. In the proportional hazard model, stopover departure hazard increased 11% for every additional 1000 km of migration distance ($\beta = 0.11 \pm 0.03$, $z = 3.29$, $p < 0.01$, Figure 2-8a). Departure hazard also increased 5% for each one $\mathrm{m \cdot s^{-1}}$ increase in tailwind ($\beta = 0.049 \pm 0.014$, $z = 3.40$, $p < 0.01$, Figure 2-8b) and 3% for each additional day of year ($\beta = 0.026 \pm 0.005$, $z = 5.26$, $p < 0.01$). Departure hazard was not affected by crosswinds ($p = 0.18$). Post-departure migratory movements can be seen in Appendix A.

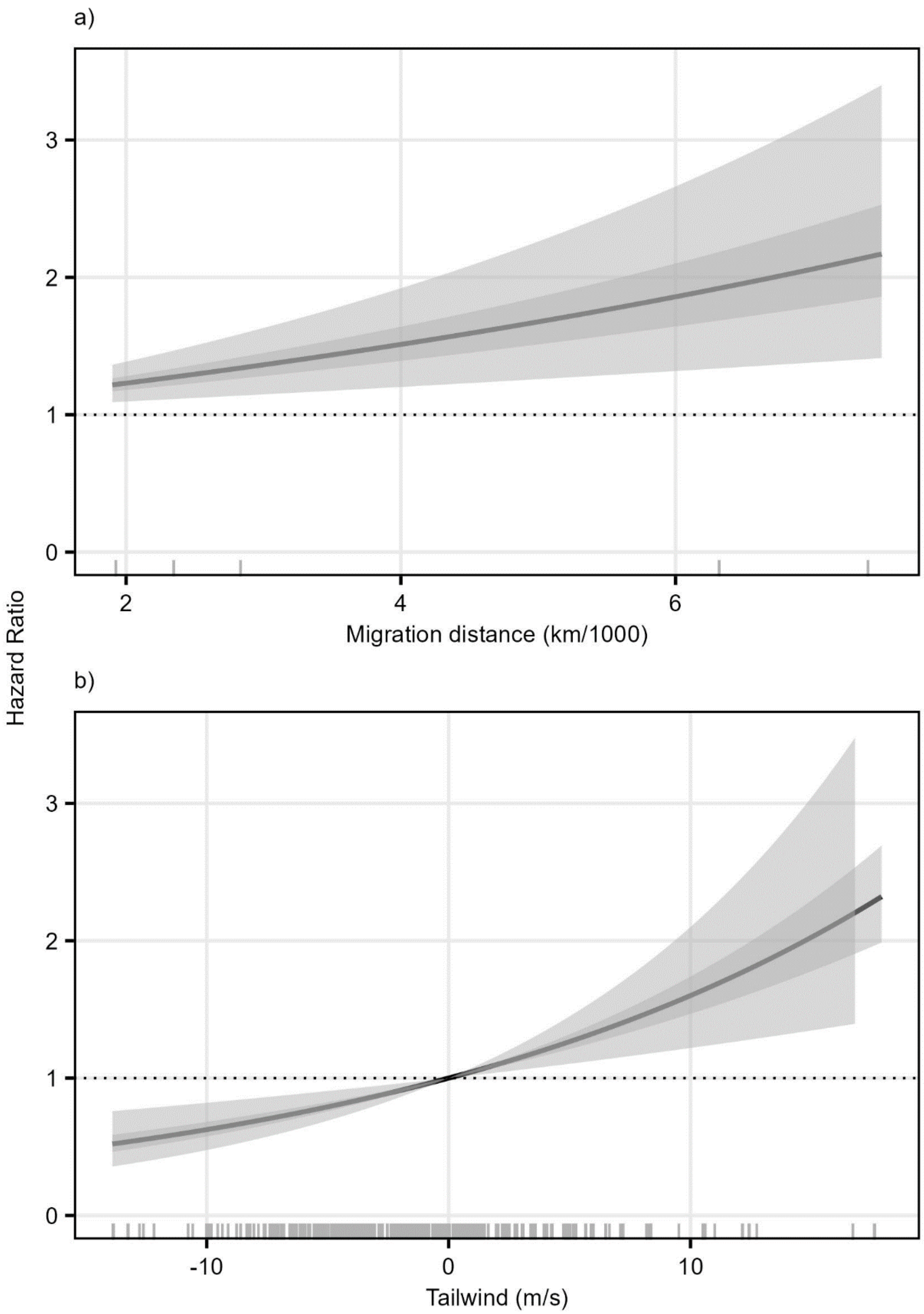


Figure 2-8. The effect of a) migration distance and b) tailwind on the hazard ratio for migratory departure simulated across varying values for songbird captured during autumn migratory stopover in eastern New Brunswick. The dark line represents the mean hazard ratio, with the dark grey and light grey representing the 50% and 95% confidence interval respectively.

2.4 Discussion

I combined individual-level physiological profiling and with measurement of behaviour made using automated telemetry to explore the covariation among diel activity timing, refuelling rate, stopover duration, and migration distance. The onset, end, and duration of diel activity varied among species, but only onset timing varied according to species migration distance and by body size as a proxy visual acuity. In line with my predictions, both capture refuelling rate index and stopover departure hazard increased with migration distance among the species examined, providing evidence that greater instantaneous rates of refuelling and shorter stopover duration facilitate the greater overall migration speed in long-distance migrants.

All diel activity timing measures differed among the five species in this study, but only the onset of activity was associated with migration distance or visual acuity. This discrepancy may stem from differences in the energetic states of migrants between dawn and dusk, which may affect the capacity or motivation to extend refuelling later in the day. After a prolonged overnight fasting, migrants in a lower energetic state may be more motivated to begin refuelling as early as possible in the morning. Conversely, the greater energetic state following a day of feeding may reduce the motivation to extend refuelling later into the evening. Extending feeding into the evening may also be limited if there is a need to digest food consumed earlier in the day (Kenward and Sibly 1977, Diamond et al. 1986, Kersten and Visser 1996). Reduced motivation or limited ability to continue refuelling in the evening may then limit any consistent relationship between visual acuity or migration distance and the end of activity. Starting foraging earlier in the day may also be more profitable if resources become progressively depleted or more difficult to acquire over the course of the day (Moore and Yong 1991). For example, the lower activity of flying insects in cooler morning temperatures may make it easier to glean flying insects, reducing the energy invested in obtaining prey. This greater profitability may offset any potential increases in predation risk associated with activity in the low-light conditions of early morning, a benefit which may not be available at the end of day.

Longer distance migrants commenced activity earlier than short distance migrants, providing support for the hypothesis that greater fuelling intensity facilitates longer distance migration via the earlier onset of refuelling. In the face of environmental variability, starting activity earlier in the day represents a consistent behavioural mechanism to ensure the greatest amount of time for refuelling is available each day given the conditions intrinsic and extrinsic conditions at the time of activity onset. Subsequent changes to weather conditions, increased predation threat, variation in local food availability, or other environmental variation may limit activity later in the day, preventing consistent extension of the refuelling period. Extending activity may also be unnecessary if individuals are able to reach a state of satiety or are limited by the need to digest prey. As such, selection pressures for greater migration speed via faster fuel deposition may only act consistently on the start of activity.

The onset of activity also varied with visual acuity, modelled using tarsus length as proxy for eye size and the known relationship between vertebrate eye-size and visual capabilities. As visual predators, a greater ability to detect prey under low light conditions likely contributes to this pattern in birds. In previous research, captive Great Tits (*Parus major*) hunted for longer and had greater prey handling times under lower light conditions (Kacelnik 1979). Birds may also limit foraging and other activities (e.g. dawn chorus timing: Thomas et al. 2002) in low light conditions when their ability to detect predators is compromised.

Separating the competing explanations for the species-level differences in the onset of activity is limited in this dataset by the positive correlation between migration distance and body size among the species in this study ($r = 0.26$, $p < 0.01$). Given that visual acuity, eye size, and body size are positively correlated (Kiltie 2000), and that body size and migration distance are independent among passerines (Schmaljohann 2019), difference in the onset of activity may be more associated with simple differences in visual acuity stemming from larger eye and body size. Larger eyes are also more metabolically expensive, and the aerodynamic, mechanical, physiological cost of proportionally larger eyes may constrain variation in eye size relative to body size (Brooke et al. 1999) particularly in long distance migrants adapted for energy efficient flight. Qualitatively, the species with the earliest onset of activity were also all ground foraging species, with the two thrush species typically found in dense wooded habitat throughout the annual cycle (Dellinger et al. 2020, Mack and Yong 2020). As such, species level differences may have also contributed to this pattern. In this wooded microhabitat, greater low-light visual acuity may be more important relative to the microhabitats used by the other species in this study, and this may also enable these species to extend their activity further into the earlier periods. Comparative studies that include species with a greater variety of body sizes, migration distances, and more direct microhabitat overlap (e.g. Ovenbird [*Seiurus aurocapilla*], Hermit Thrush, Swainson's Thrush, and Wood Thrush [*Hylocichla mustelina*]) may help distinguish the source of this pattern.

The overall duration of activity decreased with later capture date. These results illustrate how migrating earlier in the year can provide greater time to refuel each day, and an early migration date may represent an important facet of the annual migration strategy of long-distance migrants like the Swainson's Thrush. The duration of activity decreased approximately 3 minutes per-day of year, approximating the daily decrease in daylength for this region during the study period and suggesting the activity patterns largely mirror daylight trends. As similar pattern was observed in Swainson's Thrush by Morales et al. (2022) during autumn migratory stopover. Comparing between species, this rate of decrease in activity corresponds to a difference of approximately 84 minutes for birds refuelling on the median passage date of Swainson's Thrush and the median passage date of Hermit Thrush, the two earliest passing species in this study. Migrating earlier in the year to avoid shorter late-season daylengths may be of particular importance for migrants departing from latitudes higher than eastern New Brunswick, where the rate of daylength change across the autumn is more pronounced than at lower latitudes.

This study is the first to evaluate how species-level differences in the onset of activity affect instantaneous refuelling rate in free living songbirds. Capture refuelling rate was negatively associated with activity onset timing relative to local sunrise, indicating that species with a later onset of activity had a lower refuelling rate index for a given time of day. The sensitivity of metabolite-based measurement of refuelling to collection time of day likely reflects the transition of the plasma metabolite profile from the overnight fasting state to refuelling state after commencement of diurnal feeding and has been observed in previous studies that have assayed metabolite concentrations (Jenni and Jenni-Eiermann 1996, Brown et al. 2014, Hoh et al. 2018). This effect can be controlled for statistically by including capture time relative to sunrise as an analysis covariate, but doing so assumes all individuals begin foraging at the same time. My data illustrates how this assumption can influence the measured refuelling rate index, with a 10-minute difference in activity onset resulting in a 0.6 difference in refuelling rate index. This represents approximately 10% of the total refuelling rate index scale.

Instantaneous refuelling rate was positively associated with migration distance after controlling for the onset of activity and time of day, indicating that long distance migrants were depositing energy faster for a given period of activity. Behavioural, morphological, and physiological differences among the species in this study could all contribute to this pattern. Behaviourally, more intensive foraging by long-distance migrants could increase the amount of nutrients being metabolised, and differences in the relative size and activity of the alimentary or hepatic systems could facilitate the intake and rapid processing of food items consumed. Long-distance migrants may also select more energy-rich resources to promote greater refuelling, or these food items may be more available during the period in which these species a present at stopover. In a long-term study of the refuelling of three thrush species during autumn stopover, Pagano et al. (2023) suggest that Hermit Thrush utilise a greater amount of food items with lower nutrient quality as a method to compensate for a lack of more energy-rich foods, which can become locally depleted later in the migratory season (Smith et al. 2015). Differences in both behavioural and physiological mechanisms have been observed in the two subspecies of the Northern Wheatears, with greater foraging intensity (Dierschke and Delingat 2001) and higher mass gain per gram of prey consumed (Corman et al. 2014) in the long-distance migrant *leucorhoa* subspecies. Inferences from the comparisons of these metrics in wild birds may be challenging in an interspecific framework due to species-specific basal metabolic requirements, diet variation, and variation in local food available. Captive experiments that include measurement of energy assimilation may help to elucidate physiological and morphological differences enabling greater refuelling in long-distance migrants (Klaassen and Biebach 1994, Corman et al. 2014).

Stopover departure hazard was positively associated with migration distance, providing evidence for the link between greater migration speed and distance among the five species examined. Shorter stopover duration in species with greater migration distances has been observed previously in passerines, both from individual tracking-based studies (e.g. Packmor et al. 2020) and as estimated from banding recapture data (e.g. de Zwaan et al. 2022). Departure hazard was also positively associated with greater tailwind assistance and later first capture date. Departure under favourable wind conditions can reduce the energetic cost of migratory flight and the correction required for crosswind drift (Alerstam and Lindström 1990, Liechti 2006). Increased departure hazard with later date may reflect motivational difference between early and late season migrants.

One caveat of this study is that refuelling was measured on the day of capture, with activity timing measured over the subsequent stopover days. As a result, inferences regarding the influence of activity onset on measured refuelling rate rely on the assumption that the onset and end of activity on the day of capture does not differ from other days of stopover. Furthermore, our measurements of refuelling rate may have been made the morning following a migratory flight if migrants were captured on their day of arrival. As the species in this study are primarily nocturnal migrants, flight likely ended prior to or as late as sunrise (Kerlinger and Moore 1989), although activity on the morning prior to capture could have also included habitat selection related behaviours in addition to refuelling (Chernetsov 2006). The landscape context of the study sites is also absent of major geographic features preceding arrival which may have reduced instances of arrival post-sunrise that would occur is birds were mid-barrier at the time of sunrise. The lack of prolonged geographic barrier crossing pre-arrival may reduce the need for extended rebuilding of depleted energy reserves and digestive organs before efficient refuelling after arrival (Lindström et al. 1999), reducing any confounding effects that pronounced post-flight recovery may have on our measurements of refuelling.

This study is the first to apply radio telemetry and plasma metabolite profiling to explore how instantaneous rate of refuelling, diel activity, and stopover duration differ according to migration distance in passerine species. Instantaneous stopover refuelling rate increased with species-level migration distance, and the duration of activity appeared to be largely governed by interspecific differences in the onset of activity, together with seasonal differences daylength. For long-distance early-season autumn migrants like the Swainson’s Thrush, these results suggest a high capacity for daily fuel deposition. Complementing these results, stopover duration decreased with increasing migration distance, providing further evidence that the fast migration speed of long-distance migrants results from shorter stopover durations. I also demonstrated the sensitivity of metabolite-based measures of refuelling rate to the onset of diurnal activity. Both migration distance and visual acuity were associated with the observed interspecific difference in the onset of activity, and additional work on a broader species set is required to determine whether this pattern is associated with species microhabitat characteristics, an emergent property of a species morphology, or an adaptation to facilitate long distance migration though rapid refuelling and reduced stopover duration.

2.5 References

Agostinelli, C., and U. Lund (2022). R package “circular”: Circular Statistics. [Online.] Available at https://r-forge.r-project.org/projects/circular/.

Agriculture and Agri-food Canada (2023). Annual Crop Inventory 2021 - Pre-packaged GeoTIF files. [Online.] Available at https://agriculture.canada.ca/atlas/data_donnees/annualCropInventory/data_donnees/tif/2021/.

Bairlein, F. (1985). Efficiency of food utilization during fat deposition in the long-distance migratory Garden Warbler, *Sylvia borin*. Oecologia 68:118–125.

Beauchamp, A. T., C. G. Guglielmo, and Y. E. Morbey (2020). Stopover refuelling, movement and departure decisions in the White-throated Sparrow: The influence of intrinsic and extrinsic factors during spring migration. Journal of Animal Ecology 89:2553–2566.

Berg, K. S., R. T. Brumfield, and V. Apanius (2006). Phylogenetic and ecological determinants of the neotropical dawn chorus. Proceedings of the Royal Society B: Biological Sciences 273:999–1005.

Birds Canada (2022). motus: Fetch and use data from the Motus Wildlife Tracking System. [Online.] Available at https://motusWTS.github.io/motus.

Bivand, R., and N. Lewin-Koh (2021). maptools: Tools for Handling Spatial Objects. [Online.] Available at https://CRAN.R-project.org/package=maptools.

Bridge, E. S., W. T. Honeycutt, A. J. Chen, R. Miller, and J. F. Kelly (2024). Social behavior among nocturnally migrating birds revealed by automated moonwatching. Ornithology 141:ukad055.

Brooke, M. de L., S. Hanley, and S. B. Laughlin (1999). The scaling of eye size with body mass in birds. Proceedings of the Royal Society of London. Series B: Biological Sciences 266:405–412.

Brown, J. M., B. J. McCabe, L. V. Kennedy, and C. G. Guglielmo (2014). Genetically-based behavioural morph affects stopover refuelling performance in White-throated Sparrows *Zonotrichia albicollis*. Journal of Avian Biology 45:522–527.

Chernetsov, N. (2006). Habitat selection by nocturnal passerine migrants en route: mechanisms and results. Journal of Ornithology 147:185–191.

Cohen, E. B., J. M. Lafleur, and F. R. Moore (2022). Density dependent refueling of migratory songbirds during stopover within an urbanizing coastal landscape. Frontiers in Ecology and Evolution 10.

Corman, A.-M., F. Bairlein, and H. Schmaljohann (2014). The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird. Behavioral Ecology and Sociobiology 68:391–402.

Crewe, T. L., J. E. Deakin, A. T. Beauchamp, and Y. E. Morbey (2019). Detection range of songbirds using a stopover site by automated radio-telemetry. Journal of Field Ornithology 90:176–189.

Dellinger, R., P. B. Wood, and T. M. Donovan (2020). Hermit Thrush (*Catharus guttatus*), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Diamond, J. M., W. H. Karasov, D. Phan, and F. L. Carpenter (1986). Digestive physiology is a determinant of foraging bout frequency in hummingbirds. Nature 320:62–63.

Dierschke, V., and J. Delingat (2001). Stopover behaviour and departure decision of Northern Wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535–545.

DMTI Spatial Inc. (2014a). National Water (WAT). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2014b). Hydrography - Regions (HYR). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2014c). Route File (RTE). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017a). Water Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017b). Major Roads Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017c). Contour Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2021). Administrative Area Region. [computer file]. Markham, Ontario, Canada.

Dykstra, C. R., and W. H. Karasov (1992). Changes in gut structure and function of House Wrens (*Troglodytes aedon*) in response to increased energy demands. Physiological Zoology 65:422–442.

Ellegren, H. (1993). Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. Ornis Scandinavica (Scandinavian Journal of Ornithology) 24:220–228.

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, S. Ligocki, O. Robinson, W. Hochachka, L. Jaromczyk, A. Rodewald, C. Wood, I. Davies, and A. Spencer (2022). eBird Status and Trends.

Gifford, C. E., and E. P. Odum (1965). Bioenergetics of lipid deposition in the Bobolink, a trans-equatorial migrant. The Condor 67:383–403.

Gow, E. A., L. Burke, D. W. Winkler, S. M. Knight, D. W. Bradley, R. G. Clark, M. Bélisle, L. L. Berzins, T. Blake, E. S. Bridge, R. D. Dawson, et al. (2019). A range-wide domino effect and resetting of the annual cycle in a migratory songbird. Proceedings. Biological Sciences 286:20181916.

Grambsch, P. M., and T. Therneau (1994). Proportional hazards tests and diagnostics based on weighted residuals. Biometrika 81:515–526.

Guglielmo, C. G., D. J. Cerasale, and C. Eldermire (2005). A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological and Biochemical Zoology 78:116–125.

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-Level / mixed) regression models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Hedenström, A., and T. Alerstam (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Hoh, C. M., S. S. Pagano, and C. J. Norment (2018). Spatial variation in White-throated Sparrow (*Zonotrichia albicollis*) refueling rate near a migratory barrier. The Wilson Journal of Ornithology 130:891–901.

Hothorn, T., F. Bretz, and P. Westfall (2008). Simultaneous inference in general parametric models. Biometrical Journal 50:346–363.

Jenni, L., and S. Jenni-Eiermann (1996). Metabolic responses to diurnal feeding patterns during the postbreeding, moulting and migratory periods in passerine birds. Functional Ecology 10:73–80.

Jenni-Eiermann, S., and L. Jenni (1994). Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the Garden Warbler. The Auk 111:888–899.

Kacelnik, A. (1979). The foraging efficiency of Great Tits (*Parus major* L.*)* in relation to light intensity. Animal Behaviour 27:237–241.

Karasov, W. H., and B. Pinshow (2000). Test for physiological limitation to nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological and Biochemical Zoology 73:335–343.

Kemp, M. U., E. Emiel van Loon, J. Shamoun-Baranes, and W. Bouten (2012). RNCEP: global weather and climate data at your fingertips. Methods in Ecology and Evolution 3:65–70.

Kenward, R. E., and R. M. Sibly (1977). A Woodpigeon (*Columba palumbus*) feeding preference explained by a digestive bottle-neck. Journal of Applied Ecology 14:815–826.

Kerlinger, P., and F. R. Moore (1989). Atmospheric Structure and Avian Migration. In Current Ornithology (D. M. Power, Editor). Springer US, Boston, MA, pp. 109–142.

Kersten, M., and W. Visser (1996). The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. Functional Ecology 10:440–448.

Killick, R., and I. A. Eckley (2014). changepoint: an R package for changepoint analysis. Journal of Statistical Software 58:1–19.

Kiltie, R. A. (2000). Scaling of visual acuity with body size in mammals and birds. Functional Ecology 14:226–234.

Klaassen, M., and H. Biebach (1994). Energetics of fattening and starvation in the long-distance migratory Garden Warbler, *Sylvia borin*, during the migratory phase. Journal of Comparative Physiology B 164:362–371.

Kvist, A., and Å. Lindström (2000). Maximum daily energy intake: it takes time to lift the metabolic ceiling. Physiological and Biochemical Zoology 73:30–36.

La Sorte, F. A., D. Fink, W. M. Hochachka, J. P. DeLong, and S. Kelling (2013). Population-level scaling of avian migration speed with body size and migration distance for powered fliers. Ecology 94:1839–1847.

Lenth, R. V. (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means. [Online.] Available at https://CRAN.R-project.org/package=emmeans.

Liechti, F. (2006). Birds: blowin' by the wind? Journal of Ornithology 147:202–211.

Lindström, A. (2003). Fuel deposition in migrating birds: causes, constraints and consequences. In Avian Migration (P. Berthold, E. Gwinner and E. Sonnenschein, Editors). Springer-Verlag Berlin, Heidelberg.

Lindström, Å., T. Alerstam, and A. Hedenström (2019). Faster fuelling is the key to faster migration. Nature Climate Change 9:288–289.

Lindström, A., M. Klaassen, and A. Kvist (1999). Variation in energy intake and basal metabolic rate of a bird migrating in a wind tunnel. Functional Ecology 13:352–359.

Mack, D. E., and W. Yong (2020). Swainson's Thrush (*Catharus ustulatus*), version 1.0. In The Birds of the World (A. F. Poole and Gill, F.B., Editors). Cornell Lab of Ornithology, Ithaca, NY, USA.

McNeil, R., A. McSween, and P. Lachapelle (2005). Comparison of the retinal structure and function in four bird species as a function of the time they start singing in the morning. Brain Behavior and Evolution 65:202–214.

McWilliams, S. R., E. Caviedes-Vidal, and W. H. Karasov (1999). Digestive adjustments in Cedar Waxwings to high feeding rate. Journal of Experimental Zoology 283:394–407.

Mitchell, G. W., B. K. Woodworth, P. D. Taylor, and D. R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Movement Ecology 3:19.

Møller, A. P., J. Balbontín, J. J. Cuervo, I. G. Hermosell, and F. de Lope (2009). Individual differences in protandry, sexual selection, and fitness. Behavioral Ecology 20:433–440.

Moore, F. R., and W. Yong (1991). Evidence of food-based competition among passerine migrants during stopover. Behavioral Ecology and Sociobiology 28:85–90.

Morales, A., B. Frei, G. W. Mitchell, C. Bégin-Marchand, and K. H. Elliott (2022). Reduced diurnal activity and increased stopover duration by molting Swainson's Thrushes. Ornithology 139:ukab083.

Morbey, Y. E., A. T. Beauchamp, S. J. Bonner, and G. W. Mitchell (2020). Evening locomotor activity during stopover differs on pre-departure and departure days in free-living songbirds. Journal of Avian Biology 51.

Morbey, Y. E., C. G. Guglielmo, P. D. Taylor, I. Maggini, J. Deakin, S. A. Mackenzie, J. M. Brown, L. Zhao, and D. Stephens (2018). Evaluation of sex differences in the stopover behavior and post departure movements of wood-warblers. Behavioral Ecology 29:117–127.

Morbey, Y. E., and A. Hedenström (2020). Leave earlier or travel faster? Optimal mechanisms for managing arrival time in migratory songbirds. Frontiers in Ecology and Evolution 7.

Packmor, F., T. Klinner, B. K. Woodworth, C. Eikenaar, and H. Schmaljohann (2020). Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? Movement Ecology 8:6.

Pagano, S. S., G. L. Orfanides, A. J. Bros, R. L. Hoh, E. S. Delles, A. E. Frawley, and C. P. Carrington (2023). Patterns in the physiological condition of three species of thrushes during autumn stopover near the south shore of Lake Ontario. The Wilson Journal of Ornithology 135:210–223.

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10:439–446.

Price, T. (1981). The ecology of the Greenish Warbler *Phylloscopus trochiloides* in its winter quarters. Ibis 123:131–144.

R Core Team (2022). R: a language and environment for statistical computing. [Online.] Available at URL https://www.R-project.org/.

Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Schad, D. J., S. Vasishth, S. Hohenstein, and R. Kliegl (2020). How to capitalize on a priori contrasts in linear (mixed) models: A tutorial. Journal of Memory and Language 110:104038.

Schaub, M., and L. Jenni (2000). Fuel deposition of three passerine bird species along the migration route. Oecologia 122:306–317.

Schmaljohann, H. (2019). The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: a cross-continental analysis. Movement Ecology 7:25.

Smith, R. J., F. R. Moore, and C. A. May (2007). Stopover habitat along the shoreline of northern Lake Huron, Michigan: emergent aquatic insects as a food resource for spring migrating landbirds. The Auk 124:107–121.

Smith, S. B., A. C. Miller, C. R. Merchant, and A. F. Sankoh (2015). Local site variation in stopover physiology of migrating songbirds near the south shore of Lake Ontario is linked to fruit availability and quality. Conservation Physiology 3:cov036.

Taylor, P. D., T. Crewe, S. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. Francis, C. Guglielmo, D. Hamilton, R. Holberton, et al. (2017). The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:8.

Therneau, T. (2023). A Package for Survival Analysis in R. [Online.] Available at https://CRAN.R-project.org/package=survival.

Thomas, R. J., T. Széskely, I. C. Cuthill, D. G. C. Harper, S. E. Newson, T. D. Frayling, and P. D. Wallis (2002). Eye size in birds and the timing of song at dawn. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:831–837.

Zajac, R., D. J. Cerasale, and C. G. Guglielmo (2006). The rapid response of plasma metabolites to changes in feeding rate in a small passerine *Wilsonia pusilla*. Journal of Avian Biology 37:405–408.

de Zwaan, D. R., A. Huang, Q. McCallum, K. Owen, M. Lamont, and W. Easton (2022). Mass gain and stopover dynamics among migrating songbirds are linked to seasonal, environmental, and life-history effects. Ornithology 139:ukac027.

Chapter 3

3 Ecological drivers of refuelling and behaviour at coastal and inland stopover sites during autumn migration in eastern New Brunswick.

3.1 Introduction

Few of the millions of songbirds that migrate between breeding and non-breeding areas can complete their long-distance journeys without stopping periodically to rest and rebuild energy stores to fuel further flight (McWilliams et al. 2004). This energy is stored primarily as fat which is accumulated during stopovers at a much slower rate than it is used to power migratory flight (Alerstam and Lindström 1990, Hedenström and Alerstam 1997). As a consequence, the duration of the time spent refuelling at stopover sites, together with the total number stopover bouts across the migratory route, can have a drastic impact on the overall speed of migration and arrival timing at end destinations (McKinnon et al. 2014). Selection pressure for faster migration arising from high enroute mortality (Sillett and Holmes 2002) and the survival and reproductive benefits of earlier arrival at the migratory destinations (Marra et al. 1998, Norris et al. 2004, Kokko et al. 2006) may favour migrants that can reduce the time spent migrating (Alerstam 2011). As a key factors governing migration speed is refuelling (Lindström et al. 2019), the environmental and individual traits that shape refuelling may also determine the speed and success of migration.

How intrinsic and extrinsic factors interact to shape refuelling and the impact of variation in refuelling on stopover behaviour remains largely uncertain. As refuelling is ultimately dependent on local food availability, deposition rates should be higher where food is more plentiful. This relationship has been demonstrated at the site level using inter-individual banding data and regression techniques (e.g. Smith et al. 2007) and at the individual level using recapture data (Schaub and Jenni 2000), yet other studies employing automated mass balances (Dänhardt and Lindström 2001) or metabolite profiling report conflicting evidence for this relationship (Cerasale and Guglielmo 2010, Macdade et al. 2011). Refuelling rate can also be negatively affected by migrant density

(Moore and Yong 1991, Kelly et al. 2002, Ottich and Dierschke 2003), either through the division of locally available resources between individuals or through interference competition between migrants. Difference in foraging ability (Heise and Moore 2003), social status (Moore et al. 2003), or physiology (McCabe and Guglielmo 2019) may also contribute to class-based differences in refuelling, although there is mixed evidence for this phenomenon (Seewagen et al. 2013, Morbey et al. 2018, Beauchamp et al. 2020) suggesting that variable extrinsic factors may dominate over innate class-based differences in stopover refuelling performance.

Studies that relate variation in refuelling rate to the stopover behaviour of migrants remain relatively rare, owing to the challenge of measuring these aspects in free living songbirds. Movement at the stopover site scale can vary in relation to food availability (Cohen et al. 2012), suggesting that movement can be used to facilitate refuelling at the local scale. Optimal migration theory suggests that faster refuelling rates should reduce the time needed to refuel and shorten stopover duration, but migrants may also opt to forgo prolonged refuelling bouts if local refuelling conditions are poor (Kuenzi et al. 1991, Ottich and Dierschke 2003, Schaub et al. 2008). The relationship between environment, refuelling, and movement may be further modified by individual level differences in experience, social status, or physiology, particularly between age classes. For example, younger age-class birds may remain at stopover locations longer than older age-class birds (Ellegren 1991, Morris et al. 1996, Rguibi-Idrissi et al. 2003, Mills et al. 2011, Collet and Heim 2022, but see McKinnon et al. 2014), however, is uncertain if this pattern arises from differences in fuelling performance or represents an innate difference in behaviour between age classes. Wind conditions are another major factor governing migratory departure (Dossman et al. 2016, Morbey et al. 2018, Beauchamp et al. 2020, Packmor et al. 2020), but the influence of wind relative to the refuelling rate experienced during stopover remains uncertain. Energetically favourable tailwinds reduce the energetic cost of travel (Liechti 2006) by extending the range migrant can achieve for a given amount of fuel used, and departure strategies based on the availability of tailwinds may yield faster and less energetically costly migration (Weber et al. 1998). Individuals can also respond differently to wind availability based on intrinsic characteristics such as age class (Mitchell et al. 2015) further modifying relationship between departure decisions, refuelling, and tailwind. The lack of combined evaluations of individual-level refuelling rate and departure behaviour leaves it uncertain whether the availability of favourable wind conditions or local refuelling conditions are a greater driver of stopover duration and departure decisions in songbirds.

Differences in stopover behaviour might also arise at the edge of ecological barriers, which may require both high departure energy stores to surmount and constrain the habitat available in the region for refuelling. Large waterbody crossings, such as the Mediterranean Sea, Gulf of Mexico, or the Laurentian Great Lakes, represent portions of the migratory journey where landing to rest and refuel is not possible, and migrants may need to conduct extended stopovers in coastal areas to accumulate energy stores sufficient to safely fly the required distance prior to crossing (Schaub et al. 2008, Goymann et al. 2010, but see Dossman et al. 2016). Migrants that encounter resource-poor sites in these regions may move among coastal habitats or relocate inland to refuel prior to crossing (Deutschlander and Muheim 2009, Smolinsky et al. 2013, Woodworth et al. 2014). This can lead to the accumulation of refuelling migrants in areas of suitable habitat (Buler and Diehl 2009, Buler and Dawson 2014), which may result in lower fuel deposition rates (Kelly et al. 2002). This effect can also be further exacerbated by the high levels of natural and anthropogenic habitat fragmentation often found in coastal areas (Buler and Moore 2011, Cohen et al. 2014, 2022). Much of what we understand about songbird stopover in coastal habitats comes from regions where migrants must transit an ecological barrier to progress their migration, owing to the vital role of these regions in successful trans-barrier migratory movements. Relatively few studies have assessed migratory behaviour and refuelling along coastlines either aligned with the direction of migratory travel or in situations where direct transit of the adjacent ecological barrier is not required. In this context, migrant ecology at coastal sites may better reflect the influence of the coastal habitat features separately from any specialised behaviours associated with preparation for or recovery from crossing an ecological barrier.

I applied habitat assessment, physiological profiling, and automated radio telemetry to test how key environmental and individual characteristics influence the refuelling rate and movement behaviour of migrants at coastal and inland stopover sites in eastern New Brunswick during autumn migration. Direct overwater transit of the adjoining Bay of Fundy and Gulf of Maine is not required to progress southward migration from the study region. Using a multi-stage analysis framework, I tested how refuelling rate, local movement, and stopover duration differed between coastal and inland sites, or whether variation in these aspects of stopover ecology were better explained by local variation in resource availability and migrant abundance or by variation in broader temporal covariates. I then tested how individual characteristics such as age class and capture body condition explained variation in refuelling, movement, and stopover duration. As refuelling rate and movement behaviour was measured at the individual level, I also evaluated how local movement and stopover duration was influenced by capture refuelling rate.

3.2 Methods

Research was conducted at four sites in eastern New Brunswick, Canada (Figure 3-1) over three autumn migratory season, 13 September to 28 October 2019, 6 September to 28 October 2020, and 28 August to 24 October 2021. Two sites were located coastally near Waterside (45°37’30.4” N 64°47'30.47"W) (WAT) and Mary’s Point (45°43'28.07"N 64°40'31.16"W) (MPT). The other two sites were located approximately 25 km inland at the Mapleton Acadian Forest Nature Preserve (45°49'19.94"N 65° 3'33.49"W) (MAF) and the Community Forest International Whaelghinbran Property (45°44'4.88"N 65°18'2.41"W) (CFI). Sites featured similar forest structure intermixed with patches of open habitat, with the compositions of tree species at CFI, MPT, and WAT, primarily including a mixture of spruce (*Picea* spp.), fir (*Abies* spp.), birch (*Betula* spp.), and pine (*Pinus* spp.). Hardwood species were also prevalent at the MAF site, primarily maple (*Acer* spp.), beech (*Fagus* spp.), and aspen (*Populus* spp.). Local temperature was recorded using two Onset UA-002-64 temperature loggers at each site (www.onsetcomp.com). Study sites were sampled on a four-day rotation. Five to eight mist nets were used to passively capture birds, with netting commencing one hour after local sunrise to minimise the strong time-of-day effect (Guglielmo et al. 2005) and ceasing approximately seven hours after local sunrise. Daily netting effort was recorded to account for variability in netting effort arising from wind and weather conditions which prevented the safe capture of birds using all available nets. On rare-instances, nets were also closed temporarily due a processing backlog of captured birds or for other immediate logistical concerns. Birds were banded with the appropriate size U.S. Fish and Wildlife Service/Canadian Wildlife Service aluminum leg band, and wing chord, tarsus length, mass, and fat score (Kaiser 1993) were measured. Sex and age were provisionally assigned in the field following Pyle (1997), and sex was later confirmed using genetic analysis (Griffiths et al. 1998). Data collection was conducted under the banding permit 10911C issued by Environment and Climate Change Canada to ATB, with approval by the University of Western Ontario's Animal Care Committee (AUP # 2017-160).

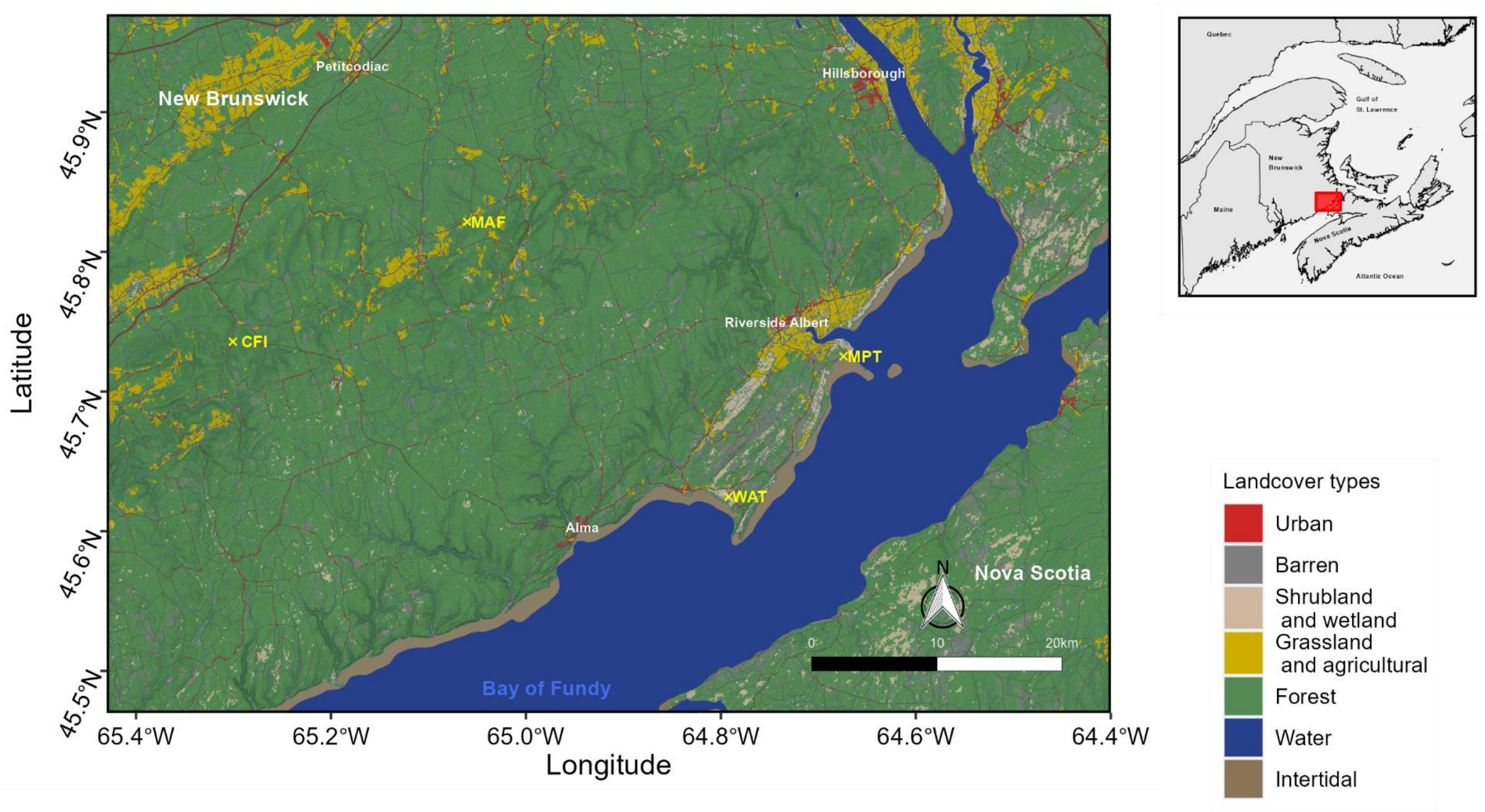


Figure 3-1. Location of study sites and 2021 landcover classification in eastern New Brunswick, Canada. Also indicated are roadways, watercourses, and topography at intervals of 10 meters. Sites labels; CFI = Community Forest International Whaelghinbran Property; MAF = Mapleton Acadian Forest Nature Preserve; WAT = Waterside; MPT = Mary’s Point. Raster landcover classification data adapted from (Agriculture and Agri-food Canada 2023), vector data from (DMTI Spatial Inc. 2014a, b, c, 2017a, b, c, 2021).

3.2.1 Plasma metabolite profiling and movement

Plasma metabolite profiling was used to measure refuelling (Guglielmo et al. 2005, Beauchamp et al. 2020) in White-throated Sparrow (*Zonotrichia albicollis*), Song Sparrow (*Melospiza melodia*), Slate-colored Junco (*Junco hyemalis hyemalis*), Swainson's Thrush (*Catharus ustulatus*), Hermit Thrush (*Catharus guttatus*), Yellow-rumped Warbler (*Setophaga coronata*) and Blackpoll Warbler (*Setophaga striata*). These species were selected because they were sufficiently abundant at the study sites, and because they represent a mixture of taxonomic families and both long and short-distance migrants. Mist nets were continuous monitored where possible or were otherwise checked every eight to 10 minutes. A digital stopwatch was used to record the time elapsed between last check of a net, and the completion of blood extraction (bleed time). Following collection, blood samples were centrifuged at 2000 *g* for 10 min to separate plasma, which was transferred into cryogenic tubes and stored in a liquid nitrogen dry shipper (Taylor-Wharton CX 100). Remaining blood cells were retained to confirm sex (Griffiths et al. 1998, Beauchamp et al. 2020 SI). Plasma concentrations of β-OH butyrate, glycerol, and triglyceride (mmol*L^{-1}) were measured using colorimetric assays (R Biopharm: 10907979035, SIGMA: Trinder reagent A and B) following Guglielmo et al. (2005). Birds ingesting enough food to deposit fat have elevated plasma triglyceride concentration, whereas birds unable to ingest sufficient quantities of food to deposit fat will have elevated plasma β-OH butyrate concentration (Guglielmo et al. 2005). Plasma concentrations of triglyceride (correcting for free glycerol) and β-OH butyrate were log10(x + 1) transformed, and principal component analysis was applied to create a refuelling index (RI) (Guglielmo et al. 2005). Samples with a bleed time greater than 20 minutes were omitted from this analysis, due to the rapid turnover of these metabolites from feeding to fasting following capture (Zajac et al. 2006). Granivorous species sampled in 2020 were also omitted from this analysis, as resource manipulations targeting granivorous species occurred in 2020 as part of chapter 4. This resulted in 290 birds from the seven target species with triglyceride and β-OH butyrate concentrations measured and with complete data on analysis covariates across all years of study.

Following blood collection digitally encoded radio transmitters (model NTQB2-1 and NTQB2-2, Lotek Wireless, www.lotekwirelss.ca) were used to measure local movement and stopover duration in five of these species (White-throated Sparrows, Swainson's Thrush, Hermit Thrush, Yellow-rumped Warblers, and Blackpoll Warblers). Tags weighed approximately 0.29 – 0.35 g, and were affixed to the bird using a leg-loop harness constructed of elastic thread (Rappole and Tipton 1991). Pulse interval of the tags varied depending in the tag model and year, and ranged from 6.10 s to 12.5 s. Manual telemetry was used to track local movement during stopover with attempts made to locate tagged birds once each visit to the capture site (every 2 to 4 days) using the homing method (White and Garrott 2012), working outward from the last known location of an individual. Coordinates were recorded when a tagged bird was observed, or the position was estimated using a combination of high signal strength at low gain. Geographic Positioning System coordinates were recorded for the position of the observer (Garmin eTrex 20x) and adjusted for the direction and distance to a bird using a laser rangefinder (Leupold Marksman 1000 or Nikon Prostaff 1000) and magnetic compass. These data were used to estimate the spatial extent of the stopover for migrants captured at each site.

Stopover duration and post-departure movement bearing was measured using the Motus Wildlife Tracking System (Motus; Taylor et al. 2017). Detections of radio signals from tagged individuals on the receiver located at each site was used to determine that a bird was still within the region of capture. Stopover duration was calculated as the number of days between tagging and departure + 1, providing the minimum length of stopover. Post-departure detections were processed following (Birds Canada 2022) to remove false-detections, and the bearing between the capture site and the next detection on the Motus array was averaged across all individuals using the package "circular" (Agostinelli and Lund 2022) to provide the average post-departure flight bearing.

Wind data for the analysis of departure risk was obtained from the NCEP/DOE Reanalysis 2 data set (http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis2.html) which provides meteorological data four times each day at 2.5° x 2.5° spatial resolution. Wind speed in $m \cdot s^{-1}$ in the easterly and northerly direction was extracted using the "RNCEP" package (Kemp et al. 2012), and interpolated for an individual's stopover site using the function NCEP.interpol with the option for linear interpolation. Wind was interpolated for ground level for 21:00 ADT. Tailwind component was estimated as V_w*cos(β), where V_w is wind speed ($m \cdot s^{-1}$) and β is average post-departure flight bearing.

