

USING LIGHT-LEVEL GEOLOCATION AND STABLE HYDROGEN ISOTOPES TO  
DETERMINE THE MIGRATORY CONNECTIVITY OF CANADIAN WOOD THRUSH  
(*HYLOCICHLA MUSTELINA*)

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## **Abstract**

The Wood Thrush is a declining forest passerine that is listed as threatened in Canada. Using light-level geolocators, and analysis of stable hydrogen isotopes in feathers, this study established the migratory connectivity of Canadian Wood Thrush. Understanding migratory connectivity is essential to creating effective management strategies for a long-distance migrant. Ninety percent of the birds tracked wintered in a narrow band of the species' winter range in eastern Honduras, Nicaragua, and northern Costa Rica. The most important stopover sites were Cuba, the Yucatan peninsula, and the Mississippi River delta. Ninety-eight percent of all feathers sampled in Nicaragua had  $\delta D$  values consistent with the northernmost part of the breeding range. Tropical deforestation on the wintering grounds is likely a leading cause of population decline in the Wood Thrush, and future conservation efforts should be directed toward habitat protection.

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## Introduction

The Wood Thrush, *Hylocichla mustelina*, is a medium-sized forest songbird, unobtrusive in appearance, most easily recognized by its clear, flute-like song. Like so many songbirds, it has undergone steep population declines across its range in the last several decades (-1.8%/year, Sauer et al. 2014, Breeding Bird Survey [BBS]), to the extent that, in December 2012, it was listed as a threatened species in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Globally, the International Union for Conservation of Nature upgraded the Wood Thrush's status from least concern to near threatened in 2014. Data on the population dynamics of this species are critical for effective conservation efforts to stabilize population levels. Because scientists are concentrated in the northern hemisphere on the breeding grounds of most Neotropical and Palearctic migrants, research on population dynamics has historically been skewed toward the breeding phase of the life cycle (Sillett and Holmes, 2002). Much is already known about the breeding productivity of Wood Thrushes in both continuous forest and in fragmented landscapes (Simons et al. 2000; Friesen et al. 1999), but relatively little is known about the nonbreeding phase (Rappole et al. 1989; Stanley et al. 2015).

Despite the increasing concerns about the status of the Wood Thrush, at present, it remains a fairly common forest passerine in Southeastern Canada. It is an excellent study species for population dynamics studies because breeding males are readily identified and located by their song, and the nests are relatively easy to find. Being a large-bodied passerine (ca. 50 g), the Wood Thrush was one of the first songbirds to be tracked throughout its annual cycle with light-level geolocators, with no apparent ill effect (Stutchbury et al. 2009; Stutchbury et al. 2011; Stanley et al. 2012; Stanley et al. 2015).

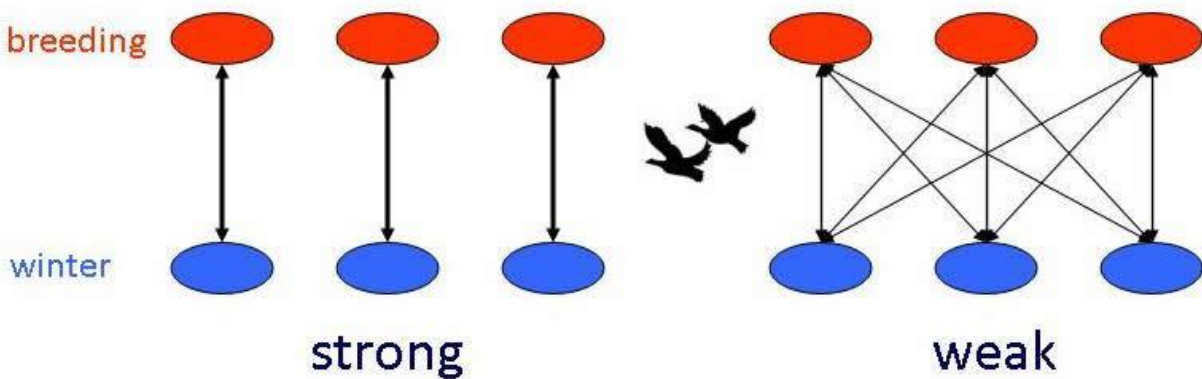
The focus of this research is the migratory connectivity of breeding populations of Canadian Wood Thrushes, the objective being to identify important nonbreeding areas, as well as key migration routes and stopover points. I have used light-level geolocation to track both breeding and wintering birds throughout their annual cycle, and have used the complementary technique of analyzing stable hydrogen isotopes in feathers to determine the locations of breeding origin of wintering birds.

### Breeding-wintering Connectivity and Migration Routes

For a migratory bird, the stages of the life cycle are physically divided between a breeding habitat, a nonbreeding habitat, and (usually) migratory stopover sites in between. Many North American species are also Central or South American species, and form part of the ecosystem on two continents. Environmental conditions during one phase of the annual cycle will affect a bird's condition when it moves to the next phase; these extended impacts are termed carryover effects (Hostetler et al. 2015). Thus, the productivity of breeding birds is influenced by events in their nonbreeding habitat, and a knowledge of where that winter habitat is and what conditions prevail there is essential to a complete understanding of breeding success (Norris et al. 2003). As migration is not (with a few notable exceptions) a non-stop affair, having appropriate re-fuelling points en route is likely just as important to the survival of a neotropical migrant as having appropriate habitat in which to breed and to spend the winter. One of the biggest challenges in migratory bird conservation has been determining the links between breeding declines measured in North America and threats elsewhere in the birds' life cycles (Sherry and Holmes 1996, Sillett et al. 2000, Webster et al. 2002) because, until recently, there was little or no information on where specific breeding populations migrate to, or how they get there (Webster and Marra 2005).



Effective conservation strategies for migratory birds require that “connectivity” of breeding and wintering populations be determined. Migratory connectivity is a relatively new concept in the scientific literature that is used to describe the level of segregation of different subpopulations of a migratory species on both the breeding and wintering grounds (Hobson 2005). A species with a low degree of migratory connectivity is one where individuals from many disparate parts of the breeding range occupy the same wintering locale (Webster et al. 2002). Conversely, a species with high migratory connectivity has separate breeding populations that also occupy separate wintering locations. Figure 1 provides a simple illustration of high and low connectivity patterns. In a mathematical sense, high connectivity means that nonbreeding coordinates are predictive of breeding coordinates. The term “migratory connectivity” is somewhat counterintuitive in that the level of “connectedness” does not reflect interactions between subpopulations, but rather the uniqueness of geographic linkages between breeding and wintering locations. One might almost define the concept in terms of segregation on the wintering grounds: high connectivity means high segregation, low connectivity means little segregation. High connectivity implies that breeding populations are very vulnerable to habitat loss in specific wintering regions. To properly document connectivity is challenging because many populations must be sampled, but comprehensive studies have begun to emerge for such species as American Redstart (Norris et al. 2006) and Common Nightingale (Hahn et al. 2013), as well as Wood Thrushes (Stanley et al. 2015). The migration tracks presented in this thesis are all included in the Stanley et al. (2015) paper.



**Figure 1:** Simplified strong and weak connectivity schematics. The ovals represent distinct geographical areas and the arrows show seasonal movement between them. Taken from [bou.org.uk](http://bou.org.uk)

### Light-level Geolocation

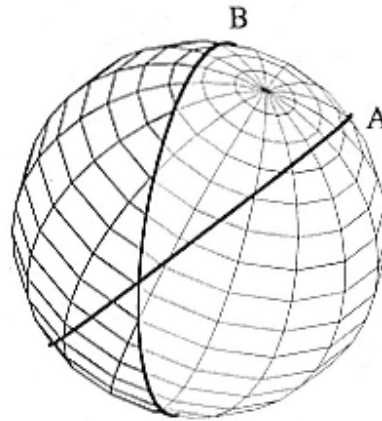
Tracking the annual movements of migratory birds has been revolutionized within the last two decades by the invention of archival light-level geolocators (hereafter geolocators) by researchers with the British Antarctic Survey (BAS) (Afanasyev and Prince 1993). Wood Thrush was the first forest passerine to be tracked with geolocator technology (Stutchbury et al. 2009), but the list of species on which geolocators have been deployed is growing rapidly (Bachler et al. 2010; Bairlein et al. 2012; DeLuca et al. 2015; Nisbet et al. 2011; Seavy et al. 2012; Tottrup et al. 2012). Geolocator units continue to shrink in size, expanding the number of candidate species. Multiple studies have demonstrated the usefulness of geolocators in establishing migratory connectivity (Fraser et al. 2012; Hallworth et al. 2015; Hobson et al. 2015; Stanley et al. 2015).

