

**MIGRATION AND WINTER ECOLOGY OF A DECLINING  
FOREST SONGBIRD**

EMILY A. MCKINNON

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## Abstract

Fundamental gaps in understanding of the year-round biology of migratory songbirds are hampering conservation of dozens of at-risk species. Until recently, determining where and when during their annual cycle migratory songbirds are most limited was not possible, because linking an individual's survival and condition across seasons and over thousands of kilometres was extremely difficult. With miniaturized tracking devices, I followed a declining migratory songbird, the Wood Thrush (*Hylocichla mustelina*) over its entire annual cycle, from well-studied breeding sites in temperate forests of eastern North America to its overwintering range in the Neotropics. As with most migratory birds, information on non-breeding ecology and habitat use is lacking for Wood Thrushes. In this dissertation, I examined demographic patterns in migration behaviour, and quantified effects of habitat occupancy in winter on condition of the birds and on spring migration performance. I found that Wood Thrush spring migration shows a distinct age-related switch from late timing and more stopovers as juveniles to earlier timing and fewer stopovers as adults. I also show, at a study site in Belize, that winter habitat quality (abundance of food and moisture) declines over the non-breeding season, and that Wood Thrushes are in the lowest body condition of the winter immediately prior to initiation of spring migration. Finally I show that despite variation in pre-migration body condition and habitat moisture, there were no carry-over effects of winter habitat occupancy to spring migration. Overall this work supports the hypothesis that Wood Thrush spring migration is primarily under genetic control, rather than condition-dependent, since winter conditions do not appear to limit migratory performance. Climate change models predict more droughts in Central America, which could decrease the condition of overwintering Wood Thrushes, and may result in detectable carry-over effects on migration in the future.

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## Table of Contents

<b>Abstract.....</b>	<b>ii</b>
<b>Acknowledgments.....</b>	<b>iii</b>
<b>Table of Contents .....</b>	<b>iv</b>
<b>List of Figures.....</b>	<b>vii</b>
<b>List of Tables .....</b>	<b>xiii</b>
<b>Chapter 1 General Introduction .....</b>	<b>1</b>
Abstract.....	2
Introduction .....	3
Geocator primer.....	5
Migratory connectivity .....	8
Migratory routes and stopovers.....	17
Multiple winter sites.....	19
Migration schedules.....	20
Future research using geolocators.....	25
Conclusion.....	30
Acknowledgments .....	31
Literature cited .....	32
<b>Chapter 2 Tracking from the Tropics reveals behaviour of juvenile songbirds on their first spring migration .....</b>	<b>40</b>
Abstract.....	41
Introduction .....	42
Materials and methods.....	45
Discussion .....	58
Literature cited .....	63
Supplemental information.....	70
<b>Chapter 3 Seasonal change in tropical habitat quality and body condition for a declining migratory songbird, the Wood Thrush .....</b>	<b>71</b>



Abstract .....	72
Introduction .....	73
Methods.....	78
Results .....	85
Discussion .....	95
Acknowledgments .....	102
Literature cited .....	102
<b>Chapter 4 Carry-over effects of winter condition on start-to-finish spring migration of a Neotropical songbird.....</b>	<b>108</b>
Abstract .....	109
Introduction .....	110
Methods.....	113
Results .....	116
Discussion .....	124
Acknowledgements.....	130
Literature cited .....	131
<b>Chapter 5 General Discussion .....</b>	<b>135</b>
Contribution to understanding of migration .....	135
Contribution to understanding of non-breeding season ecology .....	137
Contribution to conservation.....	139
Literature cited .....	141
<b>Appendix A: Abstracts and citations of related and collaborative work.....</b>	<b>145</b>
1) Stanley, C. Q., E. A. McKinnon, K. C. Fraser, M. P. MacPherson, G. Casbourn, L. Friesen, P. P. Marra, C. E. Studds, T. B. Ryder, N. Diggs, and B. J. Stutchbury. 2014. Connectivity of Wood Thrush breeding, wintering, and migration sites based on range-wide tracking. <i>Conservation Biology Early Online</i> pp 1-11. DOI:10.1111/cobi.12352.....	145
2) McKinnon, E. A., C. Q. Stanley, K. C. Fraser, M. MacPherson, G. Casbourn, P. P. Marra, C. E. Studds, N. Diggs, and B. J. M. Stutchbury. 2013. Estimating geolocator	

accuracy for a migratory songbird using live ground-truthing in tropical forest.	
Animal Migration 1:31-38.....	146
3) Chin, S., E. A. McKinnon, K. C. Fraser, J. Rotenberg, and B. J. M. Stutchbury. 2014.	
No sex bias in Wood Thrushes ( <i>Hylocichla mustelina</i> ) captured by using audio	
playback during the non-breeding season. Wilson Journal of Ornithology	
126(3):599-605. ....	147
4) Stanley, C. Q., MacPherson, M., K. C. Fraser, E. A. McKinnon, and B. J. M.	
Stutchbury. 2012. Repeat tracking of individual songbirds reveals consistent	
migration timing but flexibility in route. PLOS ONE 7(7): e40688. ....	148

## List of Figures

Figure 1-1 Since their deployment on the first migratory landbirds in 2007, geolocators have been used to track individual birds in the Palearctic–tropical, Nearctic–Neotropic, and austral migratory systems. Colors that frame the photographs match the colors that indicate migratory routes. One individual’s spring migration is shown for each subspecies (two subspecies are shown for Purple Martin and Swainson’s Thrush, and three for Northern Wheatear), except for Fork-tailed Flycatcher (yellow) and Thrush Nightingale (bright green), whose fall migrations are shown. Maps are modified from references in Table 1. .... 4

Figure 1-2 Examples of migratory connectivity patterns described using geolocator data: (a) weak connectivity within subspecies of Purple Martin (eastern subspecies, *Progne subis subis*, shown by thick arrows to indicate multiple breeding sites) but strong connectivity across subspecies (*P. subis arctica*, shown by thin arrow) (Fraser et al. 2012); and (b) three breeding populations (shown by thick arrow) of Red-backed Shrike tracked to the same wintering region—likely weak connectivity (Tøttrup et al. 2012b). This example illustrates how multiple breeding populations are needed to determine connectivity strength..... 11

Figure 1-3 (A) Average ( $\pm$  SE where available) spring migration rate ( $n = 13$  species) and (B) fall migration rate ( $n = 15$ ) for birds tracked using geolocators, in order of decreasing average body mass. Dashed lines indicate mean values (206 km day<sup>-1</sup> for spring and 135 km day<sup>-1</sup> for fall). Data points without error bars are from papers that did not report standard error or full data sets, with the exception of the Canadian Arctic Wheatear and Western Yellow-billed Cuckoo, which represent single individuals. Sample sizes (spring and fall, if different): Eurasian Hoopoe,  $n = 2$ ; Western Yellow-billed Cuckoo,  $n = 1$ ; Purple Martin,  $n =$

84, 89; Wood Thrush,  $n = 61, 28$ ; Northern Black Swift,  $n = 3$ ; Common Swift,  $n = 6$ ; Snow Bunting,  $n = 11$  (spring only); Veery,  $n = 5$ ; Swainson's Thrush (inland),  $n = 4$ ; Swainson's Thrush (coastal),  $n = 4, 5$ ; Red-backed Shrike,  $n = 9$ ; Fork-tailed Flycatcher,  $n = 5$  (fall only); Thrush Nightingale,  $n = 2$  (fall only); Northern Wheatear (Germany),  $n = 5$ ; Northern Wheatear (Canadian Arctic),  $n = 1$ ; Northern Wheatear (Alaska),  $n = 3$ . ..... 23

Figure 2-1 Juvenile wood thrushes exhibit a significantly different migration strategy in spring than adults. A) Juveniles (solid symbols) were later than adults (hollow symbols) at winter departure, entering the U. S. along the northern Gulf of Mexico coast, and when arriving at breeding sites. Triangles represent average for females and squares for males. Vertical bars indicate standard error. Inset map shows an example of locations where timing was measured for an individual wood thrush. B) Spring migration speed (total distance/duration) was slower for juvenile wood thrushes. C) Juveniles had more stopovers during spring migration relative to adults, and D) had more stopover nights in the U. S. than adults. Note that 1 stopover night = 2 consecutive noons in the same location. Boxplots extend to 25<sup>th</sup> and 75<sup>th</sup> quartiles with dark lines showing the median value and circles indicating outliers. Sample size is  $n = 17$  for juveniles, and  $n = 30$  for adults, except for winter departure ( $n = 16, 26$ ) migration speed ( $n = 15, 25$ ), and stopovers in the U. S. ( $n = 16, 29$ ). ..... 52

Figure 2-2 Migration routes at the Gulf of Mexico are not significantly different for A) adult ( $n = 30$ ) and B) juvenile ( $n = 17$ ) wood thrushes. Lines point to the longitude on the northern Gulf of Mexico coast where birds made landfall. Thickness of a line is proportional to the percent of birds within age-class using that route. Birds are all shown crossing the Gulf from a single point on the Yucatan peninsula of Mexico for simplicity; there were slight variations in takeoff locations that are not shown here. The arrow around the Gulf indicates

the proportion of birds that did not fly directly across but instead used an overland route (n = 3 of 17 juveniles, n = 3 of 30 adults)..... 54

Figure 2-3 Body condition of adult (n = 78) and juvenile (n = 107) wood thrushes captured in Belize in late winter was not significantly different, but wing length was significantly shorter for juveniles, within sexes. A) Percent lean body mass, and B) fat (n = 122 adults, n = 173 juveniles) and pectoral muscle scores (n = 88 adults, n = 129 juveniles) were not different by age-class. C) Wing length was smallest for juvenile females (n = 92), followed by adult females (n = 73), juvenile males (n = 99), and adult males (n = 72). Boxplots show 25<sup>th</sup> to 75<sup>th</sup> quartiles with open circles indicating outliers..... 56

Figure 2-4 Within-winter recaptures of birds wearing geolocators ('Geo add') (n = 15) and those which did not receive a geolocator ('No geo') (n = 10) did not show differences in percent lean body mass. In general, all birds declined in body condition as the winter progressed from wet season (Oct-Dec) to dry season (Jan-Apr). A) Birds that were relatively heavy on first capture tended to lose more mass over time, and the same pattern was shown in both 'Geo add' and 'No geo' groups. B) Birds recaptured after more days tended to decrease slightly more in percent lean body mass, with no effect of geolocators. C) Individual birds showed no consistent pattern in changes in percent lean body mass from first to second capture. Symbols indicate: 'Geo add' (filled), 'No geo' (hollow), males (squares), females (triangles), juveniles (dashed lines), and adults (solid lines). D) Average percent lean body mass of all birds was significantly higher in the wet season (n = 66) relative to the dry season (n = 88) (vertical lines show standard error). ..... 70

Figure 3-1 Map of study sites and habitats in Belize. A) Wood Thrush winter range in Mexico and Central America shown in blue shading (natureserve.org) with star indicating study site. B) Map of Belize (yellow shading) with districts outlined and study site indicated by a star. C-E) Three habitat types used by Wood

Thrushes: mature moist forest, forest disturbed by buildings and trails, and dense riparian scrub. Habitat types are described in detail in Methods. .... 80

Figure 3-2 Seasonal changes in biotic (A-C) and abiotic (D) resources for Wood Thrushes in three habitat types. Sample size (# transects) for wet and dry seasons, respectively, in each habitat were: forest, n=15,16; disturbed, n=9,21; scrub, n = 16,16. Each 10-m transect consisted of 3 pitfall traps and 3 soil samples, and fruit was surveyed in a 4x10x2m area. A) Arthropod abundance declined significantly from wet to dry seasons in all habitats. B) Edible arthropod biomass (dry weight of ants, beetles, and spiders) varied by habitat and season. C) Fruit abundance score was higher in the wet season relative to the dry season. Fruit scores were based on the number of fruits multiplied by the number of types of fruit. Scores of 0=no fruit, low = <10, moderate = 10-20, high = >20. D) Soil moisture (average % moisture by weight) declined significantly across all habitats from wet to dry. Vertical bars in A, B, and D indicate standard error. .... 90

Figure 3-3 Seasonal and habitat differences in four measures of condition for Wood Thrushes in Belize (number above bars indicates sample size). A) Body condition declined significantly from wet to dry seasons. B) Hematocrit (% packed red blood cells) did not differ significantly by season or habitat. C) Fat scores (scale of 0-4) were significantly higher in the wet season relative to the dry season in all habitats. D) Pectoral muscle scores were higher (scale of 0-4) in all habitats during the wet season, and tended to be higher in the forest relative to disturbed and scrub habitat. .... 92

Figure 3-4 Seasonal decline in body condition of n = 418 Wood Thrushes overwintering in Belize from 25 Oct to 7 Apr. There was no significant difference in the slope of the decline by habitat. .... 93

Figure 3-5 Within-winter seasonal differences in sex and age ratios of Wood Thrushes in different habitats. Numbers above bars indicate sample sizes. A)

Sex ratios differed significantly by season and by habitat. The most drastic shift was in scrub habitat where sex ratios reversed between seasons. B) Age ratios were similar across habitats but the proportion of juveniles captured declined from wet to dry seasons..... 94

Figure 3-6 NDVI, an index of habitat greenness and moisture, is significantly higher at a Costa Rican study site (La Selva Biological Station) compared with a Belizean study site (BFREE). Vertical bars indicate standard deviation over the four-year span (2010-13). Values are means from a 100km-radius circle centred on the study site location, excluding areas of water. Monthly NDVI values obtained from the Land Processes Distributed Active Archive Center (lpdaac@usgs.gov). ..... 99

Figure 4-1 Body condition of Wood Thrushes captured during the dry season in Belize did not correlate with: A) spring migration departure date (n = 26), B) date individuals crossed the Gulf of Mexico (n = 26), or C) date individuals arrived at their breeding sites (n = 24). .....118

Figure 4-2 Body condition of Wood Thrushes captured during the dry season in Belize did not correlate with: A) Spring migration duration (# of days spent migrating) (n = 24), or B) spring migration speed (total distance covered/duration) (n = 24). .....119

Figure 4-3 Winter site NDVI during March for individuals from a population of Wood Thrushes that breed at the same site in Pennsylvania did not correlate with: A) spring migration departure date (n = 21), B) date crossing the Gulf of Mexico (n = 24), or C) arrival date at breeding sites (n = 23). .....121

Figure 4-4 Winter site NDVI during March for individuals from a population of Wood Thrushes that breed at the same site in Pennsylvania did not correlate with: A) spring migration duration (# of days on migration) (n = 21) or B) spring migration rate (total migration distance/duration) (n = 21). .....122

Figure 4-5 March NDVI for two wintering sites in Belize and Costa Rica did not correlate with population-level migration timing, at A) departure from site, B) date crossing the Gulf of Mexico, and C) arrival at breeding sites. March NDVI did predict timing across populations, with birds in wetter sites migrating later. ....123

Figure 4-6 Leap-frog migration patterns in Wood Thrushes result in birds from a Costa Rica study site migrating farther than individuals at a Belize study site. A) Map shows breeding and wintering range, with two study sites indicated by stars and arrows indicating general migration destination for birds in spring. B) Migration distance is significantly longer for Costa Rica birds. C) Costa Rica is consistently wetter than Belize, as assessed by monthly NDVI within a 100-km radius of the site, during the overwintering dry season for Wood Thrushes...129



## List of Tables

Table 1-1 Summary of migration variables obtained from small landbirds using geolocators. Species are listed by increasing body size. Question marks indicate areas where patterns are suggestive but sample size small. ....	14
Table 2-1 Top general linear models that explain variation in spring migration strategy of juvenile and adult wood thrushes. Letters in brackets indicate the base category for that estimate, i.e. J = juvenile, M = male. Full models for all variables included age, sex, breeding latitude and breeding longitude. We also included an interaction term for age and sex, although it was not significant in any model. ....	57
Table 3-1 ANOVA results for the effects of season and habitat on total arthropod abundance, edible arthropod biomass, and soil moisture content. Year was included as an interaction factor for arthropod abundance and biomass and as a nesting factor in soil moisture since there was one year with only dry season soil moisture measurements. Significant factors indicated by an asterisk.....	87
Table 3-2 AIC values from a generalized linear model for differences in fruit scores by habitat and season, nested by year. Asterisks indicate lowest AIC values. ...	88
Table 3-3 ANOVA results of condition indices for Wood Thrush by habitat and season.....	91
Table 3-4 AIC values for generalized linear models with fat scores, muscle scores, sex and age of wood thrushes by season and by habitat. Season is nested by year to account for some years where only one season was sampled. Asterisks indicate the lowest AIC values; any model with AIC score within 2 of the lowest score is considered an equally acceptable model. ....	91

Table 4-1 Results of general linear models of the effect of March NDVI on individual migration performance for Wood Thrushes from the same breeding site (PA = Pennsylvania) and population-level migration performance at two overwintering sites (BZ = Belize, CR = Costa Rica). .....	124
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## Chapter 1 General Introduction<sup>1</sup>

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<sup>1</sup> This chapter is a modified version of McKinnon, E. A., Fraser, K. C., and B. J. M. Stutchbury. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. *Auk* 130 (2): 211-222. Permission to include this paper was obtained from publishers of the *Auk* and co-authors.

## **Abstract**

The study of migration and conservation of small landbirds has been revolutionized by the miniaturization of light-level geolocators. In this perspective, we summarize results from studies using geolocators on small (<80g) landbirds. Tracking the migration of small birds from start-to-finish has revealed examples of both strong and weak migratory connectivity, previously undocumented winter (intratropical) movements, unexpected long fall and spring stopovers, surprisingly rapid migration pace, and consistent migration strategy across widely separated populations and migration routes. We made the first cross-species comparisons for start-to-finish migration of small landbirds and found that spring migration pace was significantly faster than fall migration pace, as expected, but that pace was not related to migration distance or body size. Future studies using geolocators would benefit from testing optimal migration theory, exploring age and sex patterns of migration, network modelling, understanding ecological correlates of intratropical migration, and identifying conservation priorities, such as migration bottlenecks and critical non-breeding habitat.

## Introduction

Bird migration is a spectacular natural phenomenon that has generated wonder and interest for centuries. Feats of migration inspire amazement—individual birds that weigh less than 200 g may log more than 80,000 km annually (Egevang et al. 2010), travel more than 600 km day<sup>-1</sup> (Stutchbury et al. 2009, Åkesson et al. 2012), and cross huge geographic barriers such as oceans (Bairlein et al. 2012) and inhospitable deserts (Tøttrup et al. 2012b). Despite the vast geography covered during migration, many birds return to the same territories year after year. Although incredible progress has been made in our understanding of bird migration (Newton 2008), many gaps remain in our knowledge of the migration of small birds.

The development of miniaturized tracking technology has produced a wave of research into the migratory behaviour of small birds (Fig. 1). The inaugural application of miniaturized geolocators (or “geologgers”) on small songbirds in 2007 (Stutchbury et al. 2009) initiated a rapid increase in the number of studies of small landbird migration; there are currently more than 100 permits in North America alone for attaching geolocators to small birds. This technology has been so enthusiastically applied because it provides information critical to conservation and management of declining songbird populations (Faaborg et al. 2010a), as well as the opportunity to test long-standing hypotheses related to endogenous control mechanisms, navigation, and energetics (Robinson et al. 2010). Although more accurate devices may someday be available for tracking small birds, geolocators are

currently the only option for migrants that weigh <50 g (Bridge et al. 2011).

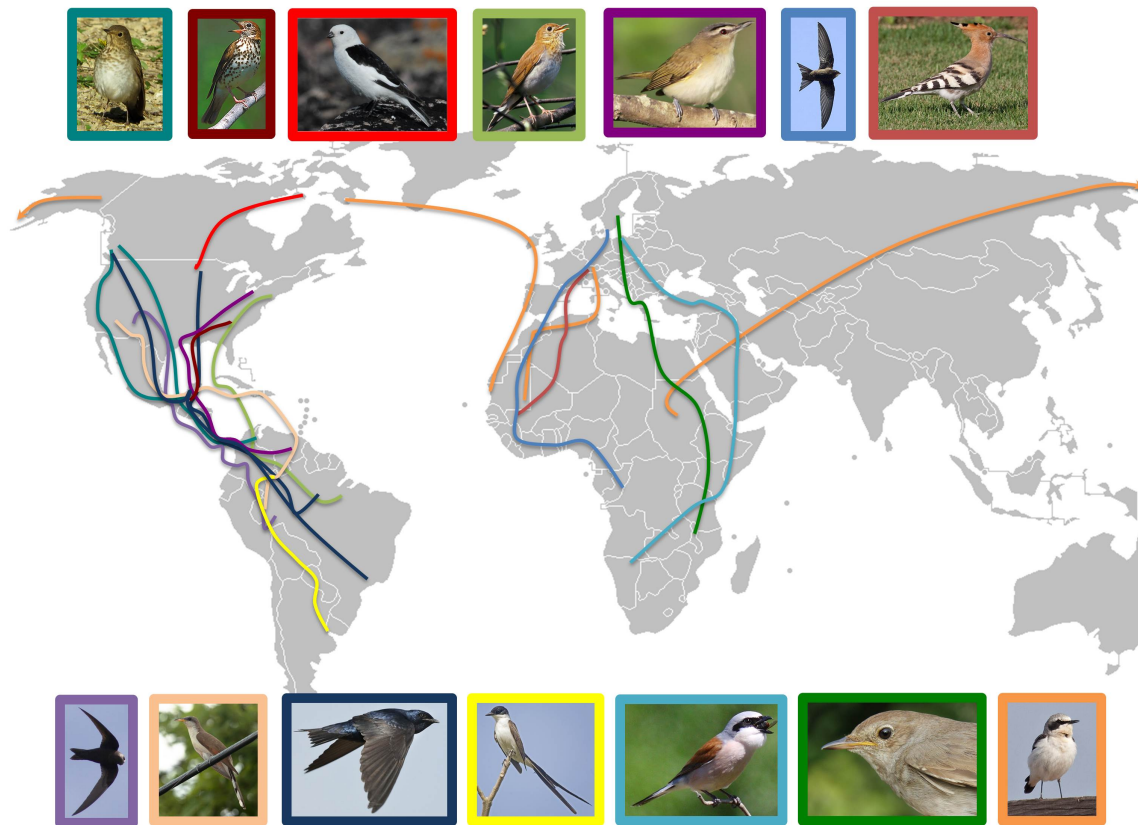


Figure 1-1 Since their deployment on the first migratory landbirds in 2007, geolocators have been used to track individual birds in the Palearctic–tropical, Nearctic–Neotropic, and austral migratory systems. Colors that frame the photographs match the colors that indicate migratory routes. One individual’s spring migration is shown for each subspecies (two subspecies are shown for Purple Martin and Swainson’s Thrush, and three for Northern Wheatear), except for Fork-tailed Flycatcher (yellow) and Thrush Nightingale (bright green), whose fall migrations are shown. Maps are modified from references in Table 1.

The main goal of many geolocator studies to date has been the description of little known migratory routes and wintering sites (e.g., Beason et al. 2012, Stach et al. 2012). As this technique becomes more widely applied (both geographically within species and taxonomically across a broad spectrum of small landbirds),

researchers can begin to test hypotheses about migration, non-breeding ecology, and behaviour to inform conservation measures. Many migratory species are declining; thus, a comprehensive understanding of the annual cycle is timely and important for management of species at risk. The purpose of our review is to summarize, for the first time, patterns emerging from geolocator studies. We review new data on (1) migratory connectivity, (2) migratory routes and stopovers, (3) intratropical migration of wintering birds, and (4) migration schedules. We then explore questions that can be answered with emerging geolocator studies, and provide a “flight plan” for future work as direct-tracking technology becomes increasingly smaller and more broadly applied.

### **Geolocator primer**

Geolocators are archival light-recording devices that are mounted on the lower back (for most small birds) following the Rappole and Tipton (1991) leg-loop harness design. The tags record light levels in relation to an internal timer. This allows the determination of sunrise and sunset times and, thus, day length and solar midday and midnight upon retrieval of the tag from the bird after it has completed its migration, usually the next year. Latitude and longitude are estimated from these light data, typically with a computer program such as LOCATOR (British Antarctic Survey) or tripEstimation in R (Sumner et al. 2009). Locations are determined using the “threshold method,” which uses calibration to determine the average sun elevation angle (the angle of the sun on the horizon) when a sunrise–sunset transition is defined, or using a “template-matching” method (Sumner et al. 2009, Lisovski et al. 2012). For more details on analysis methods, see Bridge et al. (2011),

Lisovski et al. (2012), and McKinnon et al. (2013).

Geolocator accuracy varies, depending on bird behaviour, geographic location, habitat, and weather (Fudickar et al. 2012, Lisovski et al. 2012). Ground truthing at multiple sites prior to fall migration found that geolocators mapped 91% (83 of 91) of Purple Martins accurately to within 100 km latitude and longitude (Fraser et al. 2012; scientific names of species not provided in the text can be found in Table 1). Ground-truthing tests with stationary forest birds on their tropical wintering grounds have shown that geolocators can place birds within a few degrees of latitude (365 km) and  $<1^\circ$  of longitude (66 km) of actual locations (McKinnon et al. 2013). These levels of accuracy are sufficient to elucidate unambiguous patterns of connectivity, migration timing, and so on for most species. Determination of finer-scale movements (e.g., within  $\sim 100$  km) and finer-scale mapping of birds while stationary at non-breeding sites is currently limited by technology. Geolocators, by relying on day length to determine latitude, are not able to determine the location of birds near the vernal and autumnal equinoxes (approximately 20 March and 22 September, respectively) when day length is the same everywhere. However, longitude during this time is still as accurate as at other times of the annual cycle (Fudickar et al. 2012).