3.2.2 Invertebrate prey and migrant abundance

Eight paired pitfall and sticky traps were set at each site to sample terrestrial and flying insects. At the start of the season, traps were positioned randomly along the length of one of the mist net lanes at a random perpendicular distance between six and 15 meters. Traps were collected and reset at the end of each visit to the site, leaving them exposed for a total of four days. Pitfall traps were approximately ~8 cm diameter and ~ 2 cm in depth, featuring three 50 cm drift fences spaced at 120° intervals and extending away from the trap opening and a 12 mm metal mesh screen positioned 2 cm below the rim of the trap to exclude vertebrates (Leather 2005, Smith and McWilliams 2014). Traps were set flush to the ground surface and filled with water to a depth of ~3 cm. Contents were collected at each visit to the site and stored in ~70% ethanol. In the lab, captured invertebrates were dried at 60°C for 18 to 24 h, identified to family where possible, and weighed on an electronic balance (0.1 mg). Flying insects were sampled using sticky traps (Kelly et al. 2002, Leather 2005). Five 13 cm x 20 cm yellow card-style sticky traps (LIGHTSMAX) were deployed vertically on wooden poles at a height of approximately 2.2 m, with traps having a minimum clearance from of 50 cm on all sides from any vegetation. Sticky traps replaced every visit, with the trap oriented to face a random direction selected using a random number table.

Image analysis was used to determine the percentage of the trap area covered by invertebrates to obtain an index of flying invertebrate abundance (e.g. Lukas and Stejskal 2003). Following the removal of any non-invertebrate material (leaves, dirt, etc.), traps were placed on a blue stage and photographed using a Canon Rebel T3i with and EFS 18-55 lens mounted to a tripod. Distance between the stage and lens was adjusted to 465 mm. A shutter speed of 1/30 and aperture of F5.6 and ISO of 1600 were used under low ambient lighting conditions to reduce glare from the glossy surface of the trap. The lens was leveled using a bubble level prior to photographing. Digital images of traps were then processed using a three-step process in ImageJ version 1.51w (Rasband 2018). First, the area of the image matching the colour of the trap was measured to obtain the area of the trap not covered by captured invertebrates. Second, the total area of the trap in the image was calculated by measuring the area of the blue background present around the image edge and subtracting this from the total image area. Finally, subtraction of the area in step one from the area in step two yielded the area covered by invertebrates. This was then converted to a proportion by dividing by the total area of the trap obtained in step two. Issues with storage severely limited the number of sticky traps that could be processed from the 2019 field season. As such, complete sticky trap area coverage data and pitfall capture mass data was available from 731 unique traps, representing 112 sampling days across 2019, 2020, and 2021.

To calculate an index of resource abundance, averages of the invertebrate mass from each pitfall trap and the percent of the surface covered of each sticky trap were calculated for traps set at each site and over the same four-day period. Averages for each trap type were then standardised to exposure period (four days). Following log10 (value +1) transformation, principal component analysis was then applied to the exposure-standardised average-values of the pitfall and stick traps collected across all sites, with the first principal component being used as a sites and date specific index of invertebrate resource abundance (ResI). Using this data, site- and year-specific generalised additive models (GAMs) of ResI were then fit to estimate daily invertebrate resource abundance (eResI) for the three days between consecutive visits of the same site for inclusion in the analysis of migrant departure hazard (described below).

Migrant abundance was assessed as the total number of unbanded migrants captured aggregated by taxonomic family for each sampling day, focusing on sparrows (Passerellidae), warblers (Parulidae), and thrushes (Turdidae). This taxonomic family-specific migrant catch data was available for 151 sampling days (40 from 2019, 53 from 2020, and 58 from 2021). Daily taxonomic family-specific catch rates were calculated by standardising the total number of unbanded migrants captured aggregated by taxonomic family for each sampling day by the summed total of time all nets were open on that sampling day. Recaptures of banded migrants from previous sampling days were generally infrequent (averaging < 1 recapture per-day), and as such were not considered when tallying the daily total catch. The value for the relative taxonomic family-specific catch per unit effort (CPUE) was then applied to each observation for use in the analysis of refuelling rate.

3.2.3 Analysis of invertebrate abundance and migrant catch

Differences in invertebrate abundance index (ResI) between coastal and inland stopover sites were tested using a linear mixed effect model, including site type, and the random intercept of site. Five additional models were then created by including terms for year, day of year, mean daily temperature for the site, and additive combinations of year and day or year, or year and mean temperature. The best fit model was determined using AICc. *P*-values for fixed effects were determined using the Satterthwaite approximation for degrees of freedom implemented in package “lmerTest” (Kuznetsova et al. 2017).

To test for differences in total number of bird captured by taxonomic family between coastal and inland sites across the season, a mixed-effect negative binomial model was implemented using function glmer.nb from package lme4 (Bates et al. 2015) fit using maximum likelihood. Site type, taxonomic family, year, and day of year were included as fixed effects, and an offset term for total number of net-hours each day *(log10(nethours+1)) was included to account for difference in sampling effort among days. Site was included in the model as random effects to account for repeated measurement of catch at each site. To test for site-specific familial capture rates, a likelihood ratio test was used to determine if the interaction between site and family significantly improved model fit at $\alpha = 0.05$. This analysis was then further extended to test how local food availability influenced total catch, restricting the dataset to 2020 and 2021 where invertebrate ResI data were available. A likelihood ratio test was used to test whether inclusion of ResI increased model fit relative to the best model.

3.2.4 Analysis of Refuelling performance

Candidate linear mixed effect models were used to test how key environmental and individual covariates affected refuelling rate index. Analysis was implemented using package "lme4" (Bates et al. 2015) in R version 4.1.2 (R Core Team 2021), and models were fit using maximum likelihood. All candidate models were compared to a null model (model 1) that contained individual capture time, the time between capture and the completion of blood sampling (bleed time), and random intercepts for species and site. Capture time of day has a strong influence on measured refuelling performance, resulting from the turnover of plasma metabolite profile between nocturnal fasting and diurnal feeding (Jenni and Jenni-Eiermann 1996). Conversely, bleed time decreases the refuelling rate index as the metabolite profile rapidly changes from feeding to fasting following capture.

Analysis was conducted in two stages. In the first stage, two sets of candidate models included the model 1 covariates and spatiotemporal covariates (year, site type, day of year, and all additive combinations; models 2-8) or local-scale covariates (ResI, familial CPUE and ResI + CPUE; models 9-11) were used to contrast how covariates at the broad and local scale influence refuelling. As species may differ in their response to ResI and CPUE, two models (9a, 10a) included random slopes of ResI and CPUE respectively. The best performing random slope was then used in subsequent models. The influence of intrinsic covariates was then tested in the second stage of analysis. Starting with the best model from stage one, three additional models were created by including age, body condition (capture mass and tarsus length), or both. Sex was not considered as most of the birds captured were male. All covariates were centered and scaled prior to model analysis, and model fit was determined using AICc in both stages. Following model selection, *P*-values for fixed effect covariates were determined using the Satterthwaite approximation for degrees of freedom implemented in package lmerTest. Q-Q plots and model residuals were visually inspected to verify model assumptions were not violated.

3.2.5 Analysis of local movement behaviour

Local movement behaviour was characterised using the distance between successive relocations and maximum displacement away from the release site, calculated using the adehabitatLT package in R (Calenge 2006). For each movement metric, linear mixed effect analyses were applied in a candidate model approach to test for differences in stopover movement behaviour between coastal and inland sites and to explore how other extrinsic and intrinsic factors shaped movement during stopover. In both the analysis of movement distance and maximum displacement, all covariates were centered and scaled prior to model analysis. Models were fit using maximum likelihood and compared to the null model using AICc. Following model selection, P-values for fixed effect covariates were determined using the Satterthwaite approximation for degrees of freedom implemented in package lmerTest. Q-Q plots and model residuals were visually inspected to verify model assumptions were not violated. Stopover movement trajectories generated from recorded position were visualised using the package “ggmap” (Kahle and Wickham 2013) in R.

The analysis of movement distance started with a null model (model 1) including the difference in time between the successive relocations used to calculate the movement distance (step duration) and day of stopover. Step duration was included to control for variation in the frequency of relocations, and day of stopover was included as previous studies have observed decreasing movement across the stopover period (Paxton et al. 2008, Beauchamp et al. 2020). Separate random intercepts for site, species, and individual were included to account for repeated measures of movement distance and unaccounted variability arising from site characteristics and species-specific behaviour. The influence of intrinsic and extrinsic factors on movement was then evaluated in two-stages. In the first stage of analysis, the influence of extrinsic covariates on movement distance was tested by creating separate candidate models including the model 1 covariates and spatiotemporal covariates (year, site type, and all additive combinations; models 2-4). The influence of intrinsic covariates on movement distance was then tested in stage two. Starting with the best fit model from stage one, seven additional models were created by including age, body condition (capture mass and tarsus length), capture refuelling rate index, and all additive combinations (model 5-11). Capture refuelling rate was included as the residuals from the analysis of the refuelling rate index, representing the refuelling rate of an individual accounting for intrinsic and extrinsic covariates included in the best model of refuelling.

Following a similar approach, the influence of extrinsic and intrinsic factors on maximum displacement during stopover was tested, starting with a null model (model 1) that included the nested random effects of site and species. A two-stage candidate model approach was then applied. In the first stage, separate candidate models were created by expanding model 1 to include spatiotemporal covariates (site type, year, day of stopover, and all additive combinations). The influence of intrinsic covariates on maximum displacement was then tested in stage two by extending the best fit model from stage one with either the covariates age class, body condition (capture mass and tarsus length), capture refuelling rate (using the residual estimates), or any of the additive combination of these covariates.

3.2.6 Analysis of stopover departure hazard

The influence of extrinsic and intrinsic factors on stopover duration (departure date – capture date +1) was evaluated using survival analysis (Dossman et al. 2016, Morbey et al. 2018). I applied a mixed-effect proportional hazard framework using the package “coxme” in R (Therneau 2022) to evaluate departure risk across days of stopover, allowing for the inclusion of both time-dependent covariates and random terms. I applied a two-stage candidate model approach. The null model included day of year, as increasing departure hazard with later capture date has been observed previously (Beauchamp et al. 2020, Packmor et al. 2020). Species and site were included in the null model as a random intercept in the model to account for any intrinsic differences in departure hazard between species and for site-level clustering. In the first stage of analysis, model fit of three candidate models containing regional-scale spatiotemporal covariates were compared to three candidate models including local-scale covariates to test whether regional or local scale covariates best explained extrinsic. Each of the three regional-scale spatiotemporal models of departure hazard included all null model covariates, with separate models including year, site type, and both year and site type. Local-scale covariate models included estimated invertebrate resource abundance (eResI), tailwind assistance, and both eResI and tailwind assistance, with the fit of each being evaluated when included as either a fixed effect or random slope. Both eResI and tailwind were modelled as time-dependent covariates, with each bird being assigned tailwind and eResI on each day it was at risk of departure (i.e. still at the stopover site). Daily estimates of invertebrate resource abundance (eResI) were determined by fitting site- and year-specific generalised additive models to the measured ResI values, with local mean daily temperature and a smooth term for day of year fit using generalised cross-validation in package "mgcv" (Wood 2011). Average daily temperatures and day of year were then used to estimate year and site specific ResI values for each day. Due to the limited ResI data available in 2019 site and year specific estimates of ResI could not be obtained for this year. As such, the analysis on departure hazard was conducted using stopover data from 2020 and 2021 only.

The influence of intrinsic covariates on departure hazard was then tested in the second stage of analysis. Starting with the best model from stage one, seven additional models were created by including age, body condition (included as capture body mass and tarsus length), capture refuelling rate, all two-way combinations of each covariate additively, and an additive model including all three covariates. All covariates were centered and scaled prior to analysis, and model fit was assessed using AICc. All data analyses were conducted in R version 4.1.2 (R Core Team 2021).

3.3 Results

3.3.1 Invertebrate abundance and migrant catch

In the principal component analysis of invertebrate trap data, principal component one accounted for 64.8% of variation in invertebrate capture, with average pitfall trap mass and average sticky trap coverage loading positively (0.71%). As such, principal component one can be interpreted to represent an index of local invertebrate resource abundance on that sampling day (ResI), with increasing ResI values indicating a greater local abundance of flying and terrestrial invertebrates. The best model of ResI included the fixed effects of year, site type, and mean daily temperature for the site, and the random intercepts of site. In the best model, ResI did not differ between coastal and inland sites ($\beta_{\text{inland}} = -0.15 \pm 0.29$, $t_4 = -0.51$, $p > 0.5$, Figure 3-2). ResI increased with greater daily average temperature ($\beta = 0.02 \pm 0.005$, $t_{100} = 4.08$, $p < 0.01$), and was greater in 2021 relative to 2020 ($\beta_{2021} = 1.00 \pm 0.17$, $t_{100} = 5.88$, $p < 0.01$, Table 3-1).

Estimated differences in intercept and 95% confidence intervals for the random effect of site suggests that sites did not differ in invertebrate catch (Figure 3-2b). This model had an AICc 13.18 lower than the next best model indicating significantly greater support.

Table 3-1. Parameter estimates for the analysis of invertebrate resource abundance index (ResI) at four sites in eastern New Brunswick. Shown are the fixed effects and random effects and model marginal and conditional R^2.

Fixed effects

Parameter	Estimate ± SE	Degree of freedom	t-value	Pr (>|t|)
Intercept	-0.54 ± 0.22	5.6	-2.42	0.05
Site type (Inland)	-0.15 ± 0.29	4.0	-0.51	> 0.50
Year (2021)	**1.00 ± 0.17**	**100.0**	**5.88**	**< 0.01**
Mean daily temperature	**0.35 ± 0.09**	**100.0**	**4.08**	**< 0.01**

Random effects

Group	Variance	Model Marginal R^2	Model Conditional R^2
Site	0.06	0.39	0.44

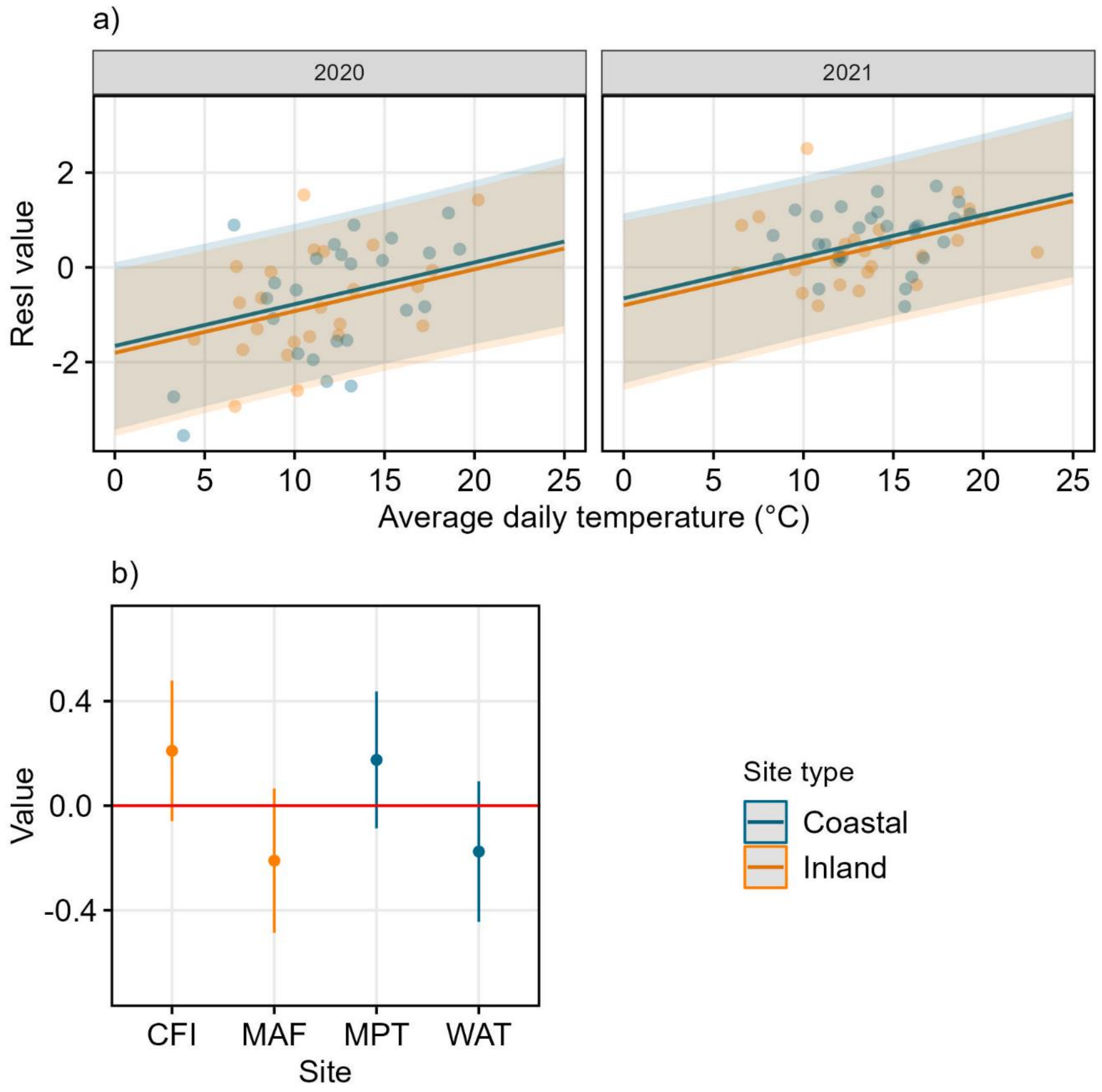


Figure 3-2. Estimated relationship for the fixed effects of average daily temperature, year, and site type (a) and the conditional modes for the random effects of site (b) from the liner mixed-effect analysis of the invertebrate resource abundance index at stopover sites in eastern New Brunswick. Also shown are the 95% prediction intervals, with colour corresponding to site type**.**

In the analysis of taxonomic family-specific migrant catch (Figure 3-3), the final model included the fixed effect of site type, taxonomic family, year, day of year, and the random of site, and was significantly improved by the inclusion of the interaction between site and family (χ_1^2= 60.28, $p < 0.01$). Inland and coastal stopover sites did not differ in taxonomic family-specific catch (β = -0.21 ± 0.87, z = -0.24, $p > 0.5$), decreased with each day of year (β = -0.28 ± 0.07, z = -3.97, $p < 0.01$) and was greater in 2020 (β = 1.27 ± 0.21, z = 6.17, $p < 0.01$) and 2021 (β = 1.03 ± 0.21, z = 4.94 , $p < 0.01$, Table 3-2, Figure 3-4). Estimated differences in intercept and 95% confidence intervals for the random effect of site suggest that catch was generally great at CFI and lower at MAF (Figure 3-4b), and that sparrow capture was greater at MPT and lower at the MAF (Figure 3-4Table **3**-**2**c). The dispersion parameter of the negative binomial family for the final model was 0.91. Including invertebrate resource abundance (ResI) resulted in a reduction of sample size to 103 sampling days across 2020 and 2021, and the addition of covariate ResI to the model was supported by a likelihood ratio test (χ_1^2= 9.88, $p < 0.01$). Migrant catch was greater with higher local invertebrate resource abundance (β = 0.25 ± 0.09, z = 2.84, $p < 0.01$, Table 3-2, Figure 3-5) The effects of the other fixed and random effects were qualitatively similar to the analysis without invertebrate resource abundance (Table 3-2).

Table 3-2. Parameter estimates for the analysis of taxonomic family-specific catch at four stopover sites in eastern New Brunswick during fall migration. Shown are the fixed and random effects for the full dataset analysis (n = 151) and the analysis including invertebrate resource abundance (ResI) excluding 2019 where ResI values were unavailable for most sampling days (n = 103).

Fixed effects

Migrant catch dataset	Parameter	Estimate ± SE	z-value	Pr (>|z|)
Full dataset (2019 – 2021, n = 151)	**Intercept**	**-2.27 ± 0.71**	**-3.18**	**< 0.01**
	Site type (Inland)	-0.21 ± 0.91	-0.24	> 0.5
	Day of year	**-0.02 ± 0.005**	**-3.94**	**< 0.01**
	Family (Thrushes)	-0.60 ± 0.57	-1.05	0.30
	Family (Warbler)	0.07 ± 0.57	0.13	> 0.5
	Year (2020)	**1.27 ± 0.21**	**6.17**	**< 0.01**
	Year (2021)	**1.03 ± 0.21**	**4.94**	**< 0.01**
ResI restricted dataset (2020 & 2021, n = 103)	Intercept	-0.77 ± 0.61	-1.27	0.20
	Site type (Inland)	-0.19 ± 0.76	-0.25	> 0.5
	ResI	**0.25 ± 0.09**	**2.84**	**0.01**
	Day of year	**-0.38 ± 0.09**	**-4.45**	**< 0.01**
	Family (Thrushes)	-0.61 ± 0.49	-1.25	0.21
	Family (Warbler)	-0.08 ± 0.49	-0.18	> 0.5
	Year (2021)	**-0.50 ± 0.18**	**-2.69**	**< 0.01**

Random effects

Migrant catch dataset	Group	Variance	Inter-class correlation coefficient	Model Marginal R^2	Model Conditional R^2
Full dataset (2019 – 2021, n = 151)	Site	0.54	0.18	0.13	0.49
	Site:family	0.57	0.19		
ResI restricted dataset (2020 & 2021, n = 103)	Site	0.41	0.15	0.12	0.44
	Site:family	0.64	0.16		

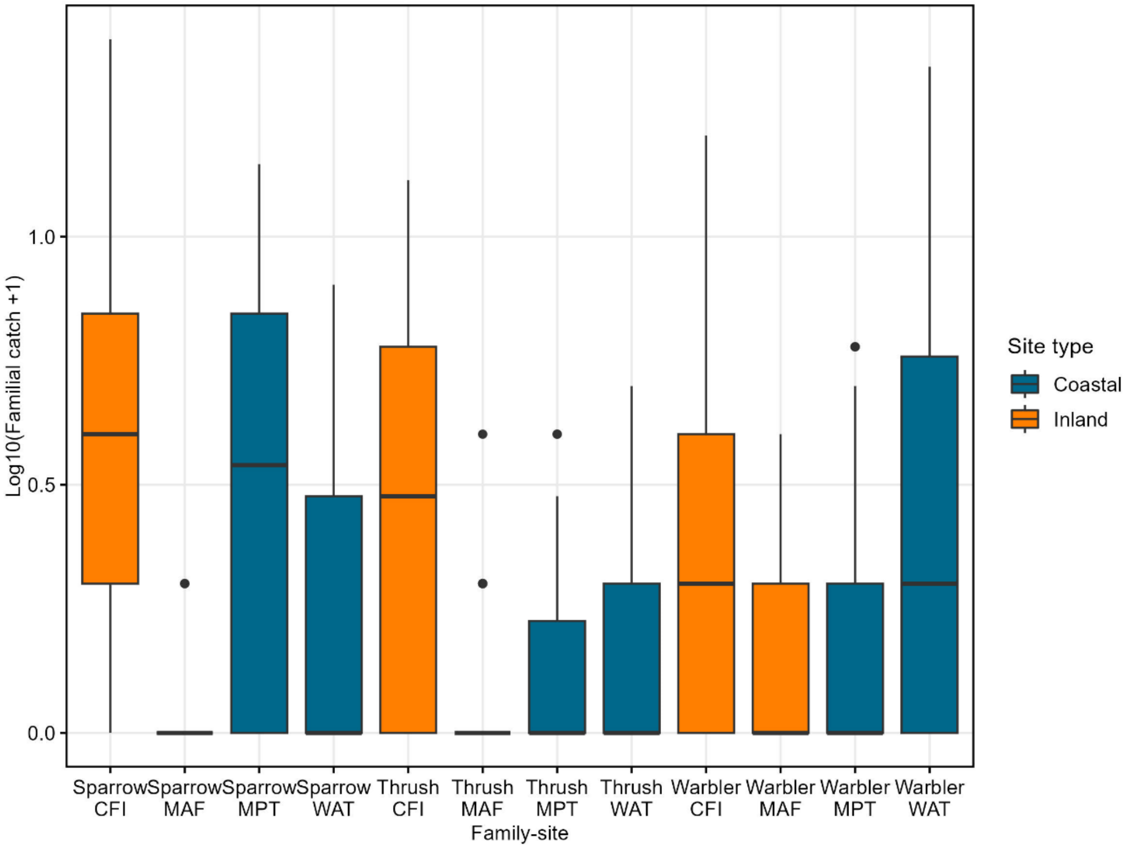


Figure 3-3. Taxonomic family-specific catch for four stopover sites in eastern New Brunswick, labeled with site initials and site type. Median is indicated by the dark bar, with boxes encompassing the first and third quartiles, and whiskers indicating values 1.5 times the interquartile range.

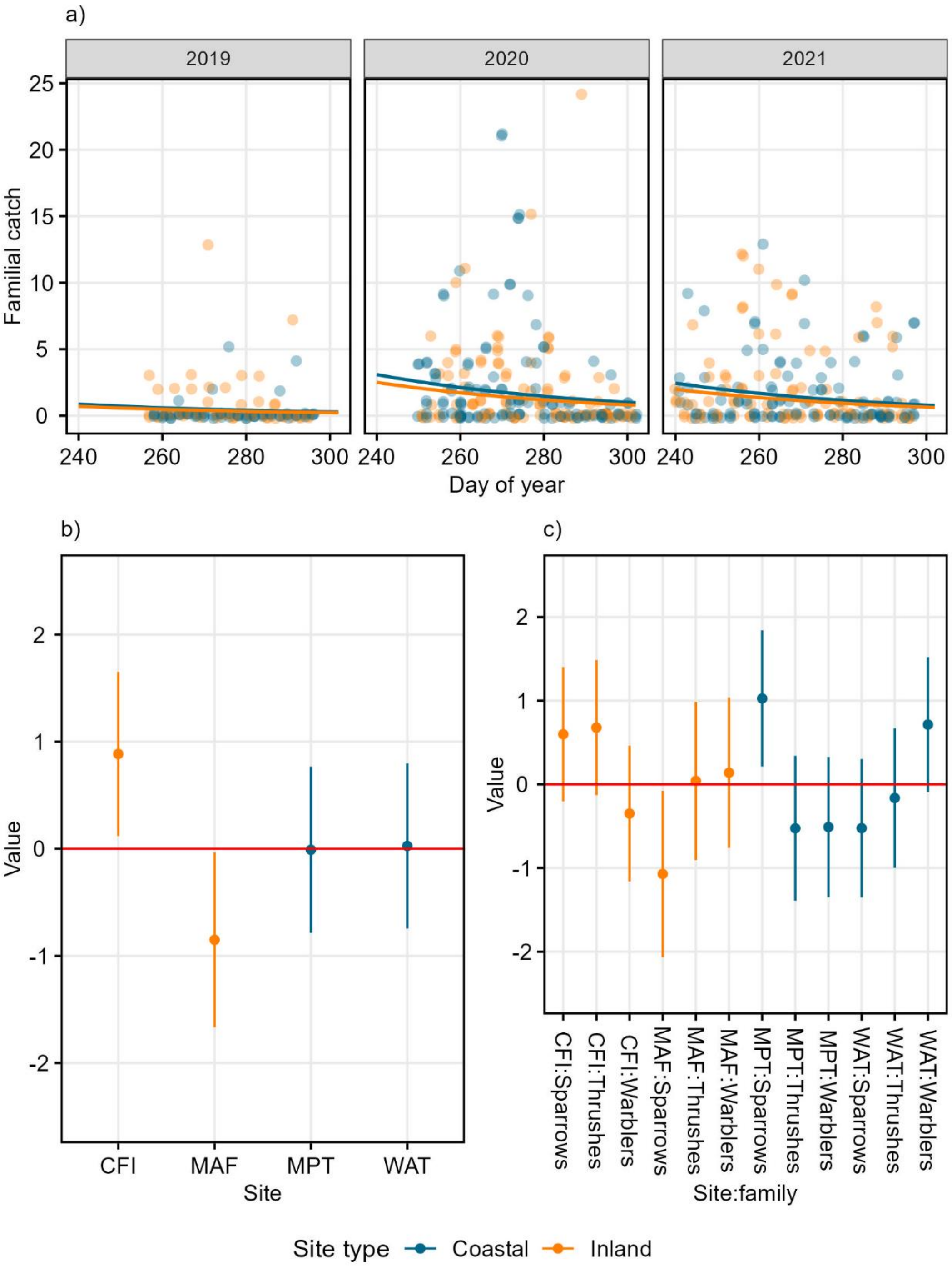


Figure 3-4. The relationship between fixed effects of day of year on taxonomic family catch for each year (a) from the mixed-effect negative binomial model of taxonomic family catch of migratory songbirds captured during autumn stopover in eastern New Brunswick. Also shown are the conditional random effect level modes and 95% prediction intervals for the random effects of site (b), and the site: taxonomic family interaction (c). Colour in all plots correspond to site type.

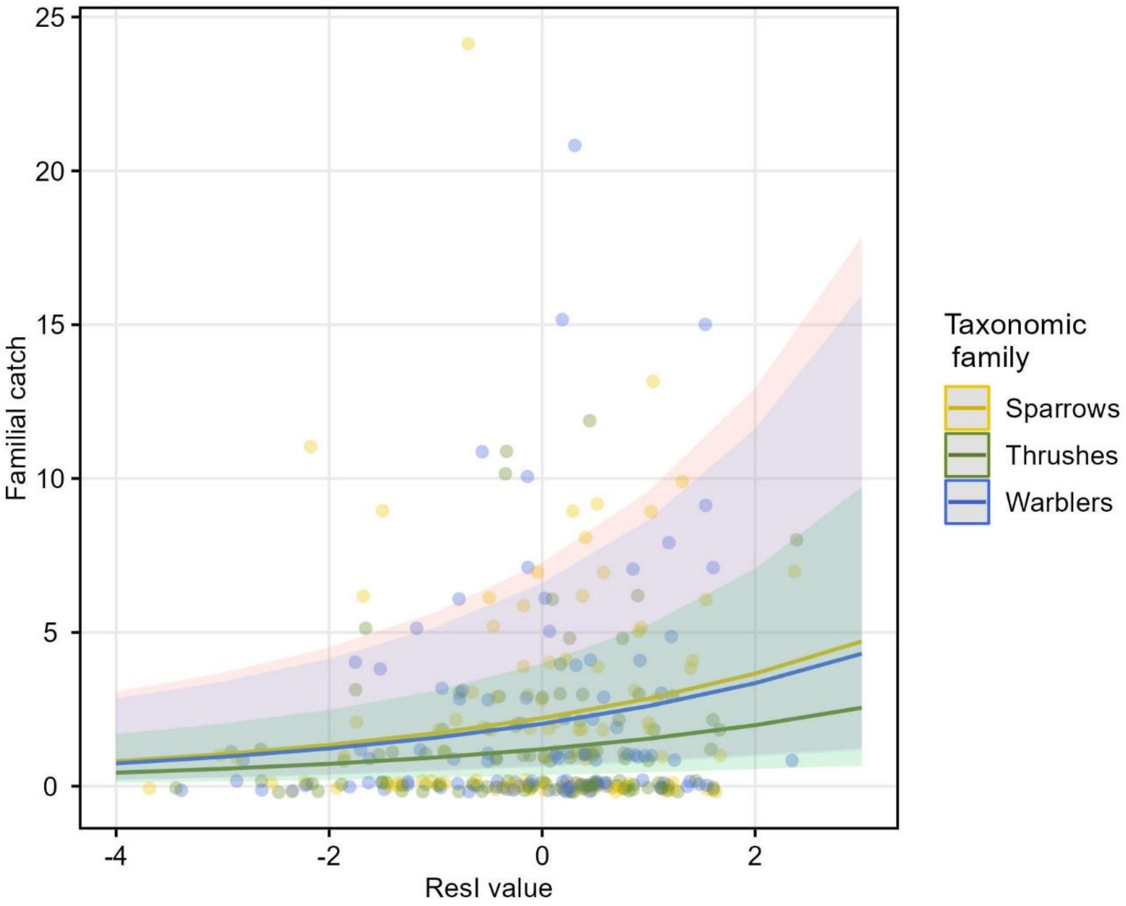


Figure 3-5. The estimated relationship between local invertebrate resource abundance (ResI) and migratory bird catch by taxonomic family from the mixed-effect negative binomial model of taxonomic family catch of migratory songbirds during autumn stopover in eastern New Brunswick. Also shown are the 95% confidence intervals and the raw data colour coded by taxonomic family.

3.3.2 Capture refuelling rate index

Plasma concentration of triglyceride and β-OH butyrate were negatively correlated (R^2 = -0.37, $p < 0.01$). The first principal component accounted for 68.6% of the variation in the dataset, with log10([triglyceride]+1) loading positively into PC1 (0.71) and log10([β-OH butyrate] +1) loading negatively (-0.71). Six birds were identified as high outliers in family-specific catch per-unit effort, and one bird was identified as a low outlier ResI value. Preliminary investigation indicated that inclusion of these individuals did not influence analysis results, and these birds were retained during final analysis. Sample sizes by species and site can be found in Table 3-3, and average metabolite concentrations for each species can be found in Table 3-4.

In stage one of model selection, the top model of RI included the fixed effects of capture time, bleed time, capture day of year, and year of capture (model 6). In stage two, model 6 with the addition of body mass and tarsus fit the best Table 3-5). After back-scaling coefficients to original units, capture refuelling index increased with each minute elapsed since sunrise ($\beta = 0.003 \pm 0.0006$, $t_{278.3} = 5.67$, $p < 0.01$) and decreased with each second of bleed time ($\beta = -0.0005 \pm 0.0002$, $t_{205.5} = -2.51$, $p < 0.01$). Refuelling rate index increased with day of year ($\beta = 0.01 \pm 0.004$, $t_{277.95} = 3.51$, $p < 0.01$), and was greater in birds with greater capture body mass (g) ($\beta = 0.10 \pm 0.02$, $t_{211.9} = 4.05$, $p < 0.01$). Finally, refuelling rate index did not differ between 2020 and 2019 ($\beta = -0.08 \pm 0.24$, $t_{281.7} = -0.33$, $p > 0.5$) but was significantly higher in 2021 compared to 2019 ($\beta = 0.42 \pm 0.20$, $t_{278.6} = 2.17$, $p = 0.03$, Table 3-6).

Table 3-3. Sample sizes by species and site for the analyses of refuelling rate, local movement behaviour, and stopover duration.

CFI – inland

Species	Refuelling rate	Movement distances	Maximum displacement	Stopover duration
White-throated Sparrow (*Zonotrichia albicollis*)	44	95	28	21
Swainson’s Thrush (*Catharus ustulatus*)	35	18	13	25
Hermit Thrush (*Catharus guttatus*)	44	78	23	20
Yellow-rumped Warbler (*Setophaga coronata*)	15	3	2	8
Blackpoll Warbler (*Setophaga striata*)	1	0	0	1
Song Sparrow (*Melospiza melodia*)	4	NA		
Slate-colored Junco (*Junco hyemalis hyemalis*)	6			

MPT – coastal

Species	Refuelling rate	Movement distances	Maximum displacement	Stopover duration
White-throated Sparrow (*Zonotrichia albicollis*)	33	71	18	20
Swainson’s Thrush (*Catharus ustulatus*)	2	2	2	1
Hermit Thrush (*Catharus guttatus*)	5	0	0	3
Yellow-rumped Warbler (*Setophaga coronata*)	6	2	1	5
Blackpoll Warbler (*Setophaga striata*)	6	2	1	2
Song Sparrow (*Melospiza melodia*)	12	NA		
Slate-colored Junco (*Junco hyemalis hyemalis*)	0			

MAF – inland

Species	Refuelling rate	Movement distances	Maximum displacement	Stopover duration
White-throated Sparrow (*Zonotrichia albicollis*)	1	0	0	0
Swainson’s Thrush (*Catharus ustulatus*)	1	0	0	0
Hermit Thrush (*Catharus guttatus*)	4	0	0	0
Yellow-rumped Warbler (*Setophaga coronata*)	0	0	0	0
Blackpoll Warbler (*Setophaga striata*)	3	1	1	1
Song Sparrow (*Melospiza melodia*)	0	NA		
Slate-colored Junco (*Junco hyemalis hyemalis*)	0			

WAT – coastal

Species	Refuelling rate	Movement distances	Maximum displacement	Stopover duration
White-throated Sparrow (*Zonotrichia albicollis*)	7	11	3	2
Swainson’s Thrush (*Catharus ustulatus*)	4	7	2	4
Hermit Thrush (*Catharus guttatus*)	11	30	7	7
Yellow-rumped Warbler (*Setophaga coronata*)	14	2	2	10
Blackpoll Warbler (*Setophaga striata*)	22	9	6	8
Song Sparrow (*Melospiza melodia*)	2	NA		
Slate-colored Junco (*Junco hyemalis hyemalis*)	8			

Table 3-4 Plasma metabolite concentrations for seven migratory songbird species captured during autumn stopover at four sites in eastern New Brunswick in 2019, 2020, and 2021.

Species	Triglyceride concentration (mmol) ± SE	β-OH butyrate concentration (mmol) ± SE
White-throated Sparrow (*Zonotrichia albicollis*)	2.35 ± 0.23	1.54 ± 0.09
Swainson’s Thrush (*Catharus ustulatus*)	2.65 ± 0.21	0.45 ± 0.05
Hermit Thrush (*Catharus guttatus*)	2.32 ± 0.17	0.65 ± 0.06
Yellow-rumped Warbler (*Setophaga coronata*)	1.66 ± 0.23	1.60 ± 0.12
Blackpoll Warbler (*Setophaga striata*)	2.66 ± 0.2	1.16 ± 0.07
Song Sparrow (*Melospiza melodia*)	1.50 ± 0.19	1.37 ± 0.12
Slate-colored Junco (*Junco hyemalis hyemalis*)	1.23 ± 0.16	1.90 ± 0.22

Table 3-5. Comparison of candidate models of stopover refuelling index from 290 birds of seven species. Only species with samples sizes greater than 12 were included, and species was included in all models as a random effect. Also indicated is models AICc, ΔAICc, Akaike weight (w_i), marginal $R^{2,}$ and conditional R^2.

Model	**Name**	**Model**	**AICc**	**ΔAICc**	**w_i**	**Marginal R^2**	**Conditional R^2**
1	Null	RI ~ Trap time + Bleed time + (1 | Species) + (1 | Site)	807.14	20.41	0.00	0.08	0.41
Stage 1 - Extrinsic local vs spatiotemporal covariates							
2	Year	RI ~ Trap time + Bleed time + Year + (1 | Species) + (1 | Site)	801.15	14.43	0.00	0.10	0.44
3	Site type	RI ~ Trap time + Bleed time + Site type + (1 | Species) + (1 | Site)	809.20	22.48	0.00	0.08	0.41
4	Day of year	RI ~ Trap time + Bleed time + Day of year + (1 | Species) + (1 | Site)	796.06	9.34	0.01	0.11	0.48
5	Year and site type	RI ~ Trap time + Bleed time + Year + Site type + (1 | Species) + (1 | Site)	803.17	16.45	0.00	0.11	0.44
6	**Year and day of year**	**RI ~ Trap time + Bleed time + Year + Day of year + (1 | Species) + (1 | Site)**	786.72	0.00	**0.69**	**0.13**	**0.50**
7	Site type and day of year	RI ~ Trap time + Bleed time + Site type + Day of year + (1 | Species) + (1 | Site)	803.17	16.45	0.00	0.11	0.44
8	Spatiotemporal	RI ~ Trap time + Bleed time + Site type + Year + Day of year + (1 | Species) + (1 | Site)	788.86	2.14	0.24	0.13	0.50
9	CPUE	RI ~ Trap time + Bleed time + CPUE + (1 | Species) + (1 | Site)	820.23	33.51	0.00	0.08	0.44
9a	Random CPUE	RI ~ Trap time + Bleed time + CPUE + (CPUE | Species) + (1 | Site)	823.66	36.93	0.00	0.08	0.46
10	ResI	RI ~ Trap time + Bleed time + ResI + (1 | Species) + (1 | Site)	806.52	19.80	0.00	0.09	0.43
10a	Random ResI	RI ~ Trap time + Bleed time + ResI + (ResI | Species) + (1 | Site)	792.63	5.90	0.04	0.09	0.46
11	Local	RI ~ Trap time + Bleed time + CPUE + ResI + (ResI | Species) + (1| Site)	793.12	6.40	0.03	0.09	0.46
Stage 2 - Best (6) with individual covariates							
6	Year and day of year	RI ~ Trap time + Bleed time + Year + Day of year + (1 | Species) + (1 | Site)	786.72	12.20	0.00	0.13	0.50
12	Age class	RI ~ Trap time + Bleed time + Year + Day of year + Age class + (1 | Species) + (1 | Site)	788.84	14.31	0.00	0.13	0.50
13	**Condition**	**RI ~ Trap time + Bleed time + Year + Day of year + Tarsus + Capture mass + (1 | Species) + (1 | Site)**	774.53	0.00	**0.75**	**0.25**	**0.52**
14	Age class and condition	RI ~ Trap time + Bleed time + Year + Day of year + Tarsus + Capture mass + Age class + (1 | Species) + (1 | Site)	776.69	2.16	0.25	0.24	0.52

RI = capture refuelling rate index, CPUE = log10 transformed family specific catch per-unit effort, ResI = Invertebrate resource abundance index. All continuous variables were centered and scaled prior to analysis.

Table 3-6. Summary table of fixed effects from the best model (9) of capture refuelling index. *P*-values were obtained using the Satterthwaite approximation for degrees of freedom implemented in package lmerTest. Coefficients and standard errors have been back-scaled to original units.

Fixed effects

Parameter	**Estimate**	**Standard error**	**Degrees of freedom**	***t*-value**	**Pr (>|t|)**
Intercept	-0.39	0.35	12.00	-1.10	0.29
Trap time (mins)	**0.003**	**0.0006**	**278.29**	**5.67**	**< 0.01**
Bleed time (secs)	**-0.0005**	**0.0002**	**205.52**	**-2.51**	**0.01**
Year (2020 vs 2019)	-0.08	0.24	281.74	-0.33	> 0.50
Year (2021 vs 2019)	**0.42**	**0.20**	**278.55**	**2.17**	**0.03**
Day of year	**0.01**	**0.004**	**277.95**	**3.51**	**< 0.01**
Tarsus length (mm)	-0.10	0.05	103.85	-1.93	0.06
Capture body mass (g)	**0.10**	**0.02**	**211.89**	**4.05**	**< 0.01**

Random effects

Group	Variance	Inter-class correlation coefficient	Model Marginal R^2	Model Conditional R^2
Species	0.50	0.41	0.25	0.52
Site	0.02	0.01		

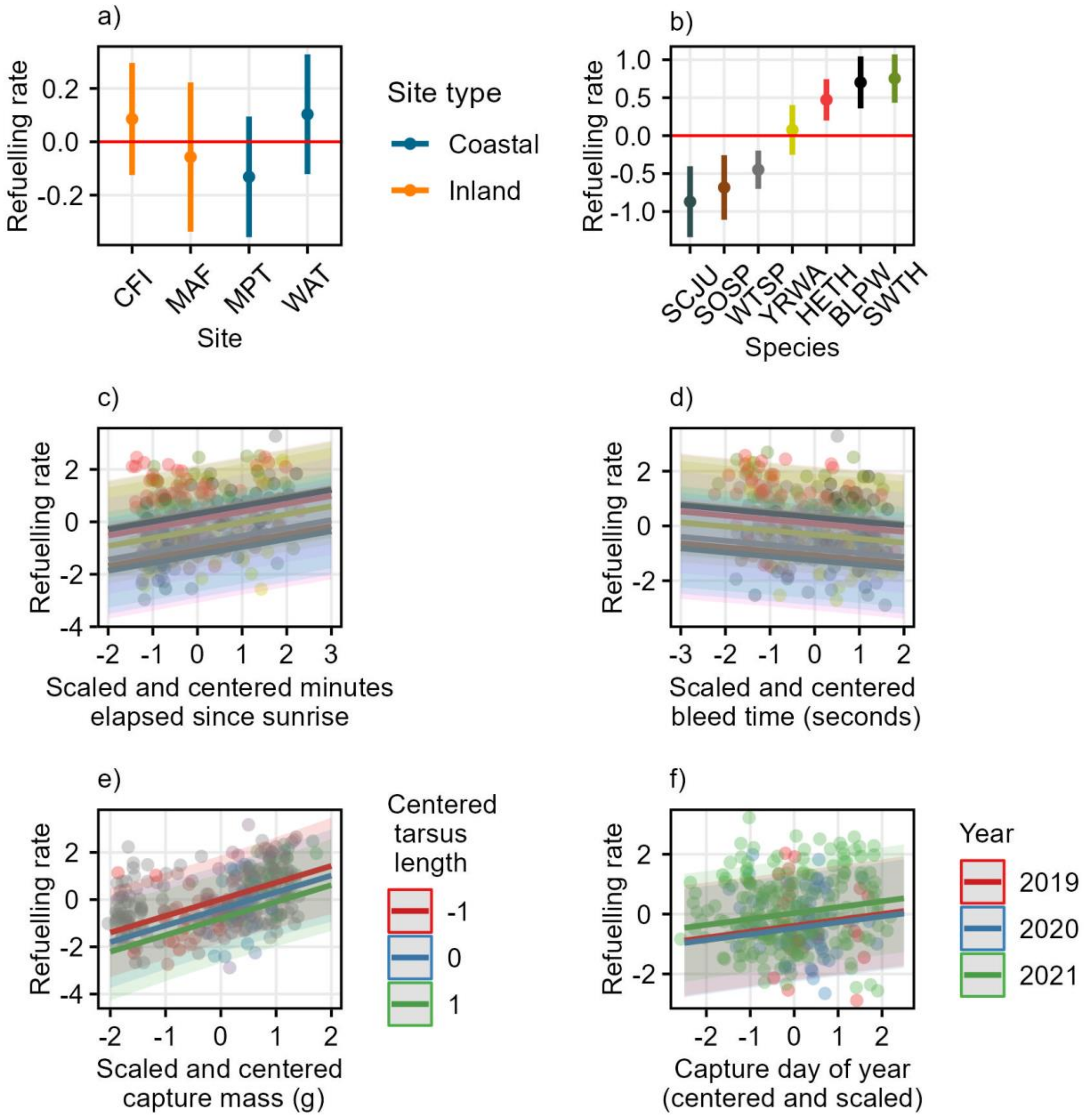


Figure 3-6. The random and fixed effects from the mixed effect analysis of refuelling rate measured in seven songbird species sampled during autumn stopover in eastern New Brunswick. Estimates of the conditional modes of the random effect of site (a) and species (b) on refuelling. Species-specific fixed effects of minutes elapsed since sunrise (c), and second between capture and the completion of blood sample collection (bleed time) (d), with colours matching those in panel b. The fixed effect of capture condition (as tarsus length and capture mass) and capture day of year on capture refuelling rate index are shown in panel (d) and (e) respectively. Also shown are 95% prediction intervals, and raw data plotted on panels c through e.