Geolocation by light developed as a cheaper alternative to satellite tracking. The prototypical devices were made for elephant seals and their design was driven in part by the need to withstand high pressure (Hill 1994). A geolocator is a type of data logger that records light intensities on a relative scale. It takes advantage of the tilt of the Earth's axis and the resulting

seasonal variation in day length to provide positional information. Models vary, but the essential components of a geolocator are a light sensor, a basic microcontroller computer chip, a memory chip, a clock, and a battery (Afanasyev and Prince 1993). These are all connected to a minute circuit board which forms the body of the geolocator, and are encased in a watertight housing. Units for passerines are mounted on the back, above the pelvis, and the light sensor is situated at the end of a stalk to keep it above the bird's plumage. The computing power of a geolocator is mostly limited to archiving the light readings and almost all analysis is carried out post-download. The simplicity of the electronics makes for minimal energy requirements, which in turn means units can be very small and lightweight. BAS models are further lightened by the fact that light readings saturate at relatively low levels, meaning that memory space fills up more slowly and the memory bank itself can be smaller. It is the size and weight of geolocators as much as anything else that makes them so ground-breaking, because they can be attached to birds much too small to carry a satellite tag.

The length of a solar day is a function of latitude, while the timing of local noon or midnight is a function of longitude. This is the entire theory of geolocation by light levels in a nutshell. Knowing the precise time of sunrise and sunset on a particular date is sufficient information to calculate latitude and longitude. Hill (1994) provides a simple and elegant explanation of the specificity of this approach. In essence, if we trace, on the globe, the great circle dividing day and night (the terminator) at the time of sunrise (Figure 2 A), then overlay the terminator at the time of sunset (Figure 2 B), the intersection of these two terminators gives the location of the observer. It should be apparent that two crepuscular events in a 24-hour period are necessary for this method, thus geolocation by light is often impossible above 60° latitude. The other important caveat is the equinoxes. At the equinox, the terminator passes through the

Earth's geographical poles, with the result that the sunrise and sunset terminators will have an infinite number of points of intersection. It should be noted that longitude data are not affected by any of these issues, and their accuracy remain constant throughout the year. Averaged across study sites, the latitude measure of geolocator devices on Wood Thrushes is accurate to within 180 km, and longitude to within 113 km (McKinnon et al. 2013).



**Figure 2:** Terminator lines on Earth's surface at sunrise (A), and sunset (B) during a single 24 hour period. The intersection of A and B represents the location of an observer experiencing these crepuscular events. Taken from Hill 1994.

### Phenology

The timing of life history events is important to the survival and fitness of an individual. Selective pressures can act differently according to sex. In migratory ecology, protandry refers to the phenomenon of males moving to a subsequent stage of the life cycle prior to females. Protandry in the timing of arrival on the breeding grounds has been well documented in many migratory animals including insects, fishes, and birds (Coppack and Pulido 2009). We lack a clear understanding of the underlying physiological and genetic mechanisms driving protandry, but some recent work on clock genes (Saino et al. 2015), known to play a role in photoperiodicity, shows a possible connection to protandry as well. Morbey and Ydenberg

(2001) enumerate seven hypotheses for the ultimate causes of the behaviour: the mate opportunity hypothesis, whereby early arriving males have access to more potential mates; the rank advantage hypothesis, which posits that the more territorial sex will arrive first; the differential susceptibility hypothesis, which suggests larger males may be less susceptible to adverse weather conditions in early spring; the evolutionary constraint hypothesis, which suggests there may be indirect selection via a trait correlated with earlier male arrival; the waiting cost hypothesis, according to which it may be beneficial to females to minimize time to mating after arrival; the mate choice hypothesis, whereby females may assess mate quality by their earlier arrival; and finally the outbreeding hypothesis, which suggests the phenomenon may be a means of preventing breeding between closely related individuals. Testing these hypotheses is complicated by the fact that they are not mutually exclusive. Using a sample that included 22 long-distance migrant species, and examining protandry in relation to sexual size dimorphism and dichromatism, Saino et al. (2010) concluded that the mate choice hypothesis was the best supported, though the only three hypotheses that were not specifically supported were rank advantage, mate opportunity, and differential susceptibility.

In recent years, the heritability and plasticity of phenological shifts in breeding activity have been under increasing scrutiny because of concerns over the impact of climate change. Multiple long-term studies have reported spring arrival dates shifting earlier (Hedlund et al. 2015; Tarka et al. 2015). In a study incorporating 117 migrant species of passerines, waterbirds, and shorebirds, Vegvari et al. (2010) found that advancement of spring arrival time was species specific and showed little constraint due to phylogenetic relationships. Species with shorter migration distances, more generalized diets, more broods per year, and minimal prebreeding molt were more likely to advance their arrival date. Greater shifts in advancement of male arrival

times in the Willow Warbler (Hedlund et al. 2015) and the Pied Flycatcher (Harnos et al. 2015), suggest that some species will show a greater degree of protandry in the future. Timing of fall migration is thought to be under weaker selective pressure and is less well studied than spring phenology, which may explain why shifts toward both earlier and later autumn departure dates have been documented in passerines (Hedlund et al. 2015, Kovacs et al. 2011, Miholcsa et al. 2009). A study on the Great Reed Warbler (Tarka et al. 2015) found evidence of significant heritability of migratory timing, and directional selection on spring arrival date in both males and females; however, the same study concluded that the observed timing change in their 20-year study was most likely due to phenotypic plasticity rather than microevolution. The fear is that climate change is advancing too rapidly for evolutionary change to keep pace with it. If it is indeed true that species that seem to be adjusting are only responding within the bounds of phenotypic plasticity, then there is real cause for concern. Phenotypic plasticity will have an upper ceiling and it's very difficult to predict when that ceiling will be reached.

Wood Thrushes are protandrous with respect to spring arrival dates, and this has most recently been shown in geolocator tracked birds (McKinnon et al. 2014). I have investigated the degree of protandry in Canadian Wood Thrush populations, comparing arrival and departure dates for both the breeding and wintering grounds. It was expected that males would depart the wintering grounds, and arrive at their breeding sites, earlier than females, but that there would be no difference between the sexes in fall migration timing. Previous geolocator work has shown that Wood Thrushes migrate at a much faster pace in spring than in fall, so the spring is where more significant phenological differences are expected. Males are the territorial sex in Wood Thrushes, so they should be under stronger selective pressure to secure territories and mates.

## Stable Isotope Analysis

Like the use of geolocators, the use of radioactively stable isotope markers in body tissues to assign individuals to a point of origin, is a relatively new approach to acquiring more specific information on long-distance animal movements (and to collecting that information more rapidly) than is possible through banding studies (Bowen 2010). A number of elements that are common in biological tissues, such as carbon, nitrogen, and hydrogen, have multiple naturally occurring stable isotopes. The ratios of these isotopes can vary in precipitation, or be altered by natural processes like nitrogen fixation. All isotopic ratios also exhibit trophic enrichment, so that heavier isotopes increase in number relative to lighter ones as one moves up a food chain (Rubenstein and Hobson 2004). The ratio of the stable isotope deuterium to protium (termed  $\delta D$ ), while fairly constant globally, and in fact anywhere in the universe where hydrogen is found, shows sufficient latitudinal variation in eastern North America to provide an indication of the origin of a substance containing a particular deuterium/hydrogen ratio. As a general rule, the relative abundance of deuterium isotopes decreases in the atmosphere (the  $\delta D$  is said to become depleted), with increasing latitude, elevation, and continentality (distance from oceans) (Bowen 2010). Isotopes in the atmospheric ratio are transferred through precipitation to the water table, and thence into plant and animal life. Thus, tissues grown at a particular latitude will bear the signature ratio of that latitude.