Aside from the accuracy and analysis issues detailed above (see also Fudickar et al. 2012, Lisovski et al. 2012, McKinnon et al. 2013), researchers have encountered several shortcomings of geolocator studies on small birds in terms of field work and study design. One of the first limitations for geolocator studies was harness and geolocator failure. This has become solvable for many species as



geolocator models and harness designs continue to be refined on the basis of field and laboratory data (Bowlin et al. 2010). We encourage the publication of details of successful and failed geolocator attachment methods to improve future studies. Battery failure occurs even for the most reliable small geolocator models (e.g., 10–15% failure rate for British Antarctic Survey MK 10 and 16 on songbirds). Researchers must take into account not only return rates of the individual birds, but also potential rates of harness or geolocator failure when determining how many geolocators should be deployed.

Another important issue to consider is the impact on the study species. Most geolocator studies assume little impact on survival or behaviour of the birds tracked. Although true tests of effects of geolocators on migratory behaviour are not possible, evidence suggests that return rates of birds with geolocators are not significantly lower than those without geolocators (E. S. Bridge et al. unpubl. data). For sensitive species, low returns may be solvable through changes in geolocator or harness design (e.g., Purple Martins had very low return rates in the first 2 years, but shortening the light stalk of the geolocator solved the problem; B. J. M. Stutchbury et al. unpubl. data). Pilot testing with dummy geolocators and various harness types is a low-cost way to establish whether negative effects occur before time, effort, and money are invested into real geolocator deployments.

In some cases, the retrieval rate of birds wearing geolocators is low because of low site fidelity (i.e., deployments on juveniles or at stopover sites). Whether or not deployment on species or demographic groups with low return rates is valuable or ethical depends on the study species and questions.

In sum, the collective experience gained around the world from tracking small birds with geolocators in the past 5 years means that most researchers should be able to confidently proceed with geocator tracking of small birds because they can (1) identify appropriate questions, species, study sites, and methods needed to get migration data; (2) understand the inherent limitations of geolocators (battery failure, temporal and spatial accuracy, shading, equinox issues with latitude, and data from survivors only); (3) ensure that they monitor possible effects on birds and conduct pilot studies in advance; and (4) anticipate return and retrieval rates in order to determine *a priori* feasibility of obtaining adequate sample sizes and statistical power for the questions posed.

### **Migratory connectivity**

One of the primary goals of tracking migratory birds between breeding and wintering areas is to determine migratory connectivity. Migratory connectivity is defined from a breeding-grounds perspective as the amount of overlap in wintering locations of individual birds from geographically distinct breeding populations (Webster et al. 2002, Boulet and Norris 2006). The degree of linkage between populations in different seasons has direct implications for density-dependent population dynamics (Norris and Marra 2007, Taylor and Norris 2010) and, therefore, conservation of migratory birds (Martin et al. 2007, Marra et al. 2011).

Broad patterns of migratory connectivity have been determined for some species by using stable isotope analysis of feathers grown at the site of interest (Hobson and Wassenaar 1997, Marra et al. 1998, Rubenstein et al. 2002), by mapping genetic structure (Clegg et al. 2003), or by using a combination of these

techniques (Chabot et al. 2012). Geolocators can reveal fine-scale connectivity patterns (i.e., locations of birds within 100–500 km) that, in most cases, cannot be elucidated by examining stable isotopes or genetic structure, which can only map birds to broad isoscapes available in the environment or to the level of genetically distinct groups (Irwin et al. 2011). An under-used source of fine-scale connectivity data is the North American bird-banding database (Ryder et al. 2011). However, for many species, band recoveries, if they exist, are too sparse to draw conclusions about migratory connectivity (e.g., Northern Black Swift [Beason et al. 2012] and Purple Martin [Fraser et al. 2012]).

For geolocators to provide information on the strength of migratory connectivity, birds should ideally be tracked from multiple breeding and/or wintering sites to determine the degree of overlap of distinct breeding populations at different points in the annual cycle (Fig. 2). To date, deployment of geolocators at such a broad scale has been relatively rare (but see Fraser et al. 2012, Laughlin et al. 2013, Renfrew et al. 2013). However, geolocators are rapidly filling in maps for single populations (or single birds; Table 1) and can be used in conjunction with other data, such as stable isotope analysis of feathers (Macdonald et al. 2012) and band recoveries (Ryder et al. 2011), to provide a snapshot of range-wide connectivity.

Two species tracked extensively using geolocators, the Wood Thrush and Purple Martin, exhibit extremes in connectivity. Wood Thrushes tracked from a single breeding population in northern Pennsylvania overwinter, almost exclusively, in a small portion of the wintering grounds in eastern Honduras and Nicaragua

(Stutchbury et al. 2009, 2011). Tracking from six other breeding sites and three wintering sites revealed a strong pattern of parallel leap-frog connectivity: northeastern populations (New York and Quebec) tend to winter in the southeast of their range (Costa Rica); central-eastern breeding birds (Pennsylvania and Ontario) winter in central Mesoamerica (Nicaragua and Honduras); and southern and Midwestern breeding birds (e.g., Indiana, Kentucky, and North Carolina) tend to winter in the northwestern winter range (Belize and Mexico) (C. Q. Stanley et al. unpubl. data).

By contrast, there was little spatial structure in winter distributions of the eastern subspecies of Purple Martin (*Progne subis subis*; Fraser et al. 2012). Similarly, Bobolinks from across the breeding range showed extensive mixing during the non-breeding period (Renfrew et al. 2013). In Purple Martins, birds from colonies across the breeding range were found in the same core wintering region in the northern Amazon basin (Fig. 2; Fraser et al. 2012). Birds from a single breeding colony wintered, on average, 900 km apart and had overlapping winter distribution with birds from breeding colonies  $\leq 2,000$  km away. This extensive mixing of breeding populations at wintering sites is a textbook example of weak migratory connectivity. However, at the subspecies level, Purple Martins exhibit strong connectivity. Purple Martins from the western North American subspecies (*P. s. arbuticola*) that were tracked using geolocators had a distinct wintering area in southeastern Brazil (Fraser et al. 2012) that did not overlap at all with the wintering range of the eastern subspecies (Fig. 2). These results emphasize the importance of scale and phylogenetics in defining patterns of connectivity.

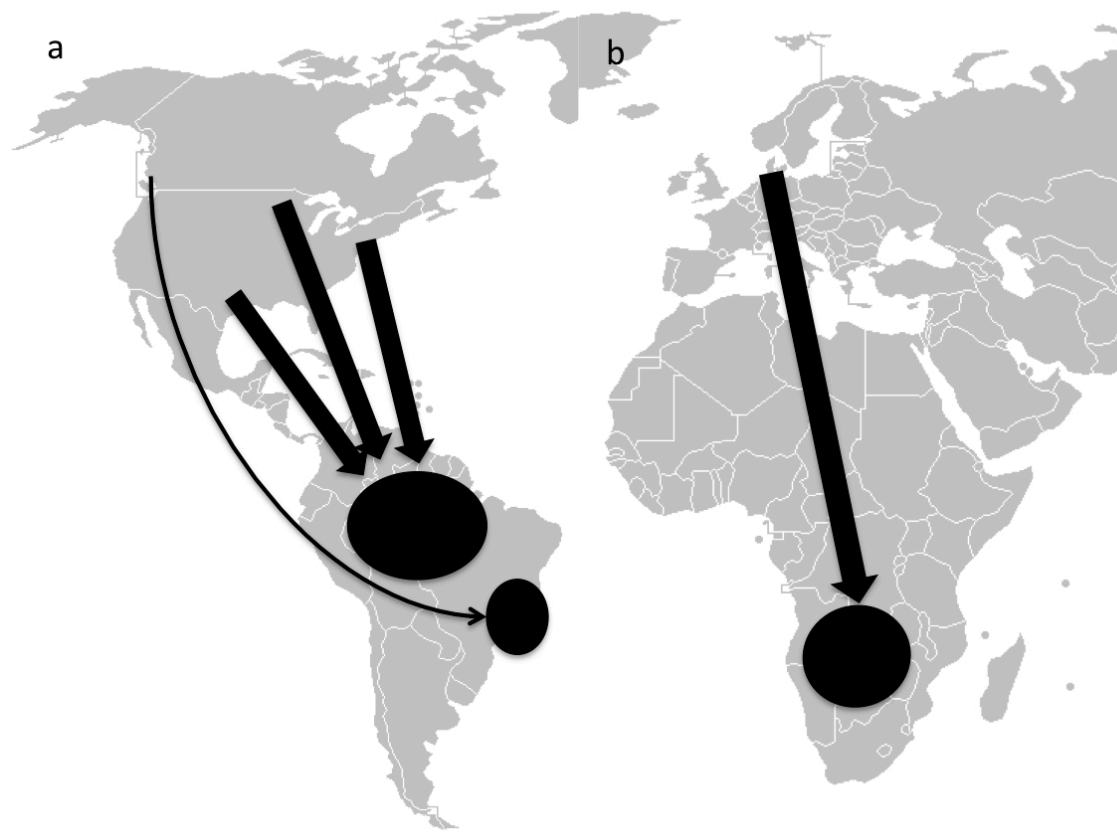


Figure 1-2 Examples of migratory connectivity patterns described using geolocator data: (a) weak connectivity within subspecies of Purple Martin (eastern subspecies, *Progne subis subis*, shown by thick arrows to indicate multiple breeding sites) but strong connectivity across subspecies (*P. subis arbuticola*, shown by thin arrow) (Fraser et al. 2012); and (b) three breeding populations (shown by thick arrow) of Red-backed Shrike tracked to the same wintering region—likely weak connectivity (Tøttrup et al. 2012b). This example illustrates how multiple breeding populations are needed to determine connectivity strength.

Macdonald et al. (2012) found strong parallel connectivity, also at the scale of subspecies, in Snow Buntings, with Greenland breeding birds wintering in eastern Canada (shown through band records) and Canadian Arctic breeding birds wintering in western Canada. Examining the banding records alone suggests a

pattern of weak connectivity within subspecies: multiple breeding populations from Greenland share a broad overlapping wintering site in eastern Canada. However, geolocator data from the Canadian Arctic revealed a migratory divide at Hudson Bay. Overall, then, the species shows a broad pattern of strong connectivity (Macdonald et al. 2012). Delmore et al. (2012) studied subspecies of Swainson's Thrush at a migratory divide and found that subspecies separated by <300 km at their breeding sites had distinct migratory routes and wintering ranges. Unlike in Snow Buntings, a pattern of strong connectivity was apparent within subspecies of Swainson's Thrush; coastal birds tracked with geolocators from a breeding population in California had a distinct wintering area in relation to coastal birds tracked from British Columbia (Cormier et al. 2013).

Most studies using geolocators have focused on qualitative measures of connectivity, such as the broad patterns described above. However, as more data are collected, quantitative measures of connectivity can be explored. To quantitatively describe migratory connectivity in Purple Martins, Fraser et al. (2012) used nearest-neighbor calculations to describe the spatial relationship among wintering birds from the same breeding populations and tested for significant correlations between breeding and wintering latitude and breeding and wintering longitude. Ambrosini et al. (2009) used band returns and distance matrices to calculate Mantel's correlations between proximity of individual Barn Swallows (*Hirundo rustica*) at breeding and winter sites, testing whether the distribution of birds in one season was random (weak connectivity) or correlated with the distribution of birds in the previous season (strong connectivity). Mantel's correlation coefficient indicated

very strong connectivity using geolocator data from Swainson's Thrushes (Cormier et al. 2013). Quantitative measures of connectivity patterns and strength would allow for more cross-species comparisons, which could lead to better understanding of the evolution of migratory behavior and, potentially, better predictions of patterns of connectivity in species that are too small for geolocator tracking

Table 1-1 Summary of migration variables obtained from small landbirds using geolocators. Species are listed by increasing body size. Question marks indicate areas where patterns are suggestive but sample size small.

Species	Body size (g)	Number of geolocator deployment sites	Loop migration <sup>a</sup>	Multiple winter sites (n)	Long stops <sup>b</sup>	Migratory connectivity <sup>c</sup>	Percentage of year at non-breeding sites <sup>d</sup>	References
Common Redstart ( <i>Phoenicurus phoenicurus</i> )	16	1	Yes	No	Yes (fall and spring)	Weak	61	Kristensen et al. 2013
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	19	1	Yes	No	Yes (spring)	NA	NA	Callo et al. 2013
Bobolink ( <i>Dolichonyx oryzivorus</i> )	25	3	NA	Yes	Yes (fall)	Weak	NA	Renfrew et al. 2013
Northern Wheatear ( <i>Oenanthe oenanthe</i> )	26	3	Yes	No	No	Strong	76 (AK) 62 (Ger) 64 (Can)	Schmaljohann et al. 2012a Schmaljohann et al. 2012b Bairlein et al. 2012
Thrush Nightingale ( <i>Luscinia luscinia</i> )	27	2	NA	Yes (3)	Yes (fall)	Strong?	NA	Stach et al. 2012
Fork-tailed Flycatcher ( <i>Tyrannus savana</i> )	30	1	NA	Yes (2)	NA	NA	NA	Jahn et al. 2013b
Veery ( <i>Catharus fuscescens</i> )	30	1	Yes	Yes (2)	Yes (fall)	NA	69	Hecksher et al. 2011
Swainson's Thrush (coastal; <i>C. ustulatus</i> )	30	2	Yes	Yes (2)	Yes (spring)	Strong	84	Delmore et al. 2012 Cormier et al. 2013
Swainson's Thrush (inland; <i>C. ustulatus</i> )	30	1	Yes	No	Yes (spring)	Strong	81	Delmore et al. 2012
Red-backed Shrike ( <i>Lanius collurio</i> )	30	3	Yes	No	Yes (fall)	Weak?	NA	Tøttrup et al. 2012b



Species	Body size (g)	Number of geolocator deployment sites	Loop migration <sup>a</sup>	Multiple winter sites ( <i>n</i> )	Long stops <sup>b</sup>	Migratory connectivity <sup>c</sup>	Percentage of year at non-breeding sites <sup>d</sup>	References
Eastern Kingbird ( <i>Tyrannus tyrannus</i> )	40	2	Yes	Yes (2)	No	NA	69	Jahn et al. 2013a
Western Kingbird ( <i>T. verticalis</i> )	40	1	NA	Yes (2)	Yes (fall)	NA	78	Jahn et al. 2013a
Scissor-tailed Flycatcher ( <i>T. forficatus</i> )	40	1	NA	No	No	NA	44	Jahn et al. 2013a
Golden-crowned Sparrow ( <i>Zonotrichia atricapilla</i> )	32	1	NA	No	NA	NA	70	Seavy et al. 2012
Snow Bunting ( <i>Plectrophenax nivalis</i> )	35	1	NA	Yes	Yes (spring)	Weak (sub-sp.) Strong (sp.)	68	Macdonald et al. 2012
Common Swift ( <i>Apus apus</i> )	44	2	No	Some individuals (2)	Yes (fall)	Weak?	81	Åkesson et al. 2012
Gray Catbird ( <i>Dumetella carolinensis</i> )	45	1	NA	No	NA	Strong (including banding data)	NA	Ryder et al. 2011
Wood Thrush ( <i>Hylocichla mustelina</i> )	45	8	Yes	No	Yes (fall)	Strong	59	C. Q. Stanley et al. unpubl. data Stanley et al. 2012 Stutchbury et al. 2009, 2011
Northern Black Swift ( <i>Cypseloides niger borealis</i> )	46	1	NA	NA	NA	NA	71	Beason et al. 2012

Species	Body size (g)	Number of geolocator deployment sites	Loop migration <sup>a</sup>	Multiple winter sites ( <i>n</i> )	Long stops <sup>b</sup>	Migratory connectivity <sup>c</sup>	Percentage of year at non-breeding sites <sup>d</sup>	References
Purple Martin ( <i>Progne subis</i> )	55	7	Yes	Yes (1–4)	Yes (fall)	Weak (sub-sp.) Strong (sp.)	66	Fraser et al. 2012
Western Yellow-billed Cuckoo ( <i>Coccyzus americanus occidentalis</i> )	60	1	Yes	No	Yes (spring and fall)	NA	79	Sechrist et al. 2012
Eurasian Hoopoe ( <i>Upupa epops epops</i> )	68	1	Yes	No	Yes (fall)	Weak	70	Bächler et al. 2010

<sup>a</sup> Loop migration: this category includes species in which spring migration was east or west of fall migration.

<sup>b</sup> Long stopover = any stopover >7 days, on average.

<sup>c</sup> Migratory connectivity: defined as overlap of wintering sites for individuals from different breeding populations.

Weak = individuals from multiple breeding populations wintering together; strong = individuals from distinct breeding populations with distinct wintering ranges. Question marks indicate studies with minimal data or no clear pattern.

<sup>d</sup> Percentage of year at non-breeding sites includes days spent at stopovers, on migration, and at wintering sites

## **Migratory routes and stopovers**

The documentation of individual migratory routes and stopover sites, from start to finish, is one of the most exciting and unique contributions of geolocators to the study of migration in small birds. Geolocators have revealed geographically and individually consistent patterns of loop migration within species (Tøttrup et al. 2012b), connections between New World Arctic and African ecosystems (Bairlein et al. 2012), and unexpectedly long spring stopovers (e.g., Red-eyed Vireos; Callo et al. 2013) and fall stopovers (e.g., Wood Thrushes; Stutchbury et al. 2011).

Many species tracked using geolocators have shown seasonal variation in migratory routes (i.e., loop migration; Table 1). For example, most Wood Thrushes exhibit fall migration routes consistently east of spring migration routes (Stanley et al. 2012). In the Palaearctic system, Red-backed Shrikes tracked from three sites in southern Scandinavia also showed a strong pattern of loop migration, with all individuals migrating farther west in fall in relation to spring routes (Tøttrup et al. 2012b). These patterns may be related to broad-scale wind patterns or spatial variation in the quality of stopover habitat (Klaassen et al. 2010); however, these hypotheses have not been explicitly tested in small landbirds.

Some species show within-season differences in migratory routes. Coastal and inland subspecies of Swainson's Thrush differed greatly in migratory route (Delmore et al. 2012), as did Alaskan and Canadian Arctic-breeding subspecies of the Northern Wheatear (Bairlein et al. 2012). Subspecific differences might be expected, but differences within populations have been documented as well. Eurasian Hoopoes tracked from the centre of their breeding range showed very

different migration routes, possibly indicative of a migratory divide (Bächler et al. 2010), and Northern Wheatears tracked from Germany also exhibited within-population variation in their migratory route (Schmaljohann et al. 2012a). Within-population variation in migratory routes is also evident in the Nearctic–Neotropic migration system. Two of five Veeries tracked from a single breeding population migrated across the western Gulf of Mexico in spring, whereas three crossed the gulf from Cuba to Florida (Heckscher et al. 2011).

It is unclear whether variation (or convergence) in migratory routes of individuals in a single population is because of endogenous control (i.e., genetic and heritable traits) or is a flexible response to environmental cues en route. Schmaljohann et al. (2012b) examined weather effects on migration decisions by Northern Wheatears and found that wind and temperature affected migration decisions in fall but not in spring. Repeat-tracking of individual Wood Thrushes showed that 7 of 10 birds used a similar spring route at the Gulf of Mexico from year to year, although, at a finer geographic scale, longitude when crossing 23.4°N was not statistically repeatable (Stanley et al. 2012). Longitudinal studies (i. e., tracking the same individuals in more than one year) using geolocators are logistically difficult because of the short life span of small birds and, thus, the large number of geolocators needed to repeat-track a sufficient sample of individuals. Nevertheless, experimental design that targets repeat-tracking is very important for addressing questions about phenotypic plasticity.

Geolocators have also revealed that some species take very long stopovers (Bächler et al. 2010, Stutchbury et al. 2011, Åkesson et al. 2012, Tøttrup et al.

2012b; Table 1); these long stops exceed the time for migratory refuelling expected on the basis of energetic models (Alerstam 1991). Studies of stopover ecology predict that food-rich sites will reduce stopover duration because birds can refuel faster and resume migration (Newton 2008), but geolocators have led to a new perspective on stopover ecology. In fact, the discovery (using geolocators) of these extended stopovers has called into question the definition of stopover, and researchers have made the case that stops longer than needed to refuel should be considered short-term residency periods that are as important for conservation as breeding and wintering periods (Stach et al. 2012, Tøttrup et al. 2012b).

Prolonged stopovers at sites with abundant food could be favoured if they improve migratory performance or condition on arrival at breeding sites (Newton 2008, Klaassen et al. 2011). Both Swainson's Thrushes and Red-eyed Vireos are omnivorous and commonly feed on fruit, a resource that is consumed by many migrants at tropical sites before and during spring migration (Blake and Loiselle 1992). Long stationary periods during spring migration in both of these species (Delmore et al. 2012, Callo et al. 2013) could be driven by high fruit availability en route. These sites may be important staging areas for refuelling for subsequent migration, as in shorebirds, but this remains to be investigated.

### **Multiple winter sites**

Another surprising discovery made with geolocators is the documentation of intratropical migrations of long-distance migratory birds within their winter range (Table 1-1). Although there was evidence that some species are "itinerant" in winter (Newton 2008), data from geolocators suggest that multiple distinct residency

periods in winter may be fairly common (Table 1-1). For example, two-thirds of Purple Martins occupied more than one long-term winter site, and some individuals had up to four distinct sites  $\leq 1,400$  km apart (Fraser et al. 2012). Intratropical movements complicate connectivity studies because the degree of connectivity with breeding areas could change over the non-breeding season as birds shift locations.

The discovery of multiple wintering sites is important for conservation and management of species at risk. Without direct tracking, these sites and the connections between them and links to breeding sites would remain unknown. Determining the year-round and full extent of habitat use is key in effective reserve design, as illustrated by a study of the Resplendent Quetzal (*Pharomachrus mocinno*); direct tracking revealed that birds spent most of their time at sites outside of reserves (Powell and Bjork 1995). Multiple non-breeding sites for temperate-breeding birds in the tropics can be compared to the more widely recognized intratropical and elevational migration of tropical species (Faaborg et al. 2010b) to determine why this pattern is evident in some species or individuals and not others.

### **Migration schedules**

Prior to the deployment of light-level geolocators on small songbirds, migration timing en route was estimated using mean passage dates between two or more points on migration (e.g., Marra et al. 2005, Tøttrup et al. 2008). One limitation of this approach is that multiple populations of birds are being measured and, hence, temporal changes within populations are not known (Newton 2008). Using this technique, actual migration rate ( $\text{km day}^{-1}$ ) of individuals cannot be calculated.

Mark-recapture is a second method used to obtain migration rates, wherein birds are banded in one location and recaptured in another (Fransson 1995). A limitation is that exactly when birds departed or arrived at each location is unknown, which influences estimates of migration rates, and such data are rare for many species and reveal only a snapshot of migration. Despite location error associated with geolocator tracking, geolocators currently provide the most accurate method to measure the specific migration rate of individual birds from start to finish and during both spring and fall migration. In this case, migration “rate” includes stopovers and flight days or nights and is usually calculated using overall migration duration divided by the number of days spent on migration. Specific migratory flight speed requires precise knowledge of stopover timing and migratory routes and is more easily obtained using geolocators for species that inhabit open landscapes with clear light data, such as the Purple Martin.

The first geolocator study of a songbird showed that migration rate, particularly in spring, was much faster than previously estimated using other methods (Stutchbury et al. 2009). Some Purple Martins travelled from South America to the northern United States at 500–600 km day<sup>-1</sup>, and Wood Thrushes returned from Central America at 250 km day<sup>-1</sup>, whereas previous estimates for spring migration pace in songbirds were 50–150 km day<sup>-1</sup> (Newton 2008). Subsequent studies using geolocators have confirmed that many species typically travel >200 km day<sup>-1</sup> on spring migration (Fig. 3). It has been hypothesized that birds travelling greater distances will migrate at a faster rate (Newton 2008). Using data from Table 1, we compared migration pace in spring and fall with migration

distance using a linear regression (R Development Core Team 2011) and found no relationship (spring:  $r^2 = 0.024$ ,  $P = 0.28$ ; fall:  $r^2 = -0.019$ ,  $P = 0.40$ ). We also tested the hypothesis that body size is related to pace, with larger birds travelling faster (Newton 2008), but larger birds did not migrate faster than smaller birds (spring:  $r^2 = -0.030$ ,  $P = 0.44$ ; fall:  $r^2 = -0.060$ ,  $P = 0.65$ ).