3.3.3 Local movement behaviour

Movement parameters were calculated for 341 movements (Figure 3-7) from 113 birds, with an average of 5.0 post-release locations recorded per-bird. Mean net displacement away from the release site was 147.0 ± 131.2 meters, with an average movement rate of 75.3 ± 123.6 meters • day^{-1} (Table 3-7). Complete data on all covariates were available for 331 movements measured in 109 individuals. Prior to analysis, movement distance was log10 transformed to satisfy the assumption of error normality in the analysis. Six birds were identified as potential outliers but were retained as inclusion of these birds did not affect the analysis outcome. In stage one of model selection, the best model of movement distance only included the null model covariate step duration (model 1). The covariates site type and year did not improve model fit. In stage two of model selection, model 1 with the addition of age class best fit the data. In the final model movement distance increased 2% with each additional day of step duration (β = 1.02 ± 1.006, t_{331} = 3.42, $p < 0.01$) and was 15% greater in hatch year birds compared to after hatch year birds (β_{HY} = 1.15 ± 1.05, t_{90} = 2.62, $p = 0.01$). Movement distance was not affected by day of stopover ($p < 0.5$).

Maximum displacement was analysed for 109 birds with complete data on all analysis covariates. Average maximum displacement by species can be found in Table 3-7. Maximum displacement was log10 transformed prior to analyses to satisfy model assumption of error normality. One bird was identified as a potential outlier but was retained as inclusion did not influence results. The null model of maximum displacement including the nested random intercepts for site and species (model 1) provided the best fit in stage one of the analysis. Model fit was not improved by the inclusion of individual level covariates.

Table 3-7. Movement parameters of five songbird species tracked during migratory stopover in eastern New Brunswick during the autumn of 2019, 2020, and 2021.

Species	Number of individuals with post-release relocations	Number of relocations per individual	Net displacement between relocations ± SD (range) meters	Average time between relocations ± SD (range) days	Movement rate (range) ± SD meters • day^{-1}	Maximum displacement ± SD (range) meters
Blackpoll Warber *Setophaga striata*	8	1.5 ± 0.5 (1-2)	117.2 ± 116.0 (7 – 346)	3.1 ± 2.8 (2.0 – 6.2)	32.7 ± 29.0 (1 – 87)	154.6 ± 123.4 (7 – 346)
Hermit Thrush *Catharus guttatus*	30	3.6 ± 2.7 (1-12)	159.6 ± 151.9 (8 – 959)	3.5 ± 2.6 (0.04 – 17.9)	57.4 ± 59.4 (3 – 426)	274.3 ± 207.3 (32 – 959)
Yellow-rumped Warbler *Setophaga coronata*	5	1.3 ± 0.5 (1-2)	117.1 ± 90.1 (61 – 338)	5.7 ± 4.2 (1.9 – 13.8)	22.5 ± 20.3 (6 – 55)	140.2 ± 110.9 (7 – 346)
Swainson's Thrush *Catharus ustulatus*	17	1.6 ± 1.0 (1-5)	134.5 ± 110.6 (33 – 465)	6.0 ± 5.6 (1.9 – 28)	25.2 ± 14.5 (5 – 70)	138.3 ± 104.1 (49 – 465)
White-throated Sparrow *Zonotrichia albicollis*	49	3.6 ± 2.5 (1-12)	147.9 ± 124.6 (9 – 724)	3.1 ± 2.8 (0.06 – 16.3)	105.3 ± 160.6 (4 – 992)	245.2 ± 172.9 (45 – 724)

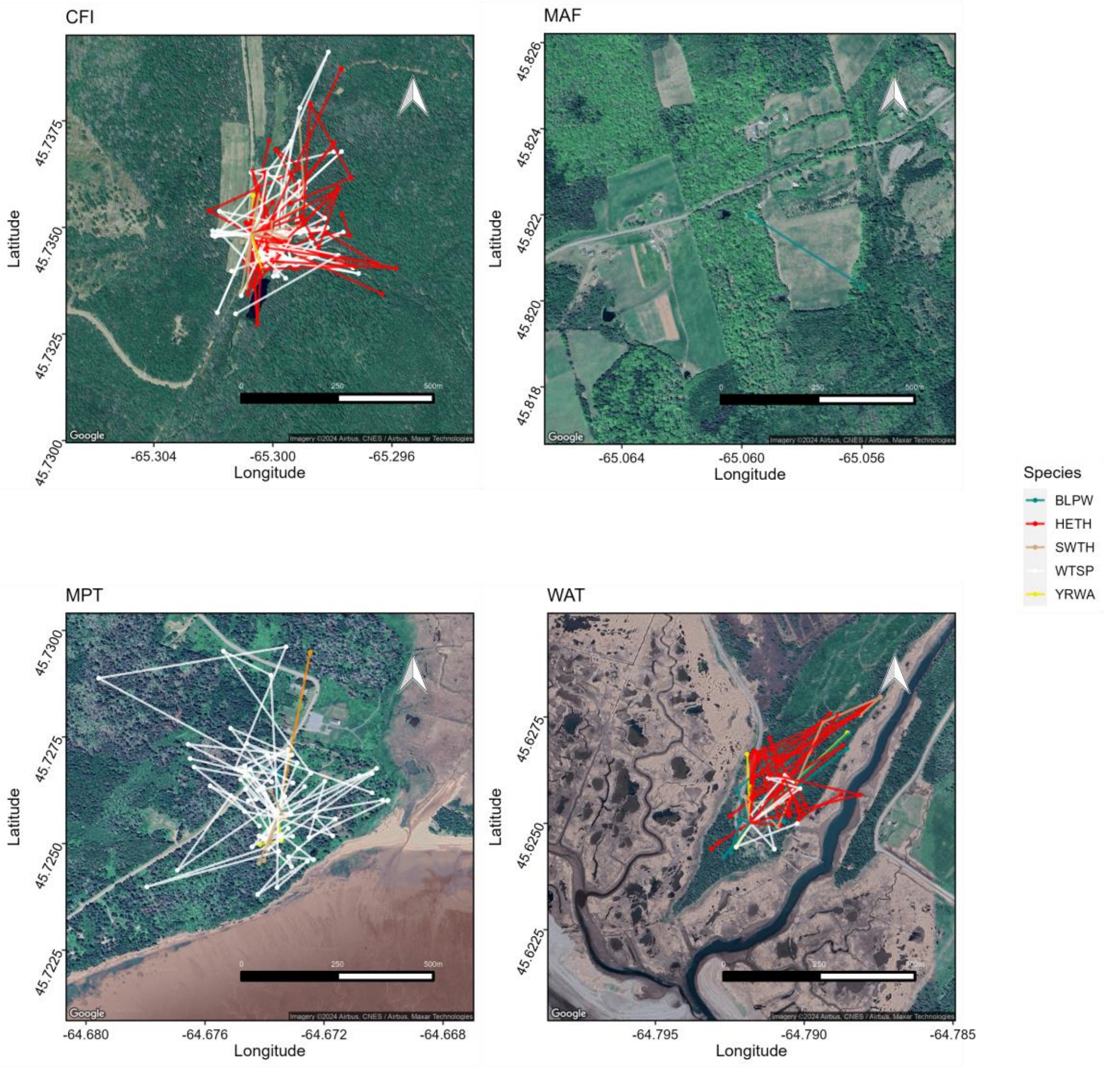


Figure 3-7. Movement trajectories for 109 songbirds of five species tracked at inland (CFI & MAF) and coastal (MPT & WAT) stopover sites in eastern New Brunswick during the autumn of 2019, 2020 and 2021.

3.3.4 Stopover duration

Stopover duration was measured for 137 birds of five species. Twenty-four birds were right-censored due to missing data for eResI after invertebrate sampling had concluded at the end of the season, leaving a total of 113 departure events (Table 3-8). One Swainson's Thrush captured early in the season was left-censored for one interval, as invertebrate sampling had not yet commenced and estimates of resource availability could not be calculated. Mean departure bearing was 243°, calculated using 115 first post-departure detections on the Motus.

Stage one of model selection indicated the best model explaining variation in departure hazard resulting from extrinsic covariates included tailwind as a fixed effect in addition to the model null covariates of capture date and the random effect of species (model 5). There was also marginal support for the inclusion of estimated invertebrate resource abundance, with an AICc 1.75 greater than the top model. In general, models containing the regional-scale spatiotemporal covariates increased AICc, suggesting that these covariates do little to explain variation in stopover duration. In stage two of the analysis, the best model included model 5 covariates, as well as body condition (modelled as tarsus length and capture body mass) and residual capture refuelling rate (model 13). This model only marginally improved fit (ΔAICc < 2) over the more parsimonious model 5, and models which included just body condition (model 9) or just residual capture refuelling (model 10, Table 3-9). In the best model, stopover departure hazard decreased 20% for every additional unit of the refuelling rate index after controlling for other covariates and back-transforming coefficients. Migrants departed under a variety of wind conditions with many birds leaving on night with wind speeds less than 5 $m \bullet s^{-1}$ (mean: -1.17 $m \bullet s^{-1}$; range: 1-9 $m \bullet s^{-1}$). Departure hazard increased 6% for every additional capture day and increased 10% for every additional $m \bullet s^{-1}$ of tailwind. Departure hazard decreased 17% for every additional millimetre of tarsus length and increased 6% for each additional gram of body mass at capture (Table 3-10).

Table 3-8. Sample sizes by species for bird included in the analysis of stopover departure hazard. Also shown are mean ± SE and range of stopover durations, and the number of departure events for each species.

Species	Sample size	Mean stopover duration ± SE	Total departure events
Blackpoll Warber *Setophaga striata*	11	8.6 ± 2.4 (1-23)	10
Hermit Thrush[1] *Catharus guttatus*	30	20.8 ± 3.4 (4 – 46)	15
Yellow-rumped Warbler *Setophaga coronata.*	23	5.2 ± 1.0 (1 – 22)	23
Swainson’s Thrush *Catharus ustulatus*	30	9.6 ± 1.0 (1 – 23)	30
White-throated Sparrow *Zonotrichia albicollis*	43	13.8 ± 1.6 (1 – 46)	35

1: No Hermit Thrush were tagged in 2019 or 2020 as this species was added to the protocol for the 2021 season.

Table 3-9. Comparison of candidate models of stopover departure hazard using 1529 stopover days from 137 birds of five species captured during autumn stopover in easter New Brunswick in 2020, and 2021. Prior to analysis, 24 birds were right-censored due to missing data on resource abundance after invertebrate sampling had concluded, for a total of 113 departure events. One bird captured early in the season was left-censored as invertebrate sampling had not yet commenced at tag deployment. Also indicated is models AICc, ΔAICc, and Akaike weight (w_i) relative to the best fit model.

Model #	**Name**	**Model**	**AICc**	**ΔAICc**	w_i
1	Null	~ Capture day of year + (1 | Species) + (1 | Site)	821.51	8.48	0.01
Stage 1 - Local vs spatiotemporal environmental covariates					
2	Site type	~ Capture day of year + Site type + (1 | Species) + (1 | Site)	822.69	9.67	0.01
3	Year	~ Capture day of year + Year + (1 | Species) + (1 | Site)	823.50	10.47	0.00
4	Spatiotemporal	~ Capture day of year + Year + Site type + (1 | Species) + (1 | Site)	824.28	11.26	0.00
5	**Tailwind fixed**	**~ Capture day of year + Tailwind + (1 | Species) + (1 | Site)**	**813.02**	**0.00**	**0.69**
5a	Tailwind random	~ Capture day of year + Tailwind + (Tailwind | Species) + (1 | Site)	873.58	60.55	0.00
6	eResI fixed	~ Capture day of year + eResI + (1 | Species) + (1 | Site)	823.50	10.48	0.00
6a	eResI random	~ Capture day of year + eResI + (eResI | Species) + (1 | Site)	875.57	62.55	0.00
7	Local conditions	~ Capture day of year + eResI + Tailwind + (1 | Species) + (1 | Site)	814.77	1.75	0.29
Stage 2 – Best environmental model and intrinsic covariates					
5	Tailwind fixed	~ Capture day of year + Tailwind + (1 | Species) + (1 | Site)	813.02	2.00	0.11
8	Age class-specific	~ Capture day of year + Tailwind + Age class + (1 | Species) + (1 | Site)	815.03	4.01	0.04
9	Capture condition	~ Capture day of year + Tailwind + Capture mass + Tarsus length + (1 | Species) + (1 | Site)	813.15	2.13	0.11
10	Refuelling	~ Capture day of year + Tailwind + Refuelling rate residual + (1 | Species) + (1 | Site)	811.85	0.83	0.20
11	Age class and condition	~ Capture day of year + Tailwind + Age class + Capture mass + Tarsus length + (1 | Species) + (1 | Site)	815.12	4.10	0.04
12	Age class and refuelling	~ Capture day of year + Tailwind + Age class + Refuelling rate residual + (1 | Species) + (1 | Site)	813.83	2.81	0.08
13	**Fuelling status**	**~ Capture day of year + Tailwind + Refuelling rate residual + Capture mass + Tarsus length + (1 | Species) + (1 | Site)**	**811.02**	**0.00**	**0.31**
14	Age class and Fuelling status	~ Capture day of year + Tailwind + Age class + Capture mass + Tarsus length + Refuelling rate residual + (1 | Species) + (1 | Site)	812.99	1.97	0.11

eResI = Estimates of invertebrate resource abundance from site and year-specific generalised additive models. Refuelling rate residual = residuals from the best model of capture refuelling rate above (9). All continuous variables were centered and scaled prior to analysis. Tailwind and eResI were modeled as time-vary covariates across each day of stopover.

Table 3-10. Summary table of fixed effects from the best mixed-effect Cox model (13) of stopover departure hazard. Coefficients, standard errors, and hazard ratios (HR) have been back-scaled to original scales.

Fixed effects

Parameter	**Coefficient**	**Standard error**	***p* - value**	**HR**
Body mass (g)	0.05	0.05	0.31	1.05
Tarsus length (mm)	**-0.19**	**0.08**	**0.02**	**0.82**
Residual refuelling index	**-0.24**	**0.11**	**0.03**	**0.79**
Capture date	**0.06**	**0.01**	**< 0.01**	**1.06**
Tailwind (m*s^{-1})	**0.10**	**0.03**	**< 0.01**	**1.10**

Random effects

Group	Variance
Species	0.73
Site	0.02

3.4 Discussion

I combined plasma metabolite analysis, radio telemetry, and habitat assessment to test how key environmental and individual characteristics shaped the refuelling and behaviour of free-living songbirds during stopover in a coastal region. Coastal and inland stopover sites did not differ systematically in the number of migrants captured or invertebrates resource abundance, and individual level refuelling rate, local movement behaviour, and stopover duration did not differ among birds using each site type. Rather than any overarching differences between stopover site types, I instead found the number of migrants captured at each site was positively associated with the abundance of invertebrates, and that much of the variation in refuelling rate, movement behaviour, and stopover duration was largely associated with variation in environmental conditions and intrinsic differences between individuals.

3.4.1 Invertebrate abundance and migrant catch

Neither invertebrate abundance nor migrant catch differed systematically between coastal and inland stopover sites, suggesting that both site types offered comparable habitat for migrants in eastern New Brunswick. In freshwater coastal ecosystems, aquatic emergent insects can significantly augment the prey available for birds using these habitats (Smith et al. 2007, Macdade et al. 2011, Génier et al. 2022), but aquatic emergent insects are generally not available on marine coastlines unless location is associated with river outflows or other sources of freshwater. Both Mary’s Point and Waterside had some nearby (< 1 km) freshwater and intertidal aquatic habitat, and this may partially explain the similarity between site types in invertebrate abundance. Despite differing proximity to an ecological barrier, coastal and inland stopover sites had similar migrant catch. This may indicate that migrants were not aggregating in coastal habitats. Given the orientation of the Fundy coast, prolonged overwater crossing are likely unnecessary for migrants travelling through eastern New Brunswick. As such, the aggregation of birds in coastal areas in preparation for prolonged overwater crossing may be unlikely. Eastern New Brunswick is also a highly forested region (Figure 3-1), with relatively low fragmentation. This may allow migrants to distribute among the suitable near-shore habitat to a greater extent relative to coastal regions where habitat fragmentation is prevalent. Both migrant catch and invertebrate abundance varied between years, although the direction of the effect was inconsistent between analyses and difficult to interpret. Migrant catch also declined with day of year and invertebrate abundance with temperature, both of which represent patterns expected for the seasonal passage of migrants and the diminishing abundance of insects with cooler temperatures.

While no relationship between refuelling rate and migrant catch or invertebrate abundance and was observed in this study, songbird catch was greater when invertebrates were more abundant. This pattern suggests that migratory songbirds use stopover habitat in eastern New Brunswick according to local invertebrate resource availability. The rapid departure of migrants that experience poorer refuelling conditions, as observed in the analysis of stopover duration, may contribute to this pattern. The use of habitat by migratory songbirds in eastern New Brunswick may then conform to a habitat-matching rule based on refuelling rate, with migrants departing or relocating soon after arrival if refuelling is limited by low per-capita invertebrate resource availability. Evaluating a similar paradigm, Shochat et al. (2002) observed that migrants refuelling at isolated stopover habitats in the northern Negev, Israel, distributed among available habitat based on local resource availability, but that differences in fuel deposition rates among sites suggested that migrants had a limited ability selecting among habitats based on refuelling conditions encountered. The fragmented nature of the suitable habitat in the Negev region may have limited the ability of migrants to assess alternate habitat patches and may have concentrated migrants in available habitat. Unlike the Negev region, the relatively contiguous and abundant forest habitat in eastern New Brunswick may have reduced the costs of moving to an alternate location for newly arrived individuals that experienced limited success refuelling at my study sites. These movements could have occurred either through extended local movements, landscape-level relocations (Taylor et al. 2011), or by nocturnal flights using the stored energy available. The use of stopover habitat based on experienced refuelling rate would also preclude any negative density or resource-dependent effects on refuelling at my study sites, a pattern which has been observed in migratory songbirds during stopover in more fragmented landscapes (Cohen et al. 2022, Zimin et al. 2023). This contrast illustrates how the availability of stopover habitat at the broader regional-scale may shape patch-level patterns of refuelling, stopover duration, and habitat use.

3.4.2 Stopover refuelling rate

Refuelling rate did not differ between coastal and inland stopover sites, and was instead best explained by the temporal covariates day of year and year and by other individual-level covariates associated with energetic condition. This similarity in site types echoes the analysis of migrant catch and invertebrate abundance, and further suggests that coastal and inland stopover sites in eastern New Brunswick provide comparable stopover habitat for migratory songbirds. Stopover refuelling rate increased with day of year and was higher in 2021 compared to 2020 and 2019. Higher refuelling with greater capture date may reflect a behavioural strategy to decrease stopover duration in the face of deteriorating weather conditions or to compensate for the shorter length of time available for refuelling in the shorter late-season days. Similar patterns have been observed in both captive and wild migrants (e.g. Fransson 1998, Schaub and Jenni 2000, Dänhardt and Lindström 2001). Alternatively, the positive relationship between refuelling and capture date may be associated with lower competition for food resources, stemming from the lower migrant abundance observed later in the season. Though initially intended, I was unable to systematically quantify the local availability of fruit resources to evaluate how this important food resource contributed to patterns of refuelling at stopover sites in eastern New Brunswick. Previous studies have found that migratory songbirds use both fruit and insects during autumn migratory stopover (Smith et al. 2007b, 2015), and that in general, the abundance and nutritional quality of remaining fruit can decline across the fall season (Smith and McWilliams 2014, Smith et al. 2015). Any seasonal decrease of non-invertebrate food abundance in this study may have been offset by the lower migrant abundance observed later in the season.

The primary individual-level covariates governing refuelling included body mass and tarsus length. After controlling for tarsus length, greater capture body mass significantly increased refuelling rate index. A positive interrelation between body condition and refuelling has been reported previously in passerines (Guglielmo et al. 2005) and non-passerine migrant (Guglielmo et al. 2002). Interpreting this relationship is challenging, as the relationship between body condition and refuelling rate is likely dynamic. Migrants with low body mass may have depleted muscle and organ mass in addition to low fat stores, limiting their ability to rapidly refuel until after an initial period of mass gain where organs are rebuilt (Carpenter et al. 1993, Karasov and Pinshow 2000, Gannes 2002). This pattern may also arise if large fat deposits contribute to elevated concentrations of triglyceride in the blood plasma, potentially through a reduced rate of uptake by adipocytes or other rate-limiting intracellular processes associated with fat storage post-circulation.

Age classes did not differ in stopover refuelling performance, with the inclusion of this term yielding substantially decreased model fit relative to competing models that did not include age class. Given the breeding range of the study species, many of the birds sampled were likely nearer to the start of migration, where the differences in foraging ability, social standing, or physiology posited to contribute to age-specific refuelling may be at their greatest. The lack of differences in refuelling at this early point in migration further suggests that differences between age classes are insufficient to yield effect refuelling rate in the context of stopover in eastern New Brunswick. One caveat to our analysis is that sample size imbalance between the age classes precluded any robust test for interactions between resource availability and age-class, and between migrant abundance and age-class. As such, I cannot preclude that a more complex functional relationship between resource availability, migrant abundance, and age-specific characteristics may moderate refuelling. Despite this, my findings further reinforce that differences in refuelling rate between age classes are either minimal or situational and are likely not a general factor governing stopover refuelling in songbirds during autumn migration.

3.4.3 Local movement behaviour

Both the distance of recorded movements and maximum displacement away from the capture sites were similar between coastal and inland stopover sites, but movement distance differed between hatch-year and after-hatch-year aged birds. After controlling for the length of time elapsed between consecutive relocations, younger hatch-year birds moved farther distance between successive relocation than older after-hatch-year birds.

The greater movement of young birds during stopover may be associated with increased foraging effort, perhaps to compensate for lower foraging proficiency (Heise and Moore 2003) or result from the need to obtain more food to satisfy a higher metabolic rate (McCabe and Guglielmo 2019). If this greater movement is associated with an increase in foraging effort, this pattern may help to explain why age classes did not differ in capture refuelling rate in this study. Alternatively, the greater distances moved by young birds may also reflect more frequent displacement by socially dominant adults (Woodrey 2000). Young birds may also react differently to predators or other disturbances, leading to greater movement local movement. Despite the greater movement exhibited by hatch-year birds, maximum displacement did not differ between age classes, suggesting that the movements of both old and young birds occurred largely within the same extent surrounding the capture sites. Local movement behaviour and maximum displacement did not differ between study years and was unaffected by initial body condition or capture refuelling rate. Previous studies have found that songbird migrants in poorer energetic condition tend to exhibit greater movement during spring stopover (Moore and Aborn 2000, Matthews and Rodewald 2010, Seewagen et al. 2010), although movement can also depend on season, local resource availability, or habitat type (Seewagen et al. 2010, Cohen et al. 2012, Slager et al. 2015).

3.4.4 Stopover departure hazard

Stopover duration did not differ between coastal and inland sites, and variation in departure hazard was best explained by capture refuelling rate, wind conditions, and capture date. In line with the other analyses in this study, the inclusion of site type did not improve model fit relative to the null model, providing no evidence that the departure behaviour of migrants differed between coastal and inland stopover sites. Accumulation of migrants in coastal habitat (e.g. Diehl et al. 2003, Buler and Moore 2011) may occur if migrants need time to accumulate the energy required to conduct barrier crossings, or if crossing are only conducted under certain wind conditions. Migrants travelling southward through eastern New Brunswick do not need to cross the Bay of Fundy to progress migration, reducing the need to conduct lengthy bouts of refuelling in coastal habitat in preparation for an overwater barrier crossing. Accumulation of migrants in coastal habitat may also result in density-dependent effects on refuelling (Cohen et al. 2022), which could act to prolong stopover duration in these regions. The absence of site type-specific refuelling rate, nor corresponding differences in resource abundance or migrant catch suggests that the pattern of stopover duration observed was not confounded by any underlying systematic differences in these associated factors between site types.

Contrary to my expectations, individuals with a greater refuelling rate index at capture had a decreased risk of departure from stopover after accounting for relevant intrinsic and environmental factors. This pattern may represent a behavioural response by migrants to avoid prolonged stopover bouts at sites were the refuelling conditions encountered early in stopover are poor. These relocations could occur either through extended local movements, short-distance relocation flights (Taylor et al. 2011), or by conducting a migratory flight using available fuel stores. Similar patterns of departure under poor fuel deposition rates have been observed previously in songbird migrants (Kuenzi et al. 1991, Schaub et al. 2008). The abundant forest habitat both in the immediate the region and southward along the coast of New Brunswick and Maine may have facilitated this behaviour, either by reducing the time and energy needed to locate suitable alternate stopover sites or removing the necessity to accumulate large fat stores for prolonged flights between disparate patches of favourable habitat.

In line with previous studies on songbird departure behaviour (Åkesson and Hedenström 2000, Dossman et al. 2016, Morbey et al. 2018, Beauchamp et al. 2020), the availability of energetically favourable tailwinds significantly increased stopover departure hazard. Timing departure to coincide with tailwinds can reduce the energetic cost of migratory travel and the amount of correction required for crosswind drift (Alerstam and Lindström 1990, Liechti 2006). In landscapes featuring an abundance of habitat suitable to forest dwelling songbirds, energetically favourable winds may also represent the more variable resource compared to the food resources available at stopover sites. This may favour a strategy where departure decisions are based on the more transitory energetic savings provided by wind assistance over the refuelling potential of a stopover site. Finally, later first capture date reduced stopover duration as in previous studies of songbird stopover (e.g. Dierschke and Delingat 2001, Beauchamp et al. 2020, Packmor et al. 2020). Increased departure hazard later in the season, together with higher late season refuelling rate, may represent a behavioural response to worsening environmental conditions or seasonal time constraints on fall migration.

When considering individual-level covariates, candidate models of departure hazard containing age class had poorer support compared to the null model, indicating that age classes did not differ in stopover duration after accounting for tailwind availability, refuelling, and capture condition. These results suggest that there is little inherent difference in departure behaviours between young and old birds, and suggest that the observed differences in local movement and any physiological or behavioural differences between age classes (e.g. McCabe and Guglielmo 2019) do not translate to differences in departure hazard. Given these differences, one possibility is that young birds departed with relatively lower fuel loads compared to adults, which could lead to a shorter post-departure flight distances and an increased number of flights and stopovers across the subsequent southbound journey. This corresponds well with observations of Wood Thrush (*Hylocichla* mustelina) migration made by McKinnon et al. (2014), finding that young birds made additional stopovers during their first northward spring migration. Advancements in tracker technologies and further development of telemetry arrays like the Motus Wildlife Tracking System will allow for additional exploration of these patterns during autumn migration.

3.4.5 Conclusion

In summary, I combined habitat assessments, physiological profiling, and radio telemetry to provide a multifaceted examinations of the ecological drivers shaping stopover refuelling and behaviour of migratory songbirds in a coastal landscape. Coastal and inland sites did not differ systematically in invertebrate resource abundance or the number of migrants at the site, and the refuelling performance, movement behaviour, and duration of stopover did not differ between site types. The results of this study suggest that stopover in coastal sites is largely comparable to stopover at inland locations in the context of eastern New Brunswick, where habitat is abundant and surmounting the adjoining ecological barrier is not required to maintain the trajectory of migration. The use of stopover sites by migrants in eastern New Brunswick was positively associated with the abundance of invertebrates, and evidence collected at the individual level suggests this pattern may arise from the more rapid departure of migrants from habitats refuelling conditions are poor. Departure was also associated with energetically favourable wind conditions, as observed in other studies of songbird migration. In habitat rich regions like eastern New Brunswick, relocating to alternate stopover sites with better fuelling prospects may be a relatively easy, and the energetic savings provided by favourable winds may represent the more variable “resource”. Under these conditions, relocation to better refuelling habitat when refuelling is poor, and departure from stopover sites based on the ephemeral energetic savings provided by winds may represent a more advantageous strategy. Future studies could explore the combined role of spatial heterogeneity in habitat and temporal heterogeneity in wind conditions together shape migratory behaviour. Modern landscapes seldom reflect the context in which migratory species evolved. Given historic losses of habitat and the current degree of fragmentation in many landscapes, it is important that we understand both the range of behaviours exhibited by migrants and how these behaviours arise from the context in which they are studied. This is crucial not only to gauge how migrants will respond to losses of habitat in the future, but also to understand how current behaviours may reflect the existing constraints and consequences of habitat alteration faced by migrants. Understanding these dynamics will strengthen our understanding of the ecology of migrant songbirds and enable the development of robust and appropriate strategies for the conservation of these species in perpetuity.

3.5 References

Agostinelli, C., and U. Lund (2022). R package “circular”: Circular Statistics. [Online.] Available at https://r-forge.r-project.org/projects/circular/.

Agriculture and Agri-food Canada (2023). Annual Crop Inventory 2021 - Pre-packaged GeoTIF files. [Online.] Available at https://agriculture.canada.ca/atlas/data_donnees/annualCropInventory/data_donnees/tif/2021/.

Åkesson, S., and A. Hedenström (2000). Wind selectivity of migratory flight departures in birds. Behavioral Ecology and Sociobiology 47:140–144.

Alerstam, T. (2011). Optimal bird migration revisited. Journal of Ornithology 152:5–23.

Alerstam, T., and Å. Lindström (1990). Optimal bird migration: the relative importance of time, energy, and safety. In Bird Migration. Springer-Verlag, New-York, NY, USA, pp. 331–351.

Bates, D. M., M. Maechler, and B. Bolker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67.

Beauchamp, A. T., C. G. Guglielmo, and Y. E. Morbey (2020). Stopover refuelling, movement and departure decisions in the White-throated Sparrow: The influence of intrinsic and extrinsic factors during spring migration. Journal of Animal Ecology 89:2553–2566.

Birds Canada (2022). motus: Fetch and use data from the Motus Wildlife Tracking System. [Online.] Available at https://motusWTS.github.io/motus.

Buler, J. J., and D. K. Dawson (2014). Radar analysis of fall bird migration stopover sites in the northeastern U.S. The Condor 116:357–370.

Buler, J. J., and R. H. Diehl (2009). Quantifying bird density during migratory stopover using weather surveillance radar. IEEE Transactions on Geoscience and Remote Sensing 47:2741–2751.

Buler, J. J., and F. R. Moore (2011). Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. Journal of Ornithology 152:101–112.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Carpenter, F. L., M. A. Hixon, C. A. Beuchat, R. W. Russell, and D. C. Paton (1993). Biphasic mass gain in migrant hummingbirds: body composition changes, torpor, and ecological significance. Ecology 74:1173–1182.

Cerasale, D. J., and C. G. Guglielmo (2010). An integrative assessment of the effects of tamarisk on stopover ecology of a long-distance migrant along the San Pedro river, Arizona. The Auk 127:636–646.

Cohen, E. B., J. M. Lafleur, and F. R. Moore (2022). Density dependent refueling of migratory songbirds during stopover within an urbanizing coastal landscape. Frontiers in Ecology and Evolution 10.

Cohen, E. B., F. R. Moore, and R. A. Fischer (2012). Experimental evidence for the interplay of exogenous and endogenous factors on the movement ecology of a migrating songbird. PLOS ONE 7:e41818.

Cohen, E. B., S. M. Pearson, and F. R. Moore (2014). Effects of landscape composition and configuration on migrating songbirds: inference from an individual-based model. Ecological Applications 24:169–180.

Collet, L., and W. Heim (2022). Differences in stopover duration and body mass change among *Emberiza* buntings during autumn migration in the Russian far east. Journal of Ornithology 163:779–789.

Dänhardt, J., and Å. Lindström (2001). Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Animal Behaviour 62:235–243.

Deutschlander, M. E., and R. Muheim (2009). Fuel reserves affect migratory orientation of thrushes and sparrows both before and after crossing an ecological barrier near their breeding grounds. Journal of Avian Biology 40:85–89.

Diehl, R. H., R. P. Larkin, J. E. Black, and F. R. Moore (2003). Radar observations of bird migration over the Great Lakes. The Auk 120:278–290.

Dierschke, V., and J. Delingat (2001). Stopover behaviour and departure decision of Northern Wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535–545.

DMTI Spatial Inc. (2014a). National Water (WAT). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2014b). Hydrography - Regions (HYR). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2014c). Route File (RTE). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017a). Water Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017b). Major Roads Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017c). Contour Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2021). Administrative Area Region. [computer file]. Markham, Ontario, Canada.

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. Behavioral Ecology 27:567–574.

Ellegren, H. (1991). Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. Ornis Scandinavica (Scandinavian Journal of Ornithology) 22:340–348.

Fransson, T. (1998). A feeding experiment on migratory fuelling in Whitethroats, *Sylvia communis*. Animal Behaviour 55:153–162.

Gannes, L. Z. (2002). Mass change pattern of Blackcaps refueling during spring migration: evidence for physiological limitations to food assimilation. The Condor 104:231–239.

Génier, C. S. V., C. G. Guglielmo, and K. A. Hobson (2022). Combining bulk stable H isotope (δ2H) measurements with fatty acid profiles to examine differential use of aquatic vs. terrestrial prey by three sympatric species of aerial insectivorous birds. Frontiers in Ecology and Evolution 10.

Goymann, W., F. Spina, A. Ferri, and L. Fusani (2010). Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. Biology Letters 6:478–481.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson (1998). A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Guglielmo, C. G., D. J. Cerasale, and C. Eldermire (2005). A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological and Biochemical Zoology 78:116–125.

Guglielmo, C. G., P. D. O’Hara, T. D. Williams, and C. Blem (2002). Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living Western Sandpipers (*Calidris mauri*). The Auk 119:437–445.

Hedenström, A., and T. Alerstam (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Heise, C. D., and F. R. Moore (2003). Age-related differences in foraging efficiency, molt, and fat deposition of Gray Catbirds prior to autumn migration. The Condor 105:496–504.

Jenni, L., and S. Jenni-Eiermann (1996). Metabolic responses to diurnal feeding patterns during the postbreeding, moulting and migratory periods in passerine birds. Functional Ecology 10:73–80.

Kahle, D., and H. Wickham (2013). ggmap: spatial visualization with ggplot2. The R Journal 5:144–161.

Kaiser, A. (1993). A new multi-category classification of subcutaneous fat deposits of songbirds. Journal of Field Ornithology 64:246–255.

Karasov, W. H., and B. Pinshow (2000). Test for physiological limitation to nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological and Biochemical Zoology 73:335–343.

Kelly, J. F., L. S. DeLay, D. M. Finch, and C. Blem (2002). Density-dependent mass gain by Wilson's Warblers during stopover. The Auk 119:210–213.

Kemp, M. U., E. Emiel van Loon, J. Shamoun-Baranes, and W. Bouten (2012). RNCEP: global weather and climate data at your fingertips. Methods in Ecology and Evolution 3:65–70.

Kokko, H., T. G. Gunnarsson, L. J. Morrell, and J. A. Gill (2006). Why do female migratory birds arrive later than males? Journal of Animal Ecology 75:1293–1303.

Kuenzi, A. J., F. R. Moore, and T. R. Simons (1991). Stopover of Neotropical landbird migrants on East Ship Island following trans-gulf migration. The Condor 93:869–883.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen (2017). lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1–26.

Leather, S. R. (2005). Insect Sampling in Forest Ecosystems. Blackwell Publishing, Malden, MA, USA.

Liechti, F. (2006). Birds: blowin' by the wind? Journal of Ornithology 147:202–211.

Lindström, Å., T. Alerstam, and A. Hedenström (2019). Faster fuelling is the key to faster migration. Nature Climate Change 9:288–289.

Lukas, J., and V. Stejskal (2003). Computer-based image analysis to estimate the area of a sticky trap occupied or contaminated by pests. Plant Protection Science 39:52–60.

Macdade, L. S., P. G. Rodewald, and K. A. Hatch (2011). Contribution of emergent aquatic insects to refueling in spring migrant songbirds. The Auk 128:127–137.

Marra, P. P., K. A. Hobson, and R. T. Holmes (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Matthews, S. N., and P. G. Rodewald (2010). Movement behaviour of a forest songbird in an urbanized landscape: the relative importance of patch-level effects and body condition during migratory stopover. Landscape Ecology 25:955–965.

McCabe, B. J., and C. G. Guglielmo (2019). Migration takes extra guts for juvenile songbirds: energetics and digestive physiology during the first journey. Frontiers in Ecology and Evolution 7.

McKinnon, E. A., K. C. Fraser, C. Q. Stanley, and B. J. M. Stutchbury (2014). Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration. PLoS ONE 9:e105605.

McWilliams, S. R., C. Guglielmo, B. Pierce, and M. Klaassen (2004). Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. Journal of Avian Biology 35:377–393.

Mills, A. M., B. G. Thurber, S. A. Mackenzie, and P. D. Taylor (2011). Passerines use nocturnal flights for landscape-scale movements during migration stopover. The Condor 113:597–607.

Mitchell, G. W., B. K. Woodworth, P. D. Taylor, and D. R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Movement Ecology 3:19.

Moore, F. R., and D. A. Aborn (2000). Mechanisms of en route habitat selection: How do migrants make habitat decisions during stopover? Studies in Avian Biology 20:34–42.

Moore, F. R., S. Mabey, and M. Woodrey (2003). Priority access to food in migratory birds: age, sex and motivational asymmetries. In Avian Migration (P. D. P. Berthold, P. D. E. Gwinner and E. Sonnenschein, Editors). Springer-Verlag, New-York, NY, USA, pp. 281–292.

Moore, F. R., and W. Yong (1991). Evidence of food-based competition among passerine migrants during stopover. Behavioral Ecology and Sociobiology 28:85–90.

Morbey, Y. E., C. G. Guglielmo, P. D. Taylor, I. Maggini, J. Deakin, S. A. Mackenzie, J. M. Brown, L. Zhao, and D. Stephens (2018). Evaluation of sex differences in the stopover behavior and post departure movements of wood-warblers. Behavioral Ecology 29:117–127.

Morris, S. R., D. W. Holmes, and M. E. Richmond (1996). A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. The Condor: Ornithological Applications 98:395–409.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:59–64.

Ottich, I., and V. Dierschke (2003). Exploitation of resources modulates stopover behaviour of passerine migrants. Journal für Ornithologie 144:307–316.

Packmor, F., T. Klinner, B. K. Woodworth, C. Eikenaar, and H. Schmaljohann (2020). Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? Movement Ecology 8:6.

Paxton, K. L., C. Van Riper, and C. O'Brien (2008). Movement patterns and stopover ecology of Wilson's Warblers during spring migration on the lower Colorado River in Southwestern Arizona. The Condor 110:672–681.

Pyle, P. (1997). Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA, USA.

R Core Team (2021). R: a language and environment for statistical computing. [Online.] Available at URL https://www.R-project.org/.

Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Rasband, W. S. (2018). ImageJ. [Online.] Available at https://imagej.nih.gov/ij/.

Rguibi-Idrissi, H., R. Julliard, and F. Bairlein (2003). Variation in the stopover duration of Reed Warblers *Acrocephalus scirpaceus* in Morocco: effects of season, age and site. Ibis 145:650–656.

Schaub, M., and L. Jenni (2000). Fuel deposition of three passerine bird species along the migration route. Oecologia 122:306–317.

Schaub, M., L. Jenni, and F. Bairlein (2008). Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19:657–666.

Seewagen, C. L., C. G. Guglielmo, and Y. E. Morbey (2013). Stopover refueling rate underlies protandry and seasonal variation in migration timing of songbirds. Behavioral Ecology 24:634–642.

Seewagen, C. L., E. J. Slayton, and C. G. Guglielmo (2010). Passerine migrant stopover duration and spatial behaviour at an urban stopover site. Acta Oecologica 36:484–492.

Shochat, E., Z. Abramsky, B. Pinshow, and M. E. A. Whitehouse (2002). Density-dependent habitat selection in migratory passerines during stopover: what causes the deviation from IFD? Evolutionary Ecology 16:469–488.

Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Slager, D. L., P. G. Rodewald, and P. J. Heglund (2015). Experimental effects of habitat type on the movement ecology and stopover duration of spring migrant Northern Waterthrushes (*Parkesia noveboracensis*). Behavioral Ecology and Sociobiology 69:1809–1819.

Smith, A. D., and S. R. McWilliams (2014). What to do when stopping over: behavioral decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions. Behavioral Ecology 25:1423–1435.

Smith, R. J., F. R. Moore, and C. A. May (2007a). Stopover habitat along the shoreline of northern Lake Huron, Michigan: emergent aquatic insects as a food resource for spring migrating landbirds. The Auk 124:107–121.

Smith, S. B., K. H. McPherson, J. M. Backer, B. J. Pierce, D. W. Podlesak, and S. R. McWilliams (2007b). Fruit quality and consumption by songbirds during autumn migration. The Wilson Journal of Ornithology 119:419–428.

Smith, S. B., A. C. Miller, C. R. Merchant, and A. F. Sankoh (2015). Local site variation in stopover physiology of migrating songbirds near the south shore of Lake Ontario is linked to fruit availability and quality. Conservation Physiology 3:cov036.

Smolinsky, J. A., R. H. Diehl, T. A. Radzio, D. K. Delaney, and F. R. Moore (2013). Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. Behavioral Ecology and Sociobiology 67:2041–2051.

Taylor, P. D., T. Crewe, S. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. Francis, C. Guglielmo, D. Hamilton, R. Holberton, et al. (2017). The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:8.

Taylor, P. D., S. A. Mackenzie, B. G. Thurber, A. M. Calvert, A. M. Mills, L. P. McGuire, and C. G. Guglielmo (2011). Landscape movements of migratory birds and bats reveal an expanded scale of stopover. PLoS ONE 6:e27054.

Therneau, T. (2022). coxme: Mixed Effects Cox Models. [Online.] Available at https://CRAN.R-project.org/package=coxme.

Weber, T. P., T. Alerstam, and A. Hedenström (1998). Stopover decisions under wind influence. Journal of Avian Biology 29:552–560.

White, G. C., and R. A. Garrott (2012). Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego, California, USA.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73:3–36.

Woodrey, M. (2000). Age-dependent aspects of stopover biology of passerine migrants. Studies in Avian Biology 20:43–52.

Woodworth, B. K., C. M. Francis, and P. D. Taylor (2014). Inland flights of young Red-eyed Vireos *Vireo olivaceus* in relation to survival and habitat in a coastal stopover landscape. Journal of Avian Biology 45:387–395.

