Stopover ecology of two moult migrating passerines: the Swainson's Thrush (*Catharus ustulatus*) and Tennessee Warbler (*Leiothlypis peregrina*) in a large peri-urban park

Vanessa Poirier
Supervised by Dr. Kyle Elliott and Dr. Barbara Frei
Department of Natural Resource Sciences
Faculty of Agricultural and Environmental Sciences
McGill University
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McGill

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ABSTRACT

Migration and moult are two energy-intensive and time-sensitive events often performed sequentially. Although rare in eastern songbirds, some individuals do undergo moult migration, stopping for long periods along their migration route to moult their feathers. Requiring intense physiological changes, moulting birds must occupy high quality habitats to successfully complete their moult. Songbirds migrating at night are attracted to artificial light emitted by cities where such high-quality green spaces are scarce. Moult migrants facing stopovers within peri-urban matrices must therefore make trade-offs between energy gained at resource-abundant sites and time gained by settling at any habitat regardless of quality. Subsequent departure decisions will depend on a bird's ability to successfully moult and refuel for migratory flight. We used radio telemetry to track the stopover behaviour of 48 moult and 41 post-moult migrating Swainson's Thrushes (*Catharus ustulatus*) and the departure decisions of 18 moulting and 4 post-moulting Tennessee Warblers (*Leiothlypis peregrina*) at the McGill Bird Observatory, within one of Canada's largest urban green spaces, from 2018 to 2022. Swainson's Thrushes inhabited densely vegetated forest margins and quickly left sparsely vegetated sites (i.e. fields and mature forests) following experimental translocations. Subsequent departure decisions made by both moult and post-moult Tennessee Warblers were independent of body condition (i.e. mass) and weather cues. Both Tennessee Warblers and Swainson's Thrushes occupied small home ranges during their stay (14 ± 17 ha and 57 ± 107 ha, respectively) which are easily contained by forest patches in cities. Overall, this research highlights the importance of resource-abundant peri-urban forests during a vulnerable time for moult migrant songbirds, and the conservation implications of maintaining these greenspaces.

RÉSUMÉ

La migration et la mue sont deux événements qui nécessaires beaucoup d'énergie et de temps à compléter. Ils sont souvent exécutés séparément. Rares chez les passereaux, certains individus de certaines espèces subissent une migration de mue : un phénomène où les migrants s'arrêtent pendant de longues périodes durant leur migration pour muer leurs plumes. Nécessitant des changements physiologiques intenses, les oiseaux en mue doivent occuper des habitats de bonne qualité pour compléter leur mue. Les passereaux qui migrent pendant la nuit sont attirés par les villes lumineux avec peu d'espaces verts. Les migrants doivent donc choisir entre (1) le temps perdu à chercher des habitats de bonne qualité et (2) l'énergie gagnée sur des sites riches en ressources. À la suite, leurs décisions de départ dépendront de leur capacité à muer et à ravitailler pour le vol migratoire. Nous avons utilisé la radiotélémétrie pour suivre le comportement d'escale de 48 grives à dos olive (*Catharus ustulatus*) en mue et de 41 post-mues et les décisions de départ de 18 parulines obscures (*Leiothlypis peregrina*) en mue et de 4 post-mues à l'Observatoire d'oiseaux de McGill dans un des plus grands parcs urbains au Canada, de 2018 à 2022. Les grives à dos olive habitaient les lisières des forêts à végétation dense et quittaient rapidement les sites à végétation clairsemée (c.-à-d. les champs et les forêts matures) à la suite de translocations expérimentales dans une matrice urbaine. De plus, les décisions de départ prises par les parulines obscures en mues et post-mues n'étaient pas basées sur leur état corporel (c.-à-d. leur grosseur) ni des indices météorologiques. Les parulines obscures et les grives à dos olive occupaient des petits domaines vitaux (14,1 ± 17,2 ha et 56,74 ± 106,9 ha, respectivement), qui sont facilement contenus par des forêts urbaines. Ces recherches démontrent l'importance des forêts urbaines pour les oiseaux migrateurs pendant une période vulnérable, et les implications pour la conservation de ces espaces verts.

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Photo of the bird tracking team in Fall 2021 at the McGill Bird Observatory

CONTRIBUTION OF AUTHORS

I developed the research questions and project design with Kyle Elliott and Barbara Frei. I planned the field work with Barbara Frei, Kyle Elliott, and Ana Morales. Field work was a big part of these experiments and I thus had help from Barbara Frei, Ana Morales, and many other interns. I analyzed the resulting data with advice from Barbara Frei and Kyle Elliott. I am the primary author of this thesis adjusted with edits, comments, and general feedback from both Kyle Elliott and Barbara Frei.

GENERAL INTRODUCTION

Billions of birds migrate every year to and from their breeding and overwintering grounds which can be thousands of kilometers apart. Traveling such long distances requires abundant energy and birds must stop periodically along their migration route to rest and refuel (McWilliams et al., 2004; Nilsson et al., 2013). Before migrating, many birds moult to produce high quality feathers that support them during flight (Hera et al., 2010; Leu & Thompson, 2002). Moult is energetically costly (Buttemer et al., 2019; Podlaszczuk et al., 2017) and an incomplete moult can lead to decreased flight efficiency and slow migration speed (Leu & Thompson, 2002). Because moult and migration are two energetically intensive and time sensitive events they are often temporally separated, however, individuals of some bird species overlap these events; stopping for long periods along their migration route to moult their feathers (known as moult migration; Cherry, 1985).

Moult migration is well-documented in waterfowl, shorebirds, and some seabirds (Leu & Thompson, 2002). Once thought to be rare in neotropical passerines, research has only recently determined its prevalence in songbirds, especially in eastern North American populations (Pyle et al., 2018). Birds must align their moult with the spatial and temporal food availability at their breeding grounds which can be a short timeframe in the North (Barta et al., 2008; Pyle et al., 2018). Individuals who miss this seasonal window migrate to a more resource-abundant site to moult their feathers (Knight et al., 2019; S. Rohwer et al., 2005). Stopover sites where birds moult must have high food availability and provide protection from predators (e.g. Fox et al. 2014; Tietz & Johnson, 2007). Migrants rely on these good quality stopover sites to successfully moult their feathers (Leu & Thompson, 2002) and refuel for migration (Lindström, 2003).

While traveling between their breeding and wintering grounds, birds encounter many human-dominated landscapes. Most passerines migrate at night and are attracted to the bright artificial lights emitted by cities (La Sorte et al., 2014; McLaren et al., 2018). Once the migrants arrive, however, they encounter many threats in the form of fatal collisions with buildings and vehicles and being hunted by cats (Loss et al., 2014; Piontek et al., 2021). Green spaces where birds can stop to moult and refuel are scarce in cities due to habitat loss, fragmentation, and homogenization

(Piano et al., 2020; Seto et al., 2012). These urban stopover sites are often small and lack familiar food sources (Matthews & Rodewald, 2010). Nevertheless, these forest fragments are extremely important for migrating songbirds. Researchers have recently identified migrants' use of spatially heterogenous forest patches in moderately urbanized areas (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023). These forest patches hold higher avian biodiversity than residential areas, city centers, and even wild (i.e. non-urban) forests (Callaghan et al., 2019). Habitat heterogeneity is abundant in the West Island of Montreal where birds encounter several large nature parks and agricultural lands with residential neighborhoods woven throughout. It is not yet known, however, how the habitat characteristics of these sites influence migrants' choices during their stopover and how that might affect their resulting energy stores and migration speed.

Considering that stopovers are the most time-consuming periods during migration (Nilsson et al., 2013; Schmaljohann, 2018; Schmaljohann & Both, 2017), stopover duration and departure timing will effect migration speed. Departure decisions, and thus stopover durations, are governed by a mix of internal (i.e. life-history, body condition, and sex) and external (i.e. weather) cues, but their degree of importance seems to be context dependent (Rappole, 2022; Tan et al., 2018). Long-distance migrants, for example, make shorter stopovers than medium and short-distance migrants (Packmor et al., 2020; Zwaan et al., 2022), as do males of many species (Briedis et al., 2019). Body condition upon arrival will also determine stopover duration as migrants must take time to refuel their fat and protein stores (Ramirez et al., 2022; Yong & Moore, 2005). Moreover, migration is more likely to occur under optimal weather conditions. For southward fall migration in the northern hemisphere, this is typically following a cold front signaled by low humidity, increased pressure, clear skies, and southward winds (Deppe et al., 2015; Packmor et al., 2020; Richardson, 1978). Migrants experiencing time pressures (e.g. long-distance migrants) are known to depart during undesirable weather conditions (Tsvey et al., 2007). Migrants who must take ~1.5 months to moult at their stopover site (Morales et al., 2022) might then similarly disregard weather cues in favour of departing as quickly as possible once their moult is complete.

According to optimal migration theory, birds employ one of two strategies during migration: time-minimization or energy-minimization (Alerstam and Lindstrom 1990). While spring migration, where birds travel from their overwintering to their breeding ground, generally prompts a time-minimization strategy, fall migration, where birds make the opposite journey, allows for energy-minimization. Time-minimizers forage to meet their energy requirements but spend all additional time traveling (Schoener 1971) while energy-minimizers acquire high refueling rates to reduce travel costs (Hedenstrom and Alerstam 1998). To successfully minimize energy expenditure, migrants must presumably target habitats that can offer abundant energy with less foraging effort. The songbirds studied in this thesis should be energy-minimizers as they complete their fall migration, a less time-sensitive period compared to spring migration. Unique individuals performing moult migration, however, have an added time investment because of their moult and may therefore favor a time-minimization strategy instead. If moult migrants were to complete migration within a similar timeframe to post-moult migrants, they would have to increase their migration speed before and after moult, either by decreasing stopover durations or increasing travel speed (Figure 0.1). Part of this thesis (see Chapter 3) will explore this trade-off between time and energy and evaluate the habitat relocation decisions of moult migrants. Primarily, I address the question: will moult migrants spend time searching for energy-abundant stopover sites (i.e. adopt an energy-minimization strategy) or settle for energy-poor sites (i.e. adopt a time-minimization strategy)?

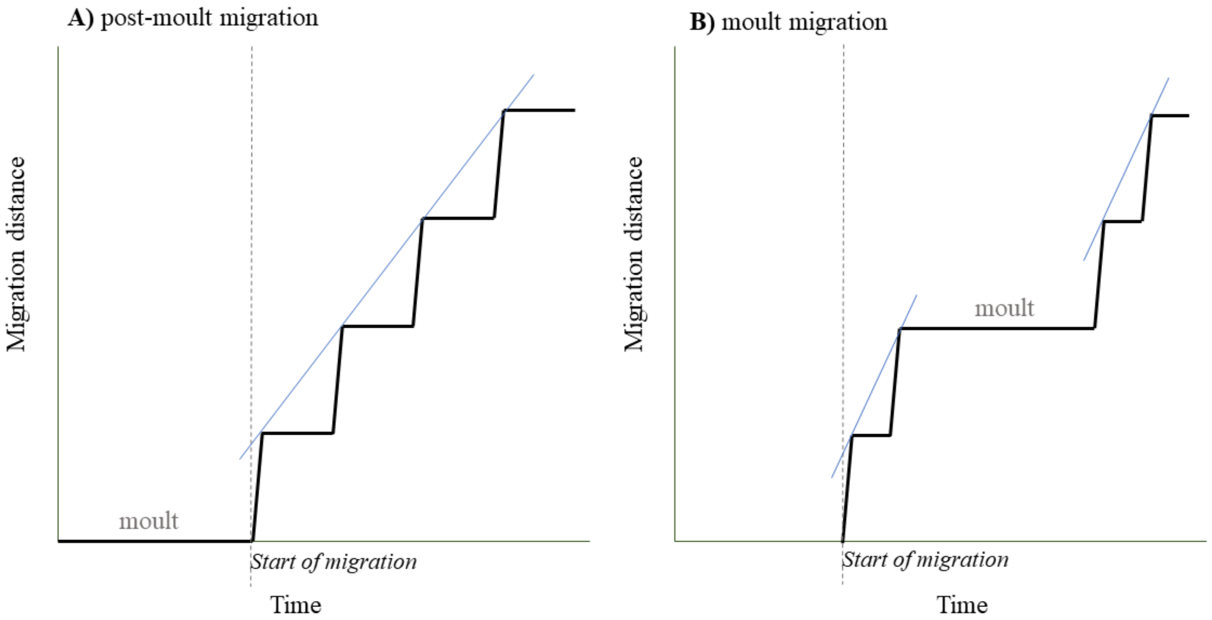

Figure 0.1. Conceptual figure showing the migration speed (distance/time) of (**A**) post-moult migrants who moult at their breeding grounds prior to migration versus (**B**) moult migrants who moult at a stopover site during migration.

Migration speed, exemplified by the slope (i.e. blue line), is steady for post-moult migrants who can undergo (more or less) uniform bouts of stopovers and migratory flights. A moult migrant attempting to migrate within the same time-frame as a post-moult migrant, however, must theoretically compensate for time loss at their moult stopover site by increasing migration speed before and/or after moulting.

In this thesis, I aim to describe the peri-urban stopover ecology of two moult migrating passerines: the Swainson's Thrush (*Catharus ustulatus*) and Tennessee Warbler (*Leiothlypis peregrina*), during their stopover at the McGill Bird Observatory (MBO) in Montreal, Quebec, Canada. Chapter 2 focuses on the stopover duration and subsequent departure decisions of both moult and post-moult migrating Tennessee Warblers. Given that moult migrants require more time and energy to moult, I expected that they spend more time at their stopover site and be less influenced by external cues when deciding to depart. Meanwhile, Chapter 3 showcases migrating Swainson's Thrushes and offers a deeper look into how moult migrants use peri-urban green spaces for their energetic needs during stopover. I employed an experimental translocation study whereby Swainson's Thrushes were captured at the MBO and relocated to sites of differing habitat types. Again, since moulting is energetically expensive (Buttemer et al., 2019; Podlaszczuk et al., 2017), I expected moult migrants to abandon sites with low food availability and protection from predators despite the extra time it would take to search for good-quality sites. In both chapters, I use the Motus Wildlife Tracking System, a global automated radio telemetry network (Griffin et al., 2020), to track the movements of these birds during their stopover in Montreal. My thesis adds to the limited literature on moult migration in eastern North America and offers a novel comparison of habitat characteristics and migrant occupancy decisions in a peri-urban setting.

Chapter 1: Literature Review

Introduction

Migration is extremely energetically costly and is a time when up to 85% mortality occurs in some species of birds (Klaassen et al., 2013; Sillett & Holmes, 2002). Birds traveling long distances must fast while flying and refuel at stopover sites between their breeding and wintering grounds (McWilliams et al., 2004). In eastern North American, some songbirds stop for long periods to moult their flight feathers (Cherry, 1985). This phenomenon, called moult migration, has been employed by some individuals of certain passerine species like the Tennessee Warbler (*Leiothlypis peregrina*) and Swainson's Thrush (*Catharus ustulatus*) (Rimmer & McFarland, 2020; Junda et al. 2020; Morales et al. 2022). Moulting requires intense changes in physiology and can cause decreased flight efficiency and subsequent migration speed if not properly completed (Leu & Thompson, 2002). The success of moult migrants should therefore depend on the quality of their stopover sites. Good quality stopover habitats have high food availability and provide protection from predators ((e.g. Fox et al. 2014; Tietz & Johnson, 2007). Urbanization and associated light pollution attracts migrating birds towards cities where food sources and anthropogenic structures threaten survival (Araújo et al., 2019). Migrating birds therefore take refuge in urban green spaces (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023) where dense vegetation offers food and protection from predators.

Moult Migration

Given that moult and migration are two energetically costly events, they are often separated in time. For example, many eastern North American songbirds perform a pre-basic moult following breeding in late July through mid-August, before beginning their migration in the fall (Pyle et al., 2018). High quality feathers are ideal for traveling long distances during migration (Hera et al., 2010; Leu & Thompson, 2002) but require substantial energy to produce (Buttemer et al., 2019; Podlaszczuk et al., 2017). After moulting, birds must prepare to migrate, a period when they can increase their food intake by as much as 40% and raise their fat reserves to between 15% and 50% of their weight (Lincoln et al., 1950). It is therefore surprising that some species overlap these energetically expensive events during moult migration.

Moult migration is well-documented in waterfowl, shorebirds, and some seabirds but was thought to be rare in neotropical passerine species and primarily restricted to the western populations in North America (Leu & Thompson, 2002). In recent years, studies have shown that moult migration occurs across multiple taxa of landbirds (Pyle et al., 2018). While past research focused on western North American populations (Pageau et al., 2020; Rohwer et al., 2008; Voelker & Rohwer, 1998), moult migration is just as prominent in the east and is even greater in the east for some species (Pyle et al., 2018). Birds with these distinct moulting sites usually find them along their migration route, presumably attracted by the resource-abundant habitats of southern climates (Rohwer et al., 2008).

Although researchers have yet to identify the exact reason why some birds perform moult migration, there is a growing literature supporting the 'push-pull hypothesis' proposed by Rohwer *et al.* (2005). Resource shortages at breeding grounds will 'push' individuals towards better habitats, while simultaneously, birds are 'pulled' towards resource-abundant sites where they can successfully complete their moult (Rohwer et al., 2005). The push away from poor breeding grounds seems to be the strongest contributor to moult migration. Pageau *et al.* (2020), for example, found that arid breeding grounds in western North America drive long-distance migrating species to moult at stopover sites. Barta *et al*. (2008) also found that birds will time their moult depending on the spatial and temporal food availability at breeding and wintering grounds. These types of large-scale movements during the non-breeding period are often related to resource availability (Knight et al., 2019). Pyle *et al.* (2018) also suggests that moult migration is more common in individuals from northern breeding populations, presumably because the north has a shorter productive window and cannot support a breeding and moulting period within the same season. As climate change causes phenological shifts and increases instances of drought in northern breeding grounds (Marra et al., 2015), songbirds may be pushed to moult at more southern and resource-abundant stopover sites (Pageau et al., 2020).

Birds who experience significant time constraints may also feel pressure to perform moult migration. Species that migrate long distances, for example, are more likely to undergo moult migration than short distance migrants, presumably due to the pressure to delay moult in favor of beginning migration as early as possible (Kjellén, 1994; Pageau et al., 2020). Females of many species have been observed performing moult migration in higher proportions than males (Briedis et al., 2019; Junda et al., 2020). This may be explained by females' increased energy and time investments in parental care. In pied flycatchers, for example, males are more likely to overlap moult and nestling feeding, especially as the season draws on (Hemborg, 1999). Males also experience protandry, a strong pressure to migrate earlier than females to reach wintering and breeding grounds first (Briedis et al., 2019). Some songbirds, however, exhibit protogyny in autumn, the opposite phenomenon where females migrate earlier than males (Mills 2005). Differences in sex and life history seem to be a potential cause of moult migration.

Moult migrants: Tennessee Warblers and Swainson's Thrushes

Tennessee Warblers (*Leiothlypis peregrina*) and Swainson's Thrushes (*Catharus ustulatus*) are two species of songbird with high proportions (>50%) of observed moult migration in southern Quebec (Junda et al., 2020). Banding stations only ~300km farther south have observed smaller proportions of moult migrants (~4% of Tennessee Warblers and ~2% of Swainson's Thrushes; Craves, 2009). Landbirds in eastern North America seem to travel shorter distances to their moulting grounds than in the west (Pyle et al., 2018), demonstrating that areas closer to their breeding grounds, like southern Quebec for boreal breeders, can be critical for moult migrants.

An adult Tennessee Warbler (left) and Swainson's Thrush (right) captured at the McGill Bird Observatory. Photo credit: Vanessa Poirier

A moulting Tennessee Warbler (left) and Swainson's Thrush (right) at the McGill Bird Observatory. Photo credit: Vanessa Poirier

Swainson's Thrush

Swainson's Thrushes are medium-sized songbirds in the thrush family (*Turdidae*) that can live up to at least 10 years (Mack & Yong, 2020). There are six recognized subspecies of Swainson's Thrush of which three are grouped into the olive-backed Swainson's Thrush variety (*swainsoni* group) that is the most common in eastern North America, while the other three are part of the russet-backed thrush (*ustulatus* group) that breed in western North America (Mack & Yong, 2020).

Swainson's Thrushes moult only once per year (Pyle et al., 1997). Hatch-year individuals perform a partial first pre-basic moult, where they only moult their head and body feathers, before their first fall migration (Pyle et al., 1997). After hatch-year adults undergo a complete basic moult where they additionally replace their flight and tail feathers (Pyle et al., 1997). Starting as early as July, juvenile and adults alike travel from their breeding grounds in the boreal forest to their wintering grounds anywhere from Mexico to Bolivia (Junda et al., 2020; Mack & Yong, 2020; Morales et al., 2022). In the following spring, individuals often migrate back to their breeding grounds from the previous year (Mack & Yong, 2020). Swainson's Thrushes do not have a breeding plumage, and only moult once every year in late summer or fall.

Swainson’s Thrushes often moult at stopover sites away from their breeding ground (Pyle et al., 2018). In fact, some stopover sites have recorded a higher proportion of moulting individuals to post-moult individuals (Junda et al., 2020). Some eastern Swainson's Thrushes travel quite far south before stopping to moult, as some have been observed moulting in the Mississippi Valley (Cherry, 1985; Pyle et al., 2018). Moult migrating Swainson's Thrushes spend an average of 47 days at their chosen stopover site, a significant portion (13%) of their annual life cycle when compared to better studied periods like breeding which is only ~8% of their life cycle (Morales et al., 2022).

Ideal stopover sites should host Swainson’s Thrushes’ dietary preferences. During migration in the spring and breeding in the summer, Swainson’s Thrushes forage primarily for insects, while during fall migration and at overwintering grounds, individuals become more frugivorous (Mack & Yong, 2020). Like most thrushes, Swainson’s Thrushes are near-ground foragers although slightly less so than other thrushes (Mack & Yong, 2020). Individuals have been observed foraging within centimeters of each other and therefore must inhabit overlapping home ranges (Mack & Yong, 2020). During their fall migration and overwinter, Swainson’s Thrushes rely primarily on fruits including elderberries (*Sambucus* sp.), blackberries and raspberries (*Rubus* spp.), twinberries (*Lonicera* sp.), and huckleberries (*Vaccinium* sp.; Beal, 1915). Swainson’s Thrushes may prefer native plants over exotic species as they are >20% more numerous in native-dominated shrublands than in exotic-dominated shrublands (Oguchi et al., 2018).

Tennessee Warbler

Tennessee Warblers are small birds in the warbler (*Parulidae*) family who can live up to 6.4 years (Klimkiewicz et al., 1983). Tennessee Warblers follow a similar life cycle to Swainson’s Thrushes. During their fall migration, starting as early as July, Tennessee Warblers travel from their breeding grounds in Canadian boreal forests and the northernmost parts of the United States to their wintering grounds in southern Mexico to northwestern South America (Rimmer & McFarland, 2020). Canada hosts virtually all the Tennessee Warbler's global breeding population (Rimmer & McFarland, 2020). Tennessee warblers often use inland routes during migration, making easy use of stopover sites (Rimmer & McFarland, 2020). Many migrating Tennessee Warblers use these stopover sites to moult their feathers (Junda et al., 2020; S. R. Morris et al., 2013; Rimmer & McFarland, 2020).

Unlike Swainson's Thrushes, Tennessee Warblers moult twice each year (Rimmer & McFarland, 2020). Between January and March, adults perform a limited pre-alternate moult at their wintering grounds (Rimmer & McFarland, 2020). Adults later perform their complete pre-basic moult between July and September like Swainson's Thrushes (Mack & Yong, 2020; Rimmer & McFarland, 2020). Juveniles also perform a partial pre-basic moult before their fall migration where they only replace body and head feathers (Rimmer & McFarland, 2020). Moult migration, however, is most often performed by after hatch-year individuals (S. R. Morris et al., 2013).

Tennessee Warblers are primarily insectivorous birds seen foraging near treetops (Rimmer & McFarland, 2020). During the breeding season, individuals become specialists of spruce budworm caterpillars, causing their populations to fluctuate with their prey (Drever et al., 2018; Rimmer & McFarland, 2020; Venier et al., 2009). Throughout migration, Tennessee Warblers' diets are primarily composed of invertebrates but become dominated by fruit during winter (Rimmer & McFarland, 2020). Individuals may also opportunistically feed on fruit and nectar during migration (Sealy, 1989; Tramer & Tramer, 1977). Tennessee Warblers have been observed feeding on *Lonicera* fruit and drinking juice from *Vitis* grapes (Mcatee, 1904; Tramer & Tramer, 1977). Studies have not yet confirmed whether individuals preferentially feed on specific plant species.

Methods of wildlife tracking: Radio telemetry

Energetically demanding life-history events such as breeding, migration, and moult, are annual occurrences for most birds. The outcome of these events can impact a bird's following life stages and overall fitness (Macias-Torres et al., 2022). Despite the importance of studying the full annual life-cycle and the significant amount of time spent at stopover sites (e.g. Morales et al., 2022; Nilsson et al., 2013; Packmor et al., 2020; Wikelski et al., 2003), research on songbirds often occur on breeding and overwintering grounds (Marra et al., 2015). Migration is a particularly unpredictable and vulnerable period for birds although their large geographical movements make this period difficult to study (Mehlman et al., 2005). These difficulties are compounded for most passerines that migrate at night (Pamula et al., 2019). In past years, researchers have relied on capture-recapture methods to study migration (see Junda et al., 2020; Schaub et al., 2001) but recent remote sensing technologies have allowed us to track birds along their migration route (Beauchamp et al., 2020; González et al., 2020; Morales et al., 2022) and at their stopover sites (Hegemann et al., 2018; Ramirez et al., 2022; Rüppel et al., 2023).

Automated radio telemetry is one such technology that allows for remote wildlife tracking. The method consists of attaching VHF (very high frequency) radio-transmitting tags to an animal which can then be detected by antennas (Griffin et al., 2020). Automated radio telemetry, in particular, allows for the constant collection of data. Towers mounted with arrays of directional antennas automatically detect and register any tagged animals within its range (Kissling et al., 2014). Although the range of these towers is estimated at ~15 km, surrounding topography and vegetation can reduce the effective range to ~0.3 to 0.6 km (Crewe et al., 2019; Taylor et al., 2017). These automated radio telemetry systems can capture data more frequently and at a lower cost than other global positioning system (GPS) tags (Kissling et al., 2014). Although the geographical locations are less precise than GPS loggers, radio telemetry expands the limits of these other technologies due to its small size and its ability to be left on the animal without retrieval (Eiler, 1995; Kissling et al., 2014). GPS loggers and satellite tags (e.g. ICARUS) that can download remotely weigh at least 5 g, which is beyond the 3% limit for most migratory birds.

While the benefits of radio telemetry are clear for studying large-scale movements, the technology can also be used on a smaller scale. One study by Morales *et al.* (2022) used radio telemetry to track moult migrating Swainson’s Thrushes’ movements during their stopover. Researchers discovered that Swainson’s Thrushes in fact have a much longer stopover length than first estimated by banding data (47 days compared to 6-9 days, see Junda et al., 2020). The use of automated radio telemetry has grown widely and now includes open-source global networks like the Motus Wildlife Tracking System (Griffin et al., 2020). The Motus Wildlife Tracking System can therefore be used to research avian behaviour at stopover sites and their subsequent migratory movements.

Migration speed and departure decisions

The speed of migration, composed of periods of flight and stopovers to refuel, is mostly determined by stopover duration rather than travel speed (Nilsson et al., 2013; Schmaljohann, 2018; Schmaljohann & Both, 2017). The time a bird chooses to depart from their stopover site will impact their overall migration speed. Departure decisions are affected by internal (i.e. sex, body condition, and life-history traits) and external factors (i.e. weather and social cues) but studies often disagree on the extent of their influence (DeSimone et al., 2022; Gill et al., 2014; Roques et al., 2021; Rüppel et al., 2023).

Wind is a well-known factor affecting a bird's travel speed and energy expenditure during long migratory flights (Deppe et al., 2015). Wind can raise or lower a bird's ground speed by up to 66%, with a direct impact on the cost of transport (Liechti, 2006; Safi et al., 2013). Smaller birds can fly as fast as ~30 k.p.h. for many hours (Tucker, 1969). The amount of energy a bird expends in strong headwinds, however, is noticeably higher than in tailwinds (Elliott et al., 2014; Tucker & Schmidt-Koenig, 1971). Migrants will therefore avoid departing on nights with strong headwinds and sometimes even settle for weak tailwinds (Liechti, 2006). Most birds depart on the earliest date of optimal wind conditions (Gill et al., 2014). With strong wind support, adult birds were able to complete flight journeys 1.4 times faster than juveniles departing in worse conditions (Mitchell et al. 2015). Appropriate wind conditions that do not hinder a bird's flight speed or deplete their energy reserves before stopover are therefore critical during these long migratory flights.

Other elements of weather including atmospheric pressure, humidity, and temperature seem to be influential mostly due to their relation to stormy weather (i.e. incoming wind and precipitation; (Richardson, 1978). Optimal departures in the fall seem to follow a passing cold front signaled by low humidity, increased pressure, clear skies (which is good for visibility), and southward winds (Deppe et al., 2015; Packmor et al., 2020; Richardson, 1978). Similarly, birds avoid departing during rainfall but may still decide to depart soon after rainfall (in the afternoon after raining in the morning, for example; Tan et al., 2018). Beauchamp *et al.* (2020) also saw greater probability of departure from stopover sites on days with strong tailwinds as well as higher temperatures. Other studies have found some species (during autumn migration) are more likely to depart on colder days even though lower temperatures are costly during flight (Packmor et al., 2020; Schmaljohann et al., 2012; Wikelski et al., 2003). The onset of frost also encourages departure as birds take off soon after frost, even with unfavourable weather (Xu and Si 2019). Despite these slight inconsistencies, weather has been argued to be the most influential factor for departure decisions (S. Morris et al., 1996; Richardson, 1990; Rüppel et al., 2023).

Although weather is important for flight, migrants experiencing strong time-constraints may depart in unfavorable weather. Long-distance migrants, for example, make shorter stopovers and are less selective about their departure conditions than shorter-distance migrants (Packmor et al., 2020). Indeed, long-distance migrants deposit fuel faster to shorten their stopover duration and migrate quicker (Zwaan et al., 2022). Migrants making these shorter stopovers leave under varied, even unfavourable, weather conditions, like on a rainy night (Tsvey et al., 2007). Contrarily, short to medium-distance migrants have the flexibility of lengthier stopovers and waiting for better weather conditions (e.g., tailwinds) on departure (Tsvey et al., 2007). Some individuals of one long-distance migratory species, Swainson’s Thrush, also undergo long stopovers (~47 days) to moult their feathers but seem to depart independent of weather conditions (Morales et al., 2022).

Sex may also influence departure decisions as males experience a great pressure to migrate earlier than their female counterparts (i.e. protandry; Briedis et al., 2019). Male white-throated sparrows (*Zonotrichia albicollis*), for example, arrived 11 days earlier to their stopover site than females during spring migration (Beauchamp et al., 2020). Males around a high proportion of females will display a stronger urge to migrate; making it clear that social cues influence migration behaviour (Deakin et al., 2021). Differences between sexes might be context dependent as another study showed similar stopover among male and female wood warblers (*Parulidae*; Morbey et al., 2018). For a majority of species the spring migration has greater time pressures than autumn migration with every part of migration (i.e. airspeed, ground speed, and stopover) being up to 1.4 times faster in spring, so the difference in speed among sexes may only be present in spring (Nilsson et al., 2013; Schmaljohann et al., 2012; Yohannes et al., 2009). The time it takes to moult itself may also differ between sexes, with females starting later but taking a shorter time to moult (Francis et al., 1991). Although recent research showed no relationship between sex and departure decisions for moult migrating Swainson’s Thrushes (Morales et al., 2022), this may be due to different moulting intensities between sexes.