Keratinous tissues like feathers and claws are commonly used in migratory studies because, once grown in, they are biologically inert. Flight feathers are replaced at least once every year, and in the case of the Wood Thrush this usually happens on the breeding grounds (Gow et al. 2012). Consequently, Wood Thrush feathers almost always bear the breeding isotopic signature, so they must be sampled on the nonbreeding territory for the purpose of

measuring connectivity. In his 1999 review paper, Hobson highlights the importance of knowing all the habitats used by an organism at different stages of its annual and/or life cycle, in order to fully understand its ecology. Some previous geolocator studies have used stable isotopes to reinforce their findings with the new technology; for instance, it was shown that East and West African wintering populations of Northern Wheatears originated from distinct breeding populations in the North American Arctic (Bairlein et al. 2012).  $\delta D_f$  (the subscript denotes the substance in which the ratio has been measured, f for feather in this case) has also been used to establish migratory connectivity in Cerulean Warblers (Jones et al. 2008), Snow Buntings (MacDonald et al. 2012), and Nightingales (Hahn et al. 2013).

Isotope analysis has several key advantages over geolocator technology: 1 – birds do not need to be recaptured after the initial sampling; 2 – it is much easier to obtain a large sample size; 3 – tissue sampling for isotopes is much cheaper than geo tracking, both in terms of equipment costs and field expenses; and 4 – high versus low connectivity can be determined with a small number of sampling sites. For all these reasons, many of the studies reporting migratory connectivity are based exclusively on isotope data, including the aforementioned Jones (2008), MacDonald (2012), and Hahn (2013) studies. Furthermore, because geolocators lack transmission capabilities, all data are lost if the unit is not recovered. Recapture rates for Wood Thrushes have been around 20% (Stanley et al. 2015). I supplemented my geolocator findings with stable isotope analysis of the hydrogen/deuterium ratio in feather samples collected from wintering Wood Thrushes fitted with geolocators.



## Methods

### Geocator Study

I used geolocators to track Wood Thrushes throughout their annual cycle. As explained above, geolocators measure and record ambient light levels with a small sensor mounted on a stalk which sits above a bird's back. Three different models were employed in this study, Mk18S and GeoTX units manufactured by the British Antarctic Survey (BAS) and MK5040 (equivalent to BAS Mk20) units made by Biotrack. The Mk18S units record peak light intensities over five-minute intervals, while the other two models record over two-minute intervals. The GeoTX model was a prototype manufactured especially for the Stutchbury lab. The unit combines a radio transmitter with a model Mk20 geocator. The radio transmitter switches on after one year on a pre-set date (May 2012 for my study) and radio signals are broadcast during daylight hours for the remainder of the battery life.

Geolocators also log time since activation. During data processing, raw light data are converted to two positional fixes per day, one at noon and another at midnight. Latitude is determined by day length, while longitude is calculated from the local noon. At the equinoxes, day length becomes equal at all latitudes. For this reason, latitudinal data for three weeks preceding, and three weeks succeeding, each equinox have been omitted from analysis. Both noon and midnight positional fixes were used for the months of June and July to estimate breeding site location, and for the months of January and February to estimate the site of winter residence. Birds are essentially stationary during these periods, so both fixes were used, whereas only noon fixes were used during the migratory periods, as Wood Thrushes are on the move at night.

All three geolocator types were mounted using the Rappole-Tipton “back-pack” method, with harness straps looping around the legs and the unit resting against the centre of the bird’s back, above the pelvis (Rappole and Tipton 1991). Harnesses were made from Teflon tubing. The Mk18S and MK5040 units had metal loops and plastic tubes through which the harness was threaded. The harness was attached to the GeoTX units with Kevlar thread. The combined weight of the geolocator and harness was approximately 1.5 g, or approximately 3% of the average Wood Thrush body mass.

I tracked Wood Thrushes from two breeding populations in Southern Ontario (Waterloo Region 43°27’ N, 80°35’ W; Kingston 44°14’ N, 76°37’ W), and one winter population in the northern highlands of Nicaragua (Reserva El Jaguar 13°14’ N, 86°3’ W). In summer 2011, 16 model Mk18S geolocators were deployed in Ontario at breeding sites in the Waterloo Region (n = 11) and in Kingston (n = 5). In addition, 10 GeoTX units were deployed on female birds, 5 at each location. Female Wood Thrushes are known to be less site faithful than their male counterparts, so the aim was to increase the number of female recoveries through the additional aid of the radio signals. During the 2012 field season, 3 units were recovered in Waterloo and 2 in Kingston. One of those retrieved at each site was a GeoTX unit. In 2012, a further 30 deployments were made in Ontario, this time using Biotrack model MK5040 units. In summer 2013, 2 MK5040 geolocators were recovered in Waterloo, and 1 in Kingston. Additionally, 1 two-year-old GeoTX unit deployed in 2011, was recovered in Waterloo. One recovered Waterloo unit (Mk18S) suffered battery failure in February, so only the fall migration track was recorded.

In Nicaragua, 64 Mk18S units were deployed in tropical cloud forest on the Reserva El Jaguar in the Jinotega Department (13°14’ N, 86°3’ W), in winter 2011-12. Of these, 4 were recovered the following winter; the data from 2 showed breeding within one latitudinal standard

deviation (~200 km) of the Canadian border. Data from 9 Wood Thrushes previously tracked from La Selva Biological Station in Costa Rica (10°24' N, 84°0' W; Stanley et al. 2015) to, or near, Canada, were also included in my analyses to better assess connectivity of Canadian breeding populations. One La Selva female was tracked for two consecutive years.

Analyses of light data were carried out using the BASTrak software package. When necessary, errors in clock drift were corrected using Decompressor. Quality of transition data was assessed with TransEdit2 using a light threshold of 16. Minimum dark period and equinox filters were used to remove all nonsensical transitions, and all data collected within 21 days of the equinoxes. Sunrise and sunset transitions were individually assessed and only those transitions with smooth curves were given high confidence values, and ultimately used in the migration analysis. For birds tracked from their breeding grounds, solar elevation angles for the winter site were estimated using the Hill-Ekstrom calibration method (Lisovski *et al.* 2012). Migration trajectories were calculated using the Locator program.

### Stable Isotope Study

Geographic variation in stable isotopic ratios provides a useful means of establishing movement patterns of migratory animals (Jones et al. 2008; Norris et al. 2006; Hobson et al. 2001). Wood Thrushes complete only a single molt each year. This is a prebasic molt and takes place on the breeding grounds just prior to fall migration. Thus, all feathers contain isotopic ratio signatures of the breeding grounds. P1 (first primary) feathers were sampled from all Nicaraguan birds that received geolocators, and the  $\delta D_f$  values were analyzed at the Queen's Facility for Isotope Research (QFIR). Feathers were treated for 24 hours in a 2:1 chloroform methanol solution to remove surface contaminants and oils. Samples were shipped to Kingston and allowed to equilibrate, for 3 weeks, with atmospheric hydrogen at the QFIR. Feathers were diced

and weighed into silver foil crucibles, then heated in a drying oven for 24 hours to remove all surface water. The crucibles were finally crushed and placed into a high temperature conversion elemental analyzer (TC/EA), and the gases resulting from sample pyrolysis were fed into a Thermo-Finnigan MAT 253 isotope ratio mass spectrometer (IRMS). The reported  $\delta D_f$  values are calculated according to the expression:

$$\delta D = (R_{sample}/R_{std} - 1) \times 1000$$

where  $R_{sample}$  is the absolute deuterium/protium ratio of the feather tissue, and  $R_{std}$  is the ratio of the Vienna standard mean ocean water (VSMOW). To account for exchangeable hydrogen in the molecular keratin structure, all  $\delta D_f$  values were linearly corrected against keratin standards (Wassenaar and Hobson 2003). The four keratin standards used were CBS ( $-157 \pm 4.2\text{‰}$ ), SPEC ( $-92 \pm 1.7\text{‰}$ ), KHS ( $-40 \pm 1.8\text{‰}$ ), and THS ( $-28 \pm 8.3\text{‰}$ ), which span the range of  $\delta D_p$  (precipitation) values over the Wood Thrush breeding range. Repeated measures of in-house mineral standards in each sample run showed precisions of  $\pm 1.7\text{‰}$  for U of M (brucite from the University of Michigan) and  $\pm 2.7\text{‰}$  for Georgia kaolinite clay. All measured  $\delta D$  values were close to known values for the standards.