Zajac, R., D. J. Cerasale, and C. G. Guglielmo (2006). The rapid response of plasma metabolites to changes in feeding rate in a small passerine *Wilsonia pusilla*. Journal of Avian Biology 37:405–408.

Zimin, S. V., A. Zimin, D. J. Burns, R. Livne, R. Paz, Y. Zvik, E. Shochat, and O. Ovadia (2023). Competition is a major limiting factor of refueling in migratory passerines during stopover. Journal of Avian Biology n/a:e03137.

Chapter 4

4 An experimental test of the effect of resource availability on refueling and stopover behaviour in free-living White-throated Sparrows (*Zonotrichia albicollis*).

4.1 Introduction

For migratory songbirds faced with the challenge of traversing vast distances, acquiring the energy needed to power migratory flight is key to successful migration. The majority of songbird species acquire this energy en route during inter-flight migratory stopovers by foraging on locally available food items and storing the energy primarily in adipose tissue (refuelling). Theories of optimal migration and stopover duration that unite models of patch-selection and bioenergetics have proposed different relationships between the rate of energy acquisition during stopover and departure fuel load depending on whether time or energy use is the “currency” to optimise (Alerstam and Lindström 1990, Hedenström and Alerstam 1997) across the migratory journey. In both scenarios, the rate at which energy is accumulated is expected to influence the length of time that migrants remain at stopover sites, with greater rates of refuelling promoting shorter migratory stopover bouts.

Both resource availability and individual traits can influence how well migrants refuel, but whether the impact of individual traits on refuelling depends on the availability of resources at a stopover site remains uncertain. Positive relationships between local food availability and refuelling rate have been reported previously in studies using recapture data and metabolite profiling to measure refuelling rate (e.g. Bibby and Green 1983, Schaub and Jenni 2000, Smith et al. 2007, Macdade et al. 2011). Intrinsic difference, such as between species, sex, or age class, can also affect refuelling rate during migratory stopover (Woodrey 2000, Seewagen et al. 2013), however, these patterns can be inconsistent within and between studies (Chapter 3) (Seewagen et al. 2013, Brown et al. 2014, Morbey et al. 2018, Beauchamp et al. 2020). Asymmetries in the ability to obtain food, resulting from differences in foraging proficiency, social rank, or competitive ability that are associated with age or sex-class are a behavioural mechanism hypothesised to underly class-specific refuelling rate (Moore et al. 2003), with reduced access to resources stemming from these asymmetries results in lower refuelling rates among poorer foragers and competitors. Critically, the impact of these behavioural asymmetries on refuelling may only occur in situations where resources are limited, and a high abundance of resource may enable all migrants to refuel near their physiological maximum regardless of any differences in ability to obtain resources (Moore et al. 2003). The availability of resources at the stopover sites may therefore acts a moderator to class-specific patterns of refuelling, with potential extended impacts on local movement and stopover duration.

Our theoretical understanding of how resource availability and individual characteristics shape songbird refuelling and stopover behaviour have been refined by observations of wild migrants (e.g. Macdade et al. 2011) and captive experiments (e.g. Moore et al. 2003, Klinner et al. 2020), yet studies that unite the experimental manipulations of resource availability typically reserved for captive experiments with the natural setting of the observational study are comparatively rare. These studies provide invaluable insight into the behaviour in the context of the natural system without needing to abstract the behaviours of captives to their free-living counterparts. Ad-libitum provisioning of wild insectivorous birds using feeding station featuring electronic balances has been applied to test the interrelation between refuelling rate, departure fuel load, and stopover duration (Lindström and Alerstam 1992, Fransson 1998, Dänhardt and Lindström 2001, Schmaljohann and Dierschke 2005). Feeding experiments conducted by temporarily confining migrants captured during stopover have been used to test how fuel stores influence stopover behaviour (Smith and McWilliams 2014), and capture and relocation of migrants to new sites has also been used to test how variation in habitat characteristics and resource availability influences stopover movement behaviour (Cohen et al. 2012, Slager et al. 2015). Few field experiments have attempted to dynamically alter the resources available to migrants while at stopover. In Rufous Hummingbirds (*Selasphorus rufus*), Hixon et al. (1983) found the spatiotemporal extent of foraging increased when nectar bearing flowers were removed and decreased with the addition of flowers during autumn migratory stopover. To my knowledge, similar dynamic experimental manipulations of stopover site resource availability have not been conducted in passerine migrants.

I combined experimental manipulations of resource availability with individual level measurements of refuelling rate, stopover-scale movement, and stopover duration to test how resource availability affects refuelling performance and behaviour in free living songbirds. To do so, I used feeding stations to dynamically alter food availability over fortnightly periods at three stopover sites during autumn migration. Refuelling rate of captured migrants was measured using plasma metabolite analysis and automated radio telemetry was used to measure local movement and stopover duration. I expected migrants to have higher refuelling rates when food was provided, as the increased access to food would enable more rapid refuelling among individuals at the site. I also expected movement during stopover would be lower when local resources when food was provided due the reduced need to travel within the stopover site to locate food. I also expected that elevated resource availability would decrease stopover duration, as the supplemental food resources would enable migrants to obtain the energy required for migratory departure faster. In addition, I also sought to explore how stopover site resource availability may modulate class differences in refuelling and stopover behaviour, testing the hypothesis that impact of class-based behavioural and physiological differences on refuelling and behaviour are moderated by resource availability. I expected that differences in refuelling rate between individuals of behaviourally and physiologically different classes would be more pronounced when experimentally provided food was not available, and that providing food would enable all individuals to refuel equally well.

To further explore how resource availability affects class-specific refuelling and behaviour, I used a study species which features a unique genetic-linked dimorphism which affects both appearance and behaviour, the White-throated Sparrow (*Zonotrichia albicollis*). During the breeding season the morph of this species can be distinguished outwardly by the colour of the crown plumage as either white-striped or tan-striped, and this dimorphism affects behaviour during breeding and throughout the annual cycle (Kopachena and Falls 1993). White-striped birds have greater competitive ability and dominance during the breeding season (Knapton et al. 1984), and slight differences in vernal migration timing (Caldwell and Mills 2006, Hoh et al. 2018). Previous studies have reported mixed support for morph differences in refuelling rate during migratory stopover (Brown et al. 2014, Hoh et al. 2018, Beauchamp et al. 2020), again demonstrating an evidentiary discrepancy for class-specific patterns of refuelling which could arise as a result of local resource availability. White-striped birds also move more during spring stopover and differ in diel activity patterns and departure timing (Beauchamp et al. 2020). Despite these difference in local behaviour, differences in stopover duration between the two morphs was not observed in the spring (Beauchamp et al. 2020). This has yet to be tested during autumn migration when morph-specific refuelling was previously observed (Brown et al. 2014).

4.2 Methods

Research was conducted between 2 September 2020 to 28 October 2020 at three sites in eastern New Brunswick, Canada (Figure 4-1). Two sites were located coastally near Waterside (45°37’30.4” N 64°47'30.47"W) (WAT) and Mary’s Point (45°43'28.07"N 64°40'31.16"W) (MPT). The other site was located approximately 25 km inland at the Community Forest International Whaelghinbran Farm (45°44'4.88"N 65°18'2.41"W) (CFI). Sites featured similar forest structure intermixed with patches of open habitat, with the compositions of tree species primarily including a mixture of spruce (*Picea* spp.), fir (*Abies* spp.), birch (*Betula* spp.), and pine (*Pinus* spp.). Local temperature was recorded using two Onset UA-002-64 temperature loggers at each site (www.onsetcomp.com).

Each site was sampled every four days, using up to eight mist nets to passively capture White-throated Sparrows (*Zonotrichia albicollis*). Mist netting commenced one hour after local sunrise to minimise the strong time-of-day effect associated with metabolite profiling (Guglielmo et al. 2005), and ceasing approximately seven hours after local sunrise. Nets were closed during periods of precipitation or in sustained winds above 15 km/hr. Mist nets were continuous monitored or were otherwise checked every eight to 10 minutes. A digital stopwatch was used to record the time elapsed between last check of a net, and the completion of blood extraction (bleed time). Blood samples were centrifuged at 2000 *g* for 10 min, and both blood cells and plasma were transferred into separate cryogenic tubes and stored in a liquid nitrogen dry shipper (Taylor-Wharton CX 100). Remaining blood cells were retained to confirm plumage morph using genetic analysis (Griffiths et al. 1998, Beauchamp et al. 2020 SI). Plasma concentrations of β-OH butyrate, glycerol, and triglyceride (mmol*L^{-1}) were measured using colorimetric assays (R Biopharm: 10907979035, SIGMA: Trinder reagent A and B) following Guglielmo et al. (2005).

Birds were banded with the appropriate size U.S. Fish and Wildlife Service/Canadian Wildlife Service aluminum leg band, and wing chord, tarsus length, mass, and fat score (Kaiser 1993) were measured. Sex and age were provisionally assigned in the field following Pyle (1997). Birds were then tagged with digitally encoded radio transmitters (model NTQB2-1 and NTQB2-2, Lotek Wireless, www.lotekwirelss.ca) to measure local movement and stopover. Tags weighed approximately 0.29 – 0.35 g, and were affixed to the bird using a leg-loop harness constructed of elastic thread (Rappole and Tipton 1991). Pulse interval of the tags varied depending in the tag model, and ranged from 6.10 s to 12.5 s. Manual telemetry was used to track local movement during stopover with attempts made to locate tagged birds once each visit to the capture site using the homing method (White and Garrott 2012). Coordinates were recorded when a tagged bird was observed, or the position was estimated using a combination of high signal strength at low gain. Geographic Positioning System coordinates were recorded for the position of the observer (Garmin eTrex 20x) and adjusted for the direction and distance to a bird using a laser rangefinder (Leupold Marksman 1000 or Nikon Prostaff 1000) and magnetic compass. These data were used to estimate the spatial extent of the stopover for migrants captured at each site.

Stopover duration and post-departure movement bearing was measured using the Motus Wildlife Tracking System (Motus; Taylor et al. 2017). Detections of radio signals from tagged individuals on the receiver located at each site was used to determine that a bird was still within the region of capture. Stopover duration was calculated as the number of days between tagging and departure + 1, providing the minimum length of stopover. Post-departure detections were processed following (Birds Canada 2022) to remove false-detections, and the bearing between the capture site and the next detection on the Motus array was averaged across all individuals using the package “circular” (Agostinelli and Lund 2022) to provide the average post-departure flight bearing of 247°.

Wind data for the analysis of departure risk was obtained from the NCEP/DOE Reanalysis 2 data set http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis2 .html) which provides meteorological data four times each day at 2.5° x 2.5° spatial resolution. Wind speed in $m \cdot s^{-1}$ in the easterly and northerly direction was extracted using the “RNCEP” package (Kemp et al. 2012), and interpolated for an individual’s stopover site using the function NCEP.interpol with the option for linear interpolation. Wind was interpolated for ground level for 21:00 ADT. Tailwind component was estimated as $V_w*\cos(\beta)$, where V_w is wind speed ($m \cdot s^{-1}$) and β is average post-departure flight bearing. All data collection was conducted under the banding permit 10911C issued to ATB by Environment and Climate Change Canada with approval by the University of Western Ontario Animal Care Committee (AUP # 2017-160).

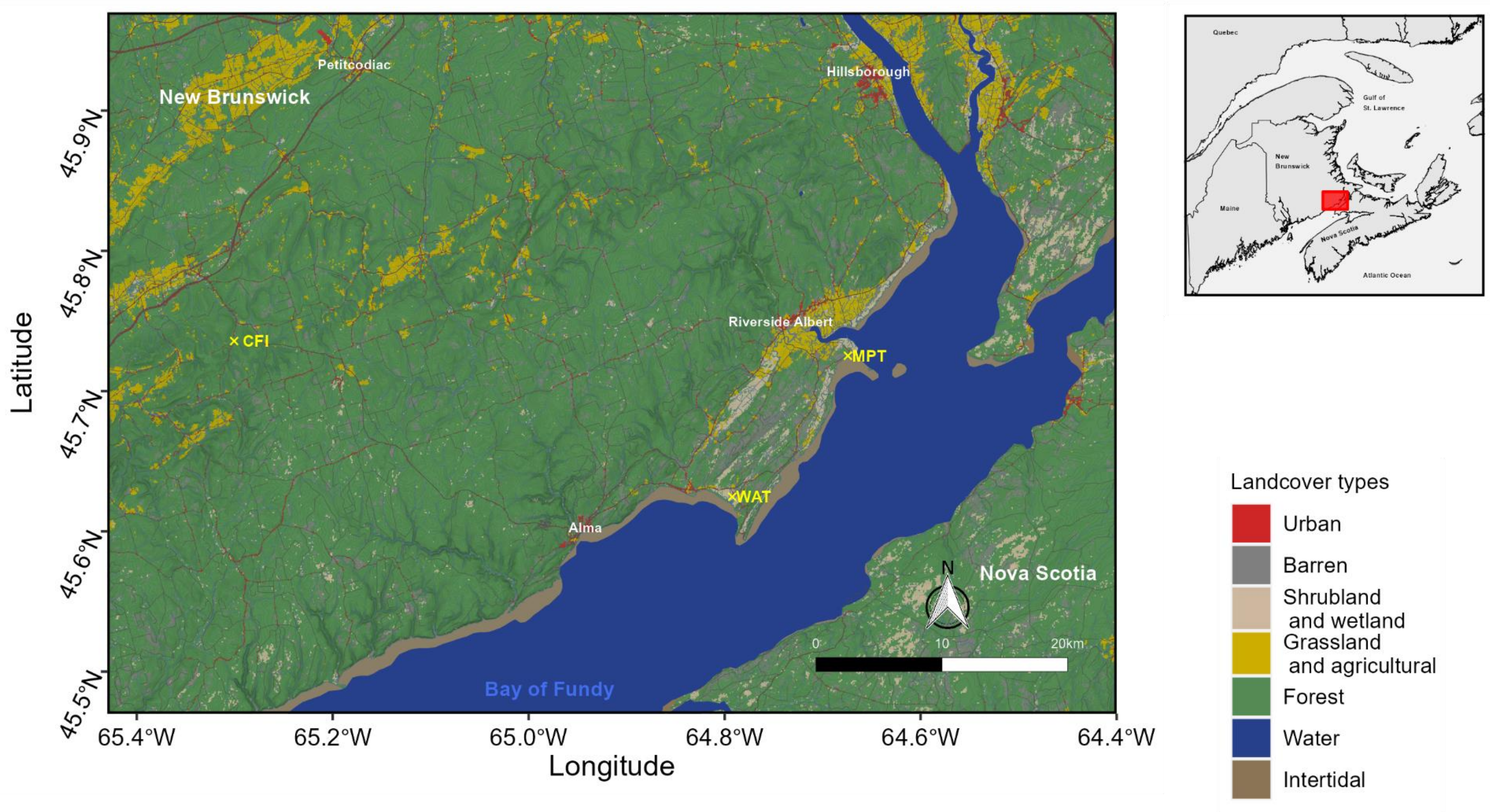


Figure 4-1. Location of study sites and 2021 landcover classification in eastern New Brunswick, Canada. Also indicated are roadways, watercourses, and topography at intervals of 10 meters. Sites labels; CFI = Community Forest International Whaelghinbran Property; WAT = Waterside; MPT = Mary's Point. Raster landcover classification data adapted from (Agriculture and Agri-food Canada 2023), vector data from (DMTI Spatial Inc. 2014a, b, c, 2017a, b, c, 2021).

Resource availability manipulation

Food resource availability was manipulated using three platform-style feeding stations deployed at each site. Platform feeding stations measured 45 cm by 55 cm and featured a fine mesh screen floor to prevent the accumulation of water. These platforms were affixed to a post approximately 2 meters above the ground and featured a baffle to deter access from the ground by mammals (Appendix B). At each site, food was provided at feeding stations in approximately 14-day blocks, with a separation of approximately 14-days where feeding stations were cleared, and no food was provided. This cycle was repeated twice during the season during autumn migration (Figure 4-2). Feeding stations were filled with locally sourced cracked corn (*Zea mays*), and the food availability status of the feeding stations was delineated as whether food was present 30 minutes following sunrise. In doing so, sites where food was scheduled to have food augmented on next day could be filled prior to leaving the site in the evening or removed at dawn prior to bird capture if local food availability was not scheduled to be augmented on that day. During periods when food was provided, feeding stations were checked, spot cleaned, and refilled every other calendar day. Feeding stations were emptied and left in place during periods when food was not provided.

Feeding stations were installed between 2 September and 4 September 2020, following which they were left filled during an initial acclimation period. The first experimental resource augmentation period began on 8 September 2020 at the coastal site MPT, followed seven days later at the inland site CFI and coastal site WAT. This seven-day offset between pairs of sites provided periods of overlap where all sites had either food augmentation or not (Figure 4-2) to control for the effect of date.

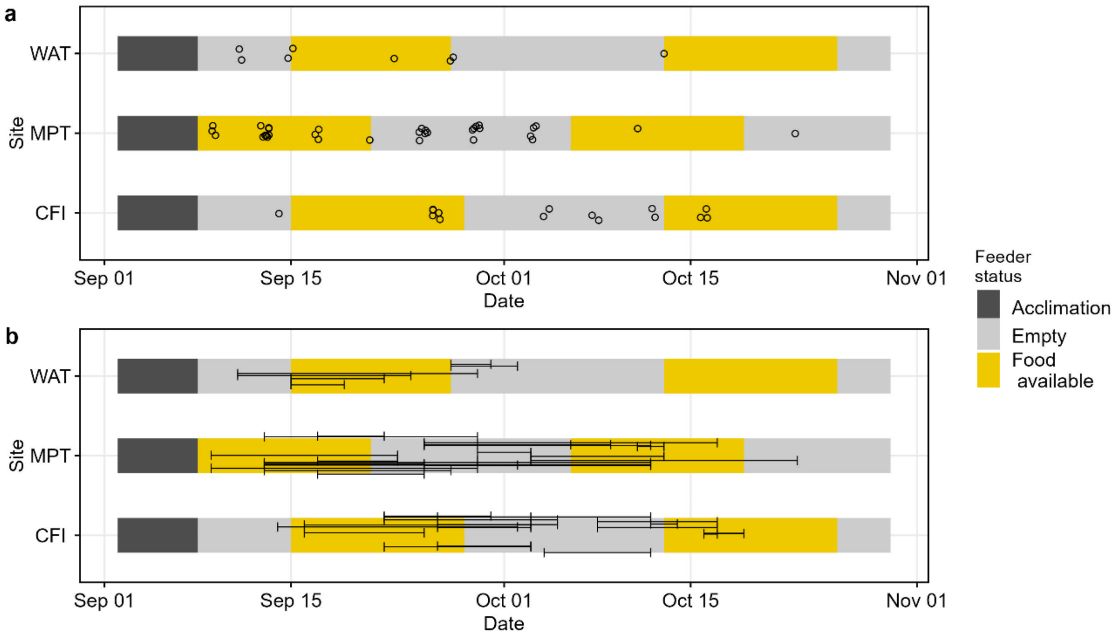


Figure 4-2. Food augmentation treatment timeline. Coloured bars indicate periods when feeding stations provided supplemental food to local migrants. Points of panel (a) indicate captures of birds included in the analysis of refuelling. The lines on panel (b) span individual stopovers. As not all capture birds were radio-tagged, only a portion of the points on panel (a) will have associated spans in panel (b).

Local invertebrate and migrant abundance,

Eight paired pitfall and sticky traps were set at each site to sample terrestrial and flying insects, positioned randomly along the length of one of the mist net lanes at a random perpendicular distance between six and 15 meters. Traps were collected and reset at the end of each visit to the site, leaving them exposed for four-day intervals. Pitfall traps were approximately ~8 cm diameter and ~ 2 cm in depth, featuring three 50 cm drift fences spaced at 120° intervals and extending away from the trap opening and a 12 mm metal mesh screen positioned 2 cm below the rim of the trap to exclude vertebrates (Leather 2005, Smith and McWilliams 2014). Traps were set flush to the ground surface and filled with water to a depth of ~3 cm. Contents were collected at each visit to the site and stored in ~70% ethanol. In the lab, captured invertebrates were dried at 60°C for 18 to 24 h, identified to family where possible, and weighed on an electronic balance (0.1 mg). Flying insects were sampled using sticky traps (Kelly et al. 2002, Leather 2005). Five 13 cm x 20 cm yellow card-style sticky traps (LIGHTSMAX) were deployed vertically on wooden poles at a height of approximately 2.2 m, with traps having a minimum clearance from of 50 cm on all sides from any vegetation. Sticky traps replaced every visit, with the trap oriented to face a random direction selected using a random number table.

Image analysis was used to determine the percentage of the trap area covered by invertebrates to obtain an index of flying invertebrate abundance (e.g. Lukas and Stejskal 2003). Following the removal of any non-invertebrate material (leaves, dirt, etc.), traps were placed on a blue stage and photographed using a Canon Rebel T3i with and EFS 18-55 lens mounted to a tripod. Distance between the stage and lens was adjusted to 465 mm. A shutter speed of 1/30 and aperture of F5.6 and ISO of 1600 were used under low ambient lighting conditions to reduce glare from the glossy surface of the trap. The lens was leveled using a bubble level prior to photographing. Digital images of traps were then processed using a three-step process in ImageJ version 1.51w (Rasband 2018). First, the area of the image matching the colour of the trap was measured to obtain the area of the trap not covered by captured invertebrates. Second, the total area of the trap in the image was calculated by measuring the area of the blue background present around the image edge and subtracting this from the total image area. Finally, subtraction of the area in step one from the area in step two yielded the area covered by invertebrates. This was then converted to a proportion by dividing by the total area of the trap obtained in step two. As such, complete sticky trap area coverage data and pitfall capture mass data was available from 358 unique traps, representing 53 days.

To calculate an index of resource abundance, averages of the invertebrate mass from each pitfall trap and the percent of the surface covered of each sticky trap were calculated for traps set at the same sites during the same four-day period. Averages for each trap type were then standardised to exposure period (four days). Following log10 (value +1) transformation, principal component analysis was then applied to the exposure-standardised average-values of the pitfall and stick traps collected across all sites, with the first principal component being used as a sites and date specific index of invertebrate resource abundance (ResI). Using this data, site-specific generalised additive models of ResI were fit to estimate daily invertebrate resource abundance (eResI) for the three days between consecutive visits of the same site. Models were fit using the function *gam* from the r package “mgcv” (Wood 2012), and included site-specific mean daily temperatures and a smooth term for day of year fit using generalised cross-validation. Site-specific values of eResI were then estimated using day of year and the daily average temperature of the site. Estimating daily invertebrate abundance was necessary to include a measure of background invertebrate food abundance in the analysis of daily departure hazard (described below).

Migrant abundance was assessed as the total number of unbanded sparrows (Passerellidae). I chose to pool the daily capture of all sparrows (Passerellidae) as the similarity in diet among these species could allow the collective use of experimentally provided food. Captured sparrows were primarily White-throated Sparrows (n = 126), Slate-colored Juncos (*Junco hyemalis hyemalis*, n = 46), and Song Sparrows (*Melospiza melodia*, n = 12), with single individuals of Lincoln’s Sparrow (*Melospiza lincolnii*), Swamp Sparrow (*Melospiza georgiana*), and Chipping Sparrow (*Spizella passerina*) captured during the study. This taxonomic family-specific migrant catch data was available for 53 days from 2020. Daily catch rate of sparrows was calculated by standardising the total number of unbanded sparrows captured for each sampling day by the summed total of time all nets were open on that sampling day, yield in a daily as catch per-unit effort of sparrows. Recaptures of banded sparrows from previous sampling days were generally infrequent (10 recaptures total across the season), and as such were not considered when tallying the daily total catch.

4.2.1 Analysis of sparrow capture

To test for a numerical response to augmented resource availability, a mixed-effect negative binomial model was implemented using function glmmTMB from package “glmmTMB” (Brooks et al. 2017). Day of year was included in the model to account for seasonal changes in sparrow abundance across the migratory period. The model also included an offset term for the number of net-hours on a sampling day (log10 (net-hours+1)) to account for difference in sampling effort, and the random intercept of site to account for repeated measures of catch at each site across multiple days within the season. Prior to assess the main effect of food treatment, a likelihood ratio test was used to test if the inclusion of a quadratic term for day of year improved model fit. Following this, a subsequent likelihood ratio test was used inclusion of local invertebrate abundance improved model fit to account for natural fluctuations in food availability. Model family was specified as “nbiom2” and fit using maximum likelihood, and model assumptions were assessed using scaled residuals simulated using the function simulateResiduals in R package “DHARMa” (Hartig 2022).

4.2.2 Analysis of refuelling rate

Plasma samples from White-throated Sparrows with a bleed time greater than 20 minutes were omitted from analysis due to the rapid turnover of metabolite profile from feeding to fasting following capture (Zajac et al. 2006). Measured plasma concentration of triglyceride (correcting for free glycerol) and β-OH butyrate were log10(x + 1) transformed, and principal component analysis was applied to create a refuelling index (RI) (Guglielmo et al. 2005). Following this, linear mixed effect models were used to test for the influence of food provision treatment and individual characteristics on refuelling rate in an information theoretic approach, starting with a null model that contained individual capture time, the time between capture and the completion of blood sampling (bleed time), capture mass, tarsus length, and the random intercept of site. Capture time and bleed time were included in the null model due to the rapid changes in metabolite concentration relative to the start of diurnal feeding and following capture. Capture mass and tarsus length was included to control for the influence of body condition on metabolite concentration, and the random intercept of site was used to account for site-level heterogeneity in refuelling.

Prior to assessing the effect of food treatment, separate likelihood ratio tests were used to test whether the inclusion of local invertebrate resource abundance (ResI), local sparrow abundance (as catch per-unit effort; CPUE sparrows), or sampling day of year, improved model fit relative to the null model. These covariates were considered to ensure the assessment of the main effects were not confounded by natural background variation in resource availability, density-dependent effects on refuelling, or by seasonal variation in refuelling rate. Covariates that significantly improved model fit were then added to the null model prior to further analysis.

After testing for potentially confounding covariates, candidate models were created to test for the additive and interactive effects of resource augmentation and individual characteristics on capture refuelling rate. Extending the null model, separate models were created to test for the effect of food treatment (model 2), age class (model 3), both food treatment and age class additively (model 4), and the interaction between food treatment and age class (model 5) on capture refuelling rate. A further set of three extended models were created to test for the effect of morph (model 6), both food treatment and morph additively (model 7), and the interaction between food treatment and morph on capture refuelling rate (model 8). Group sample size imbalance precluded a robust test of models including the three-way interaction between age class and morph and food treatment, but additive and interactive sub-models were possible. These included extended models containing the additive effect of age class and morph (model 9), the additive effect of age class, morph, and food treatment (model 10). Two additional models were developed by taking model 10 and including either the interaction between age class and food treatment (model 11) or morph and food treatment (model 12, Table

4-2). Sex was not considered all but one of the birds captured were male. All models were fit using maximum likelihood with the function *lmer* in package “lme4” (Bates et al. 2015), with model residuals were visualised to check for normality. Models fit was ranked relative to the null model using AICc, with a decrease in AICc greater than two indicating significantly improved fit over more parsimonious models. *P*-values for fixed effect covariates were determined using the Satterthwaite approximation for degrees of freedom implemented in package “lmerTest” (Kuznetsova et al. 2017)

4.2.3 Analysis of stopover duration

To test how supplemental food availability and individual characteristics affected stopover duration in White-throated Sparrows, survival analysis was applied using mixed effect Cox proportional hazard analysis with package “coxme” (Therneau 2022). Under this framework, factors that increase the hazard for migratory departure can be seen as decreasing stopover duration (Dossman et al. 2016). Stopover duration was calculated as departure date – capture date +1, providing the minimum length of stopover. A candidate model approach was used to test how age class, morph, and the food augmentation treatment affects departure hazard, starting with a null model that included the fixed effects of capture day of year, tarsus length and capture body mass as fixed effects, and nocturnal tailwind assistance as a time-vary covariate. Day of year was included in the null model as migrants captured on a later date tend to have greater departure hazard, and nocturnal tailwind was included as songbirds tend to migrate with energetically favourable tailwinds and avoid migrating when flying into the wind (i.e. with negative tailwinds) (Liechti 2006, Mitchell et al. 2015, Morbey et al. 2018, Chapters 2 & 341). Site was included as a random intercept to account for heterogeneity in stopover duration arising from unobserved site-level processes.

Prior to testing for the effect of the food augmentation treatment, the influence of local resource availability and capture refuelling rate on departure hazard was assessed to determine if naturally occurring variability in these metrics influenced departure hazard. Resource abundance was included in the analysis using the daily estimates of invertebrate abundance (eResI). Capture refuelling rate was included using the residuals from the analysis of refuelling, representing individual-level refuelling accounting for covariates relevant to this measure. Separate likelihood ratio tests were then used to test whether the addition of eResI or residual refuelling rate significantly improved the fit of the null model of stopover departure hazard.

After determining the best null model of stopover departure hazard, a separate set of extended candidate models were constructed to test for the effect of food augmentation treatment, age class, plumage morph, and all additive and interactive combination of food augmentation treatment and these individual characteristics. As in the analysis of refuelling rate, sample size imbalance across age class-morph group sizes precluded the robust assessment of models with this interaction term, leaving a total of 12 models of stopover departure hazard (Table 4-5). Candidate models were compared using AICc, with a decrease in AICc greater than two indicating significantly improved fit over more parsimonious models. In all models, the proportional hazard assumption was assessed by visualising the sum of scaled Schoenfeld residuals across time (Grambsch and Therneau 1994) using function cox.zph from the R package “survival” (Therneau 2021).

4.2.4 Local movement behaviour

To test how individual characteristics and supplemental food availability influenced stopover movement behaviour of White-throated Sparrows, separate linear mixed effect models were compared to explain variability in displacement between subsequent relocations. Starting with a null model that contained the time elapsed between consecutive relocations, the number of days since an individual was tagged (day of stopover), and random intercept terms of individual to account for repeated measures and site to account for site-level clustering of data, separate models were created through the addition of the covariates food treatment on the day status, eResI, and both covariates additively. Likelihood ratio tests were used to assess if the inclusion of a covariate increased model fit relative to the null model. Following this, the affect of age class and plumage morph was then tested by conducting likelihood ratio tests on separate extended model created through the addition of these covariates. Following assessment of single terms, separate interactions between age class and food treatment, and morph and food treatment were also tested relative to the best model using a likelihood ratio test. Prior to analysis, displacement (meters) was log10 transformed and all continuous covariates were centered and scaled.

Frequent instances of individual stopovers occurring across food treatment and non-treatment periods prevented formal analysis of whether maximum displacement differed when supplemental food was available. To test for individual-level differences in maximum displacement during stopover, a linear mixed effect model was fit including age, morph, the day of stopover on which the observation occurred, and a random intercept of site. Model assumptions were visually assessed using scaled residuals simulated from the fitted models using the function simulateResiduals in R package "DHARMa" (Hartig 2022). All data analyses were conducted in R version 4.1.2 (R Core Team 2021).

4.3 Results

4.3.1 Invertebrate resource abundance and sparrow capture

Complete data on sticky trap coverage and pitfall trap capture mass was available from 358 traps representing 49 sampling days across the autumn season. Principal component one accounted for 66.0% of the variation in invertebrate capture. Both pitfall trap mass and sticky trap coverage loaded positively, and principal component one can be interpreted as an index of local invertebrate resource abundance on the day of sampling (ResI). Sparrow catch was analysed for 49 days. One date with high sparrow capture (24 birds) was identified as an outlier but was retained in the analysis as it did not influence the analysis outcome. While the inclusion of day of year squared improved model fit (χ^2_1= 4.37, p = 0.04), the inclusion of ResI did not (χ^2_1= 0.01, p > 0.5). After controlling for netting effort, sparrow catch peaked near 16 September 2020, decreasing gradually for the remainder of the study (Day of year: β = 17.62 ± 8.45, z = 2.08, p = 0.04; Day of year^2: β = -18.04 ± 8.50, z = -2.12, p = 0.03). Sparrow capture did not differ between days where feeders were provisioned and when feeders were empty (p > 0.5). The dispersion parameter for the negative binomial model was estimated as 1.44.

4.3.2 Capture refuelling rate

Complete data on metabolite concentration and analysis covariates was available for 55 White-throated Sparrows. Plasma triglyceride (mean ± SE = 2.41 ± 0.34 mmol) and β-OH butyrate (1.48 ± 0.10 mmol) concentrations were negatively correlated, ($R^2 = -0.27$, $p = 0.04$) and the first principal component accounted for 63.5% of the variation in the dataset with log10([triglyceride]+1) loading positively into PC1 (0.71) and log10([β-OH butyrate]+1) loading negatively (-0.71), indicating greater refuelling with more positive values. Sample sizes for the factor level crossings of feeder status and age class or morph can be found in Table 4-1.Likelihood ratio tests indicated null model fit was not improved by the inclusion of local invertebrate resource abundance, catch per-unit effort of sparrows, or day of year (all $p > 0.37$). The best extended model of refuelling rate included food treatment, morph, age class, and the interaction between morph and food treatment (model 12, Figure 4-3, Figure 4-4), however, this model only marginal improved fit over the null model (Δ AICc = 0.90) and other more parsimonious models (Table 4-2).

As a result of the interaction between food treatment and morph, separate post-hoc analyses were conducted after dividing the data by plumage morph. For white-striped birds (n = 24), refuelling rate was significantly greater when food was provided ($\beta = 0.87 \pm 0.42$, $t_{24.0} = 2.08$, $p = 0.048$, Figure 4-4), and decreased with every additional minute of bleed time ($\beta = -0.001 \pm 0.0006$, $t_{24.0} = -2.07$, $p = 0.049$). Refuelling rate was not significantly affected by trap time, capture mass, tarsus length, or age class (all $p > 0.06$, Table 4-2). For tan-striped birds, refuelling rate increased with each minute since local sunrise ($\beta = 0.005 \pm 0.002$, $t_{28.06} = 2.96$, $p < 0.01$) and each gram of mass at capture ($\beta = 0.18 \pm 0.08$, $t_{27.91} = 2.25$, $p = 0.03$). Refuelling rate was also lower in younger hatch-year birds compared to after hatch year birds ($\beta_{\text{Hatch-year}} = -1.12 \pm 0.47$, $t_{28.33} = -2.41$, $p = 0.02$, Figure 4-5). Refuelling rate was not affected by the food treatment, bleed time, or tarsus in tan-striped birds (all $p > 0.10$, Table 4-2).

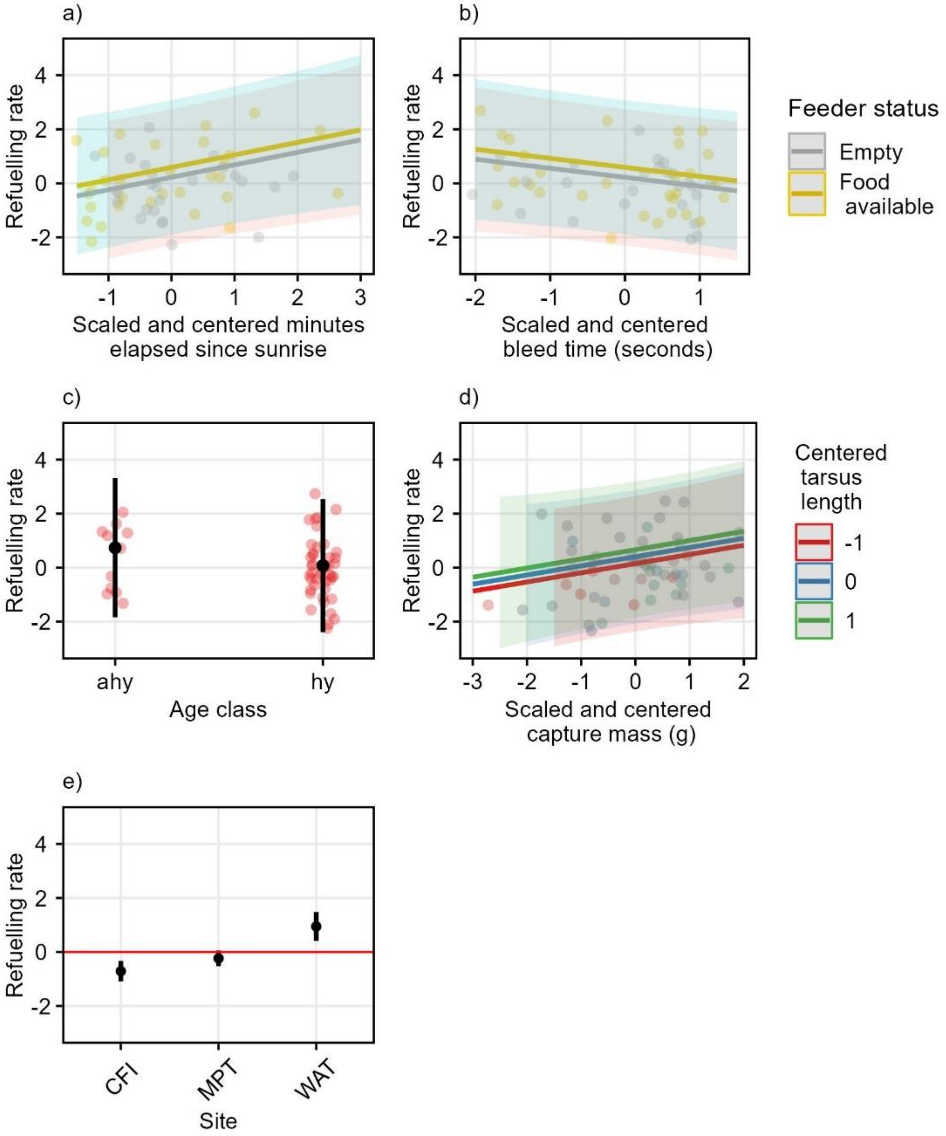


Figure 4-3. The fixed and random effects from the mixed-effect analysis of refuelling rate measured in White-throated Sparrows during autumn stopover in eastern New Brunswick. Fixed effects of minutes elapsed since sunrise (a), and second between capture and the completion of blood sample collection (bleed time) (b) coloured by feeder status. The fixed effect of age class and capture condition (as tarsus length and capture mass) are shown in panel (c) and (d) respectively. Also shown are 95% confidence intervals, and raw data. Estimates of the conditional modes and 95% confidence intervals of the random effect of site are shown in panel (e).

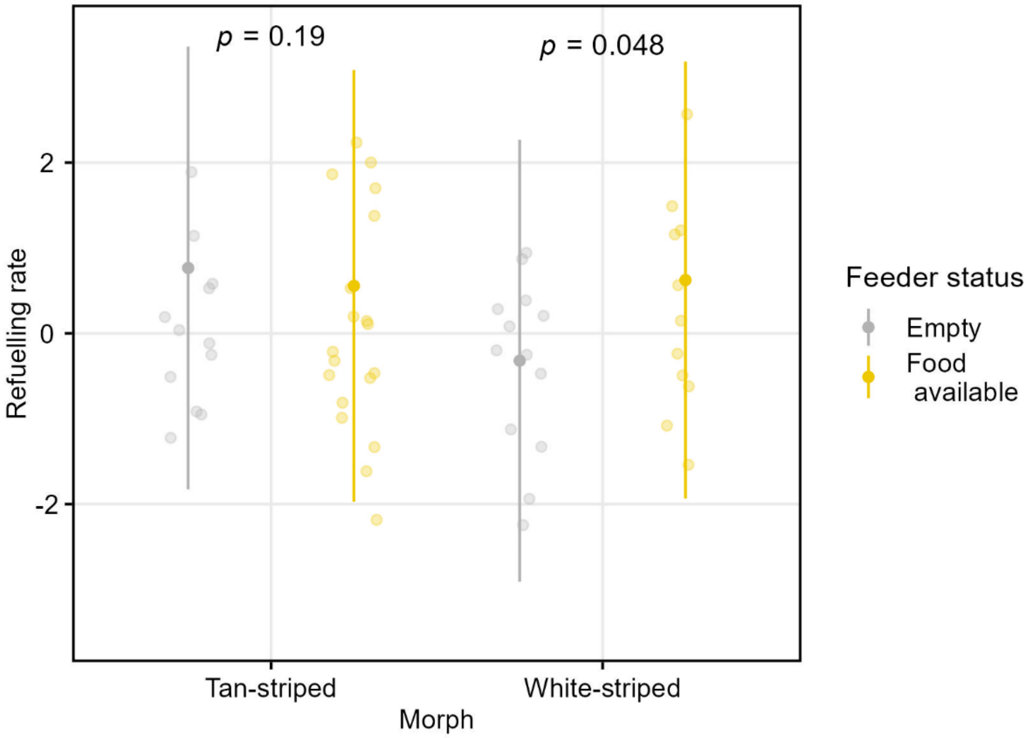


Figure 4-4. The effects of morph and food treatment on refuelling rate measured in White-throated Sparrows during autumn stopover in eastern New Brunswick. Also shown are 95% prediction intervals, and raw data.

Table 4-1. Sample sizes for the factor level crossings of feeder status, age class, and plumage morph of White-throated Sparrows captured during stopover in eastern New Brunswick in the autumn of 2020.

	Age class		**Morph**	
	Hatch year	After hatch year	White-striped	Tan-striped
Food available	22	8	11	19
Feeders empty	22	3	13	12

	Hatch year	After hatch year
White-striped	17	7
Tan-striped	27	4

Table 4-2. Comparison of candidate models of capture refuelling rate of White-throated Sparrows (*Zonotrichia albicollis*) sampled during a food resource manipulation experiment while on stopover in eastern New Brunswick in 2020. Food treatment is a two-level factor indicating whether food was available or not. Also indicated is model AICc, ΔAICc, Akaike weight (w_i), marginal $R^{2,}$ and conditional R^2

Model number	**Model name**	**Model**	**AICc**	**ΔAICc**	w_i	**Marginal R^2**	**Conditional R^2**
1	Null	RI ~ trap time + bleed time + capture body mass + tarsus length + (1|site)	171.74	0.90	0.11	0.19	0.44
2	Food treatment	RI ~ trap time + bleed time + capture body mass + tarsus length + food treatment + (1|site)	172.19	1.35	0.09	0.22	0.45
3	Age	RI ~ trap time + bleed time + capture body mass + tarsus length + age class + (1|site)	171.06	0.22	0.15	0.23	0.51
4	Age class and food treatment	RI ~ trap time + bleed time + capture body mass + tarsus length + age class + food treatment + (1|site)	172.44	1.60	0.08	0.25	0.51
5	Age class by food treatment interaction	RI ~ trap time + bleed time + capture body mass + tarsus length + age class + food treatment + age class * + food treatment + (1|site)	175.41	4.57	0.02	0.25	0.51
6	Morph	RI ~ trap time + bleed time + capture body mass + tarsus length + morph + (1|site)	173.46	2.62	0.05	0.21	0.45
7	Morph and food treatment	RI ~ trap time + bleed time + capture body mass + tarsus length + morph + food treatment + (1|site)	174.05	3.21	0.03	0.23	0.46
8	Morph by food treatment interaction	RI ~ trap time + bleed time + capture body mass + tarsus length + morph + food treatment + morph * food treatment + (1|site)	172.02	1.18	0.09	0.28	0.55
9	Age class and morph	RI ~ trap time + bleed time + capture body mass + tarsus length + age class + morph + (1|site)	171.15	0.31	0.15	0.25	0.54
10	Age class, morph, and food treatment	RI ~ trap time + bleed time + capture body mass + tarsus length + age class + morph + food treatment + (1|site)	172.91	2.07	0.06	0.27	0.54
11	Morph, and age class by food treatment interaction	RI ~ trap time + bleed time + capture body mass + tarsus length + age class + morph + food treatment + age class * food treatment + (1|site)	176.03	5.19	0.01	0.27	0.53
12	**Age class and morph by food treatment interaction**	**RI ~ trap time + bleed time + capture body mass + tarsus length + age class + morph + food treatment + morph * food treatment + (1|site)**	**170.84**	**0.00**	0.17	**0.31**	**0.62**

Table 4-3. Summary table of fixed and random effects from the best model of capture refuelling index. *P*-values were obtained using the Satterthwaite approximation for degrees of freedom implemented in package lmerTest. Coefficients and standard errors have been back-scaled to original units.