The physical condition of a bird may also affect their departure decisions. A sick bird, for example, may spend more time at a stopover site to recover (Hegemann et al., 2018). That is not to say, however, that the innate strength of a bird’s immune system influences stopover duration as healthy birds, no matter their differences in immunity, will have similar stopover lengths (Eikenaar et al., 2019). Even in the case of a sick bird, a long-distance migrant would only extend their stopover by approximately 1.2 days (or 2.9 days for short-distance migrants; Hegemann et al., 2018). Species will also change their departure behaviour depending on their body size as smaller species usually migrate in larger flocks and/or during the night to avoid predation (Götmark & Post, 1997).

Stopover duration will also depend on the speed at which a bird refuels their fat and protein stores. Birds who had depleted virtually all their stored fat in flight, for example, changed their foraging behaviour (foraging faster and on a wider range of resources) to deposit fat at a faster rate (Yong & Moore, 2005). Northern waterthrushes (*Parkesia noveboracensis*) who arrived with more lean mass spent 22% less time at their stopover site per additional gram of lean mass (Ramirez et al., 2022). While they did not find the same relationship for Swainson’s Thrushes, they did, however, find that Swainson’s Thrushes with higher plasma uric acid, which indicates increased protein catabolism, had shorter stopovers (Ramirez et al., 2022).

Overall, there is evidence that migratory departure decisions are influenced by a mix of intrinsic and extrinsic factors (Tan et al., 2018). Ideal departure conditions would be strong tailwind assistance and clear skies (Rüppel et al., 2023; Zwaan et al., 2022). Not all birds, however, wait for these perfect conditions. In these cases, individuals may be leaving in a rush to arrive early at their breeding grounds (i.e. protandry), or they are sick and must stay longer at their stopover site to recover. Perhaps the most influential factor is an endogenous spatiotemporal programme we have yet to define (Jenni & Schaub, 2003). We have no definitive answer as to how birds decide to depart for migratory flight. It seems to depend on the species, season, and the individual. The uniting factor, however, is the pressure to make a speedy migration. Considering moult migrants must take extra time to moult, this time constraint should affect their departure decisions, a subject not well understood.

Stopover within an urban landscape

Birds use stopover sites to rest and replenish their fat stores during migration (Mehlman et al., 2005). Songbirds expend twice as much energy during stopovers than in migratory flight (Wikelski et al., 2003), making it a period where resource abundance is very important. Migrants make small-scale decisions on landscape use depending on the quality of the habitat (Seewagen et al., 2010). Habitat quality of stopover sites can affect the refueling rate of migrating birds and subsequent migration speed (Lindström, 2003). Stopover sites are becoming increasingly integrated into urban matrices which threaten migrating birds (Araújo et al., 2019; La Sorte et al., 2014). Maintaining high quality stopover sites in urban areas is critical for the migration success of many passerines.

Cities emitting artificial light at night (ALAN) attracts nocturnal migrating passerines, like the Swainson’s Thrushes and Tennessee Warblers during their spring and fall migrations (La Sorte et al., 2014). In fact, the concentration of nocturnal migrants generally increases closer to cities (McLaren et al., 2018). Urban areas are dangerous places for birds, however, as fatal collisions with buildings and vehicles are quite common (Loss et al., 2014). Migrants in cities are also threatened by habitat fragmentation as stopover sites in urban areas are often quite small (Matthews & Rodewald, 2010). Swainson’s Thrushes do not spend as much time within these small forest patches (< 4.5 ha), indicating that they are unsuitable stopover sites (Matthews & Rodewald, 2010). Given the limited number of quality stopover sites in urban areas, this attraction to brightly lit cities can have a detrimental effect on migrating birds (McLaren et al., 2018).

Before migrants stop to refuel, many birds make short movements throughout a stopover site to find a suitable habitat (Mills et al., 2011; Seewagen et al., 2010). This is called the “search and settling phase” where migrants explore the landscape, comparing the relative quality of various microhabitats before settling at the better-quality microhabitats (Mills et al., 2011; Seewagen et al., 2010). Rush *et al.* (2014) demonstrated this phase in a high-elevation habitat-use study where migrating Tennessee Warblers preferentially occupied complex forests with abundant understory vegetation. Swainson's Thrushes primarily used upland forests where shrub cover, canopy cover, and tree diversity were high (La Sorte & Horton, 2021; Rodewald & Matthews, 2005). Other bird species show similar patterns of selecting vegetation-rich areas (Hadjikyriakou et al., 2020). Variation in food availability and quality was also seen to influence when and where a bird decided to moult or refuel (Leu & Thompson, 2002). Birds who choose better quality habitats should have higher refueling rates (e.g. Cohen et al., 2022; Hadjikyriakou et al., 2020) to successfully complete their moult and migration.

During this search and settling phase in cities, migrants seem to select spatially heterogenous habitat fragments (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023). Migrants preferentially inhabit deciduous and riparian forest patches in moderately urbanized areas (Guo et al., 2023). Bird diversity is higher in these 'sub-urban' areas speckled with habitat fragments as opposed to residential areas and city-centers (Buron et al., 2022; Callaghan et al., 2019). The exact habitat characteristics that attract these birds is still unknown.

Habitat preferences depend on the species and how these species budget their energy during moult (Fox et al., 2014). Habitat use may also be difficult to predict as sites which change due to drought or other external effects can be abandoned from one year to the next (example involving the Greylag Goose in Nilsson et al., 2013). Migrating songbirds are also not known to return to the same stopover sites, except for a few isolated examples (Winker et al., 1991). Even so, site fidelity has only been recorded in rare cases in Tennessee Warblers but not in Swainson's Thrushes (Morris et al., 2013). Habitat selection has also recently been seen to change seasonally. Stanley *et al.* (2021) demonstrated, using Wood Thrushes as an example, that individuals are less choosy during migratory periods. This could lead to birds occupying unsuitable habitats should they migrate through a poor quality macrohabitat, like a city.

In the city of Montreal, birds encounter skyscrapers, industrial buildings, and highly urbanized areas. At the western tip of the island, however, there is a mix of more densely vegetated land composed of nature parks and agricultural land with residential neighborhoods woven throughout (Figure 0.1). A large part of the western side of the island is included the Grand Parc de l'Ouest; Canada's largest urban park spanning ~30 km^2 (Ville de Montreal, 2022). The matrix of green space acts as a corridor for southern migrating birds which would otherwise have to settle in the eastern metropolis (Figure 0.1). The McGill Bird Observatory (45.43°N, 73.94°W) where many birds stop during migration is located in the Grand Parc de l'Ouest. Enclosed by several kilometers of green space, the site is bordered by the Ecomuseum Zoo, agricultural fields belonging to McGill University and two nature reserves: the Morgan Arboretum and the Bois-de-la-Roche Park. The habitat is characterized by a mix of wetland, shrubland, mature deciduous forests, and patches of hawthorn and sumac (Bardo et al., 2003). The western tip of Montreal therefore provides a natural haven in an otherwise weakly-vegetated city (Figure 1.1).

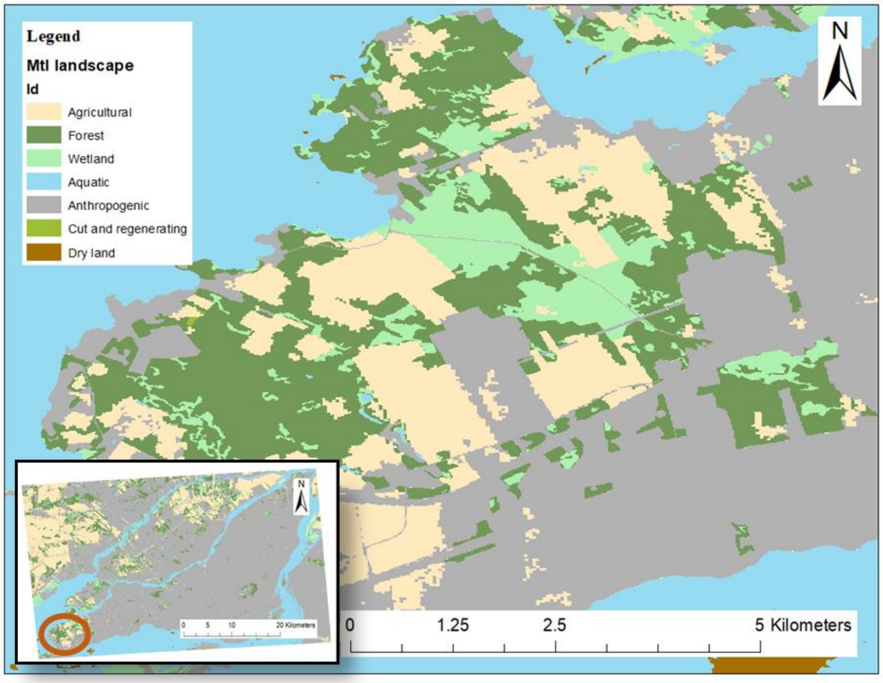

Figure 1.1. A landscape cover map of the West Island of Montreal which is the study site in this thesis. The inset map in the bottom-left corner is a zoomed-out map of the entire island of Montreal with the West Island portion circled.

Conclusion

Light pollution associated with cities attracts migrating birds towards increasingly anthropogenic stopover sites where habitat fragmentation may threaten survival (Araújo et al., 2019). Swainson's Thrushes and Tennessee Warblers are two long distance migrants that occupy stopover sites in Montreal's urban greenspaces during their fall migration (Junda et al., 2020; Morales et al., 2022). For some individuals that perform moult migration, these fall stopover periods are 13% of their annual life cycle (Morales et al., 2022). While most nocturnal migrating birds in North America likely visit cities during their migration, high quality stopover sites are rare (La Sorte & Horton, 2021; Matthews & Rodewald, 2010; McLaren et al., 2018). Birds rely on habitats with high food availability and protection from predators to meet the energetic demands of moult and migration (Dierschke, 2003; Moore et al., 1995). Identifying and conserving these suitable stopover sites is critical to the survival of moult migrating species in Montreal and other cities world-wide.

NOTE ON CHAPTER 2

Chapter 2 is a manuscript in which I am first author and has been submitted (on June 6th 2023) to the Canadian Journal of Zoology. The manuscript describes the stopover duration and departure decisions of moult and post-moult migrating Tennessee Warblers during the autumnal stopover at a peri-urban stopover site. Ana Morales (Environment and Climate Change Canada), Mathilde Lefvert (McGill University), Kyle Elliott (McGill University), and Barbara Frei (Environment and Climate Change Canada) are co-authors on this paper.

Photo of a radio-tagged Tennessee Warbler at the McGill Bird Observatory. Credit: Vanessa Poirier.

Chapter 2: Moult migrant Tennessee Warblers undergo extensive stopover in peri-urban forests of southern Quebec

Authors. Vanessa Poirier[1], Barbara Frei[2], Mathilde Lefvert[1], Ana Morales[2], and Kyle H. Elliott[1]
[1]Department of Natural Resource Sciences, McGill University
[2] Science and Technology Branch, Environment and Climate Change Canada

Abstract. Stopovers are the most energy- and time-consuming events during migration, yet individuals of certain migrants make long stopovers to moult their feathers (‘moult migration’). Time spent at stopovers is linked directly to departure decisions which are influenced by endogenous (i.e. body mass) and exogenous (i.e. weather) factors. To examine whether decisions differ between moult and post-moult migrants, we radio-tagged 18 moulting and 4 post-moult Tennessee Warblers (*Leiothlypis peregrina*) at an autumn stopover site. Moult migrants arrived earlier when breeding success (i.e. number of hatch-year individuals) was low, perhaps “pushed” by poor conditions on the breeding grounds. Moult migrants arrived at the stopover site earlier (average = 2 August) than post-moult migrants (average = 12 September) but left at approximately the same time (in mid-September). Moult migrants also stayed longer (46 ± 5 days) than post-moult migrants (8 ± 6 days) and had large and overlapping home ranges (~15 ha) that were dependent on high abundance of forest (%) and forest edge (m). Departure decisions were independent of body mass and weather. We conclude that Tennessee Warblers occupied forested stopover sites within a peri-urban landscape where they successfully moulted before continuing their migration in mid-September alongside their post-moult peers.

Résumé. Les escales sont les événements les plus longues et énergétiques durant la migration. Certains individus de passereaux s'arrêtent pendant de longues périodes durant une seule escale pour muer leurs plumes (« migration de mue »). Le temps passé aux escales est directement lié aux décisions de départ qui sont influencées par des facteurs endogènes et exogènes. Nous avons marqué par radio-télémétrie 18 parulines obscure (*Leiothlypis peregrina*) en mue et 4 parulines en post-mue entre 2018 et 2022 sur un site d’escale automnale. Les migrants en mue sont arrivés plus tôt lorsque le succès de la reproduction (c.-à-d. le nombre de jeunes individus) était faible, peut-être « poussés » par de mauvaises conditions sur les aires de reproduction. Les migrants en mue sont arrivés sur le site d'escale plus tôt (moyenne = 2 août) que les migrants post-mue (moyenne = 12 septembre) mais sont repartis en même temps (durant mi-septembre). Les migrants en mue sont restés plus longtemps (46 ± 5 jours) que les migrants post-mue (8 ± 6 jours) et avaient des domaines vitaux étendus (~15 ha) qui contenaient en grand parti des forêt (%) et des lisières de forêt (m). Les décisions de départ n’été pas influencées par leur masse ni les conditions météorologiques. Nous concluons que les parulines obscures occupaient des sites forestiers dans un paysage périurbain où elles muent avant de poursuivre leur migration à la mi-septembre.

Keywords. Moult migration, body mass, departure decisions, weather, urban stopover

Introduction

Migration is a time-sensitive and energetically costly event, coinciding with up to 85% mortality in some species (Klaassen et al., 2013; Sillett and Holmes, 2002). Through a series of migratory flights and stopovers, individual migrants must make a series of critical, and potentially costly, decisions (e.g. McWilliams et al., 2004; Nilsson et al., 2013). At every stage, from stopover duration, habitat selection, and departure, migrants must decide the best course of action that will optimize their survival. For a migrant, this entails a speedy migration and an early arrival to summer or winter grounds where they will have first pick of high-quality territories. Stopover duration is the biggest time and energy investment during migration, having an important contribution to overall migration speed (Nilsson et al., 2013; Schaub & Jenni 2001; Wikelski et al., 2003). Migrants seek food and safety at stopover sites but at times must choose habitats that cannot accommodate both (Pomeroy et al., 2008), a decision that can have important consequences for their survival and migration speed.

Despite trying to minimize time at stopovers, individuals of certain species stop for prolonged periods to moult their flight feathers (‘moult migration’; Cherry, 1985; Morales et al., 2022). While rarely studied in Neotropical passerines, moult migration is well-studied in waterfowl, shorebirds, and seabirds (Leu and Thompson, 2002). Nonetheless, there is growing awareness that moult migration may be more important for neotropical migrants than previously thought. For example, Kirtland’s Warblers (*Setophaga kirtlandii*) have an extended autumnal stopover east of Georgian Bay, Ontario, during a period when they are presumably moulting (Cooper et al. 2017). Similarly, at a stopover site in southeastern Quebec, more than half of individuals of 11 songbird species are undergoing moult (Junda et al., 2020). At this same site, moult migrant Swainson’s Thrushes (*Catharus ustulatus*) stay for ~6 times as long as post-moult migrants, a significant amount of time to spend at a single stopover (Morales et al., 2022). Birds typically moult at their breeding grounds in late summer while some perform moult migration seemingly because resource shortages at breeding grounds ‘push’ them towards better habitats, while simultaneously, they are ‘pulled’ towards resource-abundant sites (i.e. the ‘push-pull’ hypothesis proposed by Rohwer *et al.,* 2005 and observed in Barta et al., 2008; Pageau et al., 2020; Pyle et al., 2018). Little is known regarding the behaviours and strategies of Neotropical moult migrants at their stopover sites and how this may affect stopover duration.

A bird's body condition upon arrival at their stopover site will affect their subsequent behaviour (Dossman et al., 2016). Birds with minimal stored fat, for example, foraged faster and on a wider range of resources, successfully depositing fat at a faster rate (Wang and Moore, 2005). Birds arriving with more 'stored' protein also spent 22% less time at their stopover site per additional gram of lean mass (DeSimone et al., 2022; Ramirez et al., 2022). Similarly, a bird arriving with less fuel reserves will forage faster and have larger temporary home ranges (Matthews and Rodewald 2010). Migrants traveling long distances will also spend less time at their stopovers than short and medium-distance migrants (Packmor et al., 2020). In contrast to birds at a short-term refueling stopover, moult migrants are constrained to remain at the moult stopover until their feathers have regrown and they have the aerodynamic ability to continue long-distance flight. Nonetheless, as moult is energetically costly and increases their metabolic rate, we might expect that body condition upon arrival also affects stopover duration. In many cases, these analyses of stopover duration focus on spring migration (e.g. Beauchamp et al., 2020; Schmaljohann and Both, 2017) where birds seem to experience tighter time constraints (Yohannes et al., 2009; Zhao et al., 2017). Contrarily, some species migrate even faster during the fall than in spring (e.g. Mellone et al., 2015; Nuijten et al., 2014). Fall migration may therefore be more time-sensitive than previously perceived and some birds may adjust departure decisions accordingly.

Although internal conditions seem to impact departure decisions, external factors may also be very influential. Weather, particularly wind, is a strong indicator of departure, with migrants departing on the earliest dates with optimal tailwinds (Beauchamp et al., 2020; Deppe et al., 2015; Gill et al., 2014). Strong tailwinds increase travel speed and reduce energy expenditure (Richardson, 1990; Safi et al., 2013). Birds avoid departing during rainfall and prefer clear skies for visibility (Deppe et al., 2015; Tan et al., 2018). Temperature, although influential, is sometimes negatively or positively so, depending on the season (Richardson, 1990). Migrants show a preference for departing on warmer days in the spring (Beauchamp et al., 2020) and colder days in fall (Packmor et al., 2020). Many of these characteristics describe conditions following a cold front, usually the day after, where atmospheric pressure has increased, temperature decreased, and clear skies and strong northern winds support migratory flight (Richardson, 1990). There is a general decrease in the influence of these extrinsic factors, however, on long-distance migrants (Packmor et al., 2020), and may be even lower for migrants experiencing extra time constraints like moult.

A large urban park in southeastern Quebec that hosts a banding station, the McGill Bird Observatory (MBO), is a moulting stopover site for many Neotropical migrants. The park is a matrix of forest and agricultural land within an urban migratory corridor called the "Montreal Gap" stretching 600 km from Lake Ontario and the Saint Lawrence Gulf (Gahbauer et al., 2016). Tennessee Warblers (*Leiothlypis peregrina*) are a frequent moult migrant at the MBO where ~57% of individuals are moulting upon capture (Junda et al., 2020). Previous research has been conducted at this site on the stopover duration and behaviour of Swainson's Thrushes (*Catharus ustulatus*), another frequent moult migrant (Morales et al., 2022). Both Swainson's Thrushes and Tennessee Warblers migrate long distances from their breeding grounds in the North American boreal forests to their overwintering grounds in Mexico and northern South America (Mack and Yong, 2020; Rimmer and McFarland, 2020). While both passerines have a similar migration route, differences in diet may cause different patterns of moult rate, stopover use, and migration timing. Tennessee Warblers being arboreal insectivores (Rimmer and McFarland, 2020), for example, migrate earlier than Swainson's Thrushes (Junda et al, 2020) as insects become less abundant in the North later in the season (Newton, 2007). Moulting Swainson's Thrushes spent significantly more time at their stopover site than post-moult birds and were choosier of the weather conditions upon departure (Morales *et al.* 2022). Our study aims to describe the stopover duration and departure decisions of moult migrating Tennessee Warblers at the same autumnal stopover site.

Given that moulting takes no fewer than 35-40 days for passerines (Francis et al., 1991; Haukioja, 1971), we expect Tennessee Warblers to spend similarly long stopovers as observed in Swainson's Thrushes by Morales *et al.* (2022). According to the push-pull hypothesis, we should observe more moult migrants in years where conditions at the breeding grounds are poor. Tennessee Warblers are notoriously dependent on spruce budworm outbreaks during breeding (Venier et al., 2009), and poor outbreak years may lead to low breeding success and many moult migrants. The number of moult migrants should therefore be negatively correlated with the number of hatch-year individuals (as a proxy for productivity at the breeding grounds) for any given year. In addition, we expect moult migrants with limited mobility and reduced diurnal activity (Leu and Thompson, 2002; Morales et al., 2022) to occupy small home ranges and only consider departure once they are physically able. As moult migrants already spend significantly more time at their stopover site; we expect them to have the opportunity to align their departure with favourable weather conditions (similar to Morales et al., 2022 and Tsvey et al. 2007). Therefore, a moult migrant's departure decision should primarily rely on body condition but be further fine-tuned to align with favourable weather conditions (i.e. strong wind, low temperature, and decreasing atmospheric pressure).

Materials and methods

Study site and historical data

The McGill Bird Observatory (MBO) is located at the western tip of the island of Montreal (45.43°N, 73.94°W) in Quebec, Canada. Enclosed by agricultural fields belonging to McGill University and two nature reserves: the Morgan Arboretum and the Bois-de-la-Roche Park (see Figure 2.4), the habitat is characterized by a mix of wetland, shrubland, and mature deciduous forests (Bardo et al., 2003). The MBO has captured many moult migrating songbirds during their fall migration; Tennessee Warblers being the second most abundant (Junda et al. 2020). Junda *et al.* (2020) recently determined that approximately 57% of Tennessee Warblers are in the early stages of moult upon their capture at the MBO and presumably perform their entire moult on the MBO grounds each year. Since 2013, excluding 2014 and 2020, banders recorded the stage of moult for each adult individual. During these eight sampling years, the MBO collected data on 107 fall moult migrating Tennessee Warblers.

Radio-tagging and tracking

Tennessee Warblers were captured and radio-tagged at the MBO during their 2018, 2019, 2021 and 2022 fall migrations (between 30 July and 15 October). The radio-tags used were Lotek VHF nanotags and were registered with the Motus Wildlife Tracking System. After hatch-year (AHY) individuals were captured using 30mm mist-nets and banded with numbered aluminum leg bands. Standard banding measurements were taken: sex, age based on plumage and skull ossification, weight, fat, and wing chord length. Due to the lack of dimorphism in Tennessee Warblers to visually distinguish between sexes, 100ul blood samples were taken to perform DNA sexing following methods in Griffiths *et al.* (1998). We also recorded individuals' moult status using methodologies described in Newton (1966) where each primary and secondary flight feather is given a score from 0 to 1, in 0.1 increments. A score of zero indicates that the old feather has not yet fallen while a score of one means that the new feather has grown completely. These scores were cumulated to give a percent of moult completed. Birds who had completed 100% of their moult before capture were considered post-moult migrants and we assumed they moulted at a separate location besides the MBO (following methods in Morales et al. 2022). Before release, we attached 0.26 gr coded radio-transmitters (model NTQB2-1) using legloop harnesses to 42 moulting and 6 post-moult AHY Tennessee Warblers over three sampling years (see Table 2.1 in Results). Birds were banded and radio-tagged under animal use protocol 2007–5446 from McGill University, and federal banding permits 10743AE and 10743T issued by the Canadian Wildlife Service.

Tags had a burst rate of ~13 seconds and were detected by a Motus tower stationed at the MBO (45.4307ºN, -73.9385ºW) and at the McGill Macdonald Campus (45.4079ºN, -73.939ºW, Figure 2.4A). As the tower's detection ranges are dependent on the density of vegetation surrounding them, we supplemented the detections by manually tracking individuals for the first 4 days after tagging and subsequently every 3 days. Trackers recorded a GPS point when signal strength was at least 130 dB at a gain (precision) between 9 dB and 40 dB.

Home ranges

We then calculated 95% home ranges for 17 individuals that had a minimum of 5 GPS points (4 moult migrants from 2019, and 8 moult migrants and 1 post-moult migrant from 2021, and 4 moult migrants from 2022) using the *ctmm* (continuous-time movement modeling) package in R 3.2. Due to the distribution of points, the package recommended the independent and identically distributed (IID) isotropic model for the best estimation of home range, which confirmed the existence of a home range (i.e. an asymptote in semi-variance of points) rather than continuous movement. Home ranges were overlaid on a 30-meter-resolution land cover map from data collected in 2019 (from *Partenariat Données Québec*). We extracted the proportions of landscape cover type and forest edge present within the home ranges using the *raster* and *landscapemetrics* packages in R 3.2, respectively. Lastly, after scaling the variables, we performed a linear correlation comparing stopover duration and proportion of forested area within the home ranges to determine whether habitat type and size might have influenced stopover length.

Moult rate and stopover length

Rate of moult was calculated using annual data of percent moult completed. Data were collected from 107 individuals over eight years, from 2013 to 2022 (excluding 2014 and 2020). Moult scores of < 5% or > 95% were excluded from moult rate calculations as moult intensity is often reduced at the beginning and end of moult (Mumme et al., 2021). With the average moult rate, we estimated the arrival date of each individual, assuming they arrived at the MBO with 0% moult complete and began moulting the same day of arrival. We used the following equation to estimate arrival date: *arrival date = capture date – (moult completed (%)/ moult rate (%/day)*. While for post-moult migrants, we assumed they arrived the same day as their first capture.

We compared median arrival dates for both moult and post-moult migrants between years using a Kruskal-Wallis test. We also compared median arrival dates between moult and post-moult migrants across years using Mann-Whitney U tests. The number of hatch-year individuals caught in any given year was used as a proxy for productivity at the breeding grounds, assuming that good habitat conditions would lead to more chicks hatched. We investigated whether the number of hatch-year individuals was related to (1) the number of moult migrants captured and (2) the median arrival dates of moult migrants for each year using two separate linear regressions. Birds who were nearly finished moulting (i.e. having a moult score between 95% and 98%) upon capture were not included in arrival date and stopover duration calculations as it was ambiguous whether the individual had moulted at the MBO or had just arrived from another moulting site.

Departure dates and time were collected using two Motus wildlife tracking towers described above (and seen in Figure 2.4A). We considered a migratory departure to occur when a rapid increase in signal strength from all antennas at the MBO tower was followed by a decrease in signal strength until it disappeared (Packmor et al., 2020). In most cases, we were able to detect a similar change in signal at the Macdonald campus tower as the bird migrated south-west. In addition, individuals who departed before 19:00 hours were excluded from analyses as it would be unlikely for a nocturnal migrant to depart so early in the day.

Stopover duration was described as the difference between the arrival and departure dates in days. Since we could not confirm departure times for all radio-tagged birds due to inconsistent detections, stopover length could only be calculated for 4 post-moult migrating individuals (3 from 2019 and 1 from 2021) and 18 moult migrants (10 from 2018, 2 from 2019, 2 from 2021, and 3 from 2022). We then used a Mann-Whitney U test to determine whether moult and post-moult migrants spent significantly more or less time at their stopover site. Similarly, we performed additional Mann-Whitney U tests to determine whether arrival and departure dates changed significantly between moult and post-moult migrants. We also used Kruskal-Wallis tests to determine whether average arrival and departure dates changed significantly between years, keeping moult and post-moult migrant values separate for these calculations.

Use-availability analysis: migrants' resource selection

We compared 'used' to 'available' habitat to determine migrating Tennessee Warblers' resource selection in regards to landscape composition (i.e. anthropogenic, forest, and agriculture,) during their stopover. We also included forest edge (in meters) as a landscape measurement due to its appeal for migrating birds in urban and peri-urban spaces (Stanley et al., 2021; Terraube et al., 2016). The GPS coordinates obtained through manual tracking (see radio-tagging and tracking section) were our 'used' points. Two 'available' points were created for every 'used' point by placing it the same distance away from where the bird was released at a random angle from that release point. We only included migrants with more than one 'used' point (N = 17 moult and 1 post-moult migrant). All points were overlaid on a 30m-resolution landscape cover map from 2019 (obtained from *Partenariat Données Québec*). We constructed buffers of 50m, 100m, and 200m, radii around these points and extracted landscape composition and forest edge measurements from each buffer. We performed a scale of effect analysis by comparing full models of each buffer size using AICc model selection. The 100m-radius buffer had the strongest scale of effect for habitat use [see Results] and thus we used this buffer size in our subsequent analyses. Available points that were composed of 100% water were discarded as Tennessee Warblers are not aquatic birds and would not realistically be occupying those spaces.

We constructed four binomially distributed generalized linear mixed-effect models: (i) a global model including proportions of forest, and anthropogenic land, and the length of forest edge, (ii) a human disturbance model including proportion of anthropogenic land, (iii) a forest model including proportion of forest, and length of forest edge, and (iv) a null model (Table 2.2). All models also included the bird's identification (ID) number as a random effect. All variables were tested for collinearity, and we found that the proportion of forest and agriculture were highly correlated (Pearson's $r > 0.7$), and so proportion of agricultural land was excluded from the models. Finally, all four models were ranked using Akaike Information Criterion values corrected for small sample sizes (AIC_c) and analyzed for goodness of fit using the area under the curve (AUC) method for discrimination and the Hosmer-Lemeshow goodness of fit test for calibration.

Departure decisions

We collected nightly temperature, wind conditions, and change in atmospheric pressure (hereafter 'Δ atmospheric pressure') from historical data made available by Environment and Climate Change Canada (weather.gc.ca). Most climate values were taken from the Sainte-Anne-de-Bellevue weather station, less than 1 km from the study site, with few data gaps for temperature and wind values filled by the Montreal/Pierre Elliott Trudeau Intl and Montreal Intl A stations (~16 km away). We justify filling these data gaps as weather values between stations were correlated ($R^2 > 0.5$). We used these variables to determine the influence of extrinsic factors on migratory departure decisions.

The sole endogenous factor included was residual mass as a relative measurement of body size for each bird. Residual mass was calculated using the residuals of a least-squares regression of all individuals' log-transformed weight over their log-transformed wing length (including historical data from 2013 onward). The ordinary least-squares regression had an intercept of -0.350 and a slope of 0.635 ($R^2 = 0.052$, $F = 36.8$, $p < 0.001$). For individuals captured multiple times, and thus had multiple associated residual masses, we took an average of these measurements.

We used time-dependent Cox proportional hazards models to determine departure decision of the moult migrating Tennessee Warblers (Morales et al., 2022; Packmor et al., 2020). The response variable in these models was the risk of an individual departing from the stopover site on any given night. Every day, starting from the time an individual had presumably completed 75% of its moult and thus regained most of its feathers and mobility (or from their capture date if the individual already had > 75% moult complete upon capture; see similar methods in Morales et al., 2022) until their departure, was considered a potential departure day where individuals were actively deciding to 'stay' or 'leave' the site. This value, recorded as the number of days since an individual was ready to depart, is the time variable in our Cox models. We assume that, as the season draws on, individuals will feel greater pressure to leave regardless of weather conditions and thus calendar date (of every given night where a bird decided to stay or leave the stopover site) was included as a covariate in all models. One individual who had departed before having completed at least 75% of their moult, based on our moult rate estimations, was not included in our analyses.