The Wood Thrush breeding region was divided into three segments or bins: north, central, and south. The divisions are based on those in Stanley et al. (2015), but extended east-west in light of the limited longitudinal variation in  $\delta D_p$  values over eastern North America. Breeding origin was posteriorly assigned to these bins using Bayes Theorem.  $\delta D_p$  continental overlays were generated using IsoMap, which utilizes data from the Global Network of Isotopes in Precipitation (GNIP). Estimates of breeding density were made from BBS data. See Appendix A for details of the assignment calculations.

## Results

### Geolocator Study

A total of 20 annual migration tracks were collected for Canadian Wood Thrushes (Figure 3). The Wood Thrushes from both South-western and Eastern Ontario show a strong predilection for wintering in Nicaragua and northern Costa Rica. The bounding box in Figure 3 shows the winter range for 90% of the Canadian birds. Only two individuals wintered outside this range, one near Intibuca, Honduras (14.59°N, 88.04°W), and the other near Chiapas, Mexico (17.61°N, 91.69°W). The Mexican Wood Thrush was also the only bird to divide the winter stationary phase into two extended stops (>1 month) at two different locations in Central America. The two Nicaraguan birds bred in Ontario and the western part of Quebec, while the nine Costa Rican birds, on average bred farther east, in Eastern Ontario, Quebec, and New Brunswick.

All individuals followed a loop migration pattern, taking a different route north in spring than the one they travelled south in the fall.

Sixteen of the 19 spring tracks show direct flights from the Yucatan peninsula to the American coast of the Gulf of Mexico. The remaining three tracks trace routes overland through Mexico, which circumnavigated the Gulf.

Western Cuba and the tip of the Yucatan peninsula in fall, and the Mississippi delta in spring, represent the most used stopover sites.

There were no statistically significant differences between males and females in the timing of arrival at the winter site ( $t$  stat = 0.2;  $p$  = 0.42), departure from the winter site ( $t$  stat = 0.5;  $p$  = 0.33), or arrival at the breeding site ( $t$  stat = 0.1;  $p$  = 0.45) (Table 1). Owing to the small sample sizes, a power analysis was performed on the data, and the  $t$ -test was bootstrapped (Table

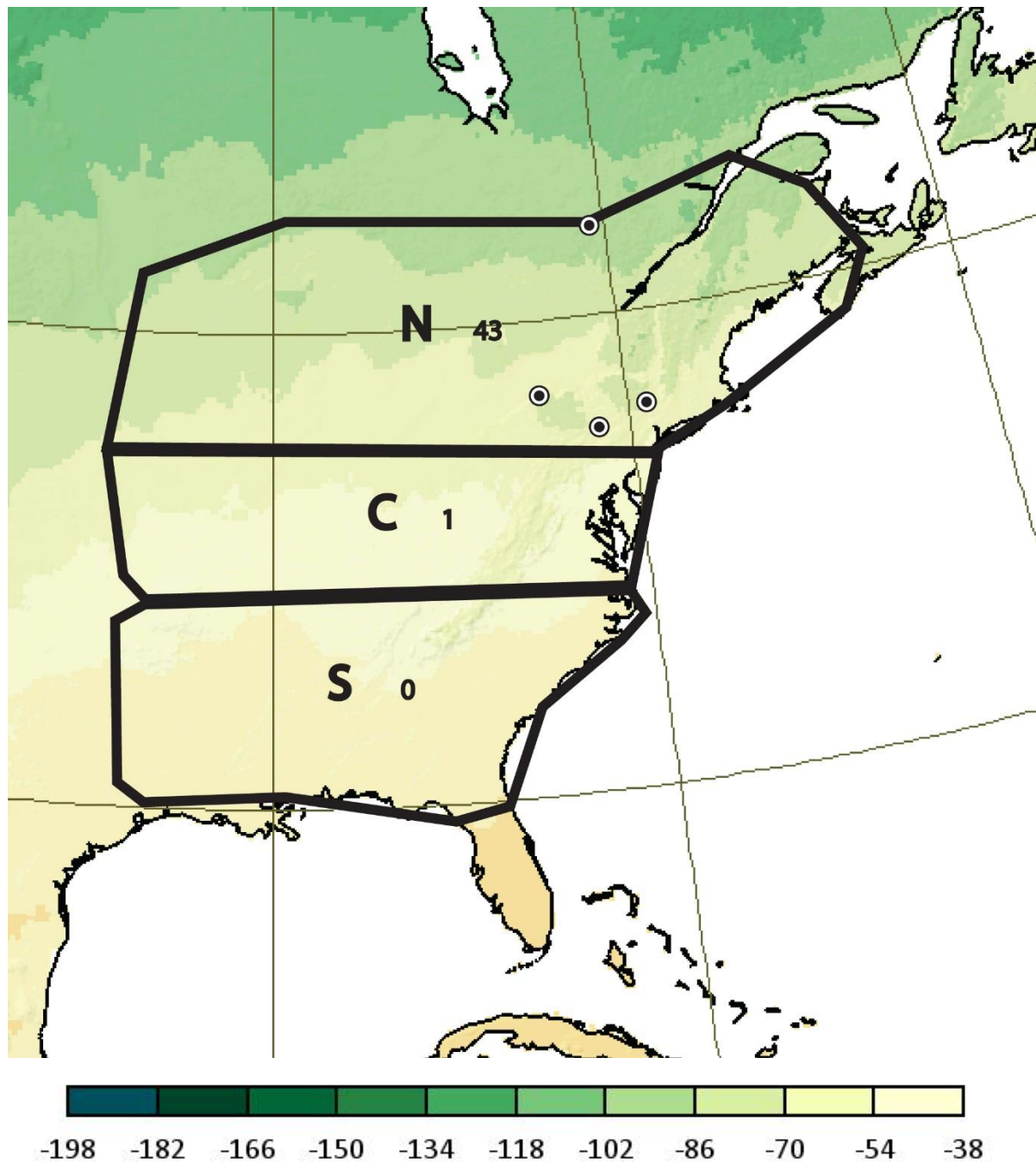
2). See Appendix 2 for the bootstrapped t value distributions. Males averaged just a day and a half earlier in winter arrival date, and less than half a day earlier in spring arrival date. Females were two and a half days earlier in spring departure from the winter grounds. Similarly, the two sexes did not differ significantly in the average longitude of either their spring or autumn migration routes. The average difference was  $0.55^{\circ}$  in fall, and  $0.18^{\circ}$  in spring. All males (n = 11) crossed the Gulf, while two of seven females took the overland route through Mexico.

### Stable Isotope Study

P1 feathers were sampled from 44 birds at El Jaguar. After linear corrections were applied, the average  $\delta D_f$  value was  $-66.8\text{‰}$  (std. dev. 13.1). All but one of the birds was mapped to breeding locations in the northern portion of the breeding range (Figure 4), with  $\delta D_f$  values ranging from  $-43.6$  to  $-93.8\text{‰}$ . The sole exception mapped to the central section of the breeding range ( $-39.9\text{‰}$ ). See Appendix A for full data set and assignment calculations.



**Figure 3:** Autumn (blue) and spring (red) migration tracks for Wood Thrushes breeding in Canada. Dashed lines indicate uncertainty in latitude due to proximity to the equinox. Filled circles represent breeding deployment sites, open circles show winter deployment sites. The black bounding box indicates the winter range for 90% of the Canadian birds. The enlargement shows the individual wintering locations.



**Figure 4:** Stable hydrogen/deuterium assignment of Wood Thrushes to north (N), central (C), and south (S) segments of the breeding range. Number of individuals assigned to each bin is indicated. Dimensionless isotope units, shown on bar, are in  $\delta$  form (‰). Circles indicate breeding sites for geolocator birds tracked from Nicaragua.



**Table 1:** Comparison of the migratory phenology and route selection of male and female Wood Thrushes. All dates are ordinal (Jan 1 = 1).

Phenological / Geographical parameter	Male		Female		Student's t-test	
	Mean	Std Dev	Mean	Std dev	t-stat	p-value
Autumn Arrival Date	307.45	14.54	309.00	17.26	t(11) = 0.2	0.42
Spring Departure Date	104.70	7.63	102.14	13.33	t(9) = 0.5	0.33
Spring Arrival Date	130.60	8.13	131.00	5.74	t(15) = 0.1	0.45
Autumn long. US exit	82.32	2.71	81.77	3.16	t(11) = 0.4	0.36
Spring long. US entry	89.72	3.13	89.90	4.65	t(10) = 0.1	0.47
Gulf crossing (Y/N)	11/0		5/2			

**Table 2:** Power analysis and bootstrapped t-tests for male/female phenological and route selection comparisons.

Parameter	Power Analysis					Bootstrap			
	n1	n2	Cohen's d	α level	Power	Alt. Hypothesis	t-stat	Std dev	p-value
Fall arr.	11	7	-0.0990	0.05	0.0543	"two.sided"	-0.04	1.10	0.47
Spr. dep.	10	7	0.2483	0.05	0.0167	"less"	0.83	1.54	0.47
Spr. arr.	10	7	-0.0550	0.05	0.0620	"less"	-0.09	1.05	0.52
Fall long.	11	7	0.1908	0.05	0.0660	"two.sided"	0.61	1.17	0.46
Spr. long.	10	7	-0.0455	0.05	0.0509	"two.sided"	-0.06	1.18	0.49

## Discussion

The primary goal of this study was to determine the core wintering grounds of Canadian Wood Thrushes so as to better inform conservation of this threatened species. Secondary goals were elucidating both the migratory routes and key stopover sites used by this same population of Wood Thrushes. Traditional band-recovery has not been successful in identifying these sites, nor the routes travelled between them. There are no examples to date of Wood Thrushes banded in June through August in Canada being recovered on the wintering grounds (Breeding Bird

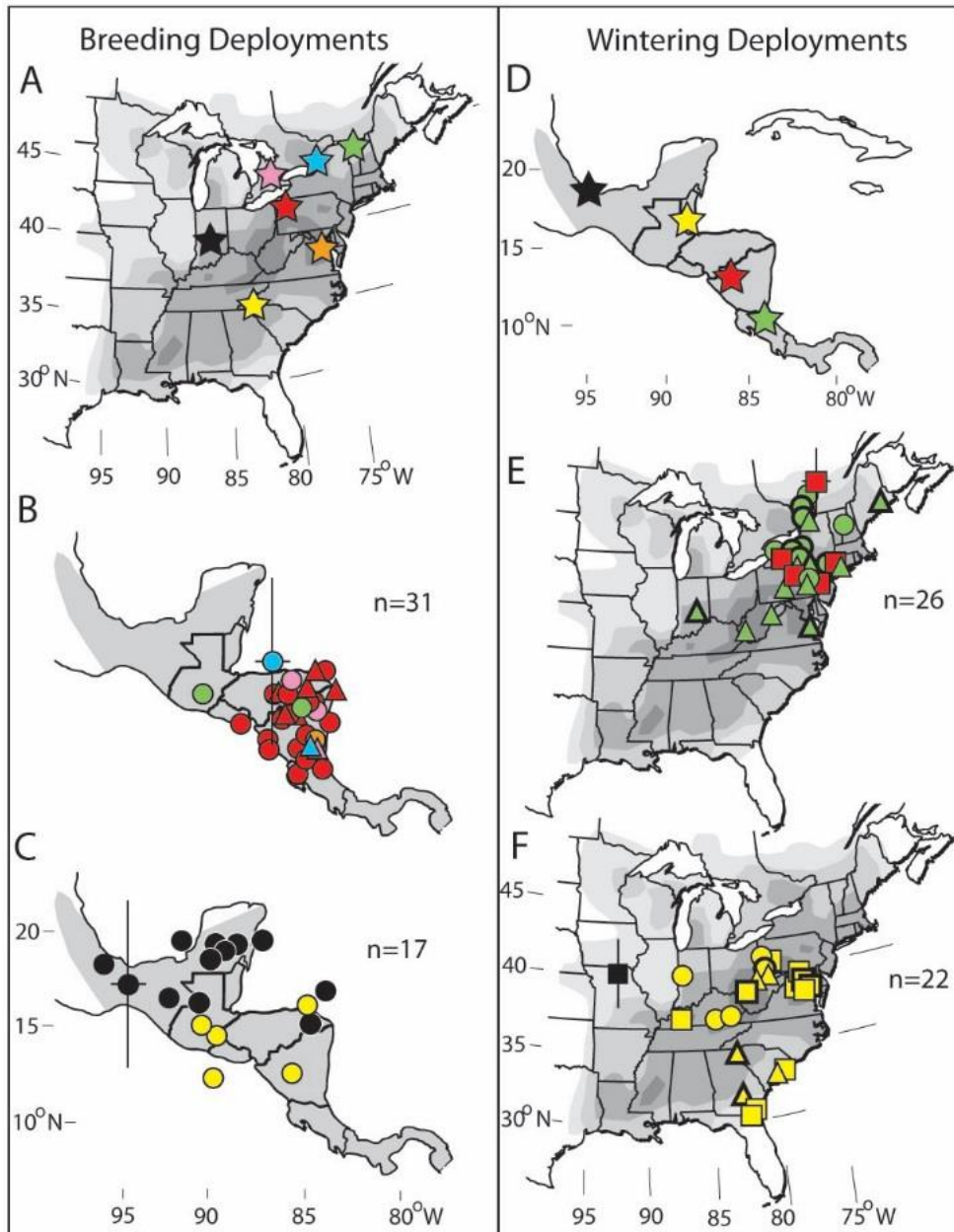
Laboratory, Patuxent MD). Using the modern approach of geolocator tracking technology, wintering sites, migratory routes, and important stopover sites (in regard to commonness of use), of 19 Wood Thrushes breeding in, or very close to, Canada were identified.

The majority of the Wood Thrushes (90%) tracked to or from breeding territories in Ontario, Quebec and New Brunswick converged on a narrow band of the winter range between 83.5 and 86.5° West. This places them in Nicaragua or eastern Honduras ( $n = 8$ ) and northern Costa Rica ( $n = 10$ ). The isotopic findings corroborate the link between Canada and this portion of the winter range. The feathers sampled in Nicaragua all had relatively negative  $\delta D_f$  values (most between -40 and -70‰); all save one of them were consistent with the northern segment of the breeding range. Canadian Wood Thrushes are the north-easternmost breeding population of Wood Thrush. Their preference for the south-eastern portion of the winter range suggests a pattern of parallel leapfrog migration.

Geographic scale becomes an important factor when evaluating migratory connectivity. Considered as a collection of separate breeding populations all sharing one winter region, Canadian Wood Thrushes show a pattern of weak migratory connectivity. The deployment sites at Waterloo and Kingston, which are 328 km apart, could have been linked to different winter locations, but my results revealed overlapping wintering sites. Thrushes tracked from El Jaguar and La Selva had breeding territories that were as much as 1000 km away from Waterloo, widening the catchment area of the winter area still further.

If, however, we consider the Canadian population as a single breeding unit of the entire Wood Thrush population, the Canadian birds fit well into a species-level migratory network that exhibits moderately strong connectivity (Stanley et al. 2015). Stanley et al. found that midwestern Wood Thrushes wintered in Mexico, birds from the South-eastern US flew to Belize

and surrounding region, and individuals from the North-eastern States and Canada wintered in eastern Central America (Nicaragua / Costa Rica) (Figure 5). The overall pattern is a leapfrog and parallel migration. The former because birds from the most northerly breeding latitudes fly to the most southerly winter ones, and the latter because all birds have approximately the same east-west distribution on the breeding range as they do on the winter range. Canadian birds are at the north and east of the breeding range, and mostly occupy the south and east of the winter range, and so fit the overall pattern.



**Figure 5:** Wood Thrush breeding and wintering linkages. Stars (A & D) represent deployment sites, matching colours of all other symbols (circle = female, square = male, triangle = sex unknown) indicate individual wintering sites (B & C), or breeding sites (E & F) from geolocator data. Taken from Stanley et al. 2015.

Being situated at the outside of a leapfrog pattern means that Canadian thrushes are flying greater distances than most of their American counterparts. This could help to explain the steeper

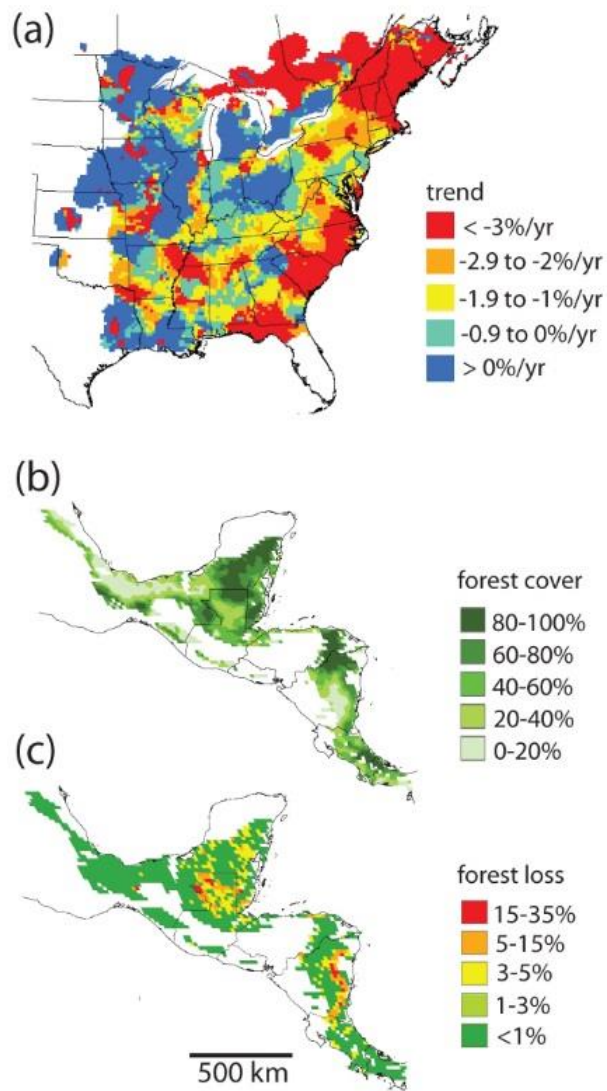
population declines in the north, though it has never been directly demonstrated that greater migratory distance leads to greater mortality in songbirds. Stanley et al. (2015) reported many different flight paths employed by Wood Thrushes, and found some patterns in route selection according to breeding location. Canadian thrushes may face particular threats during migration along preferred routes, or it may be that their limited winter range is experiencing high deforestation.

Canadian Wood Thrushes exhibit more diversity in the routes they travel in fall and spring than they do in wintering site selection. Longitude of fall exit from the United States ranged between 78 and 88° west, averaging  $82.0^\circ \pm 2.7^\circ$ . More than half ( $n = 13$ ) of the birds went through the Florida peninsula, while two went through the Bahamas, and the remaining five went south through the Florida panhandle or Alabama. Points of spring entry to the US are even more variable, ranging from 84 to 98° west (average  $89.9^\circ \pm 4.2^\circ$ ). Again, there is a clustering of tracks ( $n = 12$ ), this time along the coasts of Louisiana, Mississippi, and Alabama, between 87 and 92° west. Three tracks returned north through the Florida panhandle, and four went overland through Mexico, thus avoiding the long Gulf of Mexico water crossing. All individuals made a clockwise loop migration, with the spring route always to the west of the autumn route. Loop migrations are not really well understood, but in the Americas they may be governed by predominant wind patterns. Most high altitude winds north of the Tropic of Cancer are westerlies, while winds to the south of the Tropic are easterly trade winds. A bird crossing the Tropic from north to south in fall will encounter first westerlies, then easterlies, and exactly the opposite when traveling north in spring. This could explain the clockwise loop migrations of many North American migrants (Newton 2008).

Another puzzle is three thrushes that migrated around the Gulf of Mexico, rather than crossing it. 79% ( $n = 15$ ) of all northward migrations included a nonstop flight across the gulf, so there is clearly some form of selective pressure to undertake this feat. Increasing the speed of spring migration is a likely candidate. Many species have been shown to have a shorter spring than fall migration, with the main difference between the two periods being less time spent at stopovers (Nilsson et al. 2013). A shorter spring migration translates to early commencement of the breeding cycle (Moore et al. 2005) and greater productivity (van Noordwijk et al. 1995). The detour around the gulf adds approximately 1,400 km to the spring migration route (in comparison to the most common path from the tip of the Yucatan peninsula to the Mississippi delta) and always includes at least one additional stopover.

In a socially monogamous passerine like the Wood Thrush, where males defend breeding territories, I hypothesized that males would be under greater selective pressure than females to make it north to the breeding region as fast as possible in the spring. It was surprising, therefore, that there was no statistically significant difference between males and females for means of either departure from the wintering grounds, or arrival on the breeding grounds. This may be a result of the small sample size (only 17 birds), as other studies on the same species have found significant differences in the male/female phenology (McKinnon et al. 2014). Birds that do not exhibit protandrous migration are very much exceptions to the rule. The best known examples are species like Phalaropes where the normal parental roles of the sexes are reversed, and so too is their migratory behaviour. The power analysis confirms that the sample size is actually too small to show trends at a 95% confidence level; however, bootstrapping the data set yielded similar p-values, suggesting that the t-test is not missing any definite pattern, but the sample size, and so the statistical power, remain small. Several situations could account for the apparent lack

of protandry. As it is impossible to predict which birds will be recaptured in subsequent seasons, I couldn't set up a pair-wise experiment, and the data contain unequal numbers of the two sexes from each sampling site. The error margin of geolocators means that there is usually some estimation involved in determining arrival dates. A migrant may arrive during a spate of bad weather when the geolocator data are unusable, resulting in the first fair-weather day being incorrectly identified as the arrival date. It is possible that phenological differences between the sexes have been obscured by this alone.



**Figure 6:** Geographic patterns in population decline and habitat loss for Wood Thrush shown by:

A) Population trends across the breeding range (Sauer et al. 2014), B) Humid lowland tropical forest cover in the year 2000 (McKinnon et al. 2013) within the Wood Thrush winter range, and C) Percent forest loss in the Wood Thrush wintering range from 2000 to 2005 (Hansen et al. 2008).



High migratory connectivity implies increased vulnerability because of dependence on a subsection of the species' range (Webster et al. 2002). From a conservation standpoint, the concentration of Canadian birds within the eastern part of the winter range is of real concern because it places a strong dependency on the habitat in that region. Deforestation due to slash-and-burn agriculture is an ongoing issue in the tropics, and Nicaragua and Honduras have some of the region's highest deforestation rates (Figure 6 C). Wood Thrushes require forest habitat at all stages of their life cycle and cannot live in purely agricultural landscapes.

There have been substantial efforts towards habitat conservation in Nicaragua through the creation of a large system of national parks, including the Bosawas World Biosphere Reserve, but the Nicaraguan government has not been effective in preventing agricultural activities within park boundaries (Stocks et al. 2007). Beginning in the 1980s, some conservation projects have sought to tackle social issues in conjunction with their environmental objectives. The rationale is that, in developing countries, habitat destruction is driven by poverty and desperation, so improving the economic and social status of local peoples should alleviate stress on natural resources (Znajda 2014). While the efficacy of such projects is often difficult to gauge, studies have shown that some agroforestry initiatives, where a commercial crop is grown in a mosaic of shade trees and forest, do provide habitat that is used by migrant and resident bird species (King et al. 2007). The El Jaguar reserve where Wood Thrushes were tagged for this research is just such an agroforestry project, with coffee being grown in partial shade conditions amidst a patchwork of open pasture and cloud forest. Wood Thrushes occur there in large numbers and have been netted in both forest and plantation sections of the reserve.

## Conclusions

Canadian Wood Thrushes are spread across four provinces, but despite this, their core wintering area is only a narrow segment of the species' winter range. The areas used as stopover sites during migration are more variable among individuals, but the Florida peninsula, western Cuba, and the Mississippi delta represent the most significant stopover locations for Canadian Wood Thrushes. The greatest threat to these birds is likely deforestation in Honduras and Nicaragua, contributing more to population declines (-1.8% per year) on the breeding grounds, than any threats faced by the thrushes while in Canada.

COSEWIC lists some 30 Neotropical migrant species as at risk, of which Wood Thrush is the only one with a detailed description of its migratory connectivity. My work has shown that when considering conservation at the national level, knowledge of the total winter ranges of long-distance migrants is insufficient for directing conservation efforts. Migratory connectivity must be known in order to target the areas on which Canadian bird populations particularly depend. More research is needed to track declining migrant populations to assess patterns of connectivity, and more research is also needed in the tropics to understand the conditions experienced by Neotropical migrants during the non-breeding phase of their life cycle.

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## APPENDIX A

### Raw stable isotope data and assignment to breeding origin

**Table A1:** Measured and corrected  $\delta D_f$  values for P1 feathers collected at the Reserva El Jaguar in Nicaragua. Linear corrections adjust for exchangeable hydrogen in the feather keratin. The corrective linear equations were developed for each sample run by regressing measured values for keratin standards on their expected values.

Band #	$\delta D_f$ (‰)	Correction equation	Corrected $\delta D_f$
2301-15675	-50	$y = 1.2192x - 9.6567$	-70.5337944
2301-15676	-40		-58.705116
2301-15674	-28		-43.6772568
2301-15678	-65		-88.2963192
2301-15677	-56		-78.309852
2301-15672	-51		-72.3930744
2301-15673	-49		-69.171948
2301-15679	-30		-46.0888344
2301-15680	-41		-60.1901016
2301-15684	-64		-87.3941112
2301-15685	-64		-88.215852
2301-15686	-46		-65.9020536
2301-15687	-47		-66.7298904
2301-15657	-28	$y = 1.1781x - 14.134$	-47.3858725
2301-15656	-48		-71.0114899
2301-15655	-46		-68.2782979
2301-15647	-32		-51.9168451
2301-15663	-52		-75.7156432
2301-15665	-27		-46.4775574
2301-15648	-38		-59.4778909
2301-15666	-45		-67.4819023
2301-15664	-48		-70.3046299
2301-15658	-43		-64.7781628
2301-15659	-54		-77.7384409
2301-15661	-68		-93.8100811
2301-15646	-34		-54.3873208
2301-15660	-52		-75.6060799
2301-15671	-42		-63.5564731
2301-15688	-31	$y = 1.2229x - 1.6476$	-39.9402677

2301-15689	-66		-82.2587222
2301-15625	-36		-45.3198048
2301-15262	-48		-60.8298455
2301-15627	-56		-69.6445087
2301-15681	-49		-62.1383485
2301-15682	-53		-66.375697
2301-15628	-57		-70.7818057
2301-15683	-63		-78.4237078
2301-15629	-56		-70.3917006
2301-15630	-53		-66.0393995
2301-15631	-53		-65.886537
2301-15632	-68		-85.0530487
2301-15633	-34		-43.6150822
2301-15634	-55		-68.8679672
2301-15635	-63		-78.5606726

The simplest method of assigning birds to breeding origin based on isotope ratios assumes that the breeding populations are normally distributed in space, and so a bird with isotope ratio  $y^*$  is matched to its breeding origin  $b$ , with the normal distribution equation:

$$f(y^* | \mu_b, \sigma_b) = \frac{1}{\sigma_b \sqrt{2\pi}} \exp \left[ -\frac{1}{2\sigma_b^2} (y^* - \mu_b)^2 \right]$$

for each  $(\mu_b, \sigma_b)$ .

The marginal probability for each breeding region  $f(b)$ , was calculated as a relative abundance using averaged count data from the BBS.

**Table A2:** BBS count data from the three Wood Thrush breeding regions.

Bin	Count	Max	Min	Avg	Stn Dev	$f(b)$
North	8930	42.437	0.002	4.064	4.751	0.2775
Central	2296	42.437	0.003	6.241	7.032	0.4262
South	2580	15.372	0.003	4.338	3.057	0.2962

The conditional probability of breeding origin for a given isotopic ratio  $f(b|y)$  is calculated with Bayes' rule:

$$f(b|y) = \frac{f(b)f(y|b)}{f(y)}$$

where  $f(b)$  is the marginal probability of each breeding region  $b$ , calculated according to breeding abundance,  $f(y|b)$  is the conditional probability calculated with the normal distribution, and

$$f(y) = \sum_{b=1}^B f(y|b)f(b)$$



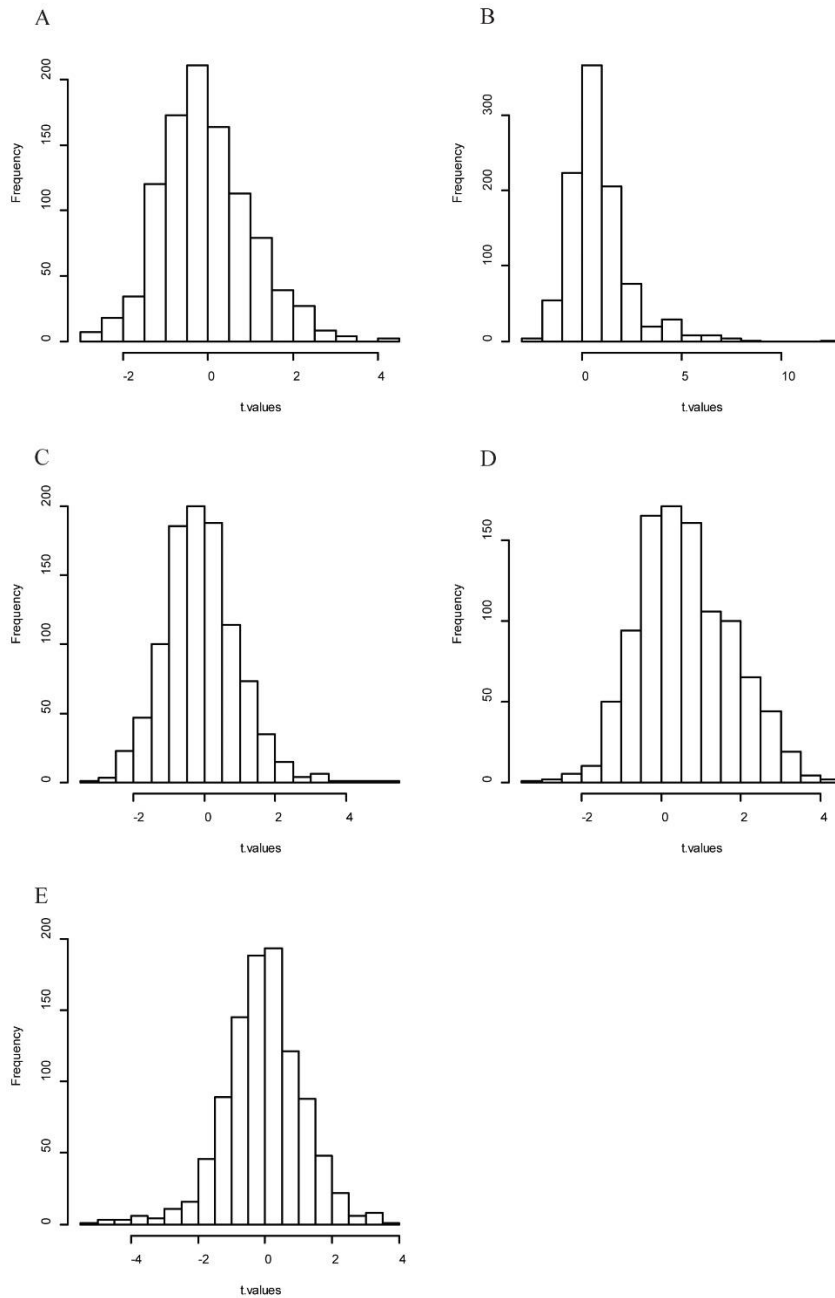
**Table A3:** Assignment of breeding origin assuming normal distribution, and using known population density with Bayes' theorem.