Parameter	**Estimate**	**Standard error**	**Degrees of freedom**	***t*-value**	**Pr (>|t|)**
Intercept	1.10	0.57	7.49	1.91	0.09
Trap time (mins)	0.006	0.002	51.79	3.73	**< 0.01**
Bleed time (secs)	-0.001	0.0004	52.43	-2.69	**< 0.01**
Capture body mass (g)	0.16	0.07	51.75	2.57	**0.01**
Tarsus length (mm)	0.36	0.18	52.08	1.79	0.08
Food treatment (food available)	-0.21	0.31	52.33	-0.67	> 0.5
Age class (hatch year)	-0.66	0.31	52.32	-2.16	**0.04**
Morph (White-striped)	-1.09	0.38	52.46	-2.89	**< 0.01**
Morph * Food treatment	1.15	0.49	52.43	2.37	**0.02**

Random effects

Group	Variance	Model Marginal R^2	Model Conditional R^2
Site	0.53	0.31	0.62

Table 4-4. Summary table of the fixed effects from post-hoc analyses of capture refuelling rate index in the white-striped and tan-striped plumage morphs of the White-throated Sparrow sampled during autumn migration in eastern New Brunswick. *P*-values were obtained using the Satterthwaite approximation for degrees of freedom implemented in package lmerTest. Coefficients and standard errors have been back-scaled to original units.

Parameter	**Estimate**	**Standard error**	**Degrees of freedom**	***t*-value**	**Pr (>|t|)**
White-striped birds (n = 24)					
Intercept	-0.54	0.46	24	-1.170	0.25
Trap time (mins)	0.006	0.003	24	1.93	0.07
Bleed time (secs)	-0.001	0.0006	24	-2.07	**0.049**
Capture body mass (g)	0.19	0.11	24	1.78	0.09
Tarsus length (mm)	0.27	0.23	24	1.13	0.27
Food treatment (provisioned)	0.87	0.42	24	2.08	**0.048**
Age class (hatch year)	-0.23	0.42	24	-0.55	> 0.5
Tan-striped birds (n = 31)					
Intercept	1.51	0.70	8.77	2.18	0.06
Trap time (mins)	0.005	0.002	28.06	2.96	**< 0.01**
Bleed time (secs)	-0.0009	0.0005	28.80	-1.61	0.12
Capture body mass (g)	0.18	0.08	27.91	2.25	**0.03**
Tarsus length (mm)	-0.07	0.40	28.63	-0.18	> 0.5
Food treatment (provisioned)	-0.42	0.31	28.30	-1.33	0.19
Age class (hatch year)	-1.12	0.47	28.66	-2.41	**0.02**

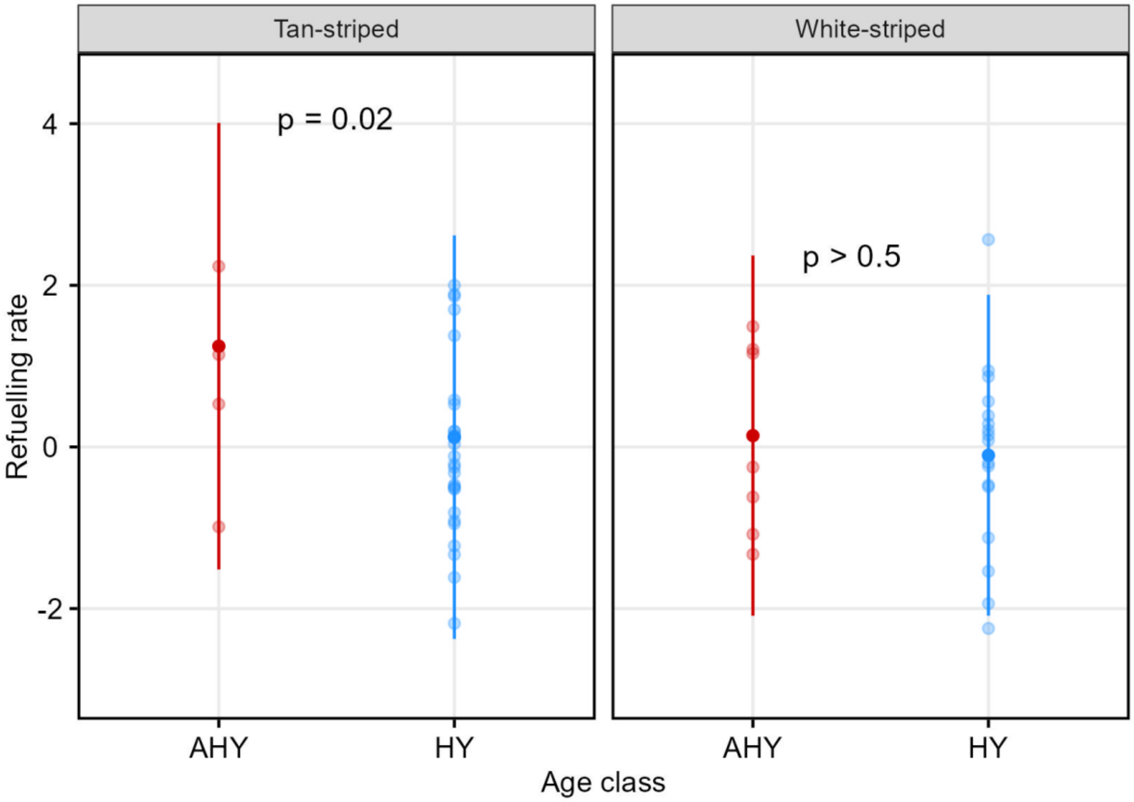


Figure 4-5. The effects of age class (AHY = after hatch year = old, HY = hatch year = young) on refuelling rate for each plumage morph of White-throated Sparrows sampled during autumn stopover in eastern New Brunswick. Also shown are 95% prediction intervals from the morph-specific post-hoc mixed-effect models of refuelling, and the raw data.

4.3.3 Movement behaviour

Distance between consecutive relocations was analysed using 65 movements from 29 tagged White-throated Sparrows. One high outlying value was identified but was retained in the final analysis as analysis results were qualitatively similar when retained. Distance between consecutive relocations ranged from 10.2 m to 407.0 m (average = 130.3 m) at intervals varying between 2 to 16 days (average = 5.3 days). Likelihood ratio tests indicated that model fit was not improved by the inclusion of food treatment (χ^2_1= 0.41, p = 0.40, Figure 4-6), local invertebrate resource availability (χ^2_1= 0.30, $p > 0.5$), nor the additive effect of food treatment and local invertebrate resource availability (χ^2_2= 2.39, p = 0.30). When assessing individual covariates, neither age class (χ^2_1= 0.01, $p > 0.5$), morph (χ^2_1= 3.73, $p = 0.053$), nor the interaction between age class and food treatment (χ^2_3= 0.75, $p > 0.5$) or morph and food treatment (χ^2_3= 5.27, $p = 0.15$) were supported over the null model. In the best (null) model, distance between successive relocations decreased ~2% for each day of stopover ($\beta = -0.01 \pm 0.007$, $t_{64.72} = -2.57$, $p = 0.01$), with a non-significant tendency to increase ~3% for each additional day between consecutive relocations ($\beta = 0.03 \pm 0.02$, $t_{63.29} = 1.88$, $p = 0.06$). The final model had a marginal r^2 of 0.12, with the random intercepts of site and individual accounting for an additional 11 percent of the variation in movement distance. Maximum displacement away from the release site was analysed for 29 individuals and was unaffected by age class, morph, or the observation day of stopover (all $p > 0.5$).

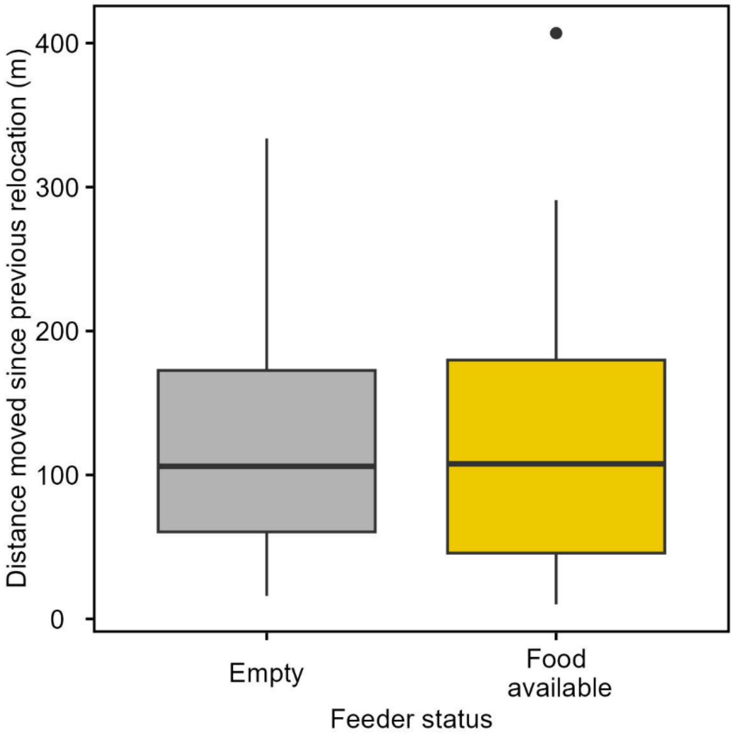


Figure 4-6. Distance between consecutive manual radio-telemetry relocations of White-throated Sparrows recorded during experimental food augmentation at stopover sites in eastern New Brunswick.

4.3.4 Stopover duration

Stopover duration was determined for 41 White-throated Sparrows, with a total of 494 stopover days. Stopover duration ranged from 1 to 30 days (median = 10 days) with all departures occurring by 23 October 2020. Likelihood ratio tests indicated that the null model fit was not improved by estimated invertebrate abundance (χ^2_1= 2.19, $p = 0.14$), or residual refuelling rate (χ^2_1= 0.26, $p > 0.5$). The best model of departure hazard included all null model covariates and plumage morph, (model 6, Table 4-2), but this model had only marginally improved fit compared to the more parsimonious null model. In the best model, stopover departure hazard increased 9% for every additional day of year ($\beta = 0.09 \pm 0.02$, $z = 4.39$, $p < 0.01$) and increased 11% for every additional m/s of tailwind assistance ($\beta = 0.10 \pm 0.03$, $z = 3.33$, $p < 0.01$). Wind assistance on nights with at least one departure was -0.72 ± 5.01 m*s^{-1} SD (range: -9.2 to 15.3 m*s^{-1}), indicating departure primarily occurred on nights with low headwind to tailwind conditions. Comparing wind conditions between night with at least one departure to those without across all sites, surface level wind speeds did not differ (ANOVA: f^1_{127}= 0.61, $p = 0.43$), but wind bearing significantly differed (Circular ANOVA: f^1_{127}= 10.53, $p < 0.01$), blowing in a more north by westerly bearing on departure night (circular mean ± circular SD = 343.5° ± 86.1°, range: 6.0° – 357.0°) compared to a more north easterly bearing on non-departure nights (50.3° ± 83.8°, range: 1° – 359.0°, Figure 4-7). Although included in the best model, departure hazard was not significantly affected by tarsus length, capture mass, or plumage morph (all $p > 0.10$).

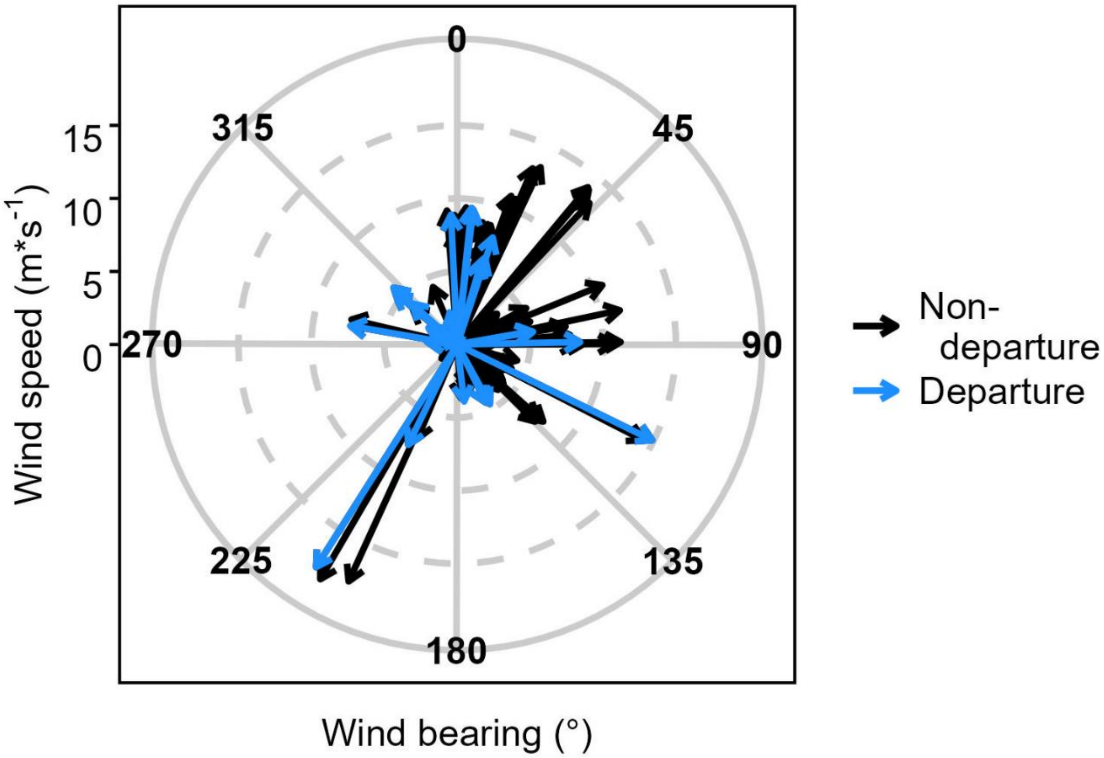


Figure 4-7. Surface level wind vectors at 21:00 hrs AST during the fall of 2020 at three stopover sites in eastern New Brunswick. Colour delineates values from nights with at least one departure (blue) and nights with no departures (black) of radio tagged White-throated Sparrows.

Table 4-5. Comparison of candidate models of stopover departure hazard using 494 stopover days from 41 White-throated Sparrows captured during a resource manipulation experiment while on autumn stopover in eastern New Brunswick in 2020. Also indicated are models AICc and ΔAICc relative to the best fit model, and Akaike weight (w_i).

Model number	Name	Model	AICc	ΔAICc	w_i
1	Null	~Day of year + Tailwind + Capture mass + Tarsus length	207.04	0.08	0.16
2	Food treatment	~Day of year + Tailwind + Capture mass + Tarsus length + Food treatment	207.55	0.60	0.13
3	Age	~Day of year + Tailwind + Capture mass + Tarsus length s + Age class	209.08	2.12	0.06
4	Age class and food treatment	~Day of year + Tailwind + Capture mass + Tarsus length + Age class + Food treatment	209.59	2.63	0.05
5	Age class by food treatment	~Day of year + Tailwind + Capture mass + Tarsus length + Age class + Food treatment + Age class * Food treatment	211.66	4.70	0.02
6	**Morph**	**~Day of year + Tailwind + Capture mass + Tarsus length + Morph**	**206.96**	**0.00**	**0.17**
7	Morph and food treatment	~Day of year + Tailwind + Capture mass + Tarsus length + Morph + Food treatment	207.17	0.21	0.15
8	Morph by food treatment	~Day of year + Tailwind + Capture mass + Tarsus length + Morph + Food treatment + Morph * Food treatment	208.89	1.93	0.07
9	Age class and morph	~Day of year + Tailwind + Capture mass + Tarsus length + Age class + Morph	208.76	1.80	0.07
10	Age class, morph, and food treatment	~Day of year + Tailwind + Capture mass + Tarsus length + Age class + Morph + Food treatment	208.67	1.71	0.07
11	Morph, and age class by food treatment interaction	~Day of year + Tailwind + Capture mass + Tarsus length + Age class + Morph + Food treatment + Age class * Food treatment	210.65	3.69	0.03
12	Age class, and morph by food treatment interaction	~Day of year + Tailwind + Capture mass + Tarsus length + Age class + Morph + Food treatment + Morph * Food treatment	210.57	3.61	0.03

All continuous variables were centered and scaled prior to analysis. Tailwind and food treatment were modeled as time-vary covariates across each day of stopover.

4.4 Discussion

I used feeding stations to experimentally test how food availability and individual characteristics shaped refuelling and behaviour in White-throated Sparrows during autumn migratory stopover in eastern New Brunswick. The influence of experimentally augmented food availability on refuelling differed between morph and age classes, but no effect of food treatment was observed on the local movement behaviour and stopover duration. Instead, local movement generally decreased the longer birds were present, and stopover duration was independent of food availability or refuelling. Together, these results illustrate how local food availability can moderate class-specific patterns of refuelling but suggest that the duration of stopover in autumn migrating White-throated Sparrows is primarily governed by exogenous factors.

4.4.1 Refuelling rate

Experimentally providing food at stopover sites yielded greater refuelling in birds of the white-striped morph of the White-throated Sparrow, but this effect was not observed in tan-striped birds. This interaction is consistent with the hypothesis that class-based differences in refuelling are moderated by the availability of resources in the environment, however, it is counter to my expectation that differences between classes would be more pronounced when resources were limited. In the context of the White-throated Sparrow plumage morphs, the greater competitive ability or social dominance exhibited by white-striped birds may have enabled them to capitalise on the food provided to increase refuelling rate. This may have been accentuated by the method used to elevate resources, with feeding stations representing localised and abundant patches of food that could be used and defended by more dominant white striped individuals. When refuelling was analysed separately in each morph, no difference in refuelling was found between age classes within white-striped birds, but younger hatch-year tan-striped birds had a lower refuelling rate compared to older after-hatch-year tan-striped birds. While largely speculative, this pattern may have arisen if the food treatment primarily increased the refuelling rate of hatch-year white-striped birds. This would both reduce the difference in refuelling between age classes in white-striped birds and increase the average refuelling rate among white-striped birds compared to tan-striped birds when food was available. Caution is likely warranted in the interpretation of these results due to the limited sample sizes and group-size imbalance, which precluded a robust test of more complex interactions between age class, morph class, and feeder status in this study.

Positive relationships between resource availability and migrant abundance have been reported by previous studies of songbird stopover (e.g. Smith et al. 2007) (Chapter 3), yet the number of sparrows captured did not increase when additional food was provided in this study. This may be due to the localised nature of the supplemental food provided at the feeding stations, representing a change in resource availability at a magnitude and spatial resolution too fine to elicit a site-scale change in sparrow abundance. Furthermore, as greater refuelling rate was found primarily in white-striped birds when food was provided, use of the supplemental food resources by these individuals may have precluded additional birds from using the habitat. Given that sparrow catch did not differ between periods when feeding stations were provisioned and empty, this finding also suggests that the analysis of refuelling rate was not confounded by an increased number of sparrows using the sites when food availability was experimentally augmented.

Variation in refuelling rate can also arise independent of invertebrate food availability. For example, predation risk can shape fuel deposition rate in songbirds (Schmaljohann and Dierschke 2005). Barring selective hunting at provisioned feeding stations by predators, the blocked treatment design and multiple feeding stations in this study was intended to control for spatiotemporal variability in predation risk across the season. Variation in refuelling rate could also be attributed to site level differences in the availability of fruit or naturally available seeds resources, representing a likely source of variation in refuelling rate attributed to site. Methodological factors can also result in variation in metabolite-based assessment of refuelling. Birds captured later in the day tend to have greater refuelling rate owing to the shift in plasma metabolite profile from overnight fasting to diurnal feeding. The interval between capture and blood collection can also drive differences in metabolite profile due to the rapid shift from feeding to capture-induced fasting (Zajac et al. 2006). High body mass at capture is also associated with greater capture refuelling rate (Guglielmo et al. 2005), although causality in this relationship is difficult to assign.

4.4.2 Local movement

Local movement distance was not affected by food addition nor invertebrate abundance, and was instead characterised by decreasing movement distance across stopover. Similar decreases in daily movement have been observed previously in the white-striped morph of the White-throated Sparrow (Beauchamp et al. 2020) and in other songbird species tracked during migratory stopover (Cohen et al. 2012). Decreased movement may stem from a reduction in foraging related movements as migrants achieve an increasingly greater fuel load across the stopover period. It may also reflect a pattern of searching and settling into a localised patch or more favourable habitat while at a stopover site (Seewagen et al. 2010, Slager et al. 2015). In the current study, these movement patterns did not differ between age or morphs classes. Differences in stopover movement between white-striped and tan-striped birds have been observed during spring migration (Beauchamp et al. 2020), and the contrast between these studies perhaps could be attributed to seasonal differences in behaviour. Movement can also differ between stopover landscapes (Cohen et al. 2012, Slager et al. 2015), and differences in habitat characteristics or resource distribution between the New Brunswick and Ontario study sites may have elicited different morph-specific movement behaviours. Further evaluation of morph-specific movement patterns across different habitats and seasons may help resolve this discrepancy.

4.4.3 Departure hazard

Stopover departure hazard was not greater when food availability was augmented, and departure hazard was also independent of local invertebrate abundance and refuelling rate. Together, these finding suggest that resource availability, and the rate at which migrants are able to refuel using these resources, are not major determinants of stopover duration in White-throated Sparrows migrating through eastern New Brunswick. One caveat to this conclusion is that fruit availability was not directly considered in the study. Previous research has used date as a proxy for the availability of fruit resources, which may be more abundant earlier in the season and deplete as autumn migration progresses (Smith and McWilliams 2014). The observed increase in departure hazard with date may then reflect a response to deteriorating fuelling conditions. On the other hand, departure hazard was independent of capture refuelling rate and refuelling rate was not affected by capture date. Together, these results suggest departure hazard is not affected by variation in fuelling conditions associated with a seasonal decline in fruit availability. Instead, the increased departure hazard may represent a behavioural response to the increasing time constraints or worsening environmental conditions unrelated to resource availability later in the season. This pattern has been observed previously in songbirds during both autumn (Chapter 2), (Ktitorov et al. 2010, Andueza et al. 2013) and spring migration (Dierschke and Delingat 2001, Beauchamp et al. 2020, Packmor et al. 2020).

Stopover departure hazard did not differ by morph or age class, and class-specific departure hazard was not altered by the addition of food. Instead, departure was primarily governed by the availability of tailwinds and by condition at capture. The similarity in stopover duration between classes echoes other stopover studies conducted on White-throated Sparrows (Beauchamp et al. 2020) and reinforces that any behaviour differences between age and morph classes do not inherently yield difference in stopover duration. These patterns were consistent despite the manipulation of food resources across the stopover period and the observed class-specific effect of the food manipulation on capture refuelling rate. As such, the greater refuelling of white-striped birds enabled by food augmentation did not directly translate to decreased stopover duration.

Consistent with previous studies of migratory departure behaviour in birds, departure hazard significantly increased with nocturnal tailwinds assistance (Åkesson and Hedenström 2000, Dossman et al. 2016, Morbey et al. 2018, Chapter 2,3). Flying with tailwinds can yield energetic saving directly through the assistance provided by following winds or from the reduced need for correct for drift resulting from crosswinds (Alerstam and Lindström 1990, Liechti 2006), representing an important resource that migrants can exploit to reduce the cost of migratory flight. Given that the average tailwind assistance was slightly negative for birds departing in this study, migrants may have been opting to "make the best of bad situation" by departing into lighter headwinds relative to other nights. Similar behaviour is predicted under situations where favourable wind conditions are relatively rare (Weber et al. 1998). Furthermore, in regions such as eastern New Brunswick where habitat to refuel is widespread, periods of energetically favourable wind conditions may be the more rare resource compared to spatial variation in habitat availability or local food resources. In this context, migrants may opt to depart when winds are most favourable regardless of local food availability and refuelling rate in order to maximise the flight range possible from current fuel stores. Finally, the use of more easterly winds on departure nights relative to the more westerly winds on non-departure nights may prevent crosswind drift towards the east, limiting the risk of being blown out over the ocean as birds travel southwest along the Atlantic coast.

One weakness of this study is that little direct individual level information on feeding station use could be obtained, and it is uncertain how any temporal variation in the use of feeding station may have contributed to the behaviour patterns observed. Future studies following in a similar framework could incorporate the use of camera traps and short-range radio receivers to further observe how feeding stations are used by untagged and tagged individuals. Integration of automated weighing stations into this setup would also provide data on fattening rates and estimates of departure fuel loads, enabling further inference regarding the interrelation between resource availability, plasma metabolite concentration at capture, fat deposition across the stopover period, and potential flight durations post-departure based on departure fuel load. Experimental suppression of local invertebrate abundance (e.g. Brown and Sherry 2006) could also be used to create a greater gradient of food availability across which to assess refuelling and behaviour. Altering the spatial and temporal aspects of the food augmentation treatment may also yield insight into potential behavioural mechanisms underlying the class-specific effect on refuelling. For example, diffuse augmentation of food across the study site may provide increased opportunities for individuals to access resources compared to the localised food treatment as in this study. This could yield a different pattern of class-specific refuelling if resources are easier to locate or harder for dominant individuals to defend.

This study manipulated food availability using feeding stations, finding class-specific effects on capture refuelling rate but finding little impact on behaviour post-capture. Moderation of the impact of spatiotemporal variation in food availability on stopover refuelling by individual characteristics in this study highlights the complexity of relationship between migrants and their stopover environment. Although local effects on behaviour were minimal, cumulative impacts of resource availability during stopover could have implication for shaping patterns of subsequent movement or successful migration post-departure, highlighting the need to further explore the complexity between, resources, refuelling, and behaviour.

4.5 References

Agostinelli, C., and U. Lund (2022). R package “circular”: Circular Statistics. [Online.] Available at https://r-forge.r-project.org/projects/circular/.

Agriculture and Agri-food Canada (2023). Annual Crop Inventory 2021 - Pre-packaged GeoTIF files. [Online.] Available at https://agriculture.canada.ca/atlas/data_donnees/annualCropInventory/data_donnees/tif/2021/.

Åkesson, S., and A. Hedenström (2000). Wind selectivity of migratory flight departures in birds. Behavioral Ecology and Sociobiology 47:140–144.

Alerstam, T., and Å. Lindström (1990). Optimal bird migration: the relative importance of time, energy, and safety. In Bird Migration. Springer-Verlag, New-York, NY, USA, pp. 331–351.

Andueza, M., J. Arizaga, E. J. Belda, and E. Barba (2013). The role of extrinsic and intrinsic factors on the departure decisions of a long-distance migratory passerine. Ardeola 60:59–72.

Bates, D. M., M. Maechler, and B. Bolker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67.

Beauchamp, A. T., C. G. Guglielmo, and Y. E. Morbey (2020). Stopover refuelling, movement and departure decisions in the White-throated Sparrow: The influence of intrinsic and extrinsic factors during spring migration. Journal of Animal Ecology 89:2553–2566.

Bibby, C. J., and R. E. Green (1983). Food and fattening of migrating Warblers in some French Marshlands. Ringing & Migration 4:175–184.

Birds Canada (2022). motus: Fetch and use data from the Motus Wildlife Tracking System. [Online.] Available at https://motusWTS.github.io/motus.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Machler, and B. M. Bolker (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R journal 9:378–400.

Brown, D. R., and T. W. Sherry (2006). Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149:22–32.

Brown, J. M., B. J. McCabe, L. V. Kennedy, and C. G. Guglielmo (2014). Genetically-based behavioural morph affects stopover refuelling performance in White-throated Sparrows *Zonotrichia albicollis*. Journal of Avian Biology 45:522–527.

Caldwell, S. S. A., and A. M. Mills (2006). Comparative spring migration arrival dates in the two morphs of White-throated Sparrow. The Wilson Journal of Ornithology 118:326–332.

Cohen, E. B., F. R. Moore, and R. A. Fischer (2012). Experimental evidence for the interplay of exogenous and endogenous factors on the movement ecology of a migrating songbird. PLOS ONE 7:e41818.

Dänhardt, J., and Å. Lindström (2001). Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Animal Behaviour 62:235–243.

Dierschke, V., and J. Delingat (2001). Stopover behaviour and departure decision of Northern Wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535–545.

DMTI Spatial Inc. (2014a). National Water (WAT). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2014b). Hydrography - Regions (HYR). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2014c). Route File (RTE). [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017a). Water Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017b). Major Roads Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2017c). Contour Line. [computer file]. Markham, Ontario, Canada.

DMTI Spatial Inc. (2021). Administrative Area Region. [computer file]. Markham, Ontario, Canada.

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. Behavioral Ecology 27:567–574.

Fransson, T. (1998). A feeding experiment on migratory fuelling in Whitethroats, *Sylvia communis*. Animal Behaviour 55:153–162.

Grambsch, P. M., and T. Therneau (1994). Proportional hazards tests and diagnostics based on weighted residuals. Biometrika 81:515–526.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson (1998). A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Guglielmo, C. G., D. J. Cerasale, and C. Eldermire (2005). A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological and Biochemical Zoology 78:116–125.

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Hedenström, A., and T. Alerstam (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Hixon, M. A., F. L. Carpenter, and D. C. Paton (1983). Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. The American Naturalist 122:366–391.

Hoh, C. M., S. S. Pagano, and C. J. Norment (2018). Spatial variation in White-throated Sparrow (*Zonotrichia albicollis*) refueling rate near a migratory barrier. The Wilson Journal of Ornithology 130:891–901.

Kaiser, A. (1993). A new multi-category classification of subcutaneous fat deposits of songbirds. Journal of Field Ornithology 64:246–255.

Kelly, J. F., L. S. DeLay, D. M. Finch, and C. Blem (2002). Density-dependent mass gain by Wilson’s Warblers during stopover. The Auk 119:210–213.

Kemp, M. U., E. Emiel van Loon, J. Shamoun-Baranes, and W. Bouten (2012). RNCEP: global weather and climate data at your fingertips. Methods in Ecology and Evolution 3:65–70.

Klinner, T., J. Buddemeier, F. Bairlein, and H. Schmaljohann (2020). Decision-making in migratory birds at stopover: an interplay of energy stores and feeding conditions. Behavioral Ecology and Sociobiology 74:10.

Knapton, R. W., R. V. Cartar, and J. B. Falls (1984). A comparison of breeding ecology and reproductive success between morphs of the White-throated Sparrow. The Wilson Bulletin 96:60–71.

Kopachena, J. G., and J. B. Falls (1993). Aggressive performance as a behavioral correlate of plumage polymorphism in the White-throated Sparrow (*Zonotrichia albicollis*). Behaviour 124:249–266.

Ktitorov, P., A. Tsvey, and A. Mukhin (2010). The good and the bad stopover: behaviours of migrant Reed Warblers at two contrasting sites. Behavioral Ecology and Sociobiology 64:1135–1143.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen (2017). lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1–26.

Leather, S. R. (2005). Insect Sampling in Forest Ecosystems. Blackwell Publishing, Malden, MA, USA.

Liechti, F. (2006). Birds: blowin' by the wind? Journal of Ornithology 147:202–211.

Lindström, A., and T. Alerstam (1992). Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. The American Naturalist 140:477–491.

Lukas, J., and V. Stejskal (2003). Computer-based image analysis to estimate the area of a sticky trap occupied or contaminated by pests. Plant Protection Science 39:52–60.

Macdade, L. S., P. G. Rodewald, and K. A. Hatch (2011). Contribution of emergent aquatic insects to refueling in spring migrant songbirds. The Auk 128:127–137.

Mitchell, G. W., B. K. Woodworth, P. D. Taylor, and D. R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Movement Ecology 3:19.

Moore, F. R., S. Mabey, and M. Woodrey (2003). Priority access to food in migratory birds: age, sex and motivational asymmetries. In Avian Migration (P. D. P. Berthold, P. D. E. Gwinner and E. Sonnenschein, Editors). Springer-Verlag, New-York, NY, USA, pp. 281–292.

Morbey, Y. E., C. G. Guglielmo, P. D. Taylor, I. Maggini, J. Deakin, S. A. Mackenzie, J. M. Brown, L. Zhao, and D. Stephens (2018). Evaluation of sex differences in the stopover behavior and post departure movements of wood-warblers. Behavioral Ecology 29:117–127.

Packmor, F., T. Klinner, B. K. Woodworth, C. Eikenaar, and H. Schmaljohann (2020). Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? Movement Ecology 8:6.

Pyle, P. (1997). Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA, USA.

R Core Team (2021). R: a language and environment for statistical computing. [Online.] Available at URL https://www.R-project.org/.

Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Rasband, W. S. (2018). ImageJ. [Online.] Available at https://imagej.nih.gov/ij/.

Schaub, M., and L. Jenni (2000). Fuel deposition of three passerine bird species along the migration route. Oecologia 122:306–317.

Schmaljohann, H., and V. Dierschke (2005). Optimal bird migration and predation risk: a field experiment with Northern Wheatears *Oenanthe oenanthe*. Journal of Animal Ecology 74:131–138.

Seewagen, C. L., C. G. Guglielmo, and Y. E. Morbey (2013). Stopover refueling rate underlies protandry and seasonal variation in migration timing of songbirds. Behavioral Ecology 24:634–642.

Seewagen, C. L., E. J. Slayton, and C. G. Guglielmo (2010). Passerine migrant stopover duration and spatial behaviour at an urban stopover site. Acta Oecologica 36:484–492.

Slager, D. L., P. G. Rodewald, and P. J. Heglund (2015). Experimental effects of habitat type on the movement ecology and stopover duration of spring migrant Northern Waterthrushes (*Parkesia noveboracensis*). Behavioral Ecology and Sociobiology 69:1809–1819.

Smith, A. D., and S. R. McWilliams (2014). What to do when stopping over: behavioral decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions. Behavioral Ecology 25:1423–1435.

Smith, R. J., F. R. Moore, and C. A. May (2007). Stopover habitat along the shoreline of northern Lake Huron, Michigan: emergent aquatic insects as a food resource for spring migrating landbirds. The Auk 124:107–121.

Taylor, P. D., T. Crewe, S. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. Francis, C. Guglielmo, D. Hamilton, R. Holberton, et al. (2017). The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:8.

Therneau, T. (2021). A Package for Survival Analysis in R. [Online.] Available at https://CRAN.R-project.org/package=survival.

Therneau, T. (2022). coxme: Mixed Effects Cox Models. [Online.] Available at https://CRAN.R-project.org/package=coxme.

Weber, T. P., T. Alerstam, and A. Hedenström (1998). Stopover decisions under wind influence. Journal of Avian Biology 29:552–560.

White, G. C., and R. A. Garrott (2012). Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego, California, USA.

Wood, S. (2012). mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness estimation. [Online.] Available at https://researchportal.bath.ac.uk/en/publications/mgcv-mixed-gam-computation-vehicle-with-gcvaicreml-smoothness-est.

Woodrey, M. (2000). Age-dependent aspects of stopover biology of passerine migrants. Studies in Avian Biology 20:43–52.

Zajac, R., D. J. Cerasale, and C. G. Guglielmo (2006). The rapid response of plasma metabolites to changes in feeding rate in a small passerine *Wilsonia pusilla*. Journal of Avian Biology 37:405–408.

Chapter 5

5 Flock together? The effects of social information from overflying migrants on the nocturnal departure time of three songbird species.

5.1 Introduction

For nocturnally migrating birds, evening departure timing defines potential flight duration, and can govern the overall speed of migration in conjunction with flight speed and the amount of time needed to rebuild energy stores between migratory flights. By departing earlier in the night, migrants maximise both the time available to fly and potential travel distance before ending flight at sunrise. If repeated across the migratory journey, travelling further each night can reduce the number of flights and inter-flight stopovers needed to reach migratory destinations. As a result, earlier nocturnal departure timing can contribute to greater overall migration speed, reducing exposure to risks encountered en route (e.g. disease, predation), and influencing arrival timing, reproductive success, and survival at the migratory destination (Smith and Moore 2005).

Despite the potential benefits of earlier evening departure, considerable variation in departure timing has been noted in migratory passerines (e.g. Åkesson et al. 1996, Schmaljohann et al. 2013, Smolinsky et al. 2013, Morbey et al. 2018, Beauchamp et al. 2020). Changes in evening locomotor activity prior to sunset suggest that the decisions to depart from a stopover site occurs prior to dusk (Morbey et al. 2020), but the factors dictating the exact timing of departure within a night remain less certain (reviewed by Müller et al. 2016). Fuel load is one of the best-understood intrinsic factors influencing nocturnal departure time, with greater fuel load resulting in earlier departure in free living birds (Schmaljohann and Naef-Daenzer 2011, Packmor et al. 2020). Changes to circadian rhythm occur in birds during migration to permit nocturnal activity (Gwinner 1996), and consistency in the timing of migratory restlessness in the absence of entraining cues suggest departure timing may be under circadian control (Coppack et al. 2008). Weather conditions are a well understood extrinsic factor that influences migratory behaviour (Richardson 1978, Liechti 2006, Nilsson et al. 2019). On a day-to-day basis, migrants are more likely to depart on nights with environmental conditions favourable to flight: when energetically favourable tailwinds are present, with minimal cloud cover, and in the absence of precipitation (Erni et al. 2002, Tsvey et al. 2007, Beauchamp et al. 2020). These factors also act within a night to govern the timing of departure, with departure delayed by conditions such as tailwinds and high cloud cover (Packmor et al. 2020). Other extrinsic factors such as impending long travel distances, barrier crossings (Müller et al. 2018), the date, or total length of night (Eikenaar et al. 2016, Sjöberg et al. 2017) can also influence the timing of nocturnal departure.

Intra and inter-specific social information may also influence departure timing, both directly as an indicator of the behaviour of other migrants or by supplementing individually acquired information on environmental conditions (Dolnik and Blyumental 1967). Songbirds are often gregarious during the migratory period, foraging collectively while on stopover and travelling in diffuse flocks. Travelling in groups can decrease navigational errors (Simons 2004), energy expenditure (Weimerskirch et al. 2001), and increase individual safety from predators (Cresswell 1994), it may also facilitate the rapid formation of foraging flocks when birds cease migratory flight together (Piersma et al. 1990). Using social information to maintain or foster a cohesive flock during the initial period of flight may be critical to obtaining the benefits from travelling with other migrants. By supplementing individually acquired information on the behaviour of other migrants, individuals can also make more rapid and accurate assessments of dynamic environmental conditions encountered during stopover (Rafacz and Templeton 2003). Endogenous factors such as migration distance and energetic condition may modify the value and capacity of an individual to use this information, resulting in differential use of social information both inter and intra-specifically (Németh and Moore 2014). Differences in experience tied to the age of a migrant can contribute to behavioural differences found between young and old migrants. Inexperienced birds are more likely to make navigational errors (Sandberg et al. 1991), are less selective of energetically favourable tailwinds (Mitchell et al. 2015), and tend to depart from stopover sites later in the night compared to adults (Schmaljohann et al. 2018). Integration of information from groups of conspecifics in addition to primary evaluation of environmental conditions may result in improved outcomes (e.g. Simons 2004), particularly if an individual's capacity to assess conditions is limited by a lack of experience.

Audio cues are likely a primary modality used to convey social information among passerine migrants, especially during periods of darkness when vison may be limited. Many species of migratory songbird utter distinct short calls while engaged in nocturnal flight, although some species can produce these calls when engaging in other activities such as foraging (Farnsworth 2005). These nocturnal flight calls (NFCs) are believed to assist in flock cohesion during travel (Farnsworth 2005) and the location of a suitable stopover sites (Chernetsov 2006, Alessi et al. 2010). NFCs can also stimulate nocturnal migratory behaviour in conspecifics. NFCs produced by captive Bobolink (*Dolichonyx oryzivorus*) undergoing nocturnal migratory restlessness elicited a mutual response in other caged conspecifics (Hamilton 1962), and playbacks of recorded NFCs induced an immediate, calling, wing-whirring, and fly-up response. Less is understood about the role of visual cues in conveying social information. Captive migrants often adopt a stereotypical "head-up" posture during migratory restlessness, and the pre-dusk "head scanning" behaviour attributed to the calibration of the magnetic compass (Mouritsen et al. 2004) could also serve to collect visual and audio information prior to departure. What affect audio and visual social information has on the departure timing of migrants remains uncertain.

Radar and acoustic monitoring data have been used for over half a century to monitor and study avian migration. Powerful weather surveillance radars can provide regional scale assessments of migrant activity (Buler et al. 2007), however, they often lack the specificity to identify individual bird targets. Radar units co-opted from maritime applications possess the resolution to detect individual birds over a shorter range, providing an ideal tool to monitor airborne migrant activity at the local scale and allowing for more precise measurement of the number of birds passing within detection range. Recording of NFCs using sensitive microphones has been used to quantify avian migration, with positive association between regional audio recordings and both radar activity (Farnsworth et al. 2004, but see Horton et al. 2015) and mist-net captures (Sanders and Mennill 2014).

The purpose of this study was to describe the departure behaviour of adult and juvenile songbirds in relation to social information and meteorological conditions encountered on their departure night, testing the hypothesis that social information from volant migrants acts as a cue for departure from migratory stopover. I expected that departure timing would be strongly associated with passage of migrants over a stopover site, and that the sensitivity to social information would differ between age classes due to experience using environmental and social cues for departure. As the modality used to convey social information between migrants is not known, I also sought to compare the effects of acoustic social information in the form of NFCs to visual social information available from the passage of migrants overhead on migratory departure timing. I also tested for the effect of local wind conditions on departure behaviour to contrast the influence of social and environmental cues on departure behaviour. Following previous work, I expected migrants to depart earlier on nights with weather condition favorable to migratory flight, and that juvenile migrants would be less selective of weather conditions.

5.2 Methods

5.2.1 Radar measurement of migrant passage

Nocturnal radar and audio data were collected in the fall of the 2020 and 2021 as part of regional migration monitoring related to wind energy development around Albert County, New Brunswick, Canada (Appendix C). Briefly, multiple Furuno Electric Co. 8252 marine radar units were operated from August through November in 2020 and in September and October of 2021. Units operated in the microwave X-band (9410 ± 30 MHz, 25 kW) with a 6-foot XN13A open-array antenna, running in short pulse mode (2100 pulses per second) at 24 rpm. Units were mounted on a custom support framework in a vertical orientation to monitor the altitude of targets, with an approximate detection range of 4.6 km with a beam width of ~22° in the horizontal plane and ~1.35° in the vertical plane (Appendix D). Prior to deployment, the radar was calibrated while in a horizontal orientation using targets at a known distance. The radar image was digitized at 4.5 m range resolution with an azimuth resolution of 1.35° using a DSPNOR ScanStreamer (Bergen, Norway). Data were saved onto external hard drives and later analyzed using Cognitive Marine Tracker (CMT) radar analysis software, from the

Cognitive Radar Corporation (Waterloo, Ontario). Periods of rain were identified through visual inspection of plotted radar returns. Targets were filtered from background noise based on target size and return signal intensity (dB) corrected for distance. A scaled signal intensity threshold of 12 *dB* was determined by correlating radar return values and NFCs, excluding hours near dusk and dawn to exclude ground calling birds. Detected targets with a scaled intensity below the threshold were excluded to avoid contamination of measured activity by non-avian targets (insect). From this filtered data, a column of air at a distance of 300 – 320 m from the radar unit and approximately 70 – 630 m in altitude was selected to monitor the passage of migrants. Detections were filtered to within this column using target azimuth (in a vertical plane given the orientation of the radar unit) and target distance.

5.2.2 Acoustic monitoring of night flight calls

Acoustic data were collected in proximity to the radar units using either Old Bird 21c microphones (http://www.oldbird.org/) or AudioMoth audio recorder units (ARU's) (https://www.openacousticdevices.info). All acoustic data were either sampled or resampled to 22 kilohertz (kHz) (encompassing the frequency range where most NFCs occur), then subset to encompass only the period of time between the end of evening civil twilight and the beginning of morning civil twilight. It is during this period that birds make NFCs while actively migrating (Evans 2005). All acoustic files were processed using a custom-built artificial intelligence NFC detection model developed by Dr. Justin Kitzes at the University of Pittsburgh using Open Sound Scape python package. The model was trained using NFCs originally identified by John Kearney of John F. Kearney & Associates (see a summary of these data at nocturnalflightcalls.com). The NFC model assigns a 'score' to each species or species group (Appendix E), which is then related to the probability that a specific acoustic detection is that species group. NFCs detected by the model were sampled for validation. Each NFC was assigned to one of three categories related to the time of night, either 'Dusk', 'Dawn' or 'Night'. NFCs categorized as 'Dusk' and 'Dawn' were detected during 30 min from the beginning or end of the civil twilight period, respectively. For validation, up to 100 NFCs were randomly selected (weighted by score) from the Dusk/Dawn period, and up to 200 calls from the Night period. These calls were visually assessed (by examining a spectrogram) and/or listened to by an expert (Tabanid Consulting Ltd.) to verify the identity of the call or call group. A statistical model was then fit for each species/species group. A binomial model, with the response being valid/not valid was fit to model score and time of night, with night as a random effect. These models were then used to predict the probability that any given call was of a given species or species group. Detections with a score lower than 2 (i.e. a low probability of being assigned to a species/species group) were then omitted from the dataset to classify each recorded NFC, and to prevent the inclusion of false detections.