For every departure date, we recorded all weather conditions the hour preceding departure. On days where birds stayed (and thus had no departure time), we calculated weather variables at 20:00 which was the median departure hour of all birds. Given that temperature was highly correlated with calendar date, we included residual temperature instead. Residual temperature was calculated by subtracting the average temperature for that date over the past 10 years from the actual recorded temperature. Change in atmospheric pressure was determined following methods in Packmor *et al.* (2020) by calculating the difference between atmospheric pressure an hour before departure and 24 hours prior. All weather variables were included as time-dependent covariates in the Cox models. Wind speed and direction were also combined into one measurement of wind support. As in Morales *et al.* (2022), we assumed that individuals traveled south-west when departing from our site and calculated wind support using the following equation: $Wind\ support = wind\ speed \times \cos(wind\ direction \times (\pi/225))$.

We created four Cox models: an endogenous model (including residual mass), an exogenous model (including temperature, wind support, and Δ atmospheric pressure), a global model (including residual mass, temperature, wind support, and Δ atmospheric pressure), and a null model. Year, calendar date (i.e. number of days since 1 January of its respective year), and moult status (i.e. moult or post-moult) were also included as random covariates in each model. We then used AIC_c model selection to rank the models.

We further compared the mean and variance of weather variables between stay and departure dates using Wilcoxon rank-sum tests and F-tests comparing two variances, respectively. In every case, data was not normal (following Shapiro Wilk's tests) but was homoscedastic (following Levene's tests). We separated data between years since, as explained in Tsvey *et al.* (2007), any given year could generally have poorer weather conditions and thus force migrants to continue migration despite the weather. Data was again separated by moult status (i.e. moult and post-moult migrants). Due to extremely low sample sizes of post-moult migrants in 2018 and 2022 (see Table 2.1), these years were excluded from analyses for this group.

Results

Moult migrating Tennessee Warblers at the MBO

From 2013 to 2022 (excluding 2014 and 2020), the MBO captured 107 actively moulting Tennessee Warblers during their fall migration. The years 2019 and 2022 recorded the lowest numbers of moult migrants (only 7 and 8 individuals, respectively) while 2018 was the highest, having captured 27 moult migrants (Table 2.1). Note that we found two radio-tagged moult migrants deceased in the wild. The average proportion of after-hatch year individuals that were moulting upon capture was 73 ± 19 % (Table 2.1). The number of hatch year individuals caught per year (as a proxy for productivity at the breeding grounds) was not significantly correlated with the number of moult migrants (Pearson's r = 0.277) but was positively correlated with moult migrants' median arrival date (Pearson's r = 0.844). Finally, years with high numbers of after-hatch year individuals had higher numbers of moult migrants as they were strongly correlated (Pearson's r = 0.831).

Table 2.1. Sample sizes for moult and post-moult after hatch year Tennessee Warblers over eight sampling years (2013 to 2022, excluding 2014 and 2020). Moult migrant arrival dates were estimated based on the calculated moult rate (2.5%/day), assuming individuals arrived at 0% moult and began moulting immediately. Post-moult (identified as birds having 100% completed moult upon capture) arrival dates are the dates of first capture. Median arrival dates for both groups include all banded birds. The comparisons of median arrival dates were performed using Wilcoxon rank sum tests. Note that values from 2013 differ slightly from numbers reported in Junda *et al.* (2020) as they classified moult migrants as birds having moult scores of > 0% and < 100% upon capture whereas we included birds with moult scores of 0%.

		sample sizes						***arrival dates***		
year	**total HY**	**total AHY**	**# moult**	**% moult**	**tagged**	**tagged moult**	**tagged post-moult**	**moult arrival *median (range)***	**post-moult arrival *median (range)***	**comparison of median arrival**
2022	26	13	8	62%	5	5	0	3 Aug (21 Jul – 18 Aug)	31 Aug (21 Aug – 18 Sep)	W = 54 $p < 0.001$
2021	63	17	14	82%	9	6	3	4 Aug (21 Jul – 3 Sep)	28 Aug (14 Aug – 22 Sep)	W = 87 $p = 0.013$
2019	105	14	7	50%	9	7	2	11 Aug (3 Aug – 20Aug)	21 Sep (8 Sep – 22 Sep)	W = 63 $p < 0.001$
2018	59	29	27	93%	25	24	1	3 Aug (8 Jul – 23 Aug)	12 Sep (26 Aug – 20 Sep)	W = 128 $p = 0.001$
2017	31	17	11	65%	0	0	0	5 Aug (20 Jul – 12 Aug)	27 Sep (5 Sep – 30 Sep)	W = 65 $p = 0.002$
2016	17	12	11	92%	0	0	0	7 Aug (21 Jul -30 Aug)	26 Sep (26 Sep -26 Sep)	NA (N = 1 for post-moult)
2015	46	23	11	48%	0	0	0	8 Aug (17 Jul – 4 Sep)	14 Sep (8 Sep – 25 Sep)	W = 169 $p < 0.001$
2013	229	20	18	90%	0	0	0	17 Aug (25 Jul – 4 Sep)	22 Sep (1 Sep – 3 Oct)	W = 99 $p = 0.002$

Moult rate and stopover length

Across all years (2013 to 2022), moult migrants were most frequently captured in early August (mode: 10 August; median: 17 August). Upon capture, the average individual had completed 39 ± 38 % of their moult. The average moult rate for Tennessee Warblers was 2.5 ± 0.6 % per day (Figure 2.1). Based on this estimation, the median arrival date for moult migrants across all sampling years (from 2013 to 2022) was 6 August (mode: 4 August). The median arrival date for moult migrants did not differ significantly between years (Kruskal-Wallis test including data from 2013 to 2022; $p = 0.068$, df = 7, $\chi^2 = 13.2$) nor did it differ for post-moult migrants ($p = 0.076$, df = 6, $\chi^2 = 11.4$). Median arrival date between moult and post-moult migrants, however, was significantly different ($p < 0.001$, df = 1, W = 5980). While moult migrants arrived in early August (median: 6 August), post-moult migrants arrived more than a month later in September (median: 14 September; see Table 2.1).

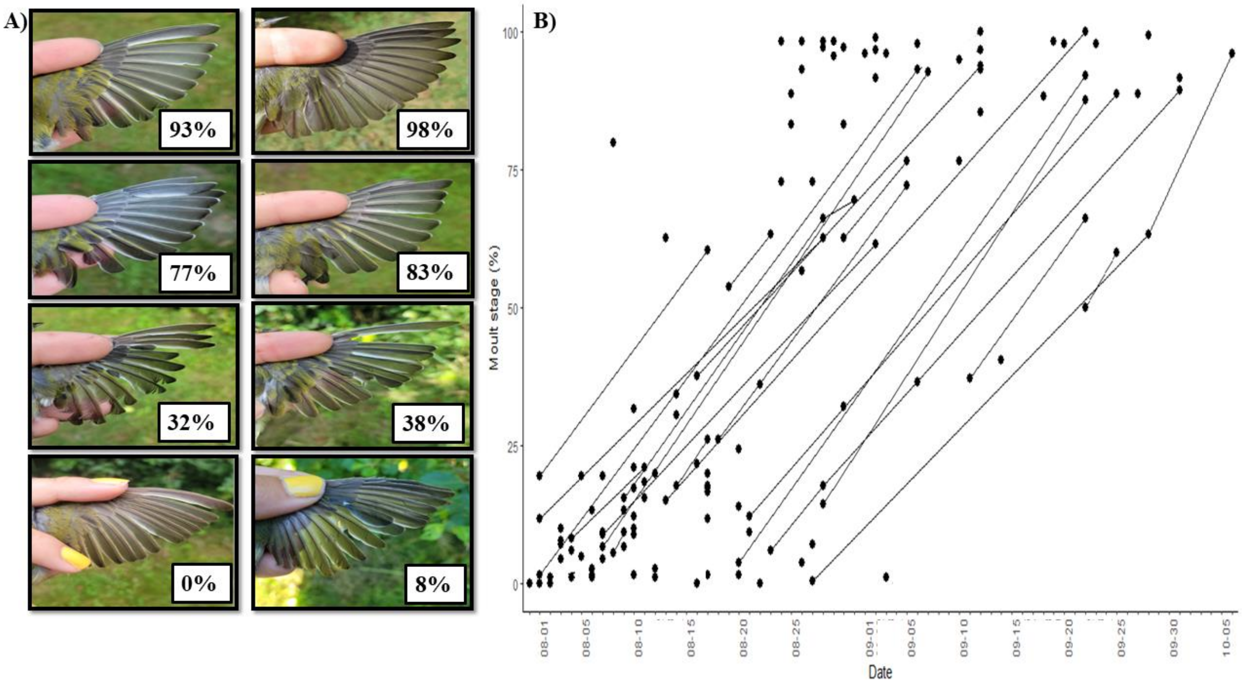

Figure 2.1. Tennessee Warblers' stage of moult (i.e. percent of moult completed) over time during their fall migration stopover at the McGill Bird Observatory (MBO). **A)** Visual representation of Tennessee Warblers' flight feather moult stages (photos taken during 2021 and 2022 fall migration). **B)** Graph showing the moult stage of individuals upon capture. Each point represents a date when an individual was captured at the MBO and their moult stage was recorded. This figure represents 72 individuals across eight years (from 2013 to 2022).

Departure dates were statistically similar between moult and post-moult migrants (p = 0.89, df = 1, W = 36). The median and mode departure date for moult migrants was 16 September while the median departure date for post-moult migrants was 20 September (with no mode; Figure 2.2). Among both moult and post-moult migrants, year had no effect on departure dates (Kruskal-Wallis test: p = 0.158, df = 3, χ^2 = 5.19).

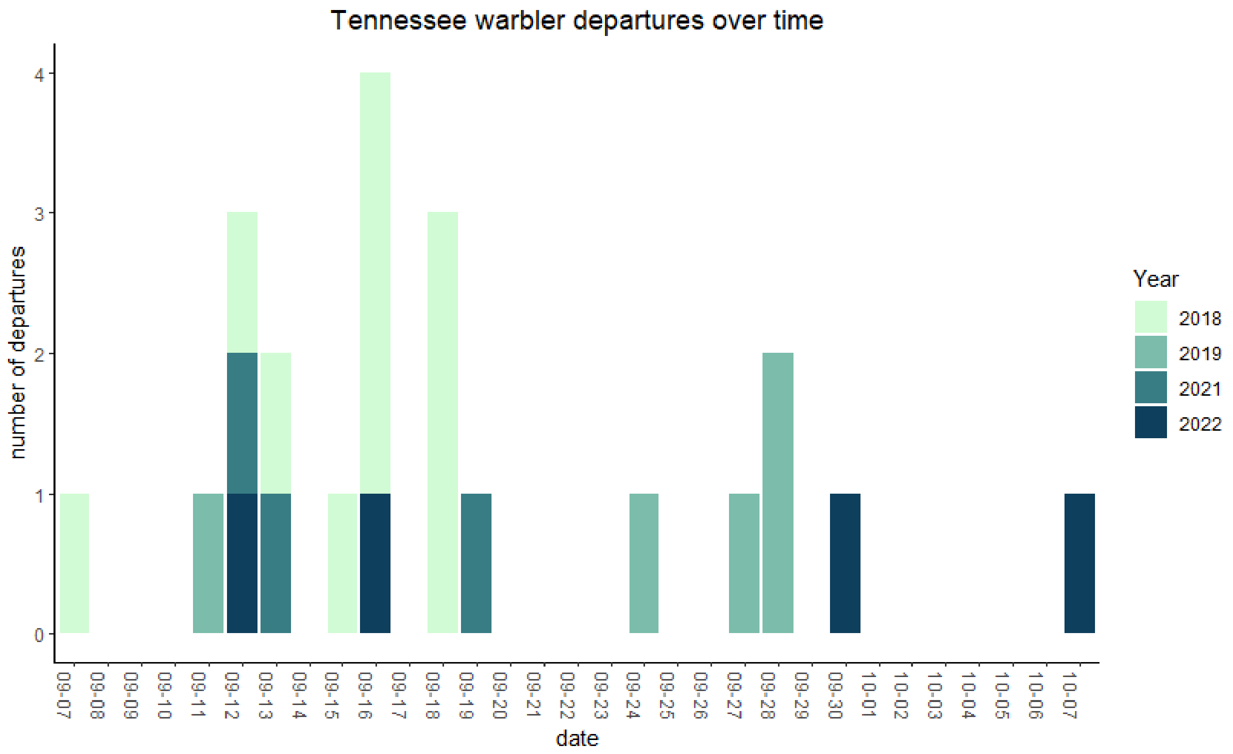

Figure 2.2. Barplot showing the number of radio-tagged Tennessee Warblers making migratory departures from the McGill Bird Observatory stopover on any given night during the fall season. Data is color-coded by year as seen in the legend.

Moult migrants spent 33 ± 11 days at the stopover site after their first capture (i.e. after tagging) while post-moult migrants stayed for 8 ± 6 days (Figure 2.3). Assuming individuals arrived at the start of their moult and maintained a constant 2.5% moult rate throughout their stay, moult migrants spent 46 ± 5 days at their stopover. The minimum stay was 39 days (in 2018) while the maximum was 56 days (in 2022). According to the estimated moult rate (2.5%/day), it would take a bird 40 days to moult their feathers, which was near~~ly~~ the average stay of moult migrants.

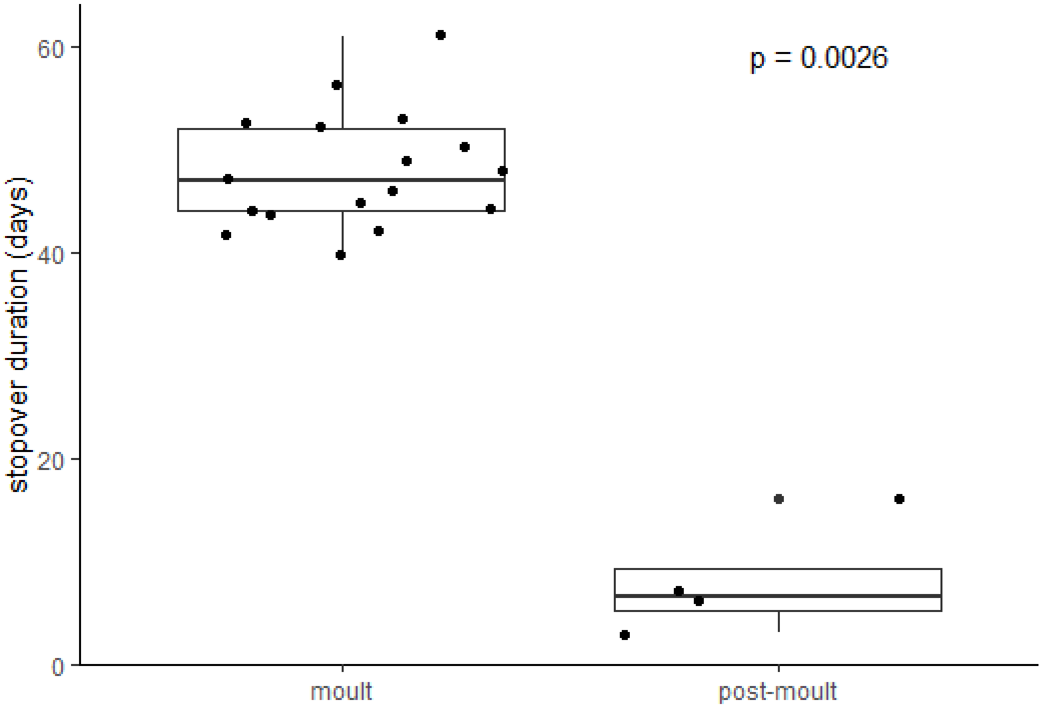

Figure 2.3. A boxplot illustrating the difference in stopover duration between moult and post-moult migrating Tennessee Warblers at the McGill Bird Observatory in southern Quebec. Stopover duration for post-moult migrants is defined as the number of days between their first capture and departure dates while, for moult migrants, it is their estimated arrival (based on their moult stage and an estimated moult rate (2.5%/day), assuming migrants arrived at the start of their moult) and their departure dates.

Home ranges

The one post-moult migrant had an estimated 95% home range of 5.79 ha (with 95% confidence intervals extending from 1.58 to 12.70 ha) while the moult migrants had an average 95% home range size of 14.6 ha (with standard error of ± 4.4 ha). The largest home range across all tagged Tennessee Warblers was 58.8 ha and the smallest was 1.33 ha, both obtained from moult migrants in 2022 and 2021, respectively (see Table S2.1 in the Supplemental materials). Figure 2.4B shows a map of the home ranges.

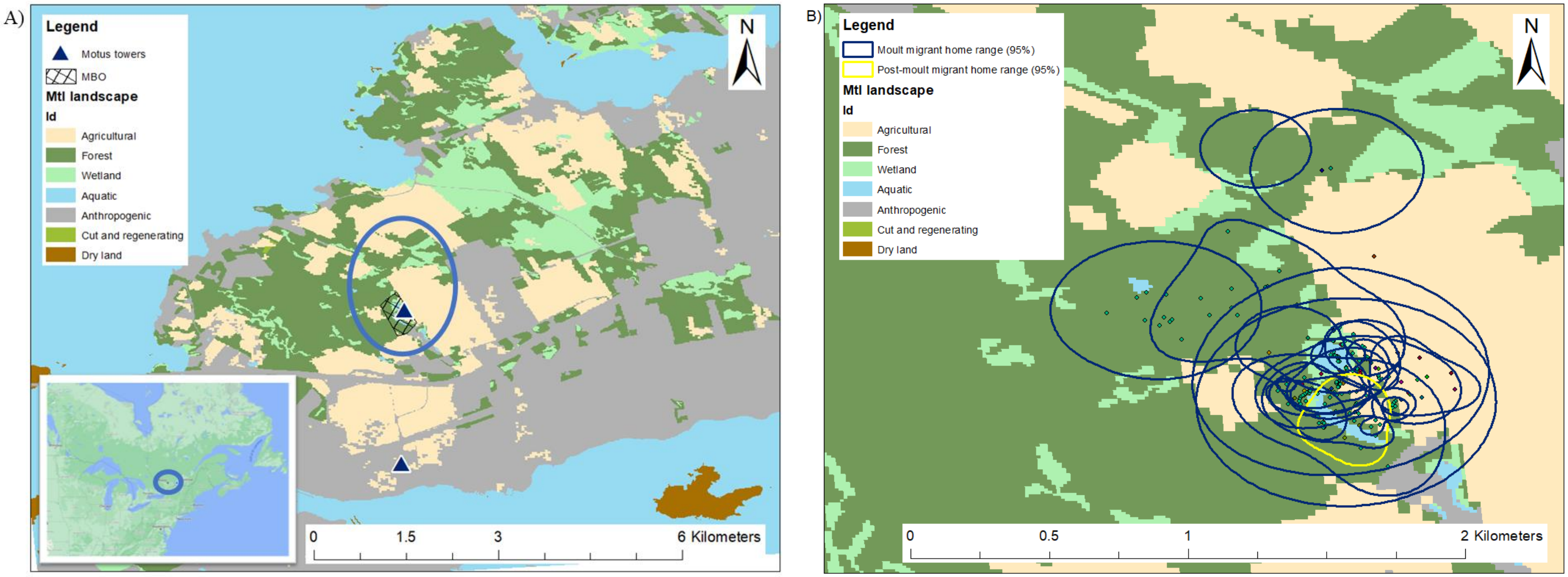

Figure 2.4. **A)** Map of the West Island of Montreal showcasing the McGill Bird Observatory and Motus tower locations. In the bottom left corner shows where the West Island of Montreal is located in northeastern North America. The blue circle indicates the area represented in map 'B'. **B)** Map of the 95% home ranges (and their associated GPS points) of moult and post-moult migrating Tennessee Warblers at the McGill Bird Observatory. Individuals were radio-tagged and tracked in 2018, 2019, 2021, and 2022. Both maps use a 30m-resolution landscape cover layer from 2019 (obtained from *Partenariat Données Québec*).

Almost half (48.83 ± 21.43 %) of the Tennessee Warblers' home ranges were composed of forests (Figure 2.4B). More than a third (33.03 ± 25.25 %) of the area spanned agricultural land. Aquatic land and wetland types covered 10.12 ± 11.20 % and 7.31 ± 5.46 % of the total area of the home ranges, respectively. The least prevalent land cover type over which the home ranges were found was anthropogenically modified habitat (excluding agriculture), which represented 0.71 ± 1.99 % of the total area. See Table S2.2 in the Supplementary materials for a summary of the land types present in each bird's home range. We found no correlation between the proportion of forested home range and stopover duration ($p = 1$, df = 16, W = 32, $R^2 = 0.164$) nor between stopover duration and home range size ($p = 0.959$, df = 16, W = 31, $R^2 = 0.095$).

Use-availability analysis: migrants' resource selection

A comparison of the global models at different buffer sizes (50m, 100m, 200m) revealed that the 100m-radius buffer was the best (> 2.0 ΔAICc between all other models). The models discussed in this section therefore include landscape measurements obtained from a 100m-radius buffer around the used and available points.

The forest model (including the proportion of forest and length of forest edge (m)) and the global model (including the same variables plus % anthropogenic land) were the two best models (> 2.0 ΔAICc between all other models) to predict resource selection of migrating Tennessee Warblers (Table 2.2). In both models, the proportion of forest and length of forest edge had a significantly positive influence on Tennessee Warbler presence ($p < 0.001$, see Table 2.3 and Figure 2.5). The conditional version of the forest model including bird ID as a random effect had a higher theoretical R^2 (= 0.82) than the marginal model excluding bird ID ($R^2 = 0.69$). These two best models also had high scores following the AUC goodness of fit test for discrimination (AUC = 0.942). Both the forest and global models, however, failed the Hosmer-Lemeshow goodness of fit test for calibration ($\chi^2 = 36500$ and 37100, df = 8, and $p < 0.001$, respectively).

Table 2.2. AICc of four generalized linear mixed-effect models comparing presence/absence coordinates (with 50m-buffer zones) of migrating after-hatch year Tennessee Warblers (N = 18) during their stopover at the McGill Bird Observatory in southern Quebec.

Model	**Variables**	**-LL**	**Δ AICc**	**Wt**
Forest	forest (%) + forest edge (m) + bird ID	-235	0.00	0.65
Global	anthropogenic (%) + forest (%) + forest edge (m) + bird ID	-234	1.25	0.35
Human disturbance	anthropogenic (%) + bird ID	-485	497	0.00
Null	bird ID	-487	500	0.00

Table 2.3. Summary of the parameter estimates of the top two resource selection models (the landscape composition and global models) predicting presence of migrating Tennessee Warblers (N = 18) during their stopover at the McGill Bird Observatory in southern Quebec.

Model	**Variables**	**estimate**	**standard error**	**z**	**p**
Forest	forest edge	3.27	0.284	11.5	< **0.001**
	% forest	0.550	0.138	3.99	< **0.001**
Global	forest edge	3.28	0.286	11.5	< **0.001**
	% forest	0.532	0.139	3.82	< **0.001**
	% anthropogenic	-0.131	0.158	-0.825	0.409

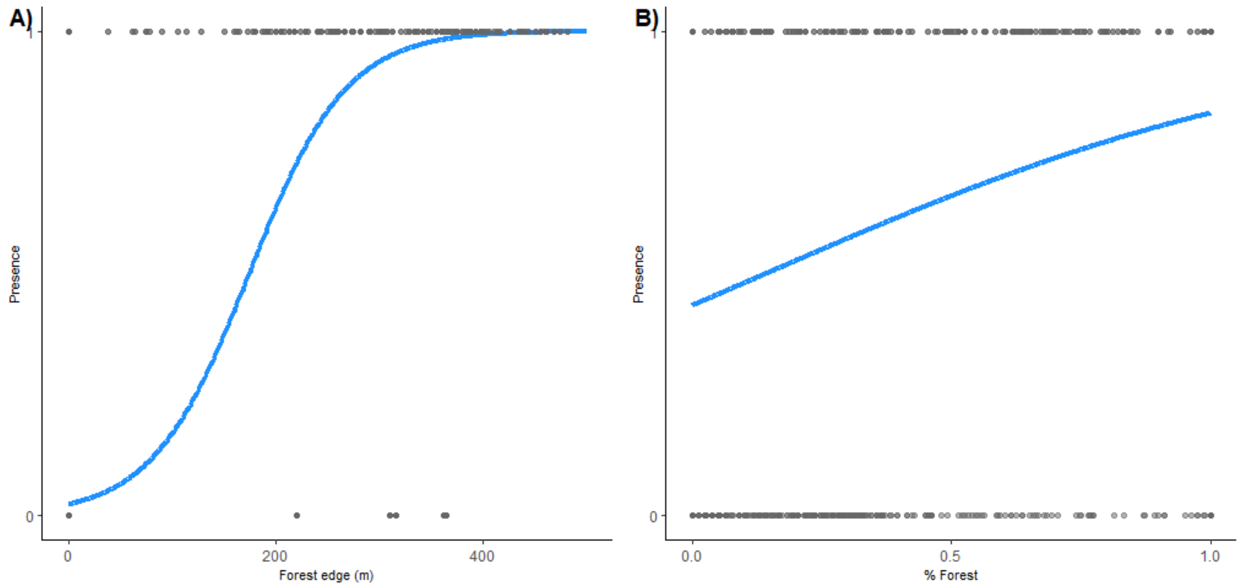

Figure 2.5. Presence of migrating Tennessee Warblers within a 100m-radius area as predicted by a generalized linear mixed effects model. Data points are areas where we observed (presence = 1) Tennessee Warblers and areas that were available but unused (presence = 0). The model's predictors include the proportion of forest and wetland, and the length of forest edge (in meters), and individual (bird ID) as a random effect. **A)** shows the positive relationship between migrants' presence and the amount of forest edge (coefficient = 3.27, p < 0.001), **B**) shows the positive relationship between migrants' presence and the proportion of forest (coefficient = 0.55, p < 0.001).

Departure decisions

The null model, which included only calendar date, year, and moult status as random effects, was the highest-ranked model for predicting a migrant's departure (Table 2.4). Although the exogenous model was ranked second-best (within < 2.0 AICc of the null model), it explained little variability in the data. The endogenous and global models were similarly poor, ranking third and fourth, respectively (both > 2.0 AICc between the null model, see Table 2.4). None of the predictor variables in any of the models were significant ($p > 0.05$) and the goodness of fit measurement of concordance for all models was similar to the null model (C = 0.5).

Table 2.4. AICc model selection performed on four models describing departure decisions for both moult (N = 18) and post-moult (N = 4) migrant Tennessee Warblers in a large urban park near the McGill Bird Observatory.

Model	**Variables**	**-LL**	**Δ AICc**	**W**
Null	calendar date + year + moult	-90.10	0.00	0.50
Exogenous	temperature + wind support + Δ atmospheric pressure + calendar date + year + moult	-87.74	1.53	0.23
Endogenous	residual mass + calendar date + year + moult	-90.09	2.04	0.18
Global	temperature + wind support + Δ atmospheric pressure + residual mass + calendar date + year + moult	-87.70	3.58	0.08

For most years, there was no significant difference between means or variance of any weather conditions between ‘stay’ and ‘leave’ dates for both moult and post-moult migrants (see Figure S2.1 in Supplementary materials). The only year with noticeable differences in mean weather was in 2018, which was also the year of our highest sample size (24 moult and 1 post-moult migrants). In 2018, residual temperature on departure dates (-4.04 ± 2.94 °C) was significantly lower than on stay dates (-1.11 ± 4.55 °C; $p = 0.044$). Change in atmospheric pressure was significantly less variable on departure dates (-0.076 ± 0.133 kPa) than on stay dates (0.0118 ± 0.434 kPa; $p < 0.001$). For all other years, however, we found no significant difference in weather conditions between stay and leave dates. Table S2.3, S2.4, and S2.5 in the Supplementary materials lists the means and standard deviations of Δ atmospheric pressure, residual temperature, and wind support, respectively, for each date category (i.e. stay or leave) in every year, along with the results of the Wilcoxon tests and f-tests comparing means and variances, respectively, for moult migrants only.

Discussion

Moult migrant Tennessee Warblers in a peri-urban greenspace spent significantly more time at their stopover site than post-moult migrants. Specifically, moult migrants spent around 46 days at their stopover site, which is just slightly more than the number of days needed to complete moult (i.e. 40 days). Meanwhile, post-moult migrants only occupied the site an average of eight days (although this did not account for days prior to first capture). This stopover duration is very similar to Swainson’s Thrushes that stayed for an average of 47 (moult migrant) vs seven (post-moult migrants) days at the same stopover site (Morales et al., 2022). This single stopover period (47 days) consists of 13% of the year, making the moult migration an important component of the annual cycle, longer than breeding (~24 days for incubation + chick-rearing; Rimmer & McFarland, 2020) or fall migration itself. This is also far longer than the 6-13 days recorded via banding data (Junda et al., 2020) or for post-moult individuals of other passerine species (2.9 days for Ovenbirds (*Seiurus aurocapilla*) observed in Seewagen et al., 2010 or < 4 days for assorted songbirds in Morris et al., 1996). Since moult takes at least 35-40 days for passerines (Francis et al., 1991; Haukioja, 1971), we presume these migrants spent most of their stopover moulting (an assumption often confirmed through recaptures) and reserved their remaining few days to refuel for migratory flight. To compensate for this extra time commitment, moult migrants arrived at the stopover site much earlier in the fall season (average = 2 August) than the post-moult individuals (average = 12 September). The earlier arrival time allowed migrants to stop for over a month to moult and still be prepared to continue migration in mid-September.

We found evidence for the ‘push’ part of the push-pull hypothesis suggesting that moult migration is driven by poor conditions at the breeding grounds that push birds towards better habitats (Rohwer et al., 2005). In years that we observed an abundance of hatch-year birds, presumably caused by a productive breeding site, we observed later arrival dates for moult migrants. Likewise, in years of poor conditions at the breeding grounds (i.e. less hatch-year birds), moult migrants arrived at the stopover site earlier presumably because they were ‘pushed’ from their breeding grounds. This push away from poor breeding grounds was similarly recorded in western North America where arid conditions drove migrants to moult at stopover sites (Pageau et al., 2020). The reason for these poor-quality years in eastern North America has not yet been investigated but may be caused by food availability. Tennessee Warblers are known to benefit from outbreaks of spruce budworm (*Choristoneura fumiferana*; Germain et al. 2021), but the resource may be quickly depleted locally and regionally. Tennessee Warblers may therefore perform moult migration as a result of a food shortage in the post-breeding season in the boreal forest following defoliation (Drever et al. 2018; Germain et al. 2021). Indeed, two abundant years for hatch year individuals was in 2019 (105 birds) and 2015 (46 birds) when nearby spruce budworm populations were high (Maine Forest Service, 2021). In these same years, moult migrants arrived at the McGill Bird Observatory later in the season presumably because they spent more time breeding in the boreal forest. Future research should investigate this relationship between resource abundance at the breeding ground and the prevalence of moult migration.

Migrating Tennessee Warblers moulted at 2.5 ± 0.7% per day. We assume a constant moult rate which is mostly likely not the case. As resources and weather conditions (like rainfall) change from day to day, so will a bird's ability to moult, presumably causing sudden drops and rises in moult rate (e.g. moult rate varied between captures for the same individuals). Most individuals were captured near the start and end of moult, presumably due to their increased mobility at these times. The Tennessee Warblers' moult rate was faster than for some other species. For example, the Swainson's Thrushes moulted their feathers at 1.9% per day at the same autumn stopover site as this study (Morales et al., 2022). Tennessee Warblers depart several weeks before Swainson's Thrushes, possibly resulting in this faster moult rate as, unlike Swainson's Thrushes, Tennessee Warblers are mainly insectivorous (Rimmer and McFarland, 2020) which may make them more vulnerable to cold snaps and necessitate an earlier migration (Newton, 2007).

Despite their limited mobility (Leu and Thompson, 2002), moult migrants occupied overlapping and relatively large home ranges (14.1 ± 17.2 ha), perhaps to search for the food and safety they require to successfully moult (Pomeroy et al., 2008). Larger home ranges encompassing multiple forest patches may alleviate the effect of small forest fragments (< 4.5 ha; Matthews and Rodewald 2010) that reduce a migrant's ability to refuel due to increased density of birds and thus higher competition (Cohen et al. 2022). Habitat variables like branch and stem densities seem to be good predictors of home range size (Anich et al. 2010) and may be why Tennessee Warblers established home ranges with high percentages of forested area (~48%). Indeed, according to our best model, migrating Tennessee Warblers chose to occupy habitats with abundant forests and forest edges and they made these decisions at a relatively small scale (within a 100m-radius or 0.785 ha). The model could not accurately predict what areas Tennessee Warblers might be using across the landscape but still informed what habitat characteristics, namely proportion of forest and forest edge, made for good stopover sites. Habitat selection also seemed to depend on the individual bird as our models performed considerably worse (theoretical $R^2 = 0.69$ compared to $R^2 = 0.82$) when we removed bird ID as a random effect. Individual-level variance in resource selection could be due to differences in orientation strategies and intraspecific competition (Alatalo 1981; Beardsworth et al., 2021) but such analyses are beyond the scope of this project. To conclude, the *Grand Parc de l'Ouest* in Montreal was capable of providing sufficient habitat (i.e. forest patches with high forest edge to interior ratios) to host migrating birds who require abundant resources to moult and refuel. Our findings on home range size of a neotropical moult migrant suggests for cities to provide critical stopover habitat for moult migrants by retaining larger forested greenspaces (e.g., of at least 15 ha in size).

The departure decisions of both moult and post-moult migrants were best described by our null model, suggesting that departure decisions are independent of the endogenous and exogenous factors we analyzed: initial body condition (i.e. residual mass) and weather (i.e. residual temperature, wind support, and change in atmospheric pressure). In other words, we cannot support nor disprove previous studies illustrating that either body condition, specifically fat reserves (see Deppe et al., 2015; DeSimone et al., 2022), nor weather (see Morales et al. 2022; Beauchamp et al., 2020; Gill et al., 2014; Richardson, 1990), are the primary factor impacting departure decisions. Considering the pressure of making a speedy migration, it is reasonable that a moult migrant stopping for ~1.5 months might disregard weather in favour of making a hurried departure. Time constraints often force migrants to be less choosy of weather conditions upon departure (see Pyle et al., 2018; Roques et al., 2021; Schmaljohann et al., 2013; Tsvey et al., 2007). We had expected a strong relationship between wind support and departure as appropriate tailwinds and their associated temperature, humidity, and pressure are often the drivers of migration (Beauchamp et al., 2020; Gill et al., 2014; Richardson, 1990), however we found no influence of wind nor pressure on departure decisions. One explanation may be that some passerines and shorebirds depart with weak winds as long as they are in the direction of flight (Lack, 1960; Schmaljohann et al., 2012; Tan et al., 2018). Finally, despite decreasing atmospheric pressure being a marker of approaching stormy weather (Abbasi et al., 2021), migrants may depart on these low-pressure nights, as recorded in Packmor *et al.* (2020). Migrants have also been recorded departing in any/all weather conditions so, although there may be trends, other deciding factors might take precedence (Richardson, 1990), namely a spatiotemporal programme we have yet to define (Jenni and Schaub, 2003).

Conclusion

Although once thought to be rare in Neotropical passerines, especially in eastern North America, a high proportion (~ 73%) of Tennessee Warblers observed at the McGill Bird Observatory perform moult migration. Individuals stop for ~1.5 months, six times longer than their post-moult counterparts. and moult intensely (completing ~2.5% of their moult per day). Breeding success was lower in years when mean arrival date was later, implying they were 'pushed' from breeding grounds due to low resources, and supporting the idea that migration timing is controlled by refueling rates. Whether a migrant stopped for 46 or 8 days, we found no evidence that their decision to depart was influenced by endogenous or exogenous factors. During their stay, Tennessee Warblers had relatively large and overlapping home ranges (~ 15 ha), meaning that they moved around to take advantage of resources in the region for refueling. They selected habitats with high proportions of forest and high ratios of forest edge to interior. Forests compose 48% of their home ranges, more than any other landscape cover type. Forests presumably offered sufficient food and protection from predators for migrants moulting and/or refueling during their stopover. In conclusion, Tennessee Warblers were able to occupy forested stopover sites in a large urban park where they could successfully moult and refuel and departed with their post-moult counterparts, presumably to complete a timely migration.

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Author contribution statement.

V.P. was involved in all aspects of the project. B.F. and K.H.E supervised the entire project and so were involved in the conceptualization, funding acquisition, formal analysis, methodology, investigation, project administration, supervision, and the writing (review and editing) process. M.L. was involved in the investigation, formal analysis, and some writing (original draft of home range analysis, which was her Honours thesis) of the project. Finally, A.M. was involved in the methodology, investigation, and some of the formal analysis of the project.

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Data availability statement

The data collected for this project is available and can be supplied by the corresponding author upon request. Bird banding data is available through the NatureCount portal (naturecounts.ca).

References

Abbasi, E., Etemadi, H., Smoak, J. M., Rousta, I., Olafsson, H., Baranowski, P., & Krzyszczak, J. (2021). ‘Investigation of Atmospheric Conditions Associated with a Storm Surge in the South-West of Iran’. *Atmosphere*, *12*(11). https://doi.org/10.3390/atmos12111429

Alatalo, R. V. (1981). ‘Habitat selection of forest birds in the seasonal environment of Finland’. Annales Zoologici Fennici, 18(2), 103–114. http://www.jstor.org/stable/23734067

Anich, N. M., Benson, T. J., & Bednarz, J. C. (2010). ‘Factors Influencing Home-Range Size of Swainson’s Warblers in Eastern Arkansas’. *The Condor*, *112*(1), 149–158. WorldCat.org. https://doi.org/10.1525/cond.2010.080103

Barta, Z., McNamara, J. M., Houston, A. I., Weber, T. P., Hedenström, A., & Feró, O. (2008). ‘Optimal moult strategies in migratory birds’. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1490), 211–229. https://doi.org/10.1098/rstb.2007.2136

Beardsworth, C.E., Whiteside, M.A., Laker, P.R., Nathan, R., Orchan, Y., Toledo, S., van Horik, J.O. and Madden, J.R. (2021). ‘Is habitat selection in the wild shaped by individual-level cognitive biases in orientation strategy?’. Ecology Letters, 24: 751-760. https://doi.org/10.1111/ele.13694

Beauchamp, A. T., Guglielmo, C. G., & Morbey, Y. E. (2020). ‘Stopover refuelling, movement and departure decisions in the white-throated sparrow: The influence of intrinsic and extrinsic factors during spring migration’. *The Journal of Animal Ecology*, *89*(11), 2553–2566. WorldCat.org. https://doi.org/10.1111/1365-2656.13315

Cherry, J. D. (1985). ‘Early Autumn Movements and Prebasic Molt of Swainson’s Thrushes’. *The Wilson Bulletin*, *97*(3), 368–370. WorldCat.org.

Cohen, E. B., Lafleur, J. M., & Moore, F. R. (2022). ‘Density Dependent Refueling of Migratory Songbirds During Stopover Within an Urbanizing Coastal Landscape’. *Frontiers in Ecology and Evolution*, *10*. https://www.frontiersin.org/articles/10.3389/fevo.2022.837790

Cooper, N. W., Hallworth, M. T., & Marra, P. P. (2017). ‘Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird’. *Journal of Avian Biology*, *48*(2), 209–219. https://doi.org/10.1111/jav.01096

Deppe, J. L., Ward, M. P., Bolus, R. T., Diehl, R. H., Celis-Murillo, A., Zenzal, T. J., Moore, F. R., Benson, T. J., Smolinsky, J. A., Schofield, L. N., Enstrom, D. A., Paxton, E. H., Bohrer, G., Beveroth, T. A., Raim, A., Obringer, R. L., Delaney, D., & Cochran, W. W. (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*(46), E6331–E6338. WorldCat.org. https://doi.org/10.1073/pnas.1503381112

DeSimone, J. G., Domschot, B. S., Fylling, M. A., Blake, W. M., & Breuner, C. W. (2022). ‘Body mass and triglycerides predict departure of free-living nomadic pine siskins’. *Functional Ecology*. WorldCat.org. https://doi.org/10.1111/1365-2435.14238

Dossman, B. C., Mitchell, G. W., Norris, D. R., Taylor, P. D., Guglielmo, C. G., Matthews, S. N., & Rodewald, P. G. (2016). 'The effects of wind and fuel stores on stopover departure behavior across a migratory barrier'. *Behavioral Ecology*, *27*(2), 567–574. https://doi.org/10.1093/beheco/arv189

Drever, M. C., Smith, A. C., Venier, L. A., Sleep, D. J. H., & MacLean, D. A. (2018). 'Cross-scale effects of spruce budworm outbreaks on boreal warblers in eastern Canada'. *Ecology and Evolution*, *8*(15), 7334–7345. https://doi.org/10.1002/ece3.4244

Francis, I. S., Fox, A. D., McCarthy, J. P., & McKay, C. R. (1991). 'Measurements and moult of the Lapland Bunting Calcarius lapponicus in West Greenland'. *Ringing & Migration*, *12*(1), 28–37. https://doi.org/10.1080/03078698.1991.9673981

Gahbauer MA, Duval S, Davey D (2016). 'McGill Bird Observatory Ten-Year Report: 2005- 2014'. Migration Research Foundation, Ste-Anne-de-Bellevue QC.

Germain, M., Kneeshaw, D., De Grandpré, L., Desrochers, M., James, P., Vepakomma, U., Poulin, J.-F., & Villard, M.-A. (2021). 'Insectivorous songbirds as early indicators of future defoliation by spruce budworm'. *Landscape Ecology*, *36*. https://doi.org/10.1007/s10980-021-01300-z

Gill, R. E., Douglas, D. C., Handel, C. M., Tibbitts, T. L., Hufford, G., & Piersma, T. (2014). 'Hemispheric-scale wind selection facilitates bar-tailed godwit circum-migration of the Pacific'. *Animal Behaviour*, *90*, 117–130. https://doi.org/10.1016/j.anbehav.2014.01.020

Griffiths, R., Double, M. C., Orr, K., & Dawson, R. J. (1998). 'A DNA test to sex most birds'. *Molecular Ecology*, *7*(8), 1071–1075. https://doi.org/10.1046/j.1365-294x.1998.00389.x

Haukioja, E. [Zool. Dept., Univ. of Turku, SF-20500 Turku 50, Finland]. (1971). '*Flightlessness in some moulting passerines in Northern Europe'*. *48*, 101–116.

Schaub, M., Jenni, L. (2001). 'Stopover durations of three warbler species along their autumn migration route.' Oecologia 128, 217–227. https://doi.org/10.1007/s004420100654

Jenni, L., & Schaub, M. (2003). 'Behavioural and Physiological Reactions to Environmental Variation in Bird Migration: A Review'. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian Migration* (pp. 155–171). Springer Berlin Heidelberg.

Junda, J. H., Duval, S., & Gahbauer, M. A. (2020). 'Use of discrete molting grounds by migrant passerines undergoing prebasic molt in southern Quebec'. *The Wilson Journal of Ornithology*, *132*(1), 72–82. WorldCat.org. https://doi.org/10.1676/1559-4491-132.1.72

Klaassen, R., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K.-M., Bairlein, F., & Alerstam, T. (2013). 'When and where does mortality occur in migratory birds? Direct evidence from long- term satellite tracking of raptors'. *The Journal of Animal Ecology*, *83*. https://doi.org/10.1111/1365-2656.12135

Lack, D. (1960). The Influence of Weather on Passerine Migration. A Review. *The Auk*, *77*(2), 171–209. WorldCat.org.

Leu, M., & Thompson, C. W. (2002). 'The potential importance of migratory stopover sites as flight feather molt staging areas: A review for neotropical migrants'. *Biological Conservation*, *106*(1), 45–56. WorldCat.org. https://doi.org/10.1016/S0006-3207(01)00228-2

Maine Forest Service. (2021). ‘Return of the Spruce Budworm to Maine’. Government of *Maine Department of Agriculture, Conservation & Forestry*. Retrieved from https://www.maine.gov/dacf/mfs/forest_health/documents/ReturnofSpruceBudworm_2021.pdf. Accessed on April 12 2023

Matthews, S. N., & Rodewald, P. G. (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*(6), 955–965. https://doi.org/10.1007/s10980-010-9475-0

McWilliams, S. R., Guglielmo, C., Pierce, B., & Klaassen, M. (2004). ‘Flying, Fasting, and Feeding in Birds during Migration: A Nutritional and Physiological Ecology Perspective’. *Journal of Avian Biology*, *35*(5), 377–393. WorldCat.org.

Mellone, U., De La Puente, J., López-López, P., Limiñana, R., Bermejo, A., & Urios, V. (2015). ‘Seasonal differences in migration patterns of a soaring bird in relation to environmental conditions: A multi-scale approach’. *Behavioral Ecology and Sociobiology*, *69*(1), 75–82. https://doi.org/10.1007/s00265-014-1818-4

Morales, A., Frei, B., Mitchell, G. W., Bégin-Marchand, C., & Elliott, K. H. (2022). ‘Reduced diurnal activity and increased stopover duration by molting Swainson’s Thrushes’. *Ornithology*, ukab083. https://doi.org/10.1093/ornithology/ukab083

Morris, S., Holmes, D., & Richmond, M. (1996). ‘A Ten-Year Study of the Stopover Patterns of Migratory Passerines during Fall Migration on Appledore Island, Maine’. *The Condor*, *98*. https://doi.org/10.2307/1369157

Newton, I. (1966). ‘THE MOULT OF THE BULLFINCH PYRRHULA PYRRHULA’. *Ibis*, *108*(1), 41–67. WorldCat.org. https://doi.org/10.1111/j.1474-919X.1966.tb07251.x

Newton, I. (2007). ‘Weather-related mass-mortality events in migrants’. *Ibis*, *149*(3), 453–467. https://doi.org/10.1111/j.1474-919X.2007.00704.x

Nilsson, C., Klaassen, R. H. G., Alerstam, T., & Natural History Editor: Mark A. McPeek. (2013). ‘Differences in Speed and Duration of Bird Migration between Spring and Autumn’. *The American Naturalist*, *181*(6), 837–845. WorldCat.org. https://doi.org/10.1086/670335

Nuijten, R. J. M., Kölzsch, A., van Gils, J. A., Hoye, B. J., Oosterbeek, K., de Vries, P. P., Klaassen, M., & Nolet, B. A. (2014). ‘The exception to the rule: Retreating ice front makes Bewick’s swans Cygnus columbianus bewickii migrate slower in spring than in autumn’. *Journal of Avian Biology*, *45*(2), 113–122. https://doi.org/10.1111/j.1600-048X.2013.00287.x

Packmor, F., Klinner, T., Woodworth, B. K., Eikenaar, C., & Schmaljohann, H. (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*(1), 6. https://doi.org/10.1186/s40462-020-0193-1

Pageau, C., Tonra, C. M., Shaikh, M., Flood, N. J., & Reudink, M. W. (2020). ‘Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines’. *Biology Letters*, *16*(6), 20200155. WorldCat.org. https://doi.org/10.1098/rsbl.2020.0155

Pomeroy, A. C., Seaman Acevedo, D. A., Butler, R. W., Elner, R. W., Williams, T. D., & Ydenberg, R. C. (2008). 'Feeding-Danger Trade-Offs Underlie Stopover Site Selection by Migrants'. *Avian Conservation and Ecology*, *3*(1), 7. WorldCat.org. https://doi.org/10.5751/ACE-00240-030107

Pyle, P., Saracco, J. F., & DeSante, D. F. (2018). 'Evidence of widespread movements from breeding to molting grounds by North American landbirds'. *The Auk*, *135*(3), 506–520. WorldCat.org. https://doi.org/10.1642/AUK-17-201.1

Ramirez, M. G., Griego, M. S., DeSimone, J. G., Elowe, C. R., & Gerson, A. R. (2022). 'Depleted lean body mass after crossing an ecological barrier differentially affects stopover duration and refuelling rate among species of long-distance migratory birds'. *Functional Ecology*, *36*(12), 2995–3006. https://doi.org/10.1111/1365-2435.14203

Richardson, W. J. (1990). 'Timing of Bird Migration in Relation to Weather: Updated Review'. In E. Gwinner (Ed.), *Bird Migration* (pp. 78–101). Springer Berlin Heidelberg.

Rimmer, C., & McFarland, K. (2020). 'Tennessee Warbler (*Leiothlypis peregrina*), version 1.0'. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.tenwar.01

Roques, S., Henry, P.-Y., Guyot, G., Bargain, B., Cam, E., & Pradel, R. (2021). 'When to depart from a stopover site? Time since arrival matters more than current weather conditions'. *Ornithology*, *139*(1), 1–13. WorldCat.org. https://doi.org/10.1093/ornithology/ukab057

Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., Cruz, S., Proaño, C., Takekawa, J. Y., Newman, S. H., Waldenström, J., Bengtsson, D., Kays, R., Wikelski, M., & Bohrer, G. (2013). 'Flying with the wind: Scale dependency of speed and direction measurements in modelling wind support in avian flight'. *Movement Ecology*, *1*(1), 4. https://doi.org/10.1186/2051-3933-1-4

Schmaljohann, H., & Both, C. (2017). 'The limits of modifying migration speed to adjust to climate change'. *Nature Climate Change*, *7*(8), 573–576. https://doi.org/10.1038/nclimate3336

Schmaljohann, H., Fox, J. W., & Bairlein, F. (2012). 'Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world'. *Animal Behaviour*, *84*(3), 623–640. WorldCat.org. https://doi.org/10.1016/j.anbehav.2012.06.018

Schmaljohann, H., Korner-Nievergelt, F., Naef-Daenzer, B., Nagel, R., Maggini, I., Bulte, M., & Bairlein, F. (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*(1), 26. https://doi.org/10.1186/1742-9994-10-26

Seewagen, C., Slayton, E., & Guglielmo, C. (2010). 'Passerine migrant stopover duration and spatial behaviour at an urban stopover site'. *Acta Oecologica*, *36*, 484–492. https://doi.org/10.1016/j.actao.2010.06.005

Sillett, T. S., & Holmes, R. T. (2002) 'Variation in Survivorship of a Migratory Songbird throughout Its Annual Cycle'. *Journal of Animal Ecology*, *71*(2), 296–308. WorldCat.org.

Stanley, C. Q., Dudash, M. R., Ryder, T. B., Shriver, W. G., Serno, K., Adalsteinsson, S., & Marra, P. P. (2021). ‘Seasonal variation in habitat selection for a Neotropical migratory songbird using high-resolution GPS tracking’. *Ecosphere*, *12*(3). WorldCat.org. https://doi.org/10.1002/ecs2.3421

Tan, K., Choi, C.-Y., Peng, H., Melville, D. S., & Ma, Z. (2018). ‘Migration departure strategies of shorebirds at a final pre-breeding stopover site’. *Avian Research*, *9*(1), 1–10. WorldCat.org. https://doi.org/10.1186/s40657-018-0108-7

Terraube, J., Archaux, F., Deconchat, M., Halder, I., Jactel, H., & Barbaro, L. (2016). ‘Forest edges have high conservation value for bird communities in mosaic landscapes’. *Ecology and Evolution*, *6*(15), 5178–5189. WorldCat.org. https://doi.org/10.1002/ece3.2273

Tsvey, A., Bulyuk, V. N., & Kosarev, V. (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*(11), 1665–1674. WorldCat.org. https://doi.org/10.1007/s00265-007-0397-z

Venier, L. A., Pearce, J. L., Fillman, D. R., McNicol, D. K., & Welsh, D. A. (2009). ‘Effects of Spruce Budworm (*Choristoneura fumiferana* (*Clem*.)) Outbreaks on Boreal Mixed-Wood Bird Communities’. *4*(1), 3. WorldCat.org. https://doi.org/10.5751/ACE-00296-040103

Wang, Y., & Moore, F. (2005). ‘Long-distance bird migrants adjust their foraging behavior in relation to energy stores’. *Acta Zoologica Sinica*, *51*, 12–23.

Wikelski, M., Tarlow, E. M., Raim, A., Diehl, R. H., Larkin, R. P., & Visser, G. H. (2003). ‘Costs of migration in free-flying songbirds’. *Nature*, *423*(6941). WorldCat.org.

Yohannes, E., Biebach, H., Nikolaus, G., & Pearson, D. J. (2009). ‘Migration Speeds among Eleven Species of Long-Distance Migrating Passerines across Europe, the Desert and Eastern Africa’. *Journal of Avian Biology*, *40*(2), 126–134. WorldCat.org.

Zhao, M., Christie, M., Coleman, J., Hassell, C., Gosbell, K., Lisovski, S., Minton, C., & Klaassen, M. (2017). ‘Time versus energy minimization migration strategy varies with body size and season in long-distance migratory shorebirds’. *Movement Ecology*, *5*(1), 23. https://doi.org/10.1186/s40462-017-0114-0

Supplementary materials

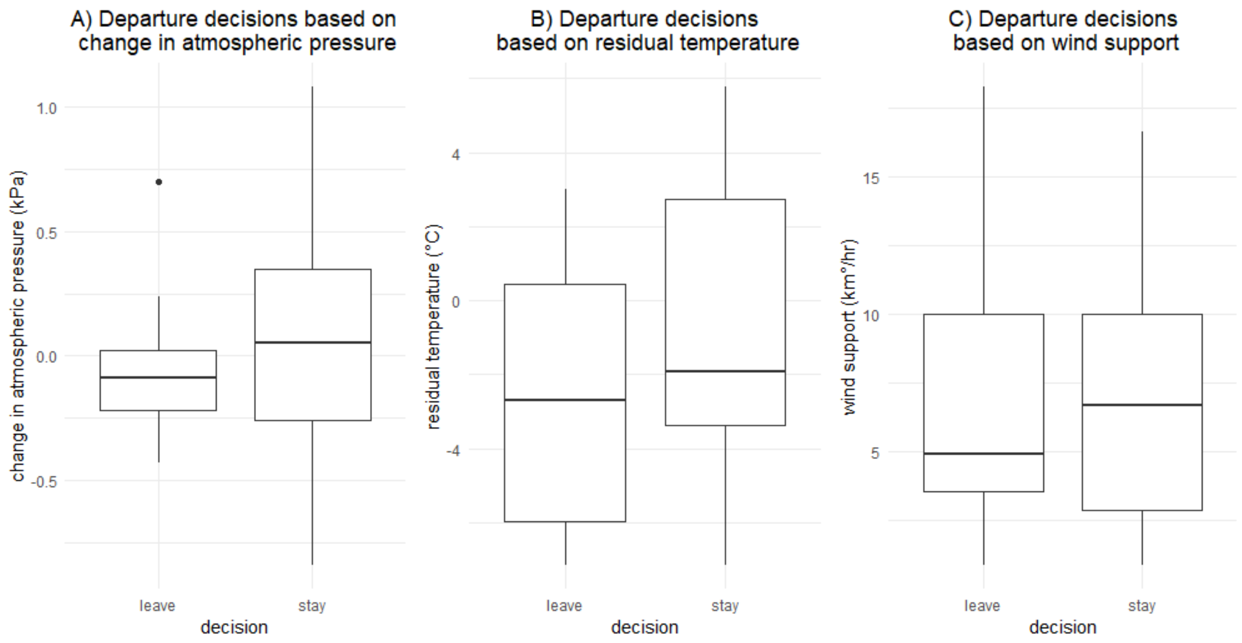
Table S2.1. 95% home range sizes of migrating Tennessee warblers (estimates using IID isotropic models), including the confidence interval (CI), at an autumnal stopover in southern Quebec. First and last detection are the dates at which the first and last GPS locations (after successful tracking) were collected for each radio-tagged bird. The most status of each bird is indicated by Y (moulting) or N (post-moult).

Tag ID	*Area (hm²)*	*Area CI (hm²)*	*Moult status*	*First detection*	*Last detection*
60	7.07	(3.96 - 11.07)	Y	2019-08-07	2019-08-27
61	23.85	(11.44 - 23.85)	Y	2019-08-13	2019-08-27
63	25.79	(14.44 - 40.39)	Y	2019-08-21	2019-09-28
64	1.60	(0.64 – 2.98)	Y	2019-09-06	2019-09-17
379	6.87	(2.97 - 12.40)	Y	2021-08-16	2021-09-10
380	1.48	(0.77 - 2.43)	Y	2021-08-15	2021-10-12
381	1.59	(0.64 – 2.96)	Y	2021-08-18	2021-10-10
382	2.96	(1.28 - 5.34)	Y	2021-08-18	2021-09-29
383	4.70	(2.43 - 7.70)	Y	2021-08-23	2021-10-12
384	50.79	(25.36 -84.92)	Y	2021-08-24	2021-10-01
385	19.39	(6.29 - 39.71)	Y	2021-08-26	2021-09-12
387	5.79	(1.58 - 12.70)	N	2021-08-29	2021-09-13
388	1.33	(0.43 - 2.73)	Y	2021-09-08	2021-10-12
37	13.12	(6.00 – 22.99)	Y	2022-08-03	2022-08-31
389	5.82	(1.59 – 12.76)	Y	2022-08-17	2022-09-03
393	9.07	(3.33 – 17.63)	Y	2022-08-17	2022-09-06
400	58.78	(29.34 – 98.27)	Y	2022-08-31	2022-10-06

Table S2.2. Proportion of landscape cover types present in each radio-tagged migrating Tennessee warbler's 95% home range (from 2018 to 2022) at an autumnal stopover in southern Quebec. All individuals are moult migrants except for ID = 387 which is a post-moult migrant.

ID	*Forest (%)*	*Agriculture (%)*	*Aquatic (%)*	*Wetland (%)*	*Anthropogenic (%)*	*Cut and regenerating land (%)*	*Dry land (%)*
379	65.41	15.77	12.01	6.80	0.00	0.00	0.00
37	34.80	50.27	8.57	6.37	0.00	0.00	0.00
380	22.52	7.28	48.34	21.85	0.00	0.00	0.00
381	61.39	18.99	10.76	8.86	0.00	0.00	0.00

382	78.93	1.34	15.72	4.01	0.00	0.00	0.00
383	43.95	27.81	16.35	11.89	0.00	0.00	0.00
384	50.14	38.34	3.44	4.52	3.57	0.00	0.00
385	51.64	30.24	5.90	4.57	7.65	0.00	0.00
387	61.68	22.34	13.57	2.41	0.00	0.00	0.00
388	32.09	65.67	2.24	0.00	0.00	0.00	0.00
389	5.77	94.23	0.00	0.00	0.00	0.00	0.00
393	65.97	9.80	11.56	12.67	0.00	0.00	0.00
400	45.34	44.14	2.61	6.98	0.93	0.00	0.00
60	38.70	35.59	12.85	12.85	0.00	0.00	0.00
61	84.45	9.53	2.63	3.38	0.00	0.00	0.00
63	66.61	20.24	2.95	10.20	0.00	0.00	0.00
64	20.63	70.00	2.50	6.88	0.00	0.00	0.00


A) Departure decisions based on change in atmospheric pressure

B) Departure decisions based on residual temperature

C) Departure decisions based on wind support

Figure S2.1. Boxplots illustrating the difference in weather conditions on nights where moult migrating Tennessee warblers decided to stay or leave the McGill Bird Observatory; an autumnal stopover in southern Quebec. Graphs include data across all sampling years (2018 to 2022). Note that y-axes show different units.

Table S2.3. Summary mean, standard deviation, and sample size of change in atmospheric pressure values on dates where moult migrating Tennessee warblers either decided to ‘stay’ at their autumnal stopover site or ‘leave’ to continue migration (number of dates in each category denoted by ‘n’). It also includes non-parametric t-test (i.e. Wilcoxon rank-sum test) and f-test (to compare two variances) values comparing means and variances, respectively, between stay and leave dates.

Decision	**stay**			**leave**			**Significance**			
	mean	SD	n	mean	SD	n	t-test		f-test	
							w	p	f	p
All years	0.03	0.48	161	-0.13	0.31	17	1157	0.30	0.35	**0.02**
2018	0.01	0.43	104	-0.08	0.13	10	455	0.52	0.09	**<0.001**
2019	0.07	0.60	28	-0.23	0.43	2	22	0.65	0.61	0.88
2021	-0.04	0.47	17	-0.29	0.17	2	14	0.69	0.13	0.56
2022	0.02	0.62	12	0.17	0.57	3	78	0.48	0.85	0.95

Table S2.4. Summary of the mean, standard deviation, and sample size residual temperature values on dates where moult migrating Tennessee warblers either decided to ‘stay’ at their autumnal stopover site or ‘leave’ to continue migration (number of dates in each category denoted by ‘n’). It also includes non-parametric t-test (i.e. Wilcoxon rank-sum test) and f-test values (to compare two variances) comparing means and variances, respectively, between stay and leave dates.

Decision	**stay**			**leave**			**Significance**			
	mean	SD	n	mean	SD	n	Wilcoxon		f-test	
							w	p	f	p
All years	-0.87	4.00	161	-2.53	3.43	17	1041	0.11	0.74	0.50
2018	-1.11	4.55	104	-4.04	2.94	10	320	**0.04**	0.42	0.16
2019	-0.17	2.97	28	0.02	1.09	2	25	0.80	0.13	0.57
2021	-0.46	1.51	17	-0.92	1.93	2	15	0.79	1.64	0.44
2022	0.14	3.27	32	0.86	3.80	3	74	0.63	1.35	0.55

Table S2.5. Summary of the mean, standard deviation, and sample size wind support values on dates where moult migrating Tennessee warblers either decided to 'stay' at their autumnal stopover site or 'leave' to continue migration (number of dates in each category denoted by 'n'). It also includes non-parametric t-test (i.e. Wilcoxon rank-sum test) and f-test (to compare two variances) values comparing means and variances, respectively, between stay and leave dates.

Decision	**stay**			**leave**			**Significance**			
	mean	SD	n	mean	SD	n	Wilcoxon		f-test	
							w	p	f	p
All years	6.72	4.15	161	7.12	4.71	17	1409	0.84	1.29	0.42
2018	6.03	4.07	104	6.00	3.99	10	499	0.83	0.96	0.96
2019	9.39	4.42	28	10.16	4.04	2	30	0.90	0.83	0.74
2021	7.54	2.56	17	6.55	5.20	2	15	0.79	4.13	0.12
2022	7.32	4.48	32	8.08	6.80	3	54	0.61	2.30	0.19

CONNECTING STATEMENT

In Chapter 2, I discovered that migrating Tennessee Warblers (*Leiothlypis peregrina*) base their departure decisions on body condition. Post-moult migrants with higher mass and thus better fat reserves will depart from their stopover site earlier than lighter birds. Moult migrants who are further along in their moult will need less time to complete their moult and will also depart earlier. How these birds obtain energy to sufficiently moult and refuel will therefore affect their departure decisions and subsequent migration speed. Of course, the energy available to migrating birds depends on the quality of their stopover site. In Chapter 3, I explore the habitat thresholds that influence a migrant's decision to stay or leave their stopover site, expecting them to prefer high quality sites that offer high energy stores. Establishing the habitat characteristics that impact migrant behaviour is especially critical in urban landscapes with few green spaces. In summary, we shift from describing the stopover duration and departure decisions of one moult migrating passerine species in Chapter 2 and move to focus on the habitat use of another moult migrating passerine, the Swainson's Thrush (*Catharus ustulatus*). Chapter 3 is therefore another critical element in understanding the stopover ecology of moult migrating passerines.

NOTE ON CHAPTER 3

Chapter 3 is a manuscript in which I am first author and has been submitted (on July 3rd 2023) to *Biological Conservation*. The manuscript describes the habitat use of moult and post-moult migrating Swainson's Thrushes during the autumnal stopover at a peri-urban stopover site. Kyle Elliott (McGill University) and Barbara Frei (Environment and Climate Change Canada) are co-authors on this paper.

Photo of a radiotagged Swainson's Thrush at the McGill Bird Observatory, taken by Vanessa Poirier.

CHAPTER 3: Peri-urban forest margins are important stopover sites for moult-migrating songbirds

Authors. Vanessa Poirier[1], Kyle H. Elliott[1], and Barbara Frei[2]
[1]Department of Natural Resource Sciences, McGill University
[2]Science and Technology Branch, Environment and Climate Change Canada

Abstract. Cities are significant barriers for migrating birds, but providing suitable greenspaces for stopovers can mitigate urban impacts. City planning for greenspaces often focusses on forests as parks, yet brushy edges and other successional habitats may be equally important especially for songbirds who spend weeks at stopovers in cities to moult their feathers ('moult migrants'). To investigate the role of peri-urban landscapes on moult migrants, we captured 48 moulting and 41 post-moult migrating Swainson's Thrushes (*Catharus ustulatus*) within a large (3000 ha) urban park in Montreal, Canada. Each bird was randomly translocated to one of eight sites of varying habitat type and tracked using radiotelemetry. We compared the time spent at each translocation site with habitat characteristics, expecting birds to spend more time in areas with high food availability and concealment from predators. Migrating thrushes spent ~4 times as much time in dense forest margins than in fields and mature forests. Berry-producing shrubs that we identified as food for thrushes (by DNA-barcoding of their feces) best characterized those margins. Home ranges were much smaller than the size of the park (50% core range: 10.6 ± 17.2 ha). This highlights the importance of urban greenspaces with dense forest margins during a vulnerable time for moult migrant songbirds, and the conservation implications of maintaining these lower-valued greenspaces. Given that city parks are often lacking understory growth, we recommend keeping 'messy' margins for migrating birds of at least 10 ha in size.

Résumé. Les villes sont des barrières pour les oiseaux migrateurs, mais des espaces verts peuvent servir comme escales migratoires pour atténuer les effets de l'urbanisation. Les gestionnaires urbaines se concentrent souvent sur les forêts en tant que parcs, mais les lisières broussailleuses et d'autres habitats de succession peuvent être aussi importants particulièrement pour les passereaux, comme les *Catharus ustulatus*, qui prennent des semaines pour muer leurs plumes (« migrateurs de mue ») à ces habitats. Pour étudier le rôle des paysages péri-urbains sur les migrateurs en mue, nous avons capturé 48 *Catharus ustulatus* en mue et 41 *Catharus ustulatus* en migration post-mue durant l'automne 2021 et 2022 dans le Grand Parc de l'Ouest (3 000 ha) : un grand parc urbain à Montréal, Canada. Chaque oiseau a été transloqué à l'un des huit sites d'habitat variable et suivi à l'aide de la radiotélémétrie. Nous avons comparé le temps passé sur chaque site de translocation avec les caractéristiques de l'habitat, en nous attendant à ce que les oiseaux passent plus de temps dans les zones avec beaucoup de nourriture et d'abri des prédateurs. *Catharus ustulatus* ont passé ~4 fois plus de temps dans les lisières de forêts denses que dans les champs et les forêts matures. Ces lisières sont caractérisées par les arbustes qui produisant des baies que nous avons identifiés comme nourriture pour les *Catharus ustulatus* (par le codage ADN de leurs excréments). Les domaines vitaux étaient beaucoup plus petits que la taille du parc (50 % du domaine vital : 10,6 ± 17,2 ha). Ceci met en évidence l'importance des espaces verts urbains avec des lisières de forêts denses pendant une période vulnérable pour les passereaux migrateurs en mue, et les implications en termes de conservation de ces espaces verts. Étant donné que les parcs urbains sont souvent dépourvus de arbustes, nous recommandons de conserver des marges « désordonnées » d'au moins 10 ha pour les oiseaux migrateurs.

Keywords. urban greenspace, forest margin, moult migration, stopover, berry-producing shrub

Introduction

Urban landscapes are rapidly expanding as our increasing human populations move toward cities (Seto et al., 2012). Urbanization causes cross-taxa declines due to habitat loss, fragmentation, and homogenization (McKinney, 2008, Piano et al., 2020, Seto et al., 2012). In response, the Kunming-Montreal Global biodiversity framework specifies, in Target 12, that urban planning should be biodiversity-inclusive (United Nations, 2022). Habitat alterations pose a particular problem for migratory birds who are an important component of temperate city biodiversity (Thompson et al., 2022). Many birds stop in urbanized areas with minimal green spaces to restore their fat reserves during migration (Rodewald & Matthews, 2005; Matthews & Rodewald 2010a, 2010b; Seewagen et al., 2010, 2011). Nocturnal migrants are particularly drawn to cities as bright artificial lights attract migrating passerines flying at night (La Sorte et al., 2014; McLaren et al., 2018; Van Doren et al., 2017). The ecological traps created by cities are particularly problematic as stopover sites in urban areas are limited in size (often < 4.5 ha), host invasive food sources that are unfamiliar to many species and provide many novel dangers (Matthews & Rodewald 2010a; Loss et al., 2014; Piontek et al,. 2020). Thus, it is critical that urban forest patches be developed so as to create refuges for migratory birds (Matthews & Rodewald, 2010a).

There is mounting evidence that migratory birds, stopping in cities, preferentially occupy spatially heterogenous forest patches (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023). These green spaces in peri-urban areas hold higher bird biodiversity than in city centers or even natural forests with less habitat heterogeneity (Callaghan et al., 2019). Migratory landbirds occur in higher densities in deciduous and riparian forest patches in otherwise weakly-vegetated regions (i.e. low density urban landscapes; Cohen et al., 2022; Guo et al., 2023). Buron *et al.* (2022) found that migratory birds prefer to use urban forest fragments during stopover rather than residential areas.

Despite the importance of heterogenous forest patches for birds (Estavo et al., 2017; Zuniga-Palacios et al., 2020), we generally consider them an eyesore (Rega-Brodsky et al., 2018). Spontaneous (i.e. non-planted) vegetation in cities is perceived as being ‘unkempt’ and is not as ‘beautiful’ as human-designed gardens (Bonthoux et al., 2019). Spontaneous vegetation generally occurs in vacant or neglected lots which is a cause for its poor perception (Rega-Brodsky et al., 2018) but these plants contribute substantially to urban biodiversity (Philips & Lindquist, 2021).

Neglected spaces have the potential to develop into early successional landscapes which offer a mix of understory vegetation and taller trees (i.e. vertical spatial complexity; Swanson et al., 2010) that increase biodiversity (Hwang, 2016). While small forest patches may not be visually appealing, to meet Target 12, cities need to conserve these fragments that host a high diversity of migratory birds.

A large portion of migratory birds in North America breed in the boreal forest and many pass through large expanses of urban areas twice per year to reach their non-breeding grounds (Cohen et al., 2022; Wells, 2011). Indeed, for billions of songbirds that migrate from the boreal forest, cities in southern Canada are the first major human barrier that they encounter, many of which are funneled through the "Montreal Gap" between the Great Lakes and Gulf of St Lawrence where songbirds do not encounter large waterbodies during migration (Gahbauer et al., 2016). Some individuals of certain passerine species spend a significant amount of time (~13% of their annual life cycle) at urban stopover sites to moult their flight feathers (Morales et al., 2022). While birds traditionally moult prior to migrating, some birds are 'pushed' by arid conditions at their breeding grounds and search for more suitable habitat to moult along their migration route ('moult migration'; Barta et al., 2008; Cherry, 1985; Pageau et al., 2020; Rohwer et al., 2005). These discrete moulting grounds exist in southern Quebec where banders have observed a high proportion (>50%) of migrants moulting at their site (Junda et al., 2020). Swainson's Thrush (*Catharus ustulatus*; hereafter "thrushes") is one such songbird species with frequent moult migrants (Junda et al., 2020; Pyle et al., 2018). Increasingly drier conditions in the boreal forests due to climate change (Price et al., 2013) could potentially push more birds towards these separate moulting grounds in cities.

To better understand what urban landscapes should be conserved for moult-migrating songbirds during this critical period of their annual cycle, we examine migrants' occupancy decisions among several different habitat types within the Grand Parc de l'Ouest in Montreal, Canada's largest municipal park. We tracked the movements of adult thrushes following their experimental translocation to three different habitat types (i.e. mature forests with low understory growth, immature forests with dense forest margins and understory growth, and open grassy fields) in southern Quebec during their fall stopover. Junda *et al.* (2020) recently determined that approximately 64% of Swainson’s Thrushes at the MBO were moulting upon capture, making them an ideal species for this study. We predict that moult migrants with high energy requirements (Hoye & Buttemer, 2011) and a general need for high food availability (e.g. thrushes commonly eat native berries during migration, Parrish, 1997) and protection from predators (i.e. concealment; Leu & Thompson, 2002; Pomeroy et al., 2008) will decide to leave field and mature forest habitats with sparse understory growth and move to immature forests with abundant berry-producing shrubs instead. In addition, based on their observed preference for heterogenous forest patches (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023), we expect migrants to select areas associated with forest edge and densely vegetated landscapes, like forest and wetlands, as opposed to open agricultural fields and anthropogenic areas.

Materials and methods

Radio-tagging and translocation

Thrushes were captured at the McGill Bird Observatory (“MBO”, 45.4307°N, 73.9385°W) during their 2021 and 2022 fall migration (between 1 August and October 21) using 30mm mist nets. After hatch-year individuals were banded with numbered aluminum leg bands and aged based on their plumage and skull ossification. We recorded the percentage of moult completed where each primary and secondary flight feather was given a score from 0 (i.e. old feather) to 1 (i.e. new feather), in 0.1 increments (Newton, 1966; Morales et al, 2022). Bird banding and radio-tagging were performed under animal use protocol 2007–5446 from McGill University, and federal banding permits 10743AE and 10743T issued by the Canadian Wildlife Service.

We translocated thrushes to habitat types within ~1200 ha of the capture site. We chose six translocation sites in 2021 and seven in 2022 (Figure S3.1). Translocation sites were chosen by in-person observation of the dominant habitat type: mature forest with sparse understory growth, immature forest with dense understory growth, or open grassy field. The capture site (MBO) was treated as an immature forest translocation site in analyses. Site size had no effect on thrushes’ occupancy decisions [see Results].

We attached 1 g and 0.35 gr coded radio-transmitters to 48 (23 in 2021 and 25 in 2022) moulting and 41 (21 in 2021 and 20 in 2022) post-moult thrushes using leg-loop harnesses. The radio-tags were NTQB-6-1, NTQB2-1, and NTQB2-4-2 models manufactured by Lotek and registered as part of the Motus Wildlife Tracking System (Frei, 2021-2022). All birds were randomly assigned to a translocation site and transported to their site by car and foot. Birds assigned to the capture site were given a minimum of 10-minute car ride to standardize the birds' treatments. Additional automated detections were collected by four Motus towers within a few kilometers of the MBO. See the detailed methods in Supplementary materials for the detailed manual tracking schedule and methods.

Habitat characteristics within and across translocation habitat types

Habitat surveys were completed from July through September 2021 and June through July 2022. We established randomized 10m-diameter circular quadrats within each site, totaling approximately 10 ± 2.5 surveys per site (range of 4 to 14; see Table S3.1 in Supplementary materials). The measurements taken in each plot included diameter at breast height (DBH) of trees > 3 cm in diameter, stand density, shrub cover, canopy cover, concealment, and density of berry-producing plants where we counted the number of shrubs by their stems and identified them by species. We only considered shrub species that we had confirmed were consumed by thrushes using DNA barcoding analysis of fecal samples collected in 2021 [see Results]. Shrub cover was measured using line transects in 2021 following methods in Higgins *et al.* (1994) and Tietz and Johnson (2007) and a cover pole in 2022 following methods in Griffith and Youtie (1988). Canopy cover was measured as the percent of canopy to open sky using ImageJ, as validated for use in Smith and Ramsay (2018). Concealment was measured based on methodologies in Tietz and Johnson (2007) whereby we observed the viability (%) of a 1 m by 1 m checkerboard sheet placed on the ground. See the detailed methods in the Supplementary materials for a detailed explanation of the DNA analysis and how these habitat characteristics were measured.

We performed a non-parametric multivariate analysis of variance (MANOVA) to compare the mean and standard deviation of all habitat variables between habitat types using the Wilks' Lambda type statistic with the *npmv* package in R.3.2. Statistically significant results ($\alpha = 0.05$) were followed with Kruskal-Wallis tests and pairwise comparisons using the Dunn method and incorporating the Benjamini-Hochberg procedure to minimize false positives. We also performed a principle component analysis comparing habitat characteristics between each translocation habitat type (see the detailed methods in Supplementary materials). Note that data was homoscedastic but not normally distributed.

Occupancy decisions at the translocation sites

We analyzed occupancy decisions (i.e. how long a bird stayed at their translocation site) based on manual tracking data. We calculated ‘length of stay’ as the percent of days each bird spent in their respective translocation site (known through manual tracking), out of their total stopover duration. Stopover duration (in days) was calculated as the difference between the capture (i.e. translocation) date and the departure date. Departure dates were recorded as the last date an individual was detected by one of the three Motus towers located in the study site.

For one moulting individual in 2022, tower detections were too weak to determine departure date. Instead, we calculated the number of days it would take that individual to completely moult (following a moult rate of 2.0 ± 0.6 % per day, calculated using data from 2013 to present from this site) as a proxy for departure date. In all, length of stay was calculated for 69 individuals (41 moult and 28 post-moult migrants; see Table S3.2 in Supplementary materials for details) and logit-transformed before all analyses.

We constructed generalized linear models (GLMs) comparing length of stay with concealment and berry-producing shrub density. We built four GLMs: a global model (including concealment and density of berry-producing shrubs), a null model, a concealment-only model, and a berry-producing shrub density model. Moult status was included as a random effect in each model. No other habitat variables were included in these models because they were all highly correlated. Predictor and response variables were scaled and centered prior to modeling. We finally ranked the four models using the Akaike information criterion method for model selection adjusted for small sample sizes (AICc).

Use-availability analysis: peri-urban resource selection

We conducted a use-availability analysis to investigate migrating thrushes’ resource selection during their stopover. The GPS coordinates collected through manual tracking were the ‘used’ points in our analysis. We only included birds that had > 1 associated GPS points (N = 64 different birds totaling 481 GPS points). We produced two available points for every used point and them at equivalent distances (to their paired used point, ranging from 1 m to 3 500 m) from the bird's release site at a randomly selected angle from that site. All points were overlaid on a 30 m-resolution landscape cover map from 2019 (obtained from *Partenariat Données Québec*). We extracted the proportion of landscape cover type (note that these are broader categories from the translocation habitat types: i.e. agriculture, anthropogenic, forest, and wetland) and length of forest edge (in meters) within 50 m, 100 m, and 200 m-radius buffers around each used and available point. Any available points that were 100% surrounded by water were removed as thrushes are not aquatic birds and would not realistically be using these areas. Data was centered and scaled before modeling.

We constructed four binomially distributed generalized linear mixed-effect models. First, we built separate global models for each buffer size and compared them through AICc model selection to determine the scale of effect. The resulting best model's buffer size (i.e. 50 m-radius, see Results) was then used to construct the following four candidate models: a 'landscape composition' model including the proportion of different landscape types (i.e. agriculture, anthropogenic, forest, wetland) in the available/used area, a 'forest edge' model including only the length of forest edge (in meters), and a global model including both landscape composition variables and forest edge, and a null model (see Table 3.2). All four models also included the habitat type of the translocation site (see Figure S3.1 in the Supplementary materials) and the bird's identification number (ID) as random effects. We also tested for multicollinearity between all the predictor variables before constructing our models and found no correlation (Pearson's $r < 0.7$). The four candidate models were ranked using AICc model selection and analyzed for goodness of fit using the Hosmer and Lemeshow test.

Distance travelled from translocation sites

We calculated the distance between chronologically consecutive GPS points (i.e. displacements) for 74 thrushes (44 moult migrants and 30 post-moult migrants). Distances were calculated using the *move* package in the R.3.2 and are presented in meters. We considered individuals translocated to immature forests, mature forests, and fields separately and compared the average first displacement between habitat types using a Kruskal Wallis and subsequent Dunn's test with the Bonferroni method.

Home range

We constructed home ranges from the GPS locations of the thrushes obtained through manual tracking. We determined 95% and 50% home ranges using independent and identically distributed (IID) isotropic models as suggested by the AICc model selection in the *ctmm* package in the R.3.2, confirming the existence of a home range rather than continuous movement. These home ranges were then overlaid on a 30 m-resolution landscape cover map from 2019 (obtained from *Partenariat Données Québec*). Calculations included data from 42 individuals across both sampling years (21 moult and 7 post-moult migrants from 2022, and 14 moult migrants from 2021) since these individuals had at least five GPS points to successfully build their home range.

Results

Habitat characteristics within and across translocation habitat types

All translocation habitat types were significantly different from one another ($p < 0.05$) across all habitat measurements ($p < 0.001$). Concealment (i.e. concealment, shrub cover, and canopy cover) and tree-related measurements (i.e. stand density and DBH) were consistently highest in mature forest sites whereas most shrub density-related measurements (i.e. shrub and berry-producing shrub density) were highest in immature forest sites (Figure S3.2). The PCAs showed the same relationships for mature and immature forests while field sites were unrelated to any habitat measurements (Figure S3.3 and Table S3.3). All habitat variables were consistently low in field sites. For sites sharing the same habitat type, only immature forest sites were statistically similar for all habitat measurements ($p > 0.05$), while there were slight differences within mature forest and field sites (Table S3.4).

We detected plant DNA in 82% of thrushes' fecal samples (N = 38), however, only 44% of detections could be identified to genus. The plant genera present were *Rubus* (13.0%), *Juglans* (13.0%), *Ambrosia* (13.0%), *Rhamnus* (8.7%), *Frangula* (8.7%), and *Boehmeria* (8.7%), of which *Rhamnus, Rubus,* and *Frangula* are berry-producing shrubs present on site.

Occupancy decisions

Average length of stay was highest in the immature forest sites (25 ± 16% of their stay or 12 ± 7 days), followed by the mature forest sites (7 ± 20% or 3 ± 9 days) and was nearly negligible in the field sites (0.15 ± 0.56% or 1 ± 3 days). Length of stay was significantly different among all habitat types ($p < 0.001$) except between mature forest and field sites ($p > 0.05$). There was no relationship between length of stay and site size (adjusted $R^2 = -0.10$ and $p = 0.66$). Average stopover duration (see Materials and methods) for moult migrants was 46 days versus 8 days for post-moult migrants.

Table 3.1. AICc of four generalized linear models comparing migrating Swainson's Thrushes' occupancy decisions (i.e. proportion of their stopover duration that they spent at their translocation site) to the sites' berry-producing shrub density and concealment. The moult status of the birds (i.e. moult or post-moult) was considered a random effect in these models.

Model	**Variables**	**-LL**	**Δ AICc**	**Wt**
Berry	berry-producing shrub density + moult	-57.07	0.00	0.75
Global	concealment + berry-producing shrub density + moult	-56.66	1.51	0.25
Null	moult	-89.01	61.62	0.00
Concealment	concealment + moult	-88.86	63.57	0.00

The best model to predict length of stay only included berry-producing shrub density (>2.0 ΔAICc values between all other models except the global model; Table 3.1). This berry model had a pseudo-R^2 (1- null deviance/ residual deviance) of 0.700. Berry-producing shrub density in this model had an estimated coefficient of 0.11 ± 0.01 ($p < 0.001$). The global model was second best, followed by the null model, and finally the concealment-only model (Table 3.1). The global model had a similar goodness of fit value (0.705) and estimated coefficient for berry-producing shrub density (0.11 ± 0.01; $p < 0.001$). In both the global and concealment models, concealment had no significant effect on length of stay ($p > 0.05$).

Use-availability analysis: peri-urban resource selection

The global model which extracted habitat measurements from a 50m-radius around the used and available points was significantly better than the models of buffer sizes 100m and 200m (> 2.0

ΔAIC). The global model including the proportion of landscape types (i.e. agriculture, anthropogenic, forest, and wetland) and the length of forest edge was the best (> 2.0 ΔAIC difference between all other models, see Table 3.2) for predicting used versus available areas (i.e. thrushes' presence). Three of the global model's five fixed variables significantly effected thrush presence: proportion of agricultural land ($p = 0.004$), proportion of forest ($p = 0.006$), and the amount of forest edge ($p < 0.001$; see Figure 3.1). The second-best model, the landscape composition model, had similarly significant predictor variables: proportion of agricultural ($p < 0.001$) and anthropogenic land ($p = 0.002$). We found very similar R^2 values between the marginal and conditional global models (R^2 conditional = 0.2 and R^2 marginal = 0.18). A Hosmer and Lemeshow goodness of fit test showed that the global model poorly fit the data ($\chi^2 = 1396$, df = 8, $p < 0.001$).

Table 3.2. AICc of four resource selection (i.e. binomial generalized linear mixed-effects) models comparing 64 migrating Swainson's Thrushes' used versus available (50 m-radius) locations based on their landscape composition and the length of forest edge (in meters). Habitat type of the area and the individual's identification (ID) are included as random effects in each model.

Model	**Variables**	**-LL**	**Δ AICc**	**Wt**
Global	agriculture + anthropogenic + forest + wetland + forest edge + habitat type + bird ID	-816	0.00	0.99
Landscape composition	agriculture + anthropogenic + forest + wetland + habitat type + bird ID	-822	9.66	0.01
Forest edge	forest edge + habitat type + bird ID	-856	72.83	0.00
Null	habitat type + bird ID	-899	156.58	0.00

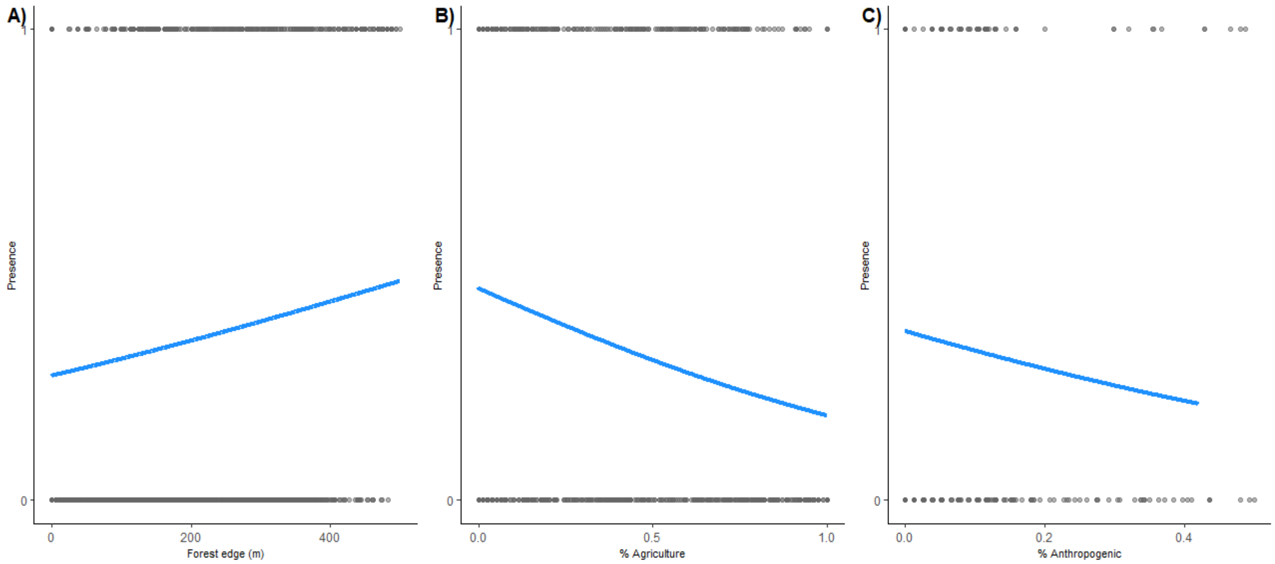


Figure 3.1. Presence of migrating Swainson's Thrushes in a given 50m-radius area as predicted by a generalized linear mixed effects model. The model's fixed effect variables include the percentage of agricultural, anthropogenic, forested land, and wetland, and the length of forest edge (in meters). Random effects in the model were translocation site and bird ID. **A)** shows Swainson's Thrush presence as influenced by the amount of forest edge (coefficient = 0.26, $p < 0.001$), **B)** shows Swainson's Thrush presence as influenced by the proportion of agricultural land (coefficient = -0.51, $p = 0.004$), and **C)** shows Swainson's Thrush presence as influenced by the proportion of anthropogenic land (coefficient = -0.3, $p < 0.006$).

Distance travelled from translocation sites

Thrushes generally made one large movement before settling in their home range for the rest of their stopover (Figure S3.4). This first displacement was significantly shorter for individuals translocated to immature forest sites (195 ± 425 m) than those from mature forest sites (419 ± 633 m, $p = 0.013$). Meanwhile, first displacements made from field sites (266 ± 377 m) were neither significantly longer nor shorter than those from immature forests or mature forests, respectively ($p > 0.05$).

Home range

According to independent and identically distributed (IID) isotropic models we determined that the average (95%) home range size of thrushes across both years was 56.74 ± 106.9 ha. The average 95% home range size was approximately two times larger for moult migrants (62.97 ± 116.3 ha) than post-moult migrants (27.39 ± 30.23 ha; Figure S3.5, Table S3.5). Core (50%) home ranges averaged 10.55 ± 17.16 ha across both years (Figure 3.2). Moult migrants still had ~2 times larger core home ranges (11.68 ± 18.85 ha) than post-moult migrants (5.92 ± 5.33 ha; Table S3.6).

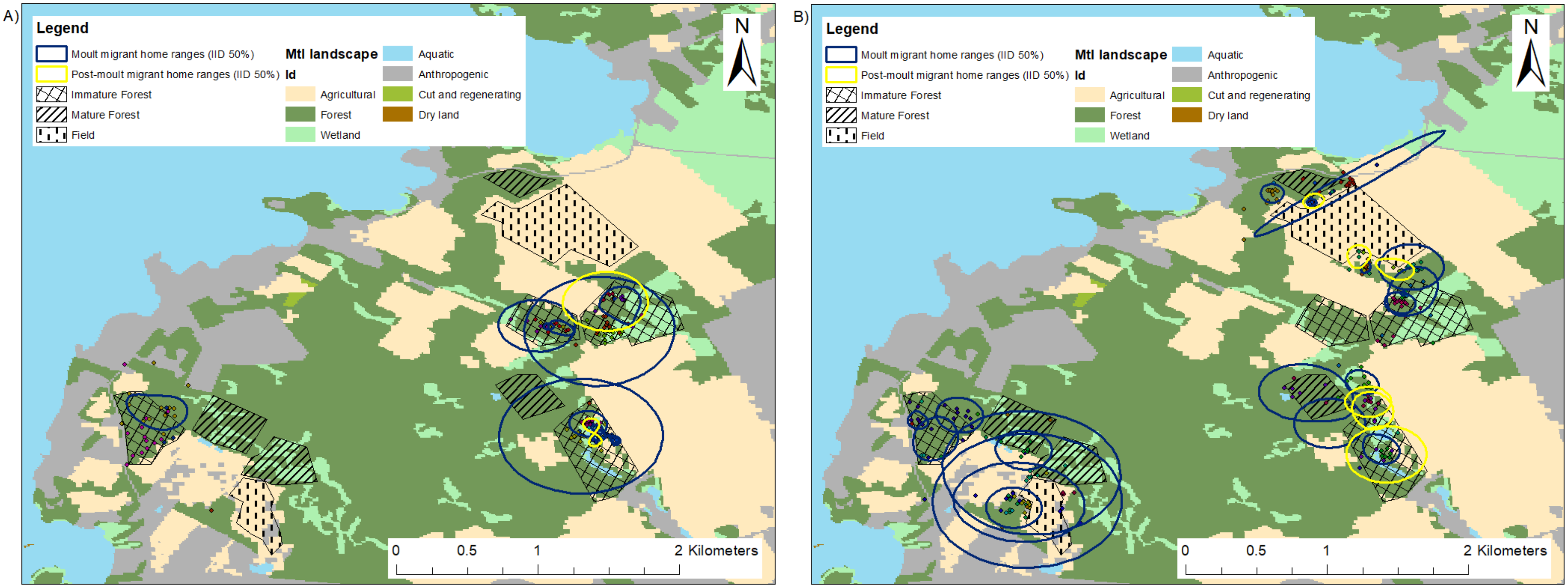


Figure 3.2. Maps of the 50% independent and identically distributed (IID) isotropic calculated home ranges of moult migrating (in navy blue) and post-moult migrant (in yellow) Swainson's Thrushes during their autumnal stopover in the West Island of Montreal. **A)** shows 14 moult and 2 post-moult migrants who were translocated to immature forest sites and **B)** shows 17 moult and 5 post moult migrants who were translocated to mature forests or field sites. GPS points on the maps were taken through manually tracking using radio telemetry when signal strength was at least 130 dB at a gain (precision) between 9 dB and 40 dB. Points belonging to the same bird share the same colour.

On average, the 50% core home ranges were composed of 56.65 ± 28.34% forest, 25.44 ± 25.24% agricultural land, 10.41 ± 14.62 wetlands, and a small percentage of water bodies (5.76 ± 16.94%) and anthropogenic areas (1.74 ± 4.55%). Similarly, the 95% home ranges were mainly composed of forests (50.75 ± 20.95%), followed by agricultural land (30.02 ± 19.41%), wetlands (10.55 ± 12.44%) and a small percentage of anthropogenic areas (4.06 ± 6.96%) and water sources (4.62 ± 10.25%; Table S3.3; see the tables in Supplementary materials for more details).

Discussion

Migrating thrushes in a peri-urban setting spent significantly more time in immature forest, primarily brushy edges with dense understory growth, rather than mature forests or fields. These immature forests had dense understory characteristics (i.e. shrub density and density of berry producing shrubs), while mature forests had more tree and concealment-related measurements(stand density, canopy cover, tree diameter at breast height, shrub cover, and concealment). Migrating thrushes also actively avoided agricultural and anthropogenic landscapes, preferring to occupy forest patches with abundant forest edge. Contrary to previous studies indicating that thrushes are less selective of their stopover habitat and forest types during migration (Stanley et al., 2021; Tietz & Johnson, 2007), thrushes selected habitat at a relatively small scale (within a 50 m radius or smaller). This suggests that migrants search for good-quality habitats in urban areas and that small forest fragments, despite their low value to humans, are important stopover sites. Given that songbirds are attracted to cities during migration where they must stop and refuel, cities have the responsibility of conserving these small forest fragments to meet Target 12.

Although studies suggest that berry-producing shrubs and concealment would both be critical factors for assessing habitat quality (Fox et al., 2014), density of berry-producing shrubs alone was the most influential factor when predicting occupancy decisions. Indeed, the immature forest sites which migrants preferred had the highest density of berry-producing shrubs. Common buckthorn (*Rhamnus cathartica*), an invasive species in Canada (Canadensys, 2022), was the most frequent berry-producing shrub across all sites and most abundant in immature forest sites. Other berry-producing plants found in the immature forest sites include glossy buckthorn (*Frangula alnus*), raspberry and blackberry (*Rubus spp*.), Virginia creeper (*Parthenocissus quinquefolia*), and riverbank grape (*Vitis riparia*). Thrushes are considered generalists and have been seen eating some of the berries mentioned here (Beal, 1915). Based on fecal samples collected from our tagged birds in 2021, individuals were indeed consuming *Rhamnus*, *Rubus*, and *Frangula* species. The abundance of fruit in these habitats must be attractive to migrating birds who require abundant energy to successfully moult and refuel for migration (Leu & Thompson, 2002; Ramirez et al., 2022). Non-native shrubs, however, tend to have less fat and be less energy-dense than native shrubs (Bolser et al., 2013; Smith et al., 2013; White & Stiles, 1992) and therefore may not be as beneficial for migratory birds looking to bolster their fat reserves. Thrushes preferentially inhabit native shrubland during autumnal stopovers (Oguchi et al., 2017) and individuals in our study may be relying on exotic shrubs only due to their abundance in disturbed, urban habitats (Ricotta et al., 2017). City managers should therefore support the growth of berry-producing shrubs, especially those native, naturally occurring species.

Migrants occupied densely vegetated areas that could potentially offer food and concealment; specifically, forest margins. Migrating thrushes were consistently found along the forested edges of their translocation sites. Other studies have highlighted the positive relationship between long-distance migrants and forest edges, and thus their importance for conservation (Stanley et al., 2021; Terraube et al., 2016). In cities where habitat fragmentation has created patches with higher ratios of forest edge to forest interior, migrants may find suitable habitat in these areas. The small size of these fragments seemingly not an issue as migrating thrushes occupied similarly small home ranges (50% IID isotropic distribution = 10.55 ± 17.16 ha). Thrushes made one long (a few hundred meters) movement before settling in their home range. Migrants translocated to preferable (i.e. immature forest) sites made shorter displacements than those translocated to mature forest sites. Our results support growing, though limited, evidence that migrants preferentially occupy fragmented green spaces in otherwise poorly-vegetated urban areas (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023).

This study adds to the growing literature on migratory bird habitat use in cities during the non-breeding season. While anthropogenic growth reduces habitat quality (Seto et al., 2012), migratory birds use urban forest patches (Matthews & Rodewald, 2010a, 2010b; Seewagen et al., 2010), provided that these forest fragments contain dense understory growth (Buron et al., 2022).

Similarly, we conclude that moulting migrants will leave mature forests and fields to move towards dense forest margins in an urban matrix. Whether actively moulting or simply refueling for migration, migrants did not settle for unfavourable stopover sites and instead searched for good quality habitats nearby despite the extra time it would take to find one in an anthropogenic landscape. Migrants considered the density of berry-producing shrubs in a site when deciding whether to occupy it. Indeed, individuals frequented areas that were abundant in berry-producing shrubs like common buckthorn. Areas characterized by this dense vegetation are less common in cities (Jiao et al., 2021; Threlfall et al., 2016). Although not necessarily used by humans, these areas carry high value for migrating songbirds during a particularly vulnerable stage in their life.

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Data availability statement. The data collected for this project is available and can be supplied by the corresponding author upon request. Bird banding data is available through the NatureCount portal (naturecounts.ca) and Motus Wildlife Tracking data is available on the Motus portal (motus.org).

References

Barta, Z., McNamara, J. M., Houston, A. I., Weber, T. P., Hedenström, A., & Feró, O. (2008). Optimal moult strategies in migratory birds. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1490), 211–229. https://doi.org/10.1098/rstb.2007.2136

Beal, F. E. L. Foster E. L. (1915). *Food habits of the thrushes of the United States: Vol. no.280 (1915)*. U.S. Dept. of Agriculture,. https://www.biodiversitylibrary.org/item/190602

Bolser, J. A., Alan, R. R., Smith, A. D., Li, L., Seeram, N. P., & McWilliams, S. R. (2013). Birds Select Fruits with More Anthocyanins and Phenolic Compounds During Autumn Migration. *The Wilson Journal of Ornithology*, *125*(1), 97–108. WorldCat.org. https://doi.org/10.1676/12-057.1

Bonthoux, S., Chollet, S., Balat, I., Legay, N., & Voisin, L. (2019). Improving nature experience in cities: What are people's preferences for vegetated streets? *230*, 335–344. https://doi.org/10.1016/j.jenvman.2018.09.056

Buron, R., Hostetler, M. E., & Andreu, M. (2022). Urban forest fragments vs residential neighborhoods: Urban habitat preference of migratory birds. *Landscape and Urban Planning*, *227*, 104538. https://doi.org/10.1016/j.landurbplan.2022.104538

Callaghan, C. T., Bino, G., Major, R. E., Martin, J. M., Lyons, M. B., & Kingsford, R. T. (2019). Heterogeneous urban green areas are bird diversity hotspots: Insights using continental-scale citizen science data. *Landscape Ecology*, *34*(6), 1231–1246. WorldCat.org. https://doi.org/10.1007/s10980-019-00851-6

Canadensys. (2022). *Database of Vascular Plants of Canada (VASCAN)*. Data accessed from https://data.canadensys.net/vascan/search

Cherry, J. D. (1985). Early Autumn Movements and Prebasic Molt of Swainson’s Thrushes. *The Wilson Bulletin*, *97*(3), 368–370. WorldCat.org.

Cohen, E. B., Lafleur, J. M., & Moore, F. R. (2022). Density Dependent Refueling of Migratory Songbirds During Stopover Within an Urbanizing Coastal Landscape. *Frontiers in Ecology and Evolution*, *10*. https://www.frontiersin.org/articles/10.3389/fevo.2022.837790

Estevo, C. A., Nagy-Reis, M. B., & Silva, W. R. (2017). Urban parks can maintain minimal resilience for Neotropical bird communities. Urban Forestry & Urban Greening, 27, 84–89. doi:10.1016/j.ufug.2017.06.013

Fox, A. D., Flint, P. L., Hohman, W. L., & Savard, J.-P. L. (2014). Waterfowl habitat use and selection during the remigial moult period in the northern hemisphere. *Wildfowl*, 131–168. WorldCat.org.

Frei, B. (2021-2022) Montreal Connectivity (Project373). Data accessed from Motus Wildlife Tracking System, Birds Canada. Available: https://motus.org/. Accessed: 2023-06-08

Gahbauer MA, Duval S, Davey D (2016) McGill Bird Observatory Ten-Year Report: 2005-2014. Migration Research Foundation, Ste-Anne-de-Bellevue QC.

Griffith, B., & Youtie, B. A. (1988). Two Devices for Estimating Foliage Density and Deer Hiding Cover. *Wildlife Society Bulletin (1973-2006)*, *16*(2), 206–210. WorldCat.org.

Guo, F., Buler, J. J., Smolinsky, J. A., & Wilcove, D. S. (2023). Autumn stopover hotspots and multiscale habitat associations of migratory landbirds in the eastern United States. *Proceedings of the National Academy of Sciences*, *120*(3). WorldCat.org. https://doi.org/10.1073/pnas.2203511120

Higgins, K. F., Oldemeyer, J. L., Jenkins, K. J., Clambey, G. K., & Harlow, R. F. (1994). Vegetation sampling and measurement. In The Wildlife Society (Ed.), *Research and management techniques for wildlife and habitats* (pp. 567–591). The Wildlife Society; USGS Publications Warehouse. http://pubs.er.usgs.gov/publication/70129377

Hoye, B. J., & Buttemer. (2011). Inexplicable inefficiency of avian molt? Insights from an opportunistically breeding arid-zone species, Lichenostomus penicillatus. *PloS One*, *6*(2), e16230. WorldCat.org. https://doi.org/10.1371/journal.pone.0016230

Hwang, Y. H. (2016). Observation of floristic succession and biodiversity on rewilded lawns in a tropical city. *Landscape Research*.

Jiao, M., Xue, H., Yan, J., Zheng, Z., Wang, J., Zhao, C., Zhang, L., & Zhou, W. (2021). Tree abundance, diversity and their driving and indicative factors in Beijing's residential areas. *Ecological Indicators*, *125*, 107462. https://doi.org/10.1016/j.ecolind.2021.107462

Junda, J. H., Duval, S., & Gahbauer, M. A. (2020). Use of discrete molting grounds by migrant passerines undergoing prebasic molt in southern Quebec. *The Wilson Journal of Ornithology*, *132*(1), 72–82. WorldCat.org. https://doi.org/10.1676/1559-4491-132.1.72

La Sorte, F. A., Tingley, M. W., & Hurlbert, A. H. (2014). The role of urban and agricultural areas during avian migration: An assessment of within-year temporal turnover. *Global Ecology and Biogeography*, *23*(11–12), 1225–1234. WorldCat.org.

Leu, M., & Thompson, C. W. (2002). The potential importance of migratory stopover sites as flight feather molt staging areas: A review for neotropical migrants. *Biological Conservation*, *106*(1), 45–56. WorldCat.org. https://doi.org/10.1016/S0006-3207(01)00228-2

Loss, S. R., Will, T., Loss, S. S., & Marra, P. P. (2014). Bird–building collisions in the United States: Estimates of annual mortality and species vulnerability. *The Condor*, *116*(1), 8–23. https://doi.org/10.1650/CONDOR-13-090.1

Matthews, S. N., & Rodewald, P. G. (2010a). Urban Forest Patches and Stopover Duration of Migratory Swainson's Thrushes. *The Condor*, *112*(1), 96–104. https://doi.org/10.1525/cond.2010.090049

Matthews, S. N., & Rodewald, P. G. (2010b). 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*(6), 955–965. https://doi.org/10.1007/s10980-010-9475-0

McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, *11*(2), 161–176. WorldCat.org. https://doi.org/10.1007/s11252-007-0045-4

McLaren, J. D., Buler, J. J., Schreckengost, T., Smolinsky, J. A., Boone, M., van Loon, E. E., Dawson, D. K., & Walters, E. L. (2018). Artificial light at night confounds broad-scale habitat use by migrating birds. *Ecology Letters*, *21*(3), 356–364. WorldCat.org.

Morales, A., Frei, B., Mitchell, G. W., Bégin-Marchand, C., & Elliott, K. H. (2022). Reduced diurnal activity and increased stopover duration by molting Swainson's Thrushes. *Ornithology*, ukab083. https://doi.org/10.1093/ornithology/ukab083

Newton, I. (1966). THE MOULT OF THE BULLFINCH PYRRHULA PYRRHULA. *Ibis*, *108*(1), 41–67. WorldCat.org. https://doi.org/10.1111/j.1474-919X.1966.tb07251.x

Oguchi, Y., Pohlen, Z., Smith, R. J., & Owen, J. C. (2018). Exotic- and native-dominated shrubland habitat use by fall migrating Swainson's Thrushes and Gray Catbirds in Michigan, USA. *The Condor*, *120*(1), 81–93. https://doi.org/10.1650/CONDOR-17-27.1

Pageau, C., Tonra, C. M., Shaikh, M., Flood, N. J., & Reudink, M. W. (2020). Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines. *Biology Letters*, *16*(6), 20200155. WorldCat.org. https://doi.org/10.1098/rsbl.2020.0155

Parrish, J. D. (1997). Patterns of Frugivory and Energetic Condition in Nearctic Landbirds during Autumn Migration. *The Condor*, *99*(3), 681–697. https://doi.org/10.2307/1370480

Phillips, D., & Lindquist, M. (2021). Just weeds? Comparing assessed and perceived biodiversity of urban spontaneous vegetation in informal greenspaces in the context of two American legacy cities. 62, 127151. https://doi.org/10.1016/j.ufug.2021.127151

Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hanashiro, F. T. T., Higuti, J., Lens, L., … Hendrickx, F. (2020). Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, *26*(3), 1196–1211. WorldCat.org. https://doi.org/10.1111/gcb.14934

Piontek, A. M., Wojtylak-Jurkiewicz, E., Schmidt, K., Gajda, A., Lesiak, M., & Wierzbowska, I. A. (2020). Analysis of cat diet across an urbanisation gradient. *Urban Ecosystems*, *24*(1), 59–69. WorldCat.org. https://doi.org/10.1007/s11252-020-01017-y

Pomeroy, A. C., Seaman, D. A. A., Butler, R. W., Elner, R. W., Williams, T. D., & Ydenberg, R. C. (2018). Feeding-Danger Trade-Offs Underlie Stopover Site Selection by Migrants. *Avian Conservation and Ecology*, *3*(1), 7. WorldCat.org. https://doi.org/10.5751/ACE-00240-030107

Price, D. T., Alfaro, R. I., Brown, K. J., Flannigan, M. D., Fleming, R. A., Hogg, E. H., Girardin, M. P., Lakusta, T., Johnston, M., McKenney, D. W., Pedlar, J. H., Stratton, T., Sturrock, R. N., Thompson, I. D., Trofymow, J. A., & Venier, L. A. (2013). Anticipating the consequences of climate change for Canada's boreal forest ecosystems. Environmental Reviews, 21(4), 322–365. 10.1139/er-2013-0042

Pyle, P., Saracco, J. F., & DeSante, D. F. (2018). Evidence of widespread movements from breeding to molting grounds by North American landbirds. *The Auk*, *135*(3), 506–520. WorldCat.org. https://doi.org/10.1642/AUK-17-201.1

Ramirez, M. G., Griego, M. S., DeSimone, J. G., Elowe, C. R., & Gerson, A. R. (2022). Depleted lean body mass after crossing an ecological barrier differentially affects stopover duration and refuelling rate among species of long-distance migratory birds. *Functional Ecology*, *36*(12), 2995–3006. https://doi.org/10.1111/1365-2435.14203

Rega-Brodsky, C. C., Nilon, C. H., & Warren, P. S. (2018). Balancing Urban Biodiversity Needs and Resident Preferences for Vacant Lot Management (Vol. 10). 10.3390/su10051679

Ricotta, C., Rapson, G. L., Asmus, U., Pyšek, P., Kühn, I., La Sorte, F. A., & Thompson, K. (2017). British plants as aliens in New Zealand cities: Residence time moderates their impact on the beta diversity of urban floras. *Biological Invasions*, *19*(12), 3589–3599. https://doi.org/10.1007/s10530-017-1590-2

Rodewald, P. G., & Matthews, S. N. (2005). Landbird use of Riparian and Upland Forest Stopover Habitats in an Urban Landscape. *The Condor*, *107*(2), 259–268. https://doi.org/10.1093/condor/107.2.259

Rohwer S, Butler LK, Froehlich D. 2005 Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. In Birds of two worlds: the ecology and evolution of migration (eds Greenberg R, Marra PP), pp. 87-105. Baltimore, MD: Johns Hopkins University Press.

Seewagen, C. L., Sheppard, C. D., Slayton, E. J., & Guglielmo, C. G. (2011). Plasma Metabolites and Mass Changes of Migratory Landbirds Indicate Adequate Stopover Refueling in a Heavily Urbanized Landscape. *The Condor*, *113*(2), 284–297. https://doi.org/10.1525/cond.2011.100136

Seewagen, C., Slayton, E., & Guglielmo, C. (2010). Passerine migrant stopover duration and spatial behaviour at an urban stopover site. *Acta Oecologica*, *36*, 484–492. https://doi.org/10.1016/j.actao.2010.06.005

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, *109*(40), 16083–16088. WorldCat.org. https://doi.org/10.1073/pnas.1211658109

Sillett, T. S., & Holmes, R. T. (2002). Variation in Survivorship of a Migratory Songbird throughout Its Annual Cycle. *Journal of Animal Ecology*, *71*(2), 296–308. WorldCat.org.

Smith, A. M., & Ramsay. (2018). A comparison of ground-based methods for estimating canopy closure for use in phenology research. *Agricultural and Forest Meteorology*, *252*, 18–26. WorldCat.org. https://doi.org/10.1016/j.agrformet.2018.01.002

Smith, S. B., DeSando, S. A., & Pagano, T. (2013). The Value of Native and Invasive Fruit-Bearing Shrubs for Migrating Songbirds. *Northeastern Naturalist*, *20*(1), 171–184. WorldCat.org.

Stanley, C. Q., Dudash, M. R., Ryder, T. B., Shriver, W. G., Serno, K., Adalsteinsson, S., & Marra, P. P. (2021). Seasonal variation in habitat selection for a Neotropical migratory songbird using high-resolution GPS tracking. *Ecosphere*, *12*(3). WorldCat.org. https://doi.org/10.1002/ecs2.3421

Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., Lindenmayer, D. B., & Swanson, F. J. (2011). The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, *9*(2), 117–125. https://doi.org/10.1890/090157

Terraube, J., Archaux, F., Deconchat, M., Halder, I., Jactel, H., & Barbaro, L. (2016). Forest edges have high conservation value for bird communities in mosaic landscapes. *Ecology and Evolution*, *6*(15), 5178–5189. WorldCat.org. https://doi.org/10.1002/ece3.2273

Thompson, R., Tamayo, M., & Sigurðsson, S. (2022). Urban bird diversity: does abundance and richness vary unexpectedly with green space attributes? https://doi.org/8. 10.1093/jue/juac017

Threlfall, C. G., Ossola, A., Hahs, A. K., Williams, N. S. G., Wilson, L., & Livesley, S. J. (2016). Variation in Vegetation Structure and Composition across Urban Green Space Types. *Frontiers in Ecology and Evolution*, *4*. https://www.frontiersin.org/articles/10.3389/fevo.2016.00066

Tietz, J. R., & Johnson, M. D. (2007). Stopover Ecology and Habitat Selection of Juvenile Swainson's Thrushes During Fall Migration Along the Northern California Coast. *The Condor*, *109*(4), 795–807. https://doi.org/10.1093/condor/109.4.795

United Nations Convention on Biological Diversity. (2022). COP15: Final test of Kunming-Montreal Global Biodiversity Framework. Retrieved from https://www.cbd.int/article/cop15-final-text-kunming-montreal-gbf-221222. Accessed on Apr 3, 2023.

Van Doren, B. M., Horton, K. G., Dokter, A. M., Klinck, H., Elbin, S. B., & Farnsworth, A. (2017). High-intensity urban light installation dramatically alters nocturnal bird migration. *Proceedings of the National Academy of Sciences*, *114*(42), 11175–11180. https://doi.org/10.1073/pnas.1708574114

Wells, J. V. (Jeffrey V., 1964-. (2011). *Boreal Birds of North America: A Hemispheric View of Their Conservation Links and Significance* (Vol. 1–1 online resource (xv, 136 pages) : illustrations, maps.). University of California Press; WorldCat.org. https://doi.org/10.1525/9780520950580

White, D. W., & Stiles, E. W. (1992). Bird dispersal of fruits of species introduced into eastern North America. *Canadian Journal of Botany*, *70*(8), 1689–1696. WorldCat.org. https://doi.org/10.1139/b92-208

Zuñiga-Palacios, J., Zuria, I., Moreno, C. E., Almazán-Núñez, R. C., & González-Ledesma, M. (2020). Can small vacant lots become important reservoirs for birds in urban areas? A case study for a Latin American city. *47*, 126551. https://doi.org/10.1016/j.ufug.2019.126551

Supplementary materials

Detailed methods

Manual tracking of radio-tagged Swainson's Thrushes

Each radio-tagged thrush was manually tracked between 6:00 and 13:00 hours, within the first 3 days of their release, and subsequently tracked every 4 days. In 2022, individuals were tracked more frequently: moult migrants for the first 4 days and subsequently tracked every 3 days while post-moult migrants were subsequently tracked every 2 days. Trackers recorded a GPS point, antennae bearing, wind speed, and temperature when signal strength was at least 130 dB at a gain (precision) between 9 dB and 40 dB.

Habitat characteristics

Thrushes were translocated to one of eight possible sites. Translocation sites were located on a mix of private and public land: the Morgan Arboretum, Bois-de-la-Roche Park, *Les Ecuries* farm, Senneville forest nature reserve, and the cemetery occupied by Belvedere Cemetery & Funeral Complex. Figure S3.1 shows a map of the translocation sites and study area. There totaled four mature forest sites, four immature forest sites (one being the capture site), and two grassy fields.

Density of berry-producing plants was used as a proxy for food availability and measured using 4m-diameter randomized quadrats at the center of each 10-m diameter quadrat. We counted the number of shrubs by their stems and identified them by species. Shrub species included in this variable were only those that we had confirmed were consumed by Swainson's Thrushes using DNA barcoding analysis of fecal samples collected in 2021. Swainson's Thrushes were placed in paper bags for ~5 minutes or until they defecated. Their feces were stored in ethanol before being sent to laboratory scientists at the Canadian Center for DNA Barcoding (CCDB) who extracted DNA using plant-specific primers (ITS-S2F_t1/ITS4_t1) and amplified them through polymerase chain reactions (PCR), producing > 100 bp sequences. Results were compared to a comprehensive BOLD reference library (see the Barcode of Life Data System) and assigned an identity using the Basic Local Alignment Search Tool (BLAST) algorithm. The plant genera found both in these fecal samples and in the habitats were: invasive buckthorn (*Rhamnus*), introduced buckthorn (*Frangula*), brambles (*Rubus*), and walnuts (*Juglans*) [see section 3.1]. We therefore excluded observations of hawthorn (*Crataegus*), dogwood (*Cornus*), honeysuckle (*Lonicera*), currants (*Ribes*), grapevines (*Vitis*) and plum (*Prunus*) from the berry-producing shrubs measurement.

Concealment was measured based on methodologies in Tietz and Johnson (2007) whereby a checkerboard cloth of one hundred 10 by 10 cm squares was laid on the ground and an observer standing 1m away counted the number of squares that were > 50% visible. Only three observers were used throughout the two years of sampling to minimize individual error. We measured additional habitat characteristics including shrub cover, stand density, canopy cover, and diameter at breast height (DBH) of all trees > 3 cm in diameter within each 10 m-diameter quadrat. Shrub cover was measured using line intercept methods in 2021 and a 2 m-long cover pole in 2022 (Higgins et al. 1994, Tietz and Johnson 2007). The cover pole was constructed following instructions in Toledo et al. (2008). An observer counted the number of 0.1 m increments of the pole that were > 25% concealed by vegetation while standing 5 m away at each cardinal direction, following methods in Griffith and Youtie (1988). Stand density was measured using a tree basal area factor prism. Finally, we measured canopy cover for plots sampled in 2022. Canopy cover was measured using standardized images taken at the center of each plot with a phone camera pointing positioned in the North-South plane. We determined the percent open sky versus canopy in each photo using ImageJ, as validated for use in Smith and Ramsay (2018).

Habitat measurements were used to quantify differences between the translocation sites as they may pertain to habitat quality. We pooled habitat measurements from both sampling years as a Wilcoxon paired sample t-test showed no change between years for all habitat characteristics except average DBH ($p = 0.014$). This is most likely because the Garmin GPSs used to mark the quadrat centroids were only accurate to within a few meters and thus the trees included in the same quadrat from year to year must have differed significantly. We therefore kept DBH separated by sampling year in our subsequent analyses. Similarly, shrub cover was measured differently between years (line transects in 2021 and a cover pole in 2022) but the two datasets were linearly correlated (adjusted R2 = 0.557, $p = 0.005$). We therefore transformed shrub cover measurements from 2021 to be comparable to those from 2022 using the coefficients estimated by their correlation: 'shrub cover equivalent to 2022 measurements'= −0.1647 x ('shrub cover 2021') + 17.8259.

All habitat measurements were homoscedastic but not normally distributed (following Levene’s and Shapiro-Wilk's tests, respectively). We therefore performed a non-parametric multivariate analysis of variance (MANOVA) to compare the mean and standard deviation of all habitat variables between habitat types using the Wilks' Lambda type statistic with the npmv package in R.3.2. Statistically significant results ($\alpha = 0.05$) were followed with Kruskal-Wallis tests and pairwise comparisons using the Dunn method and incorporating the Benjamini-Hochberg procedure to minimize false positives.

We also performed three principal component analysis (PCA) to further represent habitat types. A PCA was performed for each year’s sites and a third included sites from both sampling years. Each observation in the PCAs corresponds to a quadrat that was sampled within each respective habitat type. Observations were scaled and centered before performing the PCA to better compare habitat variables. The resulting PCAs were visualized with 95% ellipses grouping points from the same site. Each PCA resulted in six principal components but only the first two components of each are reported here as they explained the majority of the data’s variation (~70% combined).

Supplementary tables and figures

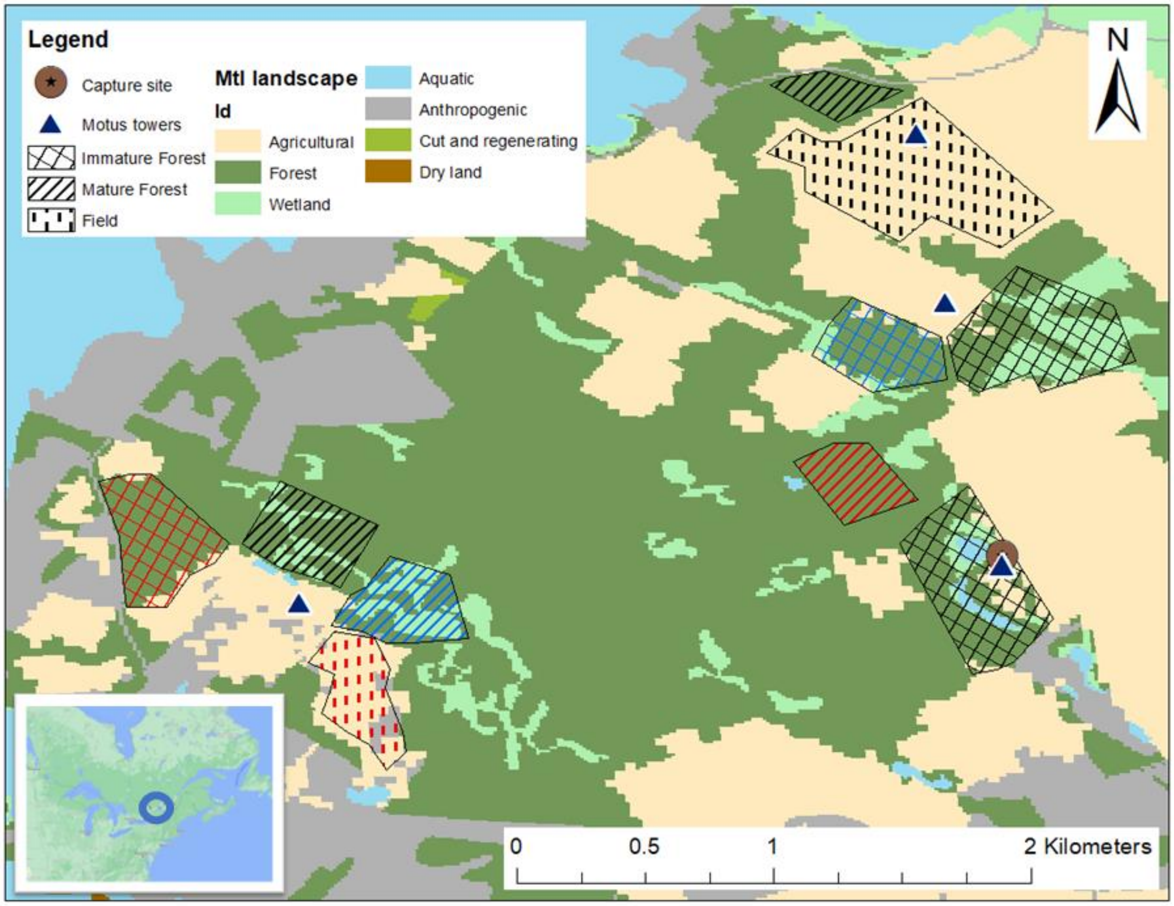

Figure S3.1. Landscape cover map of the West Island of Montreal (30m-resolution map obtained from *Partenariat Données Québec*) indicating the sites of different habitat type where moult and post-moult Swainson's Thrushes were translocated in 2021 (in blue) and 2022 (in red). Translocation sites in black were used in both sampling years (2021 and 2022). The McGill bird observatory where we captured the migrants (i.e. capture site) and Motus towers used to track the radio-tagged Swainson's Thrushes are also shown. In the bottom left corner shows where the West Island of Montreal is located in northeastern North America.

Table S3.1. Number of habitat surveying quadrats located in each translocation site where moult and post-moult migrating Swainson's Thrushes were released in 2021 and 2022 during their autumnal stopover. Quadrats were either within 50 meters of the site centroid or between 50 and 125 meters. In the site names, 'IMF' is an abbreviation for 'immature forest' and 'MF' for 'mature forest'.

Site	MBO	IMF 1	IMF 2	IMF 3	MF 1	MF 2	MF 3	MF 4	Field 1	Field 2
n within 50m-radius	7	6	2	5	10	4	4	6	5	5
n within 125m-radius	4	6	2	2	3	5	3	5	6	5
n total	11	12	4	7	13	9	7	11	11	9

Table S3.2. Number of tagged moult and post-moult migrating Swainson's Thrushes successfully radio-tagged and tracked in each translocation sites' habitat type in each sampling year. These values correspond to the sample sizes used in occupancy decision analyses.

Habitat types	Year				Total	
	2021		2022			
	moult	post-moult	moult	post-moult	moult	post-moult
Immature forest	9	5	9	7	18	12
Mature forest	7	5	8	5	15	10
Field	3	2	5	4	8	6

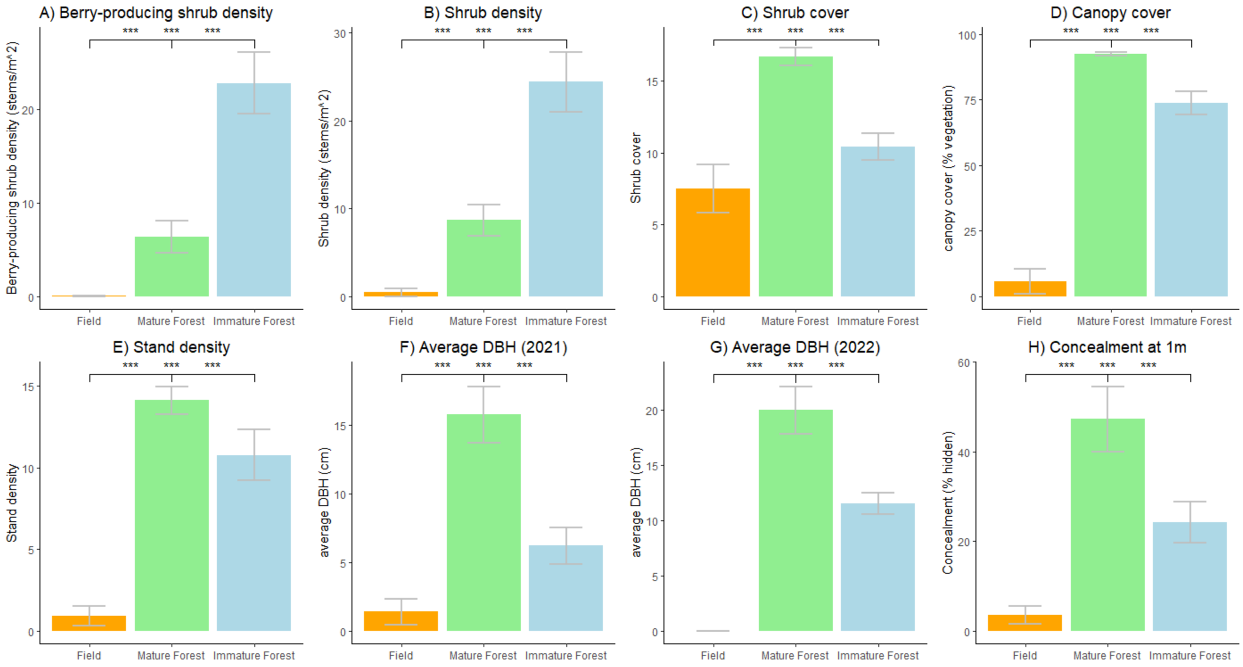

Figure S3.2. Barplots comparing the various habitat measurements between habitat types located at and around the McGill Bird Observatory where moult and post-moult migrating Swainson's Thrushes were translocated. Note that y-axes are different in each graph. Values were unique (i.e. significantly different, p < 0.001) for every habitat variable of each habitat type as indicated by the '***' notations.

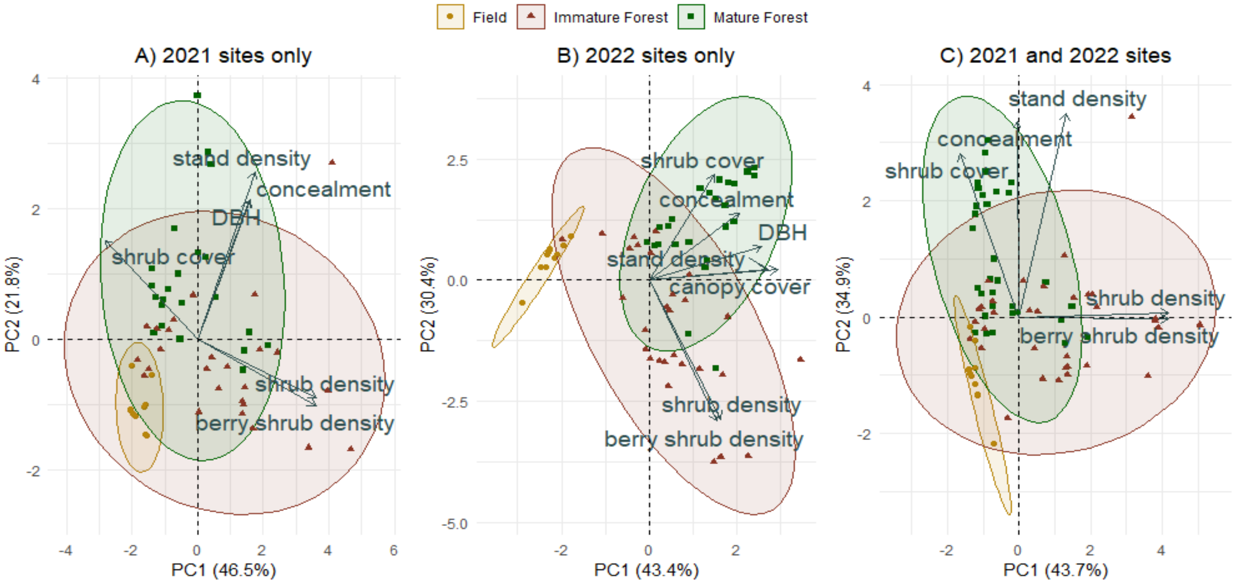

Figure S3.3. The principal component analysis comparing habitat characteristics between sites of different habitat types where moult and post-moult migrating Swainson's Thrushes were translocated to in fall 2021 and 2022. Graph **A** includes all translocation sites of 2021, graph **B** shows sites from 2022, and graph **C** combines both years. Note that canopy cover was only measured in 2022. Note that DBH = average tree diameter at breast height.

Table S3.3. Summary of principle component analyses (PCA) performed on habitat variables of translocation sites where migrating Swainson's Thrushes were released in 2021 and 2021 during their autumnal stopover in peri-urban areas. Three PCAs were performed: one for each sampling year separately and one with both years combined. Note that DBH = average tree diameter at breast height.

Habitat variable	PCA of translocation sites in 2021 only		PCA of translocation sites in 2022 only		PCA of translocation sites in 2021 and 2022	
	PC1 (46.5%)	PC2 (21.8%)	PC1 (43.4%)	PC2 (30.4%)	PC1 (43.7%)	PC2 (34.9%)
Canopy cover	NA	NA	25	0.2	NA	NA
Stand density	7	33	22	0.2	4	39
DBH	6	23	19	2	NA	NA
Shrub cover	19	12	7	20	7	25
Concealment	6	23	12	8	0	36
Shrub density	31	4	8	34	44	0
Berry-producing shrub density	32	5	7	35	44	0

Table S3.4. A table showing the average (± the standard error) of all measured habitat characteristics for each translocation site from both sampling years. Immature forest is abbreviated to 'IMF' and mature forest to 'MF'. Habitat variables were the same for all immature forest sites ($p > 0.05$). Mature forest 4 had significantly lower shrub density than mature forest 3 but higher concealment ($p < 0.05$). Mature forest 1 had significantly less stand density and concealment than mature forest 2 and 4 ($p < 0.05$). Finally, mature forest 4 had significantly higher shrub cover than all other mature forest sites ($p < 0.05$). Similarly, field sites differed by three habitat measurements: shrub cover, concealment, and canopy cover. For each variable, field 2 had significantly lower amounts than field 1 ($p < 0.05$).

Site	*Stand density*	*Shrub density*	*Shrub cover*	*DBH (2022)*	*DBH (2021)*	*Concealment*	*Berry-shrub density*	*Canopy cover*
Field 1	2 ± 1	1 ± 1	14 ± 1	0 ± 0	1 ± 1	6 ± 4	0 ± 0	11 ± 9
Field 2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	NA	0 ± 0	0 ± 0	0 ± 0
IMF 1	13 ± 4	26 ± 4	9 ± 2	12 ± 1	8 ± 0	31 ± 11	24 ± 4	79 ± 4
IMF 2	13 ± 1	28 ± 16	14 ± 3	7 ± 1	5 ± 2	11 ± 7	26 ± 16	NA
IMF 3	14 ± 2	33 ± 8	13 ± 2	14 ± 1	NA	19 ± 5	31 ± 8	72 ± 6
MBO	6 ± 2	16 ± 6	10 ± 2	11 ± 3	6 ± 3	25 ± 7	16 ± 6	68 ± 11
MF 1	10 ± 1	10 ± 4	16 ± 1	24 ± 8	19 ± 3	7 ± 3	8 ± 4	93 ± 2
MF 2	16 ± 1	8 ± 3	16 ± 2	19 ± 3	13 ± 3	53 ± 16	4 ± 2	94 ± 1
MF 3	13 ± 2	16 ± 4	15 ± 2	12 ± 2	10 ± 2	21 ± 5	14 ± 5	92 ± 2
MF 4	17 ± 1	2 ± 1	19 ± 0	25 ± 4	NA	94 ± 2	1 ± 1	91 ± 1

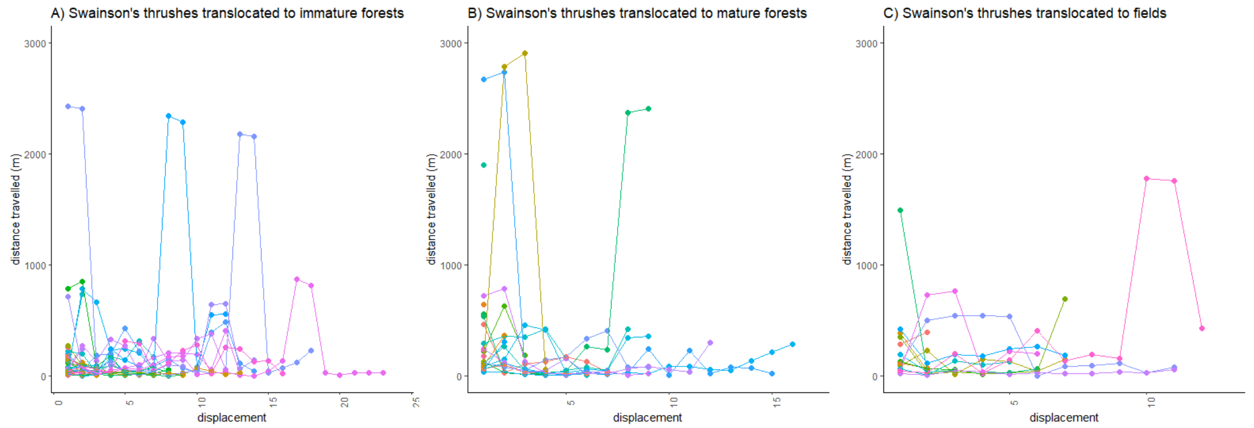

Figure S3.4. Distance travelled by radio-tagged Swainson's Thrushes translocated to **A**) immature forests, **B**) mature forests, and **C**) grassy fields. Distance travelled was the distance (in meters) measured between consecutive GPS points. Displacement signifies the chronological movement of the bird. Lines were drawn between points belonging to the same bird and colored to differentiate between birds.

Table S3.5. Moult and post-moult migrating Swainson's Thrushes' home range sizes and landscape cover composition based on Independent and identically distributed (IID) isotropic models (at 95% utilization distribution) at a autumnal peri-urban stopover site. Note that moult code "Y" indicates a moult migrant and code "N" indicates a post-moult migrant.

ID	Moult	Home range in ha *mean (range)*	Agriculture (%)	Anthropogenic (%)	Aquatic (%)	Cut and regenerating land (%)	Forest (%)	Wetland (%)
82	Y	0.87 (0.38 ± 1.6)	0	0	0	0	100	0
83	Y	9.8 (0.50 ± 1.6)	59.18	0	7.14	0	26.53	7.14
84	Y	3.7 (1.2 ± 7.6)	1.35	17.57	0	0	81.08	0
85	Y	0.90 (0.33 ± 1.8)	47.83	0	0	0	52.17	0
86	Y	0.21 (0.077 ± 0.41)	0	0	0	0	45	55
121	Y	1.9 (0.71 ± 3.7)	7.33	0	38.22	0	23.56	30.89
128	Y	170 (85 ± 280)	47.82	5.03	19.7	0	22.28	5.16
130	Y	63 (26 ± 120)	39.3	0	1.46	0	48.95	10.29
131	Y	460 (180 ± 770)	21.74	22.32	5.22	0	45.21	5.49
132	Y	0.72 (0.26 ± 1.4)	0	0	48.61	0	18.06	33.33
134	Y	8.2 (3.0 ± 16)	54.57	0	0	0	45.43	0
135	Y	0.024 (0.01 ± 0.043)	0	0	0	0	100	0
136	Y	46 (17 ± 90)	58.63	0.48	0	0	31.84	9.05
137	Y	4.0 (1.6 ± 7.4)	0	0	0	0	99.5	0.5
210	Y	16 (6.2 ± 29)	19.35	0	0	0	48.43	32.22

214	N	3.7 (1.5 ± 6.8)	12.53	0	21.53	0	31.06	34.88
218	N	70 (26 ± 140)	40.73	0	0.27	0	42.26	16.74
219	N	71 (26 ± 140)	45.95	2.93	2.62	0	39	9.5
220	N	19 (7.8 ± 36)	22.87	0	0.57	0	67.48	9.09
221	N	19 (39 ± 6.1)	26.98	0	5.27	0	57.59	10.17
223	N	3.4 (0.92 ± 7.4)	43.53	0	0	0	56.47	0
224	N	5.4 (1.5 ± 12)	74.82	0	0	0	25.18	0
226	Y	33 (14 ± 59)	40.26	5.57	1.04	0	41.14	12
227	Y	7.4 (4.2 ± 11)	21.98	0.27	0	0	77.75	0
229	Y	270 (140 ± 450)	48.98	8.42	0.54	0	35.07	6.99
230	Y	27 (14 ± 44)	26.29	19.11	0	0	54.6	0
231	Y	27 (9.8 ± 52)	21.37	0	0	0	52.06	26.57
232	Y	66 (36 ± 110)	36.58	7.3	8.92	0	30.86	16.34
233	Y	320 (18 ± 490)	38.97	8.1	2.01	0	45.61	5.32
234	Y	32 (15 ± 55)	56.16	12.5	1.06	0	26.94	3.34
235	Y	67 (29 ± 120)	24.89	0.1	2.6	0	65.31	7.09
237	Y	1.2 (0.59 ± 1.9)	38.26	0	0	0	61.74	0
242	Y	24 (12 ± 39)	14.39	11.24	0	0	73.08	1.29
243	Y	360 (150 ± 640)	21.86	21.09	3.57	0	48.33	5.16
244	Y	23 (12 ± 37)	17.73	0.57	1.48	0	73.99	6.23
245	Y	170 (89 ± 270)	25.75	19.84	2.09	0	43.94	8.39
246	Y	15 (9.4 ± 22)	35.3	0	5.56	0	48.96	10.18
247	Y	0.57 (0.15 ± 1.2)	55.93	0	1.69	0	37.29	5.08
248	Y	9.8 (5.6 ± 15)	23.34	0	0	0	53.72	22.94
249	Y	12 (6.1 ± 20)	28.12	0	3.6	0	52.64	15.65

Table S3.6. Moult and post-moult migrating Swainson's Thrushes' home range sizes and landscape cover composition based on Independent and identically distributed (IID) isotropic models (at 50% utilization distribution) at a autumnal peri-urban stopover site. Note that moult code "Y" indicates a moult migrant and code "N" indicates a post-moult migrant**.**

ID	Moult	Home range (ha) *mean (range)*	Agriculture (%)	Anthropogenic (%)	Aquatic (%)	Cut and regenerating land (%)	Forest (%)	Wetland (%)
82	Y	0.17 (0.07 ± 0.31)	0	0	0	0	100	0
83	Y	0.25 (0.13 ± 0.41)	66.67	0	0	0	33.33	0
84	Y	0.96 (0.31 ± 1.96)	0	11.58	0	0	88.42	0
85	Y	0.17 (0.06 ± 0.34)	70.59	0	0	0	29.41	0

86	Y	0.06 (0.02 ± 0.10)	0	0	0	0	33.33	66.67
121	Y	0.44 (0.16 ± 0.85)	2.33	0	81.4	0	2.33	13.95
128	Y	27.83 (13.9 ± 46.5)	65.66	2.01	8.02	0	22.15	2.16
130	Y	11.00 (4.42 ± 20.5)	22.33	0	0	0	62.53	15.13
131	Y	70.4 (30.39 ± 127)	38.46	21.04	0.71	0	29.38	10.41
132	Y	0.17 (0.06 ± 0.33)	0	0	64.71	0	23.53	11.76
134	Y	2.12 (0.78 ± 4.12)	55.4	0	0	0	44.6	0
135	Y	0.006 (0.003 ± 0.01)	0	0	0	0	100	0
136	Y	8.15 (2.99 ± 15.85)	40.05	0	0	0	59.95	0
137	Y	0.96 (0.28 ± 1.78)	0	0	0	0	100	0
210	Y	3.91 (1.57 ± 7.29)	1.29	0	0	0	61.08	37.63
214	N	1.00 (0.40 ± 1.87)	0	0	37.62	0	18.81	43.56
218	N	13.83 (5.07 ± 26.9)	30.35	0	0	0	51.01	18.64
219	N	12.59 (4.62 ± 24.49)	27.3	0	12.22	0	53.57	6.9
220	N	3.83 (1.54 ± 7.15)	18.18	0	0	0	75.84	5.97
221	N	4.25 (1.38 ± 8.72)	16	0	1.88	0	63.76	18.35
223	N	0.81 (0.22 ± 1.78)	53.09	0	0	0	46.91	0
224	N	1.41 (0.38 ± 3.09)	89.29	0	0	0	10.71	0
226	Y	6.03 (2.6 ± 10.86)	35.28	1.51	3.18	0	41.14	18.9
227	Y	1.18 (0.68 ± 1.83)	7.38	0	0	0	92.62	0
229	Y	45.1 (23.31 ± 74)	39.91	0	0	0	39.89	20.2
230	Y	5.39 (2.87 ± 8.68)	5.01	1.86	0	0	93.14	0
231	Y	6.78 (2.49 ± 13.19)	4.14	0	0	0	72.38	23.49
232	Y	11.05 (6.04 ± 17.54)	64.26	4.39	0	0	20.48	10.88
233	Y	51.89 (29.66 ± 80.2)	37.47	0.06	2.97	0	54.64	4.86
234	Y	6.20 (2.97 ± 10.59)	47.66	5.01	0	0	47.33	0
235	Y	18.23 (7.87 ± 32.86)	2.92	0	3.91	0	87	6.17
237	Y	0.27 (0.14 ± 0.45)	7.41	0	0	0	92.59	0
242	Y	5.79 (2.99 ± 9.50)	0	0	0	0	100	0
243	Y	60.84 (26.27 ± 110)	36.34	7.61	0.56	0	41.63	13.87
244	Y	4.53 (2.41 ± 7.31)	0	0	0	0	100	0
245	Y	28.63 (15.25 ± 46.2)	56.27	16.21	0	0	26.44	1.08
246	Y	2.65 (1.66 ± 3.86)	6.54	0	18.85	0	41.54	33.08
247	Y	0.15 (0.04 ± 0.32)	50	0	0	0	50	0
248	Y	1.82 (1.04 ± 2.81)	11.17	0	0	0	73.18	15.64
249	Y	2.21 (1.14 ± 3.62)	20.81	0	0	0	51.58	27.6
298	N	9.67 (4.17 ± 17.43)	13.6	0	0	0	86.4	0

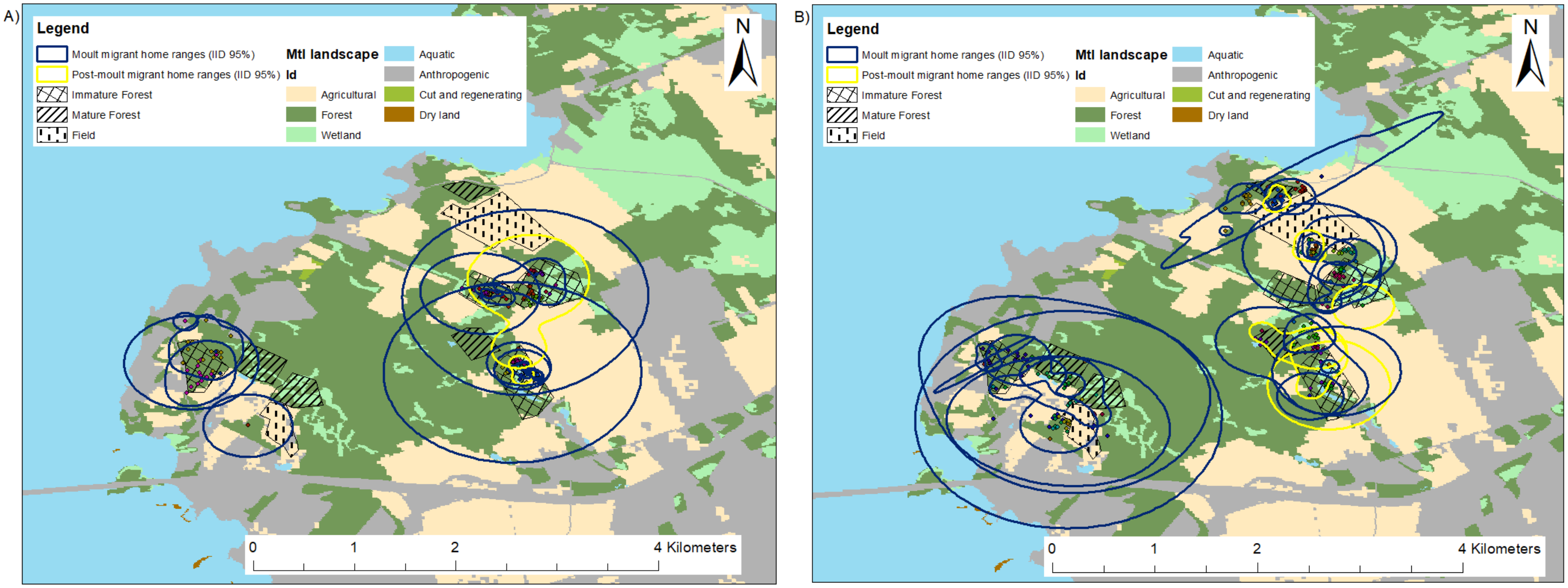

Figure S3.5. Maps of the 95% independent and identically distributed (IID) isotropic calculated home ranges of moult migrating (in navy blue) and post-moult migrant (in yellow) Swainson’s Thrushes during their autumnal stopover in the West Island of Montreal. **A)** shows 14 moult and 2 post-moult migrants who were translocated to immature forest sites and **B)** shows 17 moult and 5 post moult migrants who were translocated to mature forests or field sites. GPS points on the maps were taken through manually tracking using radio telemetry when signal strength was at least 130 dB at a gain (precision) between 9 dB and 40 dB. Points of the same color belong to the same bird.

GENERAL DISCUSSION

Our increasing global human population and our move towards cities (i.e. urbanization) have caused massive habitat loss, fragmentation, and homogenization (Piano et al., 2020; Seto et al., 2012). The bright artificial lights emitted by cities attract birds migrating at night which is the case for many passerines (La Sorte et al., 2014; McLaren et al., 2018). Migrating birds who require abundant energy to refuel during migration (McWilliams et al., 2004; Nilsson et al., 2013) are faced with anthropogenic threats, unfamiliar food sources, and restricted habitat size in cities (Loss et al., 2014; Piontek et al., 2021). Despite the challenging urban landscape, migrants have found refuge in forest fragments (Matthews and Rodewald, 2010). While most migrants spend approximately one week at these sites, individuals of some passerines ~1.5 months to moult at these sites; a significant amount of time (13% of their life-cycle) during a particularly vulnerable period (Morales et al., 2022). The peri-urban stopover ecology of these moult migrating birds, who must balance the energy and time requirements of moult and migration, is not well-known; a knowledge gap I aimed to address in this thesis.

In Chapter 2, I evaluated the stopover duration and departure decisions of one such moult migrating passerine, the Tennessee Warbler (*Leiothlypis peregrina*). I compared their departure decisions to certain internal (i.e. residual mass) and external (i.e. weather conditions) factors. Following their capture, radio-tagging, and tracking during their stopover and subsequent departure from a peri-urban stopover site, departure decisions were independent of body and weather conditions. We may have failed to detect a relationship between the departures and these internal and external factors due to the small sample size of Tennessee Warblers (17 moult migrants and 4 post-moult migrants). Although studies have shown the importance of fat reserves (e.g. Deppe et al., 2015; DeSimone et al., 2022) and weather (e.g. Morales et al. 2022; Beauchamp et al., 2020; Gill et al., 2014; Richardson, 1990) on departure decisions, we found no predictable patterns. We expected migrants to wait for cooler nights (Beauchamp et al., 2020; Packmor et al., 2020) and strong tailwinds (Gill et al., 2014) but perhaps the time constraint of moult urges migrants to depart as soon as they are capable: a time-minimization strategy.

Considering the pressure of making a speedy migration, it is reasonable that a moult migrant stopping for ~1.5 months might disregard weather in favour of making a hurried departure. Time constraints often force migrants to be less choosy of weather conditions upon departure (see Pyle et al., 2018; Roques et al., 2021; Schmaljohann et al., 2013; Tsvey et al., 2007). Birds making long stopovers, like moult migrants, will depart when they are physically ready, regardless of weather conditions (Packmor et al., 2020; Tsvey et al., 2007; Zwaan et al., 2022). We had expected a strong relationship between wind support and departure as appropriate tailwinds and their associated temperature, humidity, and pressure are often the drivers of migration (Beauchamp et al., 2020; Gill et al., 2014; Richardson, 1990), however we found no influence of wind nor pressure on departure decisions. One explanation may be that some passerines and shorebirds depart with weak winds as long as they are in the direction of flight (Lack, 1960; Schmaljohann et al., 2012; Tan et al., 2018). Finally, despite decreasing atmospheric pressure being a marker of approaching stormy weather (Abbasi et al., 2021), migrants may depart on these low-pressure nights, as recorded in Packmor *et al.* (2020). Migrants have also been recorded departing in any and all weather conditions so, although there may be trends, other deciding factors might take precedence (Richardson, 1990), namely a spatiotemporal programme we have yet to adequately describe (Jenni and Schaub, 2003).

During their lengthy stay at the stopover site, Tennessee Warblers maintained home ranges of ~15 ha in forest patches with high proportions of forest edge to forest interior compared to the surrounding area. We explored this habitat use, given that migrants must obtain high amounts of energy to successfully moult and refuel before departure, in Chapter 3. We translocated moult and post-moult migrating Swainson’s Thrushes to sites of varying habitat type, expecting them to remain in energy-abundant sites with high food availability and concealment from predators. Indeed, migrants stopped 4 times as long in immature forests with dense understory growth and dense forest margins than mature forests and fields. We also found that Swainson’s Thrushes presence was positively associated with forest edge (similar to the Tennessee Warblers) and negatively correlated with agricultural and anthropogenic landscapes. Forest edge was a hotspot for migrants in this study and others (see Stanley et al., 2021; Terraube et al., 2016) which is ideal in an urban setting with lots of forest fragments (with high forest edge to forest interior ratios).

This research lends support to Connell's (1978) intermediate-disturbance hypothesis that species diversity is higher in moderately (in frequency and intensity) disturbed areas. We indeed found that migrating songbirds will readily occupy small (< 0.6 km^2) forest fragments surrounded by human-disturbed land (i.e. agricultural and residential areas). These intermediate disturbances allow for forests of diverse successional stages where understory vegetation is abundant (see Chace and Walsh, 2006 and Faeth et al., 2011). Traditionally, cities undergo much more frequent disturbances (i.e. mowing) that keep areas in a continuous early successional stage (i.e. lawn; Niemela 1999). In addition, cities often practice a 'land sparing' (Green et al., 2005) approach where they conserve large nature reserves and parks separate from human activity (Stott et al., 2015). A 'land sharing' (Green et al., 2005) plan may be better suited for songbirds who require heterogenous habitats (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023) afforded by a mix of human disturbances and forest patches.

Immature forest sites where migrants spent the most time were characterized by high shrub density and specifically high berry-producing shrub density. In fact, berry-producing shrub density was the most significant predictor of occupancy; migrants chose to leave sites with low berry-producing shrub density and remain at sites with high berry-producing shrub density. Food availability in a stopover habitat therefore seems to be the most important component influencing a migrant's decision to stay or leave their habitat. Since these sites were densely vegetated, migrants also benefited from concealment from predators. Other sites with high shrub cover and canopy cover (i.e. mature forests) could also provide concealment but were not occupied presumably because they did not provide sufficient food. In the immature forests where migrants stayed, an invasive plant species, common buckthorn (*Rhamnus cathartica*; Canadensys, 2022), was the most frequent berry-producing shrub. DNA analyses of fecal samples taken in 2021 confirmed that the birds consumed common buckthorn on site. To my knowledge, we are the first to document this clear preference for berry-producing shrubs for migrants deciding whether to occupy a stopover site.

Fruit-producing plants are invaluable during a migrant's stopover as they must build fat reserves quickly (Bairlein 2002). Many insectivorous birds shift to a fruit-dominated diet during migration because of its high fat content (Bairlein 1990). Native berries are also generally more fatty and energy-dense than exotic fruits (Bolser et al., 2013; Smith et al., 2013; White & Stiles, 1992) but they were not as numerous in our study site. In fact, invasive buckthorn was the most abundant berry-producing shrub we observed. Similarly, a nature reserve ~250 km southward in New York showed that migrating songbirds consume the most available berries: common buckthorn (Mudrzynski & Norment 2013). Many boroughs in Montreal currently have programs underway to eradicate buckthorn from their green spaces (Schwartz, 2021; Ville de Montreal, 2019; Ville de Pointe-Claire, 2022). While buckthorn's invasive nature is certainly harmful to native wildlife (Moser et al. 2009), removing these plants without a berry-abundant replacement could create a nutritional void for migrating birds.

Despite the different energy and time requirements of moult and post-moult migrants, both groups decided to leave undesirable habitat types; expending the energy and time to relocate to a better-quality site. Acquiring abundant energy allows a migrant to successfully moult and refuel so that their next migratory flight can be efficient and quick (Alerstam, 1991; Leu & Thompson, 2002). It can therefore be said that the fall migrants in this study, moult and post-moult alike, employ an energy-minimization strategy where they targeted habitats that could presumably offer them high refueling rates at lower foraging efforts. While time-minimization may not be their priority, moult migrants seem to be compensating for their lengthy stopovers by arriving more than a month earlier to their stopover site (in early August) than their post-moult counterparts. Following their stopover, moult and post-moult migrants left on similar dates (mid-September) and presumably completed their subsequent migration within a similar timeframe (Figure 4.1).

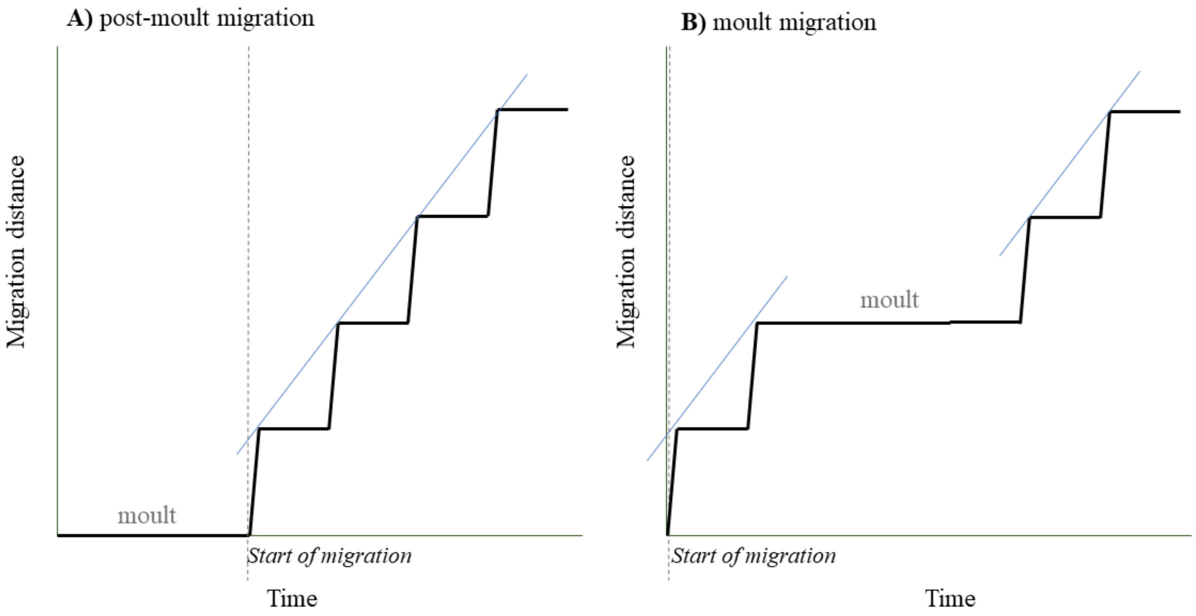

Figure 4.1 Conceptual figure showing the migration speed (distance/time) of (A) post-moult migrants who moult at their breeding grounds prior to migration versus (B) moult migrants who moult at a stopover site during migration. Migration speed, exemplified by the slope (i.e. blue line), is steady for post-moult migrants who can undergo (more or less) uniform bouts of stopovers and migratory flights. Moult migrants start their migration earlier (see dotted line) than post-moult migrants but depart from their moulting stopover site at the same time, theoretically completing their migration in a similar timeframe to post-moult migrants despite their difference in overall migration speed. Note that this is a conceptual figure expanding on Figure 0.1.

While Canada is investing in nature-based solutions for climate change, such as the Nature Smart Climate Solutions Fund and the 2 Billion Trees Commitment, decision-makers must consider the importance of peri-urban forest patches. Conservation efforts often focus on planting trees for parks but city planners should consider structural diversity and native berry-producing shrubs when deciding what to plant and where. Montreal has also recently agreed to incorporate the Kunming-Montreal Global biodiversity framework Target 12 (United Nations Convention on Biological Diversity, 2022) in their urban planning which specifies a biodiversity-inclusive approach to conservation. This research supports growing evidence highlighting the value of ‘messy’ urban greenspaces (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023) and further illustrates the importance of conserving densely vegetated areas that are traditionally under-valued in cities (Bonthoux et al., 2019; Rega-Brodsky et al., 2018). Supporting biodiversity equally means to conserve habitat heterogeneity for migrating songbirds and other wildlife.

GENERAL CONCLUSION AND SUMMARY

In conclusion, my thesis adds to the growing but still scarce research on moult migration in eastern North American passerines, and specifically their stopover behaviour in cities. Due to increasing urbanization, habitat quality of stopover sites stands to decrease globally (Seto et al. 2012). While city managers plan to conserve urban forests, they may consider the value of densely vegetated areas. I found that migrants preferentially inhabit immature forests with high densities of berry-producing shrubs over mature forests and fields. Migrating birds benefit from the high food availability and concealment from predators that these dense forest patches provide. During their stopover, migrants acquire sufficient energy to moult and refuel which allows them to comfortably depart for their next migratory flight. The conclusions reached in this thesis demonstrate the importance of conserving densely vegetated peri-urban forests for migratory passerines.

Photos of me (Vanessa Poirier) with a Swainson's Thrush (left) and a Tennessee Warbler (right)

References

Alerstam, T. (1991). Bird flight and optimal migration. *Trends in Ecology & Evolution*, *6*(7), 210–215. WorldCat.org. https://doi.org/10.1016/0169-5347(91)90024-R

Alerstam, T., Lindström, Å. (1990). Optimal Bird Migration: The Relative Importance of Time, Energy, and Safety. In: Gwinner, E. (eds) Bird Migration. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-74542-3_22

Araújo, P. M., Viegas, I., Rocha, A. D., Villegas, A., Jones, J. G., Mendonça, L., Ramos, J. A., Masero, J. A., & Alves, J. A. (2019). Understanding how birds rebuild fat stores during migration: Insights from an experimental study. *Scientific Reports*, *9*(1), 1–11. WorldCat.org. https://doi.org/10.1038/s41598-019-46487-z

Barta, Z., McNamara, J. M., Houston, A. I., Weber, T. P., Hedenström, A., & Feró, O. (2008). Optimal moult strategies in migratory birds. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1490), 211–229. https://doi.org/10.1098/rstb.2007.2136

Beal, F. E. L. (Foster E. L. (1915). *Food habits of the thrushes of the United States: Vol. no.280 (1915)*. U.S. Dept. of Agriculture,. https://www.biodiversitylibrary.org/item/190602

Beauchamp, A. T., Guglielmo, C. G., & Morbey, Y. E. (2020). Stopover refuelling, movement and departure decisions in the white-throated sparrow: The influence of intrinsic and extrinsic factors during spring migration. *The Journal of Animal Ecology*, *89*(11), 2553–2566. WorldCat.org. https://doi.org/10.1111/1365-2656.13315

Briedis M, Bauer S, Adamík P, Alves JA, Costa JS, Emmenegger T, Gustafsson L, Koleček J, Liechti F, Meier CM, Procházka P, & Hahn S. (2019). A full annual perspective on sex-biased migration timing in long-distance migratory birds. *Proceedings. Biological Sciences*, *286*(1897), 20182821. WorldCat.org. https://doi.org/10.1098/rspb.2018.2821

Buron, R., Hostetler, M. E., & Andreu, M. (2022). Urban forest fragments vs residential neighborhoods: Urban habitat preference of migratory birds. *Landscape and Urban Planning*, *227*, 104538. https://doi.org/10.1016/j.landurbplan.2022.104538

Buttemer, W. A., Addison, B. A., & Klasing, K. C. (2019). The energy cost of feather replacement is not intrinsically inefficient. *Canadian Journal of Zoology*, *98*(2), 142–148. WorldCat.org. https://doi.org/10.1139/cjz-2019-0170

Callaghan, C. T., Bino, G., Major, R. E., Martin, J. M., Lyons, M. B., & Kingsford, R. T. (2019). Heterogeneous urban green areas are bird diversity hotspots: Insights using continental-scale citizen science data. *Landscape Ecology*, *34*(6), 1231–1246. WorldCat.org. https://doi.org/10.1007/s10980-019-00851-6

Cherry, J. D. (1985). Early Autumn Movements and Prebasic Molt of Swainson’s Thrushes. *The Wilson Bulletin*, *97*(3), 368–370. WorldCat.org.

Craves, J. (2009). A Fifteen-year Study of Fall Stopover Patterns of Catharus Thrushes at an Inland, Urban Site. *Wilson Journal of Ornithology*, *121*, 112–118. https://doi.org/10.1676/08-055.1

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. WorldCat.org. https://doi.org/10.1111/jofo.12291

Deppe, J. L., Ward, M. P., Bolus, R. T., Diehl, R. H., Celis-Murillo, A., Zenzal, T. J., Moore, F. R., Benson, T. J., Smolinsky, J. A., Schofield, L. N., Enstrom, D. A., Paxton, E. H., Bohrer, G., Beveroth, T. A., Raim, A., Obringer, R. L., Delaney, D., & Cochran, W. W. (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*(46), E6331–E6338. WorldCat.org. https://doi.org/10.1073/pnas.1503381112

DeSimone, J. G., Domschot, B. S., Fylling, M. A., Blake, W. M., & Breuner, C. W. (2022). Body mass and triglycerides predict departure of free-living nomadic pine siskins. *Functional Ecology*. WorldCat.org. https://doi.org/10.1111/1365-2435.14238

Dierschke, V. (2003). Predation hazard during migratory stopover: Are light or heavy birds under risk? *Journal of Avian Biology*, *34*(1), 24–29. https://doi.org/10.1034/j.1600-048X.2003.03049.x

Drever, M. C., Smith, A. C., Venier, L. A., Sleep, D. J. H., & MacLean, D. A. (2018). Cross-scale effects of spruce budworm outbreaks on boreal warblers in eastern Canada. *Ecology and Evolution*, *8*(15), 7334–7345. https://doi.org/10.1002/ece3.4244

Eikenaar, C., Packmor, F., Schmaljohann, H., & Hegemann, A. (2019). Stopover departure decisions in autumn are not associated with constitutive immune function in Northern Wheatears Oenanthe oenanthe. *Journal of Ornithology*, *160*(3), 813–817. WorldCat.org. https://doi.org/10.1007/s10336-019-01665-8

Eiler, J. H. (1995). A Remote Satellite-Linked Tracking System for Studying Pacific Salmon with Radio Telemetry. *Transactions of the American Fisheries Society*, *124*(2), 184–193. https://doi.org/10.1577/1548-8659(1995)124<0184:ARSLTS>2.3.CO;2

Fox, A. D., Flint, P. L., Hohman, W. L., & Savard, J.-P. L. (2014). Waterfowl habitat use and selection during the remigial moult period in the northern hemisphere. *Wildfowl*, 131–168. WorldCat.org.

Francis, I. S., Fox, A. D., McCarthy, J. P., & McKay, C. R. (1991). Measurements and moult of the Lapland Bunting Calcarius lapponicus in West Greenland. *Ringing & Migration*, *12*(1), 28–37. https://doi.org/10.1080/03078698.1991.9673981

Gill, R. E., Douglas, D. C., Handel, C. M., Tibbitts, T. L., Hufford, G., & Piersma, T. (2014). Hemispheric-scale wind selection facilitates bar-tailed godwit circum-migration of the Pacific. *Animal Behaviour*, *90*, 117–130. https://doi.org/10.1016/j.anbehav.2014.01.020

González, A. M., Bayly, N. J., & Hobson, K. A. (2020). Earlier and slower or later and faster: Spring migration pace linked to departure time in a Neotropical migrant songbird. *The Journal of Animal Ecology*, *89*(12), 2840–2851. https://doi.org/10.1111/1365-2656.13359

Götmark, F., & Post, P. (1997). Prey selection by sparrowhawks, Accipiter nisus: Relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *351*(1347), 1559–1577. https://doi.org/10.1098/rstb.1996.0141

Griffin, A. S., Brown, C., Woodworth, B. K., Ballard, G.-A., Blanch, S., Campbell, H. A., Crewe, T. L., Hansbro, P. M., Herbert, C. A., Hosking, T., Hoye, B. J., Law, B., Leigh, K., Machovsky-Capuska, G. E., Rasmussen, T., McDonald, P. G., Roderick, M., Slade, C., Mackenzie, S. A., & Taylor, P. D. (2020). A large-scale automated radio telemetry network for monitoring movements of terrestrial wildlife in Australia. *Australian Zoologist*, *40*(3), 379–391. https://doi.org/10.7882/AZ.2019.026

Guglielmo, C., Cerasale, D., & Eldermire, C. (2005). A Field Validation of Plasma Metabolite Profiling to Assess Refueling Performance of Migratory Birds. *Physiological and Biochemical Zoology : PBZ*, *78*, 116–125. https://doi.org/10.1086/425198

Guo, F., Buler, J. J., Smolinsky, J. A., & Wilcove, D. S. (2023). Autumn stopover hotspots and multiscale habitat associations of migratory landbirds in the eastern United States. *Proceedings of the National Academy of Sciences*, *120*(3). WorldCat.org. https://doi.org/10.1073/pnas.2203511120

Hedenström, A., & Alerstam, T. (1998). Optimum Fuel Loads in Migratory Birds: Distinguishing Between Time and Energy Minimization. 189, 227–34. 10.1006/jtbi.1997.0505

Hadjikyriakou, T. G., Nwankwo, E. C., Virani, M. Z., & Kirschel, A. N. G. (2020). Habitat availability influences migration speed, refueling patterns and seasonal flyways of a fly-and-forage migrant. *Movement Ecology*, *8*(1), 10. https://doi.org/10.1186/s40462-020-0190-4

Hegemann, A., Alcalde Abril, P., Sjöberg, S., Muheim, R., Alerstam, T., Nilsson, J.-Å., & Hasselquist, D. (2018). A mimicked bacterial infection prolongs stopover duration in songbirds—But more pronounced in short-than long-distance migrants. *Journal of Animal Ecology*, *87*(6), 1698–1708.

Hemborg, C. (1999). Sexual Differences in Moult-Breeding Overlap and Female Reproductive Costs in Pied Flycatchers, Ficedula hypoleuca. *Journal of Animal Ecology*, *68*(2), 429–436. WorldCat.org.

Hera, I. de L., Pérez-Tris, J., & Tellería, J. L. (2010). Migratory Behavior and Differential Resource Allocation between Wing and Tail Feathers in a Passerine Bird. *The Auk*, *127*(3), 647–652. WorldCat.org. https://doi.org/10.1525/auk.2010.09120

Jenni, L., & Schaub, M. (2003). Behavioural and Physiological Reactions to Environmental Variation in Bird Migration: A Review. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian Migration* (pp. 155–171). Springer Berlin Heidelberg.

Junda, J. H., Duval, S., & Gahbauer, M. A. (2020). Use of discrete molting grounds by migrant passerines undergoing prebasic molt in southern Quebec. *The Wilson Journal of Ornithology*, *132*(1), 72–82. WorldCat.org. https://doi.org/10.1676/1559-4491-132.1.72

Kissling, D. W., Pattemore, D. E., & Hagen, M. (2014). Challenges and prospects in the telemetry of insects. *Biological Reviews*, *89*(3), 511–530. WorldCat.org. https://doi.org/10.1111/brv.12065

Kjellén, N. (1994). Moult in relation to migration in birds—A review. *Ornis Svecica*, *4*(1), 1–24. https://doi.org/10.34080/os.v4.23028

Klaassen, R., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K.-M., Bairlein, F., & Alerstam, T. (2013). When and where does mortality occur in migratory birds? Direct evidence from long- term satellite tracking of raptors. *The Journal of Animal Ecology*, *83*. https://doi.org/10.1111/1365-2656.12135

Klimkiewicz, M. K., Clapp, R. B., & Futcher, A. G. (1983). Longevity Records of North American Birds: Remizidae through Parulinae. *Journal of Field Ornithology*, *54*(3), 287–294. WorldCat.org.

Knight, S. M., Gow, E. A., Bradley, D. W., Clark, R. G., Bélisle, M., Berzins, L. L., Blake, T., Bridge, E. S., Burke, L., Dawson, R. D., Dunn, P. O., Garant, D., Holroyd, G. L., Hussell, D. J. T., Lansdorp, O., Laughlin, A. J., Leonard, M. L., Pelletier, F., Shutler, D., … Norris, D. R. (2019). Nonbreeding season movements of a migratory songbird are related to declines in resource availability. *The Auk*, *136*(3), 1–13. WorldCat.org. https://doi.org/10.1093/auk/ukz028

Ktitorov, P., Tsvey, A., & Mukhin, A. (2010). The good and the bad stopover: Behaviours of migrant reed warblers at two contrasting sites. *Behavioral Ecology and Sociobiology*, *64*(7), 1135–1143. WorldCat.org.

La Sorte, F. A., Tingley, M. W., & Hurlbert, A. H. (2014). The role of urban and agricultural areas during avian migration: An assessment of within-year temporal turnover. *Global Ecology and Biogeography*, *23*(11–12), 1225–1234. WorldCat.org.

La Sorte, F., & Horton, K. (2021). Seasonal variation in the effects of artificial light at night on the occurrence of nocturnally migrating birds in urban areas. *Environmental Pollution (Barking, Essex : 1987)*, *270*, 116085. WorldCat.org. https://doi.org/10.1016/j.envpol.2020.116085

Lack, D. (1960). The Influence of Weather on Passerine Migration. A Review. *The Auk*, *77*(2), 171–209. WorldCat.org.

Leu, M., & Thompson, C. W. (2002). The potential importance of migratory stopover sites as flight feather molt staging areas: A review for neotropical migrants. *Biological Conservation*, *106*(1), 45–56. WorldCat.org. https://doi.org/10.1016/S0006-3207(01)00228-2

Liechti, F. (2006). Birds: Blowin' by the wind? *Journal of Ornithology*, *147*(2), 202–211. https://doi.org/10.1007/s10336-006-0061-9

Lincoln, F. C. 1892-1960., Hines, Bob., & U.S. Fish and Wildlife Service. (1950). *Migration of birds*. U.S. Dept. of the Interior, Fish and Wildlife Service; WorldCat.org.

Lindström, Å. (2003). Fuel Deposition Rates in Migrating Birds: Causes, Constraints and Consequences. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian Migration* (pp. 307–320). Springer Berlin Heidelberg.

Loss, S. R., Will, T., Loss, S. S., & Marra, P. P. (2014). Bird–building collisions in the United States: Estimates of annual mortality and species vulnerability. *The Condor*, *116*(1), 8–23. https://doi.org/10.1650/CONDOR-13-090.1

Mack, D. E., & Yong, W. (2020). Swainson's Thrush (Catharus ustulatus). In *In Birds of the World* (1.0). Cornell Lab or Ornithology. https://doi.org/10.2173/bow.swathr.01

Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, *11*(8). WorldCat.org. https://doi.org/10.1098/rsbl.2015.0552

Matthews, S. N., & Rodewald, P. G. (2010). Urban Forest Patches and Stopover Duration of Migratory Swainson's Thrushes. *The Condor*, *112*(1), 96–104. https://doi.org/10.1525/cond.2010.090049

Mcatee, W. F. (1904). Warblers and Grapes. *The Auk*, *21*(4), 489–491. https://doi.org/10.2307/4070142

McLaren, J. D., Buler, J. J., Schreckengost, T., Smolinsky, J. A., Boone, M., van Loon, E. E., Dawson, D. K., & Walters, E. L. (2018). Artificial light at night confounds broad-scale habitat use by migrating birds. *Ecology Letters*, *21*(3), 356–364. WorldCat.org.

McWilliams, S. R., Guglielmo, C., Pierce, B., & Klaassen, M. (2004). Flying, Fasting, and Feeding in Birds during Migration: A Nutritional and Physiological Ecology Perspective. *Journal of Avian Biology*, *35*(5), 377–393. WorldCat.org.

Mehlman, D., Mabey, S., Ewert, D., Duncan, C., Abel, B., Cimprich, D., Sutter, R., & Woodrey, M. (2005). Conserving stopover sites for forest-dwelling migratory landbirds. *Auk*, *122*. https://doi.org/10.1642/0004-8038(2005)122[1281:CSSFFM]2.0.CO;2

Mills, A., Thurber, B., Mackenzie, S., & Taylor, P. (2011). Passerines Use Nocturnal Flights for Landscape-Scale Movements during Migration Stopover (Los Paseriformes Usan Vuelos Nocturnos para Movimientos a Escala de Paisaje durante las Paradas Migratorias). *The Condor*, *113*, 597–607. https://doi.org/10.1525/cond.2011.100186

Mills, A. M. (2005). Protogyny in Autumn Migration: Do Male Birds ”Play Chicken”? *The Auk*, *122*(1), 71–81. https://doi.org/10.1093/auk/122.1.71

Moore, F., Gauthreaux, S., Kerlinger, P., & Simons, T. (1995). *Habitat requirements during migration: Important link in conservation*.

Morales, A., Frei, B., Mitchell, G. W., Bégin-Marchand, C., & Elliott, K. H. (2022). Reduced diurnal activity and increased stopover duration by molting Swainson’s Thrushes. *Ornithology*, ukab083. https://doi.org/10.1093/ornithology/ukab083

Morbey, Y. E., Guglielmo, C. G., Taylor, P. D., Maggini, I., Deakin, J., Mackenzie, S. A., Brown, J. M., & Zhao, L. (2018). Evaluation of sex differences in the stopover behavior and postdeparture movements of wood-warblers. *Behavioral Ecology*, *29*(1), 117–127. https://doi.org/10.1093/beheco/arx123

Morris, S., Holmes, D., & Richmond, M. (1996). A Ten-Year Study of the Stopover Patterns of Migratory Passerines during Fall Migration on Appledore Island, Maine. *The Condor*, *98*. https://doi.org/10.2307/1369157

Morris, S. R., Andrijevic, A. S., Sullivan, R., Keith, R. S., Keith, B. S., & Sheets, D. H. (2013). AN 18-YEAR STUDY OF MIGRATION AND STOPOVER ECOLOGY OF TENNESSEE WARBLERS IN KALAMAZOO COUNTY, MICHIGAN. *The Wilson Journal of Ornithology*, *125*(1), 70–78. WorldCat.org.

Nilsson, C., Klaassen, R. H. G., Alerstam, T., & Natural History Editor: Mark A. McPeek. (2013). Differences in Speed and Duration of Bird Migration between Spring and Autumn. *The American Naturalist*, *181*(6), 837–845. WorldCat.org. https://doi.org/10.1086/670335

Oguchi, Y., Pohlen, Z., Smith, R. J., & Owen, J. C. (2018). Exotic- and native-dominated shrubland habitat use by fall migrating Swainson’s Thrushes and Gray Catbirds in Michigan, USA. *The Condor*, *120*(1), 81–93. https://doi.org/10.1650/CONDOR-17-27.1

Packmor, F., Klinner, T., Woodworth, B. K., Eikenaar, C., & Schmaljohann, H. (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*(1), 6. https://doi.org/10.1186/s40462-020-0193-1

Pageau, C., Tonra, C. M., Shaikh, M., Flood, N. J., & Reudink, M. W. (2020). Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines. *Biology Letters*, *16*(6), 20200155. WorldCat.org. https://doi.org/10.1098/rsbl.2020.0155

Pamula, H., Pocha, A., & Kłaczyński, M. (2019). Towards the Acoustic Monitoring of Birds Migrating at Night. *Biodiversity Information Science and Standards*, *3*. https://doi.org/10.3897/biss.3.36589

Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hanashiro, F. T. T., Higuti, J., Lens, L., … Hendrickx, F. (2020). Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, *26*(3), 1196–1211. WorldCat.org. https://doi.org/10.1111/gcb.14934

Piontek, A. M., Wojtylak-Jurkiewicz, E., Schmidt, K., Gajda, A., Lesiak, M., & Wierzbowska, I. A. (2021). Analysis of cat diet across an urbanisation gradient. *Urban Ecosystems*, *24*(1), 59–69. https://doi.org/10.1007/s11252-020-01017-y

Podlaszczuk, P., Włodarczyk, R., Janiszewski, T., Kaczmarek, K., & Minias, P. (2017). When moult overlaps migration: Moult-related changes in plasma biochemistry of migrating common snipe. *PeerJ*, *5*, e3057–e3057. PubMed. https://doi.org/10.7717/peerj.3057

Pyle, P. 1957-, Howell, S. N. G., Ruck, Siobhan., Institute for Bird Populations., & Point Reyes Bird Observatory. (1997). *Identification guide to North American birds: A compendium of information on identifying, ageing, and sexing 'near-passerines' and passerines in the hand*. Slate Creek Press; WorldCat.org. http://www.birdpop.org/pyleguide.htm

Pyle, P., Saracco, J. F., & DeSante, D. F. (2018). Evidence of widespread movements from breeding to molting grounds by North American landbirds. *The Auk*, *135*(3), 506–520. WorldCat.org. https://doi.org/10.1642/AUK-17-201.1

Ramirez, M. G., Griego, M. S., DeSimone, J. G., Elowe, C. R., & Gerson, A. R. (2022). Depleted lean body mass after crossing an ecological barrier differentially affects stopover duration and refuelling rate among species of long-distance migratory birds. *Functional Ecology*, *36*(12), 2995–3006. https://doi.org/10.1111/1365-2435.14203

Rappole, J. H. (2022). *Bird migration: A new understanding* (Vol. 1–1 online resource (xix, 323 pages) : illustrations). Johns Hopkins University Press; WorldCat.org. https://search.ebscohost.com/login.aspx?direct=true&scope=site&db=nlebk&db=nlabk&AN=3108815

Richardson, W. J. (1978). Timing and Amount of Bird Migration in Relation to Weather: A Review. *Oikos*, *30*(2), 224–272. WorldCat.org.

Richardson, W. J. (1990). Timing of Bird Migration in Relation to Weather: Updated Review. In E. Gwinner (Ed.), *Bird Migration* (pp. 78–101). Springer Berlin Heidelberg.

Rimmer, C., & McFarland, K. (2020). Tennessee Warbler (*Leiothlypis peregrina*), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.tenwar.01

Rodewald, P. G., & Matthews, S. N. (2005). Landbird use of Riparian and Upland Forest Stopover Habitats in an Urban Landscape. *The Condor*, *107*(2), 259–268. https://doi.org/10.1093/condor/107.2.259

Rohwer, S., Butler, L. K., Froehlich, D. R., Greenberg, R., & Marra, P. P. (2005). Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. *Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and PP Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland*, 87–105.

Rohwer, V. G., Rohwer, S., & Barry, J. H. (2008). Molt Scheduling of Western Neotropical Migrants and Up-Slope Movement of Cassin's Vireo. *The Condor*, *110*(2), 365–370. WorldCat.org. https://doi.org/10.1525/cond.2008.8321

Roques, S., Henry, P.-Y., Guyot, G., Bargain, B., Cam, E., & Pradel, R. (2021). When to depart from a stopover site? Time since arrival matters more than current weather conditions. *Ornithology*, *139*(1), 1–13. WorldCat.org. https://doi.org/10.1093/ornithology/ukab057

Rüppel, G., Hüppop, O., Lagerveld, S., Schmaljohann, H., & Brust, V. (2023). Departure, routing and landing decisions of long-distance migratory songbirds in relation to weather. *Royal Society Open Science*, *10*(2), 221420. https://doi.org/10.1098/rsos.221420

Rush, S. A., Soehren, E. C., & Miller, M. (2014). Stopover Duration and Habitat Use by Tennessee Warblers (Oreothlypis peregrina) at a High-Elevation Bald. *Southeastern Naturalist*, *13*(1), 92–100. WorldCat.org.

Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., Cruz, S., Proaño, C., Takekawa, J. Y., Newman, S. H., Waldenström, J., Bengtsson, D., Kays, R., Wikelski, M., & Bohrer, G. (2013). Flying with the wind: Scale dependency of speed and direction measurements in modelling wind support in avian flight. *Movement Ecology*, *1*(1), 4. https://doi.org/10.1186/2051-3933-1-4

Schaub, M., Pradel, R., Jenni, L., & Lebreton, J.-D. (2001). Migrating Birds Stop over Longer than Usually Thought: An Improved Capture-Recapture Analysis. *Ecology*, *82*(3), 852–859. WorldCat.org.

Schmaljohann, H. (2018). Proximate mechanisms affecting seasonal differences in migration speed of avian species. *Scientific Reports*, *8*. WorldCat.org. https://doi.org/10.1038/s41598-018-22421-7

Schmaljohann, H., & Both, C. (2017). The limits of modifying migration speed to adjust to climate change. *Nature Climate Change*, *7*(8), 573–576. https://doi.org/10.1038/nclimate3336

Schmaljohann, H., Fox, J. W., & Bairlein, F. (2012a). Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. *Animal Behaviour*, *84*(3), 623–640. WorldCat.org. https://doi.org/10.1016/j.anbehav.2012.06.018

Schmaljohann, H., Fox, J. W., & Bairlein, F. (2012b). Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. *Animal Behaviour*, *84*(3), 623–640. WorldCat.org. https://doi.org/10.1016/j.anbehav.2012.06.018

Schoener, T. W. (1971). Theory of Feeding Strategies. Annual Review of Ecology and Systematics, 2(1), 369–404. 10.1146/annurev.es.02.110171.002101

Sealy, S. G. (1989). Defense of Nectar Resources by Migrating Cape May Warblers (Defensa de Recursos Alimenticios por Parte de Dendroica Tigrina). *Journal of Field Ornithology*, *60*(1), 89–93. JSTOR.

Seewagen, C., Slayton, E., & Guglielmo, C. (2010). Passerine migrant stopover duration and spatial behaviour at an urban stopover site. *Acta Oecologica*, *36*, 484–492. https://doi.org/10.1016/j.actao.2010.06.005

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, *109*(40), 16083–16088. WorldCat.org. https://doi.org/10.1073/pnas.1211658109

Sillett, T. S., & Holmes, R. T. (2002). Variation in Survivorship of a Migratory Songbird throughout Its Annual Cycle. *Journal of Animal Ecology*, *71*(2), 296–308. WorldCat.org.

Stanley, C. Q., Dudash, M. R., Ryder, T. B., Shriver, W. G., Serno, K., Adalsteinsson, S., & Marra, P. P. (2021). Seasonal variation in habitat selection for a Neotropical migratory songbird using high-resolution GPS tracking. *Ecosphere*, *12*(3). WorldCat.org. https://doi.org/10.1002/ecs2.3421

Tan, K., Choi, C.-Y., Peng, H., Melville, D. S., & Ma, Z. (2018). Migration departure strategies of shorebirds at a final pre-breeding stopover site. *Avian Research*, *9*(1), 1–10. WorldCat.org. https://doi.org/10.1186/s40657-018-0108-7

Taylor, P. D., Crewe, T. L., Mackenzie, S. A., Lepage, D., Aubry, Y., Zoe Crysler, George Finney, Charles M. Francis, Christopher G. Guglielmo, Diana J. Hamilton, Rebecca L. Holberton, Pamela H. Loring, Greg W. Mitchell, D. Ryan Norris, Julie Paquet, Robert A. Ronconi, Jennifer R. Smetzer, Paul A. Smith, Linda J. Welch, & Bradley K. Woodworth. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology*, *12*(1), 8. WorldCat.org. https://doi.org/10.5751/ACE-00953-120108

Terraube, J., Archaux, F., Deconchat, M., Halder, I., Jactel, H., & Barbaro, L. (2016). Forest edges have high conservation value for bird communities in mosaic landscapes. *Ecology and Evolution*, *6*(15), 5178–5189. WorldCat.org. https://doi.org/10.1002/ece3.2273

Tietz, J. R., & Johnson, M. D. (2007). Stopover Ecology and Habitat Selection of Juvenile Swainson's Thrushes During Fall Migration Along the Northern California Coast. *The Condor*, *109*(4), 795–807. https://doi.org/10.1093/condor/109.4.795

Tramer, E. J., & Tramer, F. E. (1977). Feeding Responses of Fall Migrants to Prolonged Inclement Weather. *The Wilson Bulletin*, *89*(1), 166–167. WorldCat.org.

Tsvey, A., Bulyuk, V. N., & Kosarev, V. (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*(11), 1665–1674. WorldCat.org. https://doi.org/10.1007/s00265-007-0397-z

Tucker, V. A. (1969). The Energetics of Bird Flight. *Scientific American*, *220*(5), 70–81. JSTOR.

Tucker, V. A., & Schmidt-Koenig, K. (1971). Flight Speeds of Birds in Relation to Energetics and Wind Directions. *The Auk*, *88*(1), 97–107. JSTOR. https://doi.org/10.2307/4083964

Venier, L. A., Pearce, J. L., Fillman, D. R., McNicol, D. K., & Welsh, D. A. (2009). *Effects of Spruce Budworm (Choristoneura fumiferana (Clem.)) Outbreaks on Boreal Mixed-Wood Bird Communities*. *4*(1), 3. WorldCat.org. https://doi.org/10.5751/ACE-00296-040103

Voelker, G., & Rohwer, S. (1998). Contrasts in Scheduling of Molt and Migration in Eastern and Western Warbling-Vireos. *The Auk*, *115*(1), 142–155. https://doi.org/10.2307/4089119

Wikelski, M., Tarlow, E. M., Raim, A., Diehl, R. H., Larkin, R. P., & Visser, G. H. (2003). Costs of migration in free-flying songbirds. *Nature*, *423*(6941). WorldCat.org.

Winker, K., Warner, D. W., & Weisbrod, A. R. (1991). Unprecedented Stopover Site Fidelity in a Tennessee Warbler. *The Wilson Bulletin*, *103*(3), 512–514. WorldCat.org.

Yohannes, E., Biebach, H., Nikolaus, G., & Pearson, D. J. (2009). Migration Speeds among Eleven Species of Long-Distance Migrating Passerines across Europe, the Desert and Eastern Africa. *Journal of Avian Biology*, *40*(2), 126–134. WorldCat.org.

Yong, W., & Moore, F. (2005). Long-distance bird migrants adjust their foraging behavior in relation to energy stores. *Acta Zoologica Sinica*, *51*, 12–23.

Zwaan, D. R., Huang, A., McCallum, Q., Owen, K., Lamont, M., & Easton, W. (2022). Mass gain and stopover dynamics among migrating songbirds are linked to seasonal, environmental, and life-history effects. *Ornithology*, *139*(4), 1–16. WorldCat.org. https://doi.org/10.1093/ornithology/ukac027