With direct tracking, we can also compare both spring and fall migration rates of individual birds and species for the first time (Fig. 1-3). Using a paired  $t$ -test, we found that spring migration rate is significantly faster than fall rate, by species ( $t = 2.88$ ,  $df = 12$ ,  $P = 0.01$ ). Many factors can influence migration speeds or rates, but it is generally predicted that birds migrate at greater rates when they are under greater pressure of time to reach their destinations (Newton 2008, Tøttrup et al. 2012b). However, the associated fitness benefits of early arrival in spring do not necessarily predict faster migration rate, because birds may also achieve earlier arrival at breeding areas by leaving tropical wintering sites earlier. Departure date from overwintering areas is, in many cases, the strongest predictor of arrival date at breeding sites, with differences in rate en route between individuals contributing relatively little to variation in arrival dates (Stanley et al. 2012, Tøttrup et al. 2012b, Callo et al. 2013, Jahn et al. 2013a). With more geolocator studies, we will be able to answer the question of what ecological factors select for a fast (e.g., Purple Martin and Wood Thrush) or a slow (e.g., Red-eyed Vireo and Swainson's Thrush) rate of spring migration.



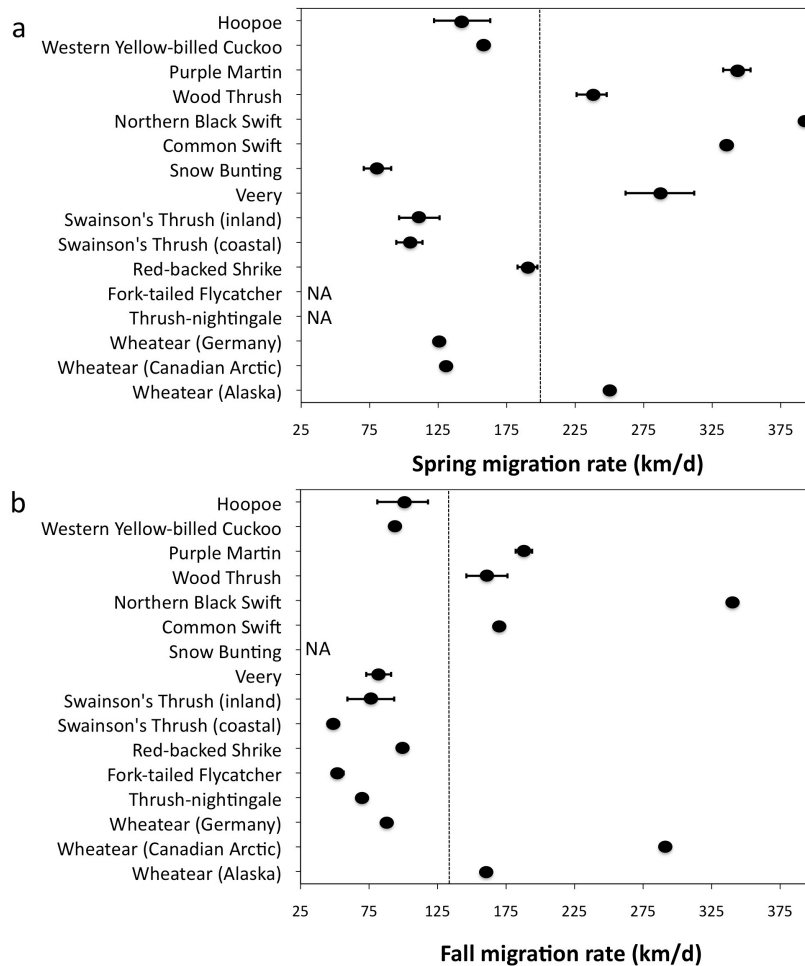


Figure 1-3 (A) Average ( $\pm$  SE where available) spring migration rate ( $n = 13$  species) and (B) fall migration rate ( $n = 15$ ) for birds tracked using geolocators, in order of decreasing average body mass. Dashed lines indicate mean values ( $206 \text{ km day}^{-1}$  for spring and  $135 \text{ km day}^{-1}$  for fall). Data points without error bars are from papers that did not report standard error or full data sets, with the exception of the Canadian Arctic Wheatear and Western Yellow-billed Cuckoo, which represent single individuals. Sample sizes (spring and fall, if different): Eurasian Hoopoe,  $n = 2$ ; Western Yellow-billed Cuckoo,  $n = 1$ ; Purple Martin,  $n = 84, 89$ ; Wood Thrush,  $n = 61, 28$ ; Northern Black Swift,  $n = 3$ ; Common Swift,  $n = 6$ ; Snow Bunting,  $n = 11$  (spring only); Veery,  $n = 5$ ; Swainson's Thrush (inland),  $n = 4$ ; Swainson's Thrush (coastal),  $n = 4, 5$ ; Red-backed Shrike,  $n = 9$ ; Fork-tailed Flycatcher,  $n = 5$  (fall only); Thrush Nightingale,  $n = 2$  (fall only); Northern Wheatear (Germany),  $n = 5$ ; Northern Wheatear (Canadian Arctic),  $n = 1$ ; Northern Wheatear (Alaska),  $n = 3$ .

It will also be important to establish what ecological or genetic factors constrain spring departure date and, thus, prevent individuals from departing early. Constraints on departure date may be related to habitat moisture gradients and associated insect abundance (Smith et al. 2011, Studds and Marra 2011). It is now possible, with geolocators, to test how individual condition and habitat quality, measured at wintering sites, affect not only departure date but also subsequent spring migration rate and arrival date. Fall migration departure and rate also remain largely un-investigated; moult and food availability in late summer are likely major predictors of fall migration strategy for some species (e.g., *Tyrannus* spp.; Jahn et al. 2013a).

We can also use geolocators to examine the relative flexibility of timing of migration. It is much debated whether birds can mount flexible responses to conditions at wintering sites or on migration, or whether these are mostly under endogenous control (Knudsen et al. 2011). This is important to determine, particularly in the context of climate change, because population declines can be expected when timing of migration does not keep pace with warming trends (Both et al. 2006). Using geolocators to track the same individual Wood Thrushes in multiple years revealed high repeatability in timing of spring migration, with individuals departing tropical non-breeding sites, on average, within 3 days of themselves in different years (Stanley et al. 2012). Such consistency of migration timing suggests that we might expect little individual flexibility in the migration schedules of some species and the strong influence of endogenous routines. By contrast, both Red-backed Shrikes and Thrush Nightingales were found to delay

their spring arrival date at European breeding sites; geolocator tracking revealed that this was in response to an extensive drought and a prolonged stopover by the birds at a major stopover site in the Horn of Africa (Tøttrup et al. 2012a). This suggests that extreme weather events may induce changes in migration strategy. Heritability of departure timing, and of other migration traits, could be established via tracking of parents and offspring, but with geolocators would require large deployments and a species with high natal return rates.

### **Future research using geolocators**

Geolocators have revealed the first detailed start-to-finish migrations of small landbirds. Although many studies are based on small sample sizes, they have nevertheless revealed surprises such as very prolonged stopovers in fall and spring, intratropical movements, and very rapid migration rate (Table 1-1 and Fig. 1-3). The growing number of direct-tracking studies will allow for novel comparative studies to test predictions for the ecological correlates that drive the evolution of these traits. Larger sample sizes for individual species will also allow more hypothesis-testing and information-theoretic approaches to explore migration behaviour (e.g., Stutchbury et al. 2011, Stanley et al. 2012) and conservation (Fraser et al. 2012).

**Optimal migration theory** Optimal migration theory provides a predictive framework that can be tested using data from individual tracks of small migratory birds. Alerstam (2011) outlined the major areas where optimal migration theory could be applied, namely flight speed, fuel deposition, response to predation risk, stopover use, transition from migration to breeding, routes, timing (daily budgets and arrival timing), foraging and migration, wind (selectivity and drift), phenotypic

flexibility, and moult schedules. For example, optimal migration theory can be used to predict duration and frequency of stopovers or which route birds should take to minimize energetic costs.

Schmaljohann et al. (2012b) applied optimal migration theory to study the migratory schedules and routes of Northern Wheatears tracked using geolocators. In fall, the birds' ratio of flight to stopover days corresponded almost exactly with theoretical predictions, and the birds also responded to wind and air pressure in a manner consistent with theory. However, contrary to optimal migration theory, Northern Wheatears did not migrate using the shortest routes between breeding and winter sites, and in spring they did not respond to environmental factors such as wind and temperature during migration. Unexpectedly prolonged fall and spring stopovers observed in other studies (see above and Table 1) also do not conform to optimal migration theory. Small migratory birds seem to be breaking "the rules" in many respects, which will launch a re-examination of what constrains the rate of migration and drives stopover duration. A limitation is that geolocators can produce data only for survivors and, thus, it is not yet possible to understand fatal errors in migration strategy.

**Sex and age patterns in migration** Different sex- and age-specific migratory strategies could be linked to differential migration risks and energetic costs for some demographic groups, with implications for our understanding of population dynamics and applications for conservation management. Tracking of males and females allows for tests of proximate factors that drive well-known patterns such as protandry in spring migration (Coppack and Pulido 2009), as well as little-studied

patterns such as protogyny in fall (Mills 2005). Tracking of juvenile birds on their first fall migration (i.e., from the nestling stage) is currently impractical (Thorup et al. 2007) because natal return rates are poor in most species, but tracking of first spring migration is more tenable. Working in the wintering sites of migratory birds allows the deployment of geolocators on hatch-year birds before their first spring migration and makes it possible to do field tests of hypotheses related to navigation and orientation of juvenile versus adult migratory birds. As expected, Wood Thrushes tracked on their first spring migration departed later from the tropics and arrived later to breeding sites than adults (Stanley et al. 2012); however, the details of juvenile versus adult migration tracks (including stopover behaviour, flight speed or rate, and migratory route) have yet to be examined using geolocators.

**Ecological correlates of major stopovers and intratropical movements** Now that multiple winter sites and prolonged stopovers have been documented in many species (Table 1-1), hypotheses related to the causes and consequences of these behaviours can be tested. Renfrew et al. (2013) provided direct evidence that large-scale intratropical movements of Bobolinks corresponded to changes in primary productivity within their non-breeding range. Heckscher et al. (2011) noted potential links between seasonal rainfall, flooding, and intratropical movement of Veeries and speculated that individuals may be responding to this predictable seasonal change in resources. Stach et al. (2012) found a positive correlation between rainfall and intratropical movement of Thrush Nightingales, which suggests that birds are tracking high-quality habitat or food resources as they relocate throughout the winter. It has been proposed that rainfall may explain

wintering movements of an austral migrant, the Fork-tailed Flycatcher (Jahn et al. 2013b), and of the Neotropical migrants Eastern and Western kingbirds (Jahn et al. 2013a). These hypotheses are testable by comparing weather patterns and bird movements using online tools provided by Movebank (see Acknowledgments; Bridge et al. 2011, Kranstauber et al. 2011). The utility of this database was illustrated by a comparison of Northern Wheatear movements with wind and air pressure (Schmaljohann et al. 2012b). Future studies should consider the advantages of Movebank, which include long-term data storage and spatial analysis capabilities, as well as making tracking data available to the public for educational or research purposes. Thus, Movebank can facilitate collaborative studies to test hypotheses regarding interspecific and geographic differences in migration strategy.

Åkesson et al. (2012) noted a large westward detour in the spring migration route of Common Swifts tracked using geolocators; they hypothesized that this detour capitalized on the emergence of insect prey in a small area of Liberia before the birds crossed the Sahara desert. An index of food availability in Northwest Africa (vegetation greenness) did not explain autumn stopovers in Common Redstarts (Kristensen et al. 2013). Other long stopover areas may be important sites for moult (Barry et al. 2009, Jahn et al. 2013a). Macdonald et al. (2012) proposed that long spring stopovers in Snow Buntings might be “muster” points where birds gather to forage in large groups to reduce predation by migrating Peregrine Falcons (*Falco peregrinus*). As with multiple winter sites, understanding the environmental and behavioural correlates of major stopovers for migratory birds will inform conservation and management strategies for migratory species and will require on-

the-ground studies at these newly identified sites to assess food supply, extent of moult, and predation risk.

**Geolocators as a conservation tool** As connectivity maps are developed for more species, it will be important to model the effects of these spatial connections and patterns in habitat loss (or other threats) on population dynamics (Taylor and Norris 2010). Direct tracking and associated migratory-connectivity mapping can also allow us to determine connections between breeding population trends and distant habitat use in the non-breeding season to test hypotheses that relate population decline to non-breeding habitat (e.g., Fraser et al. 2012). Webster et al. (2002) predicted that birds with strong connectivity would be more vulnerable to climate change than those with weak connectivity patterns because they are likely to contain little genetic variation, reducing their ability to undergo an evolutionary response to a warmer climate. Strong connectivity also increases vulnerability of species to habitat loss and environmental change on the wintering grounds because populations connected to areas with high rates of winter habitat loss will have relatively few individuals arriving from other intact wintering sites to buffer breeding populations from severe declines (Marra et al. 2006). For the first time, geolocators allow links between populations to be mapped so that demographics (e.g., breeding success and survival) can be measured at the breeding and wintering grounds of the same population to understand what drives population dynamics and to take conservation action at both breeding and wintering sites of the same population.

The biannual migrations of small landbirds are thought to be the most “risky”

part of the annual cycle; in one species, mark–recapture data estimated that 85% of annual adult mortality occurred during migration (Sillett and Holmes 2002). Understanding where mortality occurs during migration, and why, is a critical conservation need. Geolocators cannot provide information on birds that do not survive migration, but birds that survive provide data on where and when individuals migrate and which areas are migration bottlenecks. For example, many Wood Thrushes enter the United States in spring through a very narrow range of longitude near coastal Louisiana (Stutchbury et al. 2009, Stanley et al. 2012), which suggests that this site is important for conservation of this declining species. All 10 Red-eyed Vireos tracked by Callo et al. (2013) also made landfall in this small area of Louisiana, and Tree Swallows (*Tachycineta bicolor*) from three widely separated breeding populations also shared a long stopover in this region (Laughlin et al. 2013). We can also now compare migration routes of widely separated populations and quantify the severity and nature of threats (e.g., urbanization, habitat loss, communication towers, wind turbines, and pesticide application). For example, a crucial staging area for Bobolinks, identified using geolocators, coincides with an area in northern Venezuela where seed-eating birds have been intentionally poisoned (Renfrew et al. 2013). We can also test whether migration distance is positively correlated with mortality, as is often assumed (Faaborg et al. 2010a, Taylor and Norris 2010).

## **Conclusion**

A new era of bird migration research has been launched with the use of miniaturized geolocators. The newest geolocators are small enough (0.5 g), in



theory, to be deployed safely on large warblers, so the taxonomic scope of migration data is broadening each year. Despite small sample sizes, geolocators have already changed major assumptions about migratory connectivity, migration routes, non-breeding sites, and migration timing. For example, a sample size of six geolocator returns for the Common Swift revealed more information about migration and non-breeding sites for this species than 100 years of bird banding (Åkesson et al. 2012).

Researchers should be encouraged that many of the hypotheses now testable using geolocators will also be applicable to studies using other direct-tracking technology. Aside from providing new testable hypotheses and fascinating questions, data from geolocators have provided a breakthrough for conservation of declining long-distance migratory birds. Until recently, conservation of migratory landbirds was limited by the “black box” of the migration period (Faaborg et al. 2010a). Now managers have an excellent tool for determining year-round habitat requirements of vulnerable species (e.g., Beason et al. 2012, Macdonald et al. 2012) and for testing hypotheses related to threats during the non-breeding season (Fraser et al. 2012).

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Fig. 1.1 photo credits: Red-eyed Vireo, Wood Thrush, Veery: L. Elliot; Swainson's Thrush: D. Irwin; Red-backed Shrike: P. Eckberg; Purple Martin, Fork-tailed Flycatcher: H. Stiver; Yellow-billed Cuckoo: K. Mann; Snow Bunting: S. Descamps; Northern Black Swift: S. Daly; Common Swift: S. James; Hoopoe, Northern Wheatear, Thrush Nightingale – M. Willemoes-Kristensen. We thank participants in the 2012

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## **Chapter 2 Tracking from the Tropics reveals behaviour of juvenile songbirds on their first spring migration<sup>2</sup>**

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## Abstract

Juvenile songbirds on spring migration travel from tropical wintering sites to temperate breeding destinations thousands of kilometres away, with no prior experience to guide them. We aimed to provide a first glimpse at the migration timing, routes, and stopover behaviour of juvenile wood thrushes (*Hylocichla mustelina*) on their inaugural spring migration by using miniaturized archival geolocators to track them from Central America to the U.S. and Canada. We found significant differences between the timing of juvenile migration and that of more experienced adults: juveniles not only departed later from tropical wintering sites relative to adults, they became progressively later as they moved northwards. The increasing delay was driven by more frequent short stops by juveniles along their migration route, particularly in the U. S. as they got closer to breeding sites. Surprisingly, juveniles were just as likely as adults to cross the Gulf of Mexico, an open-water crossing of 800-1000km, and migration route at the Gulf was not significantly different for juveniles relative to adults. To determine if the later departure of juveniles was related to poor body condition in winter relative to adults, we examined percent lean body mass, fat scores, and pectoral muscle scores of juvenile versus adult birds at a wintering site in Belize. We found no age-related differences in body condition. Later migration timing of juveniles relative to adults could be an adaptive strategy (as opposed to condition-dependent) to avoid the high costs of fast migration and competition for breeding territories with experienced and larger adults. We did find significant differences in wing size between adults and juveniles, which could contribute to lower flight efficiency of juveniles and thus slower overall migration speed. We provide the first step towards

understanding the ‘black box’ of juvenile songbird migration by documenting their migration timing and en route performance.

## **Introduction**

Optimal migration timing and stopover habitat selection are critical for migratory animals, since mistiming their migration relative to peaks in resource abundance at breeding sites can have negative fitness consequences [1-4]. Mismatched migration timing, e. g. making landfall in resource-poor stopover habitat, can also affect survival during migration itself [5], or have non-lethal carry-over effects that influence subsequent breeding success [6]. For songbirds exhibiting loop-migration, where spring and fall routes are distinct, first-time spring migrants must navigate along a novel route to an unknown breeding site. The migration strategies of juvenile birds during this critical life history phase have been elusive. Laboratory studies and displacement experiments have provided insights into how navigational systems of juvenile birds develop over time [7,8], but free-living juvenile songbirds have never been tracked on spring migration from start-to-finish to examine spatial and temporal patterns of migration behaviour. Differences in spring migration between adult and juvenile birds, such as the number and duration of stopovers, migratory routes, and migration timing along the route, have not been studied [9]. Recent innovations in tracking technology [10] provide the first opportunity to examine full-journey spring migration of juvenile songbirds. Now it is possible to track juvenile birds from their first wintering site in the tropics to their first temperate breeding site.

Juvenile birds nearly always arrive at breeding sites later than adults [11-13]. Late arrival at breeding sites can result in reduced pairing and mating opportunities [6], reduced access to high-quality breeding territories [14], and reduced opportunities to re-

nest after predation [15]. Late-arriving birds may find breeding territories saturated upon arrival [16], leading to breeding dispersal or settlement in poor-quality habitat. The mechanisms for delayed juvenile arrival in spring remain elusive because most birds can only be studied at a single point on migration, without knowledge of final breeding destinations or non-breeding origin [17]. Juvenile recruitment to breeding areas has been highlighted as a major contributing factor to population dynamics in some species [18], and for one migratory songbird, most mortality occurs during migration [19].

The objective of this study was to quantify the first spring migrations of juvenile wood thrushes (*Hylocichla mustelina*) tracked by using light-level geolocators from two wintering sites (Belize and Costa Rica,  $n = 17$ ) and compare them with adult migrations originating at the same sites ( $n = 30$ ). Spring and fall migrations in wood thrushes occur along significantly different routes ('loop migration') [20]; therefore, spring migration route is truly novel for juvenile birds. Adult wood thrushes return in spring to their breeding sites, often the same territories, as in previous years. Juveniles return to their natal region, but only rarely to their hatching site. Therefore adults have experience travelling their spring migration routes, and can recognize and home in on their exact breeding territory from previous year(s). In contrast, juveniles have only a general map of where they were hatched; the specifics of the migration route and their final destination are unknown.

Migration behaviour of adults and juveniles is predicted to differ in several important ways. There are two over-arching hypotheses that account for age-related differences in migration. The first hypothesis posits that juveniles are sub-par competitors/foragers and thus unable to attain sufficient fuel reserves for migration as

early, quickly, or efficiently as adults. This hypothesis leads to the prediction that juveniles would depart later than adults from winter sites. Most wood thrushes fly across the Gulf of Mexico (800-1000km) in spring, which is predicted to be the most energetically efficient route [21]. However, birds in poor condition are thought to avoid this risky open-water flight altogether by travelling the longer, over-land route [22]. Therefore, we predict that juveniles will be more likely to go around the Gulf than fly across owing to poor condition. Juveniles may also have lower foraging efficiency at migratory stopover sites [23,24] and/or lower flight efficiency owing to differences in wing morphology [25-27], and we therefore predict they will have longer and/or more frequent migratory stopovers relative to adults.

A second, non-mutually exclusive hypothesis is that juveniles have an optimal migration strategy that differs from the optimal migration strategy of adults. Game-theory models support the idea that when costs of arriving early at breeding sites are high (e.g. low chance of defending/acquiring a territory, high risk of mortality in early spring), then it could be adaptive to arrive later [16]. This hypothesis predicts that juveniles would depart consistently later on migration, regardless of condition/foraging ability, owing to an endogenous program that differs from that of adults. Birds have been shown to have endogenous programs with respect to migration preparation (lipogenesis), orientation, and even migration distance [28]. For trans-continental migrants, spring departure is presumed to be endogenously controlled [29]. It has also been shown that the experience of fall migration changes the brains of juvenile migratory birds [30], suggesting that by spring migration juveniles may be more similar to adults in their innate ability to migrate. Thus any differences in migration strategy of juveniles and adults in spring may be a result of different endogenous programs, as opposed to innate migratory ability. An age-related

‘adaptive migratory syndrome’ could function in a similar way to different endogenous programs of geographically separated subspecies which result in some populations exhibiting migration behaviour at different times or for different durations [31].

## **Materials and methods**

**Ethics Statement** Permits from the Belize Forestry Department and the Costa Rican MINAE were obtained for all research, and the York University Animal Care Committee (York University, in Toronto, Ontario), approved bird handling and research protocols.

Wood thrushes were captured at two privately owned research stations in Central America: Belize Foundation for Research and Environmental Education (BFREE) in the Toledo District of southern Belize (16.5°N, 88.7°W), and La Selva Biological Station (operated by the Organization for Tropical Studies) in Costa Rica (10.4°N, 84.0°W). Birds were captured in arrays of 10-20 mistnets (36 mm mesh, 12 x 2 m), either passively, or by attracting birds to nets using wood thrush song and call audio playback. Once captured, birds were given a unique numbered metal band and a combination of colored leg bands. Since wood thrushes are sexually monomorphic during the non-breeding season, we collected a 50 µl blood sample by brachial venipuncture for genetic sexing. Blood was stored in Queen’s Lysis Buffer at 4°C, or air-dried on filter paper and stored at room temperature (24°C) until DNA extraction in the laboratory 4-6 months later. We also collected 1 tail feather and 3-4 breast feathers as back-up DNA samples. While in the hand, birds were aged as juveniles or adults following plumage characteristics described by Pyle [32]. We took digital photographs of age-specific characters of the wing and tail of each

bird. Individuals with ambiguous plumage characteristics were not included in age-specific analyses.

Most captured wood thrushes received a geolocator backpack (n=355 deployed from 2010-2013), attached by custom-fitting a Teflon ribbon leg-loop harness. Geolocators weighed 1.6g (British Antarctic Survey/Biotrack), and including the harness, < 2g. Stalk length for the geolocator was 10mm in 2010, and 20mm in all other years, with an angle of ~15°. The entire backpack (geolocator plus harness) was equivalent to approximately 4% of the body weight of the average wood thrush (mean weight:  $46.50 \pm 0.19\text{g}$ ,  $n = 479$ ). Body weight did not differ between tagged birds and non-tagged birds, or between adults and juveniles. At our study site in Belize, mean weight of geolocator-tagged adults was  $45.95 \pm 0.39\text{g}$  ( $n = 87$ ), and mean weight of tagged juveniles was  $46.07 \pm 0.36\text{g}$  ( $n = 115$ ). Return rates of geolocator-tagged birds varied by year but did not differ from return rates of banded-only birds (overall 20% average return rate) [33]. A recent study documented possible effects of geolocators on migration and other behaviors of a small songbird [34]. Since we cannot directly compare the spring migration of backpack-wearing birds with controls (whose migration cannot be determined), we examined repeat captures of birds within the same winter in Belize, and compared body condition of birds that received geolocators ( $n = 15$ ) and those that did not receive geolocators ( $n=10$ ), to assess if the backpack was associated with lower body condition prior to migration. We found no significant difference between geolocator and non-geolocator birds in the seasonal change in percent lean body mass (see below for methods) (Fig. 2-4 A-C). Body condition of all individuals was higher in the wet season (Oct-Dec) and significantly lower in the dry season (Jan-Apr) (Fig. 2-4D). We also examined return rates of juvenile birds with and



without geolocators at our study site in Belize. Return rate of banded-only juveniles was 9% (12 of 133), while return rate of geolocator-wearing juvenile birds was 8% (6 of 74). This difference was not statistically significant (Pearson's chi-squared test,  $P = 1.0$ ).

