# PRE-MIGRATION BEHAVIOUR AND SURVIVAL OF JUVENILE WOOD THRUSHES (*HYLOCICHLA MUSTELINA*) IN A FRAGMENTED FOREST LANDSCAPE

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# Abstract

Due to the difficulty in tracking juvenile songbirds once independent and dispersed from their natal areas, little is known about survival during the first year of life, despite being important for understanding population dynamics in migratory songbirds. Using technology advancements with the Motus Wildlife Tracking System and the miniaturization of radio-tags (~1-year battery), I tracked 189 Wood Thrush nestlings from the nest to provide survival estimates at 3 key life stages: fledgling survival, pre-migration survival, and migration/wintering survival. As small forest fragments have been identified as lower quality habitat, I tested if natal fragment size was a strong predictor of either survival or the extent of pre-migratory movement, and whether juveniles from small fragments suffered from carry-over effects that delayed fall migration departures or lowered annual survival. Lastly, I was able to test hypotheses that could explain the function of pre-migratory movements: habitat optimization, prospecting for future breeding territories, homing target; and for the first time, a flight performance hypothesis that proposes that the extent of pre-migratory movement improves first migration flight performance.

Natal forest fragment size was not a strong predictor of fledgling, pre-migration, or apparent annual survival and onset of fall migration was best predicted by fledge date. Weekly survival was lowest for fledglings on their natal territory, high for juveniles as they explored the landscape prior to fall migration, and lower during their first migration/wintering season. Most juveniles that were known to survive wintering/migration, returned to the study area (81%, 25/31) within ~12km of their natal site. Long-distance exploration of the landscape occurred for a high proportion (78%) of juveniles prior to onset of fall migration and these pre-migratory movements occurred at night, mainly 2 hours before sunrise. My results best supported the homing target hypotheses as pre-migratory movements were common in juveniles but not adults, were random in orientation, and a relatively large proportion of juveniles returned the next spring. Overall, my results suggest that even small forest fragments on the breeding grounds are important as they can support high juvenile survival for Wood Thrushes and that survival is driven primarily by factors outside of the breeding grounds.

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## Joint Statement of Candidate's Contributions

**Dissertation:** Pre-migration behaviour and survival of juvenile Wood Thrushes (*Hylocichla mustelina*) in a fragmented forest landscape

**Candidate:** Susan M. Hayes

Sue is the first author of both data chapters in this dissertation paper. Sue spent four field seasons doing field work that focussed on establishing study sites and permissions to use them (public and private lands), nest searching and monitoring, manual radio-telemetry, and completing habitat/vegetation measurements of Wood Thrush territories. Sue extracted and filtered all detection data for juvenile Wood Thrushes from the automated Motus Wildlife Tracking System. She did all the data and statistical analyses, prepared the results (graphs/tables, supplementary materials) and prepared the final written manuscripts for the dissertation and submission to the journals. Sue is the corresponding author for both papers and is responsible for all the correspondence with the journal and completing any revisions requested by the editor.

**Chapter 2** of the dissertation has been accepted for publication (25 September 2023) in the international journal Ornithological Applications. The paper is co-authored and the citation is: Hayes, S.M., Boyd, B.P., Israel, A.M., and B.J.M. Stutchbury (In Press). Natal forest fragment size does not predict fledgling, pre-migration or apparent annual survival in Wood Thrushes. Ornithological Applications.

Co-authors Brendan Boyd and Alexandra Israel were graduate students under Dr. Stutchbury's supervision and were also studying Wood Thrushes in the same study sites for their own theses. Their contribution to this chapter of Sue's dissertation was through collaborative field work as they were responsible for radio-tagging all the nestlings and monitoring fledgling survival through manual radio-tracking for two weeks after the young left the nest. Dr. Stutchbury's contribution was through research funding and reviewing/editing the writing of the manuscript.

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**Chapter 3** of the dissertation was submitted to the Journal of Field Ornithology on Sept. 30. The paper is co-authored and the citation is: Hayes, S.M., Boyd, B.P., and B.J.M. Stutchbury (submitted). Why do juvenile Wood Thrushes make long distance pre-migratory movements across a fragmented landscape? Journal of Field Ornithology

Co-author Brendan Boyd's contribution to this chapter of Sue's dissertation was through the inclusion of his pre-migration movement data of adult Wood Thrushes to allow a direct comparison with juveniles. Dr. Stutchbury's contribution was through research funding and reviewing/editing the writing of the manuscript.

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# Chapter 1: General Introduction

### *Migratory songbird declines*

North American migratory bird abundance across 419 species has declined by approximately 3 billion birds (~29%) since 1970 in most biomes and bird families (Rosenberg et al. 2019). In particular, 74% of grassland species are in decline and have the largest proportional loss of individuals of any group (Rosenberg et al. 2019) which has mainly been attributed to the conversion of grasslands to agriculture (Pool et al. 2014; Stanton et al. 2018) and the use of pesticides such as neonicotinoids (Eng et al. 2019; Li et al. 2020) on both the breeding and over-wintering grounds (Rosenberg et al. 2019). Forest biomes have also experienced significant declines (~57% species in decline), especially for species that breed in eastern and western forest biomes (~64% species in decline in each biome) (Rosenberg et al. 2019). Habitat loss and subsequent forest fragmentation on both the breeding and over wintering grounds have been primarily indicated in forest bird declines (Lloyd et al. 2005; Rushing et al. 2016) and more recently attributed to urbanization near the remaining breeding forest fragments (Heide et al. 2023).

Determining the exact mechanisms that are driving these declines has proven to be a challenge (Norris and Taylor 2006; Faaborg et al. 2010). Migratory birds spend approximately half of the year on their over-wintering grounds in the tropics, a third on their breeding grounds in the temperate region, and the remainder travelling to and from these destinations on migration (Norris et al. 2004; Norris and Taylor 2006). Factors on the breeding grounds, where most studies have taken place, have been shown to be a key driver in population dynamics of some species. Habitat loss and fragmentation has led to increased nest predation (Burke and Nol 2000; Schmidt 2003; Falk et al. 2011), increased brood parasitism by cowbirds (Tewksbury et al. 2006; Hannon et al. 2009) and reduced food abundance (Burke and Nol 1998; Zanette et al. 2000), all of which have contributed to migratory bird population declines (Austen et al. 2001; Parker et al. 2005; Murphy et al. 2020). Additional research however, points to factors on the over-wintering grounds such as habitat availability (Johnson et al. 2006; Taylor and Stutchbury 2016) and quality (Norris et al. 2004; Norris 2005; Bailey and King 2019) which affect individual body condition and over-winter survival. On the wintering grounds, migratory birds need to find appropriate habitat with enough food to survive but also to gain fat reserves in preparation for the journey back to the temperate breeding grounds in the spring (Studds and Marra 2005; Faaborg et al. 2010). For any one species, the primary cause for decline is often not known (e.g., non-breeding versus breeding stressors versus migration mortality).

An emerging concept in migratory bird declines is negative carry-over effects, where events at one stage of the annual cycle have negative impacts on individuals in subsequent stages. Recognizing that population dynamics are influenced by carry-over effects across life history stages, and seasons, is critical to understanding the factors that limit migratory bird population dynamics (Norris et al. 2004; Harrison et al. 2011). For instance, poor body condition on the wintering grounds has been shown to delay spring migration and reduce reproductive success on the breeding grounds (Norris et al. 2004). The abundance of arthropod food has been identified as the main driver in individual body condition during the non-breeding period (Brown and Sherry 2006; Cooper et al. 2015). Few studies have looked at carry-over effects from the breeding ground habitat quality on fall migration and annual survival. Boyd et al. (2023) tracked adult Wood Thrushes that bred in small and large forest fragments but found no carry-over effects on fall migration timing or annual survival. With the continued loss and degradation of habitat through forest clearing and fragmentation along with the growing impacts of climate change, carry-over effects may have an increasing impact on migratory bird populations (Johnson et al. 2006; Studds and Marra 2011; Ockendon et al. 2013).

### *Forest habitat quantity and quality for temperate breeding forest birds*

The first wave of massive forest loss in eastern North America was largely completed by the mid-19th century (Foster 1992) with many areas now having less than 20% forest cover remaining (Eng et al. 2009; Falk et al. 2011; Friesen et al. 2013). Although most major temperate forest loss occurred in the past, remaining forests continue to be fragmented into smaller patches, amplifying habitat loss and resulting in novel environments of agricultural or urban land-use matrix (Haddad et al. 2015).

A large body of research has been conducted on the breeding grounds implicating forest habitat loss and fragmentation for population declines of Neotropical migratory birds due to decreased breeding success (Robinson et al. 1995; Chalfoun et al. 2002; Lloyd et al. 2005). Increased nest predation (Burke and Nol 2000; Falk et al. 2011), increased cowbird nest parasitism (Hannon et al. 2009), and decreased food availability (Robinson et al. 1995; Burke and Nol 2000) have been identified as the main issues in forest fragments to adversely affect reproductive success. In some cases, the cowbird parasitism and predation rates are so high in small fragments that they have been determined to be population sinks (Robinson et al. 1995; Burke and Nol 2000) as the number of fledged young is below replacement levels (Rush and Stutchbury 2008; Eng et al. 2009). The extent to which small forest fragments are poor quality breeding sites varies among populations and species (Hames et al. 2006; Richmond et al. 2012). For instance, a forest fragment within a largely agricultural land-use matrix versus a fragment within an urban matrix may have different food supply and predation risk, and the same can apply to forest fragments that are surrounded by differing amounts of landscape forest cover (Lloyd et al. 2005; Richmond et al. 2012; Friesen et al. 2013). Forest fragmentation of a contiguous forest results in smaller patches that have a higher perimeter-to-edge reducing the overall forest interior habitat but increasing edge habitat (Fahrig 2003). These changes can affect the breeding bird community composition as area sensitive species (those that avoid small habitat patches) may no longer have suitable habitat, but generalist species that use forest edge may increase (Austen et al. 2001; Keinath et al. 2017). For instance, Falk (2011) found significantly higher nest predation rates in small forest fragments versus large contiguous forests for Ovenbird (*Seiurus aurocapilla*; 74% vs 60%) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*; 61% vs 38%) but not for Veery (*Catharus fuscescens*; 63% vs 65%). Other studies failed to find a difference in predation rates between large versus small fragments (Rush and Stutchbury 2008), but this could occur because even large fragments are surrounded by an agricultural matrix and so have high predator abundance (Friesen et al. 2013).

Brown-headed Cowbirds (*Molothrus ater*) were once restricted to the prairies and plains of the Midwestern United States, however with the clearing of forests for agricultural purposes, their range has expanded eastward and have become more abundant (Brittingham and Temple 1983). As temperate breeding birds have not co-evolved with cowbirds, few have developed defenses against their egg laying/brood rearing strategy. Video evidence has implicated cowbirds directly removing or destroying hosts' eggs in the nest (Benson et al. 2009; Cox et al. 2012; Friesen et al. 2013) thereby immediately reducing the nesting productivity for the host. A 10-year study conducted by Hannon et al. (2009) on American Redstarts (*Setophaga ruticilla*) in a fragmented forest landscape found that parasitized nests had a 15-20% increase in predation rate compared to unparasitized nests, perhaps because parasitized nests had higher parental visitation rates and louder nestling begging by the cowbird chick.

Very few studies have quantified arthropod food abundance in forest fragments and how this relates to breeding success. One study conducted by Zanette et al. (2000) however, compared prey biomass in small versus large fragments and found a significant decrease in the small fragments. In addition, nestlings had lower body mass in the small fragments despite being fed as frequently as the nestlings in the large fragments however, the difference was that larger prey items were being delivered to the nestlings in the large fragments. In an additional study comparing prey biomass in small versus large forest fragments, it was found that large fragments had 10 to 36 times higher invertebrate biomass than in small forest fragments (Burke and Nol 1998). One reason for the paucity of studies is the difficulty of sampling arthropod prey accurately in complex three-dimensional habitats like forests.

### *Juvenile songbird survival and population dynamics*

Understanding survival at different stages over the first year of life has been an under-studied area in population dynamics of songbirds (Cox et al. 2014; Drummond et al. 2019) because of the difficulty in tracking their movements once they leave the natal territory (Mitchell et al. 2011; Tarof et al. 2011) and migrate thousands of kilometers to their overwintering grounds. Population growth rate models typically resort to estimating juvenile survival to 25 to 50% of annual adult survival (Anders and Marshall 2005; Buehler et al. 2008) but the accuracy of such models remains in question (Streby and Andersen 2011). To better predict population growth and understand how the main drivers of survival impact demographics, detailed studies of the full annual cycle of juvenile songbirds are needed (Cox et al. 2014; Raybuck et al. 2019; Carle-Pruneau et al. 2021).

My study is novel as it addresses this knowledge gap through the use of an innovative new tracking technology (Motus Wildlife Tracking System) and the advancement in miniaturization of radio-tags that allowed me to track Wood Thrushes through the first-year of life. The Motus tower system is built on a collaboration of many researchers that maintain individual towers to track bird movement over a regional scale (Taylor et al. 2017). Uniquely coded nano-tags are deployed on birds using a single radio frequency that can be detected at every receiving tower across a broad geographic scale, regardless of the specific project individual towers are maintained for, providing a location, date, and time for when the radio-tagged bird was detected (Taylor et al. 2017). The high density of Motus towers within my study area allowed remote detection of radio-tagged juveniles as they moved away from their natal areas making pre-migratory landscape movements > 5 km away, as they departed on fall migration, and as they returned to the study area the following spring. Critically, the use of long battery life tags on a relatively large-bodied migratory songbird allowed, for the first time, (i) determination of fall departure date for juveniles from known nests, (ii) proposed and tested a flight performance hypothesis to determine the function of pre-migration movements, and (iii) estimation of year-round juvenile apparent survival through radio-tracking rather than re-sighting.

The primary objective in Chapter 2 was to test the hypothesis that small forest fragments reduce nesting success and juvenile survival and delay the timing of fall migration. I explored the key predictors of survival at four stages of the life cycle: (1) nestling survival within the nest, (2) fledgling survival, (3) pre-migration survival of independent juveniles, and (4) migration/wintering survival. The second objective was to test (1) if natal site fragment size (or other predictors) explain variation among individuals in fall departure date, and (2) if delayed fall migration reduces migration survival.

The high density of Motus towers within my study area also provided a unique opportunity to quantify long distance (>5 km) landscape movements of juveniles prior to the onset of fall migration. It has been widely observed that unmarked juveniles appear in late summer within well-studied forest sites which has led to the hypotheses that this pre-migratory exploration functions as prospecting for future breeding sites and/or the movements are important for physiologically priming a naïve bird for its for its migration flight (Mitchell et al. 2010; Brown and Taylor 2015; Patchett et al. 2022). In Chapter 3, I examine what individual or natal habitat variables predict juvenile Wood Thrushes pre-migratory movement, what the function is for pre-migratory movements, and I also test the prediction that if there is a great extent of pre-migratory movement, then first migration flight performance will increase.

### *Natural history of Wood Thrush*

Wood Thrushes (*Hylocichla mustelina*) were chosen as the study species as they are Neotropical migrants that are declining across most of their range in North America, including in southern Ontario (Sauer et al. 2017). They have been the focus for many studies on forest fragmentation and nest success (Donovan et al. 1995; Hoover et al. 1995; Friesen et al. 1999; Kaiser and Lindell 2007), and have supported many tagging studies (Stutchbury et al. 2009; Gow et al. 2011; Stanley et al. 2015;) as they are able to carry tags with a long battery life (birds can carry tags for up to 1 year), so are a model species for understanding forest bird declines.

The following description of life history is based on a review conducted by Evans et al. (2020) for Wood Thrushes unless otherwise stated. Wood Thrushes breed in southeastern Canada (southern Ontario, Quebec, New Brunswick, and Nova Scotia) into the eastern United States south to northern Florida and along the Gulf Coast, west to Arkansas, Iowa, and Wisconsin, in deciduous and mixed forests. Males generally arrive in southern Ontario on breeding grounds from Central America (mostly from Belize to the western half of Panama) to set up territory during the first week of May a few days ahead of the females. Breeding pairs are socially monogamous and stay together for the duration of the breeding season, however extra-pair mating also occurs though frequency varies across populations. Initial breeding territories are defined (but can shift throughout the breeding season May to August) and nest building commences utilizing a variety of tree and shrub species placing the nest on average 2.3 m from the ground and taking 3-6 days to complete. Up to 3-4 eggs are laid (1 per day in succession) and incubation lasts for a period of approximately 13 days. Nestlings fledge the nest when 12-14 days of age but remain with the parents for approximately 2 to 3 weeks. For the first week out of the nest, nestlings are not capable of sustained flight and often will hop on the ground in vegetation while being dependent on the parents for food.  Wood Thrushes are double brooded, so will attempt a second nest if their first is successful. They are omnivores species and primarily forage on the forest floor.

Wood Thrushes undergo a loop migration whereby they depart the breeding grounds from September to October and fly south along eastern United States and launching across the Gulf of Mexico through the southern tip of Florida and across to the Yucatan Peninsula continuing down into Central America, arriving on their wintering territory by mid-October to early December. Whereas the spring migration route is further to the west funneling through a narrow region of the central U.S. Gulf Coast (Stanley et al. 2015) flying northward to the breeding grounds. Wood Thrushes fly at night during migration, typically beginning just after sunset and ending before sunrise. Migration speeds vary greatly between fall and spring, with spring speeds measured to be 2-6 times faster (Stutchbury et al. 2009). Wood Thrushes depart wintering grounds in March- April with migration period lasting just 13-15 days on average.

During the winter months Wood Thrushes are found in a variety of habitats from primary forest to scrub to agroforestry habitats. Some are territorial during this time and will often return to the same territory in following years while others do not defend territories and will forage with conspecifics (Rappole et al. 1989). Although Rappole et al. (1989) found that birds in primary forest defending territories had higher survival rates than those that those that wondered in second growth forest it is not clear if the difference in survival was due to the behaviour (territorial birds were more sedentary versus birds not on territory that wandered) or habitat quality. McKinnon et al. (2015) tracked Wood Thrushes in Belize over the winter months in three different habitats to represent a gradient in habitat quality (mature forest, riparian scrub, and mature forest with increased anthropogenic disturbance) to determine the effect on overall body condition. They found that overall body condition of birds decreased over the winter season in relation to food abundance with no significant difference between habitats.

The steep decline of the iconic Wood Thrush has made it a ‘poster bird’ for migratory forest songbird declines and adults have been well studied on the breeding and wintering grounds and during migration. Nevertheless, as with almost all other migratory songbirds, little was known about the fate of juveniles after they became independent from their parents a few weeks after leaving the nest because from the researcher’s perspective, the juveniles disappear and are never seen again. But the fate of a population depends on the production of sufficient young that will survive and return to breed, and yet for migratory songbirds, researchers did not have the tools to measure this key variable. My dissertation has taken an important step to fill this gap by re-purposing the Motus technology from its primary role in monitoring migrating birds to testing how natal conditions affect pre-migration movements and juvenile survival.

# Chapter 2: Natal forest fragment size does not predict fledgling, pre-migration, or apparent annual survival in Wood Thrushes

**This chapter is a slightly modified manuscript of Hayes, S.M., Boyd, B.P., Israel, A.M., and B.J.M. Stutchbury (2023). Natal forest fragment size does not predict fledgling, pre-migration or apparent annual survival in Wood Thrushes. Ornithological Applications.**

## Abstract

Determining the drivers and mechanisms for first year survival of migratory songbirds has been an understudied area in population dynamics due to the difficulty in tracking juveniles once they have dispersed from the natal site. With the advancement in miniaturization of radio-tags (battery life ~ 400 days) and the development of the Motus Wildlife Tracking System, we tracked 189 Wood Thrush (*Hylocichla mustelina*) nestlings through independence and to fall migration departure, and their return the following spring. Natal forest fragment size and landscape forest cover (at different spatial scales) were not strong predictors of fledgling, pre-migration or apparent annual survival and onset of fall migration was best predicted by fledge date but not natal fragment size. Survival probability was lowest the first 16 days post-fledging (70%, or 0.86 weekly survival probability), very high for juveniles as they explored the landscape prior to fall migration (89%, or 0.99 weekly survival probability) and low during their first migration and wintering season (26%, or 0.95 weekly survival probability). To our knowledge, this is the first study to directly estimate annual apparent juvenile survival in a migratory songbird using year-round radio-tracking. Our study suggests that small forest fragments are important for the conservation for forest songbirds because they can support high survival of juveniles.

*Keywords:* fragment size, fledgling survival, pre-migration survival, apparent juvenile survival, fall migration timing, Wood Thrush, Motus

## Lay Summary

- Understanding the main drivers of survival during the full annual cycle of juvenile songbirds is urgently needed to better understand population decline.
- A key question for forest songbirds is whether nesting in small forest fragments negatively

affects juvenile survival.

- The advancement in radio-tags (~ 400-day battery life for small tags) alongside the Motus Wildlife Tracking System allowed us to estimate apparent juvenile survival at three life stages (fledgling, pre-migration, and migration/wintering) for a declining migratory forest songbird, the Wood Thrush.
- We show that natal fragment size does not predict survival probability for fledgling or juvenile Wood Thrushes.
- Weekly survival was lowest for fledglings on their natal territory, high for juveniles as they explore the landscape prior to fall migration, and lower during their first migration and wintering season.
- Our study suggests that even small forest fragments on the breeding grounds are important as they can support high juvenile survival for a forest songbird and that survival is driven primarily by factors outside of the breeding grounds.

## Introduction

Understanding which breeding, migration, and overwintering factors influence survival is important in modelling the population dynamics of migratory birds (Hannon and Martin 2006; Naef-Daenzer and Grüebler 2016) and subsequently, developing effective conservation policies (Cox et al. 2014; Streby et al. 2014; Vernasco et al. 2018). Survival during the first year of life for a long-distance migratory songbird is fraught with challenges and risks as they leave their natal territory for the first time, migrate thousands of kilometers and overwinter in the tropics (Naef-Daenzer and Grüebler 2016). The drivers and mechanisms behind first year survival have been an understudied area in population dynamics of songbirds (Cox et al. 2014; Drummond et al. 2019) because of the difficulty in tracking their movements once they disperse from the natal territory (Mitchell et al. 2011; Tarof et al. 2011). Since almost all juvenile songbirds disperse away from their natal area to unknown breeding locations (e.g., Rushing et al. 2021), mark-resight methods and archival tracking devices that require recapture after migration are typically of little use for studying juvenile survival or fall migration (McKinnon et al. 2014). Stable isotopes in feathers can be used to estimate juvenile dispersal, for instance in Ovenbirds (*Seiurus aurocapilla*) most first-year breeders originated from <200 km from the study area (Hachè et al. 2014) while in Cerulean Warblers (*Setophaga cerulea*) most first-year breeders were longer-distance immigrants (Jones and Islam 2023). Detailed studies of the full annual cycle of juvenile songbirds are urgently needed (Cox et al. 2014; Streby et al. 2014; Raybuck et al. 2019; Carle-Pruneau et al. 2021) to better understand what conservation actions can improve juvenile recruitment and population stability.

Annual survival probability of juvenile migratory songbirds can be partitioned into three non-overlapping stages: fledgling survival to independence, pre-migration survival, and migration/wintering survival (Tarof et al. 2011). Factors affecting survival no doubt differ between the fledgling period (first 16 days post-fledging when still-developing young have left the nest but receive food and protection from parents) and the pre-migration period (>16 days post-fledging to on-set of fall migration) when full-grown juveniles care for themselves and often begin local dispersal movements through the landscape prior to migration. Numerous radio-tracking studies have shown that the highest risk of mortality for young songbirds is the first days after they fledge and cannot fly well (Naef-Daenzer and Grüebler 2016; Drummond et al. 2019; Evans et al. 2019; Raybuck et al. 2019). Fledglings typically have an overall ~50% chance of surviving to three weeks after fledging, when most songbirds reach independence from the parents (Eng et al. 2009; Jones et al. 2017; Raybuck et al. 2019). Although many studies have estimated fledgling survival in migratory songbirds, to our knowledge there have only been two studies that tracked independent juveniles until they departed on fall migration weeks or months after fledging, and both are for swallows. Tarof et al. (2011) radio-tracked nestling Purple Martins (*Progne subis*) after fledging and resighted birds at their pre-migration roost and at breeding colonies the next spring; pre-migration survival of independent juveniles was very high (87%). Evans et al. (2019) used the Motus automated telemetry array at the regional scale and estimated 42% of juvenile Barn Swallows (*Hirundo rustica*) survive the first month after gaining independence.

Our study on Wood Thrush (*Hylocichla mustelina*) is the first we know of to estimate annual apparent juvenile survival in a migratory songbird using year-round radio-tracking, and to estimate pre-migration juvenile survival for a forest songbird. Tracking juvenile Wood Thrushes through their first year of life has been made possible with the automated long-distance radio telemetry collaborative Motus Wildlife Tracking System (Taylor et al. 2017) combined with the miniaturization of radio-tags with >365 d battery life. This tracking system consists of an array of receiver towers that allow researchers to track tagged wildlife movements over regional and continental spatial scales. With this system many aspects of migratory bird behavior can be quantified such as patterns of connectivity (McKellar et al. 2015; Marchand et al. 2020), identifying stopover locations and duration (Smetzer and King 2018; Beauchamp et al. 2020), and departure and arrival times (Mitchell et al. 2015; Evans et al. 2019; Müller et al. 2018; Dossman et al. 2023). Although much of the research to date using this system has been on adult bird movement, some studies have addressed the knowledge gap in relation to juvenile dispersal, survival, and migration strategies (Brown and Taylor 2015; Crysler et al. 2016; Cormier and Taylor 2019).

We studied Wood Thrushes because this species is a Neotropical migrant that has declined across most of its breeding range (Rushing et al. 2016; Sauer et al. 2019), so is a model species for understanding forest bird declines. In Canada, Wood Thrushes are currently listed as a Species at Risk as populations have been declining; in Ontario a decline of 3.2% / yr. was detected from 2005–2015 (Sauer et al. 2017) representing a cumulative 27.4% decline of the population. The deciduous forests of southern Ontario are highly fragmented, but it is unknown to what extent this contributes to low juvenile survival and hence population declines in this region.

For forest birds, a key predictor of nesting success is regional forest fragmentation and forest fragment size, with reduced productivity in small fragments due to a higher incidence of nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Lampila et al. 2005; Falk et al. 2011; Richmond et al. 2012). Nest predation may decrease with increased nest distance from the edge if predators are more abundant in the agricultural matrix (Etterson et al. 2014). The presence of Brown-headed Cowbird nestlings may also increase detectability and nest predation risk (Hannon et al. 2009). Predation risk within a forest fragment can also depend on the amount of regional forest cover in the surrounding landscape (Cox et al. 2012; Etterson et al. 2014). Nest predation and cowbird parasitism have been shown to increase with decreasing regional forest cover (Lloyd et al. 2005) but this relationship can depend on predator type (Cox et al. 2012). Chiavacci et al. (2018) found that higher regional forest cover increased the risk of songbird nest predation by black rat snakes (*Pantherophis obsoletus*) and Cooper's Hawks (*Accipiter cooperii*) but not by raccoons (*Procyon lotor*). The extent to which predation rate increased with forest cover also increased with the spatial scale at which the landscape was measured (e.g., 200 m versus 2500 m). However, studies examining fledgling survival have not found a strong relationship to natal forest fragment size. Rush and Stutchbury (2008) radio-tracked fledgling Hooded Warblers (*Setophaga citrina*) and found no difference between survival rates in large versus small fragments. Eng et al. (2009) radio-tracked fledgling Hooded Warblers in Ontario and found that forest fragment size was a far weaker predictor of fledgling survival than variation in forest structure resulting from prior logging practices. A parallel study on Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) found that fledgling survival was not predicted by either fragment size or prior logging treatment (Moore et al. 2010). For Wood Thrushes in a fragmented landscape in southern Indiana, fledgling survival was significantly higher for sites with greater local (2 km radius) forest cover in drought years, but the relationship was reversed in non-drought years (Vernasco et al. 2018).  Other possible drivers of fledgling survival in songbirds include nestling body condition, habitat quality, and timing of fledging (Brown and Roth 2004; Mitchell et al. 2011; Vitz and Rodewald 2011; Blomberg et al. 2014).

Timing of migration is an important factor in full-life cycle demographic models because it can impact future survival and reproduction through negative carry-over effects. For instance, poor quality winter territory (e.g., lower arthropod abundance) can delay spring migration timing and reduce subsequent reproductive success (Norris et al. 2004). For species that are territorial on their wintering grounds, poor body condition or late fall migration may make it more difficult to secure a high-quality winter territory. For instance, adult Louisiana Waterthrush (*Parkesia motacilla*) that were in poor condition prior to fall migration obtained lower quality winter territories and ended the non-breeding season in poor condition (Latta et al. 2016). Although fall migration timing does not appear to affect arrival time on the wintering grounds for adult Wood

Thrushes (Stutchbury et al. 2011), it is not known how fall migration timing of juveniles affects winter territory quality or over-winter survival. A radio-tracking study in Mexico found that first-year Wood Thrushes were more likely to be excluded from large forest fragments and had a higher mortality as a result (Rappole et al. 1989).