$f(y b)$			Normal Distribution Assignment			$f(y)$	$f(b y)$			Bayesian Assignment		
North	Central	South	North	Central	South		North	Central	South	North	Central	South
0.002495	2.91E-08	8.38E-13	1	0	0	0.000692	0.999982	1.79E-05	3.58E-10	1	0	0
0.021045	5.59E-05	5.34E-08	1	0	0	0.005864	0.995935	0.004063	2.70E-06	1	0	0
0.037930	0.015447	0.000664	1	0	0	0.017307	0.608224	0.380419	0.011358	1	0	0
6.42E-06	1.89E-15	1.23E-22	1	0	0	1.78E-06	1.000000	4.53E-10	2.05E-17	1	0	0
0.000276	4.47E-11	1.01E-16	1	0	0	7.65E-05	1.000000	2.49E-07	3.92E-13	1	0	0
0.001561	6.88E-09	1.10E-13	1	0	0	0.000433	0.999993	6.77E-06	7.52E-11	1	0	0
0.003437	7.99E-08	3.53E-12	1	0	0	0.000954	0.999964	3.57E-05	1.09E-09	1	0	0
0.040489	0.008463	0.000207	1	0	0	0.014906	0.753866	0.242016	0.004118	1	0	0
0.017455	2.52E-05	1.59E-08	1	0	0	0.004855	0.997789	0.002210	9.70E-07	1	0	0
9.41E-06	5.10E-15	4.62E-22	1	0	0	2.61E-06	1.000000	8.32E-10	5.25E-17	1	0	0
6.64E-06	2.07E-15	1.39E-22	1	0	0	1.84E-06	1.000000	4.78E-10	2.23E-17	1	0	0
0.006851	7.80E-07	9.34E-11	1	0	0	0.001902	0.999825	0.000175	1.46E-08	1	0	0
0.005814	4.47E-07	4.17E-11	1	0	0	0.001614	0.999882	0.000118	7.66E-09	1	0	0
0.040890	0.005840	0.000105	1	0	0	0.013868	0.818282	0.179478	0.002240	1	0	0
0.002219	2.02E-08	5.01E-13	1	0	0	0.000616	0.999986	1.40E-05	2.41E-10	1	0	0
0.004197	1.52E-07	8.85E-12	1	0	0	0.001165	0.999944	5.56E-05	2.25E-09	1	0	0
0.036839	0.001231	7.17E-06	1	0	0	0.010751	0.951012	0.048791	0.000198	1	0	0
0.000617	4.43E-10	2.39E-15	1	0	0	0.000171	0.999999	1.10E-06	4.14E-12	1	0	0
0.040684	0.007599	0.000170	1	0	0	0.014580	0.774405	0.222148	0.003447	1	0	0
0.019149	3.71E-05	2.86E-08	1	0	0	0.005330	0.997031	0.002967	1.59E-06	1	0	0
0.004978	2.66E-07	1.98E-11	1	0	0	0.001382	0.999918	8.22E-05	4.24E-09	1	0	0
0.002637	3.45E-08	1.07E-12	1	0	0	0.000732	0.999980	2.01E-05	4.33E-10	1	0	0
0.008461	1.63E-06	2.72E-10	1	0	0	0.002349	0.999705	0.000295	3.43E-08	1	0	0
0.000331	7.49E-11	2.06E-16	1	0	0	9.19E-05	1.000000	3.47E-07	6.63E-13	1	0	0
5.14E-07	3.13E-18	2.50E-26	1	0	0	1.43E-07	1.000000	9.37E-12	5.20E-20	1	0	0
0.031780	0.000444	1.36E-06	1	0	0	0.009009	0.978958	0.020997	4.48E-05	1	0	0

0.000637	4.87E-10	2.73E-15	1	0	0	0.000177	0.999999	1.17E-06	4.57E-12	1	0	0
0.010484	3.51E-06	8.43E-10	1	0	0	0.002911	0.999486	0.000514	8.58E-08	1	0	0
0.030383	0.031274	0.003095	0	1	0	0.022680	0.371796	0.587777	0.040427	0	1	0
7.06E-05	1.05E-12	6.09E-19	1	0	0	1.96E-05	1.000000	2.29E-08	9.21E-15	1	0	0
0.039919	0.010382	0.000305	1	0	0	0.015594	0.710435	0.283776	0.005789	1	0	0
0.015989	1.76E-05	9.28E-09	1	0	0	0.004445	0.998310	0.001689	6.18E-07	1	0	0
0.003082	5.65E-08	2.15E-12	1	0	0	0.000855	0.999972	2.81E-05	7.45E-10	1	0	0
0.013186	8.28E-06	3.00E-09	1	0	0	0.003663	0.999037	0.000963	2.42E-07	1	0	0
0.006242	5.68E-07	5.90E-11	1	0	0	0.001733	0.999860	0.000140	1.01E-08	1	0	0
0.002349	2.41E-08	6.42E-13	1	0	0	0.000652	0.999984	1.57E-05	2.92E-10	1	0	0
0.000266	4.03E-11	8.78E-17	1	0	0	7.37E-05	1.000000	2.33E-07	3.53E-13	1	0	0
0.002582	3.23E-08	9.75E-13	1	0	0	0.000717	0.999981	1.92E-05	4.03E-10	1	0	0
0.006670	7.12E-07	8.18E-11	1	0	0	0.001851	0.999836	0.000164	1.31E-08	1	0	0
0.006871	7.88E-07	9.48E-11	1	0	0	0.001907	0.999824	0.000176	1.47E-08	1	0	0
2.44E-05	6.18E-14	1.32E-20	1	0	0	6.77E-06	1.000000	3.89E-09	5.76E-16	1	0	0
0.037836	0.015664	0.000683	1	0	0	0.017380	0.604190	0.384176	0.011634	1	0	0
0.003682	9.96E-08	4.83E-12	1	0	0	0.001022	0.999958	4.15E-05	1.40E-09	1	0	0
0.000254	3.56E-11	7.39E-17	1	0	0	7.05E-05	1.000000	2.15E-07	3.10E-13	1	0	0

## APPENDIX B

### Bootstrapped t-value distributions for comparisons of male/female phenological measures



**Figure B1:** Distributions of bootstrapped t-values for wintering ground arrival date (A), spring departure date from winter location (B), spring breeding ground arrival date (C), longitude of fall gulf crossing (D), and longitude of spring gulf crossing (E).