**Geolocator returns and analyses.** We retrieved 62 geolocators from returning wood thrushes between 2010 and 2013. Five geolocators failed to record any data. Ten individuals were tracked in multiple years, either as a result of repeated geolocator deployments ( $n = 8$ ) or because they were recaptured after carrying their geolocator for 2 years ( $n = 2$ ). We preferentially used the first migrations of repeat-track birds, if available, and omitted from analysis any migration data from the additional year. Our final sample size was 47 spring migration tracks from different individuals; 17 from juveniles on their first spring migration and 30 from adults. For most birds (83% of adults and 88% of juveniles) we were able to determine the entire spring migration route. Some variables could not be measured for a given individual due to poor-quality light data, or where geolocators failed before recording the entire migration, therefore sample size varies depending upon the variable of interest from  $n = 15$ -17 juveniles and  $n = 24$ -30 adults.

To analyze the geolocator light data, we used a threshold approach, calibrated by live ground-truthing at breeding and wintering sites to determine sun elevations [35]. For spring migration, we used a breeding-grounds based sun elevation angle to calibrate locations, following McKinnon et al. [35]. One person (E. A. M.) analyzed spring migrations of all birds independently, and without knowledge of age or sex of the bird, to avoid any observer bias in interpretation of geolocator data. We used ordinal date for all analyses, such that January 1 = 1. We relied primarily on longitude to determine movements of wood thrushes, since it is more reliable and accurate than latitude [36]. Latitudes cannot be

estimated for approximately two weeks pre- and post-vernal equinox. Longitudes that shifted by  $> 2^\circ$  were considered migration movements, except for crossing the Gulf of Mexico, which was evident by a large jump in latitude ( $10-15^\circ$ ), often with little movement in longitude. Gulf crossing occurred  $> 2$  weeks after the vernal equinox (i.e. after 2 April) for all birds.

Timing of migration was determined for each individual at three points: last noon at winter site, timing of crossing into the U.S. (date of first noon across  $23.5^\circ\text{N}$ ) and first noon at breeding site. Stopovers were defined for each individual as two or more consecutive noon fixes that differed by less than  $2^\circ$  in longitude. Two consecutive noons in the same location were considered 1 stopover night (i.e. one night with no migration; wood thrushes are nocturnal migrants). Total stopover nights were summed for each bird, and the location of each stopover was divided into two categories – ‘tropical’ ( $<23.5^\circ\text{N}$ ) or ‘U. S.’ ( $>23.5^\circ\text{N}$ ). We looked specifically at the duration of the last stopover in the tropics and the first stopover in the U. S. to assess if juvenile birds need to stopover for longer before or after the open-water 800-1000km Gulf of Mexico crossing. Since many wood thrushes use the Yucatan peninsula to cross into the temperate breeding region, we used the longitude of entry into the U. S. at the north coast of the Gulf of Mexico to quantify migration route. At this point, approximately  $30^\circ\text{N}$ , wood thrushes have a relatively broad land-base ( $80-95^\circ\text{W}$ ) across which they could enter the U. S. and move to their breeding site. We calculated the average latitude and longitude for June and July for each individual to determine its breeding region. To determine migration speed for each bird, we measured overall spring migration distance by connecting its winter site to each stop, ending at its breeding site, by using straight lines. We then divided distance by the total duration of

migration in days to get overall migration speed (km/d). To determine speed on flight nights only, we divided migration distance by duration minus the number of stop nights.

**Condition and morphology analyses.** To determine if age differences in body condition prior to spring migration could drive differences in migration behavior, we examined the condition of adult and juveniles birds captured during the dry season (Jan-Apr) at our study site in Belize, Central America in 2011 and 2013. For each bird, we recorded mass to the nearest 0.1g using a Pesola spring scale, and measured the right metatarsus bone length (hereafter, 'tarsus') to the nearest 0.1mm using Vernier calipers. One researcher (E. A. M.) conducted all field measurements for consistency. We used tarsus measurements for condition analyses because they were the most significant predictor of fat-free body weight for our dataset, when compared to other linear measurements (bill length, wing length, tail length, or the first principal components calculated from all measurements) [37]. We also recorded fat score (scale of 0-7, based on MoSI protocol [38]), pectoral muscle score (0-2, based on [39]). We regressed weight of birds with fat score of zero (n = 45) against tarsus length to derive the following equation: lean body mass =  $12.34 + 1.03 \times \text{tarsus length}$ . We then used this equation to calculate a 'predicted' lean body mass (PLBM) for each individual based on its tarsus measurement. The difference between actual mass and PLBM was calculated, and converted to a percent relative to PLBM for use as a condition index (%PLBM), following methods by Bayly et al. [40]. We used a general linear model to examine age effects on %PLBM, and included age, sex, and date of capture as factors. We also examined pectoral muscle scores and fat scores by age, including sex and capture date as covariates.

We measured unflattened right wing chord to the nearest mm for adults ( $n = 145$ ) and juvenile ( $n = 191$ ) birds from our study site in Belize. Wing length differed significantly by sex; therefore we tested for differences by age separately for males and females by using t-tests.

**Statistical analyses.** We used general linear models in the program R [41] to determine if age was a significant predictor of spring migration timing (at three points: departure, crossing into the U. S. and arrival at breeding sites) and spring migration route (longitude at entry into the U.S., and migration distance). All full models for migration timing and route included the following independent factors: age, sex, and breeding location (latitude and longitude), as well as an interaction between age and sex. We included breeding destination and sex as factors in the models since birds migrating farther (i.e. to the northern breeding range), and males (which arrive first at breeding sites) are likely to show different migration behavior than birds migrating shorter distances, and females. We also included an interaction term for age and sex to account for potential differences in migration strategy by sex within-age class. We used the function “step” in R to drop terms and determine the best-fit model using AIC values.

For stopover variables we used a different approach to summarize age-related differences, since initial examination of the data revealed no sex or breeding destination effects. We used age as the response variable in a binomial linear regression and used the following stopover variables as independent factors: total stopover nights, stop nights in the U. S., stop nights in the Tropics, mean stopover duration, number of stops, and duration of stopover before Gulf crossing and after gulf crossing. This analysis allowed us to assess which stopover variable was the most different between adults and juveniles (i.e.

significant predictor of age). We also compared stopover variables directly between adults and juveniles using t-tests in order to show the mean differences for each variable. We examined variance in longitude entering the U. S. between adults and juveniles using Fisher's *F* test, and we compared whether or not birds crossed the Gulf of Mexico overwater or took an over-land route by using Fisher's Exact test to determine if juveniles were significantly more likely to go around the gulf than adults. We report means  $\pm$  standard error unless otherwise indicated.

## Results

**Migration timing.** Juveniles departed significantly later from overwintering sites than adults (model estimate for juveniles =  $7.9 \pm 2.9$  d,  $P = 0.009$ ) (Fig. 2-1A), controlling for significant sex and breeding destination effects (Table 2-1). This timing difference was also evident at the U. S. Gulf of Mexico coast, where juveniles also arrived later relative to adults (estimate for juveniles =  $9.02 \pm 2.7$ d,  $P = 0.001$ ) (Fig. 2-1A). Age had the most pronounced effect on timing of arrival at breeding sites (estimate for juveniles =  $13.97 \pm 2.7$ d,  $P < 0.001$ ) (Fig. 2-1A). There was no significant interaction between age and sex for any timing variable.

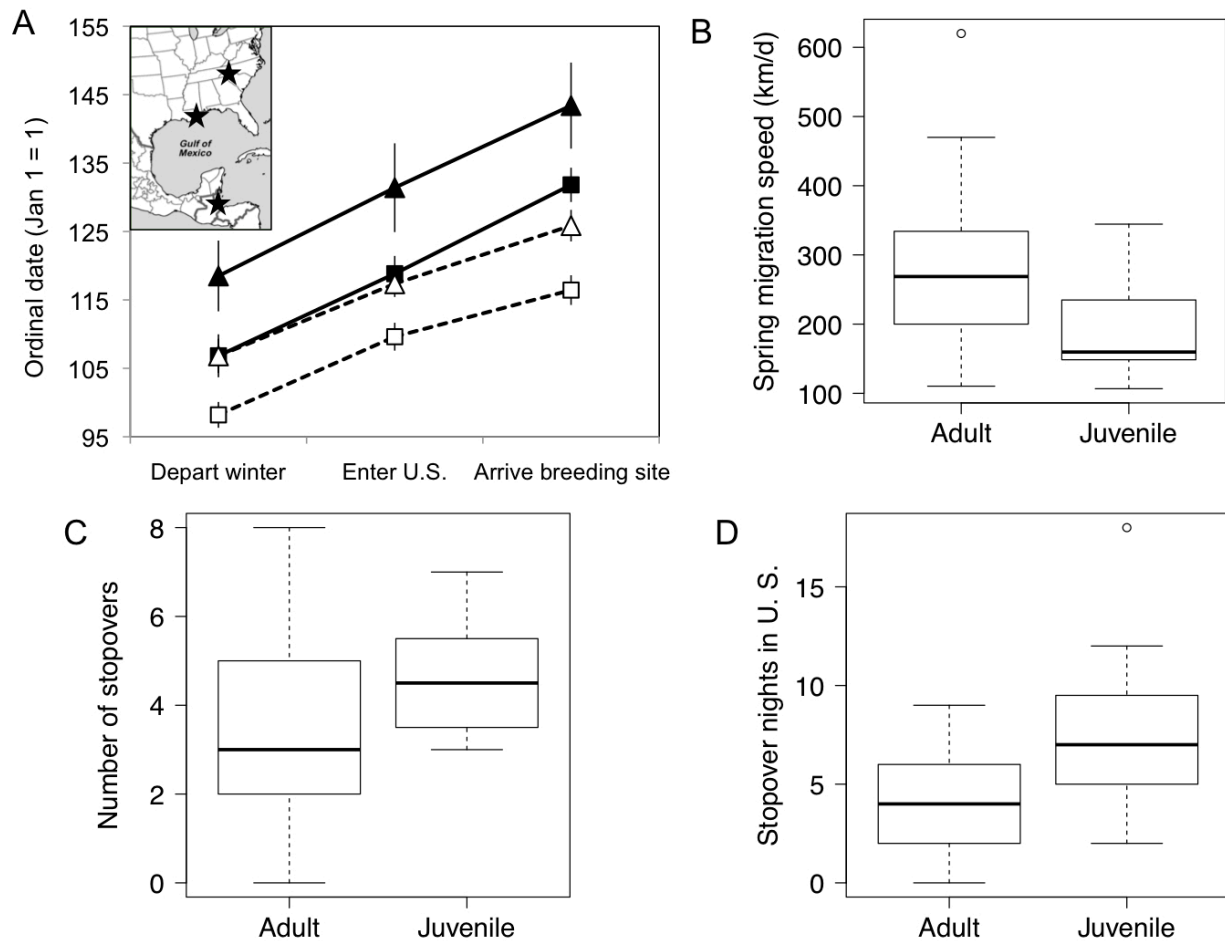


Figure 2-1 Juvenile wood thrushes exhibit a significantly different migration strategy in spring than adults. A) Juveniles (solid symbols) were later than adults (hollow symbols) at winter departure, entering the U. S. along the northern Gulf of Mexico coast, and when arriving at breeding sites. Triangles represent average for females and squares for males. Vertical bars indicate standard error. Inset map shows an example of locations where timing was measured for an individual wood thrush. B) Spring migration speed (total distance/duration) was slower for juvenile wood thrushes. C) Juveniles had more stopovers during spring migration relative to adults, and D) had more stopover nights in the U. S. than adults. Note that 1 stopover night = 2 consecutive noons in the same location. Boxplots extend to 25<sup>th</sup> and 75<sup>th</sup> quartiles with dark lines showing the median value and circles indicating outliers. Sample size is  $n = 17$  for juveniles, and  $n = 30$  for adults, except for winter departure ( $n = 16, 26$ ) migration speed ( $n = 15, 25$ ), and stopovers in the U. S. ( $n = 16, 29$ ).

**Spring migration duration and speed.** Age was the only significant factor retained in the top model for spring migration duration (estimate  $7.73 \pm 2.74$ ,  $t = 2.81$ ,  $P = 0.008$ ) (Table 2-1), indicating that the effect of age on spring migration duration is larger than effects of location of the final destination, or sex of the bird. Juveniles spent, on average, about 8d longer on spring migration than adults (mean  $24.5 \pm 2.5$  d for juveniles versus  $16.8 \pm 1.5$  d for adults). Overall migration speed (calculated as the total distance covered divided by the duration in days) was significantly slower for juveniles ( $191 \pm 18$  km/d) than adults ( $272 \pm 24$  km/d) ( $t = 2.60$ ,  $df = 35.58$ ,  $P = 0.014$ ) (Fig. 2-1B). Migration speed on flight nights only was not significantly different by age (juveniles:  $541 \pm 39$  km/d, adults  $592 \pm 35$  km/d;  $t = 0.98$ ,  $df = 33.04$ ,  $P = 0.33$ ).

**Migratory stopovers.** The only significant factor retained in our binomial linear regression with age as the dependent variable was total number of nights stopped in the U. S. (estimate for juveniles:  $0.94 \pm 0.35$ ,  $z = 2.69$ ,  $P = 0.007$ ). Comparing stopover variables between adults and juveniles using  $t$ -tests revealed that the frequency of stopovers was significantly different by age ( $t = -2.46$ ,  $df = 38.51$ ,  $P = 0.018$ ): juveniles stopped more times ( $4.6 \pm 0.3$ ) than adults ( $3.4 \pm 0.3$ ) (Fig. 2-1C). In contrast, mean stopover duration was not significantly different between adults and juveniles (mean for juveniles:  $3.4 \pm 0.3$  d, mean for adults  $3.2 \pm 0.3$  d;  $t = -0.58$ ,  $df = 35.22$ ,  $P = 0.56$ ). Juvenile birds had more stop nights over the entire migratory journey (juveniles:  $16.2 \pm 2.1$  d, adults:  $10.2 \pm 1.1$  d;  $t = -2.44$ ,  $df = 24.51$ ,  $P = 0.02$ ), and more specifically, more stopover nights in the U. S. (juveniles:  $7.4 \pm 1.0$  d, adults:  $3.9 \pm 0.5$  d;  $t = -3.09$ ,  $df = 21.989$ ,  $P = 0.005$ ) (Fig. 2-2D). There was no significant difference between adults and juveniles in the number of nights spent at stopovers in the

Tropics (juveniles:  $8.8 \pm 2.0d$ , adults:  $6.6 \pm 1.1d$ ) ( $t = -0.90$ ,  $df = 24.61$ ,  $P = 0.38$ ). We found no age-related differences in the duration of the last stopover before the Gulf of Mexico crossing ( $t = -0.08$ ,  $df = 33.97$ ,  $P = 0.93$ ), or in the duration of the first stopover on the U.S. side ( $t = -0.98$ ,  $df = 22.75$ ,  $P = 0.34$ ).

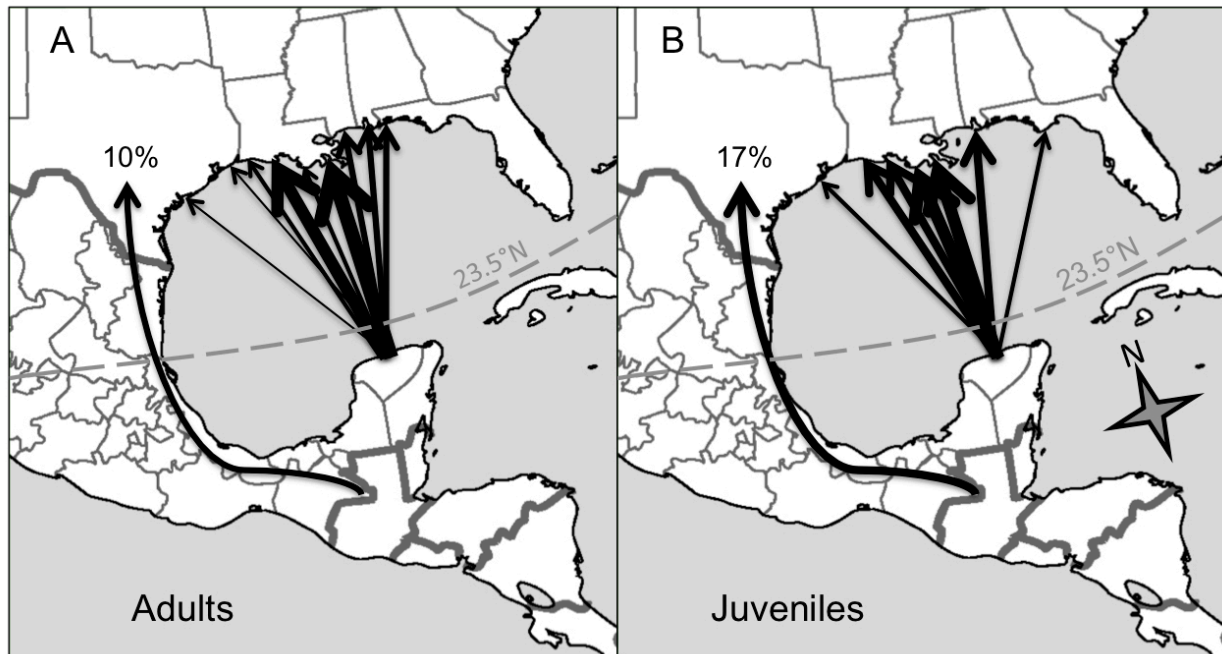


Figure 2-2 Migration routes at the Gulf of Mexico are not significantly different for A) adult ( $n = 30$ ) and B) juvenile ( $n = 17$ ) wood thrushes. Lines point to the longitude on the northern Gulf of Mexico coast where birds made landfall. Thickness of a line is proportional to the percent of birds within age-class using that route. Birds are all shown crossing the Gulf from a single point on the Yucatan peninsula of Mexico for simplicity; there were slight variations in takeoff locations that are not shown here. The arrow around the Gulf indicates the proportion of birds that did not fly directly across but instead used an overland route ( $n = 3$  of 17 juveniles,  $n = 3$  of 30 adults).

**Migration route and destination.** Age was not a significant factor explaining variation in longitude of entering the U. S. (Table 2-1). Since there were no significant effects of



breeding destination or sex on longitude entering U. S., we directly compared the longitude of adults versus juveniles at the point of entry to U. S. by using a t-test, and did not detect a significant difference by age (juveniles:  $91.7 \pm 0.7^\circ\text{W}$ , adults:  $90.6 \pm 0.5^\circ\text{W}$ ;  $t = -1.20$ ,  $df = 30.33$ ,  $P = 0.24$ ) (Fig. 2-2). Variance in longitude entering the U. S. was also not significantly different by age ( $F = 0.80$ ,  $df = 29/16$ ,  $p = 0.58$ ). Migratory distance, controlling for breeding destination, was also not significantly different by age, as would be expected if juveniles took longer routes to get to the same place (Table 2-1). A slightly higher proportion of juveniles avoided crossing the Gulf of Mexico overwater (3 of 17) compared to adults (3 of 30), although this was not significant (Fisher's Exact test,  $P = 0.65$ ) (Fig. 2-1).

**Condition and morphological differences prior to spring migration.** Age was not retained in the top model for percent lean body mass ( $P = 0.23$ ), nor was there a significant interaction between age and date of capture ( $P = 0.22$ ) in Belize. Mean %PLBM for adults was  $3.45 \pm 0.87\%$  and for juveniles  $4.04 \pm 0.73\%$  (Fig. 2-3A). We also did not find age-related differences in two other measures of body condition, pectoral muscle scores ( $F = 2.65$ ,  $P = 0.106$ ) and fat scores ( $F = 1.581$ ,  $P = 0.210$ ) (Fig. 2-3B). Juvenile wood thrushes had significantly shorter wings than adults, within sex-class (females:  $t = 4.95$ ,  $df = 135$ ,  $P < 0.001$ ; males:  $t = 3.78$ ,  $df = 132.39$ ,  $P < 0.001$ ) (Fig. 2-3C).

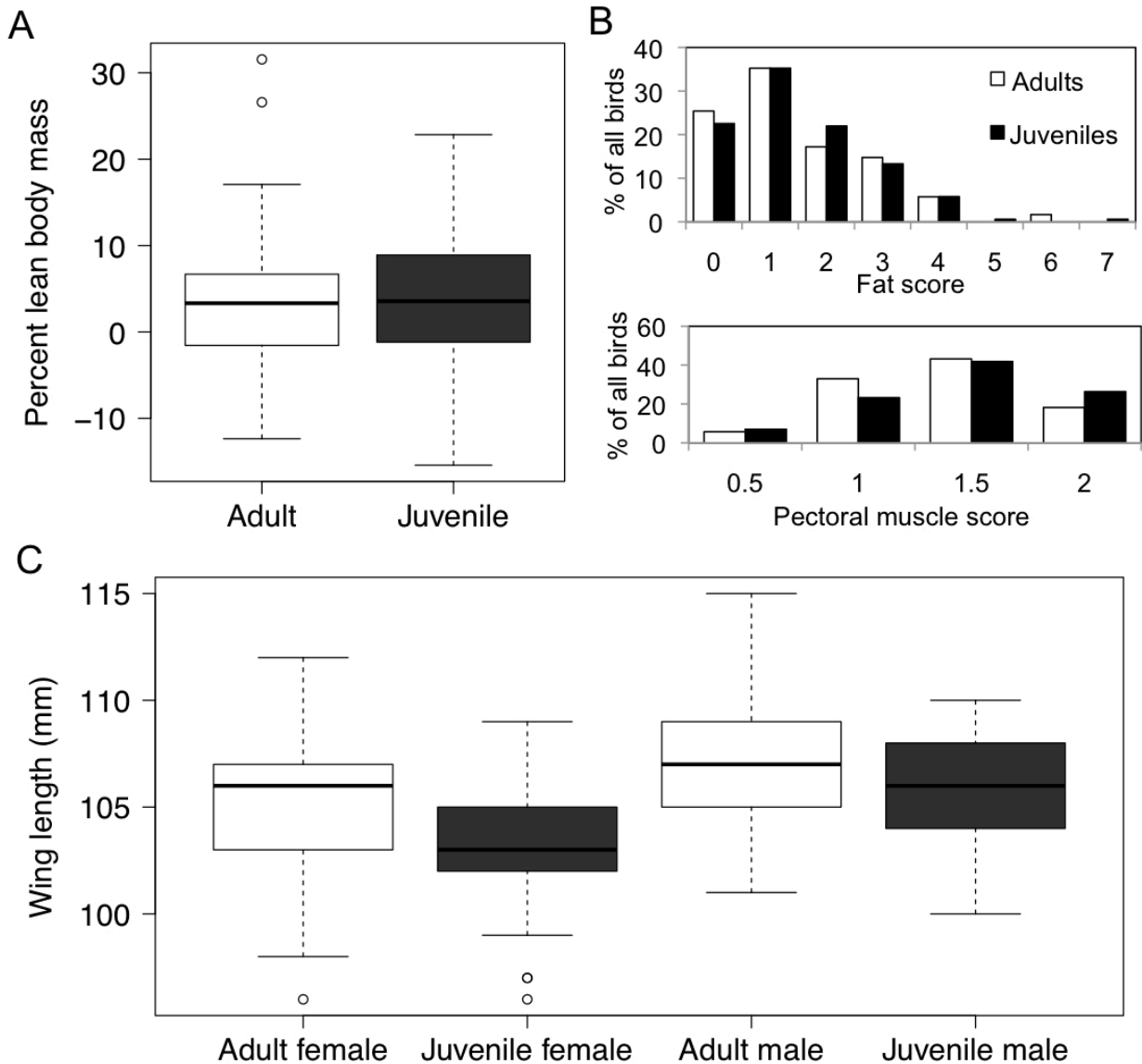


Figure 2-3 Body condition of adult ( $n = 78$ ) and juvenile ( $n = 107$ ) wood thrushes captured in Belize in late winter was not significantly different, but wing length was significantly shorter for juveniles, within sexes. A) Percent lean body mass, and B) fat ( $n = 122$  adults,  $n = 173$  juveniles) and pectoral muscle scores ( $n = 88$  adults,  $n = 129$  juveniles) were not different by age-class. C) Wing length was smallest for juvenile females ( $n = 92$ ), followed by adult females ( $n = 73$ ), juvenile males ( $n = 99$ ), and adult males ( $n = 72$ ). Boxplots show 25<sup>th</sup> to 75<sup>th</sup> quartiles with open circles indicating outliers.

**Table 2-1 Top general linear models that explain variation in spring migration strategy of juvenile and adult wood thrushes.** Letters in brackets indicate the base category for that estimate, i.e. J = juvenile, M = male. Full models for all variables included age, sex, breeding latitude and breeding longitude. We also included an interaction term for age and sex, although it was not significant in any model.