The primary objective of this study was to test if natal forest fragment size is a strong predictor of survival in the first year of life for Wood Thrushes (*Hylocichla mustelina*) at four stages of the life cycle: (1) nestling survival within the nest, (2) fledgling survival (first 16 days post-fledging), (3) pre-migration survival of independent juveniles, and (4) migration/wintering survival. We hypothesized that small forest fragments are poor quality habitat for Wood Thrush nests, fledglings, and juveniles due to higher predation risk. First, we predicted that daily nest survival is lower in small forest fragments, near forest edges. Second, we tested whether forest fragment size, percent forest cover, nestling body condition before fledging, breeding territory habitat, and timing of nesting are important predictors of fledgling survival to independence at 16 d post-fledging. Third, we tested the prediction that originating from small natal fragments delays the timing of fall migration of juvenile Wood Thrushes or reduces their pre-migration and migration survival. This could occur through negative carry-over effects such as poorer body condition and later fledge date. Juveniles from nests initiated later in the season are expected to depart on fall migration later (Mitchell et al. 2011; Evans et al. 2019), and poor body condition is expected to delay migration departure (Mitchell et al. 2011; Stutchbury et al. 2011). Fourth, we tested if small natal fragment size or late fall migration timing lowered annual juvenile survival. Birds in poorer body condition or that departed later on fall migration may experience negative carry-over effects to the wintering season, decreasing annual survival.

## Methods

### *Study Area*

This study took place from 2016 to 2019 in forest fragments in Norfolk County on the north shore of Lake Erie in Ontario Canada (42.7131ºN, 80.5372ºW). Study sites (*n* = 29 forest fragments) were selected to represent a gradient of forest size, ranging from 11 to 500 ha (median = 111.2 ha) (Figure 2-1). The percent forest cover of the Long Point Conservation Authority jurisdiction in which Norfolk County is part of, was 21% with predominant land uses being crop agriculture (LPRCA, 2019). Norfolk County lies within the Carolinian forest zone dominated by deciduous and mixed forest types consisting of species such as Sassafras (*Sassafras albidum*), Oak (*Quercus spp.*), Hickory (*Carya spp.*), Tulip tree (*Liriodendron tulipfera*), Eastern hemlock (*Tsuga canadensis*), Eastern white pine (*Pinus strobus*), and understory species such as Spicebush (*Lindera benzoin*), Witch hazel (*Hamamelis virginiana*), and Prickly ash (*Xanthoxylum Americanum*). This region was chosen because of the high-density coverage of the Motus automated telemetry system (see Supplementary Material S2-1 for study area Motus tower locations). Within the breeding range for Wood Thrushes in southeastern Canada and the eastern United States there are >300 Motus receiver towers that potentially could remotely detect juveniles during their first migration.

### *Nest Monitoring and Radio-tagging*

Beginning in mid-May of each year, we searched for Wood Thrush nests by locating singing males on territories and subsequently observing nests or nesting behavior. Nest contents were checked every 4 to 6 days using a pole with attached cellphone set to video mode. Egg incubation lasted ~14 days and nestlings fledged the nest ~26 days after the first egg was laid (Donovan et al. 1995). Only 15 nests out of 419 were abandoned during the study, in all cases during egg-laying stage, and these were not included in analyses of nest survival.

Typically, multiple nests were located and monitored at each forest fragment over the breeding season however, not all nests were selected for radio-tagging nestlings (tagging date ranged from early June to mid-August). Nests were selected to ensure representation of the gradient of forest fragment sizes during each of the first 3 field seasons. On day 10 after hatching, nestlings were banded with uniquely numbered aluminum bands (US Fish and Wildlife / Canadian Wildlife Service), a unique color band combination and mass, tarsus length, and wing chord measurements were taken. Body condition was calculated using a scaled mass index with mass and tarsus length (Peig and Green 2009). The scaled mass index has been identified as the best way to estimate energy reserves in some passerines (Peig and Green 2009, Nip et al. 2018) by adjusting mass to a standardized body length measure that is positively correlated with mass on a log-log scale.

The largest nestling (by mass) in the nest had a blood sample (25 uL) taken for genetic sexing (HealthGene Corporation) and was equipped with a uniquely coded radio transmitter (Lotek NTQB-6, 1.5-1.7g; ~ 1 yr. battery life; 12.7 sec. burst rate) using a figure-eight leg loop harness (Rappole and Tipton 1991) using 2.5 mm Teflon tubing. This unavoidable bias toward heavier nestlings to avoid potential negative impacts of radio-tags could have overestimated average juvenile survival and underestimated the effects of nestling body condition (Naef-Daenzer and Grüebler 2016; Evans et al. 2019). Three slightly different tag models were deployed due to manufacturing limitations throughout the three-year study (tag models were to be equivalent and direct replacements to the original) however, tags remained ~ 5% of the total body weight of the 10-day old nestling (total tag and harness weight = 1.7-1.9 g). Only one nestling was tagged at 131 of the160 nests (82%) however, 2 nestlings were tagged at 29 (18%)

nests. Of the 189 tagged nestlings (2016 $n = 47$, 2017 $n = 66$, 2018 $n = 76$) there was an even sex ratio of males to females (95:94).

### *Manual, Remote Radio-tracking and Aerial Telemetry*

Manual tracking of fledglings was conducted using a handheld 3 or 5 element Yagi antennae connected to an SRX 600 or SRX 800 receiver (Lotek Wireless Inc.). Each radio-tagged fledgling was relocated on or near its natal territory approximately every 4 days to determine if the bird was alive (moving and/or parents attending) or dead (stationary). If the signal appeared to be stationary, or could not be detected, a 1-hr search was made to locate the tag/carcass or the live bird. Manual tracking of fledglings continued until they either dispersed from the natal territory and could no longer be located, they died, or if still on their natal territory until the end of the field season in late August.

Remote tracking using the tower array of the Motus Wildlife Tracking System (Taylor et al. 2017) allowed us to detect the juveniles during the pre-migration period, early migration, and their return the following spring (see Supplementary Material Table A2-1 for study area Motus tower locations). The high density of automated towers within our study area, and surrounding regions in all directions allowed for the detection of juveniles up to the onset of fall migration and those that survived migration but did not return to their natal forest fragment. For juveniles that survived to begin migration, Motus towers in the U.S. detected 61% (50 of 82) after their fall departure flight and during their fall and/or spring migratory routes.

Aerial telemetry was conducted to independently locate juveniles that returned to the general study area each spring (2017, 2018, and 2019) as a supplement to Motus automated detection to determine annual survival and to estimate breeding location of birds that recruited to our study area. Approximately 5 hours was spent each year (July 18 2017, June 2 2018, and May

15 2019) following a grid pattern from north to south covering the study area, with each pass being ~2-10 km apart (extending ~20 km from the outside edge of the furthest site fragment). Smaller circles were made over forest fragments with the study area or when a detection was made to pinpoint the bird's location and record a GPS point.

### *Territory Habitat*

Vegetation measurements were taken at each nest site where a nestling was radio-tagged to assess within-fragment differences in habitat among individuals that could potentially influence fledgling survival on the natal territory (e.g., Vernasco et al. 2018). The protocol followed was a revised version of the Roberts-Pichette and Gillespie (1999) terrestrial vegetation sampling protocols that uses different plot sizes to sample trees and shrubs. First, to measure trees, three 20 m x 20 m plots were established around each nest starting with a plot 20 m and 225° from the nest, and the other two plots randomly selected within 80 m of the nest. We did not map territory boundaries of males due to time constraints and assumed that the home range was within this distance from the nest. Within each 20 m x 20 m plot all trees with >10 cm diameter at breast height (DBH) were identified to tree species and DBH to the nearest cm measured. Second, five nested 2 m x 2 m plots at the center and edges of each 20 x 20 m plot were used to document all shrub and sapling species and % cover of each stem.

### *Analytical Methods*

**Nest survival.** The percent forest cover was calculated using open access Wooded Area land cover data layer available through Land Information Ontario from Ministry of Natural Resources and Forestry (2018) and buffering each nest at the 3 spatial scales (500 m, 2 km, and 5 km from the nest to represent home ranges of different potential predators). Nest distance to forest edge and the presence/absence of Brown-headed Cowbird eggs/young were added as predictor variables.

Daily nest survival rate (DSR) was calculated with the package *RMark* 2.2.4 (Laake 2013) in R (R Core Team 2017, White and Burnham 1999). This model requires data input of the length of breeding season, age of the nest when first found, date when last checked and active (i.e., eggs/nestlings alive), and the fate of the nest (successful versus preyed upon). Nests were classed as successful if at least one nestling fledged. To test for effects of nest age (e.g., days since first egg was laid for each nest) on nest survival each nest's age on each day of the nesting season was provided, which allows for both time of season and nest age to be used as temporal predictors of nest survival (Rotella et al. 2004).

Models were run in a two-stage modeling process. First, we fit models to determine if there was a change in DSR based on temporal sources of variation which included using nest age, year, and both linear and a quadratic term for time (Supplementary Material Table A2-2). The best fit temporal model (*nest age*) was subsequently used as the base model for the predictor variables that included forest fragment size, percent forest cover at 3 different spatial scales (500 m, 2 km, and 5 km from the nest), nest distance to forest edge, and nest parasitism. The full model set included models with nest age plus one predictor variable, models with nest age plus two predictor variables (as both additive and interactive models) and models with nest age plus three additive predictor variables (Supplementary Material Table A2-3).

Model support was determined using the Akaike Information Criterion corrected for small sample size ($AIC_c$) and cumulative model weights (Arnold 2010). Model parameter and beta estimates were averaged across all models and beta estimates were used to infer biological importance. The estimated overall nest survival was determined by raising the DSR derived from the constant model to the power of 26 (number of nesting days for Wood Thrushes). The delta method (Powell 2007) was used to calculate standard error for cumulative survival probabilities.

**Fledgling survival.** Data from both the manual tracking and the Motus tower detections were used to model fledgling survival and the probability of detecting a bird given that it was alive (*p*). Fledgling survival was estimated using the Burnham model (Burnham 1993) with the *RMark* package (Laake 2013) in R (R Core Team 2017). This model incorporates both live detections on, and dead recoveries between set time intervals, which, in this study was every 4 days. The Burnham model includes a term for fidelity (*F*) to better estimate survival since individuals may permanently emigrate away from the study area where live encounters are taking place, and so would not be detectable even if still alive. For Wood Thrush fledgling survival (1-16 days old), *F* was set to 1 because all dead recoveries and live encounters occurred within the study area. Radio-tagged birds were detectable dead or alive by manual tracking on or near the natal territory and were classified as alive when detected by Motus prior to the onset of fall migration. The Burnham model also considers the probability that birds who died are encountered as dead ("r"). Known fate models consider that all dead birds can be located via radio-telemetry (e.g., r = 1), but in practice fledglings not old enough to be independent are sometimes not detected either alive or dead so their fate is unknown (e.g., Vernasco et al. 2018, this study).

All fledglings that were determined to be alive ≥ 16 days after fledging by Motus automated telemetry detections were coded as such in the encounter history on the last live encounter day (16 days). There were 9 individuals for whom there were gaps in manual tracking data due to scheduling and weather conflicts, but all 9 were subsequently detected by Motus towers within the study area in Aug. and Sept. In addition, there were 10 tagged fledglings (out of 189 tracked) that despite intensive manual tracking disappeared during the fledgling period (average of 6d post-fledging) but were detected by Motus prior to migration indicating that they had survived the fledgling period. The encounter history formats for all 19 of these birds were coded as "1" for the last encounter to signify surviving to 16-day post-fledging. There were 13 other fledglings that went undetected manually and were never detected by Motus and so their fates were coded as unknown (e.g., "0").

Similar to nest survival, a two-stage modelling process was implemented following similar methods to Vernasco et al. (2018) to model fledgling survival. The first stage of modelling determined the top temporal model for *p* while holding survival (S) and *r* constant. The probability of detecting a tagged fledgling given that it was alive (*p*) was modelled with year, linearly with age, fledge date, and two age groups (age2 - 0-8d, 9-16d; age3 - 0-8d, 9-12d, 13-16d). Detection probability could vary by year due to variation in tag design, with fledge date as later fledged birds will have a greater propensity to disperse out of receiver range, and with fledgling age because older age classes are more likely to disperse early and evade detection by manual tracking. Each parameter was modeled separately and with an additive model of year and fledge date, and the constant model for a total of 13 models (Supplementary Material Table A2-4). Next, the top *p* model was used to model *S*. Predictor variables modelled for *S* included a change in survival between calendar year (Year), linearly changing with age (Age), non-linearly changing with age (Age$^2$), time dependent (Time) and 3 age categories of 2 (age2 - 0-8d, 9-16d), 3 (age3 - 0-8d, 9-12d, 13-16d), and 4 (age4 - 0-4d, 5-8d, 9-12d, 13-16d) age groupings, and the constant model for a total of 26 models (Supplementary Material Table A2-5). A quadratic term for time (Age$^2$) was included to model *S* (and not *p*) as fledgling survival with respect to age may not be linear because flight capability increases rapidly during the first week after fledging.

The top temporal model (*S (Age) p (age3+ Year) r (constant) F (=1)*) was then used as the base model to model *S* with the set of covariates that related to the key predictions (also ran models using *S (Age) p (age3) r (constant) F (=1)* as the base model, however, did not result in substantive change to the results). The covariates in these models included forest fragment size, % forest cover at 3 different spatial scales (500 m, 2 km, and 5 km from the nest), body condition at the time of tagging, and 2 vegetation measurements that included mean number of trees with >30cm DBH, and % shrub and sapling cover in the understory as the predictor variables of survival. The full model set included models with Age plus one predictor variable, models with Age plus two predictor variables, and the constant model for a total of 38 models (as both additive and interactive models; Supplementary Material Table A2-6). Model support was determined using the Akaike information criterion corrected for small sample size ($AIC_c$) and cumulative model weights (Arnold 2010).

**Departure dates.** Motus tower data records were accessed using the *motus* and *motusData* R packages and cleaned following guidelines provided by Birds Canada (2022) (see Supplementary Material A2-7 for determination of departure date methods). We examined juvenile migration departure dates using a linear regression (*glm* function, package *lme4,* Bates et al. 2015) and gamma distribution (link="log") in program R (v. 4.0.5; R Core Team 2021). Additive models were run with natal forest fragment size, fledge date, body condition at time of fledging, sex, and year as predictor variables. Models were ranked using AIC values adjusted for small sample size (Burnham and Anderson 2002) and top models with $\Delta AIC_c < 2$ were considered equivalent to the best model. The full model was run using the *dredge* function (*MuMIn* package, Bartoń 2020), followed by model averaging.

**Pre-migration, migration/wintering, & annual survival.** The pre-migration survival period was defined as >16 days after fledging to fall migration period, migration/wintering survival was the period after fall departure to spring arrival, and annual survival from fledging the nest to spring return. Pre-migration survival was determined using Motus tower detections that were made after Aug. 25 (date of earliest fall migration departure) each year (*n* = 133). For apparent migration/wintering and annual survival analyses, birds that were detected the following spring through Motus (plus one individual detected through aerial telemetry but not Motus) were coded as alive if they were detected within or near to the study area (up to 110 km, see Supplementary Material Table A2-8).

Survival was modelled using a *glm* (family binomial with logit link) in the R package *lme4* (Bates et al. 2015) rather than other survival analysis models (i.e., RMark) as we cannot estimate the encounter probability (e.g., birds that were alive but not detected) using the Motus tower detections. We used the probability of survival as the response variable with forest fragment size, fledge date (for pre-migration and annual survival only), departure date on fall migration (for migration/wintering survival only), nestling body condition, sex, and year as predictors. To determine if departure date had a carry-over effect on migration/wintering survival, models included only the individuals that had a clear departure date (*n* = 82) based on time of day (departures just after sunset), time of year (after Aug. 25), and sequential Motus tower detections in a southerly direction (see Supplementary Material A2-7 for determination of departure date). Model support was determined using the Akaike information criterion corrected for small sample size (AICc) and cumulative model weights (Arnold 2010). The full set of models (for premigration, migration, and annual survival) were run using the *dredge* function (*MuMIn* package, Bartoń 2020), followed by model averaging.

## Results

### *Nesting Success*

Nest predation occurred at 54% (219 of 404) of nests. Nest age was overwhelming the top supported temporal model with ~100% of the model weight (Supplementary Material Table A2-2), with nest survival decreasing with increased nest age (Figure 2-2). The amount of forest cover within 5 km of the nest had a cumulative model weighting of ~44%, while models including forest fragment size had only a cumulative weighting of 21% (Table 2-1, Supplementary Material Table A2-3). As there was little to no support for models using the 500 m or 2 km spatial cover for % forest cover, they were removed from the final model set. The top two models included nest age and percent forest cover at 5 km, with the second-best model also including cowbird parasitism. Nest survival tended to decrease with increasing forest cover and with the presence of cowbirds, but these were relatively weak predictors as the confidence intervals around the *βeta* coefficient estimates slightly overlapped zero.

### *Fledgling Survival*

Observed fledgling apparent survival to 16 days after leaving nest was 70% (133 of 189) based on both manual tracking and Motus tower data. Of the 56 birds not known to have survived the fledgling period, 43 (77%) were confirmed to have been preyed upon, and 13 (23%) of the birds were never relocated alive or dead.

The top temporal model for fledgling survival was *S(Age) p(age3 + Year) r(~1) F(=1)* (Table 2-2) which had a weight of 0.26 and an increase AICc of 2.0 with the second model *S(Age + Fledge Date)*. Models that included *S(Age)* had a cumulative weight ($\sum w_i = 0.43$). Nestling body condition was a strong predictor of fledgling survival in the environmental model sets with the top models (<2 AIC) having 0.37 of the cumulative model weights (Table 2-3). Survival increased with age and nestlings in better body condition were more likely to survive to 16 days old (Figure 2-3). Models that included percent forest cover at 500 m and 2 km spatial scale had similar low support ($w_i$ = 0.07 - 0.10) and the models with forest cover within 5 km and fragment size had no support.

### *Departure Dates*

The average fall migration departure date for juvenile Wood Thrushes was Sept. 19 (range: Aug. 25 to Oct. 15) with a tendency for females to depart before males (model estimate +/- SE, 0.008 ± 0.006, $P = 0.21$). General linear regression indicated that the top models included fledge date, natal forest fragment size, body condition, sex, and year ($\sum w_i = 0.79$, <2 ΔAIC, Table 2-4), with fledge date and year (2017 and 2018) as the only significant predictors of fall migration departure (0.0009 ± 0.0001, $P < 0.001$; 0.003±0.0009, $P$=0.0014 (2017); and 0.003±0.0008, $P$=0.004 (2018)). Juvenile Wood Thrushes that fledged earlier in the breeding season (by June 22) departed on autumn migration 9 days earlier than nestlings that fledged later in the season (between July 23 and Aug. 7; Figure 2-4).

### *Pre-migration, Migration, and Annual Survival*

**Pre-migration.** Juvenile apparent pre-migration survival (from 16 days old to the onset of migration) was estimated from detection by Motus towers. Across all years, 89% (119 out of 133) of birds that survived the fledgling stage also survived the pre-migration period (duration of 52 days on average). General linear regression indicated that fledge date was not a significant predictor of pre-migration survival (0.004 ± 0.011, $P = 0.69$) and forest fragment size had little effect (-0.002 ± 0.002, $P = 0.40$). Although the top weighted model included forest fragment size ($w_i$ = 0.12; Table 2-5) there was little difference in $AIC_c$ with the second highest weighted model ($w_i$ = 0.10, ΔAIC = 0.41) which was the null model.

**Migration/wintering and annual survival.** Migration/winter apparent survival was low, as only 26% (31 out of 119) of birds that began fall migration returned the following spring. Forest fragment size had no effect (-0.002 ± 0.002, $P = 0.47$) and body condition of nestlings did not predict migration/wintering survival (0.140 ± 0.153, $P = 0.36$). Fall migration departure timing also did not predict migration/wintering survival (-0.009 ± 0.024, $P = 0.70$). Nestling body condition just before fledging was the top weighted parameter in the model set ($w_i = 0.46$) but 95% CI overlapped zero (-0.036, 0.495). None of the modelled parameters were strong predictors of Wood Thrush juvenile migration/wintering survival (Table 2-6), as models < 2 AICc included the null model ($w_i = 0.06$). Similarly, natal forest fragment size, nestling body condition and nestling fledge date were not found to be good predictors of annual survival (Table 2-6, Figure 2-5).

Across the annual cycle, from the time of fledging to returning the next spring to breed, estimated apparent annual survival was 16% (31 of 189) despite the high density of Motus towers in the region that could have detected returning juveniles (Table 2-6) and the searches conducted with aerial telemetry. Of the 31 individuals detected in spring by Motus and aerial telemetry, 6 were last detected outside of our study area ranging in distance from 28 to 110 km away (see Supplementary Material Table A2-8 for tower locations). Aerial surveys detected 9/30 (30%) of individuals that Motus had detected remotely in early spring plus 1 returning individual that had not been detected by Motus. The other first-year birds were not detected with aerial surveys within our study area and must have bred elsewhere.

## Discussion

This is one of the first studies for a forest migratory songbird to directly estimate apparent juvenile survival at three life stages (fledgling (first 16 days post-fledging), pre-migration (>16 days to onset of fall migration), and migration/wintering periods). This was possible using manual and automated radio-telemetry techniques along with technological advancements in radio-tags (small tags with >1-year battery life). We show for Wood Thrushes, a species in chronic decline across its North American breeding range (Sauer et al. 2019), that small natal forest fragments did not reduce fledgling, premigration, or annual juvenile survival and did not delay onset of fall migration. Estimating survival probability at different stages throughout the year is a first step to identifying where mortality risk is highest and how to mitigate this through conservation actions and planning. Survival probability was lowest during the 16-day fledgling periods on their natal territory (70%, or 0.86 weekly) and the 6-month migratory/wintering period (26%, or 0.95 weekly probability), and very high for juveniles during the 6-8 weeks prior to onset of fall migration (Figure 2-6).

### *Survival: From Egg to Independent Juvenile*

The daily nest survival estimate in this study (0.96 ± 0.002 SE) was similar to what others have found for Wood Thrushes in fragmented forests (0.95 to 0.96; Newell and Kostalos 2007; Etterson et al. 2014) and less than what has been documented in landscapes with very high forest cover (0.98; Schlossberg et al. 2018). Forest fragmentation effects on breeding songbirds can result in lower reproductive success due to increased nest predators (Hethcoat and Chalfoun 2015) and increased nest parasitism by Brown-headed Cowbirds (Etterson et al. 2014). In this study, however, forest fragment size was not a predictor of nest survival although the percent forest cover within 5 km of the nest and nest parasitism by Brown-headed Cowbirds had a weak negative effect. Friesen et al. (1999) conducted a study on Wood Thrushes in southern Ontario and found that nesting success was not lower in small fragments (3 to 14 ha) than larger fragments (26 to 140 ha). Etterson et al. (2014) conducted a study in Virginia USA and found that nest survival was lower in forest fragments compared with very large, contiguous (> 9000 ha) forest. The relationship between fragment size and nest survival is likely influenced by factors beyond the forest patch such as regional forest cover and configuration (Driscoll et al. 2010; Richmond et al. 2012) and land use matrix (e.g., agriculture, rural, or urban) (Phillips et al. 2005; Richmond et al. 2011). Our study region is set in a predominately agricultural land use matrix with an overall forest cover of only 21% and even the largest fragments (500 ha) did not provide a refuge from nest predators or cowbirds.

As with many fledgling survival studies on forest birds (Jenkins et al. 2016; Vernasco et al. 2018; Raybuck et al. 2019), we found that the first few days out of the nest are the most critical for fledgling survival. During this time, fledglings have no tail and only partially grown flight feathers and can flutter/hop short distances but cannot sustain powered flight which leaves them highly susceptible to predation (Naef-Daenzer and Grüebler 2016). Fledgling survival probability (0.70) was higher than for Hooded Warblers (0.51) and Rose-breasted Grosbeaks (0.62) studied in forest fragments in the same region (Moore et al. 2010; Eng et al. 2011). Natal fragment size did not predict fledgling survival, but nestling body condition (just before fledging) had a strong effect on fledgling survival, as has been found in other studies of songbirds (summarized in Cox et al. 2014; Evans et al. 2020). As the highest mortality occurs during the first few days out of the nest, birds in better body condition are likely to be better able to withstand adverse weather conditions (Jones et al. 2017) and have more developed flight capabilities and thus lower their risk of predation (Vitz and Rodewald 2011).

### *Survival: From Independent Juvenile to Breeding Adult*

Our results provide the first estimate of juvenile pre-migration survival (89 %) for a forest songbird. Only two other studies we know of have estimated pre-migration survival in juvenile migratory songbirds, and both were on swallows (Tarof et al. 2011; Evans et al. 2019) which are not comparable because they can fly well at the time of fledging and likely face a different predator community. Upon independence, juvenile forest songbirds typically leave the natal territory and make local dispersal movements through the landscape prior to migration, which may be a prospecting behavior to assess breeding sites/territories for the following spring (Nocera et al. 2006; Brown and Taylor 2015) or learning the landscape features for navigational purposes (Mitchell et al. 2010). Juvenile Wood Thrushes undertake repeated gap-crossing behaviors between forest patches to carry out this local dispersal, and thus could be exposed to higher predation risk. We found that 85% of independent juveniles were detected by Motus > 5 km from their natal site in the days and weeks prior to onset of fall migration (Hayes, unpublished data). Nevertheless, pre-migration survival was very high (89 %) in this severely fragmented landscape and natal fragment size was not an important predictor of premigration or annual survival. On average, ~52 days elapsed between fledgling independence and onset of fall migration, making the daily survival probability very high (DSR = ~0.998). This high survival rate pre-migration is surprising because juveniles are very inexperienced after the fledgling period and the landscape was highly fragmented requiring gap-crossing to disperse far. Adult Wood Thrushes routinely cross gaps during the breeding season, travelling several hundred meters between forest fragments (MacIntosh et al. 2011) and apparently naïve juveniles can do the same at low risk. Future studies could use intensive manual tracking to document the extent of natural gap-crossing behaviors in juveniles and conduct experimental translocation studies and release tagged juveniles into small fragments (e.g., Valente et al. 2019).

Few studies, and none for forest songbirds to our knowledge, have been able to track fledglings to determine their timing of fall migration months later because of limitations in radio-tag battery life and manual tracking of juveniles after they have dispersed far from their natal territory (Evans et al. 2019). In our study, early-fledged (before 15 June) individuals departed earlier on fall migration, on average by nine days, than late fledged individuals (late July/early August), but natal fragment size and sex did not predict fall migration departure (Figure 2-4). It is unknown whether early-fledged birds are better able to explore the landscape (e.g., prospecting for future breeding sites) or depart on migration in better condition than late-fledged birds. We found that fall migration departure time in juveniles does not predict migration/wintering apparent survival. For adult Wood Thrushes, fall migration timing did not predict arrival time at wintering sites due to prolonged migratory stopovers *en route* (Stutchbury et al. 2011) and it is possible that juveniles have a similar slow migration strategy. In Belize, juvenile Wood Thrushes were not in poorer body condition prior to spring migration compared to adults (McKinnon et al. 2014) suggesting that juveniles were not occupying poor quality habitat.

For both adults and juveniles, it is not known if fall migration timing influences mortality during migration itself, as opposed to after they arrive on the wintering grounds. There are many factors that affect migration survival however little is known as to where, or why, mortality happens during migration. For adult Black-throated Blue Warblers (*Setophaga caerulescens*), it has been estimated that most annual mortality (85%) happens during migration as opposed to the stationary breeding and wintering periods (Sillett and Holmes 2002) and this may also be true for independent juveniles given their inexperience with migration and stopover sites along the way. For instance, stopover habitat quality is highly variable in adult Wood Thrushes (Stanley et al. 2021) but it is not known if this affects migration survival. Very few studies have estimated juvenile survival at different life stages across the first full year of life for a songbird, as has been done for adult Black-throated Blue Warblers (Sillet and Holmes 2002) and Purple Martins (*Progne subis*) (Tarof et al.2011). Our study on Wood Thrushes estimates that after fledging 55% of all mortality in the first year occurs during the migration and wintering period (Figure 2-6). The latter result is consistent with estimates of high adult mortality during the migration period in other Neotropical migrants (Sillett and Holmes 2002; Klaassen et al. 2013).

Even with manual, aerial, and Motus telemetry methods, only 16% of birds monitored after fledging, and 26% of birds that started fall migration, were detected returning in spring. Several returning individuals were detected by Motus towers 110 km from their natal forest fragment, but many (29%) were detected with aerial telemetry within the study area and presumably breeding. It is impossible to know how many others survived without being detected by the Motus network in Ontario or elsewhere. However, a stable isotope study of Wood Thrush populations found that only 10-15% of recruits, or fewer, were long distance immigrants (> 100 km from natal site; Rushing et al. 2021).

Boyd et al. (2023) used Motus to estimate apparent annual adult Wood Thrush survival probability as 0.39, meaning that on average females must produce 0.39 female recruits per year for the population to be self-sustaining. Boyd et al. (2023) also quantified individual female Wood Thrush productivity in our study area using radiotelemetry (e.g., by finding all female's nests in each season) and estimated this to average 1.88 female fledglings per season. Since apparent annual survival of fledglings is 0.16 this would yield only 0.30 female returning recruits per year, suggesting forest fragments in this region are population sinks for this species (see also Moore et al. 2010; Eng et al. 2011). Our estimates of adult survival, female productivity, and fledgling/juvenile survival are consistent with the decline in Wood Thrush populations that has been documented in this region (Sauer et al. 2019; Heide et al. 2023). Our findings of high reproductive success and high fledgling and pre-migration juvenile survival, combined with low recent breeding habitat loss in this region (Heide et al. 2023), suggests that the drivers of population decline could be associated with threats experienced during juvenile migration and over-wintering survival.

We found no evidence of carry-over effects of small natal forest fragment size at any of the three life stages for juvenile Wood Thrush survival or on fall migration timing, and fragment size also had little effect on nest survival. Variables associated with the natal territory (e.g., nestling body condition, timing of fall migration, fragment size, regional forest cover) did not predict metrics of survival even though small forest fragments are generally considered to be poor quality habitat for nesting songbirds (Falk et al. 2011; Richmond et al. 2012). A parallel study on adult Wood Thrushes using the same radio-tag models and forest fragments found adult return rate to the study area was 39% (Boyd et al. 2023) and no effect of breeding forest fragment size on female body condition or apparent adult annual survival. Wood Thrushes appear to thrive in small forest fragments in this region and so these supposedly marginal habitats can play an important role in conservation of this declining migratory songbird. Wood Thrush are relatively tolerant to low regional forest cover and fragmentation (Torrenta et al. 2022) and so negative effects of small forest fragments on juveniles could be important for more area-sensitive species. Future studies on forest passerines could conduct a similar radio-tracking study in a landscape that includes large contiguous forest (assuming the Motus infrastructure exists) to determine if there is a threshold at which large forest area does benefit juvenile survival/migration timing.

**Table 2-1**. Top models (ΔAIC<2) for daily nest survival rate (DSR) models for Wood Thrushes across 29 forest fragments (11 to 500 ha) in southern Ontario, 2016-2018 (*n* = 404 nests). Additive and interactive models with nest age (NA), distance to forest edge (DistFE), nest parasitism (BHCO), forest fragment size (FS) and % forest cover (FC) at 5 km as predictor variables (see Supplementary Material Table A2-3 for full model set with additional spatial scales). Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with number of parameters (k), and model weight ($w_i$) given for each model. Model variable βeta coefficient estimates are given with 95% CI.

| Model | *k* | ΔAIC | $w_i$ | Variable | Estimate | SE | 95% CI |
|---|---|---|---|---|---|---|---|
| ~ NA + % FC 5 km | 3 | 0.00[a] | 0.17 | intercept | 4.524 | 0.443 | 3.656, 5.393 |
| | | | | NA | -0.058 | 0.011 | -0.080, -0.036 |
| | | | | % FC 5 km | -0.020 | 0.011 | -0.043, 0.002 |
| ~ NA + BHCO + % FC 5 km | 4 | 0.25 | 0.15 | intercept | 4.510 | 0.443 | 3.640, 5.379 |
| | | | | NA | -0.059 | 0.011 | -0.080, -0.037 |
| | | | | BHCO | -0.213 | 0.158 | -0.524, 0.097 |
| | | | | % FC 5 km | -0.018 | 0.011 | -0.041, 0.004 |
| ~ NA + BHCO | 3 | 0.90 | 0.11 | intercept | 3.839 | 0.133 | 3.579, 4.098 |
| | | | | NA | -0.059 | 0.011 | -0.081, -0.037 |
| | | | | BHCO | -0.249 | 0.158 | -0.557, 0.059 |
| ~ NA | 2 | 1.31 | 0.09 | intercept | 3.773 | 0.124 | 3.528, 4.016 |
| | | | | NA | -0.058 | 0.011 | -0.079, -0.037 |
| ~ NA + DistFE + % FC 5 km | 4 | 1.94 | 0.06 | intercept | 4.523 | 0.443 | 3.654, 5.392 |
| | | | | NA | -0.058 | 0.011 | -0.080, -0.036 |
| | | | | DistFE | 0.000 | 0.000 | -0.001, 0.001 |
| | | | | % FC 5 km | -0.021 | 0.011 | -0.044, 0.001 |
| ~ NA + FS + % FC 5 km | 4 | 2.00 | 0.06 | intercept | 4.525 | 0.443 | 3.657, 5.394 |
| | | | | NA | -0.059 | 0.011 | -0.080, -0.037 |
| | | | | FS | -0.000 | 0.001 | -0.001, 0.001 |
| | | | | % FC 5 km | -0.020 | 0.012 | -0.043, 0.003 |

[a] $AIC_c$ value = 1097.30

**Table 2-2**. Top weighted model set of time-dependent models for Wood Thrushes fledgling survival (*S*) across 29 forest fragments in southern Ontario over a 3-year period, 2016-2018 ($n$ = 189 fledglings). For all models $p$ (probability of detecting a live fledgling) was modelled as *p(age3 +Year)*. Survival models included calendar year (Year), linearly changes with fledgling age (Age), non-linearly changes with fledgling age ($Age^2$), time dependent (Time), fledge date, and 3 age categories of 2 (age2 - 0-8d, 9-16d), 3 (age3 - 0-8d, 9-12d, 13-16d), and 4 (age4 - 0-4d, 5-8d, 9-12d, 13-16d) age groupings. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with number of parameters ($k$), and model weight ($w_i$) given for each model. The full model set is shown in Supplementary Material Table A2-5.

| Model | $k$ | ΔAIC | $w_i$ |
|---|---|---|---|
| ~ Age | 8 | [a] 0.00 | 0.26 |
| ~ Age + fledge date | 9 | 2.00 | 0.10 |
| ~ age3 | 9 | 2.03 | 0.10 |
| ~ $Age^2$ | 9 | 2.05 | 0.09 |
| ~ age2 | 8 | 2.52 | 0.07 |
| ~ age4 | 10 | 2.90 | 0.06 |
| ~ Age + year | 10 | 2.96 | 0.06 |
| ~ age3 + fledge date | 10 | 4.04 | 0.04 |

[a] AICc = 913.25

**Table 2-3.** Environmental models for Wood Thrushes fledgling survival across 29 forest fragments in southern Ontario over, 2016-2018 (*n* = 189 fledglings). Survival models used the base temporal model with nestling body condition (BC) included (*S (Age) p(age3+ Year*) and additional covariates of forest fragment size (FS), % forest cover (FC) at 3 spatial scales. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with number of parameters (*k*), and model weight ($w_i$) given for each model. The full model set is shown in Supplementary Material Table A2-6.

| Model | *k* | ΔAIC | $w_i$ |
|---|---|---|---|
| ~ Age + BC | 8 | [a] 0.00 | 0.20 |
| ~ Age + % FC 2 km + BC | 9 | 1.38 | 0.10 |
| ~ Age | 7 | 1.58 | 0.09 |
| ~ Age + % FC 500 m + BC | 9 | 1.95 | 0.07 |
| ~ Age + % FC 5 km + BC | 9 | 2.07 | 0.07 |
| ~ Age+ % FC 2 km | 8 | 2.90 | 0.05 |
| ~ Age + % SC | 8 | 3.17 | 0.04 |
| ~ Age + FS | 8 | 3.37 | 0.04 |
| ~ Age + % FC 2 km * BC | 10 | 3.43 | 0.04 |
| ~ Age + % FC 500 m | 8 | 3.53 | 0.03 |

[a] AICc = 899.29

**Table 2-4.** General linear models for fall departure dates of juvenile Wood Thrushes across 29 forest fragments in southern Ontario over, 2016-2018 (*n* = 82 fledglings). Predictor variables included fledge date (FD), natal forest fragment size (FS), body condition at fledging (BC), sex, and year as additive variables. Models are ranked by Akaike's information criterion for small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model weight ($w_i$) given for each model.

| Model | df | LL | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| ~ FD + sex + year | 6 | -261.24 | [a] 0.00 | 0.23 |
| ~ FD + FS + sex + year | 7 | -260.27 | 0.47 | 0.18 |
| ~ FD + year | 5 | -262.76 | 0.72 | 0.16 |
| ~ FD + BC + sex + year | 7 | -260.72 | 1.36 | 0.12 |
| ~ FD + FS + BC + sex + year | 8 | -259.59 | 1.57 | 0.10 |
| ~FD + BC + year | 6 | -262.42 | 2.37 | 0.07 |
| ~FD + FS + year | 6 | -262.51 | 2.54 | 0.06 |

[a] AICc = 535.6

**Table 2-5**. General linear models for pre-migration survival (16d to fall migration departure) of juvenile Wood Thrushes across 29 forest fragments in southern Ontario over, 2016-2018 (*n* = 133 fledglings). Additive models for survival were run with forest fragment size (FS), nestling body condition (BC), fledge date (FD), sex, and year as predictor variables. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with number of parameters (df), log likelihood (LL), and model weight ($w_i$) given for each model.

| Model | df | LL | ΔAIC | $w_i$ |
|---|---|---|---|---|
| ~ FS | 2 | -43.52 | [a] 0.00 | 0.12 |
| ~1 | 1 | -44.75 | 0.41 | 0.10 |
| ~ FS + FD | 3 | -42.97 | 0.99 | 0.08 |
| ~ FD | 2 | -44.04 | 1.04 | 0.07 |
| ~ FS + BC | 3 | -43.00 | 1.06 | 0.06 |
| ~ BC | 2 | -44.34 | 1.64 | 0.05 |
| ~ FS + Sex | 3 | -43.31 | 1.67 | 0.04 |
| ~ Sex | 2 | -44.70 | 2.36 | 0.04 |

[a] AICc = 91.1

**Table 2-6.** General linear models for apparent migration/wintering survival (period after fall departure and spring arrival, *n* = 82) and annual survival (period from fledging the nest to spring return, *n* = 189 fledglings) of juvenile Wood Thrushes across 29 forest fragments in southern Ontario over, 2016-2018. Models for survival were run with forest fragment size (FS), body condition (BC), fledge date (FD) (for annual survival only), departure date (DD) (migration/wintering survival only), sex, and year as predictor variables. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with number of parameters (df), log likelihood (LL), and model weight ($w_i$) given for each model.

| Migration/Over-winter Survival | Model | df | LL | ΔAIC | $w_i$ |
|---|---|---|---|---|---|
| | ~ FS + BC | 3 | -45.97 | [a] 0.00 | 0.10 |
| | ~ BC | 2 | -47.07 | 0.04 | 0.10 |
| | ~ BC + Sex | 3 | -46.29 | 0.64 | 0.07 |
| | ~ 1 | 1 | -48.66 | 1.12 | 0.06 |
| | ~ FS | 2 | -47.63 | 1.16 | 0.06 |
| | ~ FS + BC + Year | 5 | -44.36 | 1.26 | 0.05 |
| | ~ FS + BC + Sex | 4 | -45.58 | 1.44 | 0.05 |
| | ~ FS + BC + DD | 4 | -45.60 | 1.47 | 0.05 |
| | ~ BC + DD | 3 | -46.77 | 1.60 | 0.04 |
| | ~ FS + Year | 4 | -45.68 | 1.64 | 0.04 |
| Annual Survival | ~ FS + BC | 3 | -81.94 | [aa] 0.00 | 0.11 |
| | ~ BC | 2 | -83.01 | 0.07 | 0.11 |
| | ~ FS | 2 | -83.31 | 0.68 | 0.08 |
| | ~ 1 | 1 | -84.35 | 0.71 | 0.08 |
| | ~ FS + FD + BC | 4 | -81.55 | 1.30 | 0.06 |
| | ~ FS + FD | 3 | -82.63 | 1.38 | 0.06 |
| | ~ FD + BC | 3 | -82.70 | 1.51 | 0.05 |
| | ~ FD | 2 | -82.87 | 1.62 | 0.05 |
| | ~ FS + BC + Sex | 4 | -81.86 | 1.92 | 0.04 |

[a] AICc = 98.2

[aa] AICc = 170.0

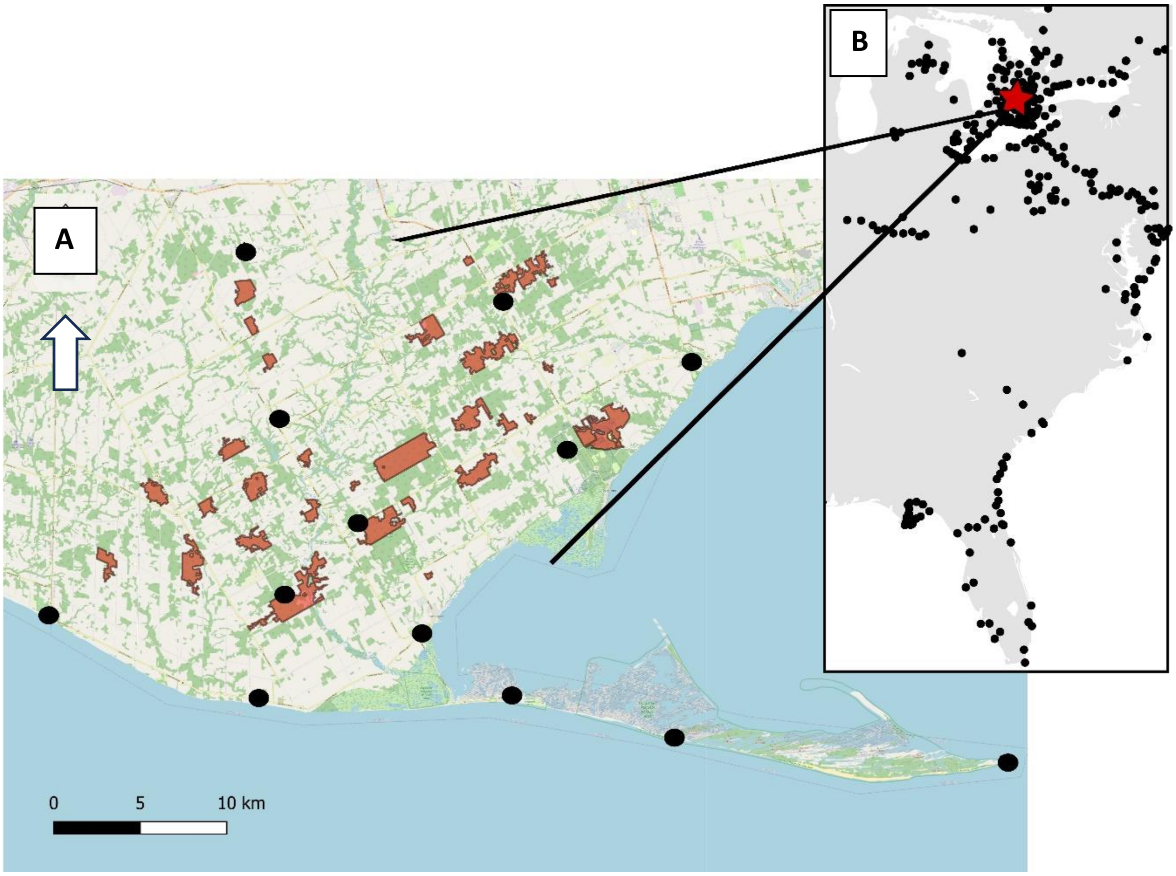

**Figure 2-1**. (**A**) Map of study sites in Norfolk County on the north shore of Lake Erie, near Port Rowan Ontario (42.7131°N, 80.5372ºW). Twenty-nine study sites (red-filled polygons) ranging from 11 ha to 500 ha were used over the course of the three field seasons (2016, 2017 and 2018). Local Motus tower network shown with filled circles, (**B**) Inset map showing study area in the broader context of eastern North America with black dots representing active Motus Wildlife Network towers in 2018.

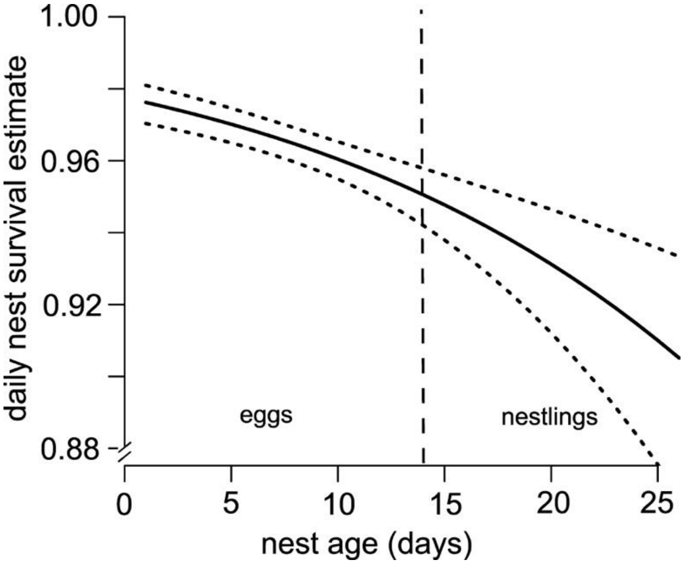

**Figure 2-2.** Nest age (calculated as 1st egg laid = day 0 on a 26-day cycle) model for daily nest survival for Wood Thrush across 29 forest fragments in southern Ontario. Dotted lines indicate 95% CIs and the vertical dashed line at day 14 represents the approximate date of eggs hatching. Daily survival probability decreased with increasing nest age but was not predicted by natal fragment size (Table 2-1).

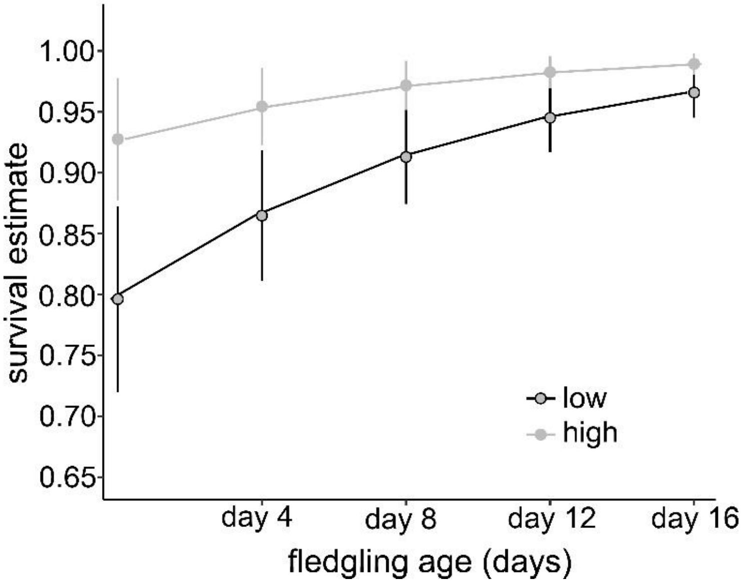

**Figure 2-3.** Predicted fledgling survival estimate (to 16d) for low (29) and high (44) levels of body condition prior to fledging with SE. Fledgling survival was predicted by nestling body condition but not by natal fragment size (Table 2-3).

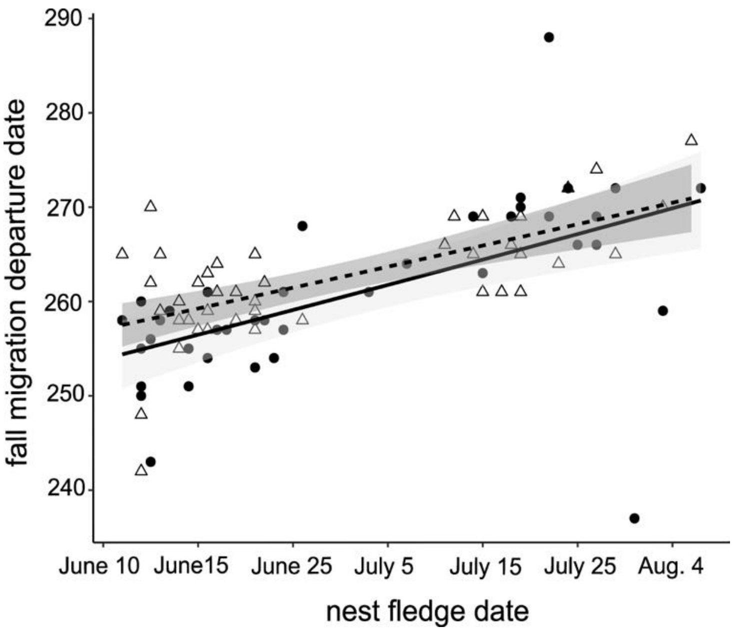

**Figure 2-4.** Relationship between autumn migration departure dates as detected by Motus automated telemetry and nest fledge dates for 82 (2016 *n* = 11, 2017 *n* = 29, 2018 *n* = 42) juvenile Wood Thrushes. Males represented with open triangles with dashed trend line and females with filled circles and solid trend line. Shading around trend lines representing 95% CIs. Departure date was strongly predicted by fledge date but not by natal fragment size (Table 2-4).

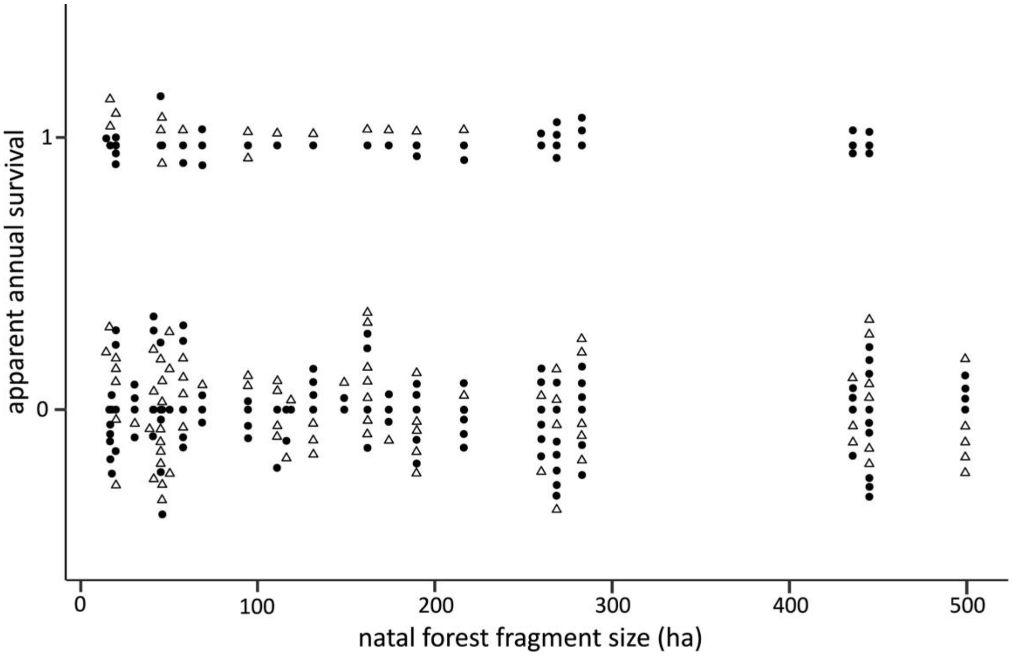

**Figure 2-5.** Scatterplot of apparent annual survival for juvenile Wood Thrushes in relation to natal fragment size (*n* = 189). On Y- axis "1" = survived, "0" = not detected. Females are represented with filled circles, males with open triangles. Points are jittered around the Y- axis for clarity. Natal fragment size did not predict apparent annual survival of juveniles (Table 2-6).

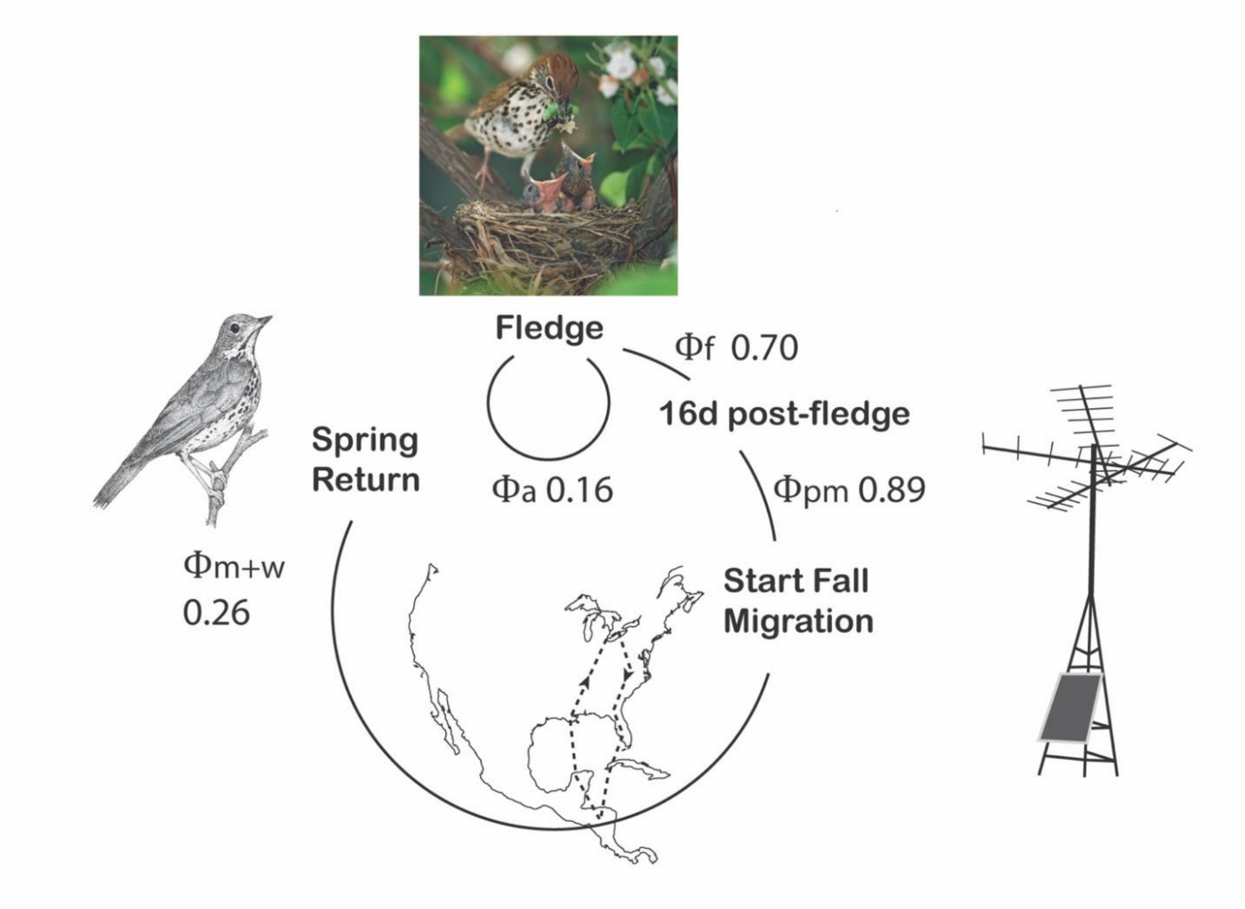

**Figure 2-6.** Apparent annual survival for 3-life stages during the first year of life of Wood Thrushes. Fledgling survival (to 16d) probability was 0.70 as determined by both manual and automated radio telemetry detections. Pre-migration (0.89), migration/wintering (0.26), and annual survival (0.16) determined using Motus automated telemetry towers (see Supplementary Material S2-9 for sample sizes at each life stage). Typical migration route of adults tracked with geolocators shown on map with dashed lines (Stanley et al. 2015). Wood Thrush drawing by Roger Hall.

# Chapter 3: Why do juvenile Wood Thrushes make long distance pre-migratory movements across a fragmented landscape?

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## Abstract

The pre-migratory period for naïve juvenile migratory songbirds is a critical stage in development as they disperse from their natal territories and prepare for their inaugural fall migration. Little is known about this period due to the difficulty in tracking individuals once they make longer dispersal movements outside the range of manual radio-tracking methods. We used the Motus Wildlife Tracking System combined with long life (~400 days) radio-tags to track juvenile Wood Thrushes from the nest up to fall migration departure, and their return the following spring. We found that 78% of juveniles made long-distance (>5 km) pre-migratory movements (PMM) at night, mainly 2 hours before sunrise, and random in orientation. We found no support for habitat optimization because adults rarely made PMM and juveniles from small forest fragments did not disperse at an earlier age or make more extensive PMM. Prospecting for future breeding territories seems unlikely because PMM occurred primarily in the two weeks prior to onset of fall migration, when social cues of territory quality are less available, and juveniles that returned in spring did not breed closer to their previous fall locations than to their natal site. Extent of PMM also did not predict flight performance (departure date, pace, orientation) as birds crossed a large water barrier on their first migration movement. Our results best support the homing target hypotheses because a large proportion (81%) of juveniles that returned the next spring were detected in the study area rather than elsewhere. The high frequency of long distance PMM in Wood Thrushes, despite the fragmented landscape, suggests that such movements could also be common in other migratory songbirds.

## Introduction

The autumn pre-migration period for juvenile migratory birds is a critical time in their development as they have become independent of their parents and may disperse from their natal territory prior to fall migration (Mitchell et al. 2010). During this pre-migration stage, naïve but independent juveniles must find adequate food not only for daily survival, but also to support a preformative feather molt and fattening in preparation for autumn migration (Mitchell et al. 2010) while being alert for predators (Anders et al. 1998, Kershner et al. 2004). Juveniles could remain in, or near, their parent's breeding territory until migration or disperse unknown distances to explore the surrounding habitat. However, little is known about pre-migration behavior of juvenile migratory songbirds despite this stage potentially being very important to survival, fall migration timing, breeding habitat selection and future reproductive success (Patchett et al. 2022). This gap in knowledge is due to the difficulty in radio-tracking individual juveniles after they leave the natal territory (Vitz and Rodewald 2011, Cox and Kesler 2012) and move out of range of manual detection.

Several studies on migratory songbirds have used a combination of manual and/or aerial radio-tracking to measure age at dispersal from the natal territory and have found much variation within and among species. For instance, Vitz and Rodewald (2011) found that most (62%) Ovenbird (*Seiurus aurocapilla*) juveniles dispersed from their natal territory and did so at an average of 29 days post-fledging while few (18%) Worm-eating Warbler (*Helmitheros vermivorum*) juveniles dispersed and did so at younger age (22 days) post-fledging. The dispersal sites for both warbler species averaged about 1.2 km from the nest site. In Wood Thrushes (*Hylocichla mustelina*), 91% of fledglings that survived to independence dispersed from their natal territory and did so an average of 32 days post-fledging, to sites about 1.5 km away (Vega

Rivera et al. 1998). It is unclear from these studies to what extent juveniles move over larger distances prior to fall migration (because such movements would be difficult to detect), and what the benefits of such movements could be.

The costs and benefits of pre-migration movements of juveniles are not well understood. Juvenile birds have no knowledge of the surrounding landscape until they begin to disperse from their parents' breeding territory (Brown and Taylor 2015). Venturing out into new areas may place higher energy demands on young birds (Weathers & Sullivan 1989) and expose them to a higher risk of predation (Yoder et al. 2004). In highly fragmented landscapes, crossing open gaps between fragments could increase predation risk, in which case dispersal may be constrained by the connectivity of the remaining forest patches and the surrounding land use (Bélisle et al. 2001, Ricketts 2001, Vitz and Rodewald 2010). But there are likely short-term and long-term benefits that can be gained from pre-migration dispersal movements by juveniles (Anders et al. 1997) and many hypotheses for the adaptive function of pre-migration movements have been proposed (Mitchell et al. 2010). Dispersal movements into habitat with an abundance of food and shelter from predators (habitat optimization hypothesis; Anders et al. 1997, Kershner et al. 2004) may increase body condition through increased energy stores and flight muscle thereby increasing chances of survival during migration (Mitchell et al. 2011). By exploring the regional landscape, juveniles may be scouting for future high quality breeding territories which could place them at a competitive advantage the following spring (territory selection hypothesis; Nocera et al. 2006, Mitchell et al. 2010, Samplonius and Both 2017, Patchett et al. 2022). Juveniles may make pre-migratory movements near the natal region to form a navigational target that will help them re-locate this region when they return in spring (homing target hypothesis; Mitchell et al. 2010). Finally, Mukhin et al. (2005) suggested that nocturnal pre-migratory flights from the natal site function to develop a stellar compass in naïve birds which is critical for navigation during nocturnal migration in songbirds.

A new technology that can be used for monitoring movements of juveniles over large distances is the Motus Wildlife Tracking System (Taylor et al. 2017) combined with the miniaturization of radio-tags. Motus has allowed researchers to remotely track wildlife movements over local, regional, and continental spatial scales via a huge network of receiver towers. Although much of the avian research to date using this system has been on adult bird migration, Motus also provides a new opportunity to study long distance pre-migration movements in juveniles. A groundbreaking study conducted by Brown and Taylor (2015) used a Motus telemetry array to document pre-migration dispersal movements of independent juveniles and adult Blackpoll Warblers (*Setophaga striata*) captured in late summer at a breeding site on an island in the eastern Gulf of Maine. The adults immediately crossed the Gulf of Maine and moved southwest along the New England coastline in a direction consistent with preparation for a cross-Atlantic long distance fall migration. The juveniles however, made long distance pre-migration movements in more random directions resulting in an average net displacement of 91 km from the breeding site. Brown and Taylor (2015) suggest juvenile warblers may have been prospecting for future breeding territories or learning landscape features for navigational purposes. Evans et al. (2019) used Motus in southwestern Ontario to show that Barn Swallows tagged as nestlings dispersed an average of 118 km from their natal colony prior to onset of fall migration. Generally, the extent to which juvenile migratory songbirds disperse prior to fall migration is not known.

To test for the occurrence and possible benefits of long distance pre-migratory movements in juveniles, we equipped nestling Wood Thrushes with radio-tags that had a 1-year battery life. Our study area, Norfolk County Ontario, had a high density of Motus towers that could detect regional movements as well as onset of fall migration and spring return. Motus tower detections of forest-dwelling birds mainly occur once a radio-tagged bird comes out of the forest and flies across an open area (Crewe et al. 2019) or flies above the forest canopy. Motus is designed to detect landscape level movements and unlike manual or aerial tracking it does not allow one to determine the actual location of a bird (i.e., whether it is at versus near its natal fragment). The first objective of this study was to test whether aspects of the nestling environment predict juvenile Wood Thrush long distance pre-migratory movement. We determined the proportion of juveniles that were detected at Motus towers long distances (> 5 km) from the natal site prior to fall migration and tested if fledge date, sex, or natal fragment size predicted age at dispersal. We also tested whether these variables were significant predictors for each of three measures of extent of premigration movement: 1) duration of premigration dispersal period > 5 km from natal fragment, 2) number of different Motus towers at which detections > 5 km occurred, and 3) the furthest distance detection (e.g., net displacement) from the natal forest prior to onset of migration.

Our second objective was to test hypotheses for the function of pre-migratory movements. The habitat optimization hypothesis predicts that adults and juveniles will have similar pre-migration movements (Brown and Taylor 2015) and that juveniles from small forest fragments (assumed to be lower quality habitat) will have earlier and/or greater pre-migration movements. The territory-selection hypothesis predicts that males (who are territorial) should have more extensive movements than females (Patchett et al. 2022), the landscape movements should be nearly randomly oriented relative to the natal site (Mitchell et al. 2010), and juveniles should exhibit far more extensive movements than adults (Brown and Taylor 2015). If juveniles are successfully locating future breeding sites, then we predicted that the distance between the last fall detection and the subsequent breeding site should be significantly less than the distance between the natal site and the breeding site (Patchett et al. 2022). The homing target hypothesis predicts that a high proportion of juveniles will return to the region and that their pre-migratory movements should be random in direction and more frequent than those of adults.

Our third objective of this study was to test, for the first time, a hypothesis that proposes that extent of pre-migratory movement improves first migration flight performance. Pre-migratory landscape movements could provide juveniles with experience that improves performance during their first migratory flight, especially if movements are nocturnal (e.g., through development of the stellar compass; Mukhin et al. 2005). Individuals that have dispersed far from their natal fragment and/or have made more frequent landscape movements may depart on fall migration earlier, travel at a faster pace on their first flight, or be more likely to fly south across the large (50 km) water barrier of Lake Erie that lies immediately south of our study site.

## Methods

### *Study area*

This study took place from 2016 to 2019 in forest fragments in Norfolk County on the north shore of Lake Erie in Ontario Canada. Study sites (*n* = 29 fragments) were selected to represent a gradient of forest size, ranging from 11 to 500 ha (median = 111.2 ha) (Figure 2-1A). Study sites were on both public (Nature Conservancy of Canada; Ministry of Northern Development, Mines, Natural Resources and Forestry; Long Point Conservation Authority) and privately-owned lands. The percent forest cover of the Long Point Conservation Authority jurisdiction in which Norfolk County is part of, was 21% with predominant land uses being crop agriculture (Long Point

Region Conservation Authority, 2019). This region was chosen because of the high-density coverage of the Motus automated telemetry system (Figure 2-1B).

### *Nest monitoring and radio-tagging*

Beginning mid-May of each year forest fragments were searched for Wood Thrush nests by locating singing males on territories and subsequently observing nests or nesting behavior. Nest contents were checked every 4 to 6 days using a pole with an attached cellphone set to video mode. Egg incubation lasted ~14 days and nestlings fledged ~26 days after the first egg was laid (Donovan et al. 1995).

Typically, multiple nests were located and monitored at each site over the breeding season but only two nests per site were selected for radio-tagging nestlings (tagging date ranged from 7 June to 17 August). On day 10 after hatching, nestlings were banded with uniquely numbered aluminum bands (US Fish and Wildlife / Canadian Wildlife Service), and a unique color band combination and mass, tarsus length, and wing chord measurements were taken.

The largest nestling (by mass) in the nest had a blood sample (25 uL) taken for genetic sexing (HealthGene Corporation) and was equipped with a uniquely coded radio transmitter (Lotek NTQB-6, 1.5-1.7g; ~ 1 yr. battery life; 12.7 sec. burst rate) using a figure-eight leg loop harness (Rappole and Tipton 1991) made of 2.5 mm Teflon tubing. Three slightly different tag models were deployed due to manufacturing limitations throughout the three-year study; however, tags remained ~ 5% of the total body weight of the 10-day old nestling tubing (total weight of tag and harness was 1.7-1.9g). Only one nestling was tagged at 131 of the 160 nests (82%) however, 2 nestlings were tagged at 29 (18%) nests. Of the 189 tagged nestlings (2016 *n* = 47, 2017 *n* = 66, 2018 *n* = 76) there was an even sex ratio of males to females (95:94).

### *Remote and aerial radio-tracking*

Remote tracking using the tower array of the Motus Wildlife Tracking System (Taylor et al. 2017) allowed us to detect tagged juveniles during the pre-migration period, during migration departure, and upon their return the following spring. The high density of automated towers within our study area, and surrounding regions in all directions (Figure 2-1A-B) allowed for possible detection of juveniles that survived migration but did not return to their natal site. Each tag detection recorded the unique tag number for the individual bird, signal strength for each antenna, along with the date and time for each detection.

Aerial telemetry was conducted to independently locate juveniles that returned to the general study area each spring as a supplement to Motus automated detection and to locate breeding sites. Approximately 5 hours was spent each year (18 July 2017, 2 June 2018, and 15 May 2019) following a grid pattern from north to south across the study area (extending ~20 km from the outside edge of the furthest forest fragment site). When a detection was made the search pattern was a series of smaller circles to pinpoint the bird's location and record a GPS point.

### *Motus data filtering*

Motus tower data records were accessed using the Motus R package and cleaned following guidelines provided in the Motus R Book (Crewe et al. 2020). The Motus filter was applied to flag detections that had a run length < 3 to minimize false positive records but on occasion were incorporated when there were additional supporting detections such as filling a time gap between towers with positive detections (3 instances). Subsequently, we manually reviewed all detections (individual hits received by each tower) that the Motus filter had flagged as true positives and removed any that had pulse rates that differed from 12.7 sec, occurred in unlikely locations (e.g., outside the breeding range), or were well outside of migration routes that have been identified for Wood Thrushes in previous geolocator studies (Stutchbury et al. 2009). For each tagged juvenile, detections were ordered by date, time of day, and each Motus tower, providing a full chronological profile of movement activity after the bird was no longer detected using manual radio telemetry at its natal territory natal site. There was a total of 788,565 individual detections made by Motus towers during pre-migration, fall, and spring periods with false detections making approximately 21% of the total.

### *Classification of pre-migratory versus migration departure detections*

Prior to the onset of migration, radio-tagged independent juveniles that had survived the fledgling period were detected by Motus towers in the study area. To classify local detections as pre-migratory movements versus a migration departure movement, we defined which Motus towers were within the study area because these could potentially detect both pre-migration local movements and fall migration departure from the study area. The Euclidean distance from each candidate tower to the nearest forest fragment was calculated in ArcGIS (version 10.8.1) and assumed that the maximum distance that a tagged bird could be detected once in the air flying outside of the forest would be 12 to 15 km (Taylor et al. 2017). We included 13 towers as falling within the study area, and these had a maximum distance of 12.5 km from the outside perimeter of the nearest forest fragment in the study area. Movements detected outside of the study area but were subsequently detected back into the study area during the pre-migratory period (i.e., before the migratory departure date) were classed as pre-migratory.

To distinguish pre-migratory from migration departure flights, we first analyzed the time of day of departure for juveniles undergoing their very first long-distance migratory flight. The location of the study area is on the north shore of Lake Erie so when a bird flew in a southerly direction overnight across the lake (~50 km) we assumed that this must represent the onset of fall migration. There were 25 tagged juveniles that were last detected by a tower within the study area and subsequently detected on the same night at a tower on the south side of Lake Erie along the lakeshore, and within a reasonable time frame (birds flying at ~50 km/hr.). We determined the average departure date and time of day of these 25 unambiguous first migratory flights. We used R package *circular* (Agostinelli and Lund 2018) to analyze if the time of migratory flight departure was non-random, as would be expected for true migratory flights which typically occur just after sunset. As expected, the time of day of these migratory movements was non-random ($\bar{R}$= 0.713, $P < 0.001$; Supplementary Material Figure B3-1A) and on average within 1 hr. and 10 mins. of local sunset (sunset on average departure date was 19:32). A directional bearing was calculated for each first migration flight measured from the individual's last Motus tower detection within the study area to the next Motus tower on the south side of Lake Erie. Migratory directional movements would be expected to be southerly which was the case ($\bar{R}$= 0.925, $P <$ 0.001; Supplementary Material Figure B3-1B). Using the range of departure dates and times of day of departure for these 25 individuals, we subsequently assigned departure dates for an additional 57 individuals whose departure dates and times of day fell within the range of the unambiguous departures (mean departure date Sept. 19, range: Aug. 25 to Oct. 15; mean departure time 20:48, range: 18:26 to 22:47; Supplementary Material Figure B3-1A-B).

Local detections away from the natal fragment that were not migration departure flights were tentatively classified as pre-migratory movements ($n$ = 425 movement detections from Motus towers of 93 individuals). To confirm that such pre-migratory movements were not migration departures, we analyzed the date and time of day to test whether they differ from known migratory flights. Most pre-migratory movements were nocturnal, but unlike migration departure flights they occurred before sunrise ($\overline{R}$= 0.383, $p < 0.001$, Supplementary Material Figure B3-1C) rather than near sunset. Pre-migratory movements also did not have an orientation bias in any cardinal direction ($\overline{R}$= 0.108, $p = 0.46$, Supplementary Material Figure B3-1D), unlike the southerly movements associated with migration flights. Thus, we assumed that these movements within the study area were pre-migratory in nature.

Motus towers cannot pinpoint the location of a bird (or the distance from the bird to the tower) and so smaller distance movements (e.g., ~ 1 km) near the natal fragment cannot be distinguished from birds that have not dispersed from the natal fragment. The detection range of Motus towers is low (~ 500 m) for radio-tagged songbirds within forest habitat (Crewe et al. 2019) but is far greater (~10 km or more) for birds that are flying in the open. The estimated antennae range varies widely among towers due to differences in tower height, antennae type and orientation, and these are shown on the Motus Wildlife Tracking System interactive mapping (https://motus.org/data/receiversMap). There were Motus towers located < 5 km from the natal site that were oriented away from the site but detected juveniles during the pre-migration period. These were included in this analysis as it was assumed that the tagged bird had to move out of the natal forest and into an area that was within range of that tower. There were 4 instances where this occurred, and the birds were added to the analysis and described as birds making > 5 km dispersal movements (i.e., included in $n = 93$).

### *Predictors of pre-migratory movements by juveniles*

For each individual ($n = 93$), age at which long distance pre-migratory movements were first detected, was calculated as the days elapsed between fledge date and the first Motus tower detection > 5 km away from the natal site. We used three different measures of the extent to which individuals moved through the local landscape prior to departing on migration. The first was the duration of this pre-migratory movement period, calculated from the date of the first detection > 5km away from the natal site to the last detection prior to the night of departure on fall migration. The time elapsed between the last pre-migratory movement and the initial migratory movement was on average 3 days (range 1 to 11 days). The second measure was the number of different Motus towers where pre-migratory movement detections occurred, regardless of how far apart the towers were. The third was the straight-line distance from the natal site to the furthest tower where a pre-migratory detection occurred.

There were 26 additional individuals that survived the fledging period but were not detected at towers > 5km away from the natal site during the pre-migratory period. Our goal was to use Motus to identify individuals that had left their natal fragment and, in most cases, where birds were detected only <5km from their natal site we could not be sure they had dispersed, and so these were excluded from further analysis. Even so, there was wide variation among individuals in extent of pre-migratory movements (duration ranged from 1 day to 68 days; # of towers detected from 1 to 11, and net displacement 5 to 85 km) and a large sample size (*n* = 93).

### *Pace, direction, and distance of first migratory flight of juveniles*

There were 20 birds with both known first migration flights (e.g., detected on same night on north and south side of Lake Erie) and who had been detected making pre-migratory movements. Since songbirds cannot land on water, the time elapsed between detections likely reflects estimates of actual ground speed. Motus tower detections provide data for a tagged bird as flying linearly as they are detected in succession by individual towers, and their actual flight path is unknown. Further, as each Motus tower has a different detection range and antenna orientation, there is uncertainty to calculating ground speed of a flying bird. To reduce this error in calculating the pace of migration we used the time of peak signal for each consecutive Motus tower detection to estimate the amount of time passed between detections (Bégin-Marchand et al. 2021). We used the straight-line distance between tower detections and divided this by the total time passed. Direction of flight used the bearing from the last Motus tower detection on the north side of Lake Erie to the first tower detection on the south side of the lake. The minimum distance between these two tower locations were used as the distance travelled during the first flight.

### *Analytical methods*

Generalized linear models in the stats package (R Core Team 2020) were used for all three measures of premigration movement with gamma distribution and link (log) for models for age of dispersal and furthest detection distance. Models for duration of detections and # of towers were modelled using a Poisson distribution. First migratory flight GLMs were fitted with gamma distribution and link (log) to determine if the pre-migratory movement measures could predict the timing of departure, pace, direction, and distance travelled during the first fall migratory flight. Fledge date, sex, and year were also included in the model sets.

We used dredge from the *MuMIn* package (Bartoń 2020) to run all combinations of additive models. All models with <2 ΔAICc were retained as competing models (Burnham and Anderson 2002) and model average coefficient estimates (full average), adjusted standard error, 95% confidence intervals, and *P* values are reported. No model averaging was conducted when only one model was <2 ΔAICc but model estimates are reported. Model residuals were checked using the *DHARMa* package (Hartig 2022) and variation inflation factors were checked for all parameters using the *car* package. All continuous predictor variables were scaled and centered.

## Results

Most juvenile Wood Thrushes (93 of 119; 78.2%) were detected making long distance (> 5km) pre-migration movements, and the duration of this pre-migration period ranged widely among individuals (mean = 12, SD ± 14, range = 1 to 68 days). Using the same methods to define pre-migration movements for a parallel study using Motus tracking of adult Wood Thrushes in the same study sites and years (Boyd et al. 2023) we found that only 5 of 60 (8.3%) adults exhibited pre-migration movements and that these movements occurred over a 1–3-day duration immediately prior to individuals beginning fall migration.

### *Predictors of age at first dispersal and extent of pre-migration dispersal movements*

A low proportion of juveniles (26 of 119; 21.8%) were never detected > 5km away from their natal fragment prior to onset of migration, and these were excluded from subsequent analyses. These individuals were from a wide range of forest fragment sizes that averaged 191.8 ± 155.1 ha), were an even split of female to males (14:12) and were on average later fledged birds (mean = July 12 ± 20.5 days).

Detections of first dispersal movements usually occurred at night (84 of 93; 90%) with 48% occurring during the period 2 hours before sunrise (Figure 3-1A). Age of dispersal from the natal fragment was highly variable even for birds fledged at a similar time of year. For instance, birds that fledged in June were first detected > 5 km from the natal site ranging from 24 days to 93 days post-fledging. Nevertheless, fledge date was a strong predictor of age at first long distance detection from the natal woodlot because birds that fledged late in the season generally were first detected at a younger age (model estimate ± SE = -0.174 ± 0.030, *P* <0.001; Table 3-1, Figure 3-1B). Those that fledged in June, on average were 20 days older when first detected > 5km from their natal woodlot than individuals that fledged in July or August. Sex was not a significant predictor of age at dispersal (0.019±0.043, *P* = 0.66), nor was natal forest fragment size (0.004±0.016, *P* = 0.79; Table 3-1, Supplementary Material Table B3-1).

The duration of the period of pre-migratory movements of juveniles, measured from first dispersal detection to last detection prior to fall migration departure, averaged 12 days (SD±14) but was highly variable (range = 1 to 68 days). Juveniles that fledged from the nest earlier in the season or were first detected > 5km away from their natal forest fragment at a younger age had a longer pre-migration dispersal period (Table 3-2; Figure 3-2 A-B). Sex was a significant predictor of pre-migration dispersal duration with males having about a 1-week longer dispersal period than females (Table 3-2; Figure 3-2A, Supplementary Material Table B3-2).

Individuals were detected at up to 11 different towers (mean = 4, SD ± 0.27, range = 1 to 11) as they moved around in the landscape prior to onset of migration. Fledge date was not significant, but juveniles that first dispersed at an older age were detected by more towers (0.148 ± 0.064, *P* = 0.02, Table 3-3) suggesting that these birds were more active in exploring the regional landscape. Sex (-0.009 ± 0.050, *P* = 0.85) and natal fragment size (0.021 ± 0.042, *P* =0.62), were not good predictors of this measure of pre-migratory movement (Table 3-3; Supplementary Material Table B3-3 and Figure B3-2).

On average the maximum distance detected away from the natal site (e.g., net displacement) was 21.8 km (SD ± 1.25) with 21 of 93 (26%) individuals detected greater than 30 km away. One individual was detected 85 km west of the natal site but returned to the study area prior to onset of fall migration. Natal forest fragment size was not a significant predictor of maximum distance detected from the natal site (0.050 ± 0.057, $P = 0.38$; Table 3-4; Supplementary Material Table B3-4 and Figure B3-3) nor was age at first dispersal (0.015 ± 0.039, $P = 0.71$).

### *Are juveniles that return in spring detected in the same region as their pre-migratory movements?*

Of the 31 juveniles that survived to return in the spring, 25 (80.6%) were detected within the study area even though the Motus tower network has the potential to detect birds over a large area in southern Ontario (Figure 2-1). One was detected through aerial tracking 7 km from the natal site, and 24 were detected at Motus towers that were within ~12 km on average (SD ± 24.5) of their natal nest site. The other 6 individuals were detected in the spring only outside of the study area (average 61.9 ± 28.0 km from natal site).

We determined the breeding sites for 9 juveniles that had been detected within the study area in spring (5 males:4 females). The last fall pre-migratory dispersal detection location of individuals did not correspond closely with either Motus spring detections or the breeding location of juveniles (Table 3-5, Supplementary Material Figure B3-4). The last spring tower detection averaged 12.2 km ± 7.2 from the fall tower, and the first breeding site was 10.7 km ± 3.6 from the last fall dispersal detection. By comparison, breeding locations were on average only 4.1 km from their natal site (SD±3.8, range = 0.6 km to 11.1km) and contrary to prediction, were significantly closer to the natal site than the last fall Motus tower detection (paired *t*-test $t_8 = 4.3$, $P = 0.001$). Two individuals returned to breed in their natal forest fragment (with territories <1 km from the natal nest site) and 7 of 9 bred <5 km from their natal site.

### *Does extent of pre-migratory movements predict fall departure date or first migratory flight performance?*

Nestling fledge date and number of towers that juveniles were detected at during pre-migratory movements were significant predictors of departure date. Individuals departed on fall migration an average of 1 week earlier if they fledged the nest during early June compared to birds that fledged at least 6 weeks later in the season (0.017 ± 0.004, $P < 0.001$). Contrary to our prediction, birds that were detected at more towers during the pre-migratory dispersal period departed later on fall migration (0.014 ± 0.0037, $P = 0.04$) (Table 3-6; Figure 3-3 A-B). The duration of pre-migratory dispersal period was not a significant predictor of departure date (0.001 ± 0.003, $P = 0.67$) and neither was maximum distance travelled from the natal nest (-0.003 ± 0.006, $P = 0.62$) (Figure 3-3 C-D; Supplementary Material Table B3-5).

To test if extent of pre-migratory dispersal influences first migratory flight performance, we used only unambiguous migration flights for which an individual was detected on the same night on the north and south side of Lake Erie ($n = 20$). The orientation of these first flights for juvenile Wood Thrushes (range 129° to 241°) was not predicted by different pre-migratory movement variables or fledge date and these models were not <2 AICc from the null model (Table 3-7, Figure 3-4 A-D, Supplementary Material Table B3-6). The average pace of first migratory flight (mean = 44.9 km/h, SD ± 18.7, range = 19.4 to 77.5 km/h) was also not predicted by fledge date or extent of pre-migration movements (Table 3-8, Figure 3-5 A-D, Supplementary Material Table B3-7). Juveniles travelled a mean distance of 74.3 km (SD ± 22.2, range = 42.7 km to 149.2 km) during their first migratory flight (straight-line between towers from the north shore to south shore of Lake Erie). None of the modelled predictors were better than the intercept model (Figure 3-6 A-D, Supplementary Material Table B3-8).

## Discussion

To our knowledge, this is the first study of a migratory songbird to tag nestlings and subsequently track their long distance (>5 km) pre-migratory movements, fall departure date, first migratory flight performance, and return in the spring. Prior studies of pre-migration movements in forest migratory songbirds, including the Wood Thrush, found that first dispersal from the natal area began 3-5 weeks after fledging and birds moved 1-2 km away (Vega Rivera et al. 1998, Vitz and Rodewald 2011). In our study, we do not know when juveniles first left their natal area or the extent to which they made short distance movements. However, we demonstrate that long-distance exploration of the landscape occurs for a high proportion (78%) of juveniles prior to onset of fall migration. These pre-migratory movements occurred at night, mainly 2 hours before sunrise, and the random orientation indicates these were not simply small-scale migration movements that would be southerly in orientation. Most juveniles began these pre-migration movements 2-3 months after fledging which suggests that juveniles do not travel far from their natal territory as soon as they are fully independent/capable. Instead, pre-migration dispersal occurred primarily during the two weeks before departure on fall migration. Long distance movements through a fragmented landscape, which require gap-crossing between forest patches, are assumed to increase risk of predation (Yoder et al. 2004, Vitz and Rodewald 2010) however, 89% of fledglings survived the premigration period (Hayes et al. in press). By the time long distance pre-migratory movements occur, juvenile Wood Thrushes may have acquired sufficient experience and flight skills to detect and evade aerial predators.

### *Benefits of pre-migration movement*

We found mixed evidence for different hypotheses for the benefits of pre-migration movements (Table 3-9). Contrary to predictions of the habitat optimization hypothesis, the extent of pre-migratory movement (> 5 km from the natal site) was not similar for juvenile and adult Wood Thrushes (Table 3-9). Furthermore, juveniles from small forest fragments did not disperse at an earlier age or have more extensive pre-migratory movements which would be expected if small forest fragments are low quality habitat. However, in a parallel study (Hayes et al. 2023) we found that small forest fragments were surprisingly good breeding sites because nesting success, fledgling survival, and juvenile survival were not lower than for large forest fragments. A more direct test of the habitat optimization hypothesis would require measurement of habitat quality at the dispersal sites and at the time they were visited by juveniles, but this is not possible for Motus detections which do not pinpoint bird locations. Vega Rivera et al. (1998) used manual and aerial telemetry to monitor dispersal of juvenile Wood Thrushes and suggested that post-fledging dispersal is driven by the location of fruiting shrubs and trees as a food source. While fruit supply may explain short distance movements (1-2 km) it does not explain why juveniles would need to travel > 5 km away in search of fruit-rich habitat which is abundant in forest edges nor why adults did not do so.

We found mixed support for the territory-selection hypothesis (Table 3-9). Pre-migration movements were far more extensive in juveniles than adults and random in orientation, but this is also predicted by the homing target hypothesis. Males had a significantly longer period of pre-migratory movements (~1 week longer than females) but other measures of extent of pre-migratory movements did not differ between the sexes. Males are expected to be under stronger selection than females to prospect for future territories so that they can compete for a good quality breeding territory soon after spring arrival. In the Cyprus Wheatear (*Oenanthe cypriaca*), males visited prospective breeding territories during pre-migration dispersal movements and were detected the next spring on breeding territories closer to their fall dispersal site rather than their natal areas, but this was not the case for females (Patchett et al. 2022). However, in our study, juvenile Wood Thrushes recruited to breeding territories that were closer to their natal site than their fall pre-migration dispersal site.

If long distance pre-migratory movements in juveniles functions to locate future high quality territories, then these movements should be timed to coincide when cues of breeding habitat quality are optimal (Johnson 1989). Public information can provide cues about breeding habitat quality (access to mates, food abundance, territory quality, and shelter from predators) and may be obtained by eavesdropping (Danchin et al. 2004) on previous breeding attempts by other conspecific (Pärt et al. 2011, Kivelã et al. 2014) or heterospecific individuals in similar habitat niches (Parejo et al. 2005, Kivelã et al. 2014, Samplonius and Both 2017) and copying their breeding location choices (Parejo et al. 2005). Betts et al. (2008) conducted one of the first experimental playback studies that documented birds' use of public information to select breeding territories for the following season. They found that juveniles returned to the treatment sites (poor quality habitats) where they used call playback of male Black-throated Blue Warbler (*Dendroica caerulescens*) song and begging calls of young during the post breeding season the year prior. A comparable call playback study conducted on Bobolinks (*Dolichonyx oryzivorus*) had similar results (Nocera et al. 2006). In our study, long distance pre-migration movements for most juveniles occurred during the two weeks prior to fall migration, in late August or early September, which may be too late in the season to use social cues to assess breeding habitat quality.

Our results provide some support for the homing target hypothesis because long distance pre-migratory movements were common in juveniles but not adults, were random in orientation, and a relatively large proportion of juveniles returned the next spring. The majority (81%, 25 of 31) of juveniles detected in the spring were within the study area. While the study site was chosen because of the high density of Motus towers, there were 34-41 other towers (depending on year) within 100 km of the study area that could have detected returning juveniles but did not (Figure 2-1). Technology to track all surviving juveniles to their breeding sites would be needed to test if extensive pre-migratory movements in fall improves the likelihood of returning to breed near natal sites.

Mukhin et al. (2005) found that Eurasian Reed Warblers (*Acrocephalus scirpaceus*) made nocturnal flights for 1-2 weeks prior to fall migration by leaving, and repeatedly returning to, their natal site. They suggested these flights could function to establish a navigational home target for next spring, but also to develop a more accurate stellar compass for their first migration. If the pre-migratory dispersal observed in juvenile Wood Thrushes functions in part to prime the navigation system, or possibly to improve flight ability, we expected that more extensive pre-migration movements would advance fall departure date and improve performance on an individual's very first migration flight (which we measured as birds crossed a water barrier, Lake Erie). Pre-migration dispersal flights were nocturnal, but we found no evidence that birds with more limited pre-migration movements were less able to orient southward or had shorter or slower flights. Individuals that were detected by more Motus towers prior to migration departed later on migration, not earlier. Wood Thrush juveniles may have already achieved good preparedness for migration by the time they undergo long distance pre-migration dispersal. Unlike Eurasian Reed Warbler juveniles that migrate only three weeks after becoming independent from their parents, Wood Thrush juveniles often have two months to prepare for their first migration.

## Conclusion

Whatever the benefit of pre-migratory movements for juvenile songbirds, future advancements in technology are needed to track individuals more precisely once they disperse from their natal territory to make larger landscape movements. Technology that can track the daily locations and habitat occupancy of juveniles once beyond the range limits of manual (~ 300 m in forest) and aerial telemetry (~ 1 km, high resource/money costs) would be needed to test hypotheses of the function of pre-migratory movements. For instance, refined movement data that followed birds throughout their first year of life, and not just during the pre-migratory period, could determine when birds leave their natal territory, where exactly they are prospecting locally, and where they return to breed. Prior studies on pre-migration movements have not quantified the survival costs of making more extensive or riskier (e.g., gap crossing) movements (Vitz and Rodewald 2010). Hayes et al. (2023) found high survival (89%) during pre-migration even though most individuals undertook long distance movements. To determine if there is a benefit to prospecting for future territories, the breeding success of birds that return to territories where prospecting occurred could be compared to individuals that did not return to prospecting sites (Patchett et al. 2022). The high frequency of long distance pre-migratory movements in Wood Thrushes, despite the fragmented landscape, suggests that such movements could also be common in other migratory songbirds.

**Table 3-1**. Age at first Motus detection > 5 km from the natal forest fragment for juvenile Wood Thrushes (*n* = 93). Generalized linear models included additive predictors of fledge date, natal forest fragment size, sex, and year. Model average estimates, adjusted standard errors (SE), 95% confidence intervals (CIs), and *P*-values for models with <2 ΔAICc are reported. *P*-values <0.05 are shown in bold. See Supplementary Material Table B3-1 for AIC model results.

| Predictor | Estimate (β) ± SE | 95% CI | *P*-value |
|---|---:|---:|---:|
| Intercept | 3.939±0.058 | 3.823, 4.054 | **<0.001** |
| Fledge date | -0.174±0.030 | -0.232, -0.116 | **<0.001** |
| Year (2017) | 0.308±0.077 | 0.157, 0.459 | **<0.001** |
| Year (2018) | 0.222±0.073 | 0.078, 0.365 | **0.003** |
| Sex | 0.019±0.043 | -0.048, 0.181 | 0.66 |
| Natal fragment size | 0.004±0.016 | -0.038, 0.079 | 0.79 |

**Table 3-2**. Duration of pre-migratory dispersal period as measured by detections > 5 km from the natal forest fragment for juvenile Wood Thrushes (*n* = 93). Dispersal period is the number of days from the first detection to the last pre-migratory detection. Generalized linear mixed models included additive predictors of age at dispersal, natal forest fragment size, fledge date, sex, and year. Model average estimates, adjusted standard errors (SE), 95% confidence intervals (CIs), and *P*-values for models with <2 ΔAICc are reported. *P*-values <0.05 are shown in bold. See Supplementary Material Table B3-2 for AIC model results.

| Predictor | Estimate (β) ± SE | 95% CI | *P*-value |
|---|---:|---:|---:|
| Intercept | 2.177±0.072 | 2.037, 2.328 | **<0.001** |
| Age at dispersal | -0.725±0.033 | -0.790, -0.658 | **<0.001** |
| Fledge date | -0.543±0.031 | -0.606, -0.482 | **<0.001** |
| Sex | 0.272±0.062 | 0.148, 0.394 | **<0.001** |
| Year (2017) | -0.027±0.093 | -0.309, -0.011 | 0.78 |
| Year (2018) | -0.159±0.075 | -0.309, -0.011 | **0.04** |

**Table 3-3.** Total number of different Motus towers at which juvenile Wood Thrushes (*n* = 93) were detected during premigration dispersal movements. Generalized linear models included additive predictors of age at dispersal, natal forest fragment size, fledge date, sex, and year. Model average estimates, adjusted standard errors (SE), 95% confidence intervals (CIs), and *P*-values for models with <2 ΔAICc are reported. *P*-values <0.05 are shown in bold. See Supplementary Material Table B3-3 for AIC model results.

| Predictor | Estimate (β) ± SE | 95% CI | *P*-value |
|---|---:|---:|---:|
| Intercept | 0.813±0.150 | 0.499, 1.097 | **<0.001** |
| Age at Dispersal | 0.148±0.064 | 0.013, 0.277 | **0.02** |
| Natal Fragment Size | 0.021±0.042 | -0.040, 0.166 | 0.62 |
| Sex | -0.009±0.050 | -0.256, 0.168 | 0.85 |
| Year (2017) | 0.468±0.185 | 0.122, 0.870 | **0.01** |
| Year (2018) | 0.927±0.165 | 0.616, 1.273 | **<0.001** |

**Table 3-4**. Maximum distance detected away from natal site during pre-migratory movements for juvenile Wood Thrushes ($n = 93$). Generalized linear models included additive predictors of age at dispersal, natal forest fragment size, fledge date, sex, and year. Model average estimates, adjusted standard errors (SE), 95% confidence intervals (CIs), and *P*-values for models with <2 ΔAICc are reported. *P*-values <0.05 are shown in bold. See Supplementary Material Table B3-4 for AIC model results.

| Predictor | Estimate (β) ± SE | 95% CI | *P*-value |
|---|---:|---:|---:|
| Intercept | 2.772±0.109 | 2.556, 2.992 | **<0.001** |
| Age at dispersal | 0.015±0.039 | -0.067, 0.180 | 0.71 |
| Fragment size | 0.050±0.057 | -0.022, 0.189 | 0.38 |
| Sex | 0.007±0.042 | -0.176, 0.256 | 0.86 |
| Year (2017) | 0.326±0.146 | 0.031, 0.614 | **0.03** |
| Year (2018) | 0.448±0.136 | 0.174, 0.714 | **0.001** |

**Table 3-5.** Distance and direction of detections from last fall Motus tower detection to breeding site and for natal site to spring breeding site for juvenile Wood Thrushes ($n = 9$). Distance of last fall tower to last spring tower is also given (See Supplementary Material Figure B3-4).

| *Tag #* | *Fall Tower to Breeding Site* | | *Natal Site to Breeding Site* | | *Fall Tower to Spring Tower* |
|---|---|---|---|---|---|
| | Dist. (km) | Bear. (°) | Dist. (km) | Bear. (°) | Dist. (km) |
| 1 | 16.1 | 37.0 | 1.2 | 208.0 | 18.3 |
| 2 | 6.9 | 282.4 | 0.8 | 307.5 | 0 |
| 3 | 6.6 | 284.0 | 0.6 | 330.1 | 25.1 |
| 4 | 7.4 | 68.3 | 4.2 | 126.5 | 6.1 |
| 5 | 13.2 | 41.7 | 3.7 | 253.1 | 13.3 |
| 6 | 10.5 | 48.5 | 4.8 | 72.0 | 9.4 |
| 7 | 8.2 | 176.9 | 8.9 | 161.0 | 9.4 |
| 8 | 11.7 | 356.1 | 1.1 | 119.2 | 15.1 |
| 9 | 15.3 | 10.7 | 11.4 | 358.7 | 13.5 |
| Avg. Dist. | 10.7 | | 4.1 | | 12.2 |
| SD | 3.6 | | 3.8 | | 7.2 |

**Table 7**. Fall migration departure date models for juvenile Wood Thrushes (*n* = 20) with AICc <2. Generalized linear models included additive predictors of three pre-migratory movements; duration of pre-migratory dispersal period, maximum distance travelled from natal site, and total number of unique Motus tower detections. Fledge date and sex were also added to the models. Model average estimates, adjusted standard errors (SE), 95% confidence intervals (CIs), and *P*-values for models with <2 ΔAICc are reported. *P*-values <0.05 are shown in bold. See Supplementary Material Table B3-5 for AIC model results.

| Predictor | Estimate (β) ± SE | 95% CI | *P*-value |
|---|---:|---:|---:|
| Intercept | 5.563±0.004 | 5.556, 5.571 | **<0.001** |
| Fledge date | 0.017±0.004 | 0.008, 0.026 | **<0.001** |
| #Towers | 0.014±0.007 | 0.0009, 0.027 | **0.04** |
| Maximum distance | -0.003±0.006 | -0.003, 0.017 | 0.62 |
| Duration | 0.001±0.003 | -0.003, 0.017 | 0.67 |

**Table 3-7.** Generalized linear model results for predictors of juvenile Wood Thrushes orientation of first migratory flight (*n* = 20). Models included additive predictors of three pre-migratory movements; duration of pre-migratory dispersal period, maximum distance travelled from natal site, and total number of unique Motus tower detections. Fledge date and sex were also added to the models. Model average estimates, adjusted standard errors, 95% CI, and *P*-values for models with <2 ΔAICc are reported. *P*-values <0.05 are shown in bold. See Supplementary Material Table B3-6 for AIC model results.

| Predictor | Estimate (β) ± SE | 95% CI | *P*-value |
|---|---:|---:|---:|
| Intercept | 5.10±0.034 | 5.031, 5.175 | **<0.001** |
| Fledge date | 0.029±0.037 | -0.015, 0.124 | 0.43 |
| #Towers | -0.005±0.018 | -0.110, 0.048 | 0.78 |
| Maximum distance | -0.009±0.023 | -0.111, 0.041 | 0.71 |
| Duration | -0.004±0.016 | -0.103, 0.048 | 0.81 |

**Table 3-8**. Generalized linear model results for predictors of juvenile Wood Thrushes pace of first migratory flight (*n* = 20). Models included additive predictors of three pre-migratory movements; duration of pre-migratory dispersal period, maximum distance travelled from natal site, and total number of unique Motus tower detections. Fledge date and sex were also added to the models. Model average estimates, adjusted standard errors, 95% CI, and *P*-values for models with <2 ΔAICc are reported. *P*-values <0.05 are shown in bold. See Supplementary Material Table B3-7 for AIC model results.

| Predictor | Estimate (β) ± SE | 95% CI | *P*-value |
|---|---:|---:|---:|
| Intercept | 3.763±0.083 | 3.593, 3.944 | **<0.001** |
| Fledge date | 0.193±0.126 | 0.019, 0.435 | 0.12 |
| #Towers | -0.032±0.076 | -0.371, 0.140 | 0.67 |
| Maximum distance | -0.050±0.088 | -0.348, 0.059 | 0.57 |
| Duration | -0.116±0.119 | -0.394, 0.005 | 0.33 |

**Table 3-9**. Summary of outcomes for each prediction of the four hypotheses for the function of pre-migratory movements (PMM) in juvenile Wood Thrushes.

| Hypothesis | Predictions | Support for Hypothesis |
|---|---|---|
| Habitat optimization | a) Juvenile PMM = Adult PMM | No |
| | b) PMM > for juveniles from small natal fragments | No |
| Territory selection | a) Male PMM > Female PMM | No (yes for duration) |
| | b) Juvenile PMM > Adult PMM | Yes |
| | c) Random orientation of PMM | Yes |
| | d) Spring return to last PMM location | No |
| Homing target | a) Juvenile PMM > Adult PMM | Yes |
| | b) Random orientation of PMM | Yes |
| | c) High return rate to region | Yes |
| Flight performance | a) Nocturnal PMM | Yes |
| | b) Extent of PMM improves performance | No |

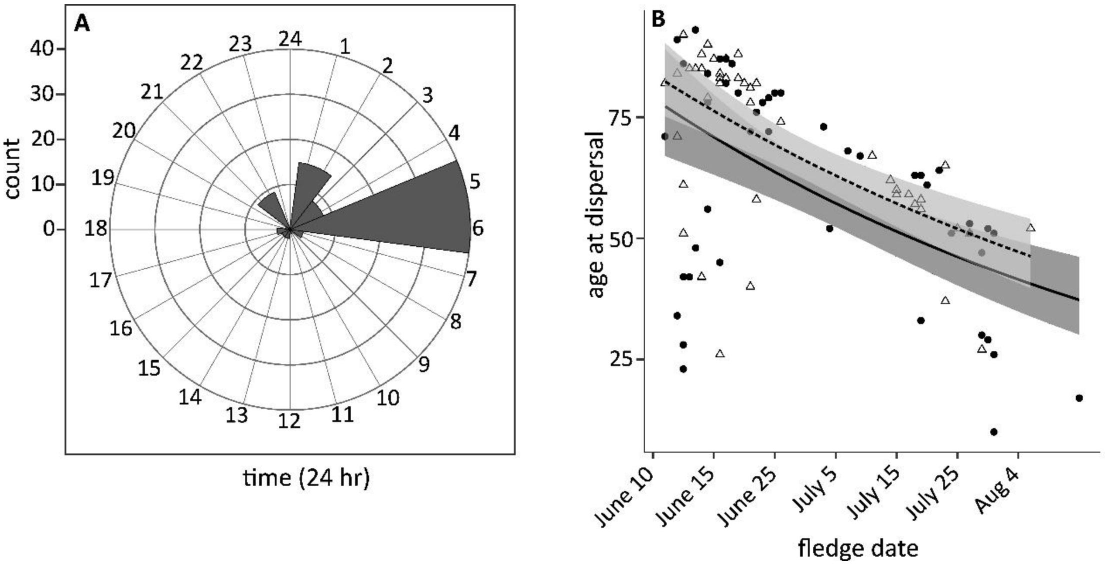


**Figure 3-1. (A)** Time of day of first dispersal movement as detected > 5 km away from natal forest site for juvenile Wood Thrushes (*n* = 93). Almost all the first dispersal movements occurred at night (397 of 425; 93%) with ~48% occurring during the 2 hours before sunrise; **(B)** Juvenile Wood Thrush fledge date and sex as predictors of age (days since fledging) at first detection > 5km from the natal forest fragment (*n* = 93). Females shown in filled circles with dashed line and males with open triangles and solid line. Grey shading indicating 95% confidence interval around trend line (Table 3-1, Supplementary Material Table B3-1).

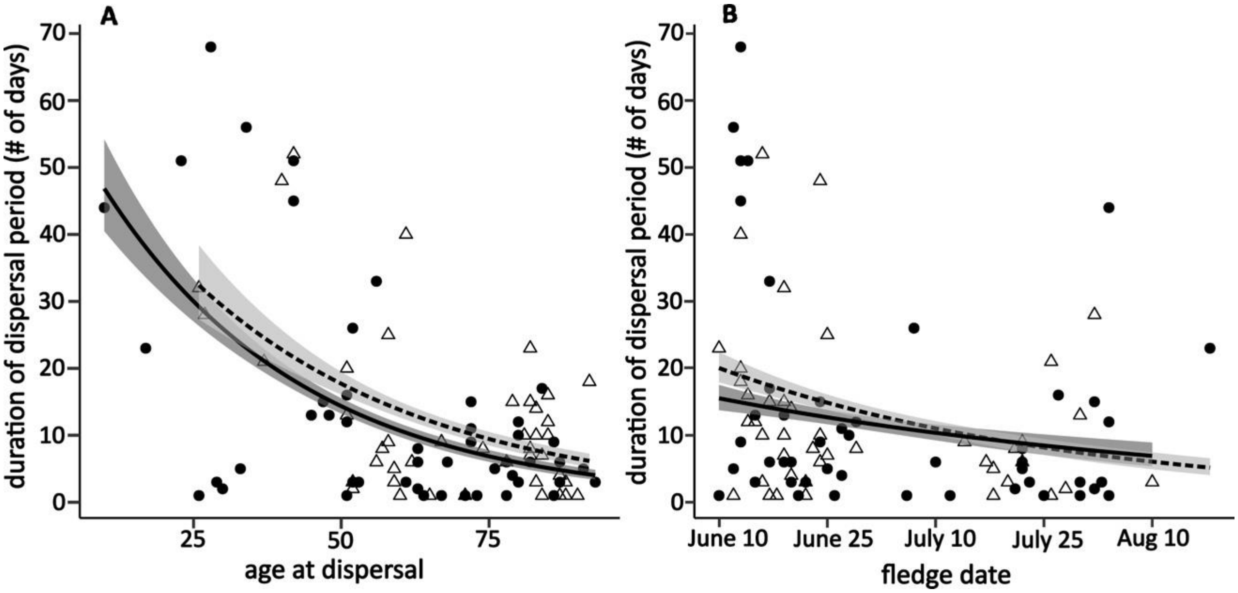


**Figure 3-2.** Duration of pre-migratory movement period for juvenile Wood Thrushes (*n* = 93) as measured from the first Motus tower detection > 5 km from the natal forest fragment to the last detection that occurred prior to fall departure with **A)** age at first detection > 5 km from natal site, and **B)** fledge date. Females shown with solid circle and dashed line, males open triangle and solid line, and grey shading indicating 95% confidence interval around trend line. Fledge date (-0.543±0.031, *P* <0.001) and age at dispersal date (-0.725±0.033, *P* <0.001) were both significant predictors in the model (Table 3-2, Supplementary Material Table B3-2).

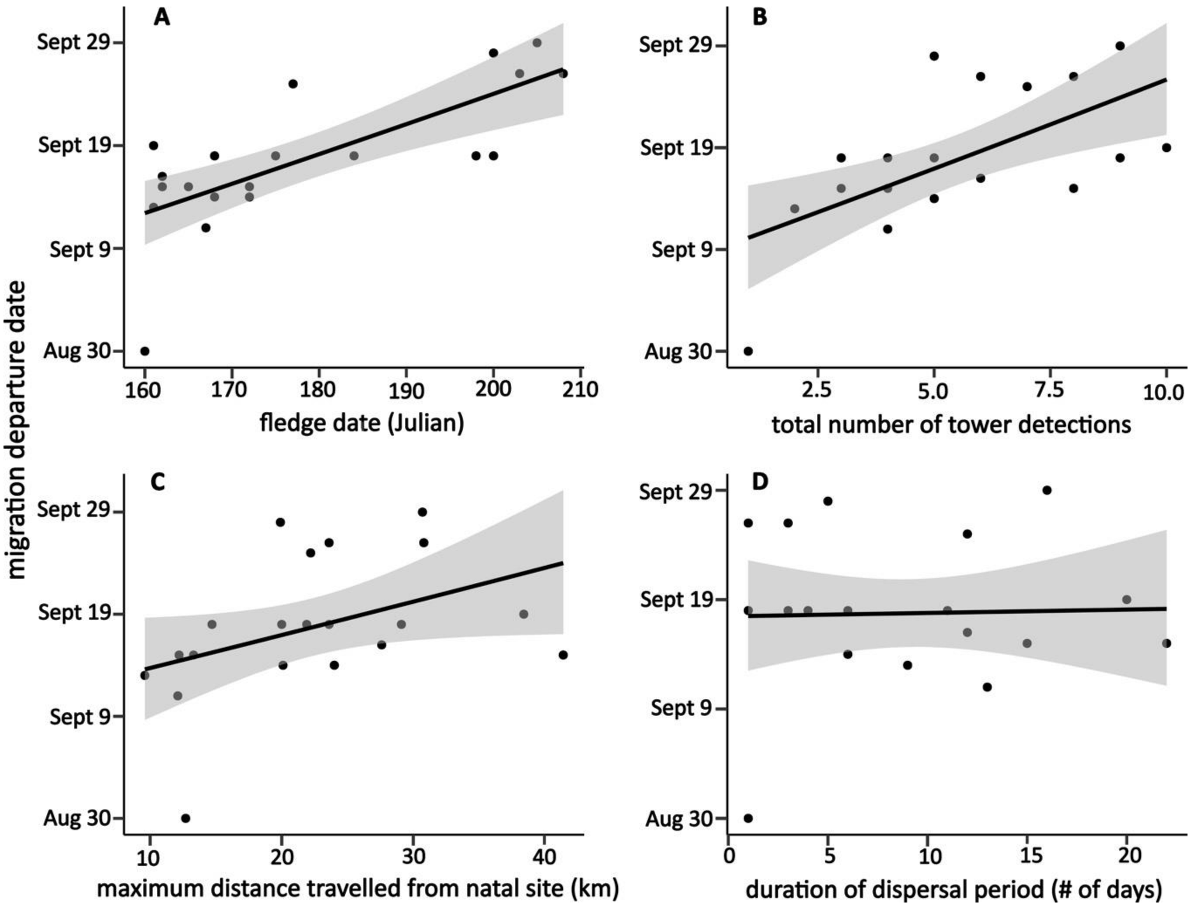


**Figure 3-3.** Fall migratory departure date of juvenile Wood Thrushes (*n* = 20) was modelled with **(A)** fledge date (*P*<0.001), and three pre-migratory movement measures of **(B)** total number of different Motus towers at which juveniles were detected > 5 km from their natal site (*P* = 0.04), **(C)** maximum distance detected from natal site (*P* = 0.62), and **(D)** duration of pre-migration dispersal period (*P* = 0.67). Top weighted models included fledge date with the total number of different Motus tower detections (Table 3-6, Supplementary Material Table B3-5). Grey shading indicating 95% confidence interval around trend line.

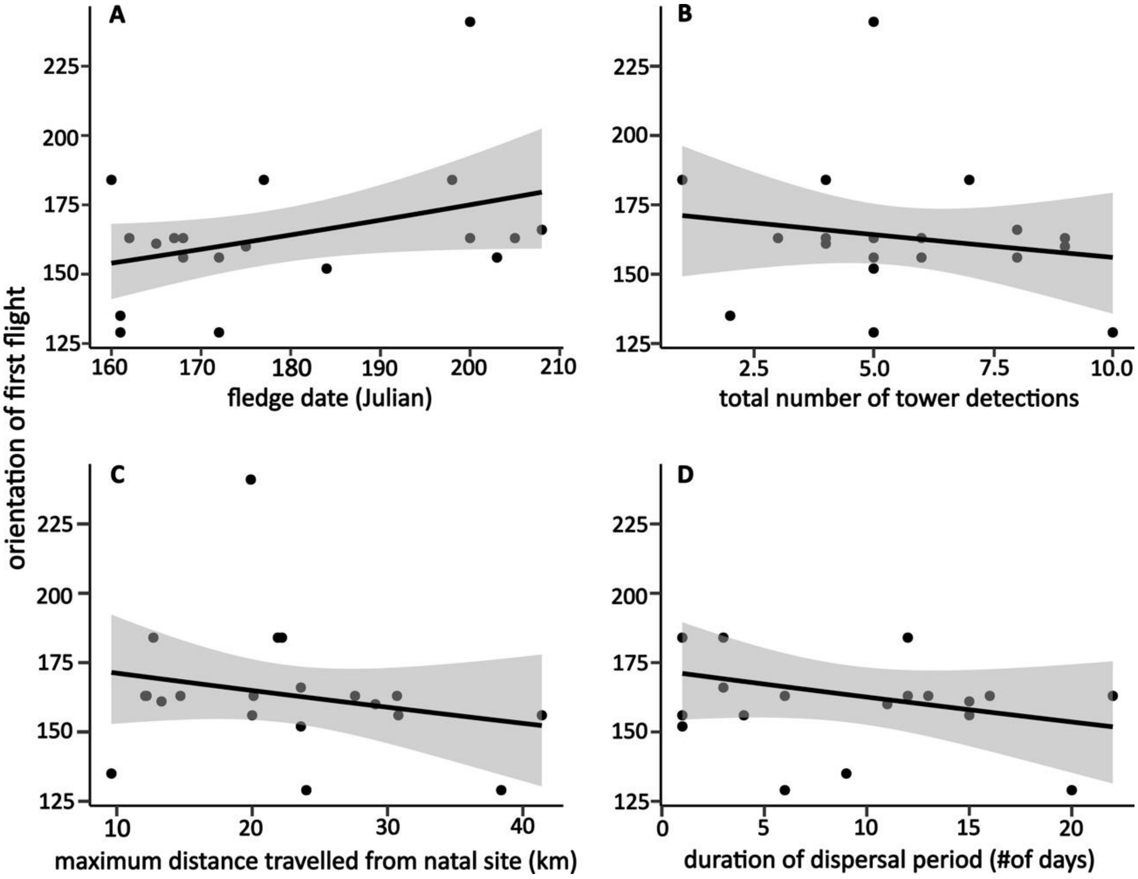


**Figure 3-4.** First migratory flight orientation of juvenile Wood Thrushes (*n* = 20) was modelled with **(A)** fledge date (*P* = 0.43), and three pre-migratory movement measures of **(B)** total number of Motus towers juveniles were detected at (*P* = 0.78), **(C)** maximum distance travelled from natal site (*P* = 0.71) and **(D)** duration of pre-migration dispersal period (*P* = 0.81). None of the models with predictors were >2 AICc from the null model (Table 3-7, Supplementary Material Table B3-6). Grey shading indicating 95% confidence interval around trend line.

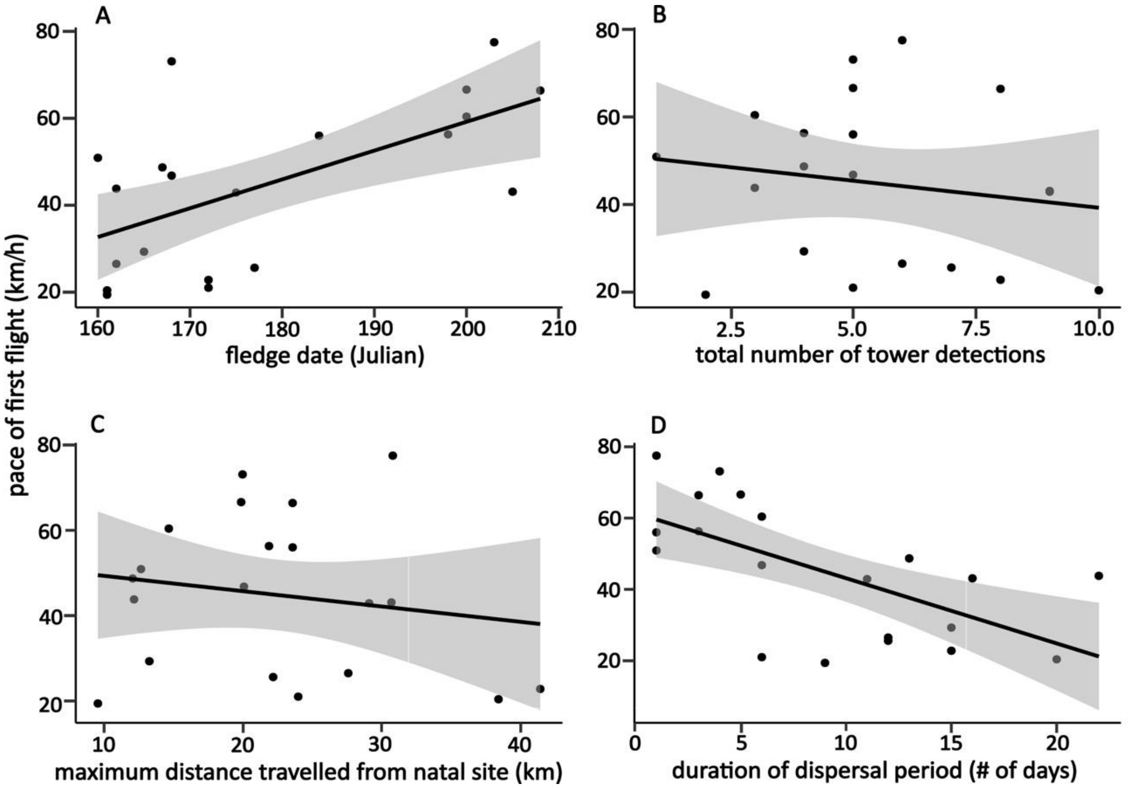


**Figure 3-5.** Pace of the first migratory flight by juvenile Wood Thrushes (*n* = 20) was modelled with **(A)** fledge date (*P* = 0.12) and three pre-migratory movement measures of **(B)** total number of Motus towers juveniles were detected at (*P* = 0.67), **(C)** maximum distance travelled from natal site (*P* = 0.57), and **(D)** duration of pre-migration dispersal period (*P* = 0.33) (Table 3-8, Supplementary Material Table B3-7). Grey shading indicating 95% confidence interval around trend line.

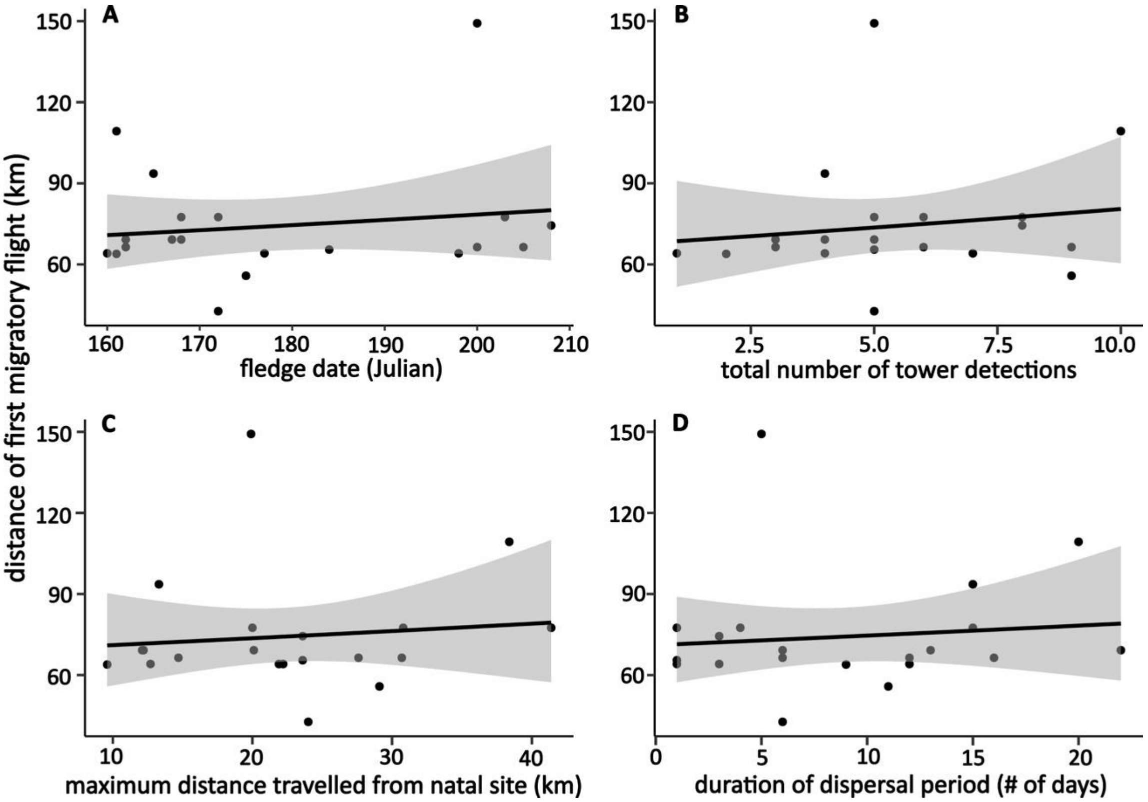


**Figure 3-6.** Distance between first and last detections of first migratory flight for juvenile Wood Thrushes (*n* = 20) with predictors of **(A)** fledge date and pre-migratory movements of **(B)** total number of Motus towers juveniles were detected at, **(C)** maximum distance travelled from natal site, and **(D)** duration of pre-migration dispersal period. None of the modelled parameters were good predictors of the distance travelled during the first flight and were all >2 ΔAICc than the intercept model (Supplementary Material Table B3-8). Grey shading indicating 95% confidence interval around trend line.

# Chapter 4: General Conclusion

This study was part of a larger body of work on the ecology of Wood Thrushes in the fragmented forest landscape in southwestern Ontario (see Supplementary Material 4-1 for paper abstracts), for which three graduate students (myself, Brendan Boyd, and Alexandra Israel) collaborated on core field activities such as nest searching, nest monitoring, manual radio-tracking, and tagging adults and nestlings. This collaboration was critical for being able to carry out field work at so many different forest fragments. This led to my co-authorship on a paper that showed that small forest fragments did not have negative effects on adult body condition, fall migration timing, or annual survival (Boyd et al. 2023), and on a paper showing that nest concealment via vegetation cover above the nest reduces risk of nest predation (Israel et al. 2023).

The Motus Wildlife Tracking System has become a widely used technology to unravel the migration routes (Brunner et al. 2022), migratory stopovers (Beauchamp et al. 2020), and migratory connectivity (Korpach et al. 2022) for dozens of migratory bird species. This system was designed to study bird migration, but my dissertation demonstrated that this system can also be used to study juvenile annual survival and pre-migration behaviour. I have made a major advancement to the understanding and knowledge of juvenile survival at key life stages. Using manual radiotelemetry, aerial telemetry, and the innovative Motus system, for the first time ever for a migratory songbird, I tracked nestlings through to independence, departure on fall migration, migration, and their return to the study area the following spring (Ch.2). I also provided measurements of pre-migration movement, that were found to be a unique behaviour observed in juveniles but not in adults, and I measured juvenile performance during their first migratory flight across a large water barrier (Ch.3).

### *Apparent survival estimates during the first year of life*

Understanding the drivers and mechanisms for survival throughout the first year of life for migratory songbirds is needed for a better understanding of population dynamics (Raybuck et al. 2019; Carle-Pruneau et al. 2021). Having this knowledge helps to identify the pinch points in survival and to assign conservation action and further directed research. This has been difficult to do once fledglings become independent and disperse from their natal areas due to logistical reasons. For this reason, much of juvenile survival during the first year of life has remained a "black box". However, with advancements in technology such as the development of the Motus system, research into this under studied area of first year of life in migratory songbirds may begin to fill these knowledge gaps. Evans et al. (2019) made an innovative first step by tagging nestling Barn Swallows and using Motus detections to estimate survival to two months following independence and to determine fall migratory departure dates.

My study takes the next step by tagging nestlings with a radio transmitter that has a 1-year battery life to estimate not only pre-migration survival, but also apparent migration/wintering survival, and apparent annual survival. No other study has successfully completed year-round tracking of juveniles for any migratory songbird, and these are also the first estimates of pre-migration survival for a forest songbird. I identified pinch points in survival (the first few days after fledging the nest and during migration/wintering) and found that being reared in a small forest fragment was not a handicap. Although this population of Wood Thrushes is not self-sustaining (e.g., a population sink), likely due to low migration/wintering survival, I show that small woodlots provide important breeding habitat for Wood Thrushes and need to be protected. Additionally, I provided evidence that most of the juveniles that were known to survive wintering/migration returned to the study area (81%, 25 of 31) within ~12 km of their natal site. The remainder of individuals (19%, 6 of 31) were last detected by Motus towers in the spring within ~110 km of the study area which suggests that these individuals dispersed to breed in distant Wood Thrush populations (Rushing et al. 2021). These longer dispersal movements away from the natal area are important for population dynamics as emigration into other populations reduces the risk of inbreeding (Szulkin and Sheldon 2008).

### *Pre-migratory movements*

Many studies have observed independent juveniles of unknown origin visiting non-natal sites (Vitz and Rodewald 2013) and some have used manual telemetry to study local landscape movements of juveniles during the pre-migration period (Styles et al. 2021). Tracking the movement of independent juveniles prior to commencing fall migration is important for understanding the purpose of these movements. Pre-migration landscape-level movements could serve the purpose of setting internal compass orientation (Mukhin et al. 2005), to form a navigational homing target (Mitchell et al. 2010), relocating to higher quality habitat (Kershner et al. 2004) or prospecting for future high-quality breeding territories (Ciaglo et al. 2020; Patchett et al. 2022). The hypothesis that juveniles are prospecting for future breeding territories is very popular (Betts et al. 2008; Patchett et al. 2022) but strong evidence would require knowledge of both the pre-migration movements and where juveniles return to breed. Motus can measure both, and so provided a unique opportunity for me to test hypotheses for how juveniles benefit from pre-migratory exploration of the landscape. The Motus system allowed me to remotely detect longer distance (> 5 km) movements (outside of manual telemetry range), and then to relate the extent of exploration to (i) fledge date, fledgling age, and natal forest fragment size, and (ii) performance on the first migration flight.

### *Applications to future research*

The study population appears to be a "sink" (juvenile recruitment is low relative to adult survival) which may be caused by low migration/wintering survival of juveniles rather than low breeding success. Future studies of juveniles are needed to map migration routes and stopover areas during both the fall and spring to identify when and where this high mortality is occurring during these times. However, traditional migration tracking methods (archival geolocators and GPS devices) are not feasible for measuring fall migration because there is such a low chance of locating the returning birds in the spring to retrieve the tags. There has only been one study to track juvenile migration, and this was done for spring migration by tagging birds with geolocators on their wintering grounds and recapturing them as they returned for their second winter (McKinnon et al. 2015). With the expanding network of Motus towers through central U.S. and into Central America, mapping migratory routes and stopover areas could be achieved for juveniles and provide valuable insight into key areas for conservation and protection that could subsequently allow for a higher recruitment of juveniles back into the breeding population.

My study found mixed support for the different hypotheses of pre-migratory movements in juveniles but most strongly supported the hypothesis that movements were related to developing a homing target for their return the following spring. The movements were common in juveniles but not in adult Wood Thrushes, were random in orientation, and a relatively large proportion of juveniles returned the following spring. More directed studies are needed into this movement behaviour with technology that can track daily locations to determine when they leave their natal territory, where they are exploring, and where precisely they return to breed.

Future studies, with more advanced technology such as GPS satellite tags that are light enough for songbirds to safely carry, are needed to track juveniles more precisely from the nest, through to migration, and return in the spring. A new collaborative ICARUS, which stands for International Cooperation for Animal Research Using Space, may be the future technology for migratory bird research as tags become progressively lighter, not cost-prohibitive, long-lasting battery, and ability for fine-scale mapping (Jetz et al. 2022). Until then, the vexing question for migratory bird conservation will remain “where do birds die, and why”?

## Literature Cited

Agostinelli, C. and U. Lund (2022). R package ‘circular’. Circular Statistics (version 0.4-95). https://r-forge.r-project.org/projects/circular/

Åkesson, S., H. Bakam, E.M. Hernandez, M. Ilieva, and G. Bianco (2021). Migratory orientation in inexperienced and experienced avian migrants. Ethology Ecology & Evolution 33: 206–229 https://doi.org/10.1080/03949370.2021.1905076

Anders, A.D., and M.R. Marshall (2005). Increasing the accuracy of productivity and survival estimates in assessing landbird population status. Conservation Biology 19:66–74 https://doi.org/10.1111/j.1523-1739.2005.00543.x

Anders, A.D., D.C. Dearborn, J. Faaborg, and F.R. Thompson III (1997). Juvenile survival in a population of neotropical migrant birds. Conservation Biology 11: 698–707

Arnold, T.W. (2010). Uninformative parameters and model selection using Akaike’s Information Criterion. Journal of Wildlife Management 74:1175–1178 https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Austen, M.J.W., C.M. Francis, D.M. Burke, and M.S.W. Bradstreet (2001). Landscape context and fragmentation effects on forest birds in southern Ontario. Ornithological Applications 103:701–714 https://doi.org/10.1093/condor/103.4.701

Bailey, B.A., and D.I. King (2019). Habitat selection and habitat quality for wintering wood thrushes in a coffee growing region in Honduras. Global Ecology and Conservation 20: e00728 https://doi.org/10.1016/j.gecco.2019.e00728

Bartoń, K. (2020). MuMIn: multi-Modal Inference. R package version 1.43.17 https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf

Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48 https://doi.org/10.18637 /jss.v067.i01

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

Bégin-Marchand, C., A. Desrochers, P.D. Taylor, J. A. Tremblay, L. Berrigan, B. Frei, A. Morales, and G.W. Mitchell (2021). Spatial structure in migration routes maintained despite regional convergence among eastern populations of Swainson's Thrushes. Movement Ecology 9: 23–33 https://doi.org/10.1186/s40462-021-00263-9

Bélisle, M., A. Desrochers, and M. Fortin (2001). Influence of forest cover on the movements of forest birds: a homing experiment. Ecology 82: 1893–1904 https://doi.org/10.1890/0012-9658(2001)082[1893:IOFCOT]2.0.CO;2

Benson, T.J., J.D. Brown, and J.C. Bednarz (2009). Identifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology 79:225–234 https://doi.org/10.1111/j.1365-2656.2009.01604.x

Betts, M.G., A.S. Hadley, N. Rodenhouse, and J.H. Nocera (2008). Social information trumps vegetation structure in breeding-site selection by a migrant songbird. Proceedings of the Royal Society B 275: 2257–2263 https://doi.org/10.1098/rspb.2008.0217

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

Blomberg, E.J., J.S. Sedinger, D. Gibson, P.S. Coates, and M.L. Casazza (2014). Carry over effects and climatic conditions influence the postfledging survival of greater sage-grouse. Ecology and Evolution 4:4488–4499 https://doi.org/10.1002/ece3.1139

Boyd, B.P., S. Hayes, A.M. Israel, B.J.M. Stutchbury (2023). Breeding season forest fragment size does not create negative carry-over for adult Wood Thrushes on fall migration timing or annual survival. Ornithological Applications duad028 https://doi.org/10.1093/ornithapp/duad028

Brittingham, M.C., and S.A. Temple (1983). Have cowbirds caused forest songbirds to decline? BioScience 33:31–35 https://doi.org/10.2307/1309241

Brown, W.P. and R.R. Roth (2004). Juvenile survival and recruitment of wood thrushes *Hylocichla mustelina* in a forest fragment. Journal of Avian Biology 35:316–326 http://dx.doi.org/10.1111/j.0908-8857.2004.03195.x

Brown, D.R., and T.W. Sherry (2006). Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149:22–32 https://doi.org/10.1007/s00442-006-0418-z

Brown, J.M. and P.D. Taylor (2015). Adult and hatch-year blackpoll warblers exhibit radically different regional-scale movements during post-fledging dispersal. Biology Letters 11: 20150593 http://dx.doi.org/10.1098/rsbl.2015.0593

Brunner, A.R., B.C. Dossman, V. Jirinec, K.L. Percy, C.M. Tonra, E.I. Johnson, and P.P. Marra (2022). Migratory behavior and connectivity revealed in a secretive Neotropical migratory songbird, the Swainson's Warbler. Journal of Field Ornithology 93: 5 https://doi.org/10.5751/JFO-00134-930305

Buehler, D.M., T. Piersma, and B.I. Tieleman (2008). Captive and free-living red knots *Calidris canutus* exhibit differences in non-induced immunity that suggest different immune strategies in different environments. Journal of Avian Biology 39:560–566 doi: 10.1111/j.2008.0908-8857.04408.x

Burke, D.M., and E. Nol (1998). Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. Ornithology 115:96–104 https://doi.org/10.2307/4089115

Burke, D.M, and E. Nol (2000). Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. Ecological Applications 10:1749–1761 https://doi.org/10.1890/1051-0761(2000)010[1749:LAFSEO]2.0.CO;2

Burnham, K.P. (1993). A theory for combined analysis of ring recovery and recapture data. In "Marked individuals in the study of bird population (J-D. Leebreton & P.M North, Eds) - Birkhäuser-Verlag, Basel https://sites.warnercnr.colostate.edu/wp-content/uploads/sites/73/2017/05/Burnham1993.pdf

Burnham, K.P. and D.R. Anderson (2002). Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag, New York, New York, USA. http://sutlib2.sut.ac.th/sut_contents/H79182.pdf

Carle-Pruneau, E., M. Bélisle, F. Pelletier, and D. Garant (2021). Determinants of nest box local recruitment and natal dispersal in a declining bird population. Oikos 2022: e08349 http://dx.doi.org/10.1111/oik.08349

Chalfoun, A.D., F.R. Thompson III, and M.J. Ratnaswamy (2002). Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16: 306–-318 https://doi.org/10.1046/j.1523-1739.2002.00308.x

Chiavacci, S.J., T.J. Benson, and M.P. Ward (2018). Linking landscape composition to predator-specific nest predation requires examining multiple landscape scales. Journal of Applied Ecology 55: 2082–2092 https://doi.org/10.1111/1365-2664.13090

Ciaglo, M., R. Calhoun, S.W. Yanco, M.B. Wunder, C.A. Stricker, and B.D. Linkhart (2020). Evidence of postbreeding prospecting in a long-distance migrant. Ecology and Evolution 11: 599–611 http://dx.doi.org/10.1002/ece3.7085

Cooper, N.W., T.W. Sherry, and P.P. Marra (2015). Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. Ecology 96:1933–-1942 https://doi.org/10.1890/14-1365.1

Cormier, D.A., and P.D. Taylor (2019). Contrasting patterns of post-fledging movements of two sympatric warbler species with different life-history strategies. Journal of Avian Biology 50:1–11 https://doi.org/10.1111/jav.02182

Cox, A.S., and D.C. Kesler (2012). Reevaluating the cost of natal dispersal: post-fledging survival of red-bellied woodpeckers. Ornithological Applications 114: 341–347 https://doi.org/10.1525/cond.2012.110070

Cox, W.A., F.R. Thompson III, and J. Faaborg (2012). Landscape forest cover and edge effects on songbird nest predation vary by nest predator. Landscape Ecology 27:659–669 https://doi.org/10.1007/s10980-012-9711-x

Cox, W.A., F.R. Thompson III, A.S. Cox, and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. Journal of Wildlife Management 78:183–193 https://doi.org/10.1002/jwmg.670

Crewe, T. L., J. E. Deakin, A. T. Beauchamp, and Y. E. Morbey (2019). Detection range of songbirds using a stopover site by automated radio telemetry. Journal of Field Ornithology 90: 176–189 https://doi.org/10.1111/jofo.12291

Crewe, T. L., Z. Crysler, and P. Taylor (2020). Motus R book a walk through the use of R for Motus automated radio-telemetry data. Available from https://motus.org/MotusRBook/index.html

Crysler, Z.J., R.A. Ronconi, and P. D. Taylor (2016). Differential fall migratory routes of adult and juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*). Movement Ecology 4:3–8 https://doi.org/10.1186/s40462-016-0067-8

Danchin, E., L. Giraldeau, T.J. Valone, and R.H. Wagner (2004). Public information: from nosy neighbors to cultural evolution. Science 305: 487–491 https://doi.org/10.1126/science.1098254

Donovan, T.M., F.R. Thompson, J. Faaborg, and J.R. Probst (1995). Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380–1395 https://www.jstor.org/stable/2387184

Dossman, B.C., A.D. Rodewald, C.E. Studds, and P.P. Marra (2023). Migratory birds with delayed spring departure migrate faster but pay the costs. Ecology 104: e3938 https://doi.org/10.1002/ecy.3938

Driscoll, M.J.L., T. Donovan, R. Mickey, A. Howard, and K.K. Fleming (2010). Determinants of wood thrush nest success: a multi-scale, model selection approach. Journal of Wildlife Management 69:699–709 http://dx.doi.org/10.2193/0022-541X(2005)069[0699:DOWTNS]2.0.CO;2

Drummond, F.M., K.A. Parker, T.G. Lovegrove, and D.P. Armstrong (2019). Distinguishing effects of juvenile mortality and dispersal on recruitment. Journal of Wildlife Management 83:1744–1752 http://dx.doi.org/10.1002/jwmg.21762

Eng, M.L., B.J.M. Stutchbury, D.M. Burke, and K.A. Elliott (2009). Influence of forest management on pre- and post-fledging productivity of a neotropical migratory songbird in a highly fragmented landscape. Canadian Journal of Forest Research 41:2009–2019 https://doi.org/10.1139/x11-119

Eng, M.L., B.J.M. Stutchbury, and C.A. Morrissey (2019). A neonicotinoid insecticide reduces fueling and delays migration in songbirds. Science. 365:1177–1180 https://doi.org/10.1126/science.aaw9419

Etterson, M.A., R. Greenberg, and T. Hollenhorst (2014). Landscape and regional context differentially affect nest parasitism and nest predation for Wood Thrush in central Virginia, USA. Ornithological Applications 116:205–214 https://doi.org/10.1650/CONDOR-13-045.1

Evans, D.R., K. A. Hobson, J.W. Kusack, M.D. Cadman, C.M. Falconer, and G.W. Mitchell (2019). Individual condition, but not fledging phenology, carries over to affect post-fledging survival in a Neotropical migratory songbird. Ibis 162:331–344. https://doi.org/10.1111/ibi.12727

Evans, M., E. Gow, R.R. Roth, M.S. Johnson, and T.J. Underwood (2020). Wood Thrush (*Hylocichla mustelina*), Version 1.0 In Birds of the World (A.F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA

Faaborg, J., R.T. Holmes, A.D. Anders, K.L. Bildstein, K.M. Dugger, S.A. Gauthreaux Jr., P. Heglund, K.A. Hobson, A.E. Jahn, D.H. Johnson, S.C. Latta, D.I.J. Levey, P.P. Marra, C.L. Merkord, E. Nol, S.I. Rothstein, T.W. Sherry, T.S. Sillett, F.R. Thompson III, and N.

Warnock (2010). Conserving migratory land birds in the New World: do we know enough? Ecological Applications 20: 398–418 https://doi.org/10.1890/09-0397.1

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515 https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Falk, K.J., E. Nol, and D.M. Burke (2011). Weak effect of edges on avian nesting success in fragmented and forested landscapes in Ontario, Canada. Landscape Ecology 26:239–251 http://dx.doi.org/10.1007/s10980-010-9543-5

Foster, D. R. (1992). Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology 80:753–771 https://doi.org/10.2307/2260864

Friesen, L., M.D. Cadman, and R.J. MacKay (1999). Nesting success of neotropical migrant songbirds in a highly fragmented landscape. Conservation Biology 13:338–346 https://doi.org/10.1046/j.1523-1739.1999.013002338.x

Friesen, L.E., G. Casbourn, V. Martin, and R. J. Mackay (2013). Nest predation in an anthropogenic landscape. The Wilson Journal of Ornithology 125:562–569 https://doi.org/10.1676/12-169.1

Gow, E.A., T.W. Done, and B.J.M. Stutchbury (2011). Radio-tags have no behavioral or physiological effects on a migratory songbird during breeding and molt. Journal Field Ornithology 82:193–201 https://doi.org/10.1111/j.1557-9263.2011.00322.x

Hachѐ, S., K.A. Hobson, E.M. Bayne, S.L. Van Wilgenburg, and M. Villard (2014). Tracking natal dispersal in a coastal population of a migratory songbird using feather stable isotope ($\delta^2$H, $\delta^{34}$S) tracers. PLoS One 9: e94437 https://doi.org/10.1371/journal.pone.0094437

Haddad, N.M., L.A. Brudvig, J. Clobert, K.F. Davies, A. Gonzalez, R.D. Holt, T.E. Lovejoy, J.O. Sexton, M.P. Austin, C.D. Collins, W.M. Cook, E.I. Damschen, R.M. Ewers, B.L. Foster, C.N. Jenkins, A.J. King, W.F. Laurance, D.J. Levey, C.R. Margules, B.A. Melbourne, A.O. Nicholls, J.L. Orock, D. Song, and J.R. Townshend (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1: https://doi.org/10.1126/sciadv.1500052

Hames, R.S., J.D. Lowe, S.B. Swarthout, and K.V. Rosenberg (2006). Understanding the risk to neotropical migrant bird species of multiple human-caused stressors: elucidating processes behind the patterns. Ecology and Society 11: http://dx.doi.org/10.5751/ES-01673-110124

Hannon, S.J. and K. Martin (2006). Ecology of juvenile grouse during the transition to adulthood. Journal of Zoology 269:422–433 http://dx.doi.org/10.1111/j.1469-7998.2006.00159.x

Hannon, S.J., S. Wilson, and C.A. McCallum (2009). Does cowbird parasitism increase predation risk to American redstart nests? Oikos 118:1035–1043 http://dx.doi.org/10.1111/j.1600-0706.2008.17383.x

Harrison, X.A, J.D. Blount, R. Inger, D.R. Norris, and S. Bearhop (2011). Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18 https://doi.org/10.1111/j.1365-2656.2010.01740.x

Hartig, F. (2022). DHARMa: residual diagnostics for hierarchical regression models. R package version 0.4.6.

Hayes, S.M., Boyd, B.P., Israel, A.M., and B.J.M. Stutchbury (2023). Natal forest fragment size does not predict fledgling, pre-migration or apparent annual survival in Wood Thrushes. Ornithological Applications https://doi.org/10.1093/ornithapp/duad054

Heide, K.T., L.E. Friesen, V.E. Martin, E.D. Cheskey, M.D. Cadman, and R.D. Norris (2023). Before-and-after evidence that urbanization contributes to the decline of a migratory songbird. Avian Conservation & Ecology 18: 15 https://doi.org/10.5751/ACE-02366-180115

Hethcoat, M.G. and A.D. Chalfoun (2015). Towards a mechanistic understanding of human-induced rapid environmental change: a case study linking energy development, nest predation and predators. Journal of Applied Ecology 52:1492–1499 http://dx.doi.org/10.1111/1365-2664.12513

Hoover, J.P., M.C. Brittingham, and L.J. Goodrich (1995). Effects of forest patch size on nesting success of Wood Thrushes. Ornithology 112: 146–155 https://doi.org/10.2307/4088774

Israel, A.M., S. Hayes, B.P. Boyd, and B.J.M. Stutchbury (2023). Effects of nest concealment on nest predation and cowbird parasitism, flight initiation distance and female stress levels in the Wood Thrush. Journal of Field Ornithology 94:9 https://doi.org/10.5751/JFO-00206-940109

Jenkins, J.M.A., F.R. Thompson III, and J. Faaborg (2016). Contrasting patterns of nest survival and postfledging survival in Ovenbirds and Acadian Flycatchers in Missouri forest fragments. Ornithological Applications 118:583–596 http://dx.doi.org/10.1650/CONDOR-16-30.1

Jetz, W., G. Tertitski, R. Kays, U. Mueller, and M. Wikelski (2022). Biological earth observation with animal sensors. Trends in Ecology & Evolution 37:293–298 https://doi.org/10.1016/j.tree.2021.11.011

Jones, T.M., M.P. Ward, T.J. Benson, and J.D. Brawn (2017). Variation in body condition and wing development predict cause-specific mortality in fledgling dickcissels. Journal of

Avian Biology 48:439–447 http://dx.doi.org/10.1111/jav.01143

Jones, L.E. and K. Islam (2023). Long-distance dispersal patterns in the Cerulean Warbler: a case study from Indiana. Avian Conservation & Ecology 18: 19 https://doi.org/10.5751/ACE-02428-180119

Johnson, M.L. (1989). Exploratory behavior and dispersal: a graphical model. Canadian Journal of Zoology 67: https://doi.org/10.1139/z89-326

Johnson, M.D., T.W. Sherry, R.T. Holmes, and P.P. Marra (2006). Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. Conservation Biology 20: 1433–1444 https://doi.org/10.1111/j.1523-1739.2006.00490.x

Kaiser, S.A., and C. Lindell (2007). Effects of distance to edge and edge type on nestling growth and nest survival in the Wood Thrush. Ornithological Applications 109:288–303 https://doi.org/10.1093/condor/109.2.288

Keinath, D.A., D.F. Doak, K.E. Hodges, L.R. Prugh, W. Fagan, C.H. Sekercioglu, S.H.M. Buchart, and M. Kauffman (2017). A global analysis of traits predicting species sensitivity to habitat fragmentation. Global Ecology and Biogeography 26:115–127 https://doi.org/10.1111/geb.12509

Kershner, E.L., J.W. Walk, and R E. Warner (2004). Postfledging movements and survival of juvenile eastern meadowlarks (*Sturnella magna*) in Illinois. Ornithology 121: 1146–1154 https://doi.org/10.1093/auk/121.4.1146

Kivelã, S.M., J. Seppänes, O. Ovaskainen, B. Doligez, L. Gustafsson, M. Mőnkkőnen, and J.T. Forsman (2014). The past and the present in decision-making: the use of conspecific and heterospecific cues in nest site selection. Ecology 95: 3428–3439 https://doi.org/10.1890/13-2103.1

Klaassen, R.H.G., M. Hake, R. Strandberg, B.J. Koks, C. Trierweiler, K. Exo, F. Bairlein, and T. Alerstam (2013). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. Journal of Animal Ecology 83:176–184 https://doi.org/10.1111/1365-2656.12135

Korpach, A.M., C.M. Davy, A. Mills, and K.C. Fraser (2022). Migratory connectivity and timing for an at-risk Canadian landbird, Eastern Whip-Poor-Will (*Antrostomus vociferus*), from two geographically distant breeding areas. Canadian Journal of Zoology 100: https://doi.org/10.1139/cjz-2021-0175

Laake, J.L. (2013). RMark: An R interface for analysis of capture-recapture data with MARK. AFSC processed rep. 2013-01, 25 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115 https://www.researchgate.net/publication/267509042_RMark_an_R_Interface_for_analysis_of_capture-recapture_data_with_MARK

Lampila, P., M. Mönkkönen, and A. Desrochers (2005). Demographic responses by birds to forest fragmentation. Conservation Biology 19:1537–1546 http://dx.doi.org/10.1111/j.1523-1739.2005.00201.x

Latta, S.C., S. Cabezas, D.A. Mejia, M.M. Paulino, H. Almonte, C.M. Miller-Butterworth, and G.R. Bortolotti (2016). Carry-over effects provide linkages across the annual cycle of a Neotropical migratory bird, the Lousiana Waterthrush *Parkesia motacilla*. Ibis 158:395–406 https://doi.org/10.1111/ibi.12344

Lloyd, P., T.E. Martin, R.L. Redmond, U. Langner, and M.M. Hart (2005). Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications 15: 1504–1514 https://doi.org/10.1890/04-1243

Long Point Region Conservation Authority (2019). Forest Management Plan 2020-2039. https://lprca.on.ca/wp-content/uploads/2020/11/LPRCA-FMP-FINAL_Public.pdf

MacIntosh, T., B.J.M. Stutchbury, and M.L. Evans (2011). Gap-crossing by Wood Thrushes (*Hylocichla mustelina*) in a fragmented landscape. Canadian Journal of Zoology 89:1091–1097 http://dx.doi.org/10.1139/z11-090

Marchand, C.B., A. Desrochers, J.A. Tremblay, and P. Côte (2020). Comparing fall migration of three Catharus species using a radio-telemetry network. Animal Migration 7:1–8 http://dx.doi.org/10.1515/ami-2020-0001

McKellar, A.E., R.K. Ross, R.I.G. Morrison, L.J. Niles, R.R. Porter, J. Burger, D.J. Newstead, A.D. Dey, and P.A. Smith (2015). Shorebird use of western Hudson Bay near the Nelson River during migration, with a focus on Red Knot. International Wader Study Group 122:201–211 http://dx.doi.org/10.18194/ws.00020

McKinnon, E.A., K.C. Fraser, C.Q. Stanley, and B.J.M. Stutchbury (2014). Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration. PLoS ONE 9: e105605 https://doi.org/10.1371/journal.pone.0105605

McKinnon, E.A., J.A. Rotenberg, and B.J.M. Stutchbury (2015). Seasonal change in tropical habitat quality and body condition for a declining migratory songbird. Oecologia 179: 363–375 https://doi.org/10.1007/s00442-015-3343-1

McKinnon, E.A., T.K. Kyser, and B.J.M. Stutchbury (2017). Does the proportion of arthropods versus fruit in the diet influence overwintering condition of an omnivorous songbird? Journal of Field Ornithology 88: 65–79 http://dx.doi.org/10.1111/jofo.12187

Ministry of Natural Resources and Forestry (2018). Data class name: Wooded area documentation. Contains information licensed under the open government license - Ontario. https://geohub.lio.gov.on.ca/datasets/lio::wooded-area/about

Mitchell, G.W., P.D. Taylor, and I.G. Warkentin (2010). Assessing the function of broad-scale movements made by juvenile songbirds prior to migration. Ornithological Applications 112:644–654 http://dx.doi.org/10.1525/cond.2010.090136

Mitchell, G.W., C.G. Guglielmo, N.T. Wheelwright, C.R. Freeman-Gallant, and D. R. Norris (2011). Early life events carry over to influence pre-migratory condition in a free-living songbird. PLoS ONE 6:e28838. http://dx.doi.org/10.1371/journal.pone.0028838

Mitchell, G.W., B.K. Woodworth, P.D. Talylor, and D.R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Movement Ecology 3:19 https://link.springer.com/content/pdf/10.1186/s40462-015-0046-5.pdf

Moore, L.C., B.J.M. Stutchbury, D.M. Burke, and K.A. Elliot (2010). Effects of forest management on postfledging survival of rose-breasted grosbeaks (*Pheucticus ludovicianus*). Ornithology 127:185–194 http://dx.doi.org/10.1525/auk.2009.09134

Mukhin, A., V. Kosarev, and P. Ktitorov (2005). Nocturnal life of young songbirds well before migration. Proceedings of the Royal Society B 272: 1535−1539 http://dx.doi.org/10.1098/rspb.2005.3120

Müller, F., G. Güppel, and J. Schmalijohann (2018). Does the length of the night affect the timing of nocturnal departures in a migratory songbird? Animal Behaviour 141:183–194 https://doi.org/10.1016/j.anbehav.2018.05.018

Murphy, M.T., L.J. Redmond, A.C. Dolan, N.W. Cooper, C.M. Chutter, and S. Cancellieri (2020). Population decline of a long-distance migratory passerine at the edge of its range: nest predation, nest replacement and immigration. Journal of Avian Biology 51: https://doi.org/10.1111/jav.02286

Naef-Daenzer, B., and M.U. Grüebler (2016). Post-fledging survival of altricial birds: ecological determinants and adaptation. Journal of Field Ornithology 87: 227–250 https://doi.org/10.1111/jofo.12157

Newell, F.L., and M.S. Kostalos (2007). Wood thrush nests in dense understory may be vulnerable to predators. The Wilson Journal of Ornithology 119: 696–702 https://doi.org/10.1676/05-036.1

Nip, E.J., B. Frei, and K.H. Elliott (2018). Seasonal and temporal variation in scaled mass index of Black-capped Chickadees (*Poecile atricapillus*). The Canadian Field-Naturalist 132: 368–377 https://doi.org/10.22621/cfn.v132i4.2015

Nocera, J.J., G.J. Forbes, and L. Giraldeau (2006). Inadvertent social information in breeding site selection of natal dispersing birds. Proceedings of the Royal Society B 273: 349–355 https://doi.org/10.1098/rspb.2005.3318

Norris, D.R., P.P. Marra, T.K. Kyser, T.W. Sherry, and L.M. Ratcliffe (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B 271:59–64 https://doi.org/10.1098/rspb.2003.2569

Norris, D.R. (2005). Carry-over effects and habitat quality in migratory populations. Oikos 109: 178–186 https://doi.org/10.1111/j.0030-1299.2005.13671.x

Norris, D.R., and C.M. Taylor (2006). Predicting the consequences of carry-over effects for migratory populations. Biology Letters 2: 148–151 doi:10.1098/rsbl.2005.0397

Ockendon, N., D. Leech, and J.W. Pearce-Higgins (2013). Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. Biology Letters 9: 20130669 https://doi.org/10.1098/rsbl.2013.0669

Parejo, D., E. Danchin, and J.M. Avilés (2005). The heterospecific habitat copying hypothesis: can competitors indicate habitat quality. Behavioral Ecology 16: 96–105 https://doi.org/10.1093/beheco/arh136

Parker, T.H., B.M. Stansberry, C.D. Becker, and P.S. Gipson (2005). Edge and area effects on the occurrence of migrant forest songbirds. Conservation Biology 19:1157–1167 https://doi.org/10.1111/j.1523-1739.2005.00107.x

Pärt, T., D. Arlt, B. Doligez, M. Low, and A. Qvarnstrőm (2011). Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. Journal of Animal Ecology 80: 1227–1235 https://doi.org/10.1111/j.1365-2656.2011.01854.x

Patchett, R., P. Styles, J.R. King, A.N.G. Kirschel, and W. Cresswell (2022). The potential function of post-fledging dispersal behavior in first breeding territory selection for males of a migratory bird. Current Zoology 68: 708–715 https://doi.org/10.1093/cz/zoac002

Peig, J. and A. J. Green (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118: 1883–1891 https://doi.org/10.1111/j.1600-0706.2009.17643.x

Phillips, J., E. Nol, D. Burke, and W. Dunford (2005). Impacts of housing developments on wood thrush nesting success in hardwood forest fragments. Ornithological Applications 107: 97–106 https://doi.org/10.1093/condor/107.1.97

Pool, D.B., A.O. Panjabi, A. Macias-Duarte, and D.M. Solhjem (2014). Rapid expansion of croplands in Chihuahua, Mexico threatens declining North American grassland bird species. Biological Conservation 170: 274–281 https://doi.org/10.1016/j.biocon.2013.12.019

Powell, L.A. (2007). Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Ornithological Applications 109: 949–954 https://doi.org/10.1093/condor/109.4.949

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rappole, J.H., M.A. Ramos, and K. Winker (1989). Wintering wood thrush movements and mortality in southern Veracruz. Ornithology 106: 402–210 https://doi.org/10.1093/auk/106.3.402

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

Raybuck, D.W., J.L. Larkin, S.H. Stoleson, and T.J. Boves (2019). Radio-tracking reveals insight into survival and dynamic habitat selection of fledgling Cerulean Warblers. Ornithological Applications 122: 1–15 https://doi.org/10.1093/condor/duz063

Richmond, S., E. Nol, and D. Burke (2011). Avian nest success, mammalian nest predator abundance, and invertebrate prey availability in a fragmented landscape. Canadian Journal of Zoology 89: 517–528 https://doi.org/10.1139/z11-017

Richmond, S., E. Nol, and D. Burke (2012). Local-versus landscape-scale effects on the demography of three forest-breeding songbirds in Ontario, Canada. Canadian Journal of Zoology 90:815–828 https://doi.org/10.1139/z2012-051

Ricketts, T. H. (2001). The matrix matters: effective isolation in fragmented landscapes. American naturalist 158: 87–99 https://doi.org/10.1086/320863

Roberts-Pichette, P. and L. Gillespie (1999). Terrestrial vegetation biodiversity monitoring protocols. EMAN Occasional Paper Series, Report No. 9. Ecological Monitoring Coordinating Office, Burlington, Ontario. http://www.muskokawatershed.org/wp-content/uploads/TerrestrialProtocol.pdf

Robinson, S.K., F.R. Thompson III, T.M. Donovan, D.R. Whitehead, and J. Faaborg (1995). Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987–1990 https://doi.org/10.1126/science.267.5206.1987

Rosenberg, K.V., A.M. Dokter, P.J. Blancher, J. R. Sauer, A. C. Smith, P.A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P.P. Marra (2019). Decline of the North American avifauna. Science 366: 120–124 https://doi.org/10.1126/science.aaw1313

Rotella, J.J., S.J. Dinsmore, and T.L. Shaffer (2004). Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205

Rotics, S., S. Turjeman, M. Kaatz, D. Zurell, M. Wikelski, N. Sapir, W. Fiedler, U. Eggers, Y. S. Resheff, F. Jeltsch, and R. Nathan (2021). Early-life behaviour predicts first-year survival in a long-distance avian migrant. Proceedings of the Royal Society B 288: 20202670 https://doi.org/10.1098/rspb.2020.2670

Rush, S.A. and B.J.M. Stutchbury (2008). Survival of fledgling hooded warblers (*Wilsonia citrine)* in small and large forest fragments. Ornithology 125: 183–191 https://doi.org/10.1525/auk.2008.125.1.183

Rushing, C.S., T.B. Ryder, A. L. Scarpignato, J.F. Saracco, and P.P. Marra (2016). Using demographic attributes from long-term monitoring data to delineate natural population structure. Journal of Applied Ecology 53: 491-500 https://doi.org/10.1111/1365-2664.12579

Rushing, C.S., T.B. Ryder, J.J. Valente, T.S. Sillett, and P.P. Marra (2021). Empirical tests of habitat selection theory reveal that conspecific density and patch quality, but not habitat amount drive long-distance immigration in a wild bird. Ecology Letters 24: 1167–1177 https://onlinelibrary.wiley.com/doi/10.1111/ele.13729

Samplonius, J.M., and C. Both (2017). Competitor phenology as a social cue in breeding site selection. Journal of Animal Ecology 86: 615–623 https://doi.org/10.1111/1365-2656.12640

Sauer, J.R., W.A. Link, and J.E. Hines (2017). The North American Breeding Bird Survey, Results and Analysis 1966-2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD. https://www.sciencebase.gov/catalog/item/5f1836a482cef313ed843104

Sauer, J.R., W.A. Link, and J.E. Hines (2019). The North American Breeding Bird Survey, Results and Analysis 1966-2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD. https://www.mbr-pwrc.usgs.gov/bbs/specl19v4.html

Schlossberg, S., D.I. King, S. DeStefano, and M. Hartley (2018). Effects of early-successional shrubland management on breeding wood thrush populations. Journal of Wildlife Management 82: 1572–1581 http://dx.doi.org/10.1002/jwmg.21559

Schmidt, K.A. (2003). Nest predation and population declines in Illinois songbirds: a case for mesopredator effects. Conservation Biology 17: 1141–1150 https://doi.org/10.1046/j.1523-1739.2003.02316.x

Sillett, T.S., and R.T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71: 296–308 https://doi.org/10.1046/j.1365-2656.2002.00599.x

Smetzer, J.R., and D.I. King (2018). Prolonged stopover and consequences of migratory strategy on local-scale movements within a regional songbird staging area. Ornithology 135: 547–560 https://doi.org/10.1642/AUK-18-4.1

Stanley, C.Q., E.A. McKinnon, K.C. Fraser, M.P. MacPherson, G. Casbourn, L. Friesen, P.P. Marra, C. Studds, T.B. Ryder, N. Diggs and B.J.M. Stutchbury (2015). Connecting breeding, wintering, and migration sites by range-wide tracking of a declining migratory songbird. Conservation Biology 29:164–174 https://doi.org/10.1111/cobi.12352

Stanley, C.Q., M.R. Dudash, T.B. Ryder, W.G. Shriver, K. Serno, S. Adalsteinsson, and P.P. Marra (2021). Seasonal variation in habitat selection for a Neotropical migratory songbird using high-resolution GPS tracking. Ecosphere 12: e03421 https://doi.org/10.1002/ecs2.3421

Stanton, R.L., C.A. Morrissey, and R.G. Clark (2018). Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agriculture, Ecosystems & Environment 254: 244–254 https://doi.org/10.1016/j.agee.2017.11.028

Streby, H.M., and D.E. Andersen (2011). Seasonal productivity in a population of migratory songbirds: why nest data are not enough. Ecosphere 2: 1–13 https://doi.org/10.1890/ES10-00187.1

Streby, H.M., J.M. Refsnider, and D.E. Andersen (2014). Redefining reproductive success in songbirds: moving beyond the nest success paradigm. Ornithology 131:718–726 https://doi.org/10.1642/AUK-14-69.1

Studds, C.E., and P.P. Marra (2005). Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86: 2380-2385 https://doi.org/10.1890/04-1145

Stutchbury, B.J.M., S.A. Tarof, T. Done, E. Gow, P.M. Kramer, J. Tautin, J.W. Fox, and V. Afanaylev (2009). Tracking long-distance songbird migration by using geolocators. Science 323: 896 https://doi.org/10.1126/science.1166664

Stutchbury, B.J.M., E.A. Gow, T. Done, M. MacPherson, J.W. Fox, and V. Afanasyev (2011). Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. Proceedings of the Royal Society B 278: 131–137 https://doi.org/10.1098/rspb.2010.1220

Styles, R., R. Patchett, J.R. King, and W. Cresswell (2021). Movements of Cyprus Wheatear *Oenanthe cypriaca* fledglings: evidence of a post-fledging home range away from the natal site prior to first migration. Journal of Ornithology 162: 339–348 https://doi.org/10.1007/s10336-020-01843-z

Szulkin, M. and B.C. Sheldon (2008). Dispersal as a means of inbreeding avoidance in a wild bird population. Proceedings of the Royal Society B 275: 703–711 https://doi.org/10.1098/rspb.2007.0989

Tarof, S.A., P.A. Kramer, J.R. Hill III, J. Tautin, and B.J.M. Stutchbury (2011). Brood size and later breeding are negatively related to juvenile survival in a neotropical migratory songbird. Ornithology 128: 716–725 https://doi.org/10.1525/auk.2011.11087

Taylor, C., and B.J.M. Stutchbury (2016). Effects of breeding versus winter habitat loss and fragmentation on the population dynamics of a migratory songbird. Ecological Applications 26: 424–437 https://doi.org/10.1890/14-1410

Taylor, P.D., T.L. Crewe, S.A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C.M. Francis, C.G. Guglielmo, D.J. Hamilton, R.L. Holberton, P.H. Loring, G.W. Mitchell, D. Norris, J. Paquet, R.A. Ronconi, J. Smetzer, P.A. Smith, L.J. Welch, and B.K. Woodworth (2017). The motus wildlife tracking system: a collaborative research network to enhance the understanding of wildlife movement. Avian Conservation & Ecology 12: 8 https://doi.org/10.5751/ACE-00953-120108

Tewksbury, J.A., L. Garner, S. Garner, J.D. Lloyd, V. Saab, and T.E. Martin (2006). Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. Ecology 87: 759–768 https://doi.org/10.1890/04-1790

Vega Rivera, J.H., J.H. Rappole, W.J. McShea, and C.A. Haas (1998). Wood thrush postfledging movements and habitat use in northern Virginia. Ornithological Applications 100: 69–78 https://doi.org/10.2307/1369898

Vitz, A.C., and A.D. Rodewald (2011). Movements of fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. Ornithology 127: 364–371 https://doi.org/10.1525/auk.2010.09048

Vitz, A.C. and A.D. Rodewald (2013). Behavioral and demographic consequences of access to early-successional habitat in juvenile Ovenbirds (*Seiurus aurocapilla*): an experimental approach. Ornithology 130:21–29 https://doi.org/10.1525/auk.2012.12006

Weathers, W. W., and K. A. Sullivan (1989). Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecological Monographs 59: 223–246 https://doi.org/10.2307/1942600

White, G. C., and K. P. Burnham (1999). Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Supplement):120–138 http://dx.doi.org/10.1080/00063659909477239

Yoder, J.M., E.A. Marschall, and D.A. Swanson (2004). The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. Behavioral Ecology 15: 469–476 https://doi.org/10.1093/beheco/arh037

Zanette, L, and B. Jenkins (2000). Nesting success and nest predators in forest fragments: a study using real and artificial nests. Ornithology 117: 445–454 https://doi.org/10.1093/auk/117.2.445

## Supplementary Material: A2

## Supplement Material: Chapter 2 tables

**Table A2-1**. Location of Motus towers within the study area forest fragments (*n* = 29) on the north shore of Lake Erie, near Port Rowan (42.7131°N, 80.5372°W) in Norfolk County, Ontario Canada.

| Motus Tower | Latitude (°N) | Longitude (°W) |
|---|---|---|
| Walsingham | 42.6353 | 80.5577 |
| Langton | 42.7259 | 80.5625 |
| Turkey Point | 42.7102 | 80.3573 |
| Zorad | 42.7877 | 80.4036 |
| Anderson | 42.6728 | 80.5033 |
| Arthur Langford | 42.6945 | 80.6478 |
| BSC | 42.6154 | 80.4581 |
| Old Cut | 42.5829 | 80.3984 |
| Clear Creek | 42.5819 | 80.5763 |
| Bolin | 42.6226 | 80.7218 |
| Falconer Farm | 42.8142 | 80.5849 |
| Werden | 42.7546 | 80.2708 |
| Waterford Quarry | 42.9155 | 80.3108 |

**Table A2-2.** Full set of temporal models for nest daily survival estimates for Wood Thrush in southern Ontario. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with number of parameters (*k*), and model weight ($w_i$) given for each model.

| Model | *k* | ΔAIC | $w_i$ |
|---|---|---|---|
| ~ *Nest age* | 2 | [a] 0.00 | 1.00 |
| ~ *Constant* | 1 | 22.36 | 0.00 |
| ~ *Time* | 2 | 24.33 | 0.00 |
| ~ *Year* | 3 | 25.31 | 0.00 |
| ~ *Time*$^2$ | 3 | 26.27 | 0.00 |

[a] AICc = 1080.3

**Table A2-3.** Full set of models for nest daily survival estimates for Wood Thrush in southern Ontario using *nest age* (age) as the base model and three spatial scales for % forest cover (FC) (500 m, 2 km, 5 km), nest parasitism (BHCO), distance to forest edge (DistFE) and forest fragment size (FS). Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with number of parameters (*k*), and model weight ($w_i$) given for each model.

| Model | *k* | ΔAIC | $w_i$ |
|---|---|---|---|
| S ~ age + % FC 5 km | 3 | [a] 0.00 | 0.13 |
| S ~ age + BHCO + % FC 5 km | 4 | 0.25 | 0.11 |
| S ~ age + BHCO | 3 | 0.90 | 0.08 |
| S ~ age | 2 | 1.31 | 0.07 |
| S ~ age + DistFE + % FC 5 km | 4 | 1.94 | 0.05 |
| S ~ age + FS + % FC 5 km | 4 | 2.00 | 0.05 |
| S ~ age + BHCO * % FC 5 km | 5 | 2.06 | 0.05 |
| S ~ age + FS + % FC 5 km + BHCO | 5 | 2.21 | 0.04 |
| S ~ age + FS + BHCO | 4 | 2.58 | 0.04 |
| S ~ age + BHCO + % FC 2 km | 4 | 2.66 | 0.03 |
| S ~ age + FS * % FC 5 km | 5 | 2.67 | 0.03 |

| | | | |
|---|---|---|---|
| S ~ age + BHCO + % FC 500 m | 4 | 2.89 | 0.03 |
| S ~ age + % FC 2 km | 3 | 3.08 | 0.03 |
| S ~ age + FS | 3 | 3.10 | 0.03 |
| S ~ age + BHCO * % FC 2 km | 5 | 3.13 | 0.03 |
| S ~ age + DistFE | 3 | 3.30 | 0.02 |
| S ~ age + % FC 500 m | 3 | 3.31 | 0.02 |
| S ~ age + DistFE * % FC 5 km | 5 | 3.42 | 0.02 |
| S ~ age + FS + % FC 5 km + DistFE | 5 | 3.86 | 0.02 |
| S ~ age + BHCO * % FC 500 m | 5 | 4.29 | 0.02 |
| S ~ age + FS * BHCO | 5 | 4.29 | 0.02 |
| S ~ age + FS + % FC 500 m + BHCO | 5 | 4.33 | 0.02 |
| S ~ age + FS + % FC 2 km + BHCO | 5 | 4.60 | 0.01 |
| S ~ age + FS + % FC 500 m | 4 | 4.87 | 0.01 |
| S ~ age + DistFE + % FC 2 km | 4 | 5.02 | 0.01 |
| S ~ age + FS + DistFE | 4 | 5.06 | 0.01 |
| S ~ age + DistFe + % FC 500 m | 4 | 5.30 | 0.01 |
| S ~ age + DistFE * % FC 500 m | 5 | 6.35 | 0.01 |
| S ~ age + DistFE * % FC 2 km | 5 | 6.55 | 0.01 |
| S ~ age + FS * % FC 500 m | 5 | 6.86 | 0.00 |
| S ~ age + FS + % FC 500 m + DistFE | 5 | 6.88 | 0.00 |
| S ~ age + FS + % FC 2 km + DistFE | 5 | 6.99 | 0.00 |
| S ~ age + FS * DistFE | 5 | 7.03 | 0.00 |
| S ~ age + FS * % FC 2 km | 5 | 7.06 | 0.00 |
| S ~ constant | 1 | 28.50 | 0.00 |

[a] AICc = 1097.30

**Table A2-4.** Full set of time-dependent models for determining the probability of detecting live tagged (*p*) fledgling Wood Thrush across 29 forest fragments in southern Ontario over a 3-year survey period, 2016-2018 (*n*=189 fledglings). Models were run holding *S* (survival) constant, r (~1) and *F* (=1). Parameters included calendar year (Year), linearly changing with age (Age), fledge date (FD) and age categories of 2 (age2 - 0-8d, 9-16d), 3 (age3 - 0-8d, 9-12d, 13-16d), age groups. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with number of parameters (*k*), and model weight ($w_i$) given for each model.

| Model | *k* | ΔAIC | $w_i$ |
|---|---|---|---|
| ~ age3 + year | 7 | [a] 0.00 | 0.59 |
| ~ age3 | 5 | 1.35 | 0.30 |
| ~ age3 + FD | 6 | 3.38 | 0.11 |
| ~ Age + year | 6 | 26.21 | 0.00 |
| ~ Age | 4 | 27.66 | 0.00 |
| ~ Age + FD | 5 | 29.66 | 0.00 |
| ~age2 + year | 6 | 32.04 | 0.00 |
| ~ age2 | 4 | 33.48 | 0.00 |
| ~ age2 + FD | 5 | 35.48 | 0.00 |
| ~ year | 5 | 37.92 | 0.00 |
| ~ 1 | 3 | 39.71 | 0.00 |
| ~ year+ FD | 6 | 39.96 | 0.00 |
| ~ FD | 4 | 41.66 | 0.00 |

[a] AICc = 929.07

**Table A2-5**. Full model set of time-dependent models for Wood Thrush fledgling survival (*S*) across 29 forest fragments in southern Ontario over a 3-year survey period, 2016-2018 *(n* =189 fledglings). For all models *p* (probability of detecting a live tagged fledgling) was modelled as *p(age3 + Year)*. Survival models included calendar year (Year), linearly changes with fledgling age (Age), non-linearly changes with fledgling age ($Age^2$), time dependent (Time), fledge date (FD), 3 age categories of 2 (age2 - 0-8d, 9-16d), 3 (age3 - 0-8d, 9-12d, 13-16d), and 4 (age4 - 0-4d, 5-8d, 9-12d, 13-16d) age groupings. Models are ranked by Akaike's Information Criterion

(AIC) with small sample size adjustment (AICc), with number of parameters ($k$), and model weight ($w_i$) given for each model.

| Model | $k$ | ΔAIC | $w_i$ |
|---|---|---|---|
| ~ Age | 8 | [a] 0.00 | 0.26 |
| ~ Age + FD | 9 | 2.00 | 0.10 |
| ~ age3 | 9 | 2.03 | 0.10 |
| ~ $Age^2$ | 9 | 2.05 | 0.09 |
| ~ age2 | 8 | 2.49 | 0.08 |
| ~ age4 | 10 | 2.90 | 0.06 |
| ~ Age + year | 10 | 4.96 | 0.06 |
| ~ age3 + FD | 10 | 4.06 | 0.03 |
| ~ $Age^2$ + FD | 10 | 4.06 | 0.03 |
| ~ age2 + FD | 9 | 4.52 | 0.03 |
| ~ Time | 11 | 4.64 | 0.03 |
| ~ age4 + FD | 11 | 4.92 | 0.02 |
| ~age3 + year | 11 | 4.97 | 0.02 |
| ~ $Age^2$ + year | 11 | 5.02 | 0.02 |
| ~Age + year + FD | 11 | 5.02 | 0.02 |
| ~age2 +year | 10 | 5.47 | 0.01 |
| ~age4 + year | 12 | 5.86 | 0.00 |
| ~age3 + year + FD | 12 | 7.04 | 0.00 |
| ~ age2 + FD + year | 11 | 7.53 | 0.00 |
| ~ age4 + FD + year | 13 | 7.94 | 0.00 |
| ~1 | 7 | 15.81 | 0.00 |
| ~ FD | 8 | 17.74 | 0.00 |
| ~ year | 9 | 18.69 | 0.00 |
| ~ year + FD | 10 | 20.71 | 0.00 |
| ~$Age^2$ + year + FD | 12 | 51.07 | 0.00 |
| ~Time + year | 13 | 51.85 | 0.00 |

[a] AICc = 913.25

**Table A2-6.** Full environmental model set for Wood Thrush fledgling survival across 29 forest fragments in southern Ontario over a 3-year survey period, 2016-2018 (*n* = 189 fledglings). Survival models used the base temporal model (*S (Age) p(age3 + Year)*) and additional covariates of forest fragment size (FS), % forest cover (FC) at three spatial scales (500 m, 2 km, 5 km), nestling body condition (BC), mean # of trees with DBH >30 cm (DBH), and mean % shrub and sapling cover (SC). Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with number of parameters (*k*), and model weight ($w_i$) given for each model.

| Model | *k* | ΔAIC | $w_i$ |
|---|---|---|---|
| ~ Age + BC | 8 | [a] 0.00 | 0.20 |
| ~Age + % FC 2 km + BC | 9 | 1.38 | 0.10 |
| ~Age | 7 | 1.58 | 0.09 |
| ~Age + % FC 500 m + BC | 9 | 1.95 | 0.07 |
| ~Age + % FC 5 km + BC | 9 | 2.07 | 0.07 |
| ~ Age+ % FC 2 km | 8 | 2.90 | 0.05 |
| ~Age + % SC | 8 | 3.17 | 0.04 |
| ~Age + FS | 8 | 3.37 | 0.04 |
| ~ Age + % FC 2 km * BC | 10 | 3.43 | 0.04 |
| ~Age + % FC 500 m | 8 | 3.53 | 0.03 |
| ~Age + DBH | 8 | 3.62 | 0.03 |
| ~ Age+ % FC 5 km | 8 | 3.63 | 0.03 |
| ~Age + %FC 500 m * BC | 10 | 4.01 | 0.03 |
| ~ Age+ % FC 5 km * BC | 10 | 4.03 | 0.03 |
| ~ Age + % FC 2 km + % SC | 9 | 4.66 | 0.02 |
| ~Age + FS + % FC 2 km | 9 | 4.91 | 0.02 |
| ~ Age + % FC 2 km + DBH | 9 | 4.95 | 0.02 |
| ~Age + FS + % SC | 9 | 5.09 | 0.02 |

|  |  |  |  |
|---|---|---|---|
| ~Age+ FS + % FC 500 m | 9 | 5.42 | 0.01 |
| ~Age + FS + DBH | 9 | 5.43 | 0.01 |
| ~Age + % FC 2 km * % SC | 10 | 5.55 | 0.01 |
| ~Age + % FC 500 m + DBH | 9 | 5.59 | 0.01 |
| ~Age + % FC 5 km * DBH | 10 | 5.65 | 0.01 |
| ~Age+ FS * % FC 5 km | 10 | 6.35 | 0.01 |
| ~Age+ FS * % FC 2 km | 10 | 6.68 | 0.01 |
| ~Age + FS * DBH | 10 | 6.77 | 0.01 |
| ~Age + FS * % SC | 10 | 7.15 | 0.01 |
| ~Age + FS + BC | 9 | 47.26 | 0.00 |
| ~Age + FS * BC | 10 | 49.31 | 0.00 |
| ~Age + % FC 5 km +% SC | 9 | 49.73 | 0.00 |
| ~Age + % FC 500 m +% SC | 9 | 49.99 | 0.00 |
| ~Age+ FS + % FC 5 km | 9 | 50.92 | 0.00 |
| ~Age + % FC 500 m * % SC | 10 | 50.98 | 0.00 |
| ~Age + % FC 5 km + DBH | 9 | 51.04 | 0.00 |
| ~Age + % FC 2 km * % SC | 10 | 51.93 | 0.00 |
| ~Age + % FC 500 m * DBH | 10 | 51.94 | 0.00 |
| ~Age+ FS * % FC 500 m | 10 | 52.68 | 0.00 |
| ~Age + % FC 2 km * DBH | 10 | 52.97 | 0.00 |

[a] AICc = 899.29

### Departure Date Methods A2-7

Motus tower data records were accessed using the *motus* and *motusData* R packages and cleaned following guidelines provided by Birds Canada (2022). The Motus filter was applied to flag detections that had a run length < 3 to minimize false positive records but on occasion were incorporated when there were additional supporting detections such as filling a time gap between towers with positive detections (3 instances). Subsequently, we manually reviewed all detections (individual hits received by each tower) that the Motus filter had flagged as true positives and removed any that had different pulse rates to 12.7 sec, occurred in unlikely locations (e.g., outside the breeding range), or were well outside of migration routes that have been identified for Wood Thrush in previous geolocator studies (Stutchbury et al. 2009). For each tagged juvenile, detections were ordered by date, time of day, and each Motus tower providing a full chronological profile of movement activity after the bird was no longer detected using manual radio telemetry at its natal site.

To determine fall migration dates for each of the tagged juveniles, we categorized the movements of each individual as either a premigration or fall migration movement. As the location of the study area is on the north shore of Lake Erie, we assumed that if a bird flew in a southerly direction across the lake (~50 km) that this must be a migratory movement. There were 27 tagged juveniles that were last detected by a tower within the study area and subsequently detected at a tower on the south side of Lake Erie on the same night and within a reasonable time frame (birds flying at ~50 km/h). We determined the average departure date and time of day of these individuals that were known to be undergoing their first migratory flight (avg. Sept. 19th, range Aug. 30h to Sept. 29th). We used the R package *circular* (Agostinelli and Lund 2022) to analyze if the time of migratory flight departure was non-random, as would be expected for true migratory flights which typically occur just after sunset. As expected, the time of day of these migratory movements was non-random ($\overline{R}$= 0.654, $P$ <0.001) and on average within 1 hr. and 18 mins. of local sunset.

Second, we used these times of first migratory flight results, to identify individuals who did not have detections the same night on both the north and south side of Lake Erie, but whose dates and time of day of departure were closely within the same range as the unambiguous fall migration movements. There were 55 individuals whose movements were categorized as a likely first migratory flight. These movements were also non-random ($\bar{R}$= 0.609, $P$ <0.001) with departures on average occurring at 21:05 about an hour after sunset (avg. departure date = Sept. 19, range = Aug. 25 to Oct. 15). We subsequently combined these 55 individuals with the unambiguous departures for analysis of departure date ($n$ = 82). Using the Motus network, we determined fall migration departure date for 82 of 133 (62%) nestlings that were known to have survived the fledgling period.

**Table A2-8.** Motus tower locations outside of the study area for 6 juveniles that were detected the following spring after being radio-tagged. Tag ID 24 was detected in the study area on several occasions from May 24 to June 8 by 4 different Motus towers leading up to the final detection.

| Motus Tag ID | Motus Tower | Latitude (°N) | Longitude (°W) | Distance from Outer Perimeter of Study Area (km) | Date of Spring Motus Detection |
|---|---|---|---|---|---|
| 211 | Hagersville Landfill (Ontario) | 42.9863 | 80.1281 | 28 | May 31 |
| 24 | Alymer (Ontario) | 42.8005 | 80.9460 | 28 | June 8 |
| 373 | West Port Bruce (Ontario) | 42.6616 | 81.0627 | 30 | May 9 |
| 18 | Rondeau Provincial Park (Ontario) | 42.2824 | 81.841 | 110 | May 10 |
| 494 | PresqueIsle (Pennsylvania) | 42.1098 | 80.1541 | 56 | May 9 |
| 400 | Girard (Pennsylvania) | 41.9856 | 80.3379 | 65 | May 22 |

**Table A2-9.** Summary of Wood Thrush apparent survival at three stages of the life cycle: (1) fledgling survival (up to 16 days after leaving the nest), (2) pre-migration survival (16 days after fledgling to fall migration period), and (3) migration/wintering survival (fall departure to spring arrival). First year annual survival was calculated from fledging to spring arrival the next year.

| Tag Year | Total Tagged | Fledgling Survival *(# fledglings survived (to 16d))* | Pre-Migration Survival *(# 16d old fledglings later detected on fall migration)* | Migration/Wintering Survival *(# juveniles detected on fall migration that returned the next spring)* | Apparent Annual Survival |
|---|---|---|---|---|---|
| 2016 | 47 | 33 (70.2%) | 31 (93.9%) | 10 (32.3%) | 21.3% |
| 2017 | 66 | 50 (75.8%) | 42 (84.0%) | 10 (23.8%) | 15.2% |
| 2018 | 76 | 50 (65.8%) | 46 (92.0%) | 11 (23.9%) | 14.5% |
| *Total* | 189 | 133 (70.4%) | 119 (89.5%) | 31 (26.1%) | 16.4% |

# Supplementary Material: B3

## Supplementary Material: Chapter 3 tables and figures

**Table B3-1.** Top competing models (with ΔAICc <2) for age at first detection > 5 km away from the natal site for juvenile Wood Thrushes (*n* = 93). Generalized linear models included additive predictors of natal forest fragment size, fledge date, sex, and year. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight ($w_i$) given for each model.

| **Model** | **df** | **LL** | **ΔAIC** | $w_i$ |
|---|---|---|---|---|
| ~ fledge date + year | 5 | -401.64 | *0.00 | 0.51 |
| ~ fledge date + year + sex | 6 | -401.09 | 1.18 | 0.29 |
| ~ fledge date + year + fragment size | 6 | -401.44 | 1.89 | 0.20 |

*AICc = 813.97

**Table B3-2.** Top competing models (with ΔAICc <2) for duration of pre-migratory period > 5 km from the natal forest fragment for juvenile Wood Thrushes (*n* = 93), as estimated from the first detection to the last pre-migratory detection. Generalized linear models included additive predictors of natal forest fragment size, fledge date, sex, and year. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight ($w_i$) given for each model.

| **Model** | **df** | **LL** | **ΔAIC** | $w_i$ |
|---|---|---|---|---|
| ~ age at dispersal + fledge date + sex + year | 6 | -396.13 | *0.00 | 0.64 |
| ~ age at dispersal + fledge date + sex | 4 | -398.95 | 1.13 | 0.36 |

*AICc = 805.23

**Table B3-3.** Top competing models (with ΔAICc <2) for total number of Motus tower detections during pre-migratory period away from the natal forest fragment for juvenile Wood Thrushes (*n* = 93). Generalized linear models included additive predictors of natal forest fragment size, fledge date, sex, and year. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight ($w_i$) given for each model.

| Model | df | LL | ΔAIC | $w_i$ |
|---|---|---|---|---|
| ~ age at dispersal + year | 4 | -189.98 | *0.00 | 0.49 |
| ~ age at dispersal + year + fragment size | 5 | -189.23 | 1.13 | 0.33 |
| ~ age at dispersal + fragment size + sex | 5 | -189.85 | 1.99 | 0.18 |

*AICc = 388.41

**Table B3-4.** Top competing models (with ΔAICc <2) for farthest distance travelled during pre-migratory period away from the natal forest fragment for juvenile Wood Thrushes (*n* = 93). Generalized linear models included additive predictors of natal forest fragment size, fledge date, sex, and year. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight ($w_i$) given for each model.

| Model | df | LL | ΔAIC | $w_i$ |
|---|---|---|---|---|
| ~ year + fragment size | 5 | -339.38 | *0.00 | 0.33 |
| ~ year | 4 | -341.13 | 0.47 | 0.26 |
| ~ year + fragment size + age at dispersal | 6 | -339.39 | 1.51 | 0.16 |
| ~ year + age at dispersal | 5 | -340.73 | 1.89 | 0.13 |
| ~ year + fragment size + sex | 6 | -339.61 | 1.95 | 0.12 |

*AICc = 690.26

**Table B3-5**. Top competing models (with ΔAICc <2) for fall migration departure date of juvenile Wood Thrushes (*n* = 20). Generalized linear models included additive predictors of three pre-migratory movements; duration of pre-migration dispersal period (Dur), maximum distance travelled from natal site (MaxDist), and total number of unique Motus tower detections (#Towers). Fledge date (FD) and sex were also added to the models. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight ($w_i$) given for each model.

| Model | df | LL | ΔAIC | $w_i$ |
|---|---|---|---|---|
| ~ FD + #Towers | 4 | -53.88 | *0.00 | 0.47 |
| ~ FD + #Towers + MaxDist | 5 | -52.54 | 0.93 | 0.29 |
| ~ FD + #Towers + Dur | 5 | -52.73 | 1.32 | 0.24 |

*AICc = 118.4

**Table B3-6.** Top competing models (with ΔAICc <2) for first flight orientation models for juvenile Wood Thrushes (*n* = 20). Generalized linear models included additive predictors of three pre-migratory movements; duration of pre-migratory dispersal period (Dur), maximum distance travelled from natal site (MaxDist), and total number of unique Motus tower detections (#Towers). Fledge date (FD) and sex were also added to the models. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight ($w_i$) given for each model.

| Model | df | LL | ΔAIC | $w_i$ |
|---|---|---|---|---|
| ~ FD | 3 | -89.01 | *0.00 | 0.26 |
| ~ 1 | 2 | -90.43 | 0.04 | 0.25 |
| ~ FD + MaxDist | 4 | -88.03 | 1.20 | 0.14 |
| ~ FD + #Towers | 4 | -88.12 | 1.39 | 0.13 |
| ~ Dur | 3 | -89.82 | 1.62 | 0.12 |
| ~ MaxDist | 3 | -89.99 | 1.96 | 0.10 |

*AICc = 185.5

**Table B3-7.** Top competing models with ΔAICc <2 for first flight pace models for juvenile Wood Thrushes (*n* = 20). Generalized linear mixed effect models included additive predictors of three pre-migratory movements; duration of pre-migratory dispersal period (Dur), maximum distance travelled from natal site (MaxDist), and total number of unique Motus tower detections (#Towers). Fledge date (FD) and sex were also added to the models with year included as a random effect. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model averaged weight ($w_i$) given for each model.

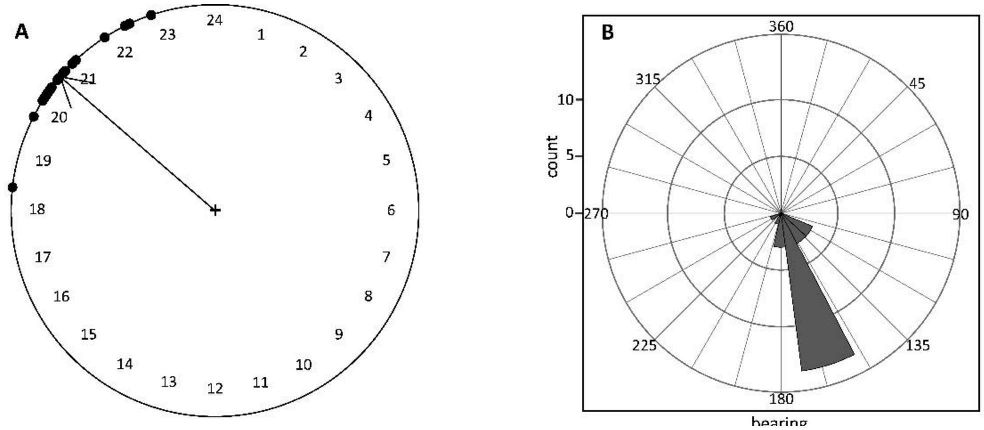
| Model | df | LL | ΔAIC | $w_i$ |
|---|---|---|---|---|
| ~ Dur + FD | 4 | -79.91 | *0.00 | 0.22 |
| ~ Dur + FD + MaxDist | 5 | -78.27 | 0.35 | 0.18 |
| ~ Dur | 3 | -81.86 | 0.75 | 0.15 |
| ~ FD + MaxDist | 4 | -80.31 | 0.81 | 0.14 |
| ~ FD + #Towers | 4 | -80.38 | 0.94 | 0.14 |
| ~ FD | 3 | -82.39 | 1.80 | 0.09 |
| ~ Dur + FD +#Towers | 5 | -79.03 | 1.87 | 0.08 |

*AICc = 170.5

**Table 8.** First flight distance travelled models with <2 ΔAICc for juvenile Wood Thrushes (*n* = 20). General linear models included additive predictors of three pre-migratory movements; duration of pre-migratory dispersal period (Dur), maximum distance travelled from natal site (MaxDist), and total number of unique Motus tower detections (#Towers). Fledge date (FD) and sex were also added to the models. Models are ranked by Akaike's Information Criterion (AIC) with small sample size adjustment (AICc), with degrees of freedom (df), log likelihood (LL), and model weight ($w_i$) given for each model. Models were not averaged as intercept model only competing model with <2 ΔAICc.

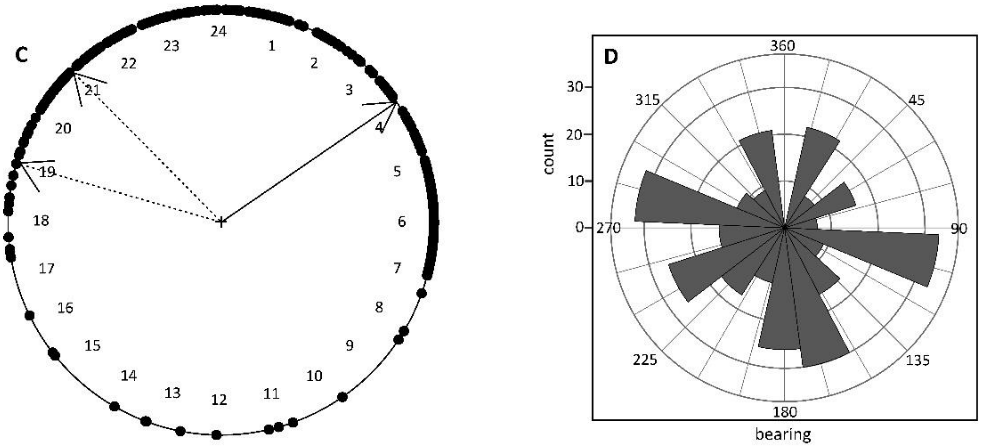
| Model | df | LL | ΔAIC | $w_i$ |
|---|---|---|---|---|
| ~ 1 | 2 | -86.93 | *0.00 | 0.32 |
| ~ FD | 3 | -86.64 | 2.21 | 0.11 |
| ~ #Towers | 3 | -86.66 | 2.25 | 0.10 |
| ~ MaxDist | 3 | -86.79 | 2.50 | 0.09 |
| ~ Dur | 3 | -86.79 | 2.51 | 0.09 |

*AICc = 178.6



mean departure time 20:48 range = 18:26 to 22:47, $\overline{R}$= 0.713, *P* < 0.001

mean =171°, $\overline{R}$= 0.925, *P* < 0.001



mean local pre-migratory flight times = 03:42, $\overline{R}$= 0.383, *P* < 0.001

mean =220°, $\overline{R}$= 0.108, *P* = 0.46

**Figure B3-1.** Circular graph depicting time of day (0 to 24 hr. clock) and directional movement for juvenile Wood Thrushes based on Motus tower detections to classify movements as pre-migratory or migratory. Unambiguous first migratory flight (*n* = 25 individuals) classed by: **(A)** Time of day for first flight; and **(B)** Direction of first fall migration flight. Pre-migratory flights (*n* = 93 individuals) classed by: **(C)** Time of day of movements; and **(D)** Direction of movements. Solid arrow indicates the average departure/movement time and dashed arrow indicating average local sunset time (range for sunset given by two broken arrows in Figure C from July 3 – 9:03 pm to Oct. 1 – 7:04).

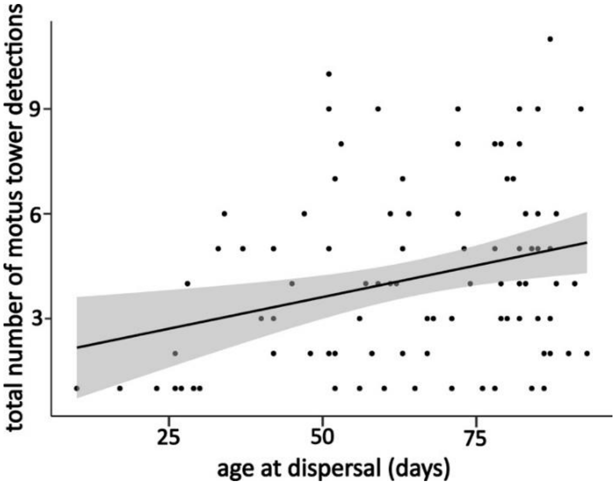


**Figure B3-2**. Total number of unique Motus tower detections for juvenile Wood Thrushes during pre-migratory movements (*n* = 93) with age at first detection > 5 km from the natal site (0.148±0.064, *P* <0.001), and grey shading indicating 95% confidence interval around trend line (Table 3-3, Supplementary Material Table B3-3).

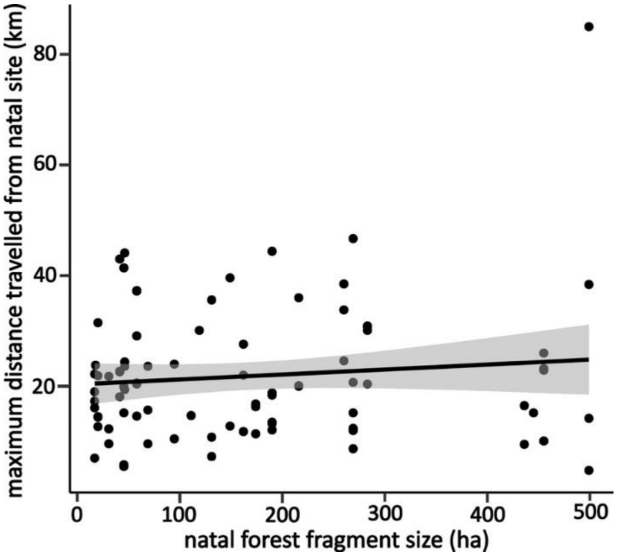


**Figure B3-3.** Maximum distance travelled from natal site as detected by the Motus tower network during pre-migratory landscape movements for juvenile Wood Thrushes (*n* =93) with natal forest fragment size (0.050±0.057, *P* = 0.38). Grey shading indicating 95% confidence interval around trend line. (Table 3-4, Supplementary Material Table B3-4).

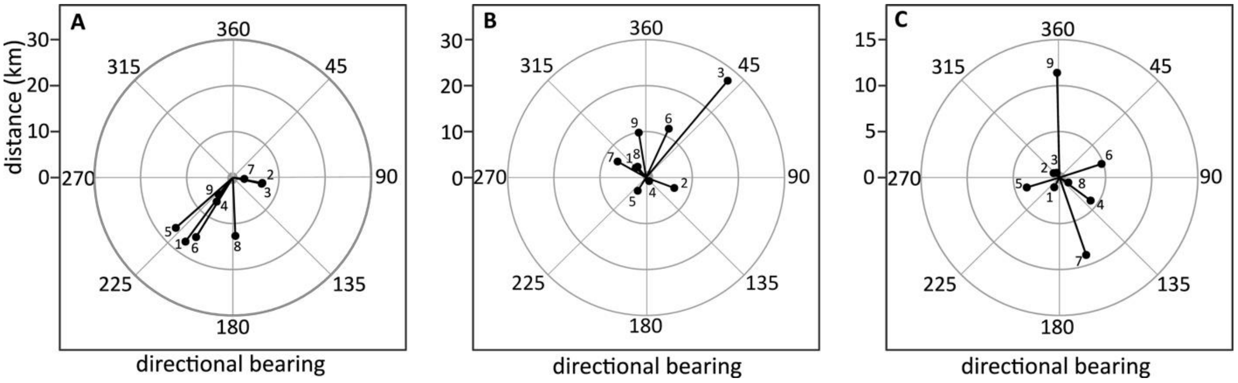


**Figure 7.** Direction and distance of Motus detections (A, B) and first breeding site (C) for juvenile Wood Thrushes with known breeding sites the next year in the study area (*n* = 9, labelled 1-9). For each bird, the center point is its natal site and distance is represented by the grey circular lines. Circular plots show the location (relative to each bird's natal site) of **(A)** last dispersal detection prior to onset of fall migration, **(B)** last spring Motus tower detection, and **(C)** location of first breeding site (Table 3-5).

# Supplementary Material: C4

## Supplement Material: Chapter 4 abstracts and citations of collaborative work

The following manuscripts were indirectly part of this thesis using data collected during this project.

1) Israel, A.M., S. Hayes, B.P., Boyd, and B.J.M. Stutchbury (2023). Effects of nest concealment on nest predation and cowbird parasitism, flight initiation distance and female stress levels in the Wood Thrush (2023). Journal of Field Ornithology 94: 9 https://doi.org/10.5751/JFO-00206-940109

Contribution: I assisted in the data collection for this project and completed the nest survival analyses for the manuscript.

Temperate zone songbirds in North America can experience high levels of nest predation and Brown-headed Cowbird (Molothrus ater) parasitism, which may contribute to population declines, and an important question is whether nesting females can mitigate these threats through greater nest concealment. However, there is little known about the pros and cons of nest concealment to the incubating female, and whether concealment influences female corticosterone levels or nest escape behavior to potentially reduce risk of predation on females. This study investigates whether nest concealment resulted in reduced risk of nest predation and Brownheaded Cowbird parasitism in the Wood Thrush (Hylocichla mustelina), a forest bird that is declining across most of its range. We monitored nests (n = 186) in a highly fragmented forest landscape in southwestern Ontario, Canada and found high nest predation (53.2%) and moderate cowbird parasitism (25.3%). Overall nest concealment, nest height, and forest fragment size were not good predictors of daily nest survival or cowbird parasitism, but greater nest concealment one meter above the nest strongly reduced nest predation risk. We speculate that because most Wood Thrush nests are relatively low (< 2.5 m above ground), above-nest concealment may be effective against detection by avian nest predators. Overall nest concealment was not negatively correlated with flight initiation distance (FID) or positively related to baseline corticosterone level. This suggests that high nest concealment does not increase stress or personal risk to incubating females; however, nest concealment manipulations are needed to further explore whether any such tradeoffs exist.

2) Boyd, B.P., S. Hayes, A.M. Israel, B.J.M. Stutchbury (2023). Breeding season forest fragment size does not create negative carry-over for adult Wood Thrushes on fall migration timing or annual survival. Ornithological Applications duad028 https://doi.org/10.1093/ornithapp/duad028

Contribution: I assisted in project start up and design (selected forest fragments, landowner permissions, data collection permits, etc.) and data collection for this project.

Although carry-over effects related to wintering habitat quality are known to influence population dynamics of migratory songbirds, the presence of breeding season carry-over is under-studied in full annual cycle models. To test whether forest fragment size on the breeding grounds can impose negative carry-over effects on a migratory songbird, we fitted adult Wood Thrushes with one-year coded radio-tags in forest fragments ranging from 11–499 ha in southwestern Ontario during the 2016–2019 breeding seasons and utilized automated telemetry via the Motus Wildlife Tracking System to record fall migration timing and returns the following spring (apparent annual survival). To examine short-term effects of fragment size on breeding females, during the 2018 and 2019 breeding seasons, we collected blood samples during incubation to measure corticosterone levels and tracked complete reproductive success and nest timing. We found that Wood Thrushes breeding in small forest fragments were not subject to strong negative effects on body condition (mass, corticosterone), reproductive success, or timing of the last nest of the season. Next, we found that the onset of fall migration departure was not delayed for birds nesting in small fragments and that apparent annual survival was not linked to breeding fragment size. This suggests that habitat differences linked to fragment size were not strong enough to trigger the kinds of negative carry-over effects (delayed migration, lower reproductive success) that have been documented in other species as a result of poor wintering ground habitat quality. The strength of breeding fragment size-induced seasonal carry-over remains a critical gap in full annual cycle models for other declining migratory songbirds. Our findings suggest that while the importance of preserving large forested areas is often prioritized in conservation projects, small forest fragments can also have high conservation value.