5.2.3 Bird capture and measurement of departure timing

Bird capture occurred at four sites in eastern New Brunswick. Two sites were located coastally near Waterside (45°37’30.4” N 64°47'30.47"W) (WAT) and Mary’s Point (45°43'28.07"N 64°40'31.16"W) (MPT). The other two sites were located approximately 25 km inland at the Mapleton Acadian Forest Nature Preserve (45°49'19.94"N 65° 3'33.49"W) (MAF) and the Community Forest International Whaelghinbran Farm (45°44'4.88"N 65°18'2.41"W) (CFI). Sites were visited in a rotation, with captures occurring every four days. Mist nets were used to passively capture migratory birds, targeting three species for radio tagging (White-throated Sparrows [*Zonotrichia albicollis*], Hermit Thrush [*Catharus guttatus*], and Swainson’s Thrush [*Catharus ustulatus*]). All birds were banded with the appropriate size U.S. Fish and Wildlife Service /Canadian Wildlife Service aluminum leg band, and wing chord, tarsus length, and mass were measured. Age was determined following Pyle (1997). All work was conducted under the banding permit 10911C issued by Environment and Climate Change Canada with approval by the University of Western Ontario’s Animal Care Committee (AUP # 2017-160).

Nocturnal departure timing was determined using automated radio telemetry. Digitally encoded radio transmitter (model NTQB, Lotek Wireless, www.lotekwirelss.ca) were affixed to birds prior to release. Tags weighed approximately 0.29g to 0.35g depending on specific tag model, and were attached using a leg-loop harness designed to drop-off after several months (Rappole and Tipton 1991). Each study site featured an automated radio receiver station, part of the Motus Wildlife Tracking System (motus.org). Detection of radio signals from tagged individuals on the receiver indicated the presence of a bird, with the time of signal loss indicating departure time. Data was downloaded using the *motus* package (Birds Canada 2022) for R Version 4.1.2 (R Core Team 2021). Detections were inspected and cleaned following methods outlined in Birds Canada (2022). Only birds with nocturnal departures occurring from the capture site were included in the analysis.

5.2.4 Statistical analyses

I applied survival analysis in a Cox Proportional Hazard framework to evaluate how social information and environmental conditions influenced the timing of departure within the departure night of an individual. In this framework, covariates that increase the hazard of a departure event are associated with earlier departure within the night. Conversely, covariates that decrease the hazard for departure within a departure night are associated with later departure. Cox Proportional Hazard models can be extended to include covariates which vary dynamically among the time intervals within an encounter history, and I leveraged this to test how within-night variation in migrant passage (measured using radar), NFC intensity (measured with ARU’s), and wind conditions affected departure hazard. The hazard for departure was modelled across consecutive fixed-length intervals within the departure night, with separate repeated analyses of departure hazard conducted using intervals of 10, 20, 30, and 40 minutes in duration to explore the sensitivity of the analysis to the interval length. The start time of each interval was assigned as an increment of the interval duration (e.g. 10 minute), with the first interval of the departure night being the first interval following the end of local evening civil twilight. In each interval, migrant passage was determined as the sum of targets detected by the radar unit closest to the stopover site during the interval. During periods of precipitation, the sum of the targets detected during the precipitation-free portion of the interval was used. If an entire interval was contaminated by rain, migrant passage was assigned a value of zero assuming that migratory activity had generally ceased during prolonged periods of precipitation (Richardson 1978, Erni et al. 2002) or that volant migrants had increased in altitude to overfly clouds, limiting any exchanging of social information. Intervals with missing radar data due to equipment malfunction were identified using the ground return signal, which provided a positive method to identify periods where the unit was operating but no airborne targets were detected. Any periods where the radar unit was not operating were excluded from the analysis, resulting in instances of left, right, and interval censoring among individuals in the dataset. NFC count was included as the sum of all passerine NFCs recorded by the local ARU within the interval.

Wind data was obtained from the NCEP/DOE Reanalysis 2 data set (http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis2.html) which provides meteorological data four times each day at 2.5° x 2.5° spatial resolution. Wind speed in $m \cdot s^{-1}$ in the easterly and northerly direction was extracted using the *RNCEP* package in R (Kemp et al. 2012), and interpolated for an individual's stopover site using the function NCEP.interp with the option for linear interpolation. Surface wind was interpolated at the start time of each interval within an individual's departure night. Tailwind assistance was calculated as $V_w * \cos(\beta)$, where V_w is wind speed ($m \cdot s^{-1}$) and β is the difference between the average flight bearing from all recorded migratory departures (244°) and wind direction. Surface wind speed was selected as this is the wind perceived by grounded birds prior to initiating migratory flight. If NFCs or the passage of migrants overhead serves as a cue to favourable wind condition at altitude, optimisation procedures to select the tailwind altitude with best fit could obscure the underlying relationship between departure hazard and NFC or overhead migrant passage.

A candidate model approach was used to separately test and compare the influence of migrant passage, NFC count, and tailwind on migratory departure hazard within the departure night, using the function "coxph" and "coxme" from the packages *Survival* (Therneau 2023) and *Coxme* (Therneau 2022) respectively. Starting with a null model of fixed departure hazard, I first tested whether the inclusion of species as a random intercept improved model fit using Akaike's information criterion corrected for small sample sizes (AICc, Burnham and Anderson 2004). This model was then extended into separate competing models which included either migrant passage, NFC count, tailwind, age class, and two-way interactions between age class and the other covariates. AICc was used to determine the model of departure hazard with the best fit, with a decrease in AICc < 2 indicating only marginally improved fit resulting from the inclusion of additional parameters. Following model selection, the shape of the time to event function (Gompertz, Weibull, Gamma, Exponential, Lognormal, Log-logistic, or Generalised Gamma) was evaluated by fitting separate parametric survival models using the function “flexsurvreg” in the *flexsurv* package and comparing model fit using AICc.

To verify that radar placement relative to capture site did not influence the analysis outcome, the analyses were again rerun using only data collected in 2021 at CFI and MPT radar units. These units were located directly at the study sites in this year and not at nearby wind energy facilities as in 2020. The units were also more easily monitored and serviced compared to 2020 due to the easing of travel guidelines related to the COVID-19 pandemic. In all analyses, migrant passage and NFC counts were log10(Value + 1) transformed, and both migrant passage, NFC count, and tailwind values were centred and scaled. Prior to analysis, the distribution of these covariates was visualised to check for birds with outlying values. The assumption of proportional hazards were assessed using the “cox.zph” function in package *Survival* (Therneau 2021).

5.3 Results

Nocturnal departures were identified for 124 birds, occurring among 55 unique nights in 2020 and 2021 that contained a total of 1994 10-minute within departure night intervals. Among these intervals, radar data of migrant passage was available for 1602 intervals (80%), collected during the departure nights of 103 birds. Of these, 41 birds were left-censored prior to departure as radar data was unavailable during the interval of departure. The final dataset included data from 22 birds across 15 nights at two stopover sites in 2020 and 81 birds across 29 nights at four stopover sites in 2021. These birds included 27 Hermit Thrush, 25 Swainson’s Thrush, and 51 White-throated Sparrows for a total of 103 birds during the fall of 2020 and 2021. One White-throated Sparrow had a high outlying departure night tailwind value and was removed from the dataset prior to analysis. Preliminary visualisation of departure behaviour using a Kaplan-Meier estimator suggested the assumption of proportional hazards was not satisfied among species

(Figure 5-1), and separate analyses of departure hazard were conducted for each species. In Hermit Thrush, only four individuals were of the adult age-class, and three of these were right-censored. This precluded robust analyses of age differences in departure behaviour in this species. Sample sizes by species and age class can be found in Table 5-1.

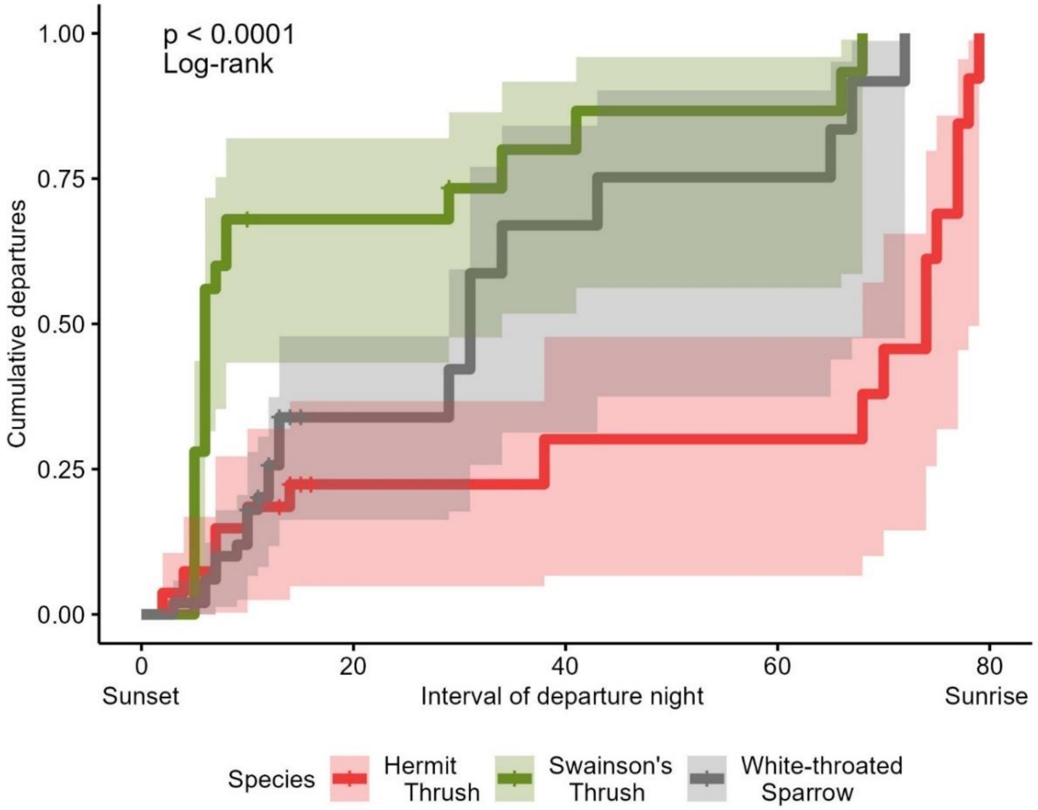


Figure 5-1. Kaplan-Meier curves showing the cumulative incidence of departure from stopover across the departure night for three species of migratory songbird during autumn migration in eastern New Brunswick.

Table 5-1. Summary statistics from the 10-minute interval dataset for each species.

Metric	White-throated Sparrow	Swainson’s Thrush	Hermit Thrush
Sample sizes (HY, AHY)	50 (31, 19)	25 (17, 8)	27 (4, 23)
Departure date range	13 September – 21 October	13 September – 14 October	16 September – 26 October
Mean nocturnal departure interval (range)	12 (1, 72)	6 (1,68)	47 (2, 79)
Mean migrant traffic (range) [birds • interval^{-1}]	25 (0, 325)	58 (0, 337)	32 (0, 212)
Mean passerine NFC (range) [NFCs • interval^{-1}]	2 (0, 165)	2 (0, 58)	4 (0, 165)
Mean tailwind assistance (range) [m·s^{-1}]	-1.4 (-10.1, 5.3)	-0.8 (-6.0, 5.4)	-0.5 (-7.6, 5.3)

For White-throated Sparrows, departures occurred ranged from 13 September to 21 October. Within departure nights, the median departure interval was 12 (120 minutes after sunset), ranging from interval 1 - 72 (approximately 12 hours after the end of evening civil twilight). Among all departure nights and locations, total migrant traffic within the 10-minute intervals ranged from 0 to 325 targets (mean = 42) measured within the monitored air column, representing a peak passage rate of ~33 birds per-minute. The number of passerine NFCs recorded during nocturnal intervals range from 0 to 165 (mean = 2). Tailwind assistance among departure night intervals ranged from -10.1 $m \cdot s^{-1}$ to 5.3 $m \cdot s^{-1}$ (mean = -0.9 $m \cdot s^{-1}$), indicating the average wind was a low headwind rather than tailwind. Tailwind assistance was weakly but positively correlated with migrant passage ($r = 0.06$, $p = 0.03$) and NFC count ($r = 0.05$, $p = 0.03$) within each interval. Values for Swainson’s Thrush and Hermit Thrush can be found in Table 5-1.

Among all species, analyses of nocturnal departure hazard based on different within-night interval durations were qualitatively similar for intervals from 10 to 30 minutes, with the best model for each species including only tailwind assistance (model 3). There was also some support for models including age class and the interaction between age class and tailwind in Swainson’s Thrush only but only in the analysis based on the 10-minute and 40-minute interval dataset. Models with either nocturnal migrant passage (model 2), NFC count (model 4), or age class (model 5) alone had poorer fit relative to the model with just tailwind (model 3), and neither migrant passage, passerine NFC counts, nor age class were significant in their respective models (all p values > 0.05). When analysed using a 40-minute interval dataset, the best model was the null model for both White-throated Sparrow and Swainson’s Thrush, but marginal support was also found for models with tailwind, NFCs, age class, and interactions (models 4,5,6,7,10. Table 5-2). Below I present the results of the analysis based on 10-minute interval duration for each species, with the models for the 20 to 40-minute intervals available in Appendix G.

In the best model of nocturnal departure hazard for White-throated Sparrows (model 3) the departure hazard increased 28% for every additional $m \cdot s^{-1}$ of tailwind assistance during the 10-minute interval ($\beta = 0.25 \pm$ SE 0.08, z = 3.09, $p < 0.01$, Figure

5-2). The log-logistic model with scale parameter (a) = 17.40 ± SE 2.32 and shape parameter (β) = 3.23 ± SE 0.59 was the best fitting function of departure hazard (Figure 5-3). In the range of shape parameter values $\beta > 1$, the distribution of the hazard for departure is unimodal with decreasing dispersion with greater values of β (Wienke 2010). For Swainson's Thrush, the best model of departure hazard included only tailwind (model 3), with departure hazard increased by 19% for every additional $m \cdot s^{-1}$ of tailwind assistance ($\beta = 0.18 \pm$ SE 0.08, z = 2.23, $p = 0.03$, Figure 5-2). There was also marginal support for model containing age class and the interaction between age class and tailwind, but neither of these terms were significant when included ($p > 0.05$). The log-logistic model with scale parameter (a) = 7.11 ± SE 0.65 and shape parameter (β) = 3.94 ± SE 0.77 was the best fitting function of departure hazard (Figure 5-3). For Hermit Thrush, the best model included tailwind (model 3). Unlike the other two species, departure hazard decreased 12% for each additional $m \cdot s^{-1}$ of tailwind assistance ($\beta = -0.25 \pm$ SE 0.10, z = -2.40, $p = 0.02$, Figure 5-2). For Hermit Thrush, the Gompertz model with shape parameter (b) = 0.03 ± SE 0.01 and rate parameter (η) = 0.008 ± SE 0.005 was the best fitting function of departure hazard, indicating an increasing hazard for departure across the night (Figure 5-3). Model rankings remained the same when using the dataset restricted to data from 2021 only.

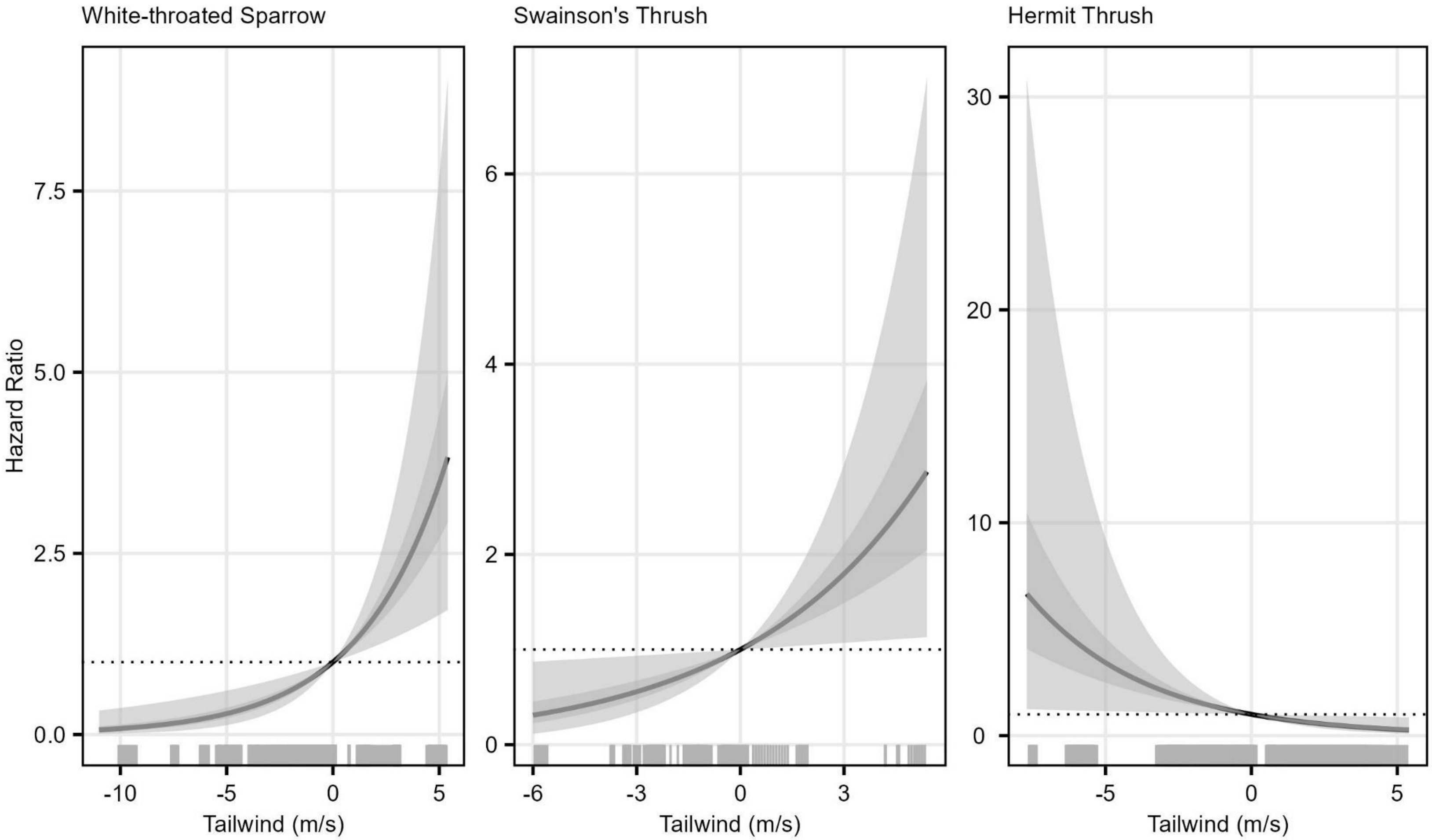


Figure 5-2. The estimated effect of tailwind on the within-night departure hazard ratio for three songbird species tagged during autumn migratory stopover in eastern New Brunswick. Greater hazard ratio indicates earlier departure. The dark line represents the hazard ratio for a given tailwind value, with the dark grey and light grey representing the 50% and 95% confidence interval respectively.

Table 5-2. Comparison of candidate models of within-night departure hazard for 121 birds of three species captured during autumn stopover in eastern New Brunswick in 2020, and 2021. Also indicated is models AICc and ΔAICc relative to the best fit model, and Akaike weight (w_i) for each model.

Model #	**Name**	**Model**	**White-throated Sparrow**			**Swainson's Thrush**			**Hermit Thrush**		
10-minute interval			**AICc**	**ΔAICc**	**w_i**	**AICc**	**ΔAICc**	**w_i**	**AICc**	**ΔAICc**	**w_i**
1	Null	~ 1	117.27	7.29	0.02	102.46	2.3	0.11	67.97	3.28	0.14
2	Migrant passage	~ Migrant passage	119.45	9.47	0.01	104.66	4.5	0.04	69.64	4.95	0.06
3	**Tailwind**	**~ Tailwind**	**109.98**	**0**	**0.65**	**100.16**	**0**	**0.34**	**64.69**	**0**	**0.72**
4	NFC	~ NFCs	119.18	9.2	0.01	102.9	2.74	0.09	69.18	4.49	0.08
5	Age class	~ Age class	119.45	9.47	0.01	104.39	4.23	0.04	Insufficient sample size		
6	Tailwind and age class additive	~ Tailwind + Age class	111.92	1.94	0.25	101.91	1.75	0.14			
7	Tailwind and age class interaction	~ Tailwind + Age class + Tailwind * Age class	114.53	4.55	0.07	101.19	1.03	0.2			
8	Migrant passage and age class additive	~ Migrant passage + Age class	121.87	11.89	0	106.82	6.66	0.01			
9	Migrant passage and age class interaction	~ Migrant passage + Age class + Migrant passage * Age class	124.49	14.51	0	109.33	9.17	0			
10	NFC and age class additive	~ NFCs + Age class	121.57	11.59	0	105.33	5.17	0.03			
11	NFC and age class interaction	~ NFCs + Age class + NFCs * Age class	124.12	14.14	0	107.23	7.07	0.01			

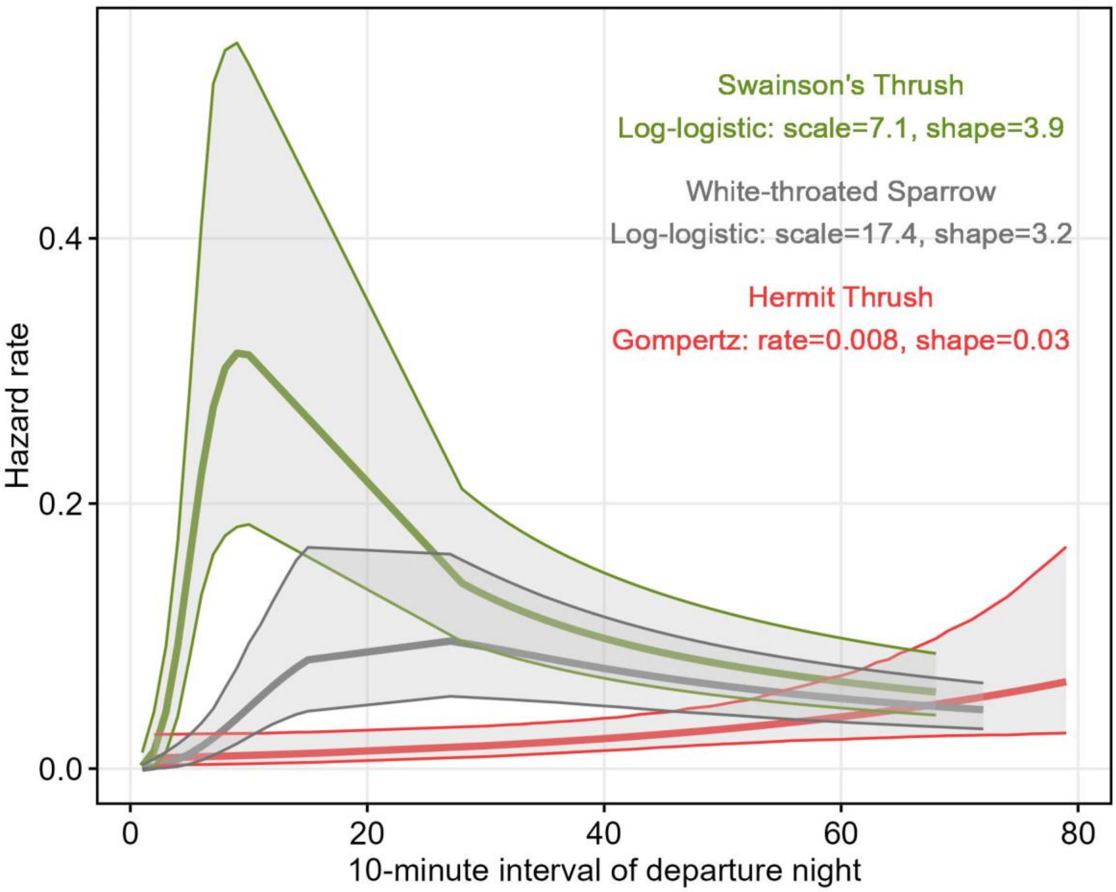


Figure 5-3. Estimated hazard functions for migratory departure across 10-minute intervals within the departure nights of three species studied during fall migration in eastern New Brunswick. Also show is the 95% confidence intervals. Distribution and associated parameter estimates are also shown.

5.4 Discussion

I combined data from acoustic monitoring, short range radar, and automated radiotelemetry in a novel analytical framework to test hypotheses regarding the influence of visual and auditory social information on the within-night departure timing of three migratory songbird species. Contrary to my expectations, I found little evidence that visual and auditory information from passing migrants serves as a cue for nocturnal departure, and this pattern was consistent for adult and the less experienced hatch-year migrants. Instead, within-night departure hazard was sensitive to tailwind conditions, increasing departure hazard and leading to and earlier nocturnal departure in White-throated Sparrow and Swainson's Thrush while decreasing departure hazard and leading to a later nocturnal departure in Hermit Thrush.

For two of the three species studied, the hazard for migratory departure increased with more energetically favourable wind conditions. The sensitivity of migratory songbirds to favourable wind conditions within their departure night echoes the patterns between departure nights in this study system (Chapter 3,4) and in others (Dossman et al. 2016, Beauchamp et al. 2020, Packmor et al. 2020). Earlier nocturnal departure under favourable wind conditions may be generally beneficial for migratory songbirds, providing both greater time for migratory flight and extending the potential flight distance through reduced energetic costs. Why the within night departure hazard for Hermit Thrush decreased with increasing tailwind assistance is uncertain. Many of these individuals were young birds, and this pattern could be attributed to inexperience and poor selectivity of winds during departure by younger birds. Unfortunately, I was not able to test for separate effect of age class nor interactions with wind conditions in this species, but there was marginal evidence for differential use of wind conditions between age classes found in Swainson's Thrush. Similar age-specific effect of wind condition on departure timing were observed in Savannah Sparrows (*Passerculus sandwichensis*) in a study occurring south of my study region (Mitchell et al. 2015), although the absence of this effect in White-throated Sparrows suggests this pattern may be variable among species and contexts.

Experiential and physiological differences between age classes have been posited to underly previously observed differences in migratory movement behaviour in songbirds (Heise and Moore 2003, Mitchell et al. 2015, Dossman et al. 2016), and these differences are likely at their greatest during fall migration (Wheelwright and Templeton 2003). The similar effect of wind conditions on departure behaviour may indicate that juveniles have gained sufficient experience to behave comparable to adults by the time they pass through the study region, or that poorer performing younger individuals are selectively lost from the study population prior to being encountered (Nol and Smith 1987, van de Pol and Verhulst 2006). Given the proximity of the study region to the breeding areas, both scenarios imply these processes occur quite early in the migration period, potentially following as little as a single flight. Alternatively, the sensitivity of departure behaviour to meteorological conditions may be largely innate among the songbird species studied. Establishing the specific processes that underly ontogenetic development of songbird movement behaviour will likely require individual-level data collected across multiple migratory periods at higher spatial and temporal resolutions.

Within-night departure timing and shape of the best-fit hazard function also differed between species. The hazard for migratory departure in Swainson’s Thrush accelerated quickly following sunset, whereas the hazard for departure gradually increased in the other species and only decreasing after approximately five hours post sunset in White throated Sparrows. Of the species in this study, Swainson’s Thrush migrate the greatest distance, travelling from temperate and boreal breeding sites to non-breeding areas in northern South America. For long distance migrants that travel at night, maximising the nocturnal flight distance by departing closer to sunset maximises the time available for flight in a given night, and fewer, longer flights may yield salient differences in the total number of stopovers across the migratory journey. This can reduce the overall time require to complete migration (McKinnon et al. 2014), and decrease exposure to threats encountered enroute such as inclement weather conditions (Ward et al. 2018), predators (Alerstam 2011), and pathogens (Hegemann et al. 2018). A similar pattern of early departure by longer distance migrants was found by Packmor et al. (2020) in a study of three nocturnally migrating songbird species in Europe, suggesting this phenomenon may form a facet of the migratory movement strategy in long distance migrant songbirds. Several individuals, including many of the Hermit Thrush in this study, departed closer to dawn. While these departures are unlikely to lead to prolonged migratory flight, I elected to retain these individuals in the analysis to investigate if social cues elicited the departure of these individuals.

While I found little evidence that visual and auditory cues between grounded and volant migrants act as a cue for migratory departure, the behaviour of songbirds may still be influenced by social information from other sources. This study does preclude the use of social information exchanged between individuals on the ground prior to departure, as observed in non-passerine bird species (Piersma et al. 1990). Like waders, songbirds are often observed foraging in flocks during migratory stopover, and form diffuse flocks during nocturnal flight. Whether these groups are composed of the same individuals, or if these social associations emerge following the transition from one behaviour to the next requires further investigation.

The use of social information for migratory departure decisions may also vary between spring and fall migration. During spring, earlier arrival at the breeding area relative to conspecifics can increase reproductive success (Aebischer et al. 1996, Smith and Moore 2005, Velmala et al. 2015), possibly through priority access to nesting locations and mates (Kokko 1999, Kokko et al. 2006). These reproductive benefits are balanced by the increased risk of encountering adverse weather conditions with earlier migration and arrival, favouring individuals that arrive earlier than conspecifics but not so early as to encounter inclement spring weather (Kokko 1999, Kokko et al. 2006). Hypothetically, visual and auditory cues from overflying conspecifics could provide information about the movements and migratory progress of other individuals in the population. This information could be used to make the movement decisions required to arrive earlier than other birds. For example, by commencing migratory flight when a conspecific is perceived passing overhead, a leading migrant that departed earlier in the year from the overwintering area would likely be able to maintain its lead given similar energetic conditions between each bird at the time of their departure. The benefits of earlier arrival at destinations are thought to be greatest when associated with the breeding grounds, and captive studies on Yellow-rumped Warblers (*Setophaga coronata*) has demonstrated that variation in the social environment can influence the behaviour patterns of songbirds during spring migration (Deakin et al. 2021). Future studies could seek to evaluate sensitivity to visual and auditory social cues on departure during spring migration.

The findings of this study are also limited to the species studied, and the proclivity to use social information when making migratory departure decisions may vary among songbird species. Travelling group size is positively associated with migration distance among North American bird species (Beauchamp 2011), possibly due to the increased value and more numerous opportunities to benefit from of socially acquired information across a longer migration route. The use of social information by long-distance migrants to synchronise behaviours such as departure from stopover and other events throughout migration, could contribute to larger travelling group sizes in these species. Captive studies of the migratory restlessness response to conspecific or heterospecific NFCs (following Hamilton 1962) in a variety of species would help to further elucidate the role of social information on departure behaviour, and how the sensitivity to this information may differ between songbird species.

This is the first study to combine automated radio telemetry data with data from radar and acoustic recording devices to link individual level movement behaviour with the behaviour of other migratory birds. While the results of this study suggest that social information obtained from passing migrants is not used by migratory songbirds when making departure decisions during fall migration, future studies could apply this framework to further explore the effect of social information in other contexts, or to test for the effect of other dynamic within-night covariates on the departure behaviour of songbirds. This method could also be adapted to test for the effects of lagged or cumulative exposure to migrant passage and NFC on departure hazard, and these types of processes may help to explain the patterns observed in the analysis using the 40-minute interval dataset. Further refinement of acoustic monitoring technology and post-processes of recordings may also allow for evaluations of behaviour using species-specific social cues.

5.5 References

Aebischer, A., N. Perrin, M. Krieg, J. Studer, and D. R. Meyer (1996). The role of territory choice, mate choice and arrival date on breeding success in the Savi's Warbler *Locustella luscinioides*. Journal of Avian Biology 27:143–152.

Åkesson, S., T. Alerstam, and A. Hedenström (1996). Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. Journal of Avian Biology 27:95–102.

Alerstam, T. (2011). Optimal bird migration revisited. Journal of Ornithology 152:5–23.

Alessi, M. G., T. J. Benson, and M. P. Ward (2010). Nocturnal social cues attract migrating Yellow-breasted Chats. The Wilson Journal of Ornithology 122:780–783.

Beauchamp, A. T., C. G. Guglielmo, and Y. E. Morbey (2020). Stopover refuelling, movement and departure decisions in the White-throated Sparrow: The influence of intrinsic and extrinsic factors during spring migration. Journal of Animal Ecology 89:2553–2566.

Beauchamp, G. (2011). Long-distance migrating species of birds travel in larger groups. Biology Letters 7:692–694.

Birds Canada (2022). motus: Fetch and use data from the Motus Wildlife Tracking System. [Online.] Available at https://motusWTS.github.io/motus.

Buler, J. J., F. R. Moore, and S. Woltmann (2007). A multi-scale examination of stopover habitat use by birds. Ecology 88:1789–1802.

Burnham, K. P., and D. R. Anderson (2004). Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Chernetsov, N. (2006). Habitat selection by nocturnal passerine migrants en route: mechanisms and results. Journal of Ornithology 147:185–191.

Coppack, T., S. F. Becker, and P. J. J. Becker (2008). Circadian flight schedules in night-migrating birds caught on migration. Biology Letters 4:619–622.

Cresswell, W. (1994). Flocking is an effective anti-predation strategy in Redshanks, *Tringa totanus*. Animal Behaviour 47:433–442.

Deakin, J. E., C. G. Guglielmo, and Y. E. Morbey (2021). Effect of the social environment on spring migration timing of a songbird. Frontiers in Ecology and Evolution 9.

Dolnik, V. R., and T. I. Blyumental (1967). Autumnal premigratory and migratory periods in the Chaffinch (*Fringilla coelebs coelebs*) and some other temperate-zone passerine birds. The Condor 69:435–468.

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. Behavioral Ecology 27:567–574.

Eikenaar, C., F. Müller, S. Kämpfer, and H. Schmaljohann (2016). Fuel accumulation advances nocturnal departure: a migratory restlessness study on northern wheatears at stopover. Animal Behaviour 117:9–14.

Erni, B., F. Liechti, L. G. Underhill, and B. Bruderer (2002). Wind and rain govern the intensity of nocturnal bird migration in central Europe - A log-linear regression analysis. Ardea 90:155–166.

Farnsworth, A. (2005). Flight calls and their value for future ornithological studies and conservation research. The Auk 122:733–746.

Farnsworth, A., S. A. G. Jr, and D. van Blaricom (2004). A comparison of nocturnal call counts of migrating birds and reflectivity measurements on Doppler radar. Journal of Avian Biology 35:365–369.

Gwinner, E. (1996). Circadian and circannual programmes in avian migration. Journal of Experimental Biology 199:39–48.

Hamilton, W. J. (1962). Evidence concerning the function of nocturnal call notes of migratory birds. The Condor 64:390–401.

Hegemann, A., P. Alcalde Abril, R. Muheim, S. Sjöberg, T. Alerstam, J.-Å. Nilsson, and D. Hasselquist (2018). Immune function and blood parasite infections impact stopover ecology in passerine birds. Oecologia 188:1011–1024.

Heise, C. D., and F. R. Moore (2003). Age-related differences in foraging efficiency, molt, and fat deposition of Gray Catbirds prior to autumn migration. The Condor 105:496–504.

Horton, K. G., W. G. Shriver, and J. J. Buler (2015). A comparison of traffic estimates of nocturnal flying animals using radar, thermal imaging, and acoustic recording. Ecological Applications 25:390–401.

Kemp, M. U., E. Emiel van Loon, J. Shamoun-Baranes, and W. Bouten (2012). RNCEP: global weather and climate data at your fingertips. Methods in Ecology and Evolution 3:65–70.

Kokko, H. (1999). Competition for early arrival in migratory birds. Journal of Animal Ecology 68:940–950.

Kokko, H., T. G. Gunnarsson, L. J. Morrell, and J. A. Gill (2006). Why do female migratory birds arrive later than males? Journal of Animal Ecology 75:1293–1303.

Liechti, F. (2006). Birds: blowin' by the wind? Journal of Ornithology 147:202–211.

McKinnon, E. A., K. C. Fraser, C. Q. Stanley, and B. J. M. Stutchbury (2014). Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration. PLoS ONE 9:e105605.

Mitchell, G. W., B. K. Woodworth, P. D. Taylor, and D. R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Movement Ecology 3:19.

Morbey, Y. E., A. T. Beauchamp, S. J. Bonner, and G. W. Mitchell (2020). Evening locomotor activity during stopover differs on pre-departure and departure days in free-living songbirds. Journal of Avian Biology 51.

Morbey, Y. E., C. G. Guglielmo, P. D. Taylor, I. Maggini, J. Deakin, S. A. Mackenzie, J. M. Brown, L. Zhao, and D. Stephens (2018). Evaluation of sex differences in the stopover behavior and post departure movements of wood-warblers. Behavioral Ecology 29:117–127.

Mouritsen, H., G. Feenders, M. Liedvogel, and W. Kropp (2004). Migratory Birds Use Head Scans to Detect the Direction of the Earth's Magnetic Field. Current Biology 14:1946–1949.

Müller, F., C. Eikenaar, Z. J. Crysler, P. D. Taylor, and H. Schmaljohann (2018). Nocturnal departure timing in songbirds facing distinct migratory challenges. Journal of Animal Ecology 87:1102–1115.

Müller, F., P. D. Taylor, S. Sjöberg, R. Muheim, A. Tsvey, S. A. Mackenzie, and H. Schmaljohann (2016). Towards a conceptual framework for explaining variation in nocturnal departure time of songbird migrants. Movement Ecology 4:24.

Németh, Z., and F. R. Moore (2014). Information acquisition during migration: A social perspective. The Auk 131:186–194.

Nilsson, C., A. M. Dokter, L. Verlinden, J. Shamoun-Baranes, B. Schmid, P. Desmet, S. Bauer, J. Chapman, J. A. Alves, P. M. Stepanian, N. Sapir, et al. (2019). Revealing patterns of nocturnal migration using the European weather radar network. Ecography 42:876–886.

Nol, E., and J. N. M. Smith (1987). Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. Journal of Animal Ecology 56:301–313.

Packmor, F., T. Klinner, B. K. Woodworth, C. Eikenaar, and H. Schmaljohann (2020). Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? Movement Ecology 8:6.

Piersma, T., L. Zwarts, and J. H. Bruggemann (1990). Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. Ardea 78:157–184.

van de Pol, M., and S. Verhulst (2006). Age-dependent traits: a new statistical model to separate within- and between-individual effects. The American Naturalist 167:766–773.

Pyle, P. (1997). Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA, USA.

R Core Team (2021). R: a language and environment for statistical computing. [Online.] Available at URL https://www.R-project.org/.

Rafacz, M., and J. J. Templeton (2003). Environmental unpredictability and the value of social Information for foraging starlings. Ethology 109:951–960.

Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Richardson, W. J. (1978). Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272.

Sandberg, R., J. Pettersson, and K. Persson (1991). Migratory orientation of free-flying robins *Erithacus rubecula* and Pied Flycatchers *Ficedula hypoleuca*: release experiments. Ornis Scandinavica (Scandinavian Journal of Ornithology) 22:1–11.

Sanders, C. E., and D. J. Mennill (2014). Acoustic monitoring of nocturnally migrating birds accurately assesses the timing and magnitude of migration through the Great Lakes. The Condor 116:371–383.

Schmaljohann, H., F. Korner-Nievergelt, B. Naef-Daenzer, R. Nagel, I. Maggini, M. Bulte, and F. Bairlein (2013). Stopover optimization in a long-distance migrant: the role of fuel load and nocturnal take-off time in Alaskan Northern Wheatears (*Oenanthe oenanthe*). Frontiers in Zoology 10:26.

Schmaljohann, H., F. Müller, T. Klinner, and C. Eikenaar (2018). Potential age differences in the migratory behaviour of a nocturnal songbird migrant during autumn and spring. Journal of Avian Biology 49:e01815.

Schmaljohann, H., and B. Naef-Daenzer (2011). Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. Journal of Animal Ecology 80:1115–1122.

Simons, A. M. (2004). Many wrongs: the advantage of group navigation. Trends in Ecology & Evolution 19:453–455.

Sjöberg, S., T. Alerstam, S. Åkesson, and R. Muheim (2017). Ecological factors influence timing of departures in nocturnally migrating songbirds at Falsterbo, Sweden. Animal Behaviour 127:253–269.

Smith, R. J., and F. R. Moore (2005). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231–239.

Smolinsky, J. A., R. H. Diehl, T. A. Radzio, D. K. Delaney, and F. R. Moore (2013). Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. Behavioral Ecology and Sociobiology 67:2041–2051.

Therneau, T. (2021). A Package for Survival Analysis in R. [Online.] Available at https://CRAN.R-project.org/package=survival.

Therneau, T. (2022). coxme: Mixed Effects Cox Models. [Online.] Available at https://CRAN.R-project.org/package=coxme.

Therneau, T. (2023). A Package for Survival Analysis in R. [Online.] Available at https://CRAN.R-project.org/package=survival.

Tsvey, A., V. N. Bulyuk, and V. Kosarev (2007). Influence of body condition and weather on departures of first-year European Robins, *Erithacus rubecula*, from an autumn migratory stopover site. Behavioral Ecology and Sociobiology 61:1665–1674.

Velmala, W., S. Helle, M. P. Ahola, M. Klaassen, E. Lehikoinen, K. Rainio, P. M. Sirkiä, and T. Laaksonen (2015). Natural selection for earlier male arrival to breeding grounds through direct and indirect effects in a migratory songbird. Ecology and Evolution 5:1205–1213.

Ward, M. P., T. J. Benson, J. Deppe, T. J. Zenzal, R. H. Diehl, A. Celis-Murillo, R. Bolus, and F. R. Moore (2018). Estimating apparent survival of songbirds crossing the Gulf of Mexico during autumn migration. Proceedings of the Royal Society B: Biological Sciences 285:20181747.

Weimerskirch, H., J. Martin, Y. Clerquin, P. Alexandre, and S. Jiraskova (2001). Energy saving in flight formation. Nature 413:697–698.

Wheelwright, N. T., and J. J. Templeton (2003). Development of foraging skills and the transition to independence in juvenile Savannah Sparrows. The Condor 105:279–287.

Wienke, A. (2010). Frailty Models in Survival Analysis. CRC Press.

Chapter 6

6 General discussion

6.1 Summary of findings

In this dissertation, I evaluated how environmental characteristics and individual traits interact to drive stopover refuelling performance and behaviour of songbirds during autumn migration in eastern New Brunswick. In this context, I first evaluated how refuelling rate and behaviour differ among species according to migration distance to test the proximate ecological hypothesis that stopover refuelling intensity facilitates long-distance migration (Chapter 2). I found that species with greater refuelling performance had longer migration distances, and this pattern was significant after accounting for the negative relationship between metabolite-based measurement of refuelling performance and the species-specific onset time of diel activity. I also found that the onset of diel activity was earlier and stopover duration was shorter in species with longer migration distances. Together, these results illustrate how migration distance is an ecological driver of stopover behaviour, with long-distance migration starting each day of stopover earlier, refuelling more intensively, and remaining at a stopover site for less time.

After evaluating how refuelling and stopover duration differed in an interspecific framework, I then built on this by testing how broad and local-scale environmental characteristics, together with individual traits, interact to shape individual-level refuelling and behaviour at coastal and inland stopover sites (Chapter 3). Refuelling performance did not differ between coastal and inland sites in eastern New Brunswick and was invariant to the abundance of songbird migrants or invertebrate prey at the site level. When evaluating intrinsic factors, young migrants did not have poorer refuelling rates than adults, but refuelling was greater in birds captured in better energetic condition. After accounting for the effect of bleed time, capture time of day, date, year, and condition on the metabolite-based measure of refuelling, migrants captured with poorer refuelling rate had higher hazards for departure and shorter stopover durations, illustrating how refuelling rate experienced at arrival acts as an ecological driver of subsequent stopover behaviour. This pattern may also help explain why effects of migrant or resource abundance on individual refuelling rate were not observed, as it suggests recently arrived migrants that experience poor refuelling from lack of food or high competition for resources depart after only a brief stopover. Corresponding to this departure behaviour, local migrant abundance was positively related to invertebrate abundance across the season. This suggests that higher invertebrate abundance enabled more individuals to satisfy the energetic demands of refuelling, and would also explain why no direct relationship between invertebrate abundance and refuelling rate was observed.

To further explore how local resource availability and individual traits interact to affect refuelling, and behaviour, I conducted a food augmentation experiment at three study sites (Chapter 4). Feeding stations were used to dynamically alter local food availability in two-week intervals to test how resource availability affects refuelling performance and behaviour in free living songbirds, and to test the hypothesis that patterns of class-specific refuelling and behaviour are moderated by local resource availability. The focus of this study was the White-throated Sparrow, a species which has two genetic morphs distinct in behaviour that provide an additional axis along which to study stopover behaviour. When food supply was augmented, no numerical response of local sparrow abundance was observed, but birds of the white-striped morph had greater refuelling rates. Both effects may be attributed to the localised and more defensible nature of the food source available from the feeding station. Local movement and stopover duration did not differ by morph or age and were unaffected by the availability of extra food.

In my final chapter (Chapter 5), I used marine radar and acoustic recorders to test the hypotheses that social information from passing migrants acts as a cue for migratory departure within the departure night of an individual, and that sensitivity to this information differs between young first-time migrants and more experienced older migrants. Within-night departure hazard did not vary according to the number of migrants passing overhead or the number of night flight calls recorded for either young or old birds, indicating social information from passing migrants does not act as an important ecological driver of departure time in this system. Migrants were sensitive to wind conditions encountered on their departure night, and departure timing was earlier in long distance migrants. Below I discuss the implication of my findings on our understanding of the ecological drivers of autumn stopover in songbirds and provide some perspectives for future studies.

6.2 Expanding basic knowledge

6.2.1 Intrinsic traits that drive stopover

Interspecific variation was observed in almost every aspect of stopover ecology examined, and in general, the observed differences among species mirrored species-level differences in total migration distance (Chapter 2,3,5). Travelling longer distances during migration inherently represents a greater energetic challenge, and prolonged periods of migration can increase exposure to enroute risks and may lead to temporal constraints on the annual cycle (Gow et al. 2019). Species that migrate longer distances typically have faster migrations, and physical attributes such as greater wing-pointedness, faster fuel depositions rates (de Zwaan et al. 2022), and earlier nocturnal departure (Packmor et al. 2020) are thought to represent some of the specialised adaptations to overcome these challenges. By combining measurements of diel activity patterns and refuelling rate at the individual level, my work shows that both an earlier onset to daily refuelling and a higher instantaneous rate of refuelling forms part of the suite of adaptations underlying interspecific differences in migration speed via differences in stopover duration.

For young songbirds in their first fall migration, stopovers occurring in eastern New Brunswick may be among the first in a journey that can extend to Central and South America. As such, I placed an emphasis on testing for age-class based differences in migration ecology, as ontogenetic or adaptive differences between young and old birds are expected to be the greatest during this early phase of autumn migration. Contrary to my expectation, young songbirds did not have poorer refuelling performance or longer stopovers than adults (Chapter 3,4). However, young birds moved more while on stopover (Chapter 3). On breeding areas, aviary trials and field observations generally suggest that the ability of juvenile migrants to locate food items is initially inferior to old birds, but rapidly improves to reach an efficiency similar to adult birds by the start of autumn migration (Sullivan 1988, Wheelwright and Templeton 2003, Heise and Moore 2003). The unfamiliar habitats and novel food items encountered during stopover, together with poorer competitive ability, could limit access to food for young birds. My results indicate this is not the case in my study system, and that any differences in the ability to obtain food that may exist between young and old birds do not translate to differences in stopover refuelling rate in eastern New Brunswick, even in the early stages of autumn migration. Given the greater local movement observed, one potential explanation is that young were able to compensate for any differences in foraging proficiency or frequent displacement by dominant birds by increasing foraging effort and moving over a broader area. Alternatively, young birds may have been focusing their foraging efforts on different food types or sub-habitats to minimise competition with adults, which may also yield both differences in the patterns of movement and similar refuelling rates.

By measuring both refuelling and stopover duration at the individual level, and then including refuelling rate in my analysis of stopover duration (Chapter 3), I provided a test of age-specific stopover duration that controlled for any confounding differences in refuelling rate between age classes. Stopover durations did not differ between young and old birds, suggesting that age classes do not differ inherently in stopover duration despite differences in basal metabolic rate (McCabe and Guglielmo 2019) and movement that may affect energy expenditure and storage. Previously reported patterns of age-specific stopover duration may have resulted indirectly from poorer refuelling performance of young birds, perhaps under circumstances where any behavioural compensation for lower foraging proficiency or adaptive partitioning of habitat was limited. For example, Rguibi-Idrissi et al. (2003) found the stopover of young Reed Warblers (*Acrocephalus scirpaceus*) was generally longer at two sites located in northern Morocco, although a consistent relationship between fuel deposition rate and stopover duration was not observed. Determining how the broader landscape context affects local patterns of refuelling and movement will require similar measurement of these aspects in a wider variety of contexts. Such knowledge may reveal important demographic specific impact of habitat quality on migratory movement behaviours.

6.2.2 Extrinsic drivers of stopover behaviour

Refuelling and movement behaviour were similar between coastal and inland stopover sites in eastern New Brunswick. Stopover in coastal landscapes has often been evaluated in the context where crossing the associated ecological barrier is required. In such circumstances, the behaviour of migrants using coastal sites may primarily reflect the processes involved in surmounting the adjoining barrier (Weber et al. 1998, Delingat et al. 2008, Goymann et al. 2010), rather than behaviours more typical of elsewhere along the migratory route. For example, navigating barriers may result in longer pre-crossing stopovers as migrants accumulate the energy required to make the crossing (Delingat et al. 2008), and to use marginal habitat after the barrier is crossed and birds are energy-depleted (Moore et al. 1990, Gutierrez Ramirez et al. 2022). A similar phenomenon has been observed in migrants refuelling prior to crossing the Sahara Desert (Schaub et al. 2008), in which departure does not occur until fuel loads sufficient to safely cross the barrier are achieved. Coastal regions often also feature high degrees of habitat fragmentation for forest-dwelling songbirds, further entangling the behavioural effects of coastal habitat with other landscape-scale processes (Cohen et al. 2012). With the notable exception of the Blackpoll Warbler, most of the migrants I studied in eastern New Brunswick were unlikely to be preparing for prolonged overwater flights, and the coastal landscape of the study region generally lacks the pronounced habitat fragmentation seen in other coastal areas. Local-scale characteristics of the coastal and inland study sites were broadly similar, lacking any pronounced differences in invertebrate food availability or migrant abundance observed in other studies, particularly those associated with freshwater coastal environments (Smith et al. 2007, Macdade et al. 2011, Ewert et al. 2011). Correspondingly, migrants did not refuel or behave differently while at coastal stopover sites compared to sites further inland.

Indices of local invertebrate availability and migrant abundance had no direct effect on refuelling rate or stopover duration in my studies. However, there was a positive relationship between the spatiotemporal variation in taxonomic family-specific migrant catch and invertebrate abundance. The more rapid departure of birds experiencing poorer refuelling rate, observed in Chapter 3, may have contributed to this pattern, and together, these findings suggest local resource availability and migrant abundance may act indirectly on stopover behaviour via the refuelling rate individuals experience shortly after arrival. The availability of habitat and relatively low degree of fragmentation in eastern New Brunswick is likely an important factor enabling this pattern. Observations of density and resource-dependent effects on refuelling are often made in regions where habitat is fragmented and availability is constrained (Moore and Yong 1991, Kelly et al. 2002, Shochat et al. 2002, Cohen et al. 2022, de Zwaan et al. 2022, Zimin et al. 2023). Under these circumstances, the ability of migrants to assess alternate habitat may be limited and relocation to alternate sites may carry a greater risk of ultimately not encountering more favourable habitat, limiting the ability for migrants to use stopover habitat according to the refuelling rate achieved. These findings further suggest how habitat fragmentation at the landscape scale is detrimental to migratory forest birds.

Contrasting the effect of natural resource availability, augmenting food supply influenced refuelling performance (Chapter 4), but the number of migrants captured at a site did not differ according to the food treatment. The difference between the patterns of refuelling and resource availability observed in Chapters 3 and 4 may be due to a combination of the localised nature of the food provided at the feeding station and the general magnitude of the change made. As clumped resources against a background of naturally available food sources, dominant individuals may have been able to maintain exclusive access the feeding station without encountering high rates of intrusion or competition (Maher and Lott 2000). This dynamic, and the fact that only three feeding stations were deployed at each site, likely explains why no numeric effect on migrant abundance was observed, as the overall site-level increase in food availability was likely low and largely capitalised on by a few dominant individuals. While this combination of factors may have provided the context in which to observe class-specific refuelling, future studies could also manipulate the spatial aspects of resource availability in addition to overall quantity available.

In Chapter 5, I was the first to test the hypothesis that visual and auditory information from passing migrants act as a cue for migratory departure in free living songbirds, expecting that birds would depart when more migrants were passing. Contrary to my expectations, I found no evidence that information from volant migrants was used when making departure decisions in the three songbird species studied during fall migration. Previous research on captive Bobolink (*Dolichonyx oryzivorus*) has suggested that auditory information from conspecifics can influence nocturnal migratory behaviour (Hamilton 1962), and information and association with conspecifics can provide numerous benefits during migration (Piersma et al. 1990, Cresswell 1994, Simons 2004). How flocks are formed and maintained during migration is largely unknown for small-bodied songbirds, and individuals that travel together are unlikely to remain together across multiple stages in migration (Newton 2008). While my results suggest social information conveyed from passing migrants is not used, the conveying of social information among grounded migrants in the leadup to during a departure event has been noted in shorebirds (Piersma et al. 1990) and likely also occurs in Nearctic passerines. The sensitivity to social information may also vary among species, as does the propensity to give night flight calls (NFCs) (Farnsworth 2005) or to engage in other social behaviours during migration. For example, G. Beauchamp et al. (2011) observed that North American bird species with longer migration distances generally tended to travel in larger flocks. Seasonal differences may also exist in the sensitivity to night flight calls, particularly if the value of this information differs in accordance with motivational difference between seasons. Captive studies (following Hamilton 1962) using a variety of species and in different seasons could help address some of these uncertainties. Doing so would help to determine if the behavioural responses of species like the Bobolink to NFCs are atypical among passerine migrants, or perhaps a feature of species which migrate more gregariously (Renfrew et al. 2020). Field manipulations of NFCs could also be used to experimentally test for the effect of social information on departure behaviour under real-world settings.

Wind conditions were a predominant driver of departure behaviour in songbirds in eastern New Brunswick, both on a night-to-night basis (Chapter 2,3,4) and within the departure night of an individual (Chapter 5). In line with previous studies of migratory stopover, birds were more likely to depart on nights with greater tailwind assistance (Åkesson and Hedenström 2000, Dossman et al. 2016, Packmor et al. 2020), indicating a preference for flying in winds more energetically favourable to migratory fight. Apart from Hermit Thrush, this pattern was also consistent within departure nights for two of the species I evaluated, with increasing tailwinds leading to earlier nocturnal departure. Of the 27 Hermit Thrush included in my analysis, 23 were young first-time migrants and three of the remaining four older birds were censored from the dataset prior to departure. This differences in wind use may also then reflect a difference between age classes in the sensitivity to wind conditions, and similar though not statistically significant interaction was observed in Swainson's Thrush. Similar age-related differences in the use of tailwind conditions have been observed previously in songbirds (Mitchell et al. 2012, 2015). These differences may provide young birds with a greater flexibility in their departure schedule, which could be beneficial if the cost of waiting for favourable tailwinds exceeds the energetic saving provided by departing with tailwinds (Mitchell et al. 2015). Differences between age classes could also be attributed to a lack of experience (Åkesson et al. 2021) or little time for selective loss to occur among the young migrants (Sergio et al. 2014, 2019) given the relatively proximity of the study region to the breeding areas of the study species.

6.2.3 Interrelation between individual-level refuelling and movement

Contrary to my expectations, migrants that had higher capture refuelling rates had longer stopover durations after controlling for interspecific differences in refuelling rate and stopover duration. These findings suggest that migrants travelling through eastern New Brunswick do not conform to the simple model of optimal stopover duration based on fuel deposition rate, in which faster refuelling rates are generally expected to reduce stopover duration under either a time or energy minimising migration strategy (Alerstam and Lindström 1990). Instead, my findings suggest an initial assessment of a site and decision to remain at a location is made based on refuelling rate, with subsequent departures occurring when favourable wind conditions temporarily increase the range that fuel stores could carry an individual. In landscapes where stopover habitat is common and the time required to locate and settle at new stopover sites is minimal, penalties from departing with a lower fuel load to take advantage of energetically favourable tailwinds may also be minimal. The influence of spatial heterogeneity in habitat availability and temporal heterogeneity in wind conditions on migratory stopover dynamics have been considered separately using simulation-based frameworks. Farmer and Wiens (1998) showed that low spatial heterogeneity in the availability of high-quality stopover sites could allow individuals to conduct migration using either short or long-distance flights without impacts on arrival date or arrival condition on breeding areas under uniform wind conditions. McCabe et al. (2018) showed that patterns of migratory movement could also be explained by wind selectivity in a uniform landscape. Future research could evaluate how spatial heterogeneity in habitat availability and temporal heterogeneity in wind conditions, together with variability in refuelling conditions during inter-flight stopovers, shape migratory movement patterns of songbirds.

6.3 Significance

Understanding how environmental characteristics and individual traits drive stopover refuelling performance and movement behaviour is vital both to our broader understanding of avian migratory ecology, and for how we evaluate habitats and landscapes for migratory birds during stopover. This knowledge will improve both our capacity to predict how migratory species will respond to the ongoing changes in our world, and for us to react accordingly to mitigate or remediate conditions that negatively impact migratory bird species where opportunities arise. Our current understanding suggests that much of the annual mortality in songbirds and other bird species occurs during migration (Sillett and Holmes 2002, Lok et al. 2015, Paxton et al. 2017), and maintaining or improving the functionality of stopover habitat is a fundamental aspect of preventing further declines in migratory bird species (e.g. Studds et al. 2017).

By combining habitat assessment and physiological profiling with advanced radio telemetry, radar, and acoustic monitoring methods, my dissertation research has furthered our understanding of intrinsic and extrinsic drivers of songbird migratory stopover behaviour and developed novel methods application of these technologies for testing hypotheses about avian behaviour. By measuring refuelling and stopover duration at the individual level, my findings affirm a link between refuelling and stopover duration, but suggest this relationship is primarily related to the initial selection of a stopover site based on assessment of local refuelling conditions. This process may in turn help to curtail pronounced density or resource dependent effects on refuelling performance observed in other studies (e.g. Cohen et al. 2022, de Zwaan et al. 2022). In the context of autumn stopover in eastern New Brunswick where habitat suitable for forest songbirds is common, this pattern suggests that sites with a high abundance of migrants are likely resource-rich sites that can support a greater number of refuelling migrants. This pattern may not be the case in more fragmented landscapes. The more rapid departure of poor refuelling individuals also has ramification for studies using recapture techniques to estimate refuelling and stopover duration, as these individuals may be more likely to leave a site prior to recapture.

Interspecific differences were observed in many of the aspects of stopover I studied, and these differences were generally associated with the migration distance of a species. This pattern provides further evidence that the constraints and challenges of traversing long distances between breeding and non-breeding areas may shape the migratory behaviour of songbirds. Long distance migrants, particularly those that reproduce at high latitudes, may face greater difficulty in maintaining synchrony between migratory arrival timing and breeding ground resource phenology in the face of anthropogenic climate change (Both and Visser 2001, Both et al. 2006, Saino et al. 2011, Mayor et al. 2017). Understanding how species vary in migratory behaviour may highlight unique vulnerabilities and opportunities for conservation of these species. For example, emphasis on window and wind turbine collision risk mitigation early in the night may be particularly beneficial to long-distance migrants who commence flight shortly after dusk. In addition, by showing that the onset of diel activity differed between species, I highlight an important consideration for future studies that employ metabolite profiling to compare refuelling in an interspecific framework.

My research has enhanced our understanding of the migration ecology of the forest songbirds of New Brunswick, revealing both broad similarities and key differences in the autumn migratory behaviour of songbirds in this region compared to others. I have provided some of the first measurements of refuelling rates, local movement behaviour, and stopover durations in multiple forest songbird species at both coastal and inland locations in the province. Although direct comparisons may be confounded by factors such as bleed time and time of day, species of songbird in eastern New Brunswick had similar or greater average plasma triglyceride and similar or lower β-OH butyrate concentration (Smith and McWilliams 2010, Seewagen et al. 2011, Brown et al. 2014, Kaplin et al. 2023, Pagano et al. 2023), suggesting that migrants in eastern New Brunswick were depositing fat at comparable or greater rates relative to previous studies of autumn refuelling. My findings show that refuelling and stopover behaviour are generally similar between coastal and inland sites in eastern New Brunswick, as is the abundance of invertebrate resources and number of migrants present. These findings indicate that both coastal and inland locations can provide stopover habitat of broadly similar quality, and that forest songbird migrants do not aggregate in habitat along the ecological barrier of the Fundy Coast.

While refuelling rate was largely invariant to invertebrate resource abundance and abundance of migrants at the study site, the interrelation between invertebrate and migrant abundance suggests that migrants may use stopover habitat according to refuelling rate, moderated by per-capita resource availability. This differs from the density-dependent patterns of refuelling reported by stopover studies occurring more fragmented landscapes, suggesting that the high degree of forest cover in the region may enable songbirds to avoid prolonged refuelling under poor local conditions, fundamentally shaping the stopover behaviour of songbirds in the province. The option to distribute according to food resource availability may have also buffered the impact of any experiential or dominance related disadvantages in young migrants on refuelling, precluding age-related differences in refuelling.

As in other studies of songbird stopover behaviour, my results show the migratory departure behaviour of songbirds in New Brunswick is sensitive to wind conditions, both between days of stopover and within the night of departure. Previous radar observations of nocturnal migratory activity have indicated that the orientation migrants is broadly towards the southwest during autumn migration (Richardson 1972), and this generally matched the average post-departure bearing from the tracking data. This information could be applied to mitigate the collisions with wind turbines in the region, by restricting their usage on nights during the migratory period where winds are most energetically favourable for birds travelling in a southwesterly direction.

6.4 Concluding remarks

Migration is a complex and dynamic behaviour that occurs through complex and dynamic landscapes. Unfortunately, these landscapes seldom reflect the context in which migratory species evolved. Given historic losses of habitat and the current and continued fragmentation of landscapes and anticipated changes wrought by anthropogenic climate change (Albert et al. 2023), it is important that we understand both the range of behaviours exhibited by migrants and how these behaviours may arise from the context in which they are studied. This is crucial not only to gauge how migrants will respond to losses of habitat in the future, but also to understand how current behaviours may reflect the existing constraints and consequences of habitat alteration faced by migrants. Tools such as radio telemetry, radar, and metabolite profiling can be applied to further our understanding of songbird migratory behaviour, and co-application of these techniques can reveal novel insights into the environmental characteristic and individual traits that drive stopover ecology. Understanding these dynamics will strengthen our understanding of the ecology of migrant songbirds and enable the development of robust and appropriate strategies for the conservation of these species in perpetuity.

6.5 References

Åkesson, S., H. Bakam, E. Martinez Hernandez, M. Ilieva, and G. Bianco (2021). Migratory orientation in inexperienced and experienced avian migrants. Ethology Ecology & Evolution 33:206–229.

Åkesson, S., and A. Hedenström (2000). Wind selectivity of migratory flight departures in birds. Behavioral Ecology and Sociobiology 47:140–144.

Albert, C., A. R. Taylor, T. Logan, and L. D’Orangeville (2023). The Acadian Forest of New Brunswick in the 21st century: what shifting heat and water balance imply for future stand dynamics and management. Environmental Reviews 31:690–707.

Alerstam, T., and Å. Lindström (1990). Optimal bird migration: the relative importance of time, energy, and safety. In Bird Migration. Springer-Verlag, New-York, NY, USA, pp. 331–351.

Beauchamp, G. (2011). Long-distance migrating species of birds travel in larger groups. Biology Letters 7:692–694.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser (2006). Climate change and population declines in a long-distance migratory bird. Nature 441:nature04539.

Both, C., and M. E. Visser (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298.

Brown, J. M., B. J. McCabe, L. V. Kennedy, and C. G. Guglielmo (2014). Genetically-based behavioural morph affects stopover refuelling performance in White-throated Sparrows *Zonotrichia albicollis*. Journal of Avian Biology 45:522–527.

Cohen, E. B., J. M. Lafleur, and F. R. Moore (2022). Density dependent refueling of migratory songbirds during stopover within an urbanizing coastal landscape. Frontiers in Ecology and Evolution 10.

Cohen, E. B., F. R. Moore, and R. A. Fischer (2012). Experimental evidence for the interplay of exogenous and endogenous factors on the movement ecology of a migrating songbird. PLOS ONE 7:e41818.

Cresswell, W. (1994). Flocking is an effective anti-predation strategy in Redshanks, *Tringa totanus*. Animal Behaviour 47:433–442.

Delingat, J., F. Bairlein, and A. Hedenström (2008). Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*). Behavioral Ecology and Sociobiology 62:1069–1078.

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. Behavioral Ecology 27:567–574.

Ewert, D. N., M. J. Hamas, R. J. Smith, M. E. Dallman, and S. W. Jorgensen (2011). Distribution of migratory landbirds along the northern Lake Huron shoreline. The Wilson Journal of Ornithology 123:536–547.

Farmer, A. H., and J. A. Wiens (1998). Optimal migration schedules depend on the landscape and the physical environment: a dynamic modeling view. Journal of Avian Biology 29:405–415.

Farnsworth, A. (2005). Flight calls and their value for future ornithological studies and conservation research. The Auk 122:733–746.

Gow, E. A., L. Burke, D. W. Winkler, S. M. Knight, D. W. Bradley, R. G. Clark, M. Bélisle, L. L. Berzins, T. Blake, E. S. Bridge, R. D. Dawson, et al. (2019). A range-wide domino effect and resetting of the annual cycle in a migratory songbird. Proceedings. Biological Sciences 286:20181916.

Goymann, W., F. Spina, A. Ferri, and L. Fusani (2010). Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. Biology Letters 6:478–481.

Gutierrez Ramirez, M. G., A. H. Kneidel, L. A. Lester, M. Temburni, and C. M. Heckscher (2022). Arrival condition and refueling performance of long-distance migratory songbirds at a spring stopover site in the eastern Gulf of Mexico. The Wilson Journal of Ornithology. https://doi.org/10.1676/20-00121

Hamilton, W. J. (1962). Evidence concerning the function of nocturnal call notes of migratory birds. The Condor 64:390–401.

Heise, C. D., and F. R. Moore (2003). Age-related differences in foraging efficiency, molt, and fat deposition of Gray Catbirds prior to autumn migration. The Condor 105:496–504.

Kaplin, M., M. Gutierrez Ramirez, S. Deckel, J. Tatten, D. I. King, and A. R. Gerson (2023). Refueling performance of migratory passerines stopping at an inland stopover site in the Connecticut River Valley. The Wilson Journal of Ornithology 135:103–117.

Kelly, J. F., L. S. DeLay, D. M. Finch, and C. Blem (2002). Density-dependent mass gain by Wilson’s Warblers during stopover. The Auk 119:210–213.

Lok, T., O. Overdijk, and T. Piersma (2015). The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. Biology Letters 11:20140944.

Macdade, L. S., P. G. Rodewald, and K. A. Hatch (2011). Contribution of emergent aquatic insects to refueling in spring migrant songbirds. The Auk 128:127–137.

Maher, C. R., and D. F. Lott (2000). A Review of Ecological Determinants of Territoriality within Vertebrate Species. The American Midland Naturalist 143:1–29.

Mayor, S. J., R. P. Guralnick, M. W. Tingley, J. Otegui, J. C. Withey, S. C. Elmendorf, M. E. Andrew, S. Leyk, I. S. Pearse, and D. C. Schneider (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. Scientific Reports 7:1902.

McCabe, B. J., and C. G. Guglielmo (2019). Migration takes extra guts for juvenile songbirds: energetics and digestive physiology during the first journey. Frontiers in Ecology and Evolution 7.

McCabe, J. D., B. J. Olsen, B. Osti, and P. O. Koons (2018). The influence of wind selectivity on migratory behavioral strategies. Behavioral Ecology 29:160–168.

Mitchell, G. W., A. E. M. Newman, M. Wikelski, and D. Ryan Norris (2012). Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. Journal of Animal Ecology 81:1024–1033.

Mitchell, G. W., B. K. Woodworth, P. D. Taylor, and D. R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Movement Ecology 3:19.

Moore, F. R., P. Kerlinger, and T. R. Simons (1990). Stopover on a Gulf Coast barrier island by spring trans-gulf migrants. The Wilson Bulletin 102:487–500.

Moore, F. R., and W. Yong (1991). Evidence of food-based competition among passerine migrants during stopover. Behavioral Ecology and Sociobiology 28:85–90.

Newton, I. (2008). The migration ecology of birds. First edition. Academic Press, London, UK.

Packmor, F., T. Klinner, B. K. Woodworth, C. Eikenaar, and H. Schmaljohann (2020). Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? Movement Ecology 8:6.

Pagano, S. S., G. L. Orfanides, A. J. Bros, R. L. Hoh, E. S. Delles, A. E. Frawley, and C. P. Carrington (2023). Patterns in the physiological condition of three species of thrushes during autumn stopover near the south shore of Lake Ontario. The Wilson Journal of Ornithology 135:210–223.

Paxton, E. H., S. L. Durst, M. K. Sogge, T. J. Koronkiewicz, and K. L. Paxton (2017). Survivorship across the annual cycle of a migratory passerine, the Willow Flycatcher. Journal of Avian Biology 48:1126–1131.

Piersma, T., L. Zwarts, and J. H. Bruggemann (1990). Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. Ardea 78:157–184.

Renfrew, R., A. M. Strong, N. G. Perlut, S. G. Martin, and T. A. Gavin (2020). Bobolink (*Dolichonyx oryzivorus*), version 1.0. In Bird of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Rguibi-Idrissi, H., R. Julliard, and F. Bairlein (2003). Variation in the stopover duration of Reed Warblers *Acrocephalus scirpaceus* in Morocco: effects of season, age and site. Ibis 145:650–656.

Richardson, W. J. (1972). Autumn migration and weather in eastern Canada: a radar study. American Birds. American Birds 26:10–16.

Saino, N., R. Ambrosini, D. Rubolini, J. von Hardenberg, A. Provenzale, K. Hüppop, O. Hüppop, A. Lehikoinen, E. Lehikoinen, K. Rainio, M. Romano, and L. Sokolov (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proceedings of the Royal Society B: Biological Sciences 278:835–842.

Schaub, M., L. Jenni, and F. Bairlein (2008). Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19:657–666.

Seewagen, C. L., C. D. Sheppard, E. J. Slayton, and C. G. Guglielmo (2011). Plasma metabolites and mass changes of migratory landbirds indicate adequate stopover refueling in a heavily urbanized landscape. The Condor 113:284–297.

Sergio, F., A. Tanferna, R. De Stephanis, L. L. Jiménez, J. Blas, G. Tavecchia, D. Preatoni, and F. Hiraldo (2014). Individual improvements and selective mortality shape lifelong migratory performance. Nature 515:410–413.

Sergio, F., G. Tavecchia, A. Tanferna, J. Blas, G. Blanco, and F. Hiraldo (2019). When and where mortality occurs throughout the annual cycle changes with age in a migratory bird: individual vs population implications. Scientific Reports 9:17352.

Shochat, E., Z. Abramsky, B. Pinshow, and M. E. A. Whitehouse (2002). Density-dependent habitat selection in migratory passerines during stopover: what causes the deviation from IFD? Evolutionary Ecology 16:469–488.

Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Simons, A. M. (2004). Many wrongs: the advantage of group navigation. Trends in Ecology & Evolution 19:453–455.

Smith, R. J., F. R. Moore, and C. A. May (2007). Stopover habitat along the shoreline of northern Lake Huron, Michigan: emergent aquatic insects as a food resource for spring migrating landbirds. The Auk 124:107–121.

Smith, S. B., and S. R. McWilliams (2010). Patterns of fuel use and storage in migrating passerines in relation to fruit resources at autumn stopover sites. The Auk 127:108–118.

Studds, C. E., B. E. Kendall, N. J. Murray, H. B. Wilson, D. I. Rogers, R. S. Clemens, K. Gosbell, C. J. Hassell, R. Jessop, D. S. Melville, D. A. Milton, et al. (2017). Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. Nature Communications 8:14895.

Sullivan, K. A. (1988). Ontogeny of time budgets in Yellow-eyed Juncos: adaptation to ecological constraints. Ecology 69:118–124.

Weber, T. P., B. J. Ens, and A. I. Houston (1998). Optimal avian migration: a dynamic model of fuel stores and site use. Evolutionary Ecology 12:377.

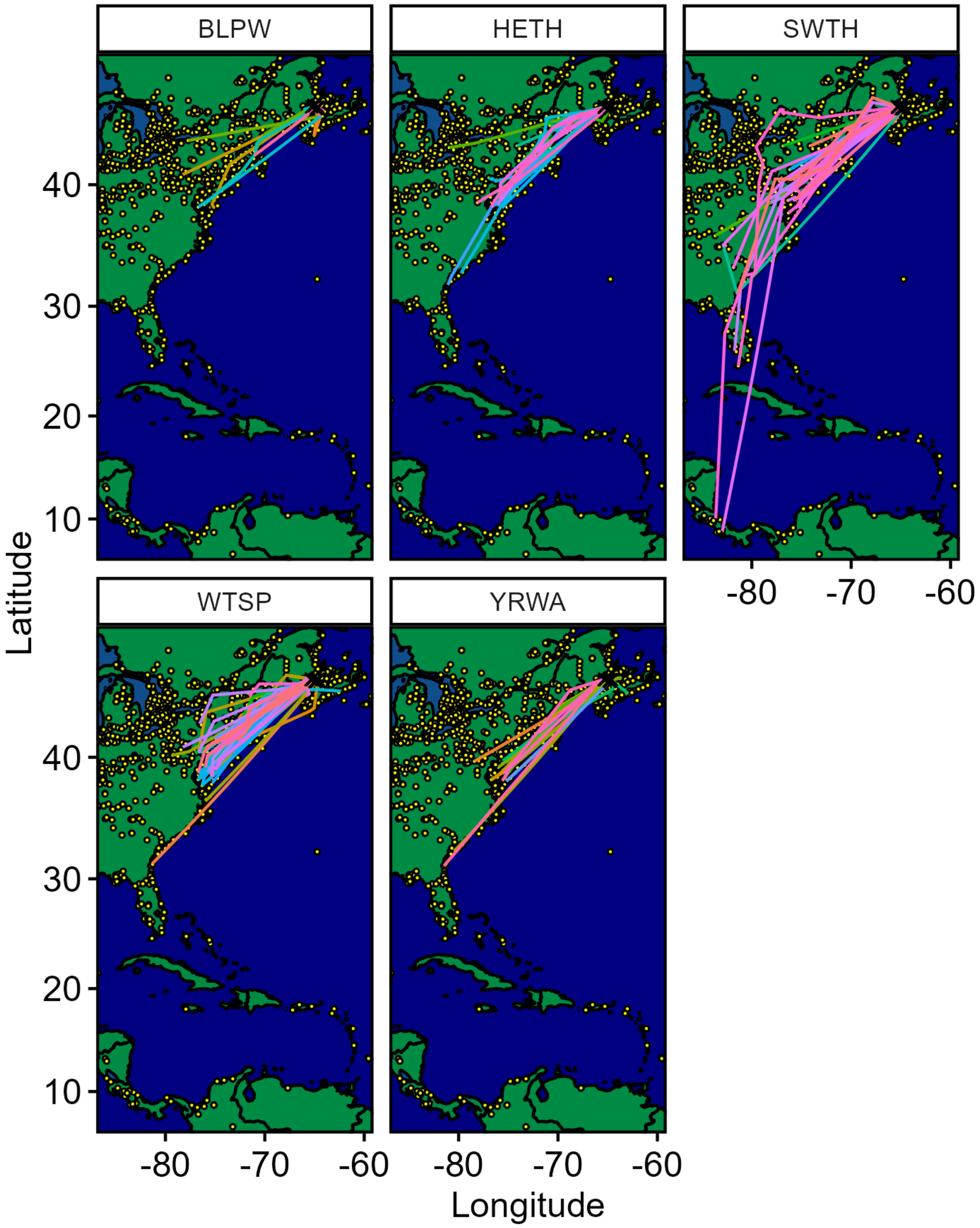
Wheelwright, N. T., and J. J. Templeton (2003). Development of foraging skills and the transition to independence in juvenile Savannah Sparrows. The Condor 105:279–287.

Zimin, S. V., A. Zimin, D. J. Burns, R. Livne, R. Paz, Y. Zvik, E. Shochat, and O. Ovadia (2023). Competition is a major limiting factor of refueling in migratory passerines during stopover. Journal of Avian Biology n/a:e03137.

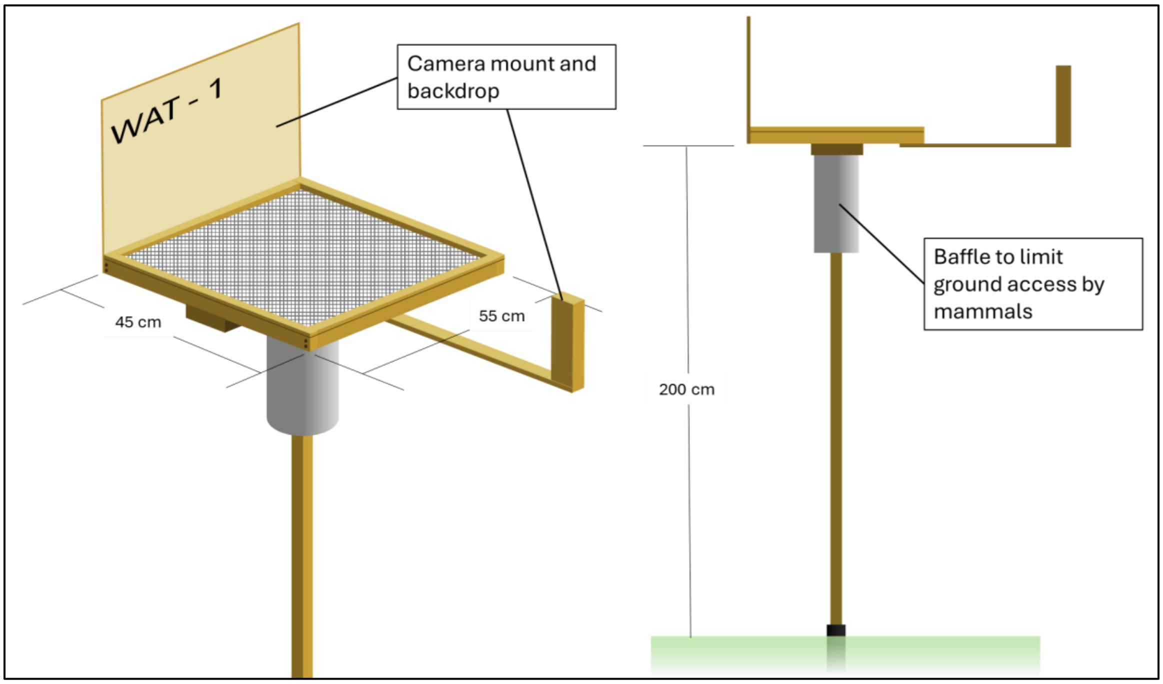
de Zwaan, D. R., A. Huang, Q. McCallum, K. Owen, M. Lamont, and W. Easton (2022). Mass gain and stopover dynamics among migrating songbirds are linked to seasonal, environmental, and life-history effects. Ornithology 139:ukac027.

Appendices

Appendix A. Post-departure movements of five songbird species tagged in eastern New Brunswick during autumn stopover in 2019, 2020, and 2021. Lines are colour-coded by individual, yellow points indicate the location of active Motus Wildlife Tracking System stations.



Appendix B. Schematic of the platform feeding stations used in Chapter 4. Dimensions in the diagram are not to scale.



Appendix C. Excerpt from Wisokolamson Energy Project Radar and Acoustic Monitoring final report. Data collected from this location were used for MTP and WAT in 2020 in chapter 5.

Wisokolamson Energy Project Radar and Acoustic Monitoring Final Report

Philip D. Taylor, Hilary Mann and Jacob Walker
Acadia University, Wolfville, NS.

2021-12-23

3 Methods

3.1 Study area

Placement of radar and acoustic equipment was dependent on access to power, site security and an unobstructed view of the sky. The Wisokolamson radar was placed in the backyard of a homeowner near the substation approximately 10 km from the nearest wind turbine (45.732991°, -64.758943°), with the acoustic unit ~28 m away. At that distance, the radar and audio data collected will be representative of the dynamics of the movements of birds through the Wisokolamson windfarm area.

Figure 1: Map of study area showing the locations of proposed turbines (red points), the position of the radar and acoustic units (blue point) and the approximate detection range of the radar (white lines). The location of the sampled ‘air column’ used for analysis is highlighted (300-320 m from the radar unit).

3.2 Radar equipment

One Furuno Electric Co. (Camas, Washington, USA) 8252 marine radar operating in the microwave X-band (9410 ± 30 MHz, 25 kW) with a 6-foot XN13A open-array antenna was deployed at the site in each season. The radar was mounted on a custom support framework in a vertical orientation to monitor the altitude of targets (See Figure 2), and was run in short pulse mode (2100 pulses per second) at 24 rpm. The approximate maximum range of detection was 4.6 km with a beam width of ~22° in the horizontal plane and ~1.35° in the vertical plane.

Prior to deployment, the radar was calibrated while in a horizontal orientation using targets at a known distance. The radar image was digitized at 4.5 m range resolution with an azimuth resolution of 1.35° using a DSPNOR ScanStreamer (Bergen, Norway). Data were saved onto external hard drives and later analyzed using Cognitive Marine Tracker (CMT) radar analysis software, from the Cognitive Radar Corporation (Waterloo, Ontario).

Figure 2: Photo of radar unit setup.

3.3 Acoustic equipment

We deployed a microphone and recorder for detecting night flight calls (NFCs) in proximity to the radar in all seasons. The unit consisted of a ‘21c microphone system’

(Old Bird Inc., Ithaca, New York, USA) mounted in a bucket with the top oriented to the sky and connected to a secondary booster amplifier and power supply. Audio was recorded with iSound Recorder 7 (Abyss Media) and saved onto external hard drives. The microphone was programmed to start recording up to an hour prior to sunset, and to stop after sunrise.

3.4 Dates monitored

In 2020, the initial work plan included monitoring throughout the spring season. However, due to the Covid- 19 pandemic and associated border restrictions we were not able to deploy equipment in spring 2020. In fall 2020, radar and acoustic units were deployed between 22 Jul and 18 November, but power failures and other malfunctions caused loss of radar data during the following time periods: Aug 1 - Sep 25, Oct 11-12, Nov 2, Nov 5, Nov 13-14 (61 nights total). Therefore, we only present data from 2021 in this report.

In 2021, radar deployment was delayed again due to Covid-19 related border restrictions, and the radar and acoustic units were run continuously from 23 April to 17 November. However, in this report we only consider the spring and fall migratory periods; from 23 April to 12 Jun for spring migration and 1 August to 17 November for fall migration. Power failures and other malfunctions caused loss of radar data during the following time periods in the spring: May 13, Jun 7-9 (4 nights total). These issues also caused loss of radar data during the following time periods in the fall: Sept 15-21 and Oct 16-18 (9 nights total).

3.5 Radar data filtering and processing

Radar data were collected continuously (24 hours per day) but for this report we analyse only data from the period between a half hour before the beginning of evening civil twilight and one half hour after the end of morning civil twilight.

Targets within that period were extracted over background noise if they were at least 6 pixels in size, and the sensitivity to detect targets over the threshold in the CMT software (Pfa setting) was set at 0.02. These settings allowed for weak targets at long range to be identified over background noise, but also were sensitive enough to pick up insects at short range and birds at the edge of the radar beam. To filter out insects and birds on the periphery of the beam at close range, we used the peak power of the radar return for each target (peak_val setting) and corrected it for range, since returned power decreases with range to the fourth power. We refer to the resulting variable as scaled intensity, which was calculated using the following formula:

$$scaledintensity = peakval(dB) - 10 \_ log_{10}(1e13/Range(m)_{4})$$

We used correlations between radar and acoustic data from the nearby Saint John site to discriminate between insect and bird targets using the scaled intensity. We selected 32 nights with numerous flight calls (and no rain) to focus on times when birds were unequivocally flying overhead. We excluded time periods within an hour of civil sunset and sunrise so that birds calling from the ground would not contaminate the correlations.

We computed correlations with targets below 300 m, which is the maximum theoretical range of the Old Bird 21C microphone (for most small species) and compared correlations between the number of bird calls detected and the number of radar targets detected in 30 min intervals for each night selected, and at intervals of 100 m extending along the ground away from the radar. The correlations were strongest for targets at scaled intensities between 12 and 20, but dropped off rapidly for targets below 12 (Figure 3). Hence, we filtered out all targets below a scaled intensity of 12 to avoid contamination from insect targets.

While this filtering helps to exclude non-bird detections, we are unable to confirm that all targets retained for analysis are birds. This is an ongoing issue associated with the use of radar to monitor birds, and we are continuing to develop better ways to determine the identity of targets with more confidence.

We used this information to provide a standardized index of the relative density of targets at different altitudes. From the full data stream we then selected all targets in a “column” of air at a distance along the ground of 300-320 m from the radar. Based on our analysis, targets with a minimum scaled intensity of 12 are detected by the radar at ranges up to about 700 m; this means that smaller birds will have a more-or-less equal probability of detection at altitudes from about 70 - 630 m altitude (from above the ground clutter to the altitude sampled at range 700 m at a distance of 310 m from the base of the radar).

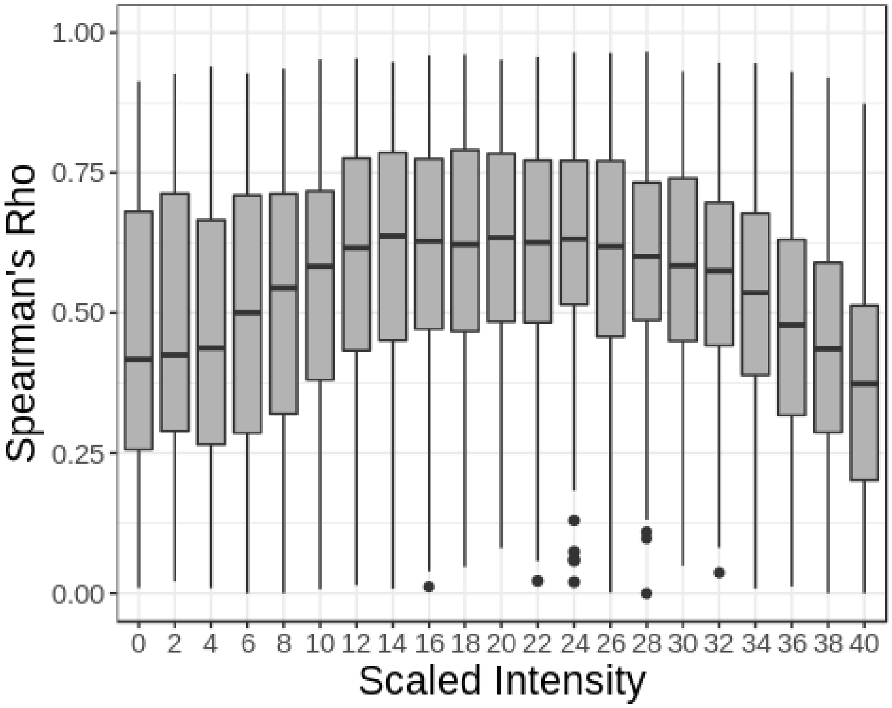


Figure 3: Correlation between the number of bird calls detected and the number of radar targets detected at different scaled intensity levels.

The tracking algorithm included in the CMT software was used to combine targets into tracks for the same nights selected above for comparing audio and radar data, and subsetted to include only targets that passed through the column of air between 300-320 m ground distance from the radar. Of these 1063 tracks that passed through this column of air, 994 (93.5%) were only detected on two or fewer scans, so the number of targets detected is likely comparable to the actual number of birds detected in that airspace. Detections of the smallest targets start to diminish at a range of about 700 m, so beyond a height of about 600 m, detection probability declines.

Radar data was visually inspected to determine periods of rain, which were subsequently excluded from analysis. Additionally, the lower limit of the altitude considered was 70 m above ground level, to eliminate ground clutter.

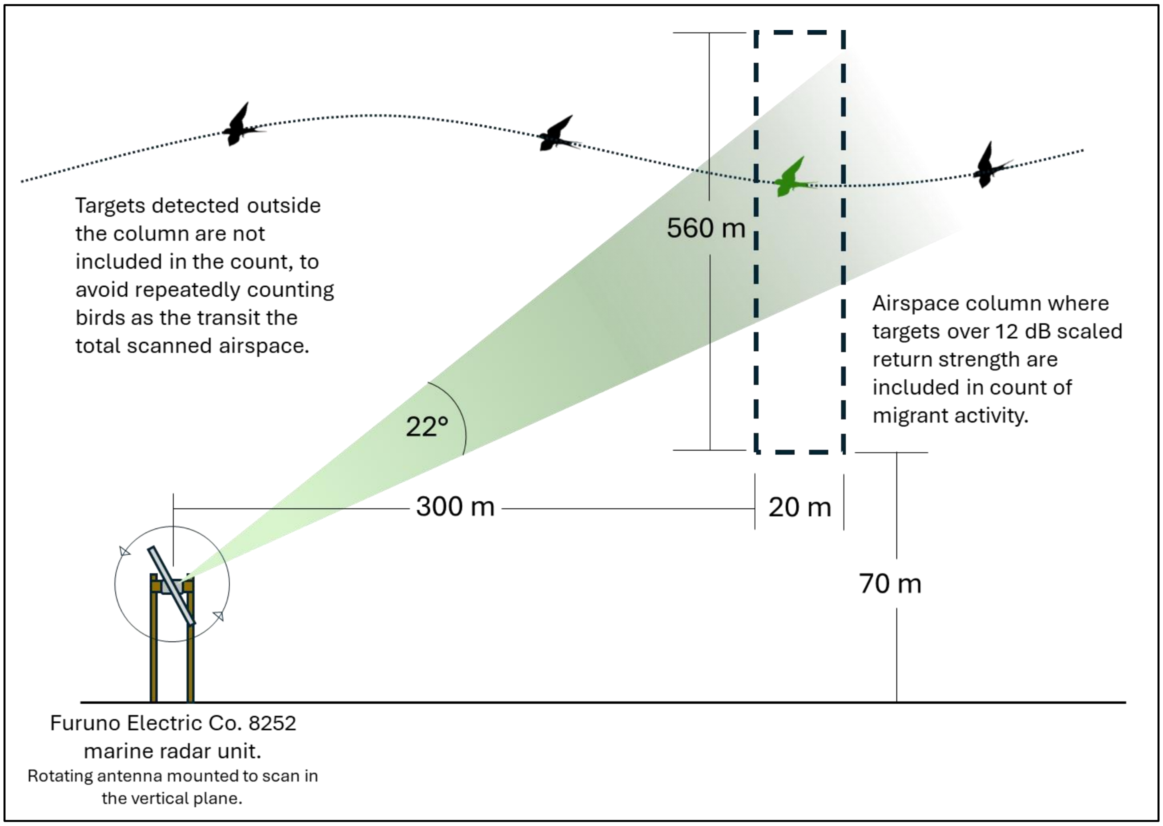
3.6 Acoustic data processing

Acoustic data were collected in conjunction with radar data in both seasons. All data collected were first subsampled to encompass only the period of time between the end of evening civil twilight and the beginning of morning civil twilight. It is during this period that birds make NFCs while actively migrating.

In 2021, acoustic files were processed using custom-built night flight call detectors developed using the OpenSoundScape program (www.opensoundscape.org). Briefly, a library of about 50,000 identified groups of calls (modified from groups presented in Appendix 1 in Sanders and Mennill 2014) were used to train a convolutional neural network model which was used to classify the recordings for the study. The classifier assigns a ‘score’ to each species (or group), which is related to the probability that the detection is actually that species. We developed statistical models to formally assess how that score related to the probability of detecting a species extracting a subset of calls across a range of novel recordings, and had an expert assess them.

While the development of the NFC classifier continues to be refined, the current rates of classification precision (the proportion of calls the classifier correctly identifies) and rates of recall (the proportion of calls that the classifier actually detects) ranges from about 60 to 90% for the thresholds that we used for each species. Here we present classifications amalgamated into two larger groups (sparrows and warblers) for ease of presentation and interpretation. We are still working on the identification of thrush calls, which are difficult to separate from spring peeper calls. In this report, we present data for a subset of nights in 2021, which are representative of activity through both seasons.

Appendix D. Schematic of the marine radar setup and the detection column for monitoring the passage of migrants over a stopover site in Chapter 5. Dimensions in the diagram are not to scale.



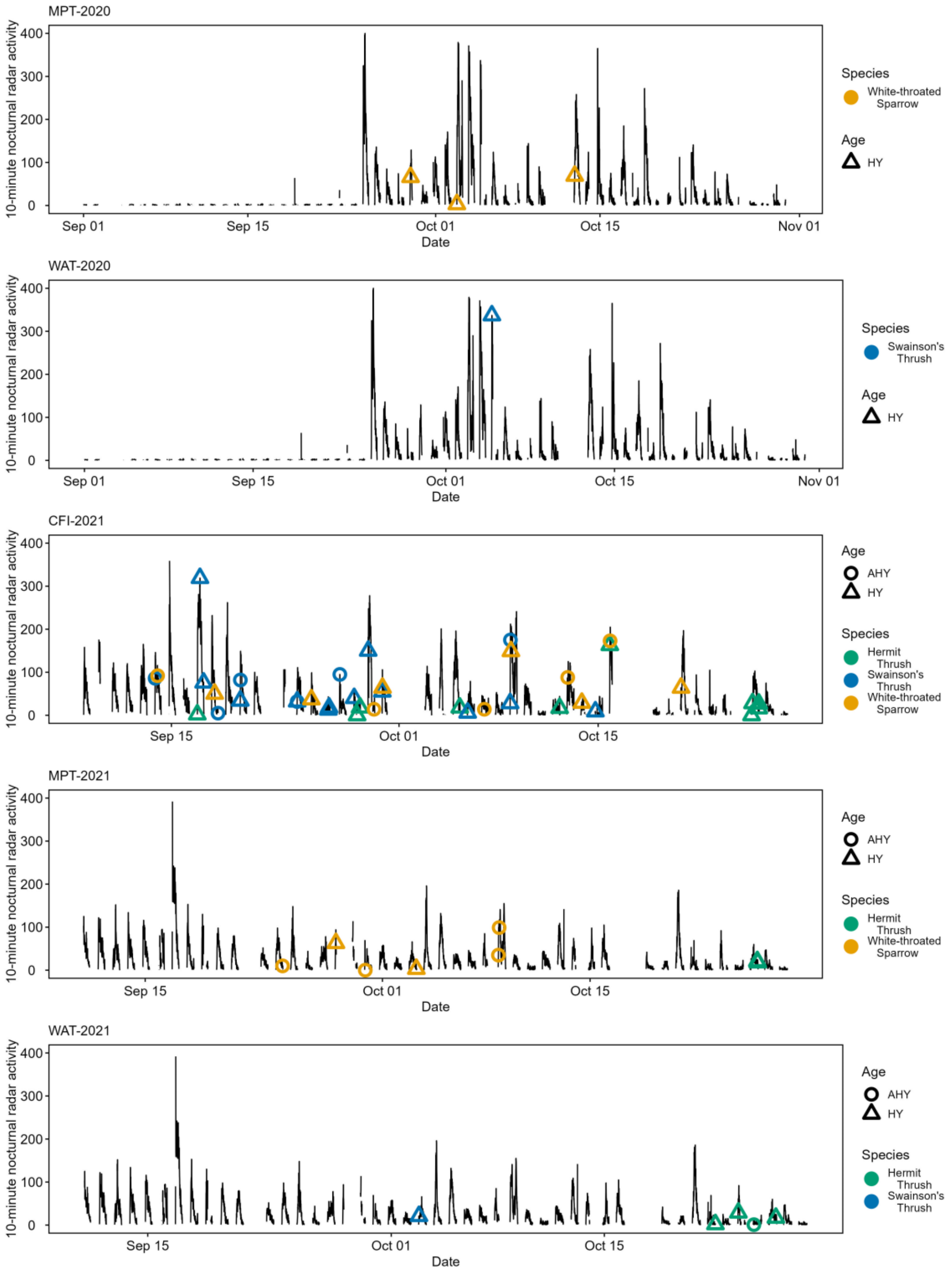
Appendix E. Species and species-groups that could be identified by the artificial intelligence night flight call detection model used in Chapter 5.

Species / Species grouping	**Potential Species**
Cup-Sparrows	☐ Chipping Sparrow (*Spizella passerine*) ☐ Field Sparrow (*Spizella pusilla*) ☐ American Tree Sparrow (*Spizelloides arborea*)
Fox / Song Sparrow Complex	☐ Fox Sparrow (*Passerella iliaca*) ☐ Song Sparrow (*Melospiza melodia*)
Zeep	☐ Bay-breasted Warbler (*Setophaga castanea*) ☐ Blackburnian Warbler (*Setophaga fusca*) ☐ Blackpoll Warbler (*Setophaga striata*) ☐ Cape May Warbler (*Setophaga tigrine*) ☐ Magnolia Warbler (*Setophaga magnolia*) ☐ Northern Waterthrush (*Parkesia noveboracensis*) ☐ Yellow Warbler (*Setophaga petechia*)
Single-banded down sweep	☐ Pine Warbler (*Setophaga pinus*) ☐ Northern Parula (*Setophaga americana*) ☐ Yellow-throated Warbler (*Setophaga dominica*) ☐ Prairie Warbler (*Setophaga discolor*)
Double-up	☐ Black-throated Green Warbler (*Setophaga virens*) ☐ Tennessee Warbler (*Leiothlypis peregrina*) ☐ Nashville Warbler (*Leiothlypis ruficapilla*) ☐ Orange-crowned Warbler (*Vermivora celata*)
Thrushes	☐ Hermit Thrush (*Catharus guttatus*) ☐ American Robin (*Turdus migratorius*) ☐ Swainson’s Thrush (*Catharus ustulatus*) ☐ Veery (*Catharus fuscescens*) ☐ Grey-cheeked Thrush (*Catharus minimus*) ☐ Bicknell’s Thrush (*Catharus bicknelli*) ☐ Eastern Bluebird (*Sialia sialis*) ☐ Wood Thrush (*Hylocichla mustelina*) ☐ Rose-breasted Grosbeak (*Pheucticus ludovicianus*) ☐ Scarlet Tanager (*Piranga olivacea*)

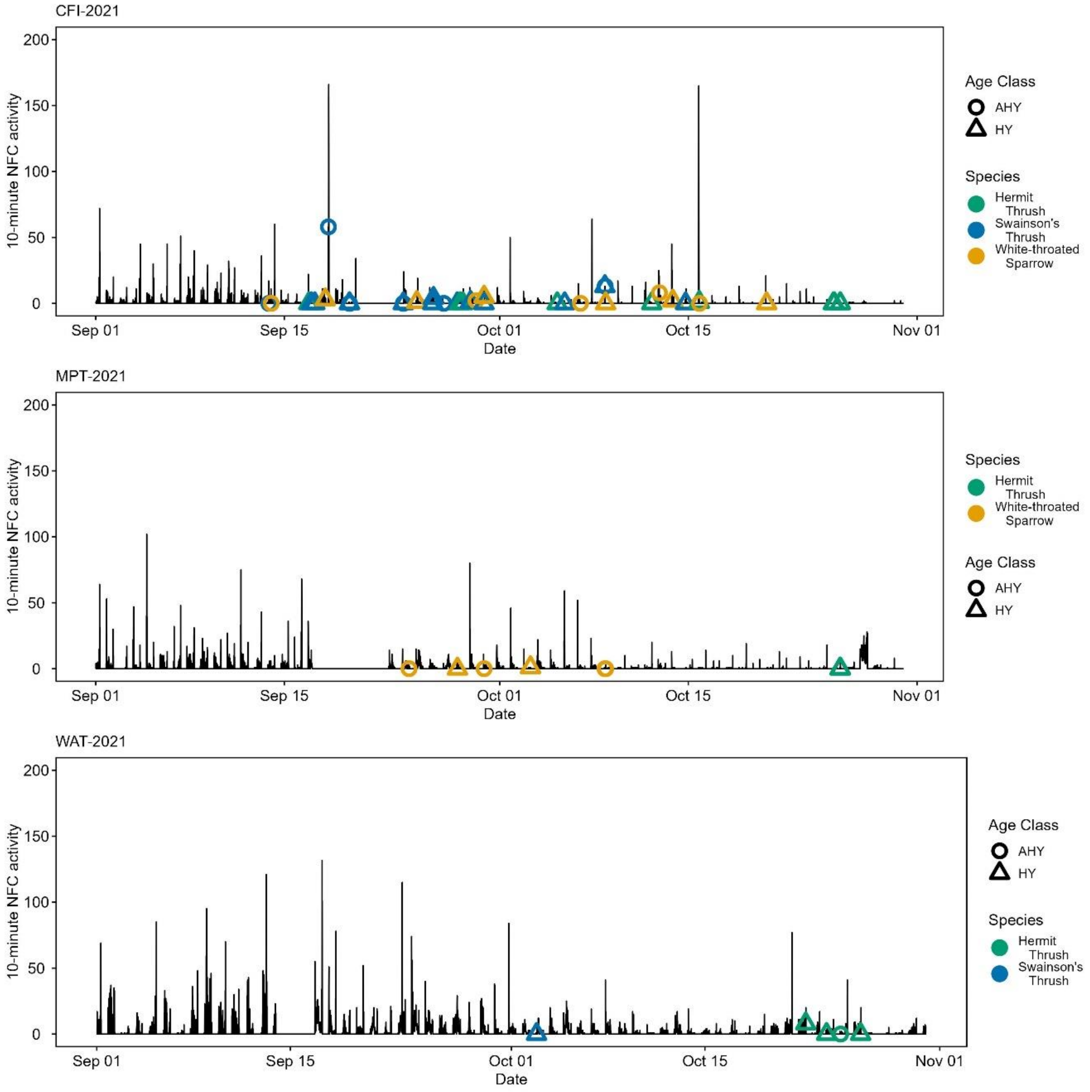
Appendix E (continued). Species and species groups that could be identified by the artificial intelligence night flight call detection model used in Chapter 5.

Full Species	Sparrows: ☐ White-throated sparrow (*Zonotrichia albicollis*) ☐ Savannah Sparrow (*Passerculus sandwichensis*) Warblers: ☐ American Redstart (*Setophaga ruticilla*) ☐ Black-and-white Warbler (*Mniotilta varia*) ☐ Black-throated Blue Warbler (*Setophaga caerulescens*) ☐ Canada Warbler (*Cardellina canadensis*) ☐ Chestnut-sided Warbler (*Setophaga pensylvanica*) ☐ Common Yellowthroat (*Geothlypis trichas*) ☐ Mourning Warbler (*Geothlypis philadelphia*) ☐ Ovenbird (*Seiurus aurocapilla*) ☐ Palm Warbler (*Setophaga pinus*) ☐ Yellow-rumped Warbler (*Setophaga coronata*) Other: ☐ Common Nighthawk (*Chordeiles minor*) ☐ American Woodcock (*Scolopax minor*) Poorly detected/classified: ☐ Wilson's Warbler (*Cardellina pusilla*) ☐ Red-breasted Nuthatch (*Sitta canadensis*) ☐ Pine Siskin (*Spinus pinus*) ☐ Golden-crowned Kinglet (*Regulus satrapa*)

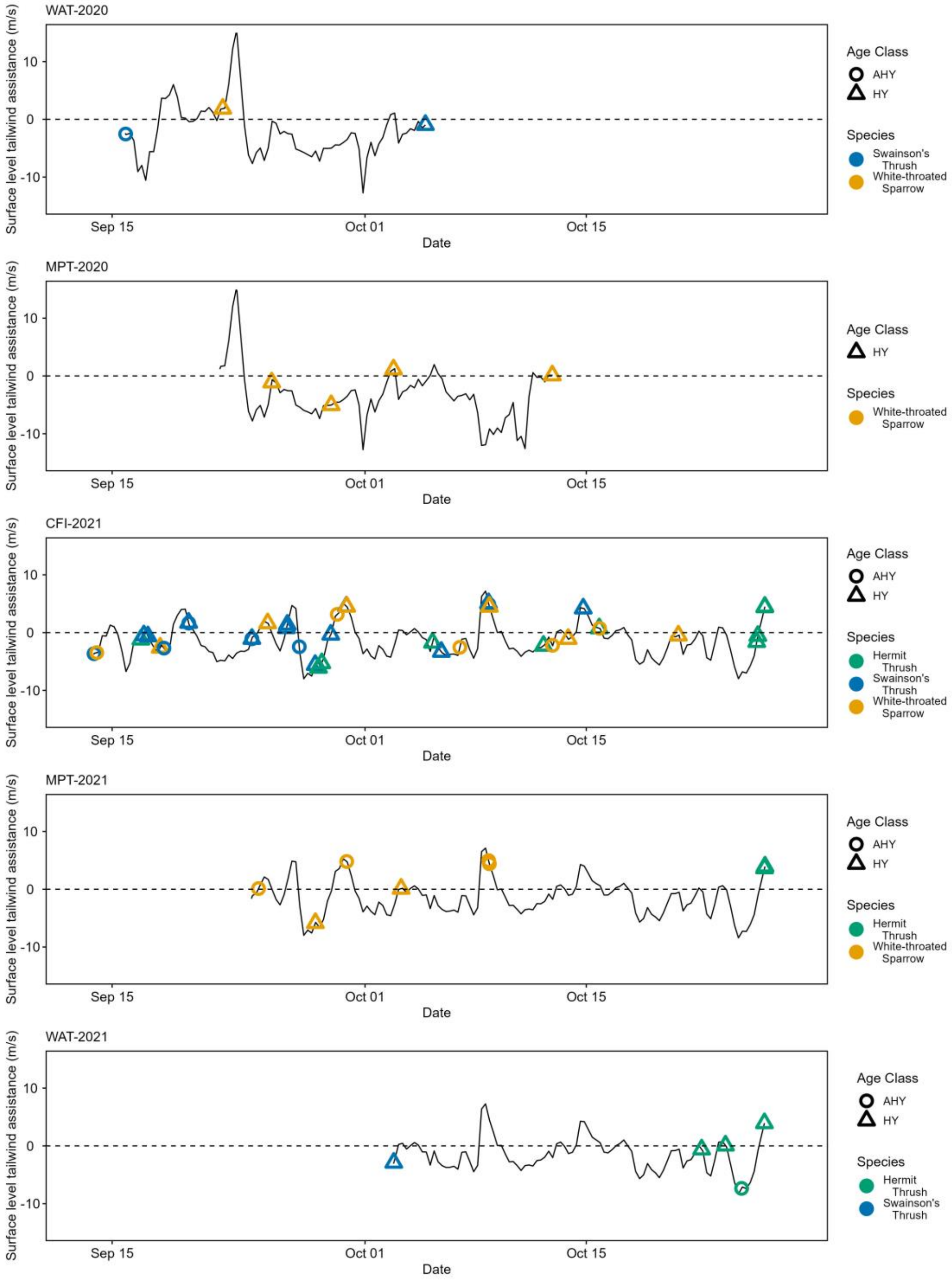
Appendix F. Radar activity, night flight calls, and tailwind assistance relative to the average travel direction of 244° for sites and years where these data were available in Chapter 5. Symbols indicate departure events for each species and age class, with the position on the y-axis indicating the value at the time of departure.



Appendix F (continued). Radar activity, night flight calls, and tailwind assistance relative to the average travel direction of 244° for sites and years where these data were available in Chapter 5. Symbols indicate departure events for each species and age class, with the position on the y-axis indicating the value at the time of departure.



Appendix F (continued). Radar activity, night flight calls, and tailwind assistance relative to the average travel direction of 244° for sites and years where these data were available in Chapter 5. Symbols indicate departure events for each species and age class, with the position on the y-axis indicating the value at the time of departure.



Appendix G. Comparison of candidate models of within-night departure hazard for three bird species captured during autumn stopover in eastern New Brunswick, associated with analysis conducted in Chapter 5. Indicated are model AICc, ΔAICc relative to the best fit model, and Akaike weights (w_i) for each model.

Model #	**Name**	**Model**	**White-throated Sparrow**			**Swainson's Thrush**			**Hermit Thrush**		
10-minute interval			**AICc**	**ΔAICc**	w_i	**AICc**	**ΔAICc**	w_i	**AICc**	**ΔAICc**	w_i
1	Null	~ 1	117.27	7.29	0.02	102.46	2.3	0.11	67.97	3.28	0.14
2	Migrant passage	~ Migrant passage	119.45	9.47	0.01	104.66	4.5	0.04	69.64	4.95	0.06
3	**Tailwind**	**~ Tailwind**	**109.98**	**0**	**0.65**	**100.16**	**0**	**0.34**	**64.69**	**0**	**0.72**
4	NFC	~ NFCs	119.18	9.2	0.01	102.9	2.74	0.09	69.18	4.49	0.08
5	Age class	~ Age class	119.45	9.47	0.01	104.39	4.23	0.04	Insufficient sample size		
6	Tailwind and age class additive	~ Tailwind + Age class	111.92	1.94	0.25	101.91	1.75	0.14			
7	Tailwind and age class interaction	~ Tailwind + Age class + Tailwind * Age class	114.53	4.55	0.07	101.19	1.03	0.2			
8	Migrant passage and age class additive	~ Migrant passage + Age class	121.87	11.89	0	106.82	6.66	0.01			
9	Migrant passage and age class interaction	~ Migrant passage + Age class + Migrant passage * Age class	124.49	14.51	0	109.33	9.17	0			
10	NFC and age class additive	~ NFCs + Age class	121.57	11.59	0	105.33	5.17	0.03			
11	NFC and age class interaction	~ NFCs + Age class + NFCs * Age class	124.12	14.14	0	107.23	7.07	0.01			

Appendix G (continued). Comparison of candidate models of within-night departure hazard for three bird species captured during autumn stopover in eastern New Brunswick, associated with analysis conducted in Chapter 5. Indicated are model AICc, ΔAICc relative to the best fit model, and Akaike weights (w_i) for each model.

20-minute interval			**AICc**	**ΔAICc**	w_i	**AICc**	**ΔAICc**	w_i	**AICc**	**ΔAICc**	w_i
1	Null	~ 1	133.3	8.43	0.01	103.85	3.7	0.08	61.46	5.15	0.07
3	Migrant passage	~ Migrant passage	135.07	10.2	0	105.99	5.84	0.03	63.28	6.97	0.03
4	**Tailwind**	**~ Tailwind**	**124.87**	**0**	**0.67**	**100.15**	**0**	**0.5**	**56.31**	**0**	**0.88**
5	NFC	~ NFCs	135.3	10.43	0	104.37	4.22	0.06	63.37	7.06	0.03
6	Age class	~ Age class	135.46	10.59	0	105.83	5.68	0.03	Insufficient sample size		
7	Tailwind and age class additive	~ Tailwind + Age class	127.03	2.16	0.23	102.29	2.14	0.17			
8	Tailwind and age class interaction	~ Tailwind + Age class + Tailwind * Age class	129.18	4.31	0.08	103.56	3.41	0.09			
9	Migrant passage and age class additive	~ Migrant passage + Age class	137.4	12.53	0	108.22	8.07	0.01			
10	Migrant passage and age class interaction	~ Migrant passage + Age class + Migrant passage * Age class	139.72	14.85	0	110.77	10.62	0			
11	NFC and age class additive	~ NFCs + Age class	137.69	12.82	0	106.77	6.62	0.02			
12	NFC and age class interaction	~ NFCs + Age class + NFCs * Age class	139.38	14.51	0	109.11	8.96	0.01			

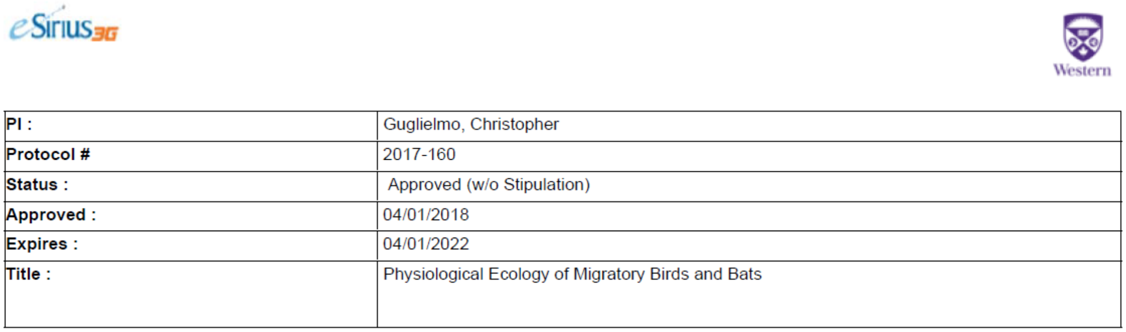
Appendix G (continued). Comparison of candidate models of within-night departure hazard for three bird species captured during autumn stopover in eastern New Brunswick, associated with analysis conducted in Chapter 5. Indicated are model AICc, ΔAICc relative to the best fit model, and Akaike weights (w_i) for each model.

30-minute interval			**AICc**	**ΔAICc**	**w_i**	**AICc**	**ΔAICc**	**w_i**	**AICc**	**ΔAICc**	**w_i**
1	Null	~ 1	133.41	8.85	0.01	105.52	2.56	0.13	68.37	1.81	0.23
3	Migrant passage	~ Migrant passage	135.26	10.7	0	107.67	4.71	0.04	70.64	4.08	0.07
4	**Tailwind**	**~ Tailwind**	**124.56**	**0**	**0.67**	**102.96**	**0**	**0.45**	**66.56**	**0**	**0.58**
5	NFC	~ NFCs	135.6	11.04	0	107.01	4.05	0.06	69.76	3.2	0.12
6	Age class	~ Age class	135.57	11.01	0	107.71	4.75	0.04	Insufficient sample size		
7	Tailwind and age class additive	~ Tailwind + Age class	126.7	2.14	0.23	105.34	2.38	0.14			
8	Tailwind and age class interaction	~ Tailwind + Age class + Tailwind * Age class	128.88	4.32	0.08	105.92	2.96	0.1			
9	Migrant passage and age class additive	~ Migrant passage + Age class	137.59	13.03	0	110.08	7.12	0.01			
10	Migrant passage and age class interaction	~ Migrant passage + Age class + Migrant passage * Age class	139.25	14.69	0	112.73	9.77	0			
11	NFC and age class additive	~ NFCs + Age class	137.98	13.42	0	109.26	6.3	0.02			
12	NFC and age class interaction	~ NFCs + Age class + NFCs * Age class	138.71	14.15	0	111.37	8.41	0.01			

Appendix G (continued). Comparison of candidate models of within-night departure hazard for three bird species captured during autumn stopover in eastern New Brunswick, associated with analysis conducted in Chapter 5. Indicated are model AICc, ΔAICc relative to the best fit model, and Akaike weights (w_i) for each model.

40-minute interval			**AICc**	**ΔAICc**	***w*_i**	**AICc**	**ΔAICc**	***w*_i**	**AICc**	**ΔAICc**	***w*_i**
1	**Null**	**~ 1**	**98.81**	**0**	**0.23**	**68.64**	**0**	**0.19**	43.01	2.72	0.15
3	Migrant passage	~ Migrant passage	101.04	2.23	0.08	70.18	1.54	0.09	42.41	2.12	0.21
4	Tailwind	~ Tailwind	99.7	0.89	0.15	69.01	0.37	0.16	**40.29**	**0**	**0.6**
5	NFC	~ NFCs	99.91	1.1	0.13	70.74	2.1	0.07	45.45	5.16	0.05
6	Age class	~ Age class	100.55	1.74	0.1	69.34	0.7	0.14	Insufficient sample size		
7	Tailwind and age class additive	~ Tailwind + Age class	101.34	2.53	0.07	69.51	0.87	0.13			
8	Tailwind and age class interaction	~ Tailwind + Age class + Tailwind * Age class	99.88	1.07	0.14	72.18	3.54	0.03			
9	Migrant passage and age class additive	~ Migrant passage + Age class	103.06	4.25	0.03	71.28	2.64	0.05			
10	Migrant passage and age class interaction	~ Migrant passage + Age class + Migrant passage * Age class	104.47	5.66	0.01	70.47	1.83	0.08			
11	NFC and age class additive	~ NFCs + Age class	101.63	2.82	0.06	71.88	3.24	0.04			
12	NFC and age class interaction	~ NFCs + Age class + NFCs * Age class	104.03	5.22	0.02	72.79	4.15	0.02			

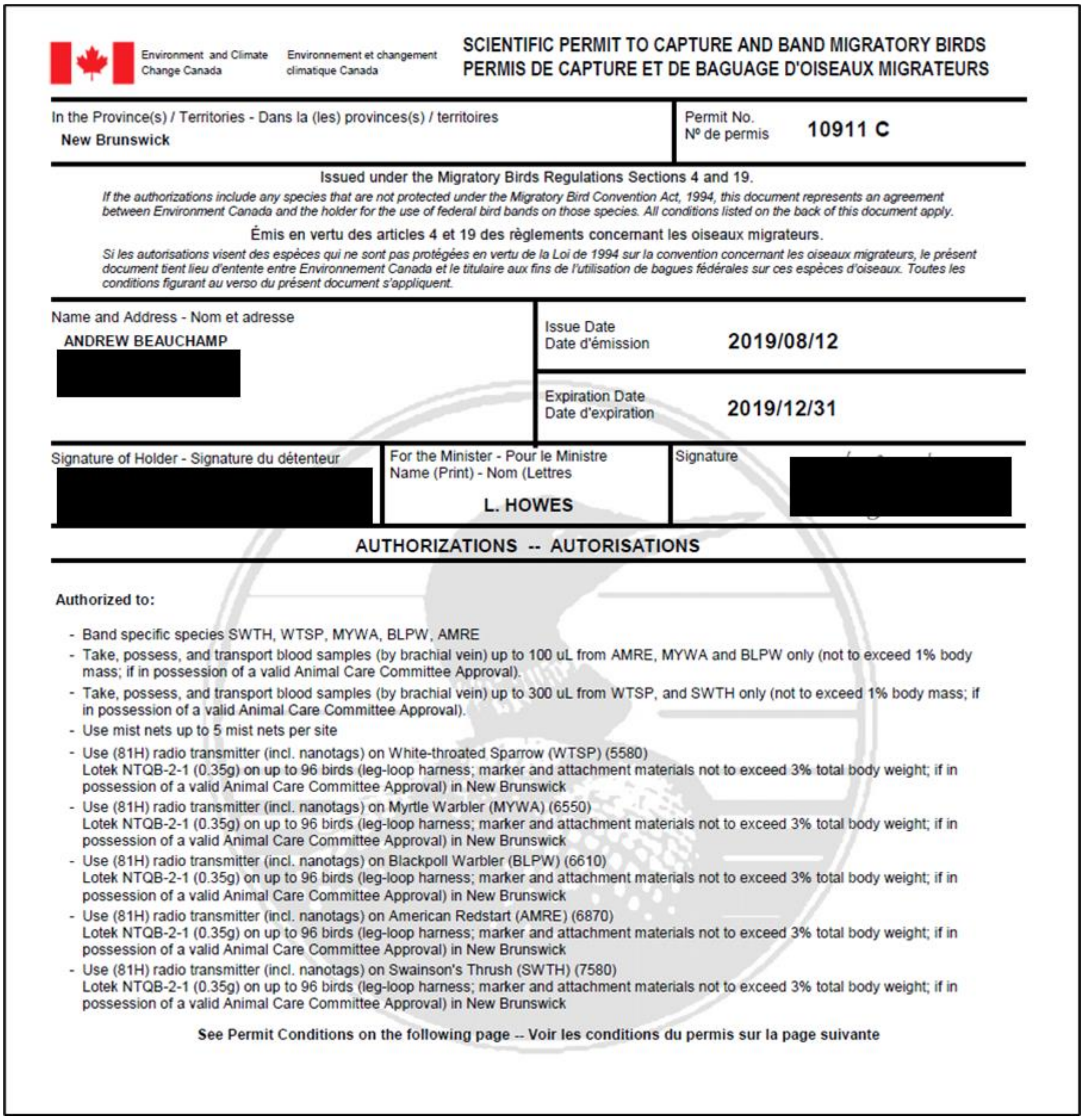
Appendix H. Ethics approvals and permits.



eSirius3G

Western

PI :	Guglielmo, Christopher
Protocol #	2017-160
Status :	Approved (w/o Stipulation)
Approved :	04/01/2018
Expires :	04/01/2022
Title :	Physiological Ecology of Migratory Birds and Bats



Environment and Climate Change Canada
Environnement et changement climatique Canada

SCIENTIFIC PERMIT TO CAPTURE AND BAND MIGRATORY BIRDS
PERMIS DE CAPTURE ET DE BAGUAGE D'OISEAUX MIGRATEURS

In the Province(s) / Territories - Dans la (les) provinces(s) / territoires **New Brunswick**	Permit No. Nº de permis **10911 C**

Issued under the Migratory Birds Regulations Sections 4 and 19.

If the authorizations include any species that are not protected under the Migratory Bird Convention Act, 1994, this document represents an agreement between Environment Canada and the holder for the use of federal bird bands on those species. All conditions listed on the back of this document apply.

Émis en vertu des articles 4 et 19 des règlements concernant les oiseaux migrateurs.

Si les autorisations visent des espèces qui ne sont pas protégées en vertu de la Loi de 1994 sur la convention concernant les oiseaux migrateurs, le présent document tient lieu d'entente entre Environnement Canada et le titulaire aux fins de l'utilisation de bagues fédérales sur ces espèces d'oiseaux. Toutes les conditions figurant au verso du présent document s'appliquent.

Name and Address - Nom et adresse **ANDREW BEAUCHAMP** [redacted]	Issue Date Date d'émission	**2019/08/12**
	Expiration Date Date d'expiration	**2019/12/31**

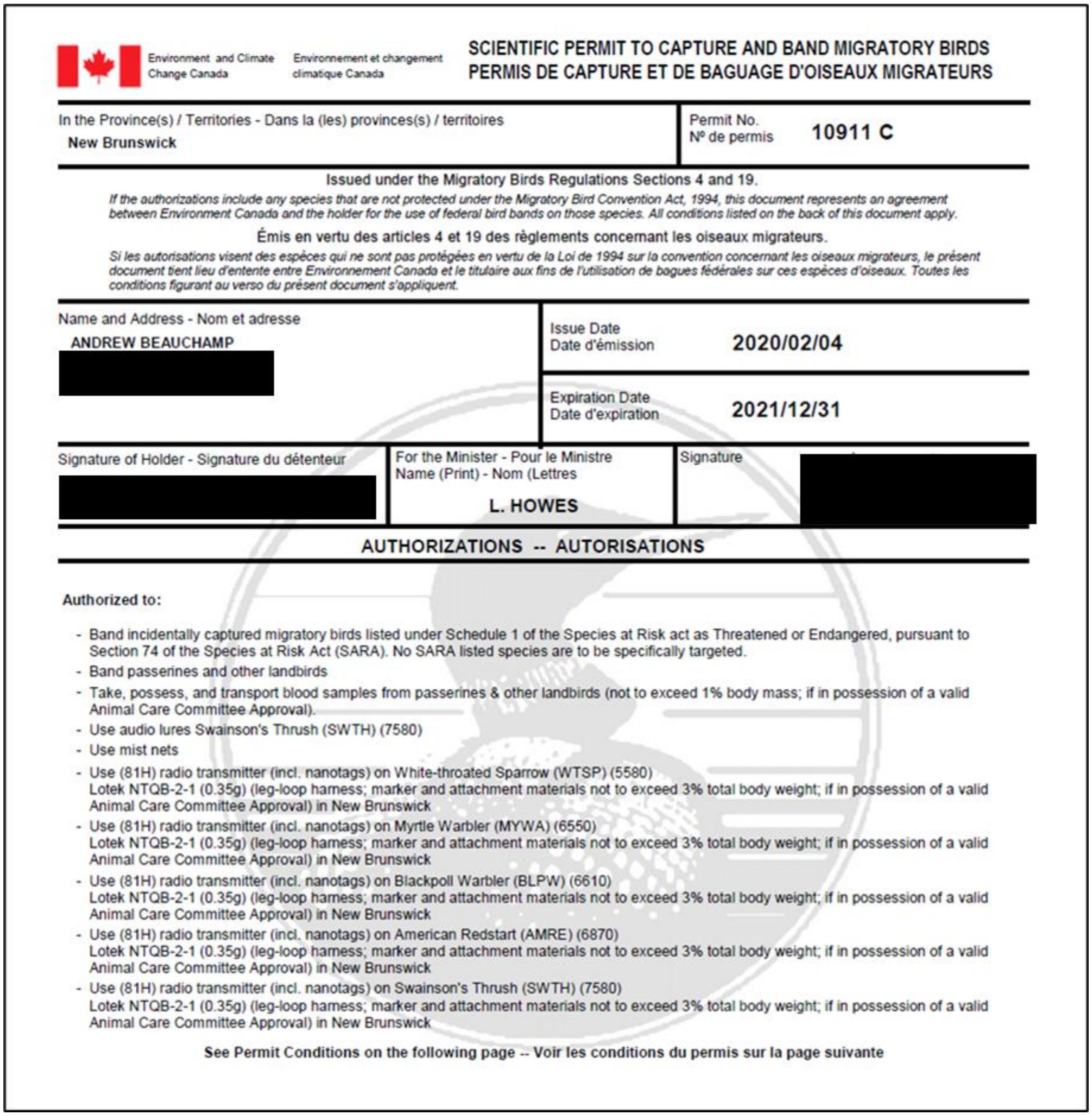
Signature of Holder - Signature du détenteur [redacted]	For the Minister - Pour le Ministre Name (Print) - Nom (Lettres **L. HOWES**	Signature [redacted]

AUTHORIZATIONS -- AUTORISATIONS

Authorized to:

- Band specific species SWTH, WTSP, MYWA, BLPW, AMRE
- Take, possess, and transport blood samples (by brachial vein) up to 100 uL from AMRE, MYWA and BLPW only (not to exceed 1% body mass; if in possession of a valid Animal Care Committee Approval).
- Take, possess, and transport blood samples (by brachial vein) up to 300 uL from WTSP, and SWTH only (not to exceed 1% body mass; if in possession of a valid Animal Care Committee Approval).
- Use mist nets up to 5 mist nets per site
- Use (81H) radio transmitter (incl. nanotags) on White-throated Sparrow (WTSP) (5580)
  Lotek NTQB-2-1 (0.35g) on up to 96 birds (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick
- Use (81H) radio transmitter (incl. nanotags) on Myrtle Warbler (MYWA) (6550)
  Lotek NTQB-2-1 (0.35g) on up to 96 birds (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick
- Use (81H) radio transmitter (incl. nanotags) on Blackpoll Warbler (BLPW) (6610)
  Lotek NTQB-2-1 (0.35g) on up to 96 birds (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick
- Use (81H) radio transmitter (incl. nanotags) on American Redstart (AMRE) (6870)
  Lotek NTQB-2-1 (0.35g) on up to 96 birds (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick
- Use (81H) radio transmitter (incl. nanotags) on Swainson's Thrush (SWTH) (7580)
  Lotek NTQB-2-1 (0.35g) on up to 96 birds (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick

See Permit Conditions on the following page -- Voir les conditions du permis sur la page suivante



Environment and Climate Change Canada
Environnement et changement climatique Canada

SCIENTIFIC PERMIT TO CAPTURE AND BAND MIGRATORY BIRDS
PERMIS DE CAPTURE ET DE BAGUAGE D'OISEAUX MIGRATEURS

In the Province(s) / Territories - Dans la (les) provinces(s) / territoires
New Brunswick

Permit No.
Nº de permis **10911 C**

Issued under the Migratory Birds Regulations Sections 4 and 19.

If the authorizations include any species that are not protected under the Migratory Bird Convention Act, 1994, this document represents an agreement between Environment Canada and the holder for the use of federal bird bands on those species. All conditions listed on the back of this document apply.

Émis en vertu des articles 4 et 19 des règlements concernant les oiseaux migrateurs.

Si les autorisations visent des espèces qui ne sont pas protégées en vertu de la Loi de 1994 sur la convention concernant les oiseaux migrateurs, le présent document tient lieu d'entente entre Environnement Canada et le titulaire aux fins de l'utilisation de bagues fédérales sur ces espèces d'oiseaux. Toutes les conditions figurant au verso du présent document s'appliquent.

Name and Address - Nom et adresse
ANDREW BEAUCHAMP
[redacted]

Issue Date
Date d'émission **2020/02/04**

Expiration Date
Date d'expiration **2021/12/31**

Signature of Holder - Signature du détenteur
[redacted]

For the Minister - Pour le Ministre
Name (Print) - Nom (Lettres)
L. HOWES

Signature
[redacted]

AUTHORIZATIONS -- AUTORISATIONS

Authorized to:

- Band incidentally captured migratory birds listed under Schedule 1 of the Species at Risk act as Threatened or Endangered, pursuant to Section 74 of the Species at Risk Act (SARA). No SARA listed species are to be specifically targeted.
- Band passerines and other landbirds
- Take, possess, and transport blood samples from passerines & other landbirds (not to exceed 1% body mass; if in possession of a valid Animal Care Committee Approval).
- Use audio lures Swainson's Thrush (SWTH) (7580)
- Use mist nets
- Use (81H) radio transmitter (incl. nanotags) on White-throated Sparrow (WTSP) (5580)
  Lotek NTQB-2-1 (0.35g) (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick
- Use (81H) radio transmitter (incl. nanotags) on Myrtle Warbler (MYWA) (6550)
  Lotek NTQB-2-1 (0.35g) (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick
- Use (81H) radio transmitter (incl. nanotags) on Blackpoll Warbler (BLPW) (6610)
  Lotek NTQB-2-1 (0.35g) (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick
- Use (81H) radio transmitter (incl. nanotags) on American Redstart (AMRE) (6870)
  Lotek NTQB-2-1 (0.35g) (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick
- Use (81H) radio transmitter (incl. nanotags) on Swainson's Thrush (SWTH) (7580)
  Lotek NTQB-2-1 (0.35g) (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; if in possession of a valid Animal Care Committee Approval) in New Brunswick

See Permit Conditions on the following page -- Voir les conditions du permis sur la page suivante

Curriculum Vitae

Name: Andrew Beauchamp

Post-secondary Education and Degrees:

Trent University
Peterborough, Ontario, Canada
2011-2016 B.Sc.

The University of Western Ontario
London, Ontario, Canada
2016-2018 M.Sc.

The University of Western Ontario
London, Ontario, Canada
2018-Present Ph.D.

Honours and Awards:

Irene Uchida fellowship
Department of Biology, Western University
October 2023

James L. Baillie Memorial Fund for Bird Research and Preservation & **The Bill and Betty Wasserfall Award**
Birds Canada & The Ontario Bird Banding Association
May 2023

Malcolm Ferguson Award
Department of Biology, Western University
November 2022

Mitacs Accelerate Fellowship
Georgian Bay Land Trust and Birds Canada
May 2022

James L. Baillie Memorial Fund for Bird Research
Society of Canadian Ornithologists Ornithologists-Société des ornithologistes du Canada
March 2022

Mitacs Accelerate Fellowship
Georgian Bay Land Trust
May 2021

Geoff Peach Scholarship

Lake Huron Centre for Coastal Conservation
May 2021

Faculty of Science Graduate Student Teaching Award
Western University
July 2021

Natural Sciences and Engineering Research Council of Canada Alexander Graham Bell Canada Graduate Scholarship-Doctoral
Western University
May 2020 to January 2023

Queen Elizabeth II Graduate Scholarships in Science and Technology
Western University
May 2020 (Declined)

Ruth Horner Arnold Fellowship in Biology
Western University
October 2019

Queen Elizabeth II Graduate Scholarships in Science and Technology
Western University
May 2019 – April 2020

David E. Laudenbach Scholarship
Western University
September 2018

Taverner Student Research Award
Society of Canadian Ornithologists Ornithologists - Société des ornithologistes du Canada
May 2018

Queen Elizabeth II Graduate Scholarships in Science and Technology
Western University
September 2017 – August 2018

Ontario Graduate Scholarship
Western University
September 2016 – August 2017

President's Honour Roll

Trent University
2016

Trent National Renewable Scholarship
Trent University
September 2012 – April 2016

Related Work Experience	Teaching Assistant The University of Western Ontario 2017-2024

Publications:

Guglielmo, C.G., Morbey, Y.E., Kennedy, L.V., Deakin, J., Brown, J.M., & **Beauchamp, A.T.** (2022). A scaling approach to understand the dynamics of fat and lean mass in refueling migrant songbirds measured by quantitative magnetic resonance. *Frontiers in Ecology and Evolution* 10:787623.

Beauchamp, A. T., Kusack, J. W., Hobson, K. A., & Guglielmo, C. G. (2021). Testing the utility of condition indices in nestling swallows: a quantitative magnetic resonance approach. *Journal of Ornithology*, 162(1), 207-219.

Morbey, Y.E., **Beauchamp, A.T.**, Bonner, S.J., Mitchell, G.W. (2020). Evening locomotor activity during stopover differs on pre-departure and departure days in free-living songbirds. *Journal of Avian Biology* 51(11).

Beauchamp, A. T., Guglielmo, C. G., & Morbey, Y. E. (2020). Stopover refueling, movement and departure decisions in the white-throated sparrow: The influence of intrinsic and extrinsic factors during spring migration. *Journal of Animal Ecology*, 89(11), 2553-2566

Crewe, T. L., Deakin, J. E., **Beauchamp, A. T.**, & Morbey, Y. E. (2019). Detection range of songbirds using a stopover site by automated radio-telemetry. *Journal of Field Ornithology*, 90(2), 176-189.