<b>Dependent variable</b>	<b>Factors retained in top model</b>	<b>Estimate <math>\pm</math> standard error</b>	<b>t</b>	<b>P</b>
Spring departure date	Age (J)	7.93 $\pm$ 2.91	2.73	0.009
	Sex (M)	-10.88 $\pm$ 2.89	-3.76	<0.001
	Breeding latitude	0.74 $\pm$ 0.38	1.96	0.057
Spring enter U.S.	Age (J)	9.02 $\pm$ 2.66	3.39	0.001
	Sex (M)	-10.57 $\pm$ 2.53	-4.17	<0.001
	Breeding latitude	1.02 $\pm$ 0.34	2.98	0.005
Breeding arrival date	Age (J)	13.97 $\pm$ 2.66	5.25	<0.001
	Sex (M)	-11.58 $\pm$ 2.53	-4.57	<0.001
	Breeding latitude	1.12 $\pm$ 0.34	3.03	0.002
Spring migration duration	Age (J)	7.73 $\pm$ 2.74	2.81	0.008
Longitude entering N.A.	No significant factors	-	-	-
Spring migration distance	Breeding latitude	79.78 $\pm$ 26.81	2.98	0.002
	Breeding longitude	-107.49 $\pm$ 25.81	-4.16	<0.001
Spring migration speed (distance/ migration duration)	Age (J)	-80.70 $\pm$ 33.99	-2.37	0.023

## Discussion

For the first time, we tracked juvenile songbirds from start-to-finish on their inaugural spring migration and found significant differences in migration strategy between juveniles and adults tracked from the same wintering sites. After accounting for the effects of sex and breeding destination, juveniles were a week later than adults in departing from wintering sites and two weeks later in arriving at breeding sites (Fig. 2-1A). The slower migration speed of juveniles overall (Fig. 2-1B) was the result of juveniles stopping for more nights than adults (Fig. 2-1C, D), which resulted in a ~50% longer spring migration duration for juveniles. Juveniles did not take significantly longer routes, or significantly different migration paths at the Gulf of Mexico, nor were they more likely to go around a major ecological barrier (Fig. 2-2).

Differences in spring migration departure date from the tropics suggest either that juveniles are unable to optimally respond to photoperiod cues in spring, or that they respond to later or different migration initiation cues, relative to adults. Photoperiod may be only one of several synchronizers that entrain endogenous circadian rhythms controlling migratory activities [42]. The availability of food has a large impact on body condition and timing of spring migration of an insectivorous migrant, the American redstart (*Setophaga ruticilla*) [43]. Food-rich habitat (mangrove forest) is monopolized by territorial, dominant adult males [44] and adults precede young birds on spring migration [17], with subsequent carry over effects on breeding success [14]. In wood thrushes, there is no evidence for age-related dominance patterns during the non-breeding season [45]. Nevertheless, juveniles could be less efficient at foraging than adults, resulting in delayed departures for younger birds if they are slower to achieve appropriate levels of fat and

muscle for migration [11]. We did not find evidence of age-related differences in percent lean body mass, fat scores, or pectoral muscle scores, during late winter (Fig 2-3). Our results suggest that age-related differences in condition at winter sites are not driving the overall age patterns in migration timing observed for wood thrushes. However, within-age-class variation in our study was large (range of ~2 weeks in departure dates within age and sex classes), and future studies should examine if this variation could be explained by environmental factors.

Multi-year migration tracking of adult wood thrushes showed that departure date from wintering sites, and arrival date at the breeding site, was repeatable for an individual from one year to the next [46]. We found that first-time spring migrants differ substantially in timing from experienced migrants. This suggests that a shift from “late” to “early” migration strategy occurs at the individual level between the first and second spring migration. An age-dependent shift in migratory orientation and route has been documented in raptors and shorebirds during fall migration [47, 48]. If this difference is not related to body condition of the birds, it is possible that an endogenous timing mechanism is the primary controller of spring migration departure in juveniles. Migration of juveniles in fall is under strong endogenous control [28, 42]. Laboratory studies of migration behaviour (*‘zugunruhe’*) under a constant photoperiod and resource access, similar to recent experiments with Northern wheatears (*Oenanthe oenanthe*) that showed activation of migratory behaviour in males earlier than females [49], would elucidate whether juvenile birds have an innate, later migration program relative to adults.

Arriving later at breeding sites could have evolved as an adaptive strategy for juvenile birds [16]. If there are high costs of migrating early, such as mortality from

inclement weather, or aggressive encounters with older territorial individuals [11, 50, 51], selection may favour a later endogenous program for juveniles to avoid such early-migration risks. Juveniles in general are subdominant to adults in many species, thus they would probably have a low chance at holding a breeding territory when faced with an experienced adult competitor. In rose-breasted grosbeaks (*Pheucticus ludovicianus*), juveniles with more adult-like plumage preceded more typical juvenile-plumage birds on spring migration [52], suggesting that social dominance (signalled by plumage coloration) affected arrival patterns. One scenario supported by both evolutionary and game theory models is a two-wave spring arrival pattern [16, 53], with different costs and benefits for early- versus late-arriving birds. This two-wave pattern could correlate with age, if adult birds arrive in the first peak, and juvenile birds arrive during a second wave. Juveniles could therefore avoid the increased risk of arriving early and spend more time *en route* physiologically preparing for their first breeding season [54].

More stopovers in the U. S. for juveniles (Fig. 2-1C, D) could be explained by a need for more frequent refuelling, if foraging efficiency is lower for juvenile birds [23]. However, some studies at stopover sites have found no evidence for age-related differences in condition [55] or refuelling rates [56]. If juveniles were less efficient at refuelling relative to adults, we would expect to see longer stopover duration or more frequent stopovers over the entire migratory route, as well as longer stops before or after the ~1000-km open-water crossing of the Gulf of Mexico. Our data indicate that juveniles do not stay longer at migration stopover sites than adults (mean duration of stopovers was similar), nor do they spend more time preparing for or recovering from an open-water crossing of ~1000km. It is possible that juveniles stop more frequently in the U. S. because of an adaptive strategy

to conserve or acquire resources for breeding, in contrast to a final 'sprint' migration in which birds exhaust resources in a final push to arrive early [54]. The accuracy of geolocators is currently insufficient for mapping the precise location of stopover sites. If exact stopover locations were known, remote sensing could be used to assess habitat quality of stopover sites for juveniles versus adults. Recently-developed miniature archival GPS loggers, which have a resolution of <1km and can sample up to 50 locations throughout the annual cycle, could be applied to further explore differences (or similarities) between adult and juvenile spring migration stopover behaviour.

Despite the inherent differences in experience between adults and juveniles, we did not detect any age-related differences in spring migration route. Tracking technology for small birds is currently limited in its ability to record fine-scale details of migration route. When higher resolution technology becomes available, age-related differences may become apparent. It is also possible that in wood thrushes, there are no significant differences in migratory routes by age in spring. Migratory birds can display long-distance homing abilities during their first spring migration; displaced juvenile European starlings (*Sturnus vulgaris*) managed to find their way to their natal site even after wintering in the 'wrong' place [8]. In order to navigate 'home' in spring, juveniles birds require a period of familiarization with their natal site before departing on fall migration, which may occur as short nocturnal flights prior to fall migration departure [57]. Thus, in spring, juveniles can use both their innate magnetic compass and navigational homing abilities to reach their destination [58]. We expected juvenile birds to take longer routes, or less risky routes (i.e. around the Gulf of Mexico, instead of across), but this was not the case. Many songbirds take relatively direct routes in spring to minimize time spent on migration and advance

spring arrival dates [59]. It is possible that juveniles and adults have convergent spring migration routes because of prevalent wind and weather patterns at the Gulf in spring and an innate migratory program for when and where to migrate.

Juveniles had significantly shorter wings in our study population. Wing length is related to flight efficiency [25], and it has been hypothesized that juvenile birds trade-off flight speed for maneuverability to avoid predation [26]. We broadly estimated migration speed (or 'rate', [20]) as the total migration distance divided by overall migration duration, following other migration studies [e. g. 60]. Juveniles were significantly slower overall than adults (Fig. 2-1B); however, this appeared to be due to more frequent stopovers taken by juveniles and not slower flight speed on a given night. Thus juveniles are capable of covering the same distance as adults during each migration night. Juveniles might stop more if each flight requires more days of refueling owing to greater energetic costs of flight. Shorter wings of juveniles could lead to less efficient flight. It is important to note that we measured only wing length and not wing shape; relative pointedness is an important component of wing efficiency [25]. It is also possible that adults are better able to select appropriate tail winds and therefore decrease energy expenditure while flying. Finally, it could be that juvenile birds have an innate program to stop more frequently as they approach their breeding region, in order acquire more resources for reproduction [54]. Radio-tracking studies following birds during nightly flights (e.g. [61]) could compare distance, speed, and fuel-use of juveniles versus adults directly to determine exactly how migration differs by age at a scale of a single migratory flight.

Wood thrush populations have declined on average by  $\sim 2\%$ /year over the past 50 years [62]. There is evidence that most mortality in songbirds occurs on migration [19],



and a recent tracking study of raptors showed that mortality during migration (both spring and fall) was six times higher than during stationary periods of the annual cycle [63]. This period could be especially limiting for juvenile birds, which we show spend ~50% more time on spring migration. It is also possible that juvenile birds migrate using a mortality-minimizing strategy, instead of the typical adult time-minimization strategy. Regardless, understanding demographic patterns in migration is a critical step for full-life cycle modelling of migratory species to determine where conservation funds should be prioritized to mitigate further population declines.

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## Supplemental information

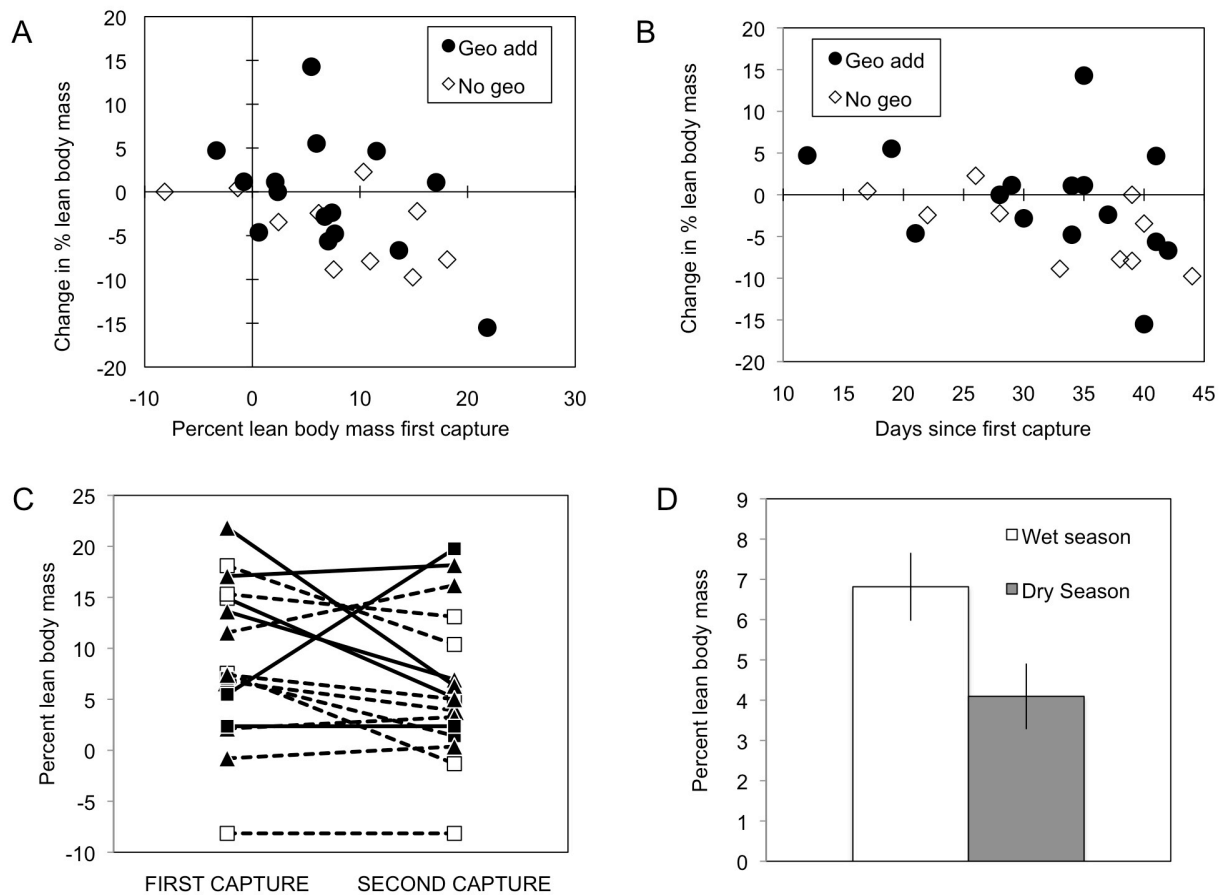


Figure 2-4 Within-winter recaptures of birds wearing geolocators ('Geo add') (n = 15) and those which did not receive a geolocator ('No geo') (n = 10) did not show differences in percent lean body mass. In general, all birds declined in body condition as the winter progressed from wet season (Oct-Dec) to dry season (Jan-Apr). A) Birds that were relatively heavy on first capture tended to lose more mass over time, and the same pattern was shown in both 'Geo add' and 'No geo' groups. B) Birds recaptured after more days tended to decrease slightly more in percent lean body mass, with no effect of geolocators. C) Individual birds showed no consistent pattern in changes in percent lean body mass from first to second capture. Symbols indicate: 'Geo add' (filled), 'No geo' (hollow), males (squares), females (triangles), juveniles (dashed lines), and adults (solid lines). D) Average percent lean body mass of all birds was significantly higher in the wet season (n = 66) relative to the dry season (n = 88) (vertical lines show standard error).



### **Chapter 3 Seasonal change in tropical habitat quality and body condition for a declining migratory songbird, the Wood Thrush**

## **Abstract**

Many Neotropical migratory songbirds spend their non-breeding season in tropical humid forests. Climate change is predicted to increase severity and frequency of droughts, and decrease rainfall in the Neotropics. For conservation of declining migratory songbirds, it is critical to understand how resources during the non-breeding season are affected by seasonal patterns of drying, and thereby predict potential long-term effects of climate change. We studied habitat quality for a declining tropical forest-dwelling songbird, the Wood Thrush, in Belize during their overwintering period (Oct-Apr). We examined habitat moisture, abundance of food resources, and condition of individual birds ( $n = 418$ ) in three habitat types: mature moist forest, disturbed (fragmented) forest, and riparian scrub. We found a strong pattern of habitat drying from early winter (wet season) to late winter (dry season; prior to spring migration) in all habitats, with concurrent declines in arthropod and fruit abundance. This paralleled declining body condition of individual Wood Thrushes. Birds were in the worst condition of the winter as they were about to depart on spring migration, regardless of habitat occupancy. Body condition, fat and muscle scores were significantly higher during the early winter (wet season), and poor condition (low body condition index, low fat and pectoral muscles scores) was equally apparent in all habitat types during late winter (dry season). Our results indicate that late winter dry seasons are particularly challenging, even for a forest-dwelling, omnivorous species. Increased forest drying, through climate change or degradation of tropical forests by fragmentation or logging, is expected to have a negative effect on the condition of individual Wood Thrushes, and may accelerate on-going population declines.

## Introduction

Effective conservation of declining populations of migratory animals requires that we understand when and where they are most limited (Martin et al. 2007, Faaborg et al. 2010). Neotropical migratory songbirds that breed in North America spend most of the year and are more spatially concentrated (Mills 2006) at overwintering sites thousands of kilometres away in the tropics. Ecological factors during the non-breeding period are expected to have a large impact on overall population dynamics (Calvert et al. 2009), but they remain relatively understudied for many species (Faaborg et al. 2010). Winter habitat can affect bird fitness directly by driving within-season mortality, and indirectly, through carry-over effects (Taylor and Norris 2010), where non-lethal consequences of habitat occupancy in winter affect subsequent fitness, either on migration or at breeding sites (Harrison et al. 2011). Predictions of a warmer and drier climate in the Neotropics under various global change scenarios (Neelin et al. 2006, Hidalgo et al. 2013) underline the importance of determining which ecological factors are most important for overwintering migratory birds.

Neotropical migratory birds arrive to Central America at the end of the wet season (~Sep-Nov), when arthropod food resources are relatively abundant (Janzen 1973). As the environment becomes increasingly dry (~Feb-May), plant productivity slows and invertebrate abundance also declines (Sherry and Holmes 1996, Johnson and Sherry 2001, but see Smith and Robertson 2008), particularly in more dry habitats (Smith et al. 2011a). For migratory birds preparing for spring migration during the dry season, accumulating and maintaining adequate levels of pre-migratory fuel (fat) and large flight muscles may be extremely challenging and food can be a major limiting factor (Johnson et al. 2006, Studds

and Marra 2011). Parallel to seasonal ecological changes, overwintering migrants may decline in condition over the non-breeding season (Sherry and Holmes 1996, Strong and Sherry 2000, Johnson et al. 2006), especially in poor-quality habitats (Marra and Holberton 1998).

Two closely related ecological factors in the non-breeding season, arthropod abundance and rainfall, have been identified as important controllers of fitness and carry-over effects for Neotropical migrant songbirds. Several studies have examined the abundance or biomass of arthropods and found correlations with individual condition (Strong and Sherry 2000) and habitat occupancy (Smith et al. 2011a) of migratory songbirds. Territorial movements of Northern Waterthrush (*Parkesia noveboracensis*) over the winter corresponded to declines in arthropods in their original territories, indicating that food becomes more limiting later in winter, especially in more dry habitats (Smith et al. 2011b). Experimental evidence also supports the idea that arthropod abundance limits condition of overwintering Ovenbirds (*Seiurus aurocapillus*) in Jamaica (Brown and Sherry 2006).

Habitat moisture (a correlate of rainfall, mediated by habitat type) is thought to drive patterns of arthropod abundance, which supplies the mechanism for changes in the condition of birds (Studds and Marra 2007, Smith et al. 2010). Indeed in years where moisture is low but arthropod abundance is high, bird condition corresponds best to their prey and not the moisture at the site. Habitat moisture varies on a large scale by habitat type and season. Birds captured at breeding sites can retain a 'signature' of winter habitat occupancy in the ratios of stable-carbon isotopes in their tissues (Norris et al. 2005), since stable carbon isotopes vary predictably with the photosynthetic pathway of plants, and are

incorporated into the tissues of higher-order consumers. Satellite imagery can also be used to assess habitat moisture in the winter range for birds sampled at breeding sites, so that reproductive parameters can be compared to conditions in the previous winter (Saino et al. 2004). Both isotope analysis and remote sensing can be used to infer habitat occupancy in winter when birds are captured on migration or at breeding sites, assuming the winter site is known and the bird is captured before tissue turnover reflects local isotope values.

Research on the wintering grounds has found that habitat moisture correlates well with fitness in at least three migratory warblers, Ovenbird (Brown and Sherry 2006), Northern Waterthrush (Smith et al. 2010), and American Redstart (*Setophaga ruticilla*) (Studds and Marra 2007), although experimental manipulation of moisture at a non-breeding site in Jamaica was unsuccessful in affecting body condition of American Redstarts (Wilson et al. 2013).

Limitation of high-quality overwintering habitat has apparently led to despotic interactions between sex and age classes in several species of migratory songbirds. In American Redstarts, adult males monopolize high-quality wet mangrove habitat, with subsequent positive influences on their condition (Marra and Holberton 1998). Similarly, juvenile birds are often excluded from territories in high-quality habitats, as has been shown in Hooded Warblers (*Setophaga citrina*) (Stutchbury 1994). Therefore, sex and age ratios in different habitats can indicate the relative quality of that habitat. However, it is also possible that different age or sex classes have innate preferences for different habitats (Morton et al. 1987, Morton 1990), or that differential survival of age or sex classes is unrelated to wintering habitat. Regardless, it is important to understand demographic patterns in habitat occupancy for effective conservation of a species as a whole. Preserving

habitat types biased towards one particular sex- or age-class could be ineffective in long-term conservation. For example, conservation of a male- or adult-biased habitat type would be less effective than conservation of a range of habitat types, if populations are limited by the number of breeding females (Freed and Cann 2013), or juvenile survival and recruitment into breeding populations (Saracco et al. 2010).

Most studies to date on habitat quality for non-breeding migrants have focussed on species that consume primarily invertebrates (e.g. American Redstarts). Many migratory songbirds consume fruit or other non-invertebrate prey during non-breeding periods (Blake and Loiselle 1992). Migrants that can consume an alternate food source may be able to offset the costs of declining habitat moisture and arthropod abundance, if the abundance of alternate resources, such as fruit, increases or is sufficient for preparing for spring migration. Local abundance of wintering Yellow-rumped Warblers (*Setophaga coronata*) increased with experimentally increased abundance of fruit (Borgmann et al. 2004). Wood Thrushes (*Hylocichla mustelina*) in Costa Rica appeared to increase their consumption of fruit in late winter (Blake and Loiselle 1992), suggesting that they may be able to prepare for migration on a diet of fruit. Although migratory fuel (fat) can be synthesized from high-lipid fruits (such as *Viburnum dentatum*, ~41% lipids) during fall migration (Smith et al. 2007), for birds that consume both arthropods and other foods, arthropods are often assumed to be the preferred and most nutritious prey. Tropical fruits consumed by small birds tend to be relatively low in protein and lipids (Moermond and Denslow 1985). Wintering Hermit Thrushes (*Catharus guttatus*) preparing for short-distance spring migration accumulated more mass and fat when fed a high-protein diet of arthropods than when fed arthropods and *ad libitum* fruits (Long and Stouffer 2003). Other studies have

suggested that, during the non-breeding season, migrant birds consume arthropods with a high chitin-digestible nutrient ratio, such as ants and beetles, as opposed to more easily digested and nutrient-rich arthropods (Bell 1990, Poulin and Lefebvre 1996), which may increase the relative importance of fruits in the diet. It remains unclear if patterns of resource and bird condition declines through the overwintering period shown in primarily insectivorous species are also true for species with omnivorous diets.

Many overwintering Neotropical migratory songbirds occupy tropical humid forest (Hutto 1980), yet the vast majority of the research on habitat quality for migrants has occurred in relatively rare mangrove-scrub ecotones (e.g. studies of American Redstarts and Northern Waterthrush) (Studds and Marra 2007, Smith et al. 2010) or tropical dry limestone forests or thorn-scrub (e.g. Ovenbirds) (Strong and Sherry 2000, Brown and Sherry 2006). Tropical humid forests in southern Mexico, Central and South America are expected to be more moist overall, and more stable in terms of moisture and arthropod abundance, relative to coastal mangrove and scrub habitat. Forest understorey habitats are likely buffered from seasonal change during the dry season, compared with other habitats, and therefore may be preferred habitat for territorial insectivorous birds. It is not known if the strong associations between habitat moisture and migrant songbird condition would occur in a more moist and stable environment such as a tropical forest understorey, where many migrants spend the winter.

In this study, we examined overwintering habitat quality for Wood Thrushes in Belize, Central America. Wood Thrushes are rapidly declining (2.2%/year in the last 10 years alone) (Sauer et al. 2012), and information on habitat use during the non-breeding season is urgently needed to inform conservation measures. Tropical forest degradation

and loss is thought to be a major factor in population declines for this species (Stanley et al. *in press*), but the drivers of Wood Thrush condition during the non-breeding season have not been studied. We compared food abundance (arthropods and fruit), habitat moisture, and four indicators of condition for Wood Thrushes across three habitat types from early (wet season) to late winter (dry season). We predicted that Wood Thrushes would be in better condition in habitats that are wetter, and that body condition would correlate with arthropod abundance but not fruit abundance, if arthropods are a better or preferred food source. We predicted that seasonal declines in moisture and associated condition of Wood Thrushes would be buffered in high quality habitat (mature moist forests) relative to poor-quality habitat (disturbed forest and riparian scrub). Finally, we expected high quality habitat to be relatively male and adult-biased, compared with poor-quality habitat, assuming that high quality habitat is limited and there is competitive exclusion by older (adult) and larger (male) birds.

## **Methods**

**Study site.** We conducted this study at the Belize Foundation for Research and Environmental Education (BFREE), a 1153-acre private reserve in the Toledo District of Belize, Central America. The reserve is a lowland tropical evergreen forest bordering the Bladen River which runs from the Maya Mountains to join the Monkey River, eventually emptying into the Caribbean sea (Brewer et al. 2003). This site receives most of its rainfall (2500-3000mm annually) from June to January, with a strong dry season from February to May (S. Brewer, BFREE, unpubl. data). Most of the forest in this region is secondary owing to widespread destruction of primary forest during hurricane Iris in 2001; some tall canopy trees (e. g. *Ceiba* spp., *Ficus* spp.) survived. Human disturbance to the region is very



limited owing to the small population size in Toledo (population 30,538 persons; density 6.6 persons/km<sup>2</sup>) and Belize as a country (population 334,297; density 14.5 persons/km<sup>2</sup>, concentrated in 5 larger towns). Three protected areas border BFREE: the Bladen Nature Reserve (97,000 acres; off-limits for everything except research), the Cockscomb Basin Wildlife Sanctuary and Jaguar Preserve (96,000 acres; minimal tourism and research permitted) and the Maya Mountain Forest Reserve (38,000 acres; sustainable forest harvesting permitted) (Fig. 3-1).

We studied Wood Thrushes in three major habitat types: mature moist forest, disturbed forest, and 'scrub'. Each habitat type was located 700-1000m away from other study sites. The forest habitat consisted of closed canopy, secondary forest regenerating post-hurricane (i.e. natural disturbance), with a few larger residual trees. This habitat type had minimal disturbance from people; only a few narrow and infrequently used trails allowed access. In contrast the disturbed forest habitat was located within the vicinity of several buildings including relatively high-use buildings such as the communal kitchen. Disturbed forest sites included small patches between buildings, and patches of forest bordered by dirt roads used by ATVs. The third habitat type, 'scrub', is a seasonally flooded area along the Bladen River. This area consists of sandy soil, and ranges from dense shrubby riparian thickets dominated by wild cane *Gynerium sagittatum* to more established forests of *Pterocarpus*, river figs (*Ficus insipida* and *F. guajavoides*), balsa, quamwood, cecropias (*Cecropia* spp.), dogwood (*Lonchocarpus heptaphyllus*) and cantimo (*Acacia glomerosa*), where disturbance is milder. The area is usually under water for at least part of the rainy season and thus fewer taller trees and more early-succession vegetation are present.

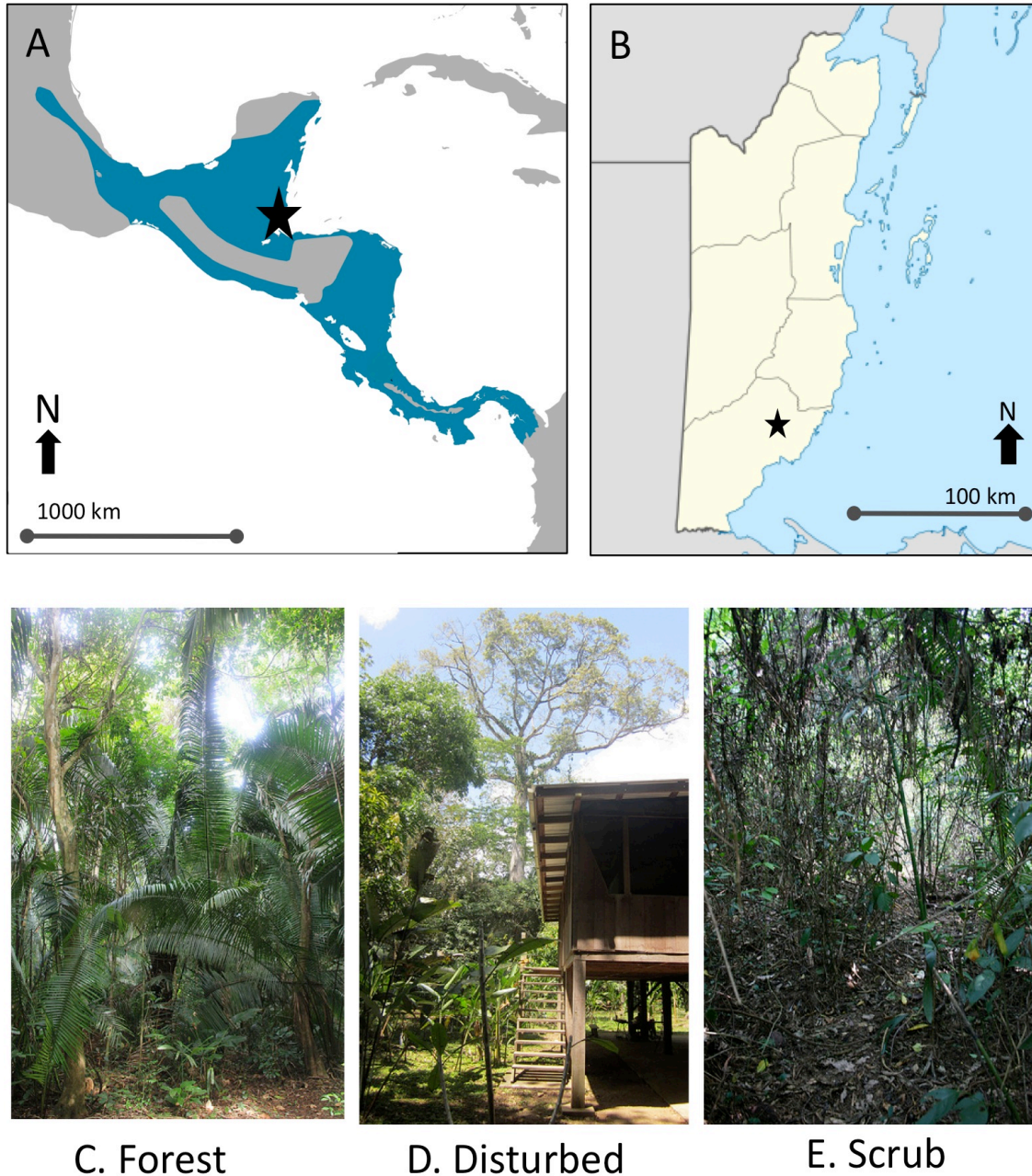


Figure 3-1 Map of study sites and habitats in Belize. A) Wood Thrush winter range in Mexico and Central America shown in blue shading (natureserve.org) with star indicating study site. B) Map of Belize (yellow shading) with districts outlined and study site indicated by a star. C-E) Three habitat types used by Wood Thrushes: mature moist forest, forest disturbed by buildings and trails, and dense riparian scrub. Habitat types are described in detail in Methods.

**General field methods.** Fieldwork was conducted from Oct-April from 2010-2013 (4 winters: 09/10, 10/11, 11/12 and 12/13). In each habitat type, we used approximately 20-40 unique net-lanes connected by narrow trails and separated by 10-30m. Wood Thrushes were captured between 550-1200hrs, and 1500-1800hrs, in arrays of 16-20 36-mm mesh mistnets. We used conspecific playback of Wood Thrush song to increase capture rates of birds. Every 2-3 days we moved all the nets to a new location to avoid repeated captures of the same individuals.

Each captured bird was given a numbered metal band and a unique combination of three plastic colour bands. Birds were aged as juveniles or adults based on three main plumage characters: shape of the 10<sup>th</sup> primary feather, tail feather shape, and shape and colouring of wing coverts (Pyle 1997). We collected a small (<100ul) blood sample for genetic sexing from each bird by using brachial venipuncture with a sterile 26½ gauge needle and a heparinised capillary tube. Blood samples were stored dried on filter paper (generic unbleached coffee filters) or in Queen's lysis buffer in a 4°C refrigerator until DNA extraction and analysis by polymerase chain reaction (PCR), using a modified primer set based on Griffiths (1998). See Chin et al. (2014) for a detailed description of PCR methods.

**Quantifying habitat moisture.** To determine habitat moisture, we collected three replicate soil samples along a 10-m transect perpendicular to each mistnet lane. Soil samples were collected from 2-4 cm depth at 1, 5 and 10-m from the centre of the net lane extending into the surrounding habitat. Soil was loosely placed into glass vials, which were capped and weighed immediately. Samples were then dried completely (24 hours at 100 °C, or until weight no longer decreased). The difference between dry and wet weight was

converted to a percentage for further analyses. The three samples per transect were averaged to create one mean soil moisture value per transect.

**Quantifying arthropod abundance.** Wood Thrushes are primarily ground foragers, therefore we focused prey sampling on the forest floor by using pitfall traps. At 8 to 16 net sites per habitat type, we deployed 3 pitfall traps along 10-m transects. Traps consisted of 16-oz plastic cups placed in holes at 1m, 5m and 10 m along the transect, so that the edge of the cup was flush with the ground. Traps were filled with water and a drop of dish soap to a depth of 2 cm, and emptied and reset every 24 hours for a total of 72 hours of trapping (3 days) in each habitat in each season. We used a plastic plate mounted on two wooden skewers to create a lid ~1cm over the top of the trap to avoid overflow from rain or capture of small vertebrates. Arthropods collected from 3 traps per transect were pooled to create one sample per transect. All arthropods collected in the traps were stored frozen or in ethanol until they were identified to family or order. The body length of each arthropod was measured to the nearest 1-mm. Since some arthropods captured in the pitfall traps are more likely to be consumed by Wood Thrush than others, we calculated an index of edible arthropod biomass. Following length-weight equations published for Neotropical arthropods (Strong and Sherry 2000), we calculated the dry weight of Coleoptera, Formicidae, and Araneae and summed them into one measure of edible arthropod biomass per transect.

**Quantifying fruit abundance.** To assess fruit abundance, we searched for fruit on trees or shrubs within 2m of the ground, and fruit on ground (fallen from canopy) in 10m x 4m plots adjacent to the net-lane where each Wood Thrush was captured. We counted the number of individual fruits and types of fruits. To create an index of fruit abundance, we

multiplied the number of fruits by the number of types of fruits. Values less than 10 were classified as 'low abundance', 10-20 as 'moderate abundance' and greater than 20, 'high abundance'.

**Condition of birds.** Condition of the birds was assessed by four measures: 1) a general body condition index (mass corrected for size) (Labocha and Hayes 2012), 2) scores of visible body fat (Conway et al. 1994), 3) scores of pectoral muscle size (Salewski et al. 2009), and 4) a measure of the packed blood cell volume (hematocrit) (Hatch et al. 2010). We used multiple measures since each may vary differently in relation to conditions experienced by an individual bird, and each measure has limitations (Labocha and Hayes 2012). Body condition provides an overall indication of nutrient stores (fat + muscle), but looking at both fuel (fat) and flight muscle separately is also useful. For example, high levels of fat may be associated with unreliable access to food, during times when birds are not actively preparing for migration (Witter and Cuthill 1993), likewise very low levels of fat may not be a sign of poor condition, but very low pectoral muscle scores are likely a sign of muscle catabolism and emaciation. Hematocrit provides a physiological index of condition. Recent studies have found that higher hematocrit (relatively more red blood cells) is associated with earlier spring arrival at breeding sites for Gray Catbirds (*Dumetella carolinensis*) (Hatch et al. 2010) and American Redstarts (Tonra et al. 2011). High hematocrit can increase flight efficiency (Jenni et al. 2006), therefore it should increase as birds prepare for migration (Hatch et al. 2010). Hematocrit should also decrease with high energy expenditures (Jenni et al. 2006), therefore birds expending more energy foraging in poor-quality habitats should have lower hematocrit than birds in high-quality habitat.

To calculate a general body condition index, we used methods similar to other studies of migrating thrushes in the Tropics (Bayly et al. 2013, Gomez et al. 2013) and estimated lean body mass for each bird using a regression equation of mass versus tarsus length for fat-free birds. The bird's actual body mass was then compared to the estimated body mass and the difference converted to a percentage. Birds with a positive body condition index were heavier than expected, i.e. body condition index of 7.2% indicates an individual 7.2% larger than its expected lean mass, and birds with negative body condition indices are lighter than expected, i.e. body condition index of -5.3% indicates an individual 5.3 % lighter than its expected lean mass. Fat was scored by examining the torso of the bird for visible fat deposits, and following a standardized 7-point scoring system to estimate the amount of visible fat (Desante et al. 2009). Few birds had fat scores greater than 4, therefore we truncated our measures at 5 categories (0-4) and considered the largest category as '4 or greater'. Pectoral muscles in birds are the primary means of powering flight and are catabolised to produce energy when needed (protein fuel) (Salewski et al. 2009). Pectoral muscles were scored by examining the muscles visually and by feel to determine a score out of 4, with 0 as concave muscle, and 4 as bulging convex muscle. Muscle scores approximate the scoring system of (Gosler 1991) only instead of a 2-point scale with half-point values, we simply used a 4-point scale.

**Statistical analyses.** For seasonal analyses, we grouped condition and environmental variables into two time periods: Oct-Nov (wet season) and Feb-Mar (dry season). We compared soil moisture, food abundance (arthropod abundance and edible biomass), and condition indices (body condition and hematocrit) across habitats by using a nested ANOVA with season and habitat as independent factors. Habitats were nested by season,

since we were interested in within-season differences by habitat type, and season was nested by year since some years were only sampled in one season (e. g. winter 2009/2010 only dry season values). To assess where significant differences were occurring (i.e. which habitats and seasons), we conducted post-hoc Tukey's HSD tests to compare means. For fat, muscle, and fruit scores, we used generalized linear models with a Poisson error distribution and assessed the best model by comparing AIC values of full models to reduced models. Full models included habitat nested by season and year. After observing that birds generally declined in condition from wet to dry seasons, we tested for differences in the slope of this decline by habitat by using an ANCOVA, with body condition of birds captured throughout the entire winter (Oct to Apr) as the response, and an interaction between date of capture and habitat as the independent factor. We compared the slope of the decline to the rate of change for 25 individual birds captured twice within the same winter to determine if the overall rate of body condition decline was similar for individual birds. To compare sex and age ratios across seasons and habitats, we used a generalized linear models with a binomial error distribution and assessed the best model by AIC. All statistical analyses were performed using the software R (R Development Core Team 2011).

## **Results**

**Soil moisture levels.** Near the beginning of the overwintering period for Wood Thrush in Belize (Nov), soil moisture levels were more than double (12-14%) that at the end of the winter (Mar; 2-6% soil moisture) when Wood Thrushes are starting to prepare for migration (~12-20 days prior to departure) (Berthold 2001). Wood Thrushes tracked from our study site departed from on average on 9 Apr, with earliest bird departing 27 Mar and

latest bird departing 25 Apr (E. A. McKinnon, unpubl. data). Soil moisture differences were significant both by season and habitat (Table 3-1, Fig. 3-2D). Post-hoc tests indicated that across seasons, scrub habitat was drier than forest, but not relative to disturbed habitat (Fig. 3-2D). The nested habitat/season/year term was significant; upon further examination, this was owing to the wet season in 2010 being significantly wetter overall than in 2011 ( $df = 1,156$ ,  $F = 17.13$ ,  $P < 0.001$ ).

**Wood Thrush food.** Arthropod abundance was related to patterns of soil moisture in that higher soil moisture was associated with higher abundance of arthropods ( $r^2=0.13$ ,  $F_{1,78} = 12.95$ ,  $P < 0.001$ ). Overall arthropod abundance declined significantly over the winter, but within-season abundance was significantly different by habitat, and not all habitats declined significantly over the winter (Fig. 3-2A, Table 3-1). Post-hoc tests revealed that in the early winter (wet season), scrub had significantly more arthropods per transect than disturbed (difference: 51.3 arthropods/transect, CI 4.18-98.5,  $P = 0.03$ ) and forest habitats (difference: 67.7 arthropods/transect, CI: 25.6-109.7,  $P = 0.0001$ ). In late winter (dry season), there was no significant difference between habitat types. In terms of seasonal change, post-hoc tests showed that only forest habitat did not differ significantly over the season ( $P=0.31$ ). Both disturbed habitat (difference: -52.6 arthropods/transect, CI: 7.6-97.6,  $P 0.01$ ) and scrub habitat (difference: -95.5 arthropods/transect, CI: 541-136.9,  $p < 0.001$ ) had significantly lower numbers of arthropods, with scrub habitat showing the greatest decline.



Table 3-1 ANOVA results for the effects of season and habitat on total arthropod abundance, edible arthropod biomass, and soil moisture content. Year was included as an interaction factor for arthropod abundance and biomass and as a nesting factor in soil moisture since there was one year with only dry season soil moisture measurements. Significant factors indicated by an asterisk.

Total arthropod abundance				
Source	d. f.	Mean square	<i>F</i>	<i>P</i>
Season	1	81256	49.38	<0.001*
Habitat	2	14821	9.01	<0.001*
Habitat/Season	2	8713	5.29	0.007*
Habitat/Season/Year	3	666	0.40	0.75
Residuals	85	1645		
Edible arthropod biomass				
Season	1	0.01	0.02	0.88
Habitat	2	1.42	2.93	0.058
Habitat/Season	2	0.46	0.94	0.39
Habitat/Season/Year	3	0.03	0.06	0.98
Residuals	84	0.48		
Soil moisture				
Season	1	2671.4	552.77	<0.001*
Habitat	2	177.6	36.76	<0.001*
Habitat/Season	2	21.4	4.44	0.014*
Habitat/Season/Year	5	37.7	7.80	<0.001*
Residuals	124	4.8		

Edible arthropod biomass was not significantly different by season, but there was a trend for differences by habitat in that forest tended to have more edible arthropod biomass (Table 3-1, Fig. 3-2B). The best model for fruit abundance was tied between habitat + season and season alone. Fruit abundance was significantly higher in the wet

season (estimate  $\pm$  SE =  $0.58 \pm 0.21$ ,  $z = 2.77$ ,  $P = 0.006$ ) and, although not significant in the model, post-hoc tests revealed that fruit abundance was higher in the forest (estimate  $\pm$  SE =  $0.16 \pm 0.31$ ,  $z = 0.50$ ,  $P = 0.62$ ) and scrub habitats (estimate  $\pm$  SE =  $0.32 \pm 0.29$ ,  $z = 1.09$ ,  $P = 0.28$ ) relative to disturbed habitat (Table 3-2, Fig. 3-2C).

Table 3-2 AIC values from a generalized linear model for differences in fruit scores by habitat and season, nested by year. Asterisks indicate lowest AIC values.

Model for fruit score	AIC values
Habitat x Season/Year	339
Habitat + Season + Habitat/Season	332
Habitat + Season	331*
Season	329*
Habitat	336

**Wood Thrush condition, age and sex ratios.** Wood Thrush body condition declined significantly from early to late winter (Table 3-3, Figure 3-2). Body condition was not significantly different by habitat on its own, but only when nested by season and year, indicating that yearly variation occurs. Examining patterns of body condition by habitat for each year separately by using a Tukey HSD post-hoc test, we found that habitat only had an effect on body condition in the wet season (in both years measured) but not in the dry season. In the wet season, body condition was significantly lower in scrub relative to disturbed habitat in 2010 ( $P = 0.005$ ), and lower in scrub relative to forest in 2011 ( $P = 0.02$ ). Examining all birds captured throughout the entire wintering period (from Oct-Apr), we found that there was no significant interaction between habitat and date of capture, indicating that the rate of decline in body condition (slope) was not significantly different

by habitat ( $df = 2, 412, F = 0.43, P = 0.65$ ). Capture date was a significant factor explaining body condition over the entire winter, with an estimated loss of  $0.04 \pm 0.008$  % body mass per day from October to April ( $df = 1, 414, F = 19.08, P < 0.001$ ) (Fig. 3-3). For 25 birds captured more than once in the same winter (on average, 27 days apart, range from 7-65 between captures) the daily rate of change in body condition was nearly identical to the overall pattern, at  $-0.038 \pm 0.04\%$  body mass lost per day.

Hematocrit did not show any significant pattern by season or habitat (Table 3-3). The top model for fat scores only included season (Table 3-4), which had a positive effect for wet season, indicating that fat scores were higher in early winter relative to late winter (estimate  $\pm$  SE =  $0.32 \pm 0.07$ ,  $z = 4.21, P < 0.001$ ). The two top models for muscle scores were habitat + season and season alone, which were equally ranked by AIC (Table 3-4). In both models, muscle scores were higher in the wet season (estimate  $\pm$  SE =  $0.15 \pm 0.06$ ,  $z = 2.55, P = 0.01$ ; season only model). In the season + habitat models, muscle scores tended to be higher in the forest (estimate  $\pm$  SE =  $0.11 \pm 0.01$ ,  $z = 1.70, P = 0.09$ ) and lower in the scrub (estimate  $\pm$  SE =  $-0.02 \pm 0.08$ ,  $z = -0.30, P = 0.76$ ), relative to disturbed habitat, but these estimates were not significant.

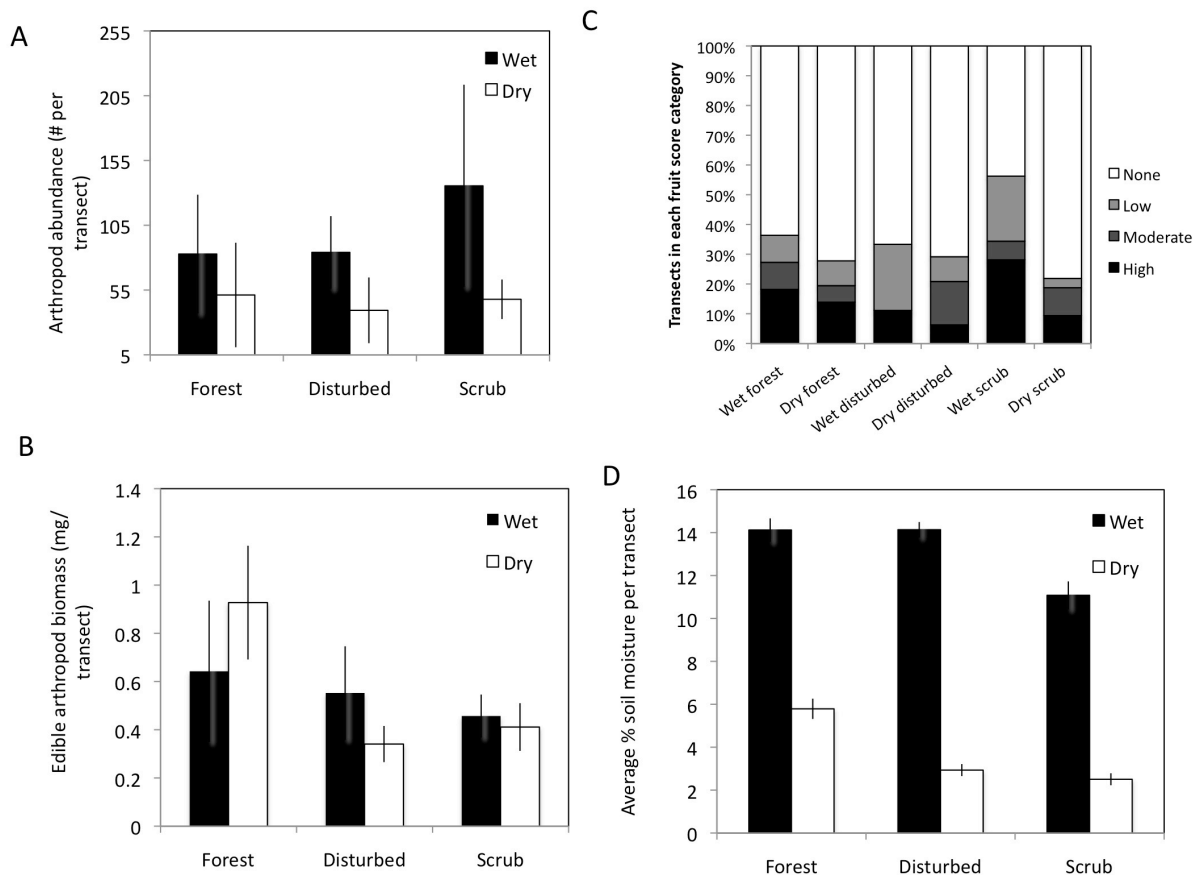


Figure 3-2 Seasonal changes in biotic (A-C) and abiotic (D) resources for Wood Thrushes in three habitat types. Sample size (# transects) for wet and dry seasons, respectively, in each habitat were: forest, n=15,16; disturbed, n=9,21; scrub, n = 16,16. Each 10-m transect consisted of 3 pitfall traps and 3 soil samples, and fruit was surveyed in a 4x10x2m area. A) Arthropod abundance declined significantly from wet to dry seasons in all habitats. B) Edible arthropod biomass (dry weight of ants, beetles, and spiders) varied by habitat and season. C) Fruit abundance score was higher in the wet season relative to the dry season. Fruit scores were based on the number of fruits multiplied by the number of types of fruit. Scores of 0=no fruit, low = <10, moderate = 10-20, high = >20. D) Soil moisture (average % moisture by weight) declined significantly across all habitats from wet to dry. Vertical bars in A, B, and D indicate standard error.

Table 3-3 ANOVA results of condition indices for Wood Thrush by habitat and season.

Body condition index				
Source	d. f.	Mean square	<i>F</i>	<i>P</i>
Season	1	1775.1	26.03	<0.001*
Habitat	2	172.4	2.53	0.08
Habitat/Season	2	54.8	0.80	0.45
Habitat/Season/Year	12	268.1	3.93	<0.001*
Residuals	400	68.2		
Hematocrit				
Season	1	99.71	2.18	0.14
Habitat	2	22.91	0.50	0.61
Habitat/Season	1	73.94	1.62	0.20
Habitat/Season/Year	3	28.76	0.63	0.60
Residuals	134	45.67		

Table 3-4 AIC values for generalized linear models with fat scores, muscle scores, sex and age of wood thrushes by season and by habitat. Season is nested by year to account for some years where only one season was sampled. Asterisks indicate the lowest AIC values; any model with AIC score within 2 of the lowest score is considered an equally acceptable model.

Models	Fat	Muscle	Sex	Age
Habitat x Season/Year	1324	1199	416	556
Habitat + Season + Habitat/Season	1310	1184	404*	553
Habitat + Season	1308	1181*	406*	549
Season	1305*	1181*	404*	545*
Habitat	1323	1186	405*	549

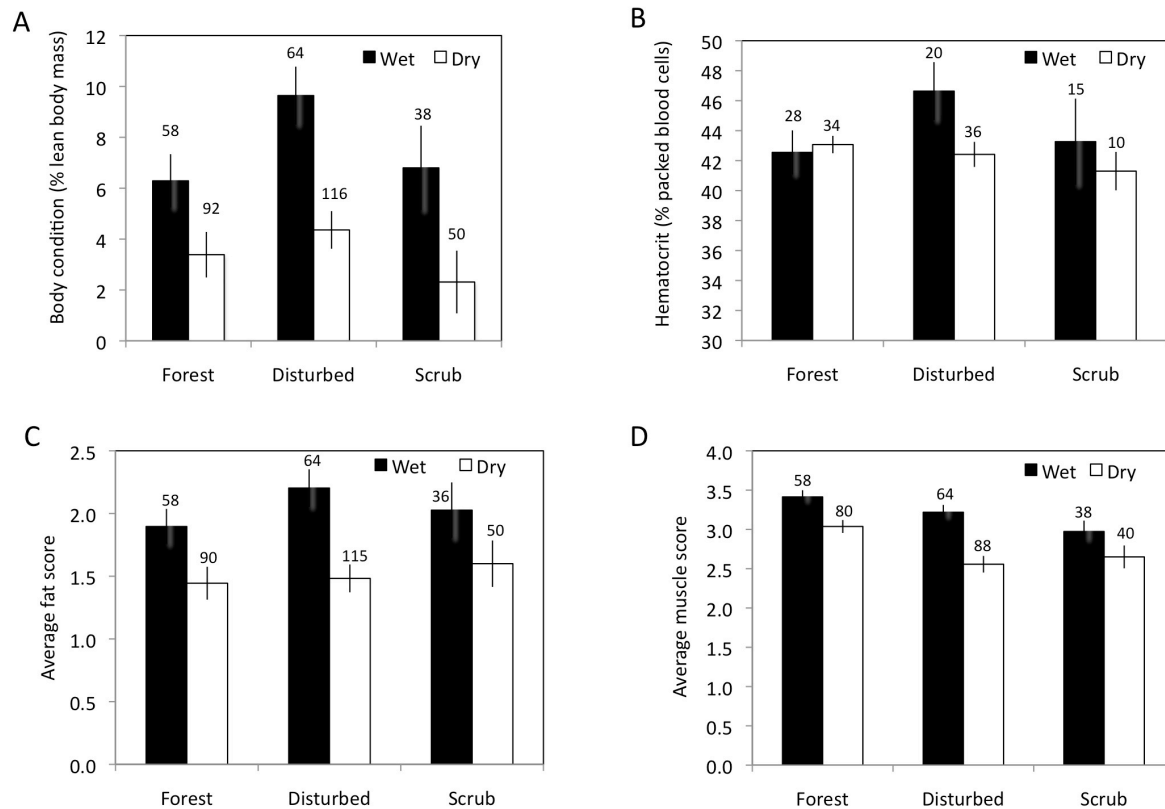


Figure 3-3 Seasonal and habitat differences in four measures of condition for Wood Thrushes in Belize (number above bars indicates sample size). A) Body condition declined significantly from wet to dry seasons. B) Hematocrit (% packed red blood cells) did not differ significantly by season or habitat. C) Fat scores (scale of 0-4) were significantly higher in the wet season relative to the dry season in all habitats. D) Pectoral muscle scores were higher (scale of 0-4) in all habitats during the wet season, and tended to be higher in the forest relative to disturbed and scrub habitat.

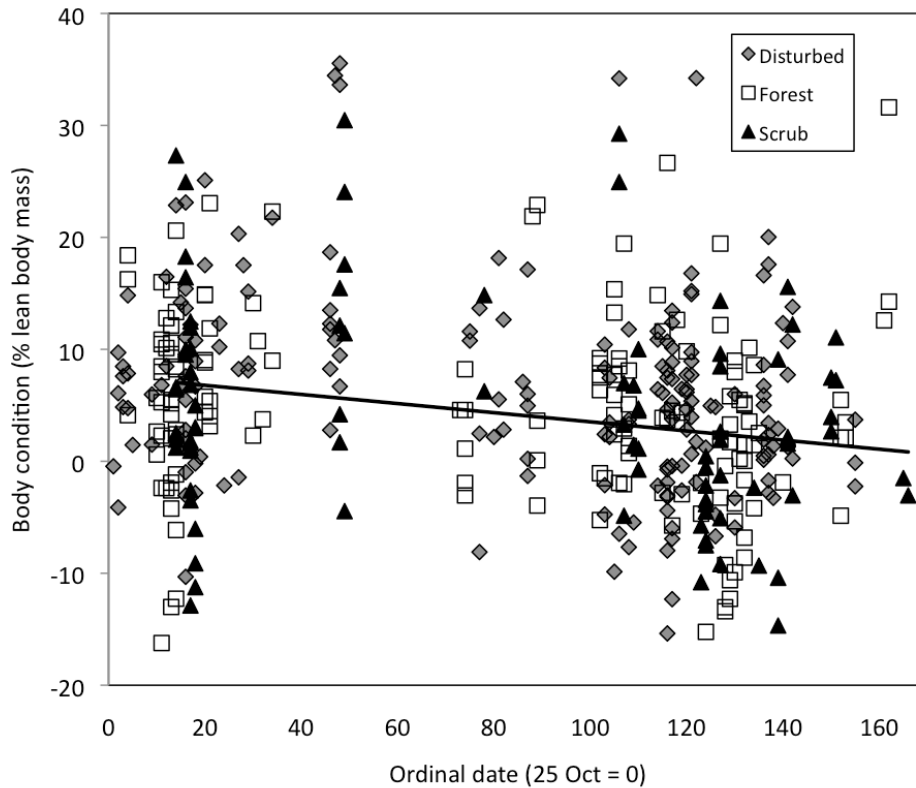


Figure 3-4 Seasonal decline in body condition of  $n = 418$  Wood Thrushes overwintering in Belize from 25 Oct to 7 Apr. There was no significant difference in the slope of the decline by habitat.

Sex ratios were significantly different by habitat and season, with an interaction between habitat and season (Fig. 3-4A, Table 3-4). The interaction occurred because sex ratios changed significantly by season only in the scrub habitat, from highly male-biased to highly female-biased. Scrub habitat had a more female-biased sex ratio overall (estimate  $\pm$  SE =  $-1.09 \pm 0.46$ ,  $z = -2.37$ ,  $P = 0.02$ ), but this was driven by the dry-season sex ratio, where there were 0.5 males captured per female (Fig. 3-4A). During the wet season, the scrub showed the opposite trend, with two males captured per female ( $1.78 \pm 0.78$ ,  $z = 2.29$ ,  $P = 0.02$ ).

The best model to explain differences in age ratios only retained season as a factor. There tended to be more juveniles captured in all habitats during the wet season (Fig. 3-4B) than dry season, although this was not significant (estimate  $\pm$  SE =  $0.31 \pm 0.21$ ,  $z = 1.47$ ,  $P = 0.14$ ).

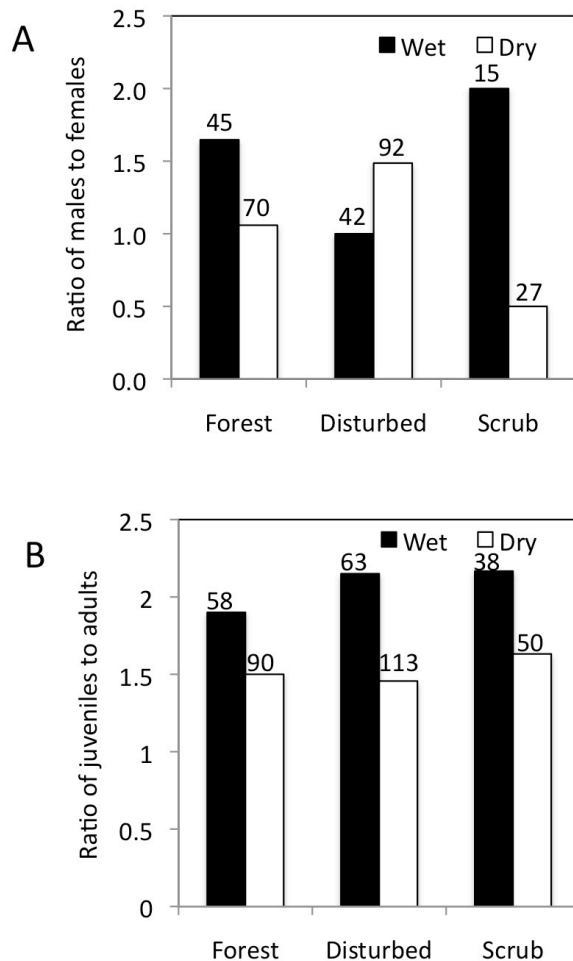


Figure 3-5 Within-winter seasonal differences in sex and age ratios of Wood Thrushes in different habitats. Numbers above bars indicate sample sizes. A) Sex ratios differed significantly by season and by habitat. The most drastic shift was in scrub habitat where sex ratios reversed between seasons. B) Age ratios were similar across habitats but the proportion of juveniles captured declined from wet to dry seasons.



## Discussion

The habitat where Wood Thrushes overwinter in Belize undergoes a strong seasonal reduction in soil moisture and food resources from early winter to late winter (Oct-Apr). The soil showed a clear pattern of drying (Fig. 3-2) which corresponded with a decline in both arthropod abundance and fruit abundance at our study site (Fig. 3-2). We also documented a decline in body condition of Wood Thrushes seasonally, parallel to declines in soil moisture and food, and similar to patterns reported for Ovenbirds in shade coffee, scrub, and dry limestone forests in Jamaica (Strong and Sherry 2000). Body condition, fat, and muscle mass of Wood Thrushes all declined over time. Patterns of sex and age-ratios were more complex, and showed significant changes from more juveniles and males in the wet season, to relatively more adults and females captured during the dry season. Unexpectedly, there was a clear reversal of sex ratios from the wet to dry season in scrub habitat only, from highly male-biased (2 males per female) to highly female-biased (0.5 males per female). Overall our results suggest that in all habitats late winter is a challenging period for this forest-dwelling omnivore, especially since birds must accumulate enough fat and muscle for upcoming spring migration, which begins as early as 28 March in this population of Wood Thrushes (see Chapters 2 and 4).

We expected forest habitat to be relatively high quality for Wood Thrushes (more food) (Sherry and Strong 2000, Richards and Windsor 2007). Surprisingly, scrub habitat had the highest abundance of arthropods during the wet season, and was not significantly lower in arthropods than other habitats during the dry season, despite being slightly drier than forest habitat. During the wet season in the tropics, arthropod abundance is related to productivity of vegetation, which is high in early-successional habitats, compared with

mature forests (Richards and Windsor 2007). This likely explains the high arthropod abundance we observed in scrub habitat during the wet season. Arthropod abundance in the dry season is limited by temperature and humidity, which both decrease in more open habitats relative to forests (Richards and Windsor 2007). Following this pattern, scrub habitat declined strongly in arthropods in the dry season, while forest habitat (more stable in terms of humidity and temperature) retained a similar abundance of arthropods in both seasons. In forest habitat, there was a trend for edible arthropod biomass (which includes dry weights of ants, beetles, and spiders) to increase from wet to dry season in the forest, possibly owing to larger arthropods taking refuge in a wetter environment (Janzen 1973). However, overall our results suggest that in the dry season, arthropod food (as measured by overall abundance and edible biomass) is equally available in all habitat types we studied.

Wood Thrush condition, as assessed by multiple indices, was not higher in forest relative to disturbed forest or scrub. We found significant condition differences by habitat only in the wet season, and different effects in different years. In the wet season, body condition was significantly higher in forest relative to scrub in 2010 and higher in disturbed relative to scrub in 2011. Both 2010-11 and 2011-12 winters were classified as La Nina years (National Weather Service 2014, [www.cpc.noaa.gov](http://www.cpc.noaa.gov)), which typically result in less rainfall on the Caribbean slope of Central America, including Belize (Malhi and Wright 2004), although 2010-11 winter had much less rainfall from Oct-Apr than in 2011-12 (578 mm vs. 998mm; Hydromet Climate Section, Government of Belize). Habitat differences could be more subtle than we expected, and only apparent in some seasons and in some years. It is possible that birds only suffer poor condition in the scrub habitat in the

driest winters (i.e. 2010-11), and the advantages of the forest habitat are most apparent in those years as well. Likewise, American Redstarts in scrub habitat were not always in poorer condition than birds in 'high quality' mangrove habitat; it depended on the amount of precipitation in a given year (Studds and Marra 2007). Wood Thrushes at our study site depart on migration in the first or second week of April. It is possible that our condition data (truncated at the end of Mar) did not capture patterns in condition by habitat that would carry-over to affect migration. However, our data showed a small but steady decline in body condition over the winter ( $-0.04\%$  per day) in all habitat types (Fig. 3-4), and it seems unlikely that this trend would drastically reverse in the week or two before birds departed on migration. The dry season in Belize continues until late May or early June, thus birds mostly likely experienced a steady decrease in habitat moisture up until they departed on migration.

One reason that body condition was not higher in forest could be because our 'high quality' forest habitat was secondary forest rather than primary forest, which is expected to be the best winter habitat for Wood Thrushes (Rappole et al. 1989). However, a recent study in Costa Rica found no differences in condition of Wood Thrushes between primary and secondary forest patches (Stanley 2012), suggesting that primary forest is not markedly higher-quality habitat. The pronounced dry season in Belize may simply result in poor quality habitat for Wood Thrushes across the board, as evidenced by the low food resources and body condition of birds, relative to early winter, and regardless of habitat type. The body condition we documented in the dry season amounted to  $\sim 5\%$  decrease in body mass from the wet season. For an average-weight Wood Thrush (45g), this translates to 2.4g. This is a much larger decline that has been documented to produce carry-over

effects in American Redstarts, which showed effects of mass differences of only 0.2g (~2.5% average body weight) (Studds and Marra 2005). However, we did not detect any effect of lower body weight on spring migration performance of Wood Thrushes (see Chapter 4).

Birds in relatively resource-poor winter habitat may migrate shorter distances, resulting in a pattern of leap-frog migration (Bell 2005). In Belize and southern Mexico, the most northern part of the Wood Thrush winter range, dry seasons are more pronounced than at lower latitudes (Fig 3-6), and habitat quality for Wood Thrushes may follow a similar gradient. Tracking Wood Thrushes on migration has revealed a pattern of leap-frog migration (Stanley et al. *in press*), where birds in the north of the winter range (i.e. our study site in Belize) migrate relatively short distances (average  $3407 \pm 112$  km, range 2200-4800 km) to southern breeding sites while birds wintering further south (e.g. Costa Rica) migrate to the farthest northern breeding range (average  $4635 \pm 111$  km, range 3931-6164 km) (E.A. McKinnon and C.Q. Stanley, unpubl. data; see also Chapter 4). The low dry-season condition we observed may not be enough affect the relatively short-distance spring migrations of Wood Thrushes overwintering in Belize. Comparative studies of Wood Thrush condition across a range of wintering latitudes would clarify if pre-migratory condition is instead more closely linked to the broad-scale patterns of moisture at the scale of the entire winter range, and not to local, fine-scale differences in habitat moisture.

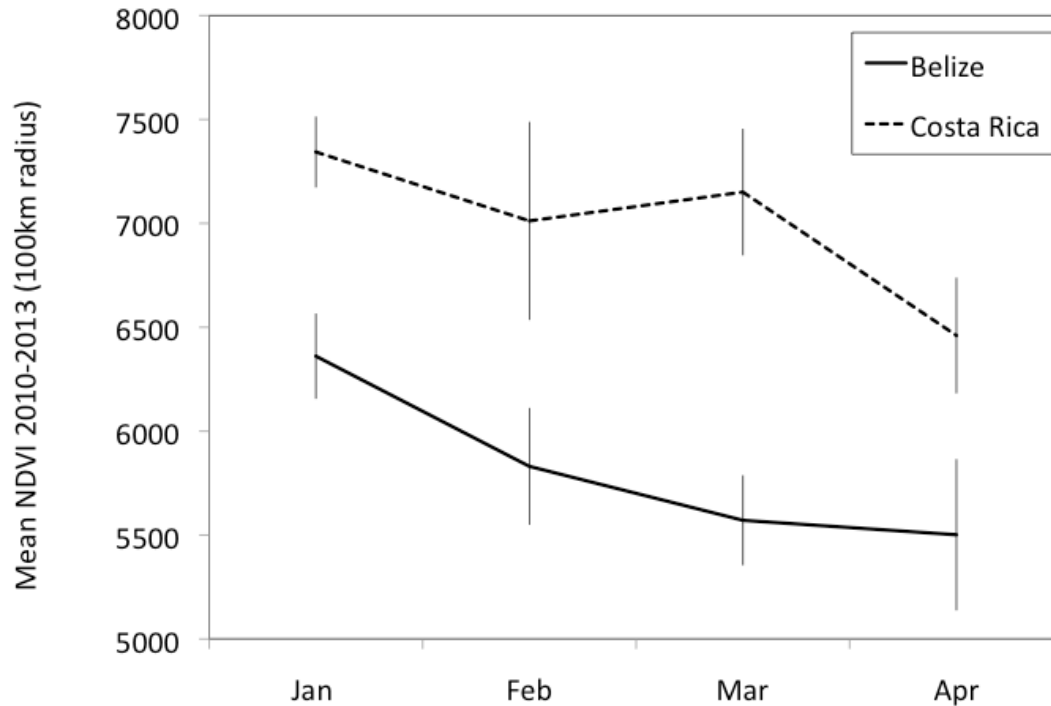


Figure 3-6 NDVI, an index of habitat greenness and moisture, is significantly higher at a Costa Rican study site (La Selva Biological Station) compared with a Belizean study site (BFREE). Vertical bars indicate standard deviation over the four-year span (2010-13). Values are means from a 100km-radius circle centred on the study site location, excluding areas of water. Monthly NDVI values obtained from the Land Processes Distributed Active Archive Center (lpdaac@usgs.gov).

At an overwintering site in Veracruz, Mexico, Wood Thrushes displayed a territorial/floater behavioural system in winter (Brown and Long 2007), with at least 50% of individuals defending exclusive territories of about ~1ha for the duration of the winter (Rappole et al. 1989). However, we had high capture rates of Wood Thrushes within relatively small areas in all habitats (e.g. up to 20 different individuals captured over a 24-hour period in a ~1 ha net array), and relatively low within-season recapture rates, suggesting that birds either occupied very large, overlapping territories or were primarily ‘floaters’. This could confound our attempts to link condition of birds with the habitat they

were captured in, if individuals are moving over a large area including a range of habitats of varying qualities. Thus individual condition may be related to the amount of time birds are able to spend in high quality habitat. Short-distance (100s of km) intratropical movements of wintering migratory birds are poorly understood (Delmore et al. 2012) but this migration is also thought to track seasonal and geographic changes in rainfall and food availability. More precise tracking devices, especially those capable of remotely transmitting location information, will be needed to provide insights into potential dry-season short- and long-distance movements of Wood Thrushes.

One surprising pattern in our data was the marked shift in sex ratio in the scrub habitat, from highly male-biased (2 males per female) in the wet season to female-biased (2 females per male) during the dry season. We have no reason to believe that males at this site experience relatively higher levels of mortality than females or males elsewhere, so we conclude that large numbers of males move to another location during the dry season. This supports the idea that overall, birds at our study site were less territorial than in other studies (Rappole et al. 1989), and that extensive within-winter movements may be a feature of Wood Thrush behaviour at our study site. While studies have used sex-ratios to infer habitat quality, we caution that this may not be the correct interpretation for Wood Thrushes, as there were no significant differences in body condition by habitat during the dry season. Juvenile birds are more likely to be non-territorial than adults (Winker et al. 1990), therefore an exodus of non-territorial juvenile males (wet season 70% juvenile males, to dry season only 30% juvenile males) could explain this pattern. But why would relatively more females remain? One possibility is that females prefer dense, shrubby habitat over more open-understorey forests, a pattern that has been suggested for

wintering female Hooded Warblers (Morton 1990) and also female Bicknell's Thrush (*Catharus bicknelli*) (Townsend et al. 2012). In American Redstarts where significant sex-segregation by habitat has been documented, there are clear negative consequences for condition of birds of both sexes occupying the female-biased habitat (Norris et al. 2004). Our data suggest instead that there may be innate habitat preferences for Wood Thrushes of each sex, possibly related to differences in spring migration strategy (i.e. males must leave earlier to arrive first at breeding sites, which could result in different resource needs in late winter).

Overall our results showed that dry season condition was lower for birds in all habitat types compared with wet season. Tropical forests are expected to face more frequent periods of severe drought, and decreased annual rainfall, under current forecasts of global climate change (Neelin et al. 2006, Karmalkar et al. 2011, Hidalgo et al. 2013). It is possible that body condition was low in all habitat types in our study because forests in this region are already experiencing more severe dry seasons with current levels of global warming. The central wintering range for Wood Thrush, including Belize and adjacent Guatemala, southern Yucatan, Mexico, and Honduras, is estimated to contain more than 50% of the remaining Wood Thrush habitat in Central America (Stanley et al. *in press*), and experiences similar rates of drying as our study site. It is unknown what effects relatively low body condition of Wood Thrushes could have on spring migration performance or mortality or, for birds surviving migration, on breeding productivity. Tracking devices that transmit locations remotely would allow assessment of the rates of mortality for birds on spring migration, and could be used to understand the more far-reaching consequences of tropical forest quality on Wood Thrush populations. Forest fragmentation and conversion

of moist forests to agriculture will exacerbate the effects of drying on habitat quality for Wood Thrushes, and many other species. Conservation measures aimed at protecting remaining areas of moist tropical forest would likely promote increased condition and survival of Wood Thrushes and other forest-understorey birds.

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## **Chapter 4 Carry-over effects of winter condition on start-to-finish spring migration of a Neotropical songbird**

## Abstract

Different periods of the annual cycle can be inextricably linked for migratory animals, where habitat quality and individual condition at the end of one season can carry-over to affect fitness in subsequent seasons. In Neotropical-Nearctic migratory songbirds, carry-over effects from the overwintering season in the tropics may influence spring migration timing: birds in poor condition and in low quality habitats are predicted to be delayed, and suffer costs for reproductive success. We examined carry-over effects of winter body condition and habitat quality on start-to-finish spring migration timing of Wood Thrushes, a songbird that journeys between breeding sites in eastern forests of North America and humid tropical forests of Central America. We compared a body condition index at a wintering study site Belize to migration performance (timing at three points, overall speed and duration). Habitat moisture levels are a proxy for habitat quality for Wood Thrushes and other songbirds, therefore we expected broad scale habitat moisture patterns to correlate with individual and population-level spring migration performance, i.e. birds in wetter sites should show improved migration performance, and populations experiencing wetter years should also show an increase in average performance. Using a larger sample of birds tracked from multiple sites, we compared winter site moisture (assessed remotely by NDVI) from across the winter range to spring migration performance. We found no evidence of carry-over effects of winter body condition or NDVI on spring migration performance, either at the individual or population-level. We documented a broader pattern in NDVI and migration timing, in that birds overwintering in the wettest areas in the southern part of the winter range departed the latest. Our results suggest that carry-over effects of winter habitat quality may be subtler for some species than expected, or

may only be apparent during extreme weather events such as droughts. The consistently later spring timing in wettest areas of the Wood Thrush non-breeding range supports the theory that high-quality habitats offset the costs of farther migration, resulting in a leap-frog migration pattern.

## **Introduction**

It has been demonstrated theoretically (Norris 2005) and with field data (Norris et al. 2004, Saino et al. 2004, Stutchbury et al. 2011) that events and processes in one part of an animal's life cycle can carry-over to influence fitness in subsequent parts of the life cycle (Harrison et al. 2011). In migratory birds, occupancy of low-quality habitat during the non-breeding season can result in poor physiological condition at spring migration departure (Marra and Holberton 1998), which in turn can influence survival to the next winter (Angelier et al. 2009). Spring departure date is often strongly linked to arrival date at breeding sites (Callo et al. 2013, Stanley et al. 2012), which is an important predictor of reproductive success (Lozano et al. 1996), therefore carry-over effects that alter migration speed or timing (e.g. date of departure from wintering site, arrival date at breeding site) can have serious consequences for individual fitness and population dynamics (Both et al. 2006).

One limitation of studies of winter to migration carry-over effects in migratory songbirds is that tracking small birds from start-to-finish on spring migration was not possible until the recent miniaturization of tracking devices (Stutchbury et al. 2009). Previous studies have relied on spring migration departure dates (Studds and Marra 2011) or timing of arrival at stopover sites (Gonzalez-Prieto and Hobson 2013) as proxies for overall migration performance, or have found links between individual performance at



breeding sites and former winter habitat quality measured indirectly through stable-isotope analysis (Rockwell et al. 2012) or remote sensing data (Saino et al. 2004). However, some research has found evidence for strong genetic control of spring migration timing (Stanley et al. 2012), suggesting that carry-over effects might be constrained by endogenous programs. It is also possible that effects of environmental conditions in winter may not be manifested until after migration departure (Tøttrup et al. 2008). Therefore it is important to measure spring migration behaviour along the entire journey to assess if carry-over effects from wintering sites occur at any point from departure to arrival at breeding sites.

We tested the hypothesis that winter habitat occupancy would carry-over to affect spring migration performance by tracking individual Wood Thrushes (*Hylocichla mustelina*) over their entire spring migration to their breeding sites in North America. Wood Thrushes are a rapidly declining forest songbird that breeds in eastern North America (Sauer et al. 2012), and threats related to non-breeding season habitat are not well understood (Evans et al. 2011). The late-winter migration preparation period (March) is the most likely time period to cause carry-over effects on spring migration, since Wood Thrushes should be preparing for their early-April migration departures at this time (Berthold 2001). Other studies have found carry-over effects of March rainfall on spring migration departure date of songbirds (Studds and Marra 2011). Body condition of Wood Thrushes is variable late in their overwintering period (dry season), and declines in parallel with habitat moisture and food availability (both arthropods and fruit; McKinnon Ch. 3), suggesting that carry-over effects on spring migration could occur. Furthermore, climate change models project decreased rainfall and stronger dry seasons in northern

Central America (Hidalgo et al. 2013), underlining the importance of understanding if habitat moisture affects fitness of Wood Thrushes via effects on spring migration performance.

We used two approaches to examine carry-over effects in Wood Thrushes. First, we compared body condition of birds tracked from a winter site in Belize ( $n = 22$ ) to their spring migration timing, overall speed, and duration ('migration performance'). We predicted that birds in poorer condition would show later migration timing over the entire migration route, spend more days on migration, and travel at a slower rate (total distance/duration). Second, we included a larger sample of birds tracked from other wintering and breeding sites (total including Belize  $n = 53$ ) and compared winter habitat moisture (as remotely assessed by NDVI index of plant productivity) to migration performance. NDVI is assumed to correlate with local food resources and therefore habitat quality (Saino et al. 2004). We predicted that birds occupying wintering sites with lower NDVI (more dry, poor habitat quality) would show negative carry-over effects on spring migration, such as later departure, slower migration speed, longer duration, and later arrival at breeding sites. For two wintering populations studied over 3 years each, we predicted that year-to-year variation in NDVI would correlate with population-level migration performance, such that in drier years the average migration performance in that population would be lower (i.e. mean departure date would be later). Finally, we predicted that between-population differences in migration performance would be related to differences in NDVI, in that sites that are consistently more wet would have birds that showed consistently better migration performance.

## Methods

**Field methods.** Wood Thrushes were captured at the Belize Foundation for Research and Environmental Education (BFREE) in the Toledo district of Belize, Central America, over the course of 4 winters, from 2010 to 2013 ( $n = 166$ ). For our range-wide sample, birds were captured at Hemlock Hill Biological Station, in Pennsylvania, USA, during the 2008-2011 breeding seasons ( $n = 96$ ), and at La Selva Biological Station in Costa Rica over three winters, from 2009 to 2012 ( $n = 109$ ). Geolocators (British Antarctic Survey model MK14S, 1.6g) were deployed on birds by using a Teflon ribbon leg-loop harness, custom fit to each bird. We attempted to capture all birds with geolocators one year after deployment. Once recaptured, we removed the geolocators and released the birds. Some studies have found effects of geolocators on survival (Gomez et al. 2014) or timing of breeding in songbirds (Arlt et al. 2013); however, previous studies on Wood Thrushes have documented no effects on return rates (Stanley et al. 2014) or short-term (i.e. within-winter) effects on body condition (McKinnon et al. 2014). To assess if birds that survived to return to our study sites with geolocators were larger than average (i.e. if geolocators disproportionately affected survival of smaller birds, for example) we compared the pre-migration body condition of returning birds with that of all birds captured during the dry season by using a t-test.

Individual birds were also marked with metal and plastic leg bands for identification in the field and upon recapture. Birds captured outside of the breeding season were genetically sexed by PCR using a small blood or feather sample, and birds were aged as juvenile (first-year) or older by examination of plumage characteristics.

**Geolocator analysis.** Geolocator data were downloaded and analyzed using the light-threshold method, following (McKinnon et al. 2013). We extracted 6 spring migration variables from the light data for further analyses: last noon at winter site ('departure date'), first noon across the Gulf of Mexico ('cross date'), first noon at breeding site ('arrival date'), total migration distance, total migration duration, and overall migration speed (distance/duration). To calculate migration distance, we used a straight-line measure starting at winter sites and connecting stopovers until arrival at breeding sites. For birds captured at our breeding study site (Pennsylvania), we calculated the location of winter home ranges by taking the average latitude and longitudes for January and February, using a winter-ground calibrated sun elevation (McKinnon et al. 2013). For birds captured at both wintering study sites (Costa Rica and Belize), we used a similar approach to calculate the average latitude and longitude for June and July, using a breeding-site calibration sun elevation (McKinnon et al. 2013).

**Body condition (Belize site only).** For birds captured during the dry season in Belize, we measured the metatarsus bone to the nearest 0.1mm, and weighed each bird to the nearest 0.1g. We also scored fat levels on a scale from 0-7, following established protocols for monitoring wintering migratory birds (Desante et al. 2009). Following methods of other studies on wintering migrants (e. g. Strong and Sherry 2000, Bayly et al. 2013, Gomez et al. 2013) we determined body condition by calculating the estimated lean mass of each individual using an equation derived from a regression of fat-free bird weight versus tarsus. We then calculated each bird's predicted lean mass based on its tarsus length, and compared the actual weight of the bird to the predicted lean mass. The difference was

converted to a percentage for easier interpretation, i.e. a condition index of 8.6% indicates a bird is 8.6% larger than its expected lean mass.

Since we captured each individual bird on a different day relative to its departure date (on average, 55 days before departure, range of 24-95 days), we adjusted the body condition of each to account for difference in capture date. Previous work (McKinnon; Ch 3) found that Wood Thrush body condition (% predicted lean body mass) at our study site declined significantly over the winter, at a rate of 0.04% per day (95% confidence intervals: 0.02-0.05). Therefore we multiplied the number of days between capture and departure date by -0.04% to estimate departure body condition for each bird. This resulted in a decrease in the % lean mass of about 2.2, on average (range of 0.96 – 3.64%).

**NDVI analyses.** To determine an estimate of habitat moisture, we used the Normalized Difference Vegetation Index (NDVI). This commonly-used ecological index is derived from satellite imagery, and higher values indicate increased leaf area and primary productivity (Pettorelli et al. 2011). Central American NDVI data for March from 2009-2013 were downloaded from the Land Processes Distributed Active Archive Center (lpdaac@usgs.gov), and clipped to the Wood Thrush wintering range (natureserve.org) by using ArcGIS 10 (ESRI). Using ArcGIS, we created a 100-km radius buffer around the estimated winter home range of each Wood Thrush from our PA breeding site. This accounts for most error in geolocator position for birds tracked from breeding to wintering sites. Within this 100-km radius circle we extracted all NDVI values, and calculated an average NDVI for each bird. For our two winter-grounds study-sites, we used a 100-km buffer centred on each field station (BFREE in Belize, and La Selva in Costa Rica) for a comparable NDVI average. We specifically focussed on NDVI in March, as this is the last

month that most Wood Thrushes were resident at their winter sites before departing on spring migration and previous work has found that rainfall in March corresponds to departure dates in another Neotropical migrant (Studds and Marra 2011).

**Statistical analyses.** To determine if late season Wood Thrush body condition predicted migration performance, we used general linear models with spring migration variables as responses and Belize Wood Thrush departure condition as our predictor of interest. Since both age and sex have strong effects on migration timing and stopover behaviour (McKinnon *et al.* 2014; Ch. 2), we also included these as independent factors. For comparison of NDVI values to migration performance of birds tracked across the Wood Thrush range, we conducted separate analyses for breeding site and winter site deployments. For breeding site birds, we used a general linear model with spring migration variables as dependent factors and March NDVI and sex as predictors. We used the March NDVI from the specific year in which each bird was tracked, therefore we did not need to include year as a separate factor. We did not include age in this analysis since all birds were adults undergoing spring migration for at least their second time. For winter site birds, we used a similar approach but we nested March NDVI by study site, to examine if yearly variation in NDVI within each site was associated with effects on population-level migration performance. We also ran the model without nesting to determine if across sites higher NDVI was related to better spring migration performance.

## Results

We recaptured 86 Wood Thrushes wearing geolocators. Some geolocators failed to record any usable data, therefore our final sample size was  $n = 26$  (Belize),  $n = 21$  (Costa Rica), and  $n = 23$  (Pennsylvania). Since we only obtained migration information from birds that

survived to return to our study sites, this may have biased our results to individuals in better condition. We tested for this by calculating an estimated body condition for all birds captured in Belize during the dry season ( $n = 190$ ), and compared with the condition of birds that returned with geolocators. The difference in condition was not significant ( $t$ -test,  $t = -0.37$ ,  $df = 32.1$ ,  $P = 0.71$ ); birds with geolocators were on average 3.8% above their expected lean body mass, while non-geolocator birds were 3.2%.

Estimated departure body condition of Wood Thrushes in Belize ranged from -15% to 23.3%. Body condition in Belize was not a significant predictor of spring migration departure timing (estimate =  $0.20 \pm 0.20$ ,  $t = 0.03$ ,  $P = 0.31$ ), date crossing the Gulf of Mexico (estimate  $-0.05 \pm 0.17$ ,  $t = -0.28$ ,  $P = 0.78$ ) or arrival at breeding site (estimate =  $-0.05 \pm 0.23$ ,  $t = -0.20$ ,  $P = 0.84$ ), when controlling for known age- and sex-effects (Fig. 4-1). Likewise, birds in better body condition were not more likely to migrate faster (migration rate estimate =  $0.80 \pm 4.29$ ,  $t = 0.19$ ,  $P = 0.85$ ) or for fewer days (migration duration estimate =  $-0.19 \pm 0.22$ ,  $t = -0.84$ ,  $P = 0.41$ ) (Fig. 4-2).

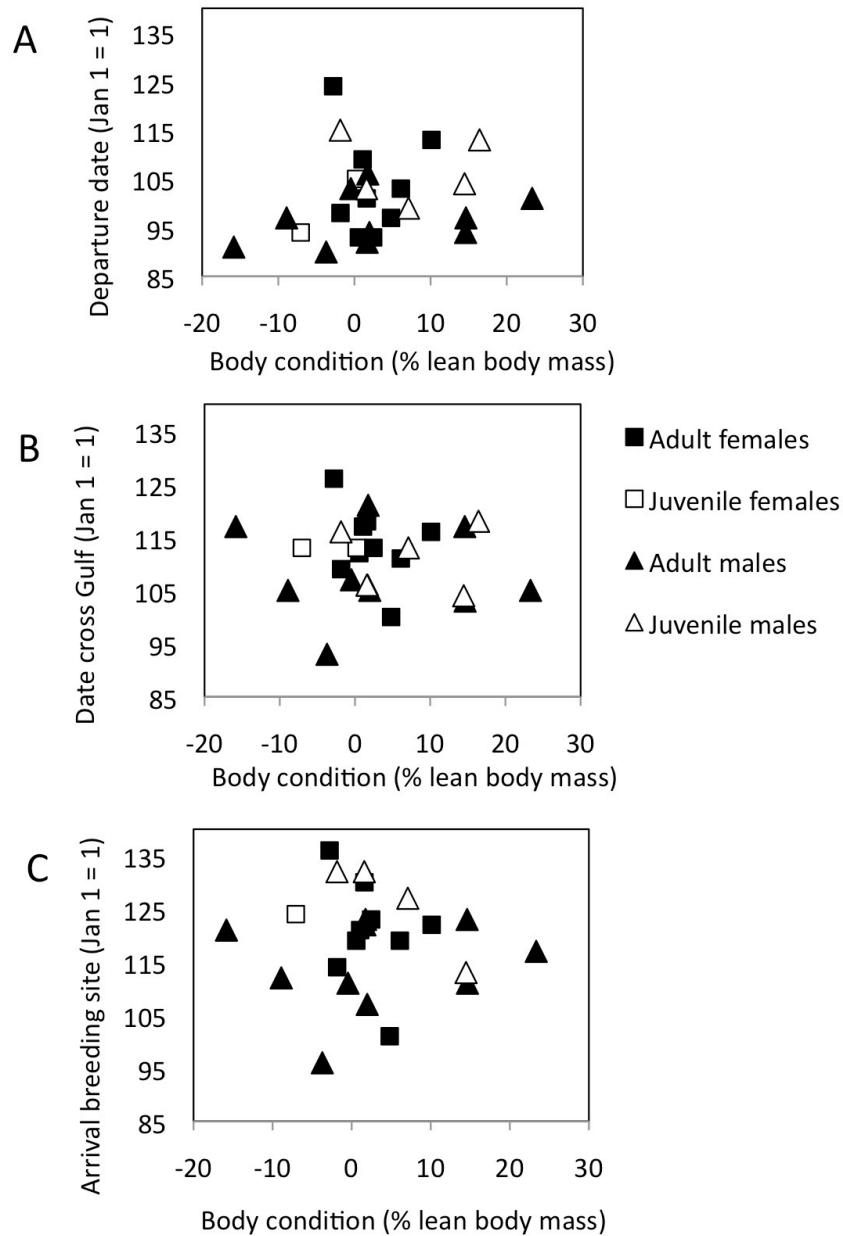


Figure 4-1 Body condition of Wood Thrushes captured during the dry season in Belize did not correlate with: A) spring migration departure date ( $n = 26$ ), B) date individuals crossed the Gulf of Mexico ( $n = 26$ ), or C) date individuals arrived at their breeding sites ( $n = 24$ ).



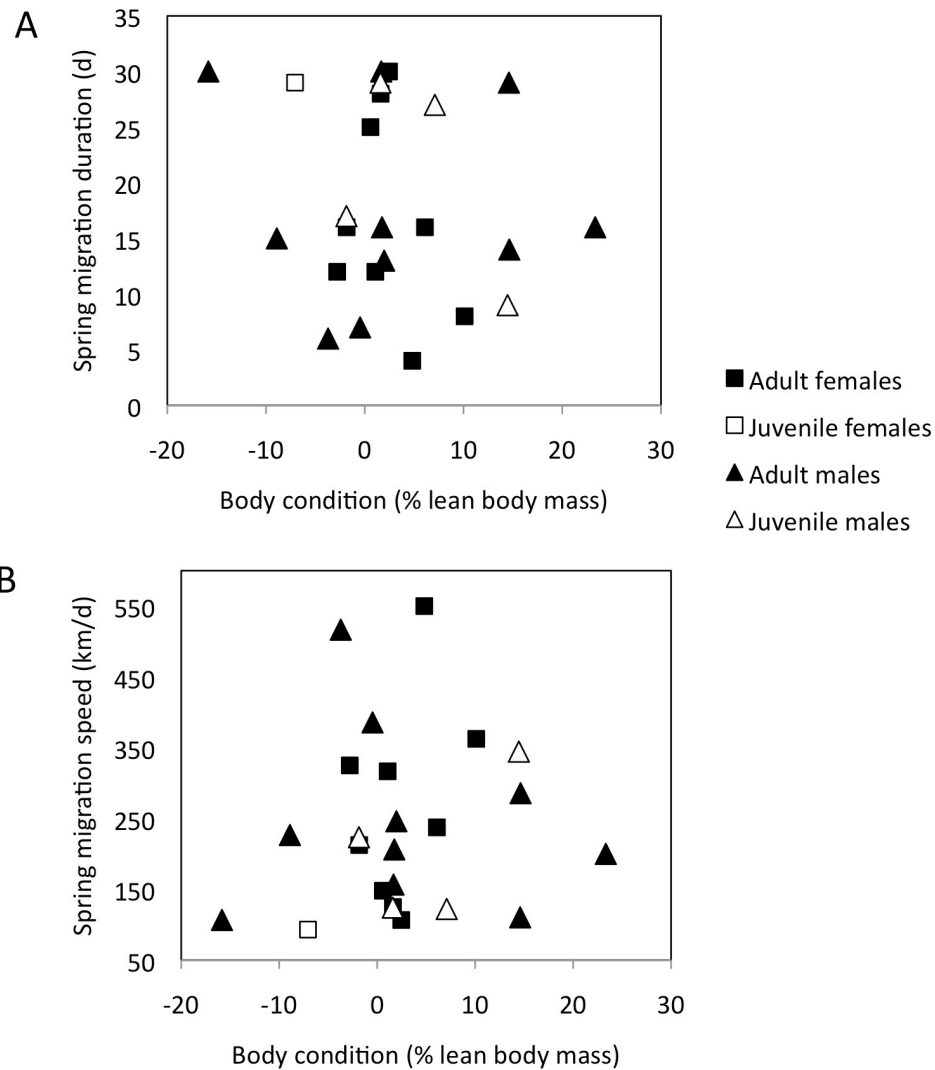


Figure 4-2 Body condition of Wood Thrushes captured during the dry season in Belize did not correlate with: A) Spring migration duration (# of days spent migrating) (n = 24), or B) spring migration speed (total distance covered/duration) (n = 24).

NDVI values varied across the winter range with consistently wetter sites in the south and drier sites in the north. If overwintering site food resources vary with average NDVI, individuals wintering in high NDVI locations should show earlier and/or faster migration relative to birds from the same breeding population (e.g. PA) that overwinter in areas with low NDVI. Breeding birds tracked from PA wintered in the central part of the

Wood Thrush range (Stanley et al. 2014), with an average NDVI of 6957, with a range of 4384-8022 depending on the year and the exact location of the bird. Despite broad variation in conditions experienced by birds from this breeding population during their overwintering period, NDVI in March was not a significant predictor of migration timing at departure, crossing the Gulf of Mexico, or arrival at breeding sites, nor overall migration duration or speed (Table 4-1, Fig. 4-3, Fig. 4-4).

For Belize and Costa Rica birds, inter-annual differences in NDVI were not related to differences in within-population spring migration performance (Table 4-1, Fig. 4-5). However, when not nested by site, NDVI in March was a significant predictor of migration timing (estimate =  $0.002 \pm 0.001$ ,  $t = 2.51$ ,  $P = 0.014$ ) between populations (Fig 4-5), and when including age and sex effects, March NDVI explained 21% of the variation in departure timing ( $F = 7.41$ ,  $df = 3, 69$ ,  $P = 0.0002$ ). This relationship was even stronger at the crossing of the Gulf of Mexico and at arrival to breeding sites, where March NDVI + sex + age explained 40% of the variation (gulf cross:  $F = 19.01$ ,  $df = 3, 76$ ,  $P < 0.001$ ; arrival date:  $F = 17.78$ ,  $df = 3, 72$ ,  $p < 0.001$ ).

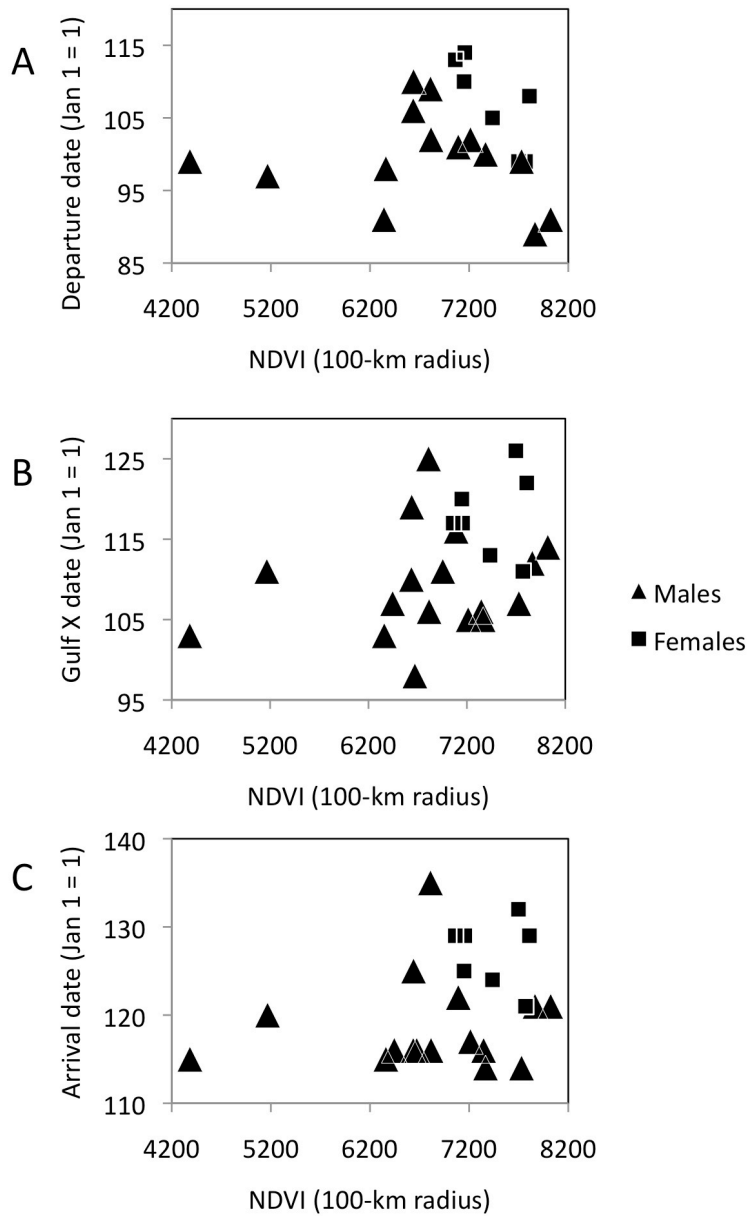


Figure 4-3 Winter site NDVI during March for individuals from a population of Wood Thrushes that breed at the same site in Pennsylvania did not correlate with: A) spring migration departure date (n = 21), B) date crossing the Gulf of Mexico (n = 24), or C) arrival date at breeding sites (n = 23).

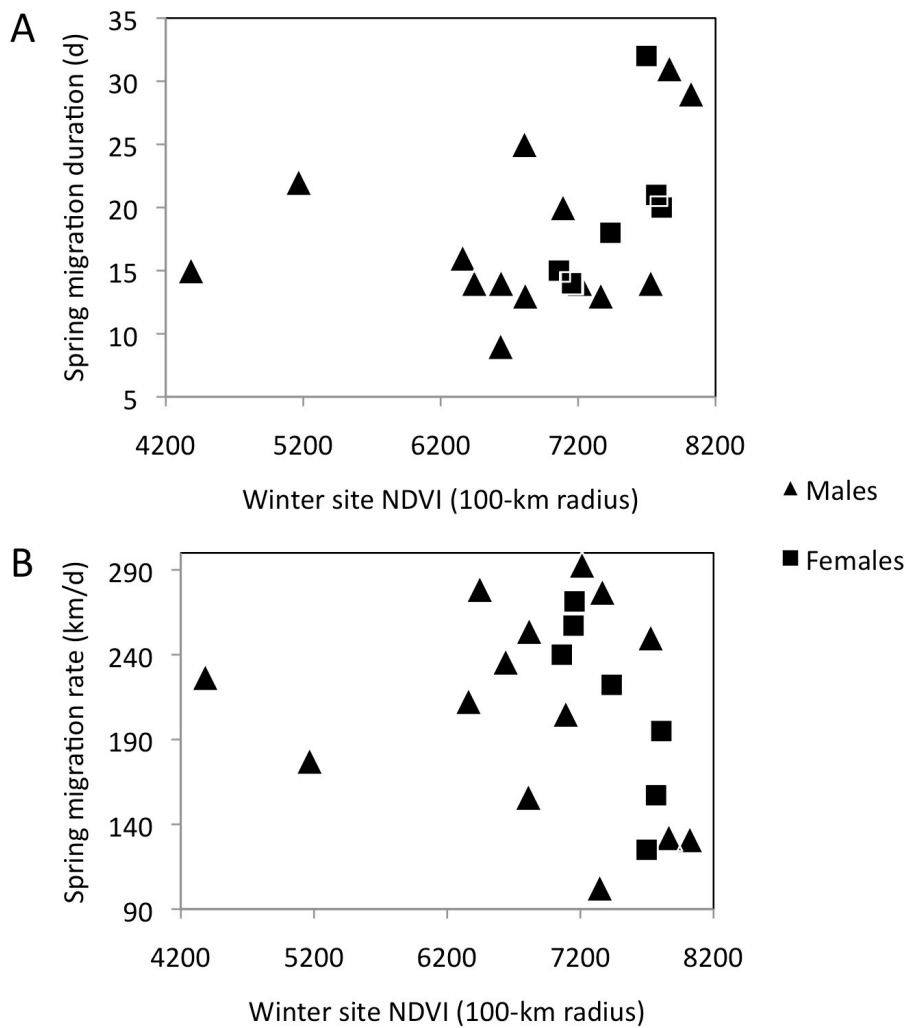


Figure 4-4 Winter site NDVI during March for individuals from a population of Wood Thrushes that breed at the same site in Pennsylvania did not correlate with: A) spring migration duration (# of days on migration) ( $n = 21$ ) or B) spring migration rate (total migration distance/duration) ( $n = