

**CARRY-OVER EFFECTS OF FOREST FRAGMENTATION ON  
BREEDING ADULT WOOD THRUSHES (*HYLOCICHLA MUSTELINA*)**

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## Abstract

Full annual cycle research has become increasingly important as more evidence is found of connections between events that occur during different periods of the annual cycle, sometimes thousands of kilometers apart. For instance, long term negative carry-over effects arising from poor quality wintering habitat in the tropics have been shown to reduce future reproductive success and survival. Habitat loss and fragmentation on the breeding grounds have a negative effect on immediate breeding success of many bird species; however, short-term impacts on adult body condition and long-term impacts on migration and survival have not been studied. Individuals occupying small forest fragments are expected to experience high rates of cowbird brood parasitism, higher nest predation, and lower food availability which could directly delay fall migration due to timing constraints from late re-nesting or indirectly delay migration if adults are in poorer condition. If small fragments are lower quality habitat, breeding adults are also expected to have lower relative mass, and higher baseline levels of blood corticosterone. During the 2016-2019 breeding seasons, I fitted 117 adult Wood Thrushes with coded radio-tags in a variety of large and small forest fragments in Norfolk County, Ontario, to track their movements using Motus. For two years of the study, I also collected blood samples to measure corticosterone levels. I found that fragment size was related to many vegetation variables (e.g. density of trees, shrubs, groundcover) as expected, but it did not have a strong effect on relative mass or blood corticosterone of adults. Contrary to prediction, season-long reproductive success was also not lower in small fragments. In addition, I found that fall migration timing and annual survival were also not related to fragment size. Overall, I found no evidence that breeding habitat quality has a significant negative short-term or long-term effect on Wood Thrushes. This suggests that small forest fragments can provide good quality breeding habitat for forest songbirds and differences in quality between small and large fragments are not strong enough to trigger the kinds of negative carry-over effects that have been documented in other species on the wintering grounds.

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**Chapter 1: General Introduction**

### *Forest fragmentation and bird conservation*

The alarming decline of North American songbirds was first brought to light in the 1980s and has become one of the most studied and publicized conservation issues today. The continent-wide North American Breeding Bird Survey began in 1966, and by the late 1980s it had documented trends pointing to a steep decrease in migratory bird populations that quickly garnered significant attention from the scientific community and national media. Forest-dwelling migrants that wintered in forests of the Neotropics were declining the most steeply (Ambuel and Temple 1982; Wilcove 1985; Robbins, Sauer et al. 1989) suggesting a link to the high rates of tropical deforestation that had occurred in recent decades. Year-round residents and short-distance migrants to the U.S. did not show the same general pattern of decrease (Robbins, Sauer et al. 1989) which further suggested that tropical deforestation was likely the driving force of observed declines.

However, other research had shown that deforestation and fragmentation on the temperate breeding grounds strongly reduced reproductive success, with some researchers even suggesting that this was likely the main culprit for population declines (Ambuel and Temple 1982; Holmes and Sherry 1988; Hutto 1988; Bohning-Gaese et al. 1993; Askins 1995, Donovan and Flather 2002). Breeding ground events could drive population declines via increased brood parasitism of nests by Brown-headed Cowbirds (*Molothrus ater*) (Brittingham and Temple 1983) and higher nest predation rates (Wilcove 1985) in small fragments. There is still debate surrounding the causes of decline in even well-studied species like the Wood Thrush, with one modelling approach suggesting breeding ground drivers while another finding strong support for wintering ground drivers (Rushing, Ryder et al. 2016; Taylor and Stutchbury

2016). The common underlying theme of these studies, whether they implicated the wintering grounds or breeding grounds, was that the fragmentation of once continuous forest habitats into smaller pieces through increased urbanization, agriculture, and other human development was creating multiple stressors on migratory songbirds.

The net loss of habitat is perhaps the most obvious result of forest fragmentation (e.g. Murcia 1995) but the destruction of forested land often leaves behind fragments that are isolated and separated by a matrix of human-transformed land cover (e.g. Haddad et al. 2015). Forest fragments are often compared to islands using the principles outlined in MacArthur and Wilson's 1967 revolutionary book *The Theory of Island Biogeography*. Specifically, MacArthur and Wilson proposed that island biodiversity is balanced by immigration and extinction, which in turn are influenced by island size and degree of isolation. The largest, least isolated islands are expected to have the highest diversity and the smallest, most isolated islands have the least diversity. In 1975, Jared Diamond used the principles of island biogeography to suggest a set of rules for the design of conservation reserves in a fragmented landscape. They proposed that a single large reserve would be superior to any combination of smaller reserves that match the same total area. Early field studies on North American birds confirmed that the number of species does increase with forest size (Galli et al. 1976) and that total area along with the degree of isolation of a fragment was more important in predicting number of species than any habitat variables (Robbins, Dawson, et al. 1989). Lynch and Whigham (1984) found that both land area and degree of isolation were significant factors in predicting the presence of many species. In Connecticut, Askins et al. (1987) also found that species richness and density were related to fragment size.

Forest fragmentation can also lead to the loss of diversity through the creation of extensive forest edge (Haddad et al. 2015). As the land area of a forest gets smaller, the proportion of edge to interior habitat of the forest also increases, and the temperature of edge habitat is typically hotter and drier, with lower humidity and less soil moisture (Kapos 1989; Saunders et al. 1991) which can lead to smaller fragments having low invertebrate diversity and abundance (Klein 1989). Many studies found that species richness of North American breeding passerines was positively correlated with the size of forest fragments and that some species had minimum size requirements (Forman et al. 1976; Galli et al. 1976; Ambuel and Temple 1983). Blake and Karr (1984) discovered that although large fragments did not necessarily have more species than combinations of smaller fragments that equaled the same land area, some long-distance migrants and interior species were only located in large fragments.

The idea of fragmentation being bad for biodiversity has been a dogma in bird conservation research since it began, but in 2003, Lenore Fahrig published a review on habitat fragmentation studies and found that many studies were looking at the effects of patch scale (e.g. fragment size) on species abundance and richness, but were not testing for fragmentation effects at the landscape scale. They concluded that there was little evidence that one large habitat patch was of greater ecological value than the same area fragmented into smaller, widely separated patches. While small fragments may have lower species richness than large ones, there could be landscape-level benefits of fragmentation that counteract the negative effects that occur at a smaller spatial scale. For instance, with the same total amount of forested habitat, avian species richness should be the same in a fragmented versus non-fragmented landscape because the former provides more diverse habitat. Testing her “habitat

amount hypothesis” would require an experimental design that compares landscapes that have the same total forest cover, but which differ widely in extent of fragmentation (Fahrig 2017). This idea was so contrary to current thinking at the time that it ignited a debate that continues to this day (Fletcher Jr et al. 2018; Fahrig et al. 2019; Fahrig 2021; Saura 2021). The studies intended to test the HAH have ended with mixed results but those conducted on migratory birds in Ontario have found strong support (De Camargo et al. 2018) and partial support (Torrenta and Villard 2017) for the hypothesis. De Camargo et al. (2018) divided the province into 100km<sup>2</sup> regions and looked at how species richness was affected by the degree of fragmentation after controlling for the total amount of habitat in each region. Overall, they found that species richness was strongly related to habitat amount, while fragmentation had no additional affect; however, they still found that 13% of forest bird species used in the study had significant negative responses to fragmentation. Torrenta and Villard (2017) opted for a different approach, conducting point counts in only five regions, and quantifying landscape at three spatial scales of 500m, 1000m, and 1500m. While they found evidence that habitat amount can provide an indication of species richness, fragment size was the better predictor in most cases. Both of these studies highlight that habitat amount may be important in predicting species richness, but in the context of migratory songbirds, degree of fragmentation also remains an important factor.

#### *Fragmentation effects on reproductive success and demography*

These studies on avian diversity in fragmented landscapes gave support to the idea that small fragments provided unsuitable habitat for many species of long-distance migrants and

concurrent research had begun to tease apart the underlying mechanisms of why this was the case. In 1983, Brittingham and Temple showed that the rate of brood parasitism by Brown-headed cowbirds decreased for nests that were farther from a forest opening or the forest edge. Later studies showed that parasitism rate was higher in small fragments and that parasitism greatly reduced host reproductive success (Bohning-Gaese et al. 1993; Donovan et al. 1995; Robinson et al. 1995; Porneluzi and Faaborg 1999). Early studies also found high nest predation near edge habitat (Gates and Gysel 1978) and an experimental study with artificial nests found higher nest predation in small fragments (Wilcove 1985). Many subsequent studies have confirmed that overall productivity is lower in small fragments (Yahner and Scott 1988; Porneluzi et al. 1993; Donovan et al. 1995; Robinson et al. 1995; Porneluzi and Faaborg 1999; Morris et al. 2015), and nesting success increases with distance to edge for forest songbirds (Burke and Nol 1998; Mancke and Gavin 2000; Batary and Baldi 2004).

Gibbs and Faaborg (1990) uncovered another reason that small fragments are detrimental to breeding success in forest songbirds, through female choice for larger fragments. They monitored Ovenbirds in small fragments and contiguous forest and found that not only was there a higher density of male Ovenbirds in contiguous tracts, but about 75% of male Ovenbirds were able to pair with females, compared to only about 25% of males in fragmented sites. They suspected this difference in pairing success was related to females preferentially choosing to nest in the contiguous forest. Later studies also found more evidence of reduced pairing success in small fragments (Villard et al. 1993; Van Horn et al. 1995; Burke and Nol 1998; Fraser and Stutchbury 2004, Lampila et al. 2005; Parker et al. 2005). Females may prefer large fragments not only because these typically provide higher nesting success but

because the extra-pair mating system means that females have more choices among neighbouring males in larger fragments. This has since been dubbed the “hidden lek” to refer to females being attracted to breeding sites (e.g. large fragments) where they can find the highest quality males as extra-pair mates (Wagner 1998).

With an increasing understanding of many of the mechanisms associated with poor nesting and mating success in small forest fragments, researchers began to investigate how small fragments in the landscape affected overall population dynamics. Using a modelling approach, Pulliam (1998) found that populations that were not viable on their own (sinks) could be maintained by immigration from nearby populations that were self-sustaining (sources). Donovan et al. (1995) used population growth models to assess the viability of populations of Wood Thrushes, Red-eyed vireos, and Ovenbirds in fragmented and contiguous landscapes. They found that nest predation and brood parasitism were so high in small fragments for Red-eyed vireos and Ovenbirds that these act as population sinks (see also Robinson et al. 1995, Trine 1998). While there was some evidence that not all small fragments act as sinks (Friesen et al. 1999), later studies continued to find more evidence for source-sink dynamics taking place in a fragmented landscape (Porneluzi and Faaborg 1999; Burke and Nol 2000; Eng et al. 2011). A source-sink relationship can occur over long distances in fragmented landscapes, with Tittler et al. (2006) finding evidence that Wood Thrush source and sink populations in Ontario could be 60-80km apart. Many studies provide support for the importance of regional forest cover in sustaining viable populations of migratory songbirds (Austen et al. 2001; Betts et al. 2006; Zuckerberg and Porter 2010; Smith et al. 2011).



Given the extensive evidence that small fragments reduce nesting success of many forest songbirds, occupying such habitat is expected to have short-term and long-term negative consequences for adults. The focus of this dissertation (Chapter 2) is to examine the novel question of how small forest fragments affect the body condition (mass, corticosterone) of breeding adults, the timing of their fall migration departure, and their annual survival.

This dissertation includes an opportunistic chapter (Chapter 3) that is also novel because the migration tracking method used (Motus Wildlife Tracking System) allows one to gather migration route data on both survivors and non-survivors. All other tracking methods for songbirds are archival; requiring the device to be retrieved from individuals after migration, and so are biased because information can be obtained only for survivors.

#### *Natural history and life cycle of the Wood Thrush*

Wood Thrushes were chosen as the focus for this study because much is known about the effects of fragmentation on their nesting success (Hoover et al. 1995; Robinson et al. 1995; Weinberg and Roth 1998; Burke and Nol 2000; Etterson et al. 2014), adults are able to carry a radio transmitter without negative effects on survival and behaviour (Vega Rivera et al. 1998; Anders et al. 1998; Gow et al. 2011), and they have been successfully tracked year-round using archival light level geolocators (Stutchbury et al. 2009; Stutchbury et al. 2010).

The information contained in the following sections that outline the breeding, migration, and wintering periods of the annual cycle for Wood Thrushes was previously reviewed by Evans et al. (2020) unless otherwise indicated. Wood Thrushes breed throughout the mixed and deciduous forests of southeastern Canada and the eastern United States. They

prefer mature forests with trees greater than 15m in height, a high diversity of deciduous trees, a somewhat open forest floor with some shrub cover, and moist ground with a decaying layer of leaves. In Canada, they arrive on the breeding grounds in early May with males arriving a few days earlier than females to secure a territory which they defend until the end of the breeding season. Once a female chooses a mate, it builds a nest that is typically less than three meters off the ground and then lays a clutch of 3-5 blue-green eggs. Wood Thrushes are socially monogamous and maintain a pair bond for the length of the breeding season, but like many temperate songbirds they are known to engage in extra-pair copulations but at a low frequency. The female is responsible for the 12-13 day incubation of the eggs, but after they hatch, the male helps to feed the nestlings. When the nestlings are 12-14 days old, they leave the nest but remain with the parents for about three weeks. Wood Thrushes are a double brooded species, so if their first nest is successful, the female will begin building a new nest to repeat the process and raise a second set of young.

Typically during mid-August after breeding but prior to migration, adult Wood Thrushes undergo a complete molt, replacing all of their feathers. After molting, Wood Thrushes migrate to Central America and Mexico where they spend the winter months, departing the breeding grounds from September to early October. During fall migration, they progress at a slower pace compared to spring migration, which can proceed 2-6 times faster. This slower pace in fall is attributed to more time spent at stopover sites, with some stops lasting 1-2 weeks. High levels of individual variation in migration pace exist, with some birds reaching their wintering territory by mid-October, and others not arriving until early December. The initiation of northward spring migration occurs during Mar-Apr when Wood Thrushes head back to their temperate

breeding sites, lasting an average of 13-15 days. Spring and fall migration routes differ, with fall migration occurring farther to the east, and spring migration more to the west. Migration in this species is nocturnal, with migratory flights typically beginning an hour after sunset and concluding 1-2 hours before sunrise.

Wood Thrushes occupy a variety of habitats in the overwintering range but are most common in the understory of low elevation primary forest with a closed canopy along the Atlantic slope from around Veracruz, Mexico, through to the western half of Panama. Rappole et al. (1989) found that Wood Thrushes exhibited two different strategies during the wintering months. Some individuals remained sedentary and defended a territory against other Wood Thrushes in primary forest, while others wandered through second growth forest and did not maintain a territory. They found that birds occupying territories in the primary forest had higher survival rates than the wanderers. In Belize, McKinnon et al. (2015) showed that scrub habitat was actually the highest quality for Wood Thrushes during the wet season but later in the dry season, there was no significant difference between forest, disturbed, and scrub habitats. While the previous studies showed relatively little movement during the non-breeding season, Stanley et al. (2021) used a combination of radio and GPS tracking to find that while some individuals were relatively sedentary, others made permanent long-distance, mid-winter relocations. They believe that these movements were in response to declining habitat suitability but found no evidence that Wood Thrushes were tracking resources or moving to higher quality habitat.

**Chapter 2: Carry-over effects of forest fragmentation on breeding adult Wood Thrushes (*Hylocichla mustelina*)**

## Introduction

### *Parental stress and forest fragmentation*

With the foundation of negative consequences of temperate forest fragmentation on the diversity, occurrence, and breeding success of Neotropical migrants well established, the field has not had any major advancement in some time. The effects of forest fragmentation are expected to lead to adverse conditions for birds breeding in small fragments. Chronic (long-term) and acute (immediate) stress levels have been used as indirect measures of habitat quality in birds and are measured through quantification of the level of a glucocorticoid found in the blood that is associated with stress response (e.g. Marra and Holberton 1998). The resting, or baseline level of this glucocorticoid, corticosterone (CORT), has been found to be elevated in birds that face unfavourable conditions (e.g. Marra and Holberton 1998). If the conditions found in small forest fragments (high brood parasitism, high nest predation) are subjecting birds residing in them to chronic stress, this is expected to translate into higher levels of baseline CORT. Stress physiology and its role in natural systems is not a new subject, but it has increased in prominence in recent years as conservation biologists have begun to link anthropogenic stressors to animal behaviour, demographics, and biodiversity loss. Measures of stress have been increasingly used as a method of gauging animal disturbance to anthropogenic changes (reviewed by Bonier, Martin et al. 2009; Sheriff et al. 2011). When these stress responses are quantified, inferences can be drawn about the relative health of individuals and populations (Bonier, Martin et al. 2009) that can have vital conservation implications (Sheriff et al. 2011; Cooke et al. 2013).

Variation in the acute stress response (i.e. CORT concentration 30min after capture) has been long thought to play an important role in survival and reproductive success (reviewed by Breuner et al. 2008). The acute stress response can vary among individuals, between sexes, and across seasons even when baseline CORT remains consistent (Wingfield et al. 1992, 1994, 1995; Angelier et al. 2009; Done et al. 2011). Response CORT has even been found to increase (Dietz et al. 2013) and decrease (Grunst et al. 2014) in response to anthropogenic disturbance. Due to the well-known detrimental effects that CORT can have on reproduction (Wingfield et al. 1998; McEwen and Wingfield 2003; Williams et al. 2008), the acute stress response is thought to represent a trade-off between survival and reproductive success, with greater suppression of the response occurring when the current value of reproduction is high (Lendvai et al. 2007). The suppression has been found to be greatest when parental care is highest, in the sex providing the most care, and when the chance of rebreeding is low (Wingfield et al. 1995). This relationship has been identified in a field study on White-crowned Sparrows (*Zonotrichia leucophrys*) where response CORT was negatively correlated with reproductive output (Patterson et al. 2014).

An increased intensity of this acute response is expected to result in an increased ability to escape the life-threatening situation responsible for its trigger, leading to increased annual survival. Though this relationship has been found (Beziers et al. 2020), most studies with this focus have ended with mixed results (reviewed by Breuner et al. 2008) and some have even found a negative correlation (MacDougall-Shackleton et al. 2009). Breuner et al. (2008) believe that there is no real evidence that the strength of an acute stress response can reliably predict an individual's chance of survival. So, what then, can the strength of an acute response tell us?

Angelier et al. (2009) suggest that using acute stress response to predict survival is useful but it may be context dependent, playing a more important role in some individuals than others. They found that the level of stress response CORT did not predict annual survival in American redstarts (*Setophaga ruticilla*) occupying high quality winter habitat; however, it was a significant predictor of annual survival for those birds occupying low quality winter habitat. The ability to mount a strong stress response might only be beneficial to birds that repeatedly face unpredictable environmental challenges. Angelier et al. (2009) conclude that the CORT acute stress response can have serious fitness consequences but it is essential to consider the environmental context and the phenotype of individuals involved.

Baseline CORT, measured upon capture, has become increasingly used as a physiological index of the relative condition or health of individuals or populations (Bonier, Martin et al. 2009). Higher baseline CORT has been linked to many environmental stressors including reduced food availability (Wingfield and Ramenofsky 1997; Buck et al. 2007; Kitaysky et al. 2007; Williams et al. 2008), higher predator abundance (Clinchy et al. 2004), increased re-nesting as a result of predation (Morris et al. 2015), anthropogenic disturbance (Wasser et al. 1997; Zhang et al. 2011; Leshyk et al. 2012), and poor habitat quality (Marra and Holberton 1998; Rivers et al. 2014; Cirule et al. 2017). The high levels of baseline CORT associated with chronic stress can have direct effects such as impaired cognitive function (McEwen and Sapolsky 1995; Wingfield et al. 1998; McEwen 1999), suppressed immune capability (McEwen and Sapolsky 1995; Dhabhar and McEwen 1997; Sapolsky et al. 2000; Saino et al. 2003), and reduced feather quality (Saino et al. 2005; DesRochers et al. 2009; Butler et al. 2010; Jenni-Eiermann et al. 2015; Vagasi et al. 2018), but are also linked to indirect, long term effects

including delayed breeding (Schoech et al. 2009), lower nesting success (Angelier et al. 2007; Angelier et al. 2010; Jaatinen et al. 2013), smaller offspring (Soursa et al. 2003; Saino et al. 2005; Morris et al. 2015), a reduced stress response (Marra and Holberton 1998; Cirule et al. 2017), poor body condition (Marra and Holberton 1998; Muller et al. 2007; Roberts et al. 2007; Morris et al. 2015; Vagasi et al. 2018; Vagasi et al. 2020), and lower rates of annual survival (Goutte et al. 2010; Cirule et al. 2017; Quirici et al. 2021). Some studies have found that the response to elevated baseline CORT varies across individuals and populations (Brown et al. 2005; Roberts et al. 2007; Bonier, Moore et al. 2009; Hennin et al. 2016; Madlinger and Love 2016a, 2016b; Fischer et al. 2020) and this has increased the popularity of the idea that the interpretation of baseline CORT should be context-dependent. Through the early stages of the study of stress response in birds, elevated baseline CORT was widely considered to be negative and associated with many detrimental effects; however, as context is increasingly included in studies, the relationship becomes less clear. Now, it seems that elevated baseline CORT can act in a positive, negative, or neutral manner that varies by individual, population, and life history stage, which further stresses the importance of recognizing and accounting for the context in which the samples are taken. The capture of Wood Thrushes for this study will necessitate some disturbance prior to capture through the process of setting up mist nets in relatively close proximity to nests. Due to the possibility that this early disturbance could initiate a stress response and compromise a true baseline CORT sample, hereafter I instead use the term “initial” CORT sample to refer to any sample collected <3 minutes after capture.



### *Seasonal carry-over effects*

It has become clear that a better understanding of how events throughout the annual cycle are interconnected is essential for conservation efforts because anthropogenic stressors in one season can have long term negative effects on survival and reproductive success. Seasonal carry-over effects are challenging to study in migratory birds, in part due to the difficulty and expense of tracking individuals between periods of their annual cycle, often across large geographic distances (Faaborg et al. 2010; Harrison et al. 2011; Catry et al. 2013; Marra et al. 2015); however, as technology continues to improve, these types of studies are becoming increasingly feasible. Adults breeding in small forest fragments may face longer-term negative consequences through seasonal carry-over effects that delay fall migration and reduce annual survival, but this has not yet been studied for a migratory songbird. In contrast, many studies have documented carry-over effects arising from differential winter habitat quality that results in differing levels of food availability. Marra et al. (1998) found that American Redstarts (*Setophaga ruticilla*) occupying lower quality winter habitat in the tropics (dry scrub) had a lower body condition which delayed their spring departure and in turn, their arrival on the breeding grounds (Studds and Marra 2005). They also found that they could identify the type of habitat the birds occupied which differs along a moisture gradient, by measuring stable isotopes in their blood. Norris et al. (2004) measured blood isotopes immediately after American redstarts arrived on the breeding grounds to show that females formerly occupying high quality winter habitat (mangrove forest) months earlier raised more offspring on the breeding grounds and fledged them at an earlier date.

Birds residing in high quality winter habitat have been found to be in better body condition (Marra et al. 1998; Bearhop et al. 2004; Studds and Marra 2005; Brown and Sherry 2006; Cooper et al. 2015), which allows them to depart for and arrive at the breeding grounds earlier (Marra et al. 1998; Studds and Marra 2005; Reudink et al. 2009; Rockwell et al. 2012; Gonzalez-Prieto and Hobson 2013; Cristol et al. 2014; Cooper et al. 2015; Paxton and Moore 2015; Saino et al. 2015; Akresh et al. 2019), and this early arrival can translate into earlier nesting (Saino et al. 2004; Rockwell et al. 2012; Drake et al. 2013; Goodenough et al. 2017; Lopez Calderon et al. 2019), higher quality young (Moller and Hobson 2004), higher overall reproductive success (Norris et al. 2004; Reudink et al. 2009; Rockwell et al. 2012; Drake et al. 2013; Rushing, Marra et al. 2016; Goodenough et al. 2017; Imlay et al. 2019; Lopez Calderon et al. 2019) and even higher annual survival (Studds and Marra 2005). With habitat quality often linked to moisture content, weather events that cause widespread drying such as El Nino can impose negative carry-over effects similar to those of poor habitat quality across entire wintering populations of some species (Rockwell et al. 2012; Paxton et al. 2014).

Breeding habitat quality is also expected to influence adult body condition because of the lower food availability (lower arthropod abundance) found in small fragments combined with the higher energetic demands associated with additional nesting attempts due to predation and brood parasitism. With habitat quality on the wintering grounds having been shown to impact body condition (Marra et al. 1998; Bearhop et al. 2004; Studds and Marra 2005; Brown and Sherry 2006; Cooper et al. 2015), this trend is expected to also be found on the breeding grounds. Most Neotropical migrants undergo an energetically taxing complete molt and replacement of their feathers prior to fall migration and this costly time period could

intensify any disparity in body condition at the end of the breeding season that could delay molt, and in turn, fall migration.

Breeding in small fragments could also cause negative carry-over effects through higher rates of nest predation, an increased number of nesting attempts, and a longer breeding season. An extended breeding season has been found to delay the initiation of fall migration in Wood Thrushes and other species (Stutchbury et al. 2011; Mitchell et al. 2012; Saino et al. 2017; Briedis et al. 2018; De Zwaan et al. 2019; Chmura et al. 2020) but this has not been linked to breeding habitat quality. The costs of a delayed fall migration likely vary among species, as some are able to make up lost time during migration by spending less time at stopover sites so they arrive at the wintering grounds simultaneously with birds that departed earlier (Stutchbury et al. 2011; De Zwaan et al. 2019). It is not known whether timing of fall migration impacts annual adult survival.

### *Research questions*

No study that I am aware of has tested for seasonal carry-over effects due to breeding ground fragmentation in a migratory songbird. Technology has now reached a point where the tools are available to not only track migratory birds across life stages, but also to assess and make inferences about their individual condition using blood samples. These advances have finally made it possible to combine these two fields and evaluate whether breeding ground fragmentation gives rise to negative physiological markers, or carry-over effects that may impact migration timing and annual survival in a free-living adult migratory bird.

In this study I use an innovative new tracking technology that has made it possible to study how habitat fragmentation could induce negative carry-over effects on migration movements of breeding adults. The Motus Wildlife Tracking System (Motus) is an automated radio telemetry system that is able to detect radio tags and thereby record individual bird movement over a regional scale (MacKenzie and Taylor, 2014). What makes this system so unique is that the coded nano-tags employ a single radio frequency that can be detected at every receiving station across a broad geographic scale, regardless of the specific project individual towers are maintained for (Taylor et al. 2017). Using Motus will eliminate one of the main problems associated with archival GPS and light-level geolocators; the need to recover the tags to retrieve the data. Archival devices, by definition, can only provide data on individuals that survive their entire migration journey, there and back. Motus will also eliminate the latitudinal inaccuracies of light-level geolocators that occur close to the autumn equinox that often make it impossible to determine onset of fall migration for birds that travel due south (Bridge et al. 2011). With Motus, the timing of onset of fall migration can be determined even for birds that are never seen again.

Until now, annual survival studies have largely relied on marking individuals and having to re-sight them at a later date, which loses its effectiveness as dispersal distances increase outside the study area (Haas 1998; Cline et al. 2013). Conventional radio tags have been used to track dispersal at moderate distances, usually in conjunction with expensive aerial telemetry (Vega Rivera et al. 1998; Vega Rivera et al. 1999). While both these methods can be effective within-year for relatively short distances, they become problematic at greater distances and between years where an individual may have dispersed so far that band re-sighting and aerial

telemetry are not effective. With long-life nano-tags, Motus provides a means for the first time to know whether an individual has successfully completed migration regardless of whether they return to their previous territory. With this knowledge, birds that have dispersed large distances between years can be more reliably separated from those that did not survive migration. Being able to distinguish between these two possibilities will allow for more accurate estimates of annual survivorship.

This project is designed to test for carry-over effects arising from forest fragmentation on the timing of fall migration and annual survivorship, and to look for underlying mechanisms by examining initial and response CORT levels of breeding adults and the timing of breeding events. Pairs occupying small fragments are expected to experience high rates of brood parasitism and nest predation as well as the generally harsher conditions associated with increased fragmentation, and this is expected to contribute to a more stressful life, which should translate to a higher initial level of CORT. These conditions may give rise to carry-over effects by extending the nesting period and delaying fall migration and/or delaying migration because adults are in poorer condition.

The predictions being tested are that adult birds in small fragments are expected to have (1) a lower body condition (higher initial CORT, lower mass) (2) later nests due to repeated nest predation (3) delayed initiation of fall migration, and (4) a lower annual survival rate.

## **Materials and methods**

### *Ethics statement*

Permits and permissions were obtained for all land access required for research, and all bird handling and research protocols were approved by the York University Animal Care Committee.

### *Study area*

This study was conducted in Norfolk County, Ontario, which lies on the north shore of Lake Erie and retains 21% forest cover composed of a wide variety of deciduous and mixed forest fragments of varying sizes (LPRCA, 2019). Norfolk County has the most extensive Motus coverage in Ontario, with 13 towers resulting in near-complete coverage for birds in migratory flight (Fig 1-1). The study was designed to compare small versus large fragments as a means to maximize expected effect size given the logistical constraints of working in, and travelling between, so many study sites. Although sample sizes varied slightly between years owing to access constraints to private land, in general there were 10 small (11-69 ha in size) and 10 large (162-499 ha in size) forest fragments (Fig 1-1; Table A-1) on a mix of public and private land. In many cases, roads acted as an edge for at least one portion of a fragment and the width of a roadway is the minimum distance between fragments in this study. Necessary permits were obtained for conducting research on public lands, and landowner permission was sought during each spring for access to private lands.

### *Study species*

Wood Thrushes were chosen for this study because much is known about the effects of fragmentation on their nesting success (Hoover et al. 1995; Robinson et al. 1995; Weinberg and Roth 1998; Burke and Nol 2000; Etterson et al. 2014), adults are able to carry a radio transmitter without negative effects on survival and behaviour (Vega Rivera et al. 1998; Anders et al. 1998; Gow et al. 2011), and they have been successfully tracked year-round using archival light level geolocators (Stutchbury et al. 2009; Stutchbury et al. 2010). They are also a long distance migrant that winters in the forests of Central America and now a federally listed Threatened Species at Risk in Canada. However, Wood Thrushes are still a common breeding species in the deciduous and mixed forests of southwestern Ontario (COSEWIC, 2012).

### *Nest searching and monitoring*

Beginning in mid-May, all of the study sites were extensively searched for nests starting at the location of each singing male. When a nest was found, the height, tree species, GPS coordinates, and number of eggs/nestlings and presence of Brown-headed cowbird eggs/nestlings was recorded. In the case of nestlings, the age was estimated based on the stage of development. If a nest was empty or contained eggs, it was checked only every eight days to minimize disturbance. If there were nestlings, it was not checked again before nestlings were 10 days old and ready to be tagged (for a different study) at which point the nest was considered successful. In order to minimize disturbance during nest checks, a camera was briefly placed over the nest, and the footage was then reviewed at a distance. When

conducting nest checks, every effort was made to continue in the same direction of travel to decrease the chance of leading potential predators to the nest.

### *Tagging*

The specifications of the radio-tags (“nanotags”) varied among years due to the manufacturer discontinuing models but all had a burst rate of 12.7 seconds and minimum expected lifespan of 400 days. During 2016, NTQBW-6-1 (~1.6g) avian coded VHF nanotag transmitters were fitted to adult Wood Thrushes of both sexes when their nestlings were 10 days old. In 2017, I followed the same protocol using ANTC-M6-1 (~1.7g) nanotags. In 2018, a combination of ANTC-M6-1 and NTQB2-6-1 (~1.6g) nanotags were fitted to adult Wood Thrushes of both sexes during the incubation period of nesting, and in 2019, NTQB2-4-2S (~1.5g) nanotags were fitted to only adult female Wood Thrushes during the incubation stage of their first nesting attempt of the season. Nanotags were attached using a backpack leg loop harness (Rappole & Tipton 1991) made from 2.5mm Teflon tubing. To catch the birds, two 12m mist nets were set up 90 degrees to each other, about 3-5 m from the nest, boxing in two sides. If an adult bird was present at the nest after net set up, we would walk steadily towards the bird opposite to the nets until it flew off the nest, usually into a net. Adults were banded with both Canadian Wildlife Service numbered aluminum bands and unique colour band combinations to allow for identification when birds were re-sighted.

Tarsus length, wing chord, and mass were measured for each bird. Sex was determined by checking for the presence of a brood patch or cloacal protuberance (Pyle et al. 1997). During the breeding season, male Wood Thrushes develop obvious external cloacal protuberances to



store sperm and assist with copulation. Female Wood Thrushes are responsible for incubation and to do this effectively, they develop a visible brood patch to more efficiently transfer body heat to the eggs. The development of a brood patch involves the loss of some feathers from the abdomen, and the wrinkling and vascularization of the resulting patch bare skin. Age was determined using plumage criteria as outlined by Pyle et al. (1997). All North American songbirds undergo a prebasic molt once per year, but the first prebasic molt in a bird's life differs from all those that succeed it. In adult Wood Thrushes, the prebasic molt involves complete replacement of all feathers, while juvenile birds retain the remiges, rectrices, alulas, primary coverts, and some or all of the greater coverts. These retained juvenal feathers were grown in the nest simultaneously and because growing many feathers at the same time is physiologically taxing, these feathers differ in quality and shape compared to adult feathers that are replaced sequentially. By examining the flight feathers and coverts of Wood Thrushes, the presence of these worn juvenal feathers indicate a bird is in its second year, while the absence of such feathers indicate that a bird is older than its second year.

#### *Blood sampling (2018-2019)*

Blood sampling for CORT focused on tagged female Wood Thrushes and was carried out during the incubation period of the first nest of the breeding season. While CORT levels can fluctuate in passerines during the course of a day, they peak just before sunrise and then remain steady during daylight hours before rising again in the evening (Breuner et al. 1999). Time constraints did not allow for sampling to be carried out consistently during the same time period each day. Instead, all samples were collected at least three hours after sunrise and three

hours before sunset. Mist nets were constantly monitored to ensure that initial blood samples were taken less than three minutes from the moment of capture to best reflect baseline conditions. Approximately 100ul of blood was taken from the brachial vein of one wing using a capillary tube, after puncture with a 26g needle. Each bird was exposed to a capture-stress protocol which involves taking an initial blood sample, holding the bird for 30 min in a fabric bag, and then taking a second blood sample (Wingfield et al. 1994). Blood samples were immediately expelled into 400ul Eppendorf tubes and stored on ice. Samples were centrifuged within twelve hours and blood plasma was separated and stored in a freezer.

Corticosterone concentration was measured using the commercially available Enzo Life Sciences Corticosterone ELISA kit (ADI-900-097) as per the manufacturer's instructions after validating and optimizing the kit using Wood Thrush plasma. Samples were run in duplicate and if both assays yielded a concentration that fell outside the standard curve, the sample was excluded from further analysis (n=1). In an effort to control instances where birds were exposed to stressors prior to capture, initial blood samples that were identified as outliers using the inter-quartile method were also eliminated from further analysis along with their corresponding stress response samples (n=8). Blood samples were also eliminated from analysis if the Wood Thrush was captured after more than two capture attempts (n=10) because capture CORT levels would not reflect baseline pre-capture CORT in these cases. The intra-assay coefficient of variation was 8.2% in the first set of samples assayed in 2018, and 13.2% for the second set of samples in 2019. The inter-assay coefficient of variation based on a standard concentration run in duplicate on each plate was 8.7% in 2018 and 6.4% in 2019.

### *Manual radio tracking, Motus detections, and aerial telemetry*

The location of tagged Wood Thrush adults was determined every four days using an SRX 600 Lotek receiver and a handheld three-element Yagi antenna until they either dispersed away from their breeding territory (absent for at least two visits), or until late-August. At each check, the approximate GPS coordinates of the bird was recorded. Starting in mid-August, movement data were acquired from Motus. Although the receiver towers rarely detected breeding birds within the forest, they were able to detect larger scale, higher altitude migratory movements.

Motus receivers sometimes record false detections due to random radio noise, duplicate tags, and overlapping tag signals when multiple tags are transmitting in the same area (Crewe et al. 2020). A number of filtering and quality control steps were taken to identify these and exclude them from analysis. First, I eliminated any detection that fell outside of my deployment dates. Next, I eliminated detections of fewer than three consecutive tag bursts because such runs are likely to be false detections (Crewe et al. 2020). Lastly, I eliminated any detection that occurred in impossible or highly unlikely locations, or represented unrealistic distances and directions based on prior knowledge of migration timing and routes from geolocator studies (Stutchbury et al. 2009; Stutchbury et al. 2010). Fall migratory detections were deemed to be those that occurred after sunset during the migratory period (September 1 to October 15), when a bird was not detected in Ontario again until the following year. Typically, a bird would be tagged in early summer and then not be detected by Motus until a single night during the migration period when a series of towers would pick it up.

After eliminating false detections, Motus recorded 361 (202 fall, 159 spring) instances of tagged Wood Thrushes passing individual towers (74 different birds) during the spring and fall migration periods (September 1 - June 1) with only 5 of these birds (7%) detected by a single tower. For all birds detected during the migration periods, only 7 had no false detections and on average each bird had  $114 \pm 39$  false detections and  $159 \pm 20$  good detections. The total number of false detections for each bird ranged from 0-2242 and made up 42% of all detections.

During June/July of 2017, 2018, and 2019 a four hour aerial telemetry survey was conducted to attempt to locate the breeding sites of returning birds and search for individuals that may not have been detected by Motus as they arrived in the area. Aerial telemetry surveys were conducted from a Cessna 172 equipped with a strut-mounted H-type antenna and SRX 600 Lotek receiver. We followed a flight pattern designed to completely cover the study area in a grid pattern search and any additional forest fragments within ~10 km of our study site boundary. Once a tag was detected, multiple passes were completed over the same area and a GPS point was taken at the location of the strongest signal.

### *Vegetation sampling*

To quantify territory-level features that could affect habitat quality, a vegetation survey was carried out at each territory where an adult Wood Thrush was tagged. Each survey consisted of three 20m x 20m plots where height, diameter at breast height (DBH), and species of each living tree with a DBH greater than 10cm was recorded. Tree heights were measured using a laser rangefinder, while DBH was measured using a diameter measuring tape. The

southwest corner of the first plot was located 20m from the nest at a bearing of 225° to ensure that the actual nest was included in the plot. The southwest corners of the second and third plots were chosen using a random number generator to generate a bearing (0-360°) and distance (20-80m) from the nest. Each side of a plot followed a primary compass direction and was formed starting from the southwest corner. To estimate canopy cover, a forest densiometer reading was taken at each corner of the 20x20m plot and averaged. At each 20x20m plot, five smaller 2x2m subplots were measured to represent the shrub and groundcover layers. Four of these 2m plots were located halfway down and 2m outside of each side of the 20x20m plot and the fifth was located directly in the center of the 20x20m plot. Within these smaller plots, all shrub stems that were 0.5-1.3m are counted, and all shrub stems that were greater than 1.3m but with a DBH of less than 10cm were counted. The percentage of cover that each range of shrub height provided was then estimated. The dominant species in each of these height ranges was also noted. Within each of these 2x2m subplots, the southwest quadrant was used as a 1x1m subplot to represent the groundcover layer. The percentage of groundcover with a height of less than 0.5m and percentage of bare soil was estimated, and the dominant species of groundcover identified.

### ***Statistical analysis***

All analyses were conducted in R 4.0.3 (R Core Team 2020) and all tests were two-tailed and expressed as means  $\pm$ SE. All scatterplots were created using the ggplot2 package (Wickham, 2016) in R. I considered models supported when their  $\Delta$ AICc = 0-2 (the top model  $\Delta$ AICc = 0) and at least 2 AICc better than the intercept-only model (Arnold 2010). When more

than one model was supported, I used model averaging in the MuMIn package (Barton 2020) to produce coefficient estimates. I considered predictor variables to be meaningful when 95% confidence intervals of coefficient estimates did not overlap zero.

#### *Territory habitat characteristics and fragment size*

To examine how fragment size affects vegetation characteristics, I used linear models in the stats package (R Core Team 2020). For each non-transformed vegetation variable, I used fragment size as the only predictor variable. In addition, I used a principal components analysis to look at the relative relationship of each vegetation characteristic with fragment size using the factoextra package (Kassambara and Mundt, 2020).

#### *Body condition and corticosterone*

To examine how fragment size affects relative mass in Wood Thrushes, I used generalized linear mixed models with gamma error distribution in the lme4 package (Bates et al. 2015) with relative mass as the dependent variable, fragment size as the predictor variable, and age, sex, and capture date as covariates. Average relative mass varied significantly by year, so I included year as a random effect in all models. I used dredge in the MuMIn package (Barton 2020) to rank the 16 candidate models using Akaike Information Criterion scores corrected for small sample size (AICc). To examine the relationship between both CORT measures and fragment size, I again used generalized linear mixed models with gamma error distribution. Using the CORT measure as my dependent variable, I used fragment size as my predictor variable and included relative mass, capture date, and capture attempt (first or second) as

covariates. Both CORT measures varied significantly by year, so year was included in all models as a random effect. I used dredge in the MuMIn package (Barton 2020) to rank the 16 resulting candidate models for each CORT measure using AICc.

#### *Nest timing and reproductive effort*

To examine how fragment size affects the timing of the last nest of a breeding season, I fitted linear mixed models in the lme4 package (Bates et al. 2015) using the non-transformed Julian date of the first egg of the last nest of the season as my dependent variable, fragment size as my predictor variable and age and relative mass as covariates. Nest timing varied by year, so year was included as a random effect in all models. I used dredge in the MuMIn package (Barton 2020) to rank the 8 resulting candidate models using AICc. To examine the relationship between reproductive success and forest fragment size I fitted generalized linear mixed models with a poisson error distribution using the number of young fledged as my dependent variable, fragment size as my predictor variable, and age and relative mass as covariates. The number of young fledged differed by year, so year was included as a random effect in all models. I used dredge in the MuMIn package (Barton 2020) to rank the 8 resulting candidate models using AICc.

#### *Fall migration*

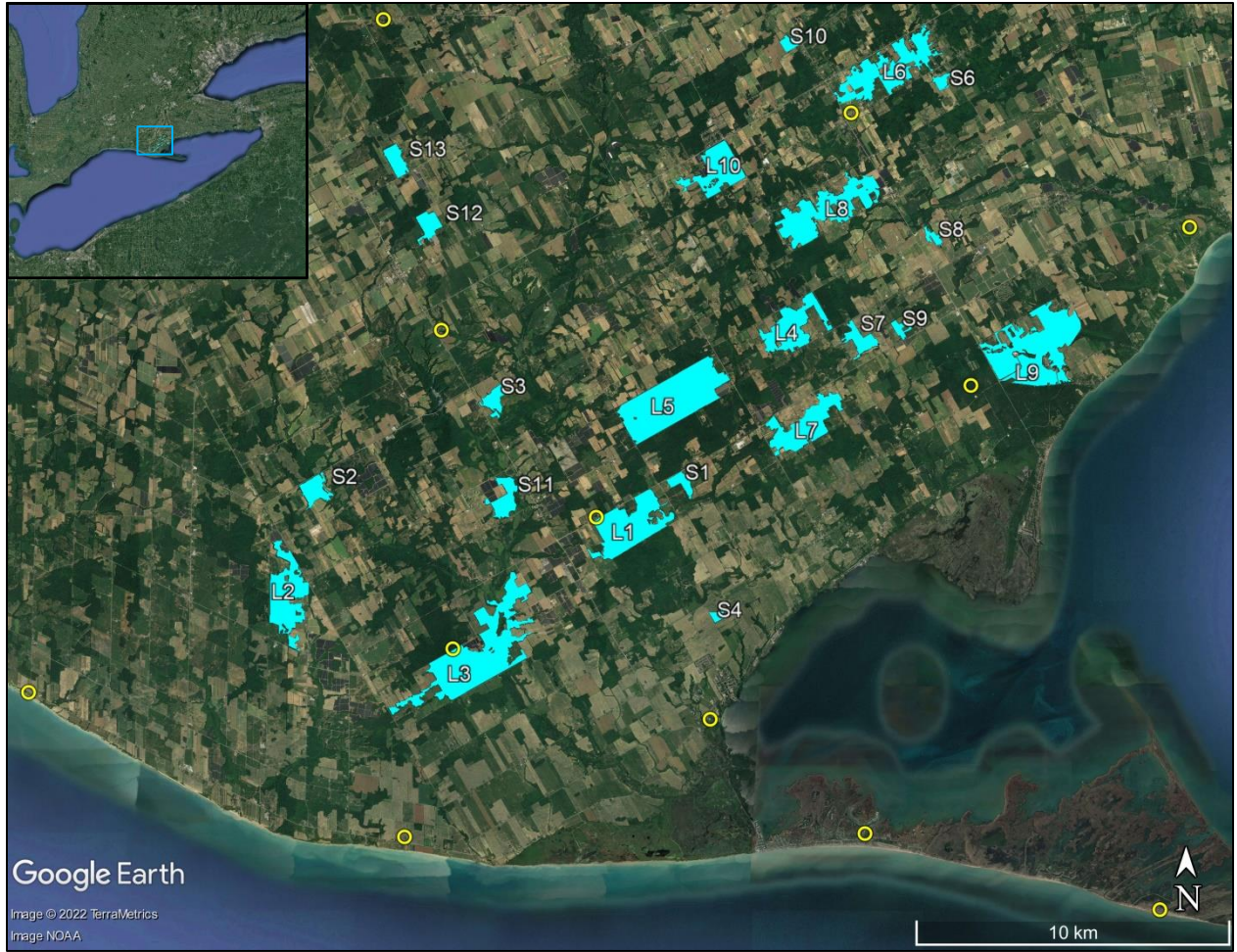
To examine the effect of fragment size on fall migration, I fitted generalized linear mixed models with gamma error distribution in the lme4 package (Bates et al. 2015) using the Julian date of the last Motus detection in Norfolk County as my dependent variable and fragment size

as my predictor with age, sex, and the interaction between fragment size and sex as covariates. Fall migration date varied by year, so year was included as a random effect in all models. I used dredge in the MuMIn package (Barton 2020) to rank the 10 resulting candidate models using AICc. To examine the relationship between the number of young fledged by tagged females and fall migration, I fitted generalized linear mixed models with gamma error distribution in the lme4 package using the Julian date of the last Motus detection in Norfolk County as my dependent variable and young fledged as my predictor with age, fragment size, and relative mass as covariates. Fall migration date varied by year, so year was included as a random effect in all models. I used dredge in the MuMIn package (Barton 2020) to rank the 10 resulting candidate models using AICc.

### *Apparent survival*

To examine how fragment size affects apparent survival, I fitted generalized linear mixed models with binomial error distribution in the lme4 package (Bates et al. 2015) using apparent survival as my dependent variable, fragment size as my predictor variable, and age, sex, and the interaction between fragment size and sex as covariates. Apparent survival varied each year, so year was included as a random effect. I used dredge in the MuMIn package (Barton 2020) to rank the 10 resulting candidate models using AICc. Birds that were tagged in 2019 were not used in estimating annual survival because the tag model used that year had a thin 0.2mm diameter antenna (other years used a 0.6-0.7mm diameter antenna), and tag failure due to broken antennas over the 11-month deployment period was suspected. Only three (10%) of the adult females tagged in 2019 were detected in spring 2020.





**Figure 1-1.** Study site (blue shading) and Motus tower (yellow circles) locations in Norfolk County, Ontario.

## Results

### *Territory habitat characteristics and fragment size*

We completed 143 vegetation surveys at the territory level, with 94 of those occurring in large fragments (162-500ha) and 49 in small fragments (16-69ha). Most (7 of 10) habitat variables had a significant relationship with fragment size as expected (Fig 1-2). The number of large trees ( $\geq 30$  cm diameter) and total number of trees increased with fragment size while number of shrubs, shrub cover, and ground cover all decreased with fragment size. The number of small trees ( $< 30$  cm diameter), percentage of canopy cover, and ratio of large to small trees did not vary with fragment size.

To further examine the relationship between habitat characteristics and fragment size, I conducted a principal component analysis (Fig A-1). Vegetation variables that were strong contributors to PC1 (number of large trees, number of large/small shrubs, percentage of large/small shrub cover) were all correlated with fragment size and PC1 explained 28% of the variation in habitat among territories. Only two variables that were strong contributors to PC2 were not related to fragment size (number of small trees, ratio of large to small trees) and PC2 explained an additional 19.5% of the variation. With most habitat characteristics of territories being related to fragment size, we decided that for our purposes, fragment size would adequately represent habitat characteristics for our remaining analyses.

### *Body condition and corticosterone*

During four field seasons I collected morphometric data on 212 adult Wood Thrushes (2016, n=45; 2017, n=59; 2018, n=64; 2019, n=44), with 136 of these birds captured in large fragments and 76 captured in small fragments. Tarsus length varied from 28.4 - 35.2mm and mass varied from 39 – 63g so I used a ratio of mass/tarsus (relative mass) to account for skeletal size variation. To examine the relationship between relative mass and fragment size (Fig 1-3), I fitted a generalized linear mixed model using a gamma error distribution, with relative mass as the dependent variable, fragment size as the predictor variable, and sex, age, and date of capture included as covariates, and year as a random effect. After ranking the 16 candidate models (Table 1), the top model used capture date and sex as predictors (weight=0.42) while the only other model to garner support ( $\Delta AICc=1.63$ ) used capture date, sex, and fragment size (weight=0.19). While fragment size did appear among the top models, only the coefficient estimates for capture date and sex were significant, with 95% confidence intervals that did not overlap zero (Table 8). On average, female birds had higher relative mass ( $1.64 \pm 0.01$ ) than males ( $1.49 \pm 0.01$ ) and relative mass declined during the course of the breeding season.

For the duration of the 2018-2019 field seasons I targeted female Wood Thrushes and collected initial CORT samples (e.g. < 3 min after capture) from 47 birds, and corresponding stress response samples (e.g. 30 min after capture) from 42 of those birds (Fig 1-4). As expected, initial CORT concentration ( $6.38 \pm 0.59\text{ng/ml}$ ) was significantly lower than stress response CORT concentration ( $33.43 \pm 2.1\text{ng/ml}$ ) taken 30 minutes later (t-test  $t(47)=-12.39$ ,  $p<0.001$ ). There was a strong year effect in both initial and response CORT. In 2018, the mean

concentration of initial ( $4.92 \pm 0.58\text{ng/ml}$ ;  $n=24$ ) and stress response ( $25.43 \pm 1.45\text{ng/ml}$ ;  $n=20$ ) CORT was significantly lower than the 2019 mean concentration of initial ( $7.89 \pm 0.94\text{ng/ml}$ ,  $n=23$ ; t-test  $t(37)=-2.82$ ,  $p<0.001$ ) and stress response ( $40.71 \pm 3.08\text{ng/ml}$ ,  $n=22$ ; t-test  $t(31)=-4.83$ ,  $p<0.001$ ) CORT.

To examine the relationship between forest fragment size and CORT concentration, I fitted generalized linear mixed models using a gamma error distribution, with CORT measures as the dependent variable, fragment size as the predictor variable, and relative mass, capture date, and capture attempt (first or second attempt) included as covariates, and year as a random effect. For initial CORT concentration, the intercept-only model had the lowest AICc value from the set of 16 candidate models (Table 2), suggesting that fragment size, along with the covariates explained little of the observed variation in initial CORT. Stress response CORT concentration had two models that received support out of the 16 candidate models (Table 3). The best model used only capture attempt as a predictor (weight=0.33), and the only other supported model ( $\Delta\text{AICc}=1.37$ ) used capture attempt + capture date (weight=0.17). Capture attempt was the only coefficient with a 95% confidence interval that did not overlap zero, having a positive relationship with response CORT concentration (Table 8). Birds sampled after the second capture attempt ( $n=17$ ) had 33% higher stress response CORT ( $39.2 \pm 3.97\text{ng/ml}$ ) than the stress response CORT ( $29.5 \pm 1.99\text{ng/ml}$ ) of those captured during the first attempt ( $n=25$ ).

### *Timing of nesting and reproductive effort*

During the 2018 and 2019 field seasons I radio-tracked females ( $n=61$ ) from mid-May to late August and was able to obtain last nesting dates for 75% ( $n=46$ ) of these birds (Fig 1-5). I was unable to determine last nesting dates of 15 females for a number of reasons. During 2018, the 3/31 tagged females without last nest dates included one bird that was never detected again after initially being tagged and two birds that were not detected again following early season nest failures. During 2019, the 12/30 tagged females without last nest dates included six birds that were not detected after early nest failures, five birds where I was unable to locate additional nests, and one bird that disappeared after a first successful nest. I used the Julian day of the first egg of the last nest of the season to represent last nesting date. I excluded last nesting dates that occurred in May ( $n=3$ ) because despite being unable to relocate these birds, it is unlikely that they ceased attempting to nest based on nest timing in a Pennsylvania study (Stutchbury et al. 2011). The earliest last nesting date for an individual female during 2018 ( $n=28$ ) and 2019 ( $n=18$ ) was June 8, and the latest nesting date occurred on July 24, with the overall average last nesting date being on June  $30 \pm 1.7$  days. In 2018 the average date of the first egg of the last nest was July  $3 \pm 1.8$  days ( $n=28$ ) and in 2019 it was June  $27 \pm 3.3$  days ( $n=18$ ), but this difference was not statistically significant (t-test  $t(27)=1.46$ ,  $p=0.16$ ). To look at the relationship between forest fragment size and last nesting date, I fitted a linear mixed model using the first egg date of the last nest of each female as the dependent variable, fragment size as the predictor variable, and included age and relative mass as covariates, and year as a random effect. After ranking the 8 candidate models (Table 4), no model was  $>2\text{AIC}$

better than the intercept-only model, suggesting that fragment size and the covariates are not strong predictors of last nest date.

Of the 46 females that I obtained last nesting dates for, I was able to track the total number of young fledged for 41 (89%) of them (Fig 1-6). The most young fledged in a season by a single female was 10 (n=1) and the least was 0 (n=7), with the overall average being  $3.76 \pm 0.38$  across both years. Females fledged an average of  $3.92 \pm 0.41$  (n=25) young in 2018 and  $3.5 \pm 0.75$  (n=16) young in 2019; however, this difference was not significant (t-test  $t(24)=0.49$ ,  $p=0.63$ ). To examine the relationship between forest fragment size and total number of young fledged, I fitted generalized linear mixed models using a poisson error distribution, with number of young fledged as the dependent variable, fragment size as the predictor variable, and included last nest date, age, and relative mass as covariates, and year as a random effect. After ranking the 16 candidate models (Table 5), no model was  $>2AIC$  better than the intercept only model, suggesting that fragment size and the covariates are not strong predictors of the total number of young fledged.

### *Fall migration timing*

From 2016-2019, 60 of 117 (51%) tagged Wood Thrushes were detected by the automated Motus system as they departed for fall migration (Fig 1-7). Initial migration detections were clustered about one hour after sunset (Raleigh test  $z= 0.85$ ,  $p<0.001$ ,  $n=60$ ; Fig 1-8a) and the first detections south of Lake Erie were clustered about two hours later (Raleigh test  $z=0.69$ ,  $p<0.001$ ,  $n=25$ ; Fig 1-8b). To examine the relationship between forest fragment size and fall departure date, I fitted a generalized linear mixed model using a gamma error

distribution, with fall departure date as the dependent variable, fragment size as the predictor variable, and included age and sex as covariates (with an interaction between sex and fragment size), and year as a random effect. The earliest (September 9) and latest (October 10) fall departures occurred during 2016 and 2017 respectively, while the average fall departure date across all years was September 29. After ranking the 10 candidate models (Table 6), the best-fitting model (weight = 0.33) used fragment size, sex, and fragment size\*sex as predictors while the only other model to receive support ( $\Delta\text{AICc}=0.61$ ) used sex as the only predictor (weight = 0.25). Sex was the only coefficient with a 95% confidence interval that did not overlap zero (Table 8), with females departing earlier on average (September 27  $\pm$  1 day) than males (October 2  $\pm$  1.6 days).

Total reproductive effort is expected to have a negative effect on female departure date due to the high cost of reproduction; however, total reproductive effort was only tracked during 2018-2019. Of the 60 Wood Thrushes that were detected departing for fall migration, 41 were female, and 32 of those were tagged during 2018-2019. I was able to determine the total number of young fledged for 24 of these birds (Fig A-2). To examine the relationship between female fall departure date and the number of young fledged, I fitted a generalized linear mixed model using a gamma error distribution, with fall departure date as the dependent variable, number of young fledged as the predictor variable, fragment size, age, and body condition as covariates, and year as a random effect. After ranking the 16 candidate models (Table A-2), the best fitting model (weight = 0.31) used fragment size as the only predictor, and the only other model to receive support ( $\Delta\text{AICc}=0.30$ ) used fragment size and number of young fledged as predictors (weight = 0.27). Fragment size was the only coefficient with a 95% confidence

interval that did not overlap zero (Table A-3), with small fragment birds on average departing earlier (September  $26 \pm 1.3$  days) than large fragment birds (September  $29 \pm 0.9$  days).

### *Apparent survival*

A total of 87 Wood Thrushes were tagged during the 2016-2018 (2016, n=20; 2017, n=27; 2018, n=40) field seasons, and 34 (39%) of these were detected by Motus returning to Norfolk County the following spring with one additional bird detected only by manual telemetry (Fig 1-9). The return rate for large sites was 25/53 (47%) while the return rate for small sites was only 10/34 (29%) but this difference in frequency was not significant (chi-square test  $\chi^2(1) = 2.72$ ,  $p = 0.1$ ). Using a combination of manual and aerial telemetry, I found that only 22/35 (63%) birds returned to the site they had nested in the previous year, consisting of 15/23 (65%) females and 7/12 (58%) males. The remaining 13 returning birds were not detected by aerial telemetry surveys, suggesting that they chose new breeding fragments outside the study area.

To examine the relationship between forest fragment size and annual survival, I fitted a generalized linear mixed model using a binomial error distribution with annual survival as the dependent variable, fragment size as the predictor variable, and included age and sex as covariates (with an interaction between sex and fragment size), and year as a random effect. Despite the overall differential return rate between large and small sites, after ranking the 10 candidate models (Table 7), the intercept-only model had the strongest support, suggesting that none of the variables are strong predictors of apparent annual survival.



**Table 1-1.** Results of AICc selection of gamma distribution generalized linear mixed models testing the influence of variables on relative mass (n=212) of birds captured during 2016-2019, including year as a random effect.

<b>model</b>	<b>LL</b>	<b>n</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta</math>_AICc</b>	<b>weight</b>
capture date + sex	180.83	212	5	-351.4	0.00	0.42
capture date + sex + fragment size	181.08	212	6	-349.7	1.63	0.19
capture date + sex + age	180.84	212	6	-349.3	2.11	0.15
sex	178.29	212	4	-348.4	2.97	0.1
capture date + sex + fragment size + age	181.09	212	7	-347.6	3.74	0.07
sex + fragment size	178.4	212	5	-346.5	4.86	0.04
sex + age	178.32	212	5	-346.4	5.01	0.03
sex + fragment size + age	178.43	212	6	-344.5	6.91	0.01
capture date	159.41	212	4	-310.6	40.75	0.00
capture date + age	159.7	212	5	-309.1	42.27	0.00
capture date + fragment size	159.65	212	5	-309	42.36	0.00
capture date + fragment size + age	159.96	212	6	-307.5	43.86	0.00
intercept	154.12	212	3	-302.1	49.27	0.00
age	154.54	212	4	-300.9	50.49	0.00
fragment size	154.17	212	4	-300.1	51.23	0.00
fragment size + age	154.61	212	5	-298.9	52.44	0.00

**Table 1-2.** Results of AICc selection of gamma distribution generalized linear mixed models testing the influence of variables on initial blood CORT concentration (n=47) of birds tagged during 2018 and 2019, including year as a random effect.

<b>model</b>	<b>LL</b>	<b>n</b>	<b>K</b>	<b>AICc</b>	<b>Δ_AICc</b>	<b>weight</b>
intercept	-123.99	47	3	254.5	0.00	0.25
capture attempt	-123.17	47	4	255.3	0.74	0.17
relative mass	-123.54	47	4	256	1.49	0.12
capture date	-123.98	47	4	256.9	2.36	0.08
fragment size	-123.99	47	4	256.9	2.39	0.08
capture attempt + relative mass	-122.96	47	5	257.4	2.84	0.06
capture attempt + capture date	-123.1	47	5	257.7	3.11	0.05
capture attempt + fragment size	-123.16	47	5	257.8	3.23	0.05
capture date + relative mass	-123.5	47	5	258.5	3.92	0.04
relative mass + fragment size	-123.53	47	5	258.5	3.98	0.03
capture date + fragment size	-122.97	47	5	259.4	4.85	0.02
capture attempt + capture date + relative mass	-122.88	47	6	259.9	5.32	0.02
capture attempt + capture date + fragment size	-122.95	47	6	260.0	5.45	0.02
capture attempt + relative mass + fragment size	-123.08	47	6	260.3	5.71	0.01
capture date + relative mass + fragment size	-123.49	47	6	261.1	6.53	0.01
capture attempt + capture date + relative mass + fragment size	-122.86	47	7	262.6	8.04	0.00

**Table 1-3.** Results of AICc selection of gamma distribution generalized linear mixed models testing the influence of variables on response blood CORT concentration (n=42) of birds tagged during 2018 and 2019, including year as a random effect.

<b>model</b>	<b>LL</b>	<b>n</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta_{AICc}</math></b>	<b>weight</b>
capture attempt	-161.95	42	4	315.3	0.00	0.33
capture attempt + capture date	-161.22	42	5	316.7	1.37	0.17
capture attempt + relative mass	-161.35	42	5	317.5	2.19	0.11
capture attempt + fragment size	-161.79	42	5	317.6	2.29	0.11
capture attempt + capture date + relative mass	-160.46	42	6	318.7	3.37	0.06
intercept	-161.06	42	3	319	3.73	0.05
capture attempt + capture date + fragment size	-161.11	42	6	319.3	3.96	0.05
capture attempt + relative mass + fragment size	-164.97	42	6	319.8	4.52	0.04
fragment size	-160.25	42	4	321	5.69	0.02
capture date	-164.56	42	4	321.1	5.78	0.02
capture attempt + capture date + relative mass + fragment size	-164.84	42	7	321.3	6.02	0.02
relative mass	-164.85	42	4	321.5	6.18	0.02
capture date + fragment size	-164.42	42	5	323.3	7.98	0.01
relative mass + fragment size	-164.43	42	5	323.5	8.21	0.01
capture date + relative mass	-164.73	42	5	323.6	8.3	0.01
capture date + relative mass + fragment size	-164.31	42	6	325.9	10.58	0.00

**Table 1-4.** Results of AICc selection of linear mixed models testing the influence of variables on first egg of last nest date (n=46) of tagged females during 2018 and 2019, including year as a random effect.

<b>model</b>	<b>LL</b>	<b>n</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta_{AICc}</math></b>	<b>weight</b>
fragment size	-176.24	46	4	361.5	0.00	0.38
intercept	-178.34	46	3	363.3	1.79	0.16
fragment size + relative mass	-175.91	46	5	363.3	1.85	0.15
fragment size + age	-176.24	46	5	364.0	2.52	0.11
relative mass	-177.76	46	4	364.5	3.03	0.09
age	-178.32	46	4	365.6	4.15	0.05
fragment size + relative mass + age	-175.90	46	6	365.9	4.48	0.04
relative mass + age	-177.71	46	5	366.9	5.45	0.03

**Table 1-5.** Results of AICc selection of poisson distribution generalized linear mixed models testing the influence of variables on number of young fledged by tagged females (n=41) during 2018 and 2019, including year as a random effect.

<b>model</b>	<b>LL</b>	<b>n</b>	<b>K</b>	<b>AICc</b>	<b>Δ_AICc</b>	<b>weight</b>
last nest	-95.54	41	3	197.7	0.00	0.19
last nest + fragment size	-94.79	41	4	198.7	0.96	0.12
last nest + relative mass	-94.87	41	4	198.8	1.11	0.11
intercept	-97.48	41	2	199.3	1.54	0.09
relative mass	-96.40	41	3	199.4	1.71	0.08
last nest + age	-95.19	41	4	199.5	1.75	0.08
last nest + fragment size + relative mass	-94.21	41	5	200.1	2.40	0.06
last nest + fragment size + age	-94.30	41	5	200.3	2.57	0.05
last nest + relative mass + age	-94.35	41	5	200.4	2.68	0.05
relative mass + age	-96.02	41	4	201.1	3.42	0.03
age	-97.27	41	3	201.2	3.46	0.03
fragment size	-97.35	41	3	201.4	3.62	0.03
last nest + fragment size + relative mass + age	-93.53	41	6	201.5	3.79	0.03
fragment size + relative mass	-96.29	41	4	201.7	3.95	0.03
fragment size + age	-97.13	41	4	203.4	5.64	0.01
fragment size + relative mass + age	-95.88	41	5	203.5	5.75	0.01

**Table 1-6.** Results of AICc selection of gamma distribution generalized linear mixed models testing the influence of variables on fall migration date (n=60) of birds tagged during 2016-2019, including year as a random effect.

<b>model</b>	<b>LL</b>	<b>n</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta</math>_AICc</b>	<b>weight</b>
fragment size + sex + fragment size*sex	-186.74	60	6	387.1	0.00	0.35
sex	-189.70	60	4	388.1	1.05	0.21
fragment size + sex	-188.65	60	5	388.4	1.34	0.18
fragment size + sex + fragment size*sex + age	-186.65	60	7	389.4	2.38	0.11
sex + age	-189.43	60	5	390.0	2.91	0.08
fragment size + sex + age	-188.48	60	6	390.5	3.48	0.06
fragment size	-193.19	60	4	395.1	8.03	0.01
intercept	-194.38	60	3	395.2	8.11	0.01
age	-194.25	60	4	397.2	10.16	0.00
fragment size + age	-193.13	60	5	397.4	10.31	0.00

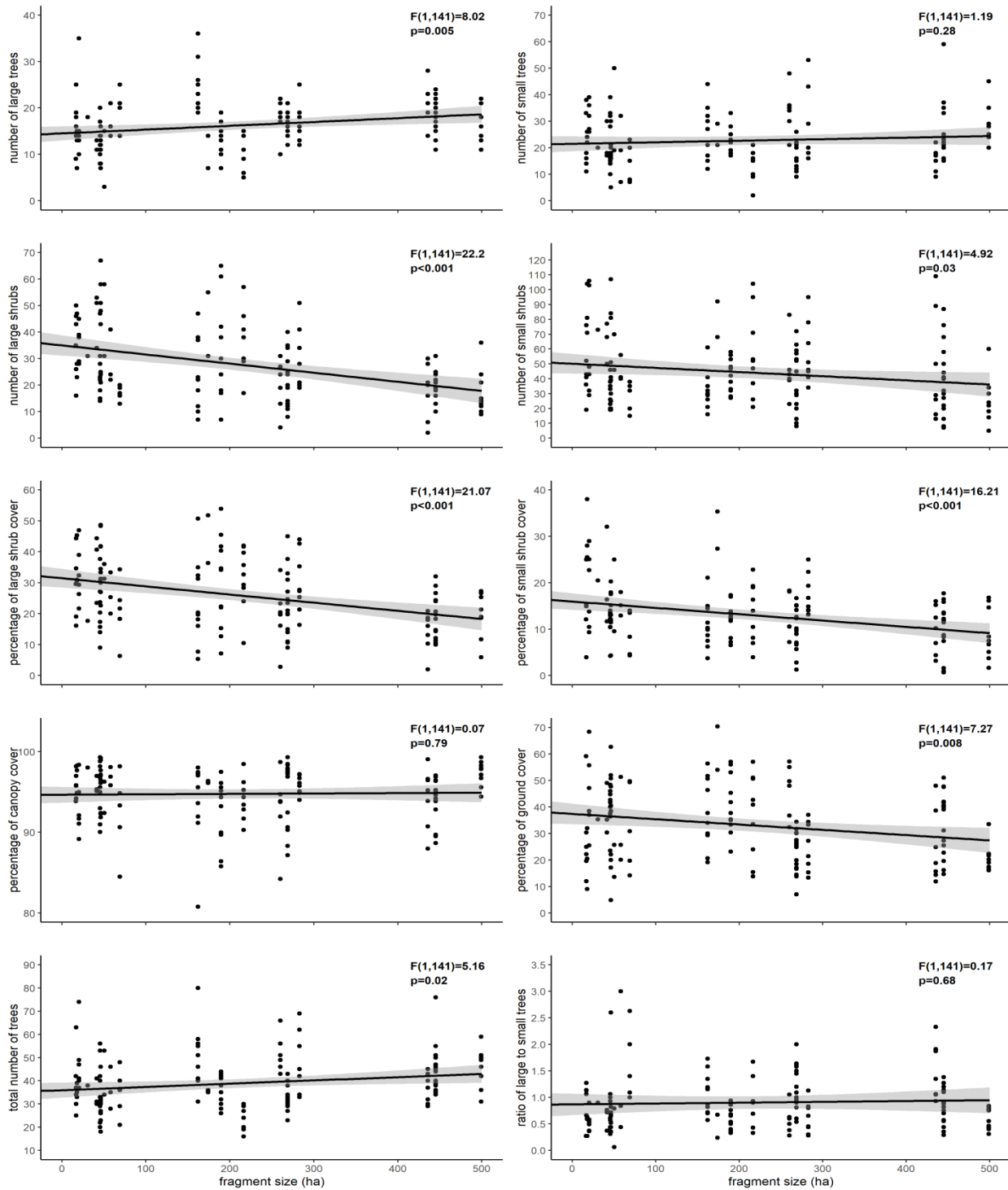
**Table 1-7.** Results of AICc selection of binomial distribution generalized linear mixed models testing the influence of variables on apparent survival (n=87) for birds tagged during 2016-2018, including year as a random effect.

<b>model</b>	<b>LL</b>	<b>n</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta</math>_AICc</b>	<b>weight</b>
intercept	-58.03	87	2	120.2	0.00	0.39
fragment size	-57.98	87	3	122.2	2.05	0.14
age	-57.98	87	3	122.2	2.05	0.14
sex	-58.02	87	3	122.3	2.12	0.13
fragment size + age	-57.93	87	4	124.4	4.15	0.05
fragment size + sex	-57.96	87	4	124.4	4.21	0.05
age + sex	-57.97	87	4	124.4	4.22	0.05
fragment size + sex + fragment size*sex	-57.17	87	5	125.1	4.88	0.03
fragment size + age + sex	-57.92	87	5	126.6	6.37	0.02
fragment size + age + sex + fragment size*sex	-57.16	87	6	127.4	7.17	0.01

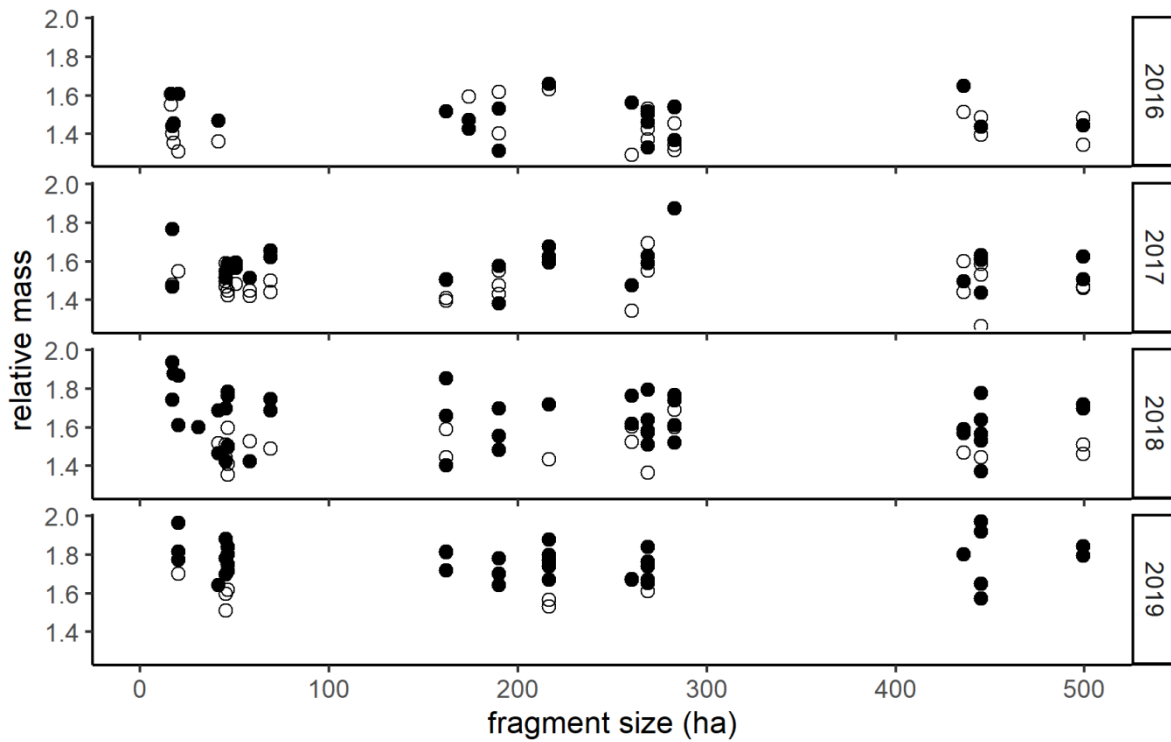
**Table 1-8.** Coefficient estimates for  $\Delta$  AICc <2 models that are also >2 AICc better than intercept-only model for relative mass (Table 1), response CORT (Table 3), and fall migration date (Table 6); coefficients appearing in multiple supported models are averaged.

<b>dependent variable</b>	<b>coefficient</b>	<b>estimate</b>	<b>s.e.</b>	<b>t-value</b>	<b>p-value</b>	<b>2.5%</b>	<b>97.5%</b>
<b>relative mass</b>	intercept	5.95e-1	4.46e-2	13.35	<0.001	5.07e-1	5.45e-1
	fragment size	-7.10e-6	1.94e-5	-3.66e-1	0.36	-4.52e-5	3.10e-5
	capture date	-6.39e-4	2.48e-4	-2.58	0.005**	-1.12e-3	-1.54e-4
	sex	-6.77e-2	9.80e-3	-6.91	<0.001***	-8.69e-2	-4.85e-2
<b>response CORT</b>	intercept	3.70	6.50e-1	5.70	<0.001	2.43	4.98
	capture attempt	2.39e-1	9.72e-2	2.46	0.007**	4.85e-2	4.29e-1
	capture date	-2.16e-3	4.17e-3	-0.52	0.3	-1.03e-2	6.03e-3
<b>fall migration</b>	intercept	5.59	5.92e-3	944.41	<0.001	5.58	5.61
	fragment size	3.45e-5	3.13e-5	1.10	0.14	-2.69e-5	1.03e-4
	sex	2.58e-2	9.71e-3	2.65	0.004**	6.75e-3	4.48e-2
	fragment size*sex	-3.74e-5	4.80e-5	-7.78e-1	0.22	-1.32e-4	5.68e-5

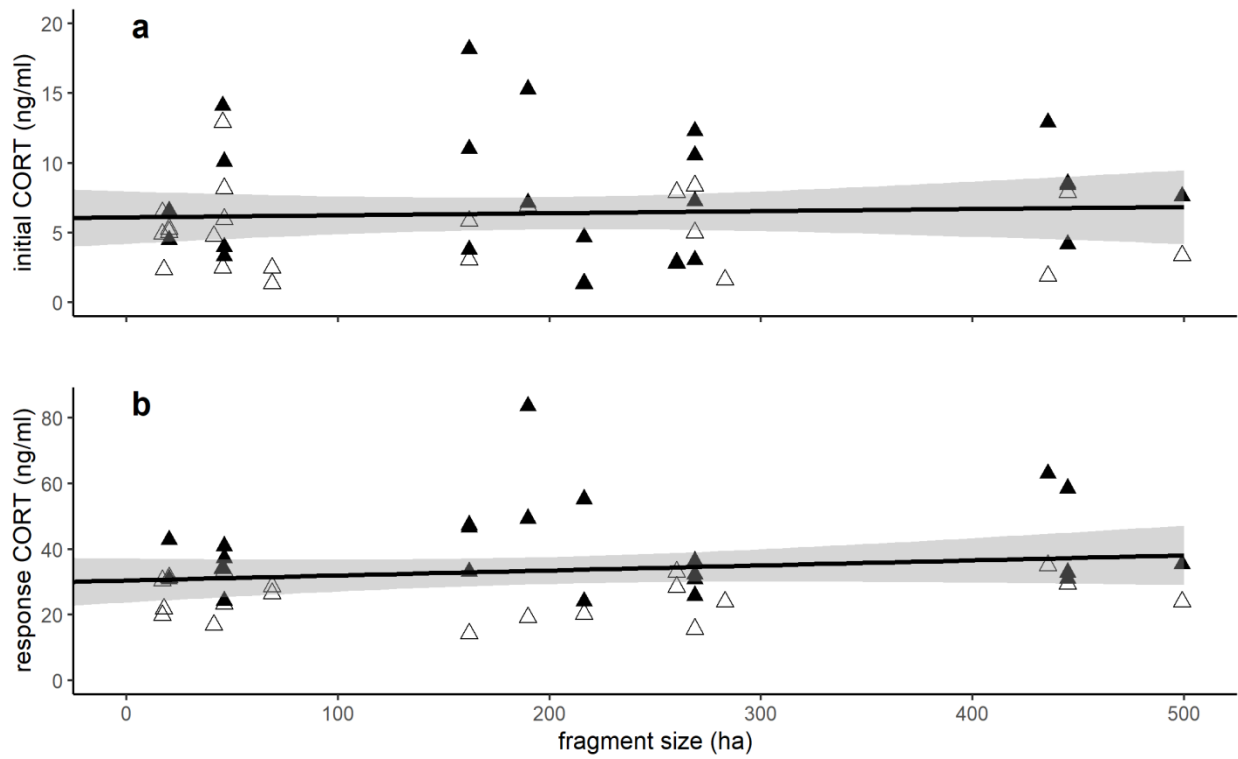




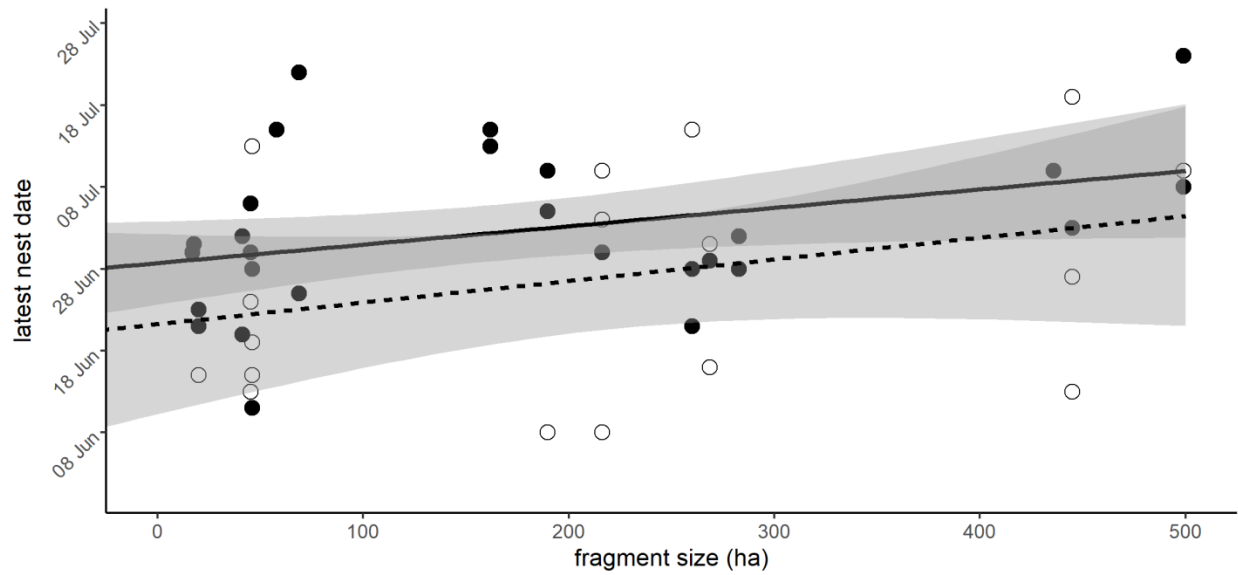
**Figure 1-2.** The relationship between vegetation characteristics and fragment size at the territory level (n=143), with large trees having a diameter at breast height (DBH) of  $\geq 30\text{cm}$ , small trees a DBH of  $10\text{-}30\text{cm}$ , large shrubs being more than  $1.3\text{m}$  tall, and small shrubs being  $0.5\text{-}1.3\text{m}$  tall.



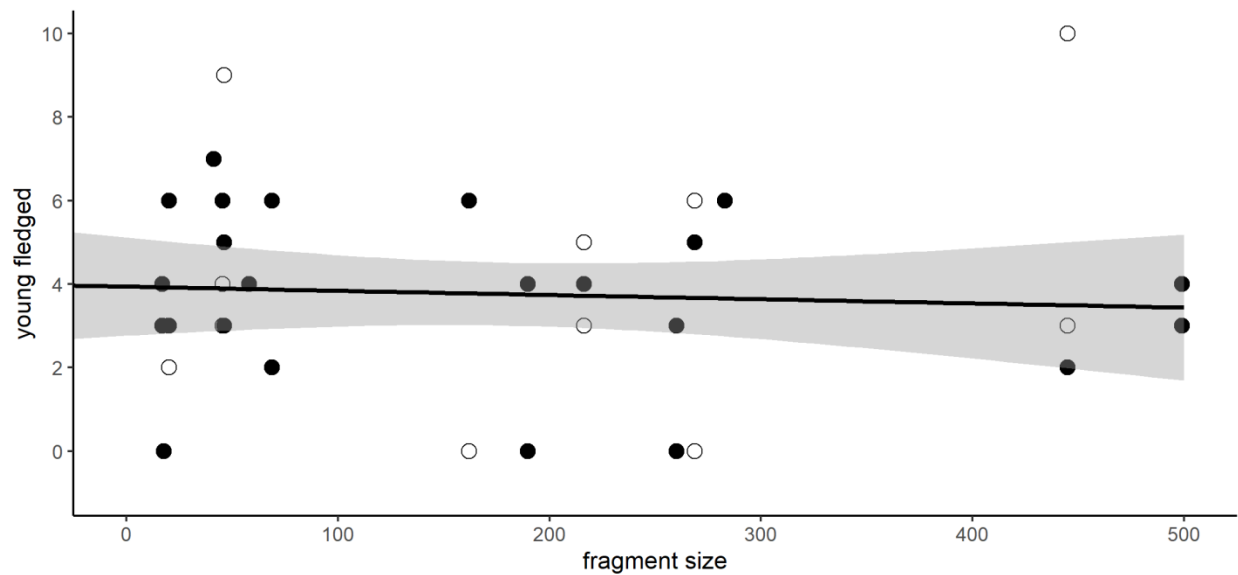
**Figure 1-3.** Fragment size did not have a significant effect on relative mass (mass/tarsus length) of female (closed symbols) or male (open symbols) Wood Thrushes in 2016 (n=45), 2017 (n=59), 2018 (n=64), or 2019 (n=44).



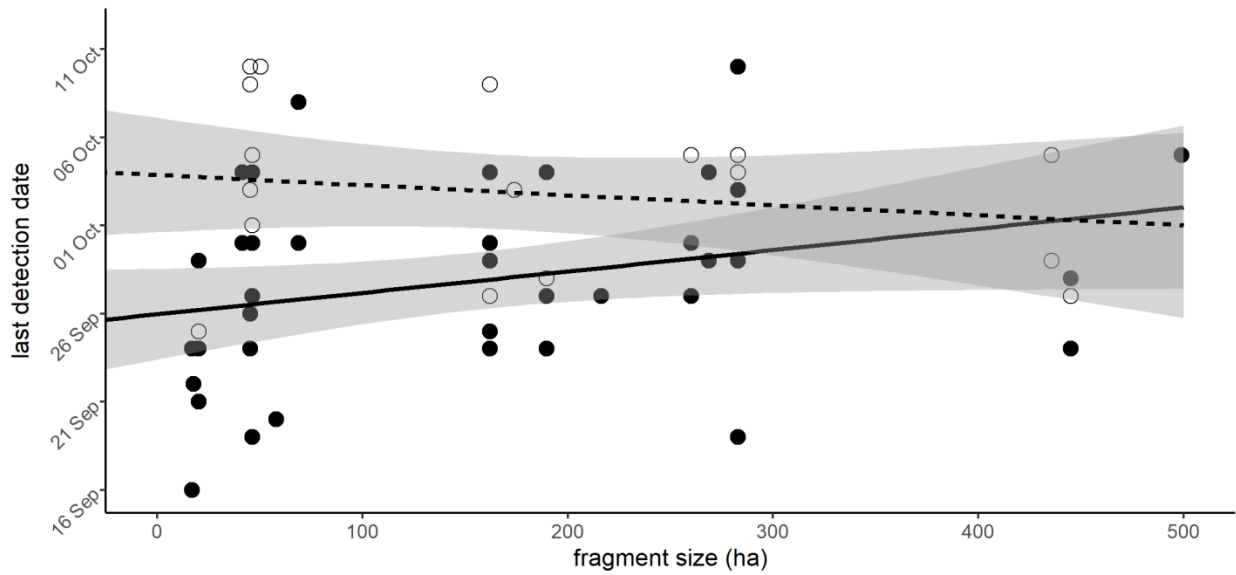
**Figure 1-4.** Fragment size did not have a significant effect on (a) initial (n=47) or (b) stress response (n=42) CORT during 2018 (open symbols) or 2019 (closed symbols).



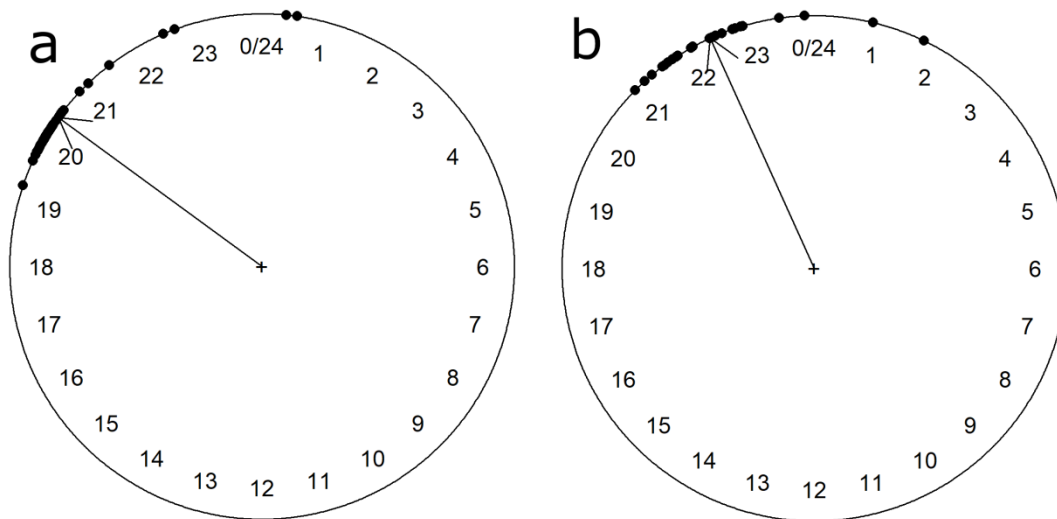
**Figure 1-5.** Fragment size was not a significant predictor of the first egg date of the last nest of individual females during 2018 (n = 28; closed symbols, solid line) and 2019 (n = 18; open symbols, dashed line).



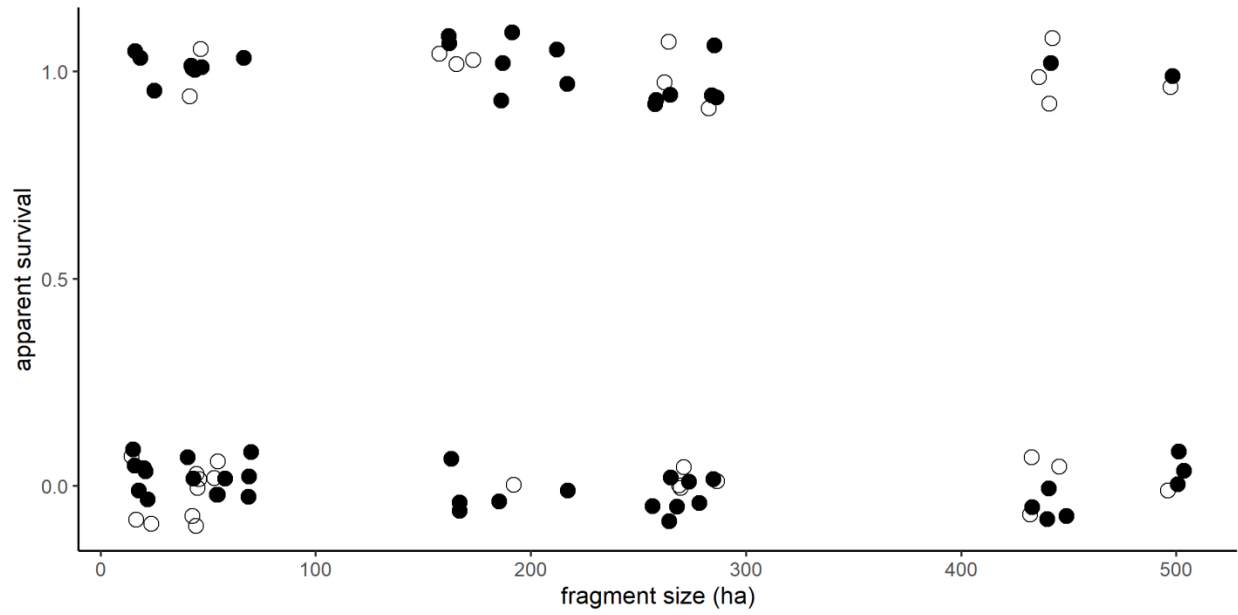
**Figure 1-6.** Fragment size was not a significant predictor of the number of total young fledged by individual females during 2018 (n = 25; closed symbols) and 2019 (n = 16; open symbols).



**Figure 1-7.** Fragment size was included in the top model for fall departure date of female ( $n = 41$ ; closed symbols, solid line) and male ( $n = 19$ ; open symbols, dashed line) Wood Thrushes, but was not a significant predictor.



**Figure 1-8.** Timing for (a) the first fall migration detection ( $n=60$ ), and (b) the first fall US migration detection ( $n = 25$ ) for Wood Thrushes had a non-random distribution plotted on a 24h clock.



**Figure 1-9.** Fragment size was not a significant predictor of survivorship of female (closed symbols) and male (open symbols) Wood Thrushes tagged during 2016 (n=20), 2017 (n=27), and 2018 (n=40) with jitter function applied to points, based on Motus detections and manual telemetry.

## Discussion

This study is the first to test whether forest fragmentation on the breeding grounds can impose negative carry-over effects on the timing of autumn migration and annual survival in a migratory songbird. This is surprising because negative carry-over effects of winter habitat quality on spring migration, and even reproductive success, have been well studied in other migratory songbirds (Marra et al. 1998; Bearhop et al. 2004; Norris et al. 2004; Reudink et al. 2009; Drake et al. 2013; Paxton and Moore 2015; Akresh et al. 2019). First, I found that habitat quality (forest fragment size) had no strong effects on adult body condition (relative body mass, corticosterone) while breeding. Second, I found that the onset of fall migration departure and annual survival were also not linked to breeding fragment size. Combined, I found no evidence for significant negative short-term or long-term effects of breeding habitat quality on adult Wood Thrushes.

### *Short-term effects of breeding season habitat quality on adults*

Relatively little research has focused on the link between breeding habitat quality and physiological condition for adult migratory Neotropical songbirds, but the relationship has been well documented on the tropical wintering grounds. Birds occupying lower quality winter territories have been found to have lower body condition (Marra et al. 1998; Latta and Faaborg 2001; Stanley et al. 2021) and elevated baseline CORT (Marra and Holberton 1998), due to the underlying ecological mechanism of lower food supply, specifically arthropods, in poor quality habitat (Brown and Sherry 2006). I found that most of my vegetation variables for breeding

habitat were linked to fragment size, with small fragments typically having fewer large trees and more shrubs, resulting in a denser, scrubbier understory. I did not quantify food abundance, but Burke and Nol (1998) sampled arthropod abundance in large and small fragments in central Ontario and found that terrestrial arthropod abundance was 10-36 times higher in large fragments which they attributed to higher ground level moisture and deeper leaf litter. However, despite arthropods forming the majority of a Wood Thrush's diet through most of the breeding season, differences in fragment size and habitat in my study did not produce significant differences in relative mass of Wood Thrushes. Although Wood Thrushes include a substantial amount of fruit in their diet later in the breeding season, most adults were sampled in late May or June before fruit becomes locally abundant. It is possible that small fragments in my study area, which by definition have a high percentage of edge habitat, did not have a lower arthropod food supply for Wood Thrushes. Supporting this possibility is a study by Kaiser and Lindell (2007) that found that in large fragments in southwestern Michigan, Wood Thrush nestling growth rate was higher for edge nests than interior nests. Despite the widespread assumption that small fragment size and edge habitat are poor quality foraging habitat, this does not appear to apply to breeding Wood Thrushes.

While relative mass was not linked to fragment size, I did find a difference between sexes, with females averaging both higher mass and shorter tarsus length, which led to a higher relative mass metric than males. Johnson et al. (1990) have suggested that the lower relative mass seen in males is likely due to the energetic costs of singing, mate guarding, and territorial defense. They explain that the higher relative mass seen in females could be a result of typical breeding season enlargement of the reproductive tract along with higher fat reserves that may



be beneficial for rapid reneating after nest predation. Body condition also decreased during the course of each breeding season and this decline was strongly driven by females. Males of many species have their lowest body condition indices early in the breeding season while frequently singing, acquiring, and defending territories, while females continue to decline in condition throughout the course of the season due to the energetic demands of repeated egg-laying, incubation, brooding and feeding nestlings (Hillstrom 1995).

During the two years of blood sampling, I found no evidence of either initial or response CORT being linked to fragment size which is consistent with my finding that breeding in small fragments does not have negative effects on the body mass of Wood Thrushes. Initial CORT samples were expected to be higher in small fragments due to an increased predation risk (Clinchy et al. 2004; Morris et al. 2015), lower food supply (Schoech et al. 2004), and general poor habitat quality (Marra and Holberton 1998; Rivers et al. 2014; Cirule et al. 2017), but small fragments in my study area may not suffer from these problems.

Both initial and response CORT were significantly higher during 2019, when birds in my study area endured an unusually cold spring which led to leaf out occurring almost two weeks later than a typical year. Despite this, Wood Thrushes began nest building at the same time as a typical year and nests initiated during May suffered high failure rates (2019 70% failed, n=27; 2018 38% failed, n=24). This year-to year pattern seems to best fit the CORT-tradeoff hypothesis (Wingfield and Sapolsky 2003; Patterson et al. 2014; Schoenle et al. 2018) which posits that higher levels of baseline CORT and a more robust stress response will direct resources away from reproduction and towards immediate survival. Low temperatures during breeding have also been linked to elevated baseline CORT in Blue tits (*Cyanistes caeruleus*)

(Henderson et al. 2017). Longer term studies are needed to assess how adverse spring weather affects CORT in breeding adults, and whether this is more severe for birds in smaller fragments, because year-to-year variation in spring environmental conditions is expected to increase with climate change.

Habitat quality carry-over effect studies that take place on the wintering grounds have often relied on a strong moisture gradient for habitat classification, with higher quality habitat associated with mesic conditions and low quality habitat associated with xeric conditions. For instance, Marra et al. (1998) studied American Redstarts occupying two distinct habitat types on the wintering grounds. High quality wet mangrove habitat was occupied by dominant birds, usually adult males, with better body condition and lower baseline CORT concentration (Marra and Holberton 1998), while subordinates were relegated to a dry scrub habitat. These two drastically distinct habitat types have also been linked to differences in body condition for other wintering Neotropical migrants (Bearhop et al. 2004; Studds and Marra 2005; Brown and Sherry 2006; Cooper et al. 2015). On the breeding grounds, the vegetation differences that occur between small and large forest fragments, or even edge versus interior sites, may not be starkly different enough in terms of food supply to produce strong carry-over effects on adult CORT while they are breeding.

Initial CORT concentration was dramatically lower than the stress response CORT concentration, as expected. However, response CORT concentration had a positive relationship with whether a bird was captured on the first or second attempt, with a 33% effect size. To capture female Wood Thrushes, I erected mist nets beside nests and then walked toward the nest steadily from the opposite direction until the female flew off the nest, usually into the net.

In some instances, female birds evaded capture by leaving the nest during net setup or missing the net entirely. In these cases they were captured either while returning to the nest or by repeating the process a second time. Interestingly, capture attempt had only a very weak effect on initial CORT suggesting that it was the strength of the induced stress that was influenced most strongly by apparent pre-capture disturbance. While every effort was made to limit disturbance while setting up mist nets around nests and female Wood Thrushes typically stay on the nest even when approached very closely, it is impossible to know if some females initiated a stress response prior to capture. Concentrations of both initial and response CORT were similar to a study of Wood Thrushes in a large forest fragment where females were not flushed from nests (Done et al. 2011). My analyses used the inter-quartile method to identify and eliminate any outliers (n=8) and I also re-ran the analyses using only birds captured on the first attempt (initial n=27; response n=25) which produced a similar result that neither CORT variable was predicted by fragment size.

Further evidence that small fragments are not necessarily poor quality habitat for Wood Thrushes is that the season-long reproductive success of individual females did not vary with fragment size. Radio-tracking revealed that the total number of young fledged per female, number of nesting attempts per female, and number of broods per female did not vary with fragment size. I am not aware of any study that has radio-tracked female migratory songbirds to test how total reproductive success varies with forest fragment size. Few studies on forest fragmentation have even banded breeding females to determine the occupant of renests and for many species, like the Wood Thrush, females may routinely disperse off territory for renesting (Gow and Stutchbury 2013) making it difficult to quantify season-long reproductive

success. The influence of fragment size on season-long reproductive success is expected to vary geographically because of regional differences in maximum fragment size (Friesen et al. 1999; Burke and Nol 2000), the amount of local forest cover (Zanette and Jenkins 2000), and differing assemblages of predators that may or may not be forest dependent (Nour et al. 1993). In my study area regional forest cover was low (21%) and fragment size ranged from 11 – 499 ha, yet fragment size was not predictive of individual reproductive success. Although many previous studies have found lower nesting success for Wood Thrushes in small fragments (Donovan et al. 1995; Robinson et al. 1995; Burke and Nol 2000) this was not the case in my study area. While forest fragment size did not predict total number of young fledged in my study, last nest date appeared in the top three models of this analysis (combined weight 0.42). Though these models were not statistically better than the intercept-only model, this may suggest that last nest date is at least weakly positively correlated with the number of young fledged, and could become a significant predictor of total reproductive success with a larger sample. Season-long and manual radio-tracking of females to locate and monitor all their nesting attempts is logistically challenging, making it difficult to attain strong statistical power.

#### *Long-term carry-over effects of breeding season habitat quality*

This is also the first study to test if nesting in small fragments creates timing delays for adults at the end of the breeding season. Radio-tracked females in large fragments averaged slightly later final nests of their season, opposite to what was expected, but this difference was only a few days and not statistically significant. Timing of last nests is potentially important in triggering carry-over effects because adults benefit from minimizing overlap between the

energetically expensive activities of feeding young, molting feathers, and migrating. Fall migration timing in Wood Thrushes is influenced by feather molt timing, which is in turn influenced by timing of the last nest (Stutchbury et al. 2011). This light-level geolocator tracking study found that birds nesting later into the season delayed their annual feather molt and this translated into these birds being delayed during fall migration. However, females in small fragments in my study did not experience poor body condition, high nest predation or more nesting attempts and so these did not culminate in later final nests.

I also found no evidence that the initiation of fall migration departure was linked to breeding fragment size, and while fall departure dates varied by more than a month, this variation was not related to fragment size. Little is known about how breeding habitat affects the timing of fall migration in migratory songbirds although some studies have found evidence that the cessation of breeding activities is tied to the initiation of fall migration (Mitchell et al. 2012; Saino et al. 2017; Briedis et al. 2018; de Zwaan et al. 2019; Chmura et al. 2020; Imlay et al. 2021). However, none of these studies attempted to account for whether habitat quality is related to the cessation of breeding activities. While small breeding fragment size does not contribute to long term carry-over effects on Wood Thrushes, studies on other forest songbirds are needed to determine if habitat induced post-breeding carry-over effects are generally weak compared with those found for wintering-to-breeding carry-over effects.

Fall migration was not related to fragment size; however, sex played a significant role in migration timing with females departing an average of five days earlier. Differential migration timing by sex has been well-studied during spring migration, with males of many species arriving earlier on the breeding grounds than females in order to secure a high quality territory

and a mate (Morbey and Ydenberg 2001). Individual autumn migration timing differences based on sex have received less study because the tracking technology has only relatively recently become available. Mills (2005) speculated that later autumn migration in males than females may occur because males benefit from defending their territories after breeding, particularly from prospecting juveniles. Male Wood Thrushes are known for having high breeding site fidelity (Roth and Johnson 1993), returning to the same territory year after year but it is unknown to what extent territory defense is important in early fall. A different possibility is that molt timing differs between sexes, with females completing molt before males, allowing for an earlier departure. In Pennsylvania, just south of my study site, Stutchbury et al. (2011) found that female Wood Thrushes began their molt earlier than males but they were not able to determine onset of fall migration timing. It is not known if earlier migration brings any advantages in terms of migration or wintering ground survival, but late molting Wood Thrushes did not arrive later at the wintering grounds (Stutchbury et al., 2011).

Based on the subset of female birds (n=24) with data for both fall Motus detections and total number of fledglings, high reproductive success did not significantly delay fall migration timing. For these females, fragment size was a significant predictor of fall departure date with large fragment birds averaging later departures, contrary to prediction. Interestingly, the apparent weak relationship between reproductive success and migration timing appears to be largely driven by small fragments (Fig A-2). For instance, in small fragments the least reproductively successful female (zero fledglings) departed almost two weeks before the most successful female (nine fledglings). Although later nesting birds average higher reproductive success, it remains unknown whether a tradeoff occurs between higher reproductive effort and

the potential benefits of early migration. This could potentially be experimentally tested by Motus tagging Wood Thrushes in a variety of large and small fragments and then inducing half of the tagged birds in each fragment to complete nesting early through removal of the second brood nest, while leaving the other half as an unmanipulated control group. Reproductive success could be monitored for all birds and migration timing and annual survival could again be determined through automated Motus detections. If birds in the experimental group have a higher rate of survival, and birds in the control group have higher season-long reproductive success, this would provide evidence of a tradeoff occurring.

Fragment size was not linked to annual survival in a logistic regression analysis although I did find that 47% of Wood Thrushes breeding in large fragments returned to the study area the following spring compared to only 29% of small fragment birds. My study is the first I am aware of to use long-lasting radio tags combined with the Motus wildlife tracking system to estimate annual survival in a migratory songbird. The mark and re-sight method is typically used to estimate annual survival but this is only accurate if returning birds have very high site fidelity (i.e., high probability of resighting birds that survived). Motus was able to significantly improve my estimates of apparent survival compared to mark and re-sight studies by detecting and confirming survival of an additional 37% of returning birds. These individuals did not return to their former breeding fragments and thus would have otherwise been considered to have not survived despite returning to the study area. In a mark and re-sight study on American redstarts (*Setophaga ruticilla*), Studds and Marra (2005) found a significant relationship between winter habitat quality and annual survival, with 59% of birds wintering in high quality habitat sighted the following year compared to only 33% of those occupying low quality habitat. As noted

earlier, differences in habitat quality between small and large breeding fragments may not be extreme enough to trigger annual survival differences.

Periods of the annual cycle are temporally and geographically separate in migratory birds but remain linked with each other through complex seasonal interactions that can make it difficult to identify the primary causes of population decline (Harrison et al. 2011). Recent calls have been made for increased full annual cycle research (Marra et al. 2015), and while studies focusing on carry-over effects are becoming more common, those examining breeding season carry-over remain rare (reviewed by Harrison et al. 2011). These breeding carry-over studies largely focus on timing of nesting vs fall migration (Mitchell et al. 2012; Saino et al. 2017; Briedis et al. 2018; De Zwaan et al. 2019; Chmura et al. 2020; Imlay et al. 2021) and little is known about whether breeding habitat quality has long term consequences at later stages of the annual cycle. Latta et al. (2016) used feather CORT to estimate conditions at the time of the post-breeding annual molt in Louisiana waterthrushes (*Parkesia motacilla*) and found that birds in better condition during the pre-migratory molt also secured better winter territories and were more likely to return the following year perhaps indicating higher quality breeding habitat. In my study, the lack of significant relationships between fragment size and key variables including body condition, timing of nesting and migration, reproductive success and annual survival may indicate that fragmentation on the breeding grounds does not impose strong negative carry-over effects on adult Wood Thrushes. It is an enigma that Wood Thrushes in my study area appear to thrive in small forest fragments, even though studies in other regions and on other species have often shown short-term negative effects of fragmentation on food supply and nesting success. The presence or absence of breeding habitat-induced seasonal



carry-over remains an unknown for other declining migrant songbirds but long-term tracking technologies, such as the Motus automated telemetry network, can now be used to fill this critical gap.

### **Chapter 3: Does migration route variation predict survival for a migratory songbird?**

## Introduction

Migration may represent the most dangerous period of the annual cycle in the lives of many songbirds (Sillett and Holmes 2002). Variation in migration routes between geographically distinct breeding populations of a species can arise through migratory connectivity when they also occupy geographically distinct wintering grounds (Webster et al. 2002); however, variation in migration routes can also exist within a breeding population that travels to the same wintering grounds (Vardanis et al. 2011). This variation in migration routes has the potential to increase or decrease the probability of survival through the avoidance of obstacles such as cities (Loss et al. 2014), or the inclusion of resources such as rich stopover sites (Mehlman et al. 2005). Being able to link survival outcomes to variation in migration routes has the potential to identify threats that occur during the most dangerous period of the annual cycle.

Past efforts to track migration routes of small songbirds traditionally had to rely on mark and recapture techniques with a very low recovery rate, such as bird banding (Wood 1945). Technological advances first allowed mapping of migration routes using light-level geolocators (Stutchbury et al. 2009) with accuracy measured in hundreds of kilometers (McKinnon et al. 2013) and later, mapping using GPS pinpoint tags accurate to within 10m (Halworth and Marra 2015); however, both of these devices are archival and rely on a bird surviving migration and being successfully recaptured to access stored data. With a detection range of ~15km, Motus is not as accurate as GPS pinpoint tags, but provides the unique opportunity to collect data from individuals that do not survive, as well as birds that are not recaptured.

Many migration tracking studies rely on tagging that takes place at stopover sites so the breeding grounds of tagged birds remain unknown (ex. Begin-Marchand et al. 2021) or are broadly estimated using indirect methods such as feather isotopes (Smetzer et al. 2017). Without accurate knowledge of breeding grounds, individuals may not be heading to the same non-breeding region, so any relationship between survival and slight migration route variation is impossible to discern. Wood Thrushes exhibit migratory connectivity (Stanley et al. 2015) so the birds tagged in this study from the same breeding population are presumed to be travelling to the same wintering location and are expected to follow a similar migration route. Using light-level geolocators, Stanley et al. (2015) found that 97% birds from the region of my breeding population migrated to Central America through the eastern Gulf or Florida and 70% wintered in a narrow band through eastern Honduras, Nicaragua, and northern Costa Rica. For the first time to my knowledge, I am able to use Motus to compare the migration routes of breeding birds that survive until the following breeding season with those that do not.

## **Materials and methods**

### *Ethics statement*

Permits and permissions were obtained for all land access required for research, and all bird handling and research protocols were approved by the York University Animal Care Committee.

### *Study area*

This study was conducted in Norfolk County, Ontario, which lies on the north shore of Lake Erie and retains 21% forest cover composed of a wide variety of deciduous and mixed forest fragments of varying sizes (LPRCA, 2019). Norfolk County has the most extensive Motus coverage in Ontario, with 13 towers resulting in near-complete coverage for birds in migratory flight (Fig 1-1). The study was designed to compare small versus large fragments as a means to maximize expected effect size given the logistical constraints of working in, and travelling between, so many study sites. Although sample sizes varied slightly between years owing to access constraints to private land, in general there were 10 small (11-69 ha in size) and 10 large (162-499 ha in size) forest fragments (Fig 1-1; Table A-1) on a mix of public and private land. In many cases, roads acted as an edge for at least one portion of a fragment and the width of a roadway is the minimum distance between fragments in this study. Necessary permits were obtained for conducting research on public lands, and landowner permission was sought during each spring for access to private lands.

### *Study species*

Wood Thrushes were chosen for this study because adults are able to carry a radio transmitter without negative effects on survival and behaviour (Vega Rivera et al. 1998; Anders et al. 1998; Gow et al. 2011), and they have been successfully tracked year-round using archival light level geolocators (Stutchbury et al. 2009; Stutchbury et al. 2010). They are also a long distance migrant that winters in the forests of Central America and now a federally listed Threatened Species at Risk in Canada. However, Wood Thrushes are still a common breeding species in the deciduous and mixed forests of southwestern Ontario (COSEWIC, 2012).

### *Tagging*

The specifications of the radio-tags (“nanotags”) varied among years due to the manufacturer discontinuing models but all had a burst rate of 12.7 seconds and minimum expected lifespan of 400 days. In 2018, a combination of ANTC-M6-1 and NTQB2-6-1 (~1.6g) nanotags were fitted to adult Wood Thrushes of both sexes during the incubation period of nesting, and in 2019, NTQB2-4-2S (~1.5g) nanotags were fitted to only adult female Wood Thrushes during the incubation stage of their first nesting attempt of the season. Nanotags were attached using a backpack leg loop harness (Rappole & Tipton 1991) made from 2.5mm Teflon tubing. To catch the birds, two 12m mist nets were set up 90 degrees to each other, about 3-5 m from the nest, boxing in two sides. If an adult bird was present at the nest after net set up, we would walk steadily towards the bird opposite to the nets until it flew off the nest, usually into a net. Adults were banded with both Canadian Wildlife Service numbered

aluminum bands and unique colour band combinations to allow for identification when birds were re-sighted.

### *Motus detections, and aerial telemetry*

Motus receivers sometimes record false detections due to random radio noise, duplicate tags, and overlapping tag signals when multiple tags are transmitting in the same area (Crewe et al. 2020). A number of filtering and quality control steps were taken to identify these and exclude them from analysis. First, I eliminated any detection that fell outside of my deployment dates. Next, I eliminated detections of fewer than three consecutive tag bursts because such runs are likely to be false detections (Crewe et al. 2020). Lastly, I eliminated any detection that occurred in impossible or highly unlikely locations, or represented unrealistic distances and directions based on prior knowledge of migration timing and routes from geolocator studies (Stutchbury et al. 2009; Stutchbury et al. 2010).

During June/July of 2018 and 2019 a four hour aerial telemetry survey was conducted to attempt to locate the breeding sites of returning birds and search for individuals that may not have been detected by Motus as they arrived in the area. Aerial telemetry surveys were conducted from a Cessna 172 equipped with a strut-mounted H-type antenna and SRX 600 Lotek receiver. We followed a flight pattern designed to completely cover the study area in a grid pattern search and any additional forest fragments within ~10 km of our study site boundary. Once a tag was detected, multiple passes were completed over the same area and a GPS point was taken at the location of the strongest signal.

### *Statistical analysis*

All analyses were conducted in R 4.1.2 (R Core Team 2022) and all tests were two-tailed with values are expressed as means  $\pm$ SE. To better visualize detection density, kernel density estimation was performed using the `stat_density_2d` function in the `ggplot2` package (Wickham 2016). Maps overlaid with kernel density estimation were retrieved from Google (Google Maps 2022) and generated using the `ggmap` package (Kahle & Wickham 2013). Migration speed plots were created using the `ggplot2` package (Wickham 2016).



## Results

### *Migration routes*

During four field seasons that took place from May-August 2016-2019, I tagged 117 adult Wood Thrushes and 60 (51%) of those were detected by the automated Motus system departing the study area during the onset of fall migration. Of these 60 birds, 33 were also detected outside of Ontario on their way to the wintering grounds in Central America. Most of these migrating birds (32 of 33) were detected at Motus towers located in the United States. Outside of the US, one was detected in Mexico and two in Belize. In total, birds were detected at 18 different Motus towers in the US (Table 2-1), one tower in Mexico, and one tower in Belize. Birds detected passing through the United States ranged from being detected by a single tower to as many as three towers with an average of  $1.55 \pm 0.13$  towers/bird. Within the United States, birds were detected heading almost directly south from the study area, with all detections occurring between longitudes of  $-79.77$  and  $-84.16$ .

After removing birds tagged during 2019 that had an unknown survival outcome due to the possibility of faulty tags ( $n=5$ ), I was left with 28 birds with apparent survival outcomes. Of these birds, 14 were detected returning to the study area the following year, while 14 were not, despite the large number of towers in the region. I produced separate kernel density plots for fall detections of birds that returned from migration (Fig 2-1) and those that did not (Fig 2-2). Birds that returned from migration had an average first US detection longitude of  $-80.74 \pm 0.26$ , compared to  $-81.67 \pm 0.64$  for birds that did not return, however this difference was not

statistically significant (t-test  $t(17)=-1.33$ ,  $p=0.20$ ). At a latitude of  $35^{\circ}$  N, this represents a difference of  $\sim 84$  km.

A total of 38 tagged Wood Thrushes were detected by the Motus system during spring migration, with 18 being detected passing through the United States, and the remaining birds only detected within Ontario. These 18 birds were detected at a total of 17 different United States towers (Table 2-2), with an average of  $1.61 \pm 0.18$  towers/bird. Within the United States, five birds were detected along the northern Gulf of Mexico, with four detections occurring in Texas, and one in Louisiana (Fig 2-3). One bird may have travelled north through Florida, as evidenced by detections at two towers located in eastern Georgia. Birds were detected at a greater range of longitudes than fall migration, especially to the west, ranging from  $-95.83$  to  $-78.74$ . The five most southerly detections occurred farther west than any fall detection, indicating that most birds must travel in a northeasterly direction in spring while traversing through the United States.

### *Migration speed*

Fall migration speeds varied remarkably by individual. To estimate fall migration speed, I plotted the migration detections of each bird that was detected both departing the southwestern Ontario study area and at least once outside of Ontario (Fig 2-4a;  $n=30$ ). During fall departure, many birds were detected at multiple Motus towers located within the study area so I treated the last detection within the study area as the first detection of fall migration and used the latitude of the southern edge of the study area ( $42.6^{\circ}$  N) to represent this first migration detection of all birds. Travelling from the southern edge of the study area located at

approximately 42.6° N, a total of five Wood Thrushes were detected crossing 35.20° N in North Carolina, located ~844km to the south. The fastest bird departed Ontario on Sept 24 and arrived in North Carolina just over 32 hours later on Sept 25. The slowest bird took 21 days to cover the same distance, while the average timing was  $12.4 \pm 3.2$  days. Five individuals were also detected crossing 30.09° N in northern Florida, ~1424km from the study area. The fastest of these birds arrived 14 days after departing the study area, while the slowest two birds both took 20 days. On average, birds took  $17.6 \pm 1.3$  days to make the journey to northern Florida. Three birds were detected reaching the tropics, with one covering the straight-line distance of ~2580km to the Yucatan in Mexico in 29 days. The other two tropical detections occurred ~2932km from the study area in Belize and the birds covered the distance in only 16 and 22 days.

Much like fall migration, spring migration speed also varied greatly by individual. To visualize spring migration speed, I plotted the detections of every bird that was detected both arriving in the study area and at least once outside of Ontario (Fig 2-4b; n=15). During spring arrival, many birds were detected at multiple Motus towers located within the study area so I treated the first detection within the study area as the last detection of spring migration and used the latitude of the southern edge of the study area (42.6°) N to represent this last migration detection of all birds. Of the three birds detected in Texas, the two detected at High Island covered the ~1901km to the study area in 19 and 22 days. The third bird detected in Texas was farther to the west and covered the ~2021km to the study area in only 10 days. This bird was in Texas later (April 30) than those detected at High Island (April 21/April 22), yet arrived at the study area earlier (May 10) than the other two birds (May 11/May 13). The only

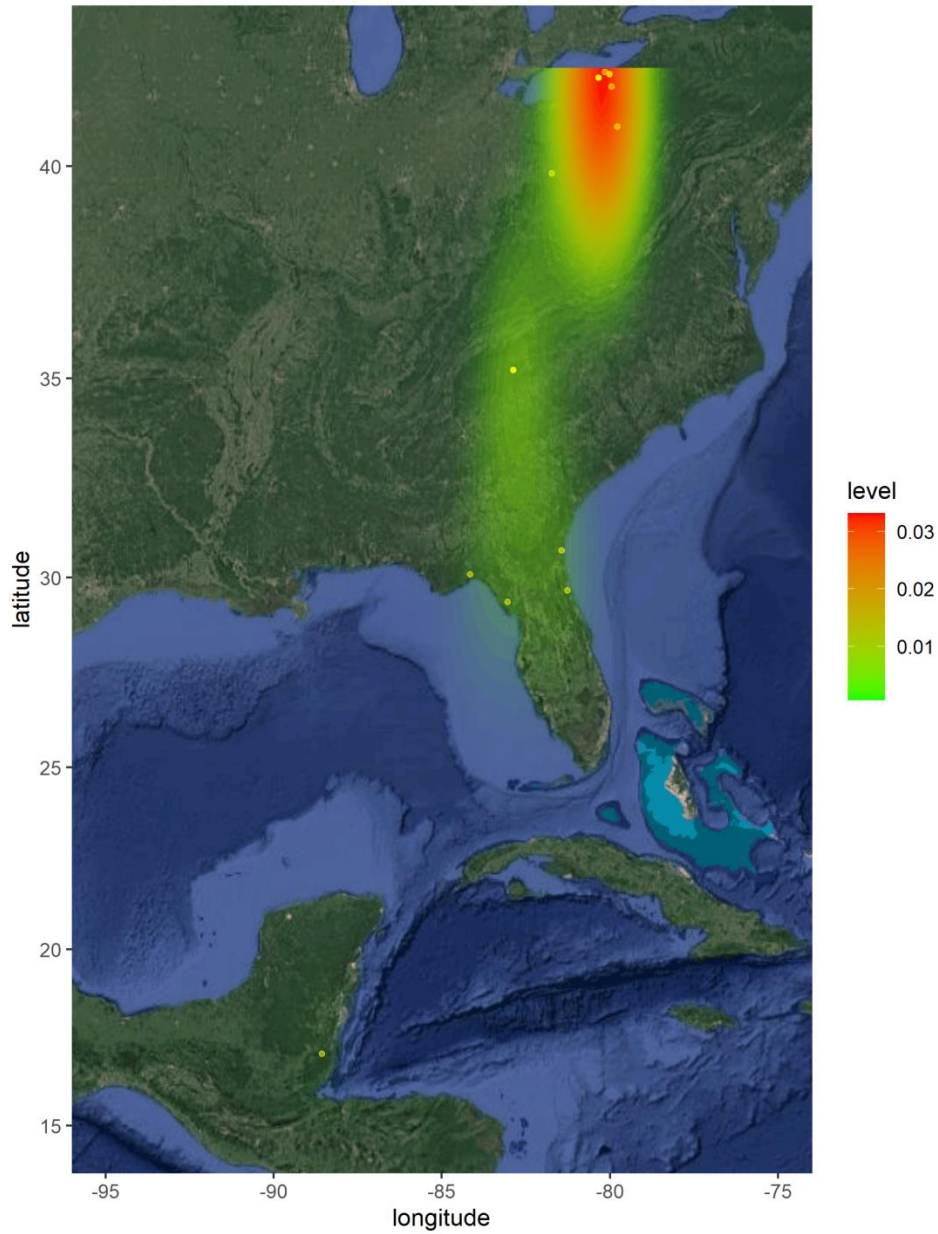
other bird detected on the Gulf coast that was also detected in the study area, was in Louisiana on Apr 26 and covered the ~1725km to the study area in only five days. The bird that was detected heading northward through eastern Georgia on April 26 reached the study area 10 days later on May 6 after covering ~1274km. Two birds were detected crossing 35.20° N in North Carolina, reaching the study area ~844km to the north, in two and eight days. These birds covered the same distance much faster than the fall average of 12.4 days.

**Table 2-1.** Number of Wood Thrushes detected at each Motus tower within the United States during fall migration (2016-2019).

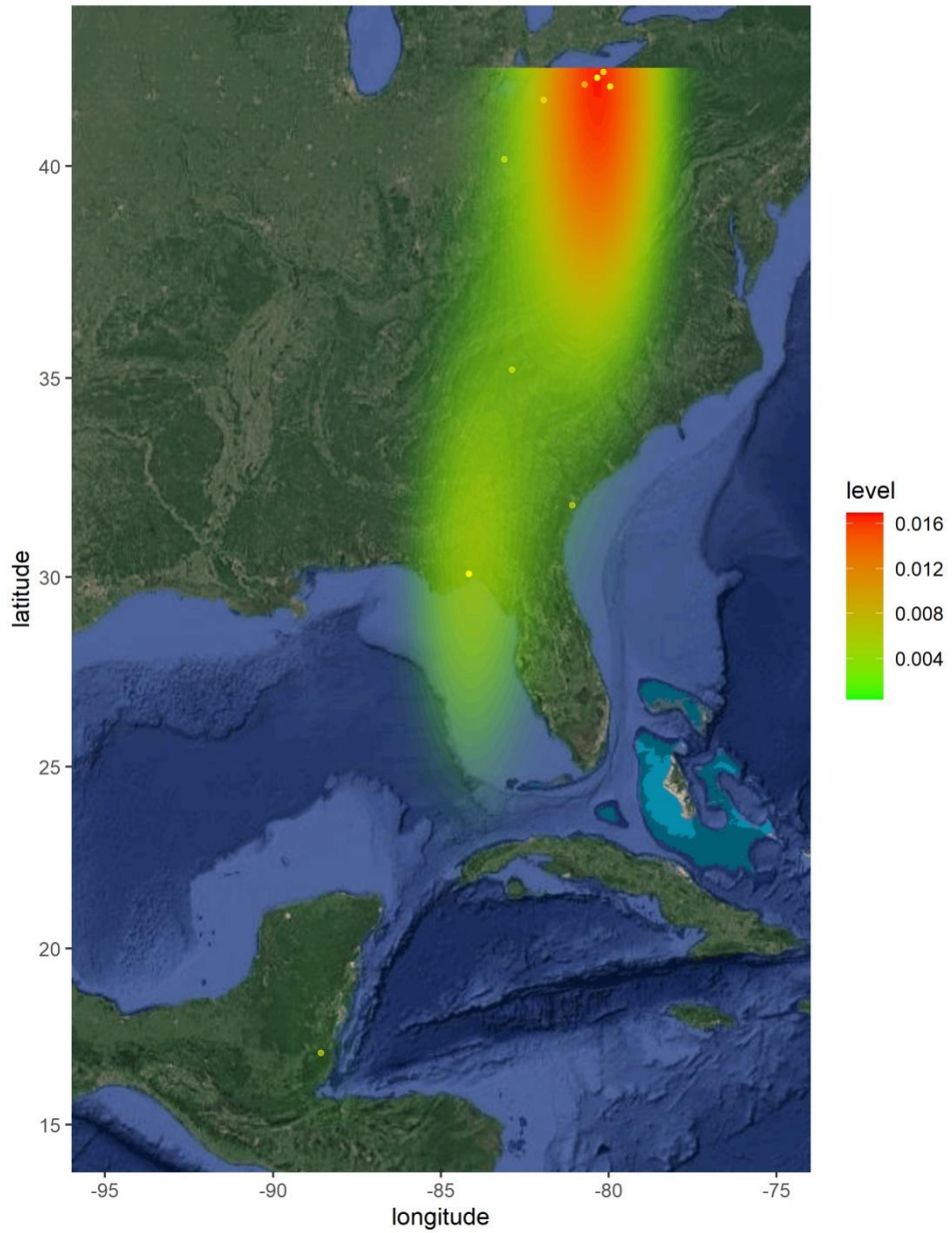
<b>state</b>	<b>tower</b>	<b>latitude</b>	<b>longitude</b>	<b>detections</b>
<b>Pennsylvania</b>	Presque Isle	42.1098	-80.1541	3
	Lakeview	42.0628	-80.0168	3
	Girard	41.9856	-80.3379	14
	Stutchbury	41.7859	-79.9504	4
	Butler	40.8906	-81.9337	1
<b>Ohio</b>	Kingsville	41.8376	-80.712	1
	Cleveland	41.5423	-81.629	1
	Honey Hut	41.4907	-81.9337	1
	Columbus Zoo	40.1602	-83.1147	2
	The Wilds	39.8298	-81.7327	2
<b>North Carolina</b>	Pisgah Astronomical	35.197	-82.8732	5
<b>Georgia</b>	Ossabaw Island	31.8406	-81.0883	1
	DNR Headquarters	31.1229	-81.4776	1
<b>Florida</b>	Fort Clinch	30.6987	-81.4321	1
	St Marks	30.088	-84.1628	5
	Lower Suwanee	29.3725	-83.0443	1
	Florida Panther	26.1872	-81.35	1

**Table 2-2.** Number of Wood Thrushes detected at each Motus tower within the United States during spring migration (2017-2020).

<b>state</b>	<b>tower</b>	<b>latitude</b>	<b>longitude</b>	<b>detections</b>
<b>Louisiana</b>	Wisner	29.1230	-90.1605	1
<b>Texas</b>	San Bernard	29.1623	-95.8254	1
	High Island	29.5622	-94.3904	3
<b>Georgia</b>	DNR Headquarters	31.1229	-81.4776	1
	St Simons	31.2956	-81.3435	1
<b>North Carolina</b>	Pisgah Astronomical	35.197	-82.8732	3
<b>Ohio</b>	The Wilds	39.8298	-81.7327	2
	Winous Point	41.4619	-82.9991	1
	Honey Hut	41.4907	-81.9337	1
	Geneva	41.8582	-80.9701	4
<b>Pennsylvania</b>	State Game Lands	40.0774	-78.7493	2
	Ford Island	41.6367	-80.4228	1
	Stutchbury	41.7859	-79.9504	2
	Girard	41.9856	-80.3379	3
	Lakeview	42.0628	-80.0168	1
	Presque Isle	42.1098	-80.1541	1
	North East	42.1755	-79.8394	1

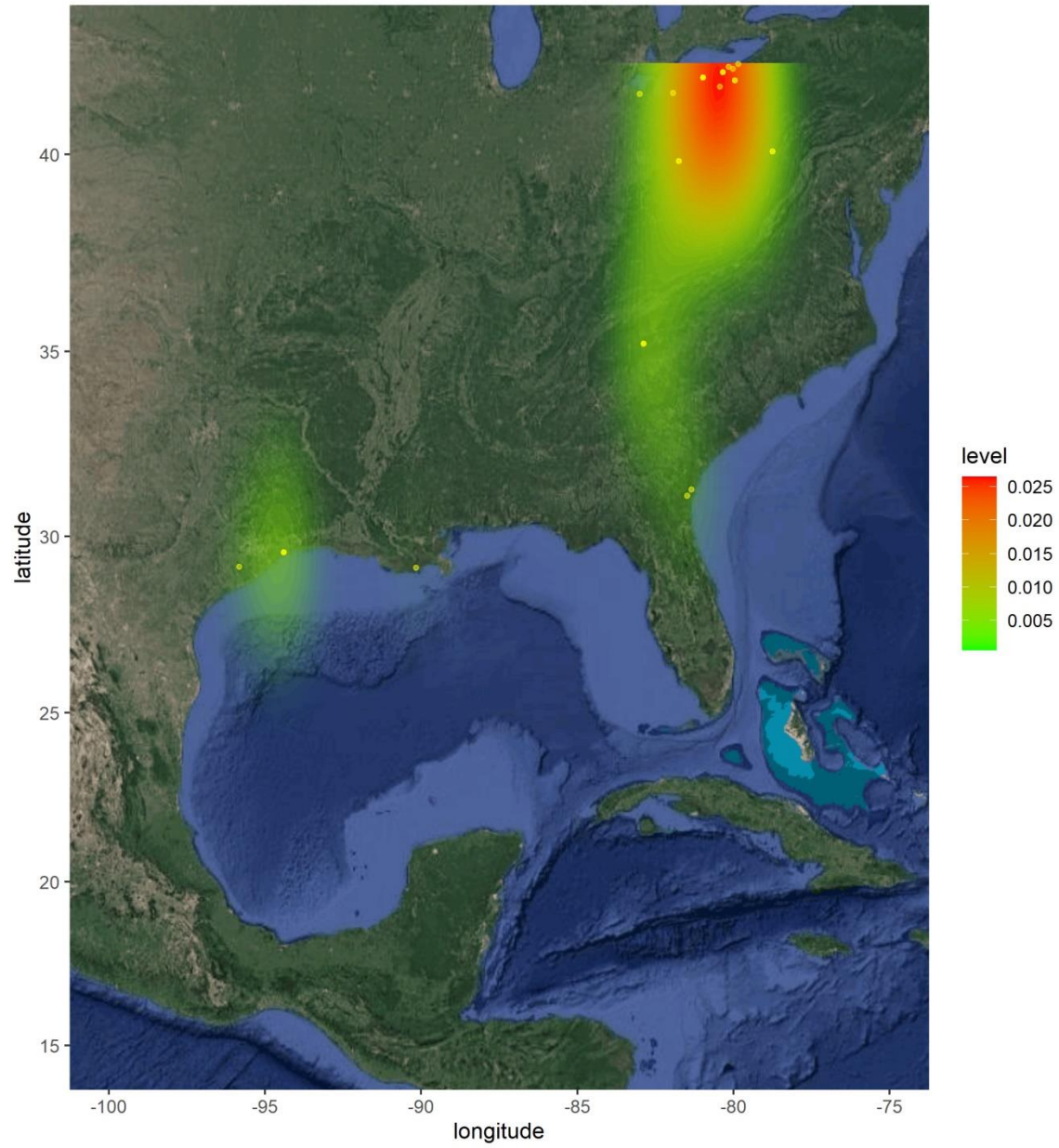


**Figure 2-1.** 2D kernel density estimation of fall migration detections of Wood Thrushes ( $n = 14$ ) that occurred south of Ontario during 2016-2019 that returned to the study area the following spring (apparent migration survival).

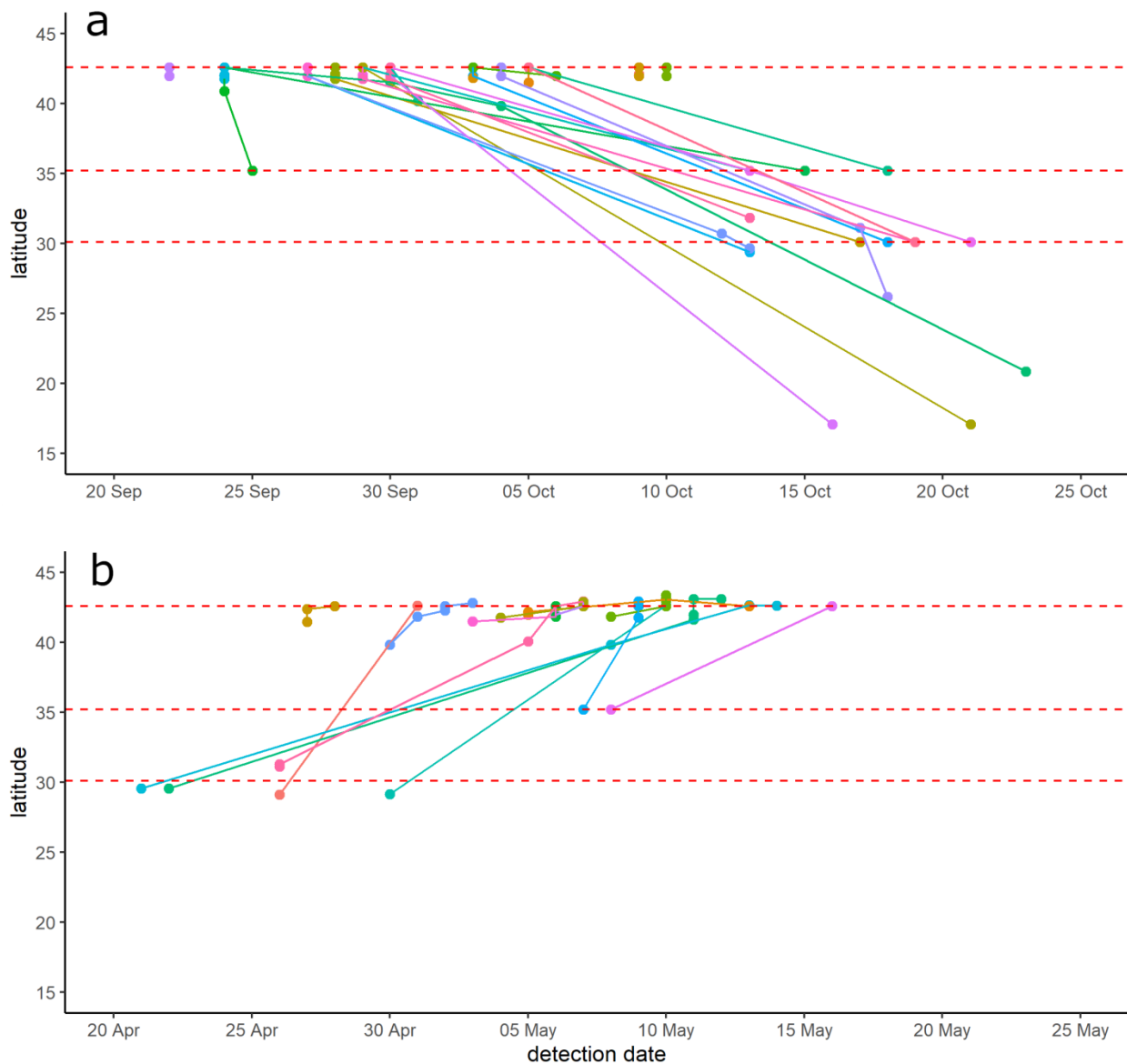


**Figure 2-2.** 2D kernel density estimation of fall migration detections of Wood Thrushes (n=14) that occurred outside of Ontario during 2016-2018 that did not return to the study area the following spring (and so were assumed to have not survived migration).





**Figure 2-3.** 2D kernel density estimation of spring migration detections of Wood Thrushes (n=18) that occurred outside of Ontario during 2017-2020.



**Figure 2-4.** Latitude plotted against date for all Wood Thrushes detected outside of Ontario during (a) fall migration 2016-2019 ( $n = 30$ ) and (b) spring migration 2017-2020 ( $n = 15$ ) that were also detected departing from or arriving to the study area in southwestern Ontario. Each colour represents an individual Wood Thrush. The uppermost dashed line represents the latitude of the study area ( $42.6^{\circ}$  N), the middle dashed line represents the latitude of Pisgah Astronomical in North Carolina ( $35.197^{\circ}$  N), and lower dashed line represents the latitude of St Marks in Florida ( $30.088^{\circ}$  N).

## Discussion

To the best of my knowledge, this study is the first to use the Motus Wildlife Tracking System to compare migration routes of birds that returned from the migration and wintering periods of the annual cycle, with those that did not. I found no evidence that fall route of eventual returning birds differed from that of non-returning. While the relatively small sample size of this study does not allow for strong conclusions to be drawn regarding the role of migration route variation in annual mortality, it does provide evidence that Motus can be used for this purpose. Wood Thrushes are relatively large songbirds (~45-55g) and so can safely carry relatively heavy radio-tags that have a one year battery life. This also allowed me to tag adults at their breeding site, and use Motus to determine fall departure date and which birds returned the next spring. Other Motus studies have radio-tagged adults of unknown origin that are already on migration (e.g. Begin-Marchand et al. 2021).

There are a number of probabilities that must be considered when estimating apparent survival using the Motus system. When a tagged Wood Thrush is detected returning to the location it was tagged in the previous year, we can say definitively that it survived the wintering and migration periods. When a tagged Wood Thrush is not detected returning the following year, there are a number of possibilities to consider besides death. The first thing to consider is whether a tagged bird has survived but returned to a location other than southwestern Ontario. Adult Wood Thrushes are known for high site fidelity (Roth and Johnson 1993) and as expected, no bird tagged in this study was detected the following year far from the study area despite the relatively high Motus coverage around the Great Lakes. The next thing to consider is whether a

tag has failed. Aside from some issues with antenna breakage in 2019 (this year was excluded from annual survival analysis for this reason) only 2/288 (<1%) tags were confirmed to have failed after deployment on adult or juvenile (Sue Hayes PhD research) Wood Thrushes. Another possibility for error is if a tag falls off before it reaches the end of its deployment. To minimize the chances of this happening, harnesses were constructed out of heavy 2.5mm Teflon tubing and knots were reinforced with super glue. All tagged birds were tracked at least weekly using a manual telemetry receiver until late August of the year they were tagged, and there was no instance of a tag falling off. The last possibility to consider is that a Wood Thrush may escape detection by Motus. Extensive manual telemetry surveys and an aerial survey were conducted each year to validate Motus and only one of the 35 (3%) birds that were known to survive the migration and wintering periods was not detected by Motus. When all of these probabilities are combined, they suggest that Motus alone can produce apparent survival estimates with >95% confidence, and when supplemented with manual and aerial telemetry this number is likely even higher.

Breeding adult Wood Thrushes that survived fall migration and returned to the breeding grounds the following year did not average a statistically different migration route than those that did not return. The relatively small number of migration detections in the US can be partially attributed to the lack of Motus coverage through large portions of the migration route in fall and spring (Fig 2-5a, 2-6; Stanley et al. 2015). A study of this type is expected to become increasingly feasible in the future as the coverage of Motus continues to grow (Fig 2-5b). During the years this study took place (2016-2020) the number of Motus towers in the eastern US within the longitudinal range of Wood Thrush fall migration (-85 to -79) grew steadily from only

45 in 2016, to 102 in 2019, reaching 128 towers operating in 2021. It is expected that a similar tagging effort today would yield a correspondingly higher number of detections.

### *Migration route and speed*

I was also able to document strong individual variation in departure date, migration route and speed within the same breeding population of Wood Thrushes, which is a similar finding to studies using geolocators (Stutchbury et al. 2009; Stutchbury et al. 2011, Stanley et al. 2015) and archival GPS tags (Stanley et al. 2021). Both geocator and Motus tracking methods show that birds breeding in southwestern Ontario and northwestern Pennsylvania travel directly south after leaving the breeding site and that variation in longitude of route increases with distance from study site (Stanley et al. 2015; Stanley et al. 2021). While the Wood Thrush is one of the best-studied songbirds when it comes to geocator tracking (Stanley et al. 2015) these devices are not well suited for detecting timing of fall departure and locations during early migration, something that only Motus can currently do. Geolocators determine latitude from estimated day length, and so have poor spatial accuracy during the weeks near the fall equinox when day length is similar everywhere, which is when Wood Thrush fall migration peaks. GPS tags must be pre-programmed to collect positions on a given date and so also cannot capture departure date.

Despite the relatively small sample size, the results of this study provide evidence that variation in the continental migration route used by Wood Thrushes across the US may not be that important in determining survival. Fall migration generally proceeds at a slower rate than spring migration, with more time allocated to the use of stopover sites (Stutchbury et al. 2009).

More time allocated to stopovers means Wood Thrushes are expected to be in better energetic condition, and as a result, better equipped to deal with obstacles they may encounter. The eastern US is composed of a heterogeneous landscape of potential stopover sites, and it may be that the quality of a stopover site is more important than its broader geographic location. During migration, Stanley et al. (2021) found that Wood Thrushes exhibit much greater behavioural flexibility in terms of habitat selection, compared to the breeding and wintering seasons when they are on territories. During stopovers they occupied a wider range of habitats (e.g. agricultural, wooded savannah). Future studies could use Motus to test how habitat quality at stopovers sites affects the timing and route of subsequent migration in fall and spring.

It is not known where birds die during migration, but mortality risk is assumed to be high when crossing large bodies of water such as the Gulf of Mexico where there is no escape from sudden inclement weather or fatigue (Newton 2007; Ward et al. 2018; Drymon et al. 2019). Wood Thrushes from the same breeding population increase their longitudinal variation as they travel south (Stanley et al. 2021), and it is possible that longitude immediately prior to the dangerous Gulf of Mexico crossing is most important to survival. In fall, geolocator tracking of surviving Wood Thrushes from southwestern Ontario and northwestern Pennsylvania has shown they either directly cross the Gulf of Mexico from northern Florida (~1000km), or travel south through Florida and cross to Cuba (~300km) before making the jump to Mexico (~270km) or Central America (~700km) (Fig 2-6; Stanley et al. 2015). With large differences in the amount of open water that must be crossed in continuous flight, variation in this portion of migration could be most important to determining survival outcomes.

Migration speed varied by individual during spring and fall, but overall, migration speed during fall was slower than spring. This supports previous findings that stopover frequency and duration is variable based on the individual (Stutchbury et al. 2011), but stopovers account for less time during spring migration (Stutchbury et al. 2009). Maximum migration speeds were comparable to those recorded by geolocators (Stutchbury et al. 2009) with the fastest fall migrant reaching Florida in 14 days (~102km/day) and the fastest spring migrant reaching the study area from the Gulf coast in only 5 days (~345km/day). The fastest spring migration movement (average distance covered per 24 hour period) occurred when a Wood Thrush travelled ~844km from North Carolina to the study area in only 52 hours. The fastest single movement overall occurred during fall migration when a bird covered the same distance to North Carolina in only 32 hours. This speed exceeds daily travel speed of Wood Thrushes recorded during a geocator study (Stutchbury et al. 2009), as well as the estimated daily flight performance in *Catharus* thrushes (Wikelski et al. 2003), and may represent the fastest recorded migration speed of a Wood Thrush.

The main focus of my research was to look at the effect of breeding habitat quality on annual survival and migration timing in Wood Thrushes (Ch 2), therefore a study area with a high density of local Motus towers was chosen for this purpose. Despite this, a relatively low 51% (60/117) of tagged birds were detected departing the study area, and only 27% (32/117) were detected at least once in the US, with 28 of those having apparent survival outcomes. There are a number of possibilities for why this was the case. Firstly, because my study area was chosen based on local Motus coverage, a study area selected for migration route coverage would offer more migration detections. Motus towers are not evenly dispersed across the

landscape (Fig 2-5), and most US detections occurred close to Lake Erie due to the relatively high density of towers there. A better location for a migration study might be northeastern Pennsylvania or south-central New York, to utilize the heavy Motus coverage that exists through Pennsylvania from the northwest to the southeast, continuing all the way to the Atlantic coast (Fig 2-5b). This high regional coverage would be expected to provide more migration detections, along with better estimates of initial migration bearing due to the larger distance between the tagging site and the towers; however, an array close to the tagging site would need to be erected to detect birds returning the following year. A large gap in coverage that exists along the western Gulf coast of Florida through to Louisiana would also need to be rectified for this study design to be effective.

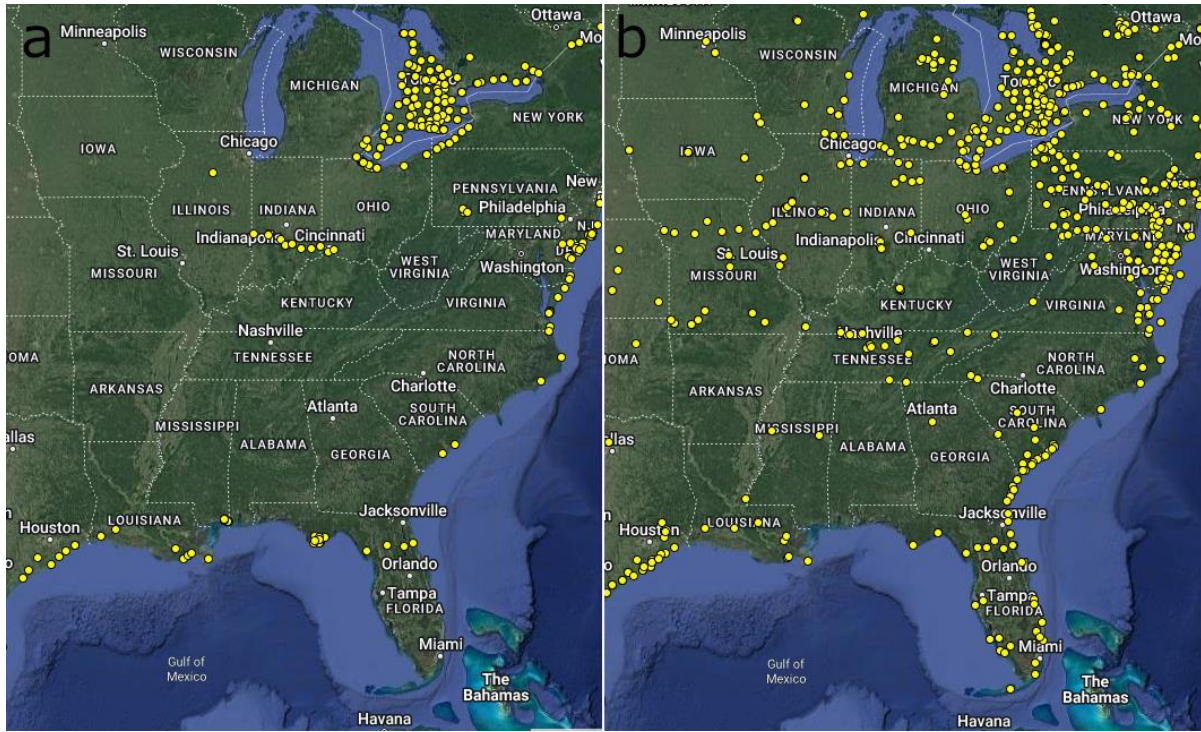
The lack of detections may also be attributed to the limitations of the Motus system itself. During breeding season, Wood Thrushes were rarely detected despite occupying breeding territories in relatively close proximity to towers (<2km). A study on stopover detection of songbirds highlights the necessity of clear line of sight for radio telemetry to be effective, finding that ground dwelling species would be sporadically detected up to ~1km away from a Motus tower, but had to be within 300m to record accurate temporal data through consistent detections (Crewe et al. 2019). Detections of Wood Thrushes initiating fall migration occurred after dark, generally at multiple towers, indicating the relatively high altitude needed to provide the clear line of sight needed between transmitter and receiver. Migration altitude has been found to be quite variable in Swainson's Thrushes (*Catharus ustulatus*) with one individual flying below 100m for more than an hour, and another flying below 40m for almost two hours (Bowlin et al. 2015). If Wood Thrushes have similar variability in migration altitude,



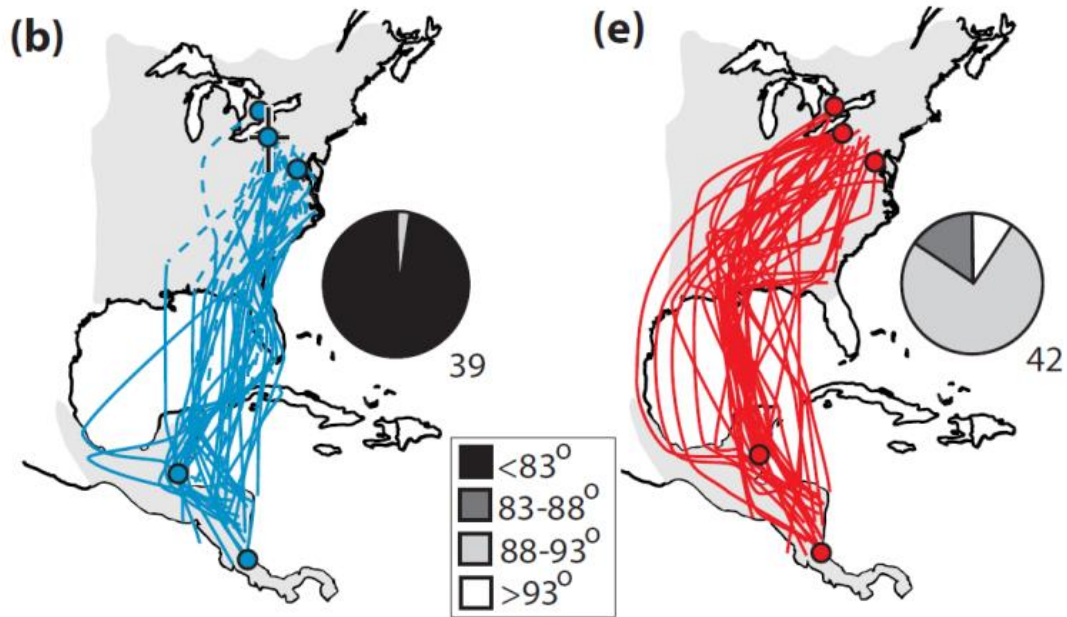
some individuals may have been at a low enough altitude to prevent detection by Motus towers. Another possibility is that the projected detection range of 15km for Motus towers (Taylor et al. 2017) is more directional and variable than previously thought. Standard Motus towers make use of three 9-element antennas, which function best through a relatively narrow band in the direction they are pointing. This leaves large gaps in coverage around each tower, potentially providing opportunity for birds to fly past undetected. In addition to directional gaps in coverage, many of the towers in the study area are expected to have overlapping detection ranges if the 15km range estimate is accurate. Despite many towers in the study area being within 10km of each other, Wood Thrushes initiating migration were rarely detected by multiple towers simultaneously. The only two towers that somewhat regularly detected birds at the same time were located at Birds Canada headquarters and Long Point Bird Observatory's Old Cut field station, only ~6km apart, and the most distant towers to simultaneously detect a bird were located ~15km from each other. Together, this suggests that the effective detection range of Motus towers for the models of tag used in this study is probably less than 4km, with inconsistent detections up to a maximum of ~8km.

Along with another recent study (Begin-Marchand et al. 2020); this study acts as a proof of concept for comparing migration routes using the Motus network. Migration route differences between adult and hatch-year birds undertaking their first migration have been rarely studied and remain an unknown for most species of migratory songbirds. McKinnon et al. (2015) used geolocators to track spring migration in first-year birds (first northward migration) versus adults wintering in Belize and found that while first-year birds departed later from the tropics and travelled more slowly, they followed the same migration route across the Gulf of

Mexico; however, this comparison was based on survivors only. Motus has also been used for testing age differences in migration route and risk-taking. Brown and Taylor (2015) used Motus to track post-breeding juvenile and adult Blackpoll warblers (*Setophaga striata*) over short distances as they left an island breeding site. They found that adult and juvenile behaviour differed. Adults generally moved southwest across the Gulf of Maine and travelled down the New England coast before beginning their long non-stop open ocean crossing. Juveniles instead explored the regional landscape prior to migration but remained constrained by Nova Scotia's shoreline, perhaps perceiving the overwater crossing to the New England coast as risky due to lacking prior knowledge of its distance. These differing strategies indicated that adults use information from previous migrations to alter their migration route, in this case shortening the distance of their non-stop open ocean crossing by initiating it farther south. A future study on Wood Thrushes could use Motus to compare the full fall and spring migration routes of adults and hatch year birds. Using Motus to look for age-specific migratory differences could help to further explain intraspecific variation seen in routes while simultaneously testing for predictors of survival in both age classes.



**Figure 2-5.** Growth of Motus network from (a) 2016 to (b) 2021 in the eastern US with individual towers represented by yellow points.



**Figure 2-6.** [Figure 2b, 2e, from Stanley et al. 2015] Estimated fall (blue) and spring (red) migration routes for Wood Thrushes that bred in (b, e) central east (gray shading, breeding and wintering range; solid circles, geolocator deployment sites; lines through top left blue circle, average location error from ground-truthing (McKinnon et al. 2013); dashed lines, migration movements where location is uncertain due to persistent shading or during fall or spring equinox when latitude cannot be resolved; pie charts, proportion of individuals in each breeding region making use of migration routes classified according to longitude along the U.S. Gulf coast; sample size appears beside pie chart).

## Chapter 4: General Conclusion

In this study I used the new Motus Wildlife Tracking System (Taylor et al. 2017) to test predictions that could not be tested by any other existing tracking method. I tested for effects of forest fragmentation on fall migration timing of a migratory songbird for the first time ever (Ch 2.). I also compared, for the first time ever, the migration routes of songbirds that return from the migration and wintering periods, with those that do not (Ch 3.). Tracking devices used on small songbirds until this point had to be retrieved to recover data, due to their archival nature. Motus tags do not have to be recovered to retrieve data and thus have finally allowed for a host of new questions to be answered while at the same time filling in gaps in existing annual cycle research. Motus also has the capability to detect migration departure date and time of day which other technologies for songbirds cannot accomplish.

#### *Breeding season carry-over*

A key innovation of my study was deploying Motus tags with 1-year battery life on breeding birds to determine subsequent fall migration timing and annual return rates. Carry-over effects relating to habitat quality on the wintering grounds were brought to the attention of the scientific community by Marra et al. (1998). Since that time, numerous studies have found evidence of wintering habitat quality having an impact on the following breeding season (Norris et al. 2004; Reudink et al. 2009; Rockwell et al. 2012; Drake et al. 2013; Rushing, Marra et al. 2016; Goodenough et al. 2017; Imlay et al. 2019; Lopez Calderon et al. 2019). Despite the attention that wintering ground carry-over has received and the recent calls for more focus on full annual cycle research (e.g. Marra et al. 2015), no study until this point has looked for carry-over from breeding season habitat quality. In this dissertation, I was able to use Motus to

successfully record the timing of initiation of fall migration of Wood Thrushes with more accuracy than ever before. I did not find strong evidence for breeding season habitat carry-over despite good sample sizes and a measurement of a comprehensive suite of individual-level variables (body condition, timing of nesting, corticosterone, onset of fall migration).

Additionally, the high temporal accuracy of migration timing data showed that female Wood Thrushes initiate fall migration earlier than males, previously unknown for this oft-studied species and the opposite of the findings of a recent meta-analysis on European songbirds that found male songbirds typically departed first during the fall (Briedis et al. 2019).

Motus was able to provide precise data on the initiation of fall migration, but also provided better estimates of apparent survival compared to traditional mark and re-sight studies. Wood Thrushes are known to have high site fidelity, especially males (Roth and Johnson 1993), and extensive manual telemetry and an aerial telemetry survey during each year of the project, found that only 22/35 (63%) birds that survived the migration and wintering periods (detected by Motus) actually returned to their previous breeding fragments. Studies relying on mark and re-sight or even traditional radio-tag methods would have assumed that the remaining 13/35 (37%) did not survive migration.

### *Migration tracking*

Migration is the most dangerous portion of the annual cycle in the lives of migratory birds (Sillett and Holmes 2002) so it makes sense that variation in migration routes between individuals could impact their probability of survival. Until this point, it has remained a necessity to recover archival tags to access data in order to discern migration routes. This means that

migration routes can only be determined for birds that survive the migration and wintering periods. Though the sample size is modest, I show that the Motus system can be used to map the migration route of birds that return from the wintering and migration periods in the same way as traditional tracking devices, but can also map the routes of birds that do not return from the migration and wintering periods. Motus can effectively do away with the sampling bias introduced into all existing studies that collected data from only surviving individuals. One of the most important questions in ornithology today is “where do birds die?” and while the new space station ICARUS tracking system (Jetz et al. 2022) will eventually be able to answer this question when the system becomes fully operational and tags are small enough, until that point Motus may be the best option to identify general regions of the highest mortality during migration.

#### *Applications to future research*

While the habitat differences in my study population may not have been stark enough to produce strong carry-over effects (as supported by relative mass and initial CORT results in Ch 2), an experimental manipulation study could create a stronger gradient in habitat quality to induce carry-over. Within a single large forest fragment, an experimental group of birds could receive supplemental feeding (Podolsky et al. 2004) to artificially increase the quality of their habitat. If early migration is beneficial and migration timing is related to habitat quality, it is expected that birds in the experimental group should depart earlier for fall migration. To test if fall migration timing is instead related to timing constraints as a result of high nest predation and more nesting attempts, another experimental manipulation could be undertaken. Within a



large forest fragment, an experimental group of birds could have their breeding season ended prematurely through nest removal. If timing constraints as a result of prolonged breeding activities dictate fall migration dates, it is expected that the experimental group of birds should initiate fall migration earlier.

Both main chapters of this dissertation represent predictions and methods that can be applied to countless other species of birds. The usage of Motus to look for the presence of breeding season carry-over paves the way for future research of this nature. Though breeding season habitat quality did not lead to discernable carry-over effects in Wood Thrushes, it remains a distinct possibility that it plays a role in other species. Areas with high regional Motus coverage provide opportunity to conduct this type of study successfully and long-life tags are now small enough to attach to many species of songbirds. The long-term decline of many migratory songbirds in North America has created an urgent need to use new technologies such as Motus to more thoroughly assess breeding habitat quality and migration threats.

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## Appendix A: Chapter 2 supplementary tables and figures

**Table A-1.** Study site names, locations, size, and matrix type

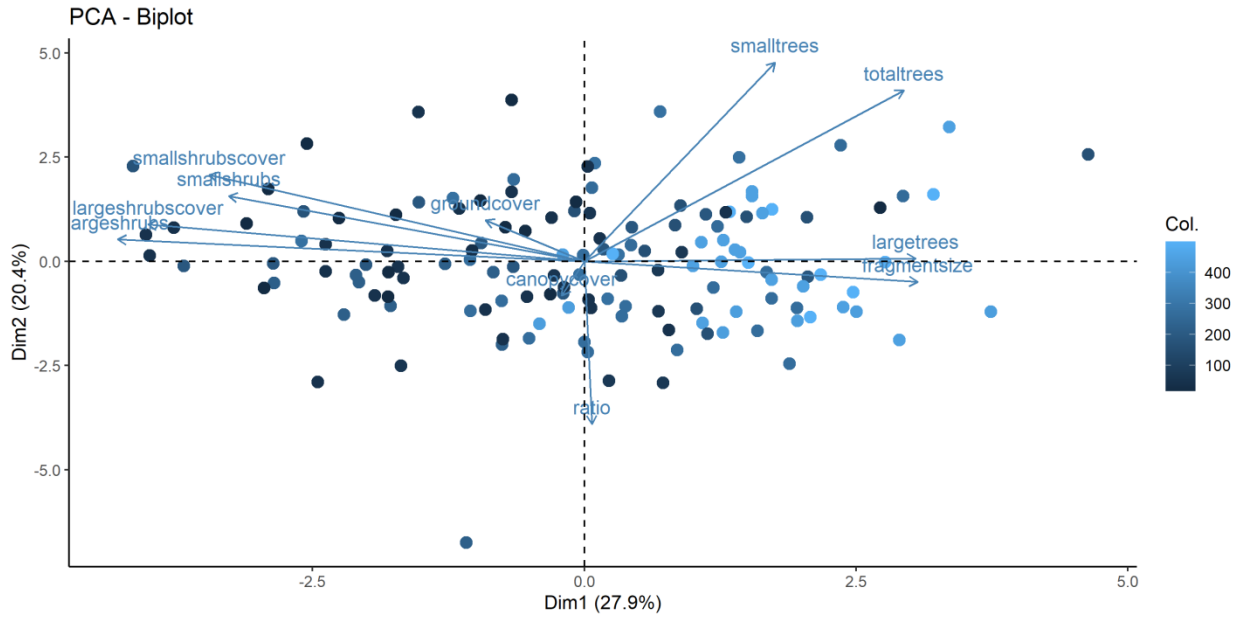
site name	latitude	longitude	area	matrix type
L1	42.67090	-80.48804	268.7	agricultural
L2	42.66671	-80.63913	216.4	agricultural
L3	42.62936	-80.55369	499.1	agricultural
L4	42.72581	-80.42808	174	agricultural
L5	42.70658	-80.47160	445	agricultural
L6	42.80377	-80.37985	260	agricultural
L7	42.69865	-80.41948	189.7	agricultural
L8	42.76279	-80.40671	282.9	agricultural
L9	42.72608	-80.32347	435.7	agricultural
L10	42.77422	-80.45275	162	agricultural
S1	42.68382	-80.46928	30.8	agricultural
S2	42.68118	-80.61204	58	agricultural
S3	42.70787	-80.54124	41.4	agricultural
S6	42.79659	-80.36841	17.8	agricultural
S7	42.72217	-80.39825	50.4	agricultural
S8	42.75198	-80.37084	16.4	agricultural
S9	42.72637	-80.38569	16.7	agricultural
S10	42.80767	-80.42739	20.1	agricultural
S11	42.67640	-80.53821	68.8	agricultural
S12	42.75679	-80.56745	46.2	agricultural
S13	42.77404	-80.58011	45.4	agricultural

**Table A-2.** Results of AICc selection of gamma distribution generalized linear mixed models testing the influence of total number of young fledged on female fall migration (n=24) of birds tagged during 2018 and 2019, including year as a random effect.

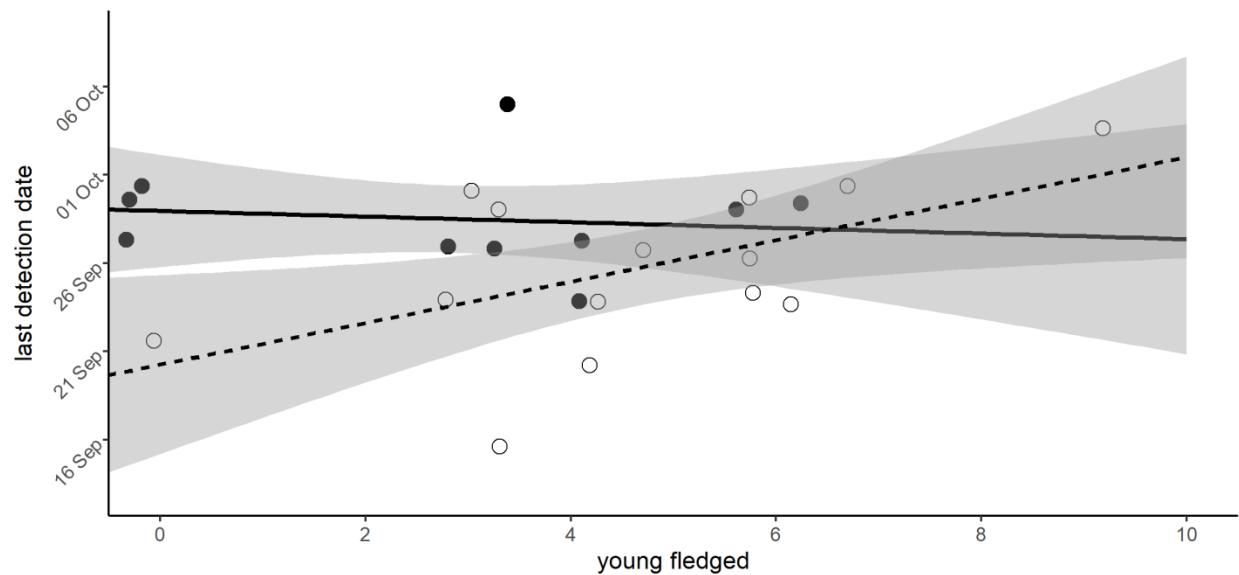
<b>model</b>	<b>LL</b>	<b>n</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta_{AICc}</math></b>	<b>weight</b>
fragment size	-65.98	24	4	142.1	0.00	0.31
fragment size + fledglings	-64.52	24	5	142.4	0.30	0.27
fragment size + relative mass	-65.75	24	5	144.8	2.77	0.08
fragment size + fledglings + relative mass	-63.99	24	6	144.9	2.84	0.08
fragment size + age	-65.91	24	5	145.1	3.08	0.07
intercept	-69.08	24	3	145.3	3.28	0.06
fragment size + fledglings + age	-64.49	24	6	145.9	3.84	0.05
fledglings	-68.60	24	4	147.3	5.24	0.02
fragment size + relative mass + age	-65.58	24	6	148.1	6.02	0.02
relative mass	-69.07	24	4	148.2	6.17	0.01
age	-69.08	24	4	148.3	6.19	0.01
fragment size + fledglings + relative mass + age	-63.76	24	7	148.5	6.45	0.01
fledglings + relative mass	-68.57	24	5	150.5	8.41	0.01
fledglings + age	-68.60	24	5	150.5	8.46	0.01
relative mass + age	-69.07	24	5	151.5	9.40	0.00
fledglings + relative mass + age	-68.58	24	6	154.1	12.02	0.00

**Table A-3.** Coefficient estimates for  $\Delta$  AICc <2 models that are also >2 AICc better than intercept-only model for female fall migration by young fledged (Table A-2); coefficients appearing in multiple supported models are averaged.

<b>dependent variable</b>	<b>coefficient</b>	<b>estimate</b>	<b>s.e.</b>	<b>t-value</b>	<b>p-value</b>	<b>2.5%</b>	<b>97.5%</b>
<b>fall migration</b>	intercept	5.59	7.04e-3	793.55	<0.001	5.57	5.60
	fragment size	6.41e-5	2.38e-5	2.69	0.004**	1.75e-5	1.11e-4
	young fledged	9.20e-4	1.29e-3	7.15e-1	0.24	-1.60e-3	3.44-3



**Figure A-1.** Principle components analysis of habitat variables relationship with fragment size.



**Figure A-2.** Number of young fledged was included in the top models for female fall departure date of large fragment (n = 10; closed symbols, solid line) and small fragment (n = 14; open symbols, dashed line) Wood Thrushes, but was not a significant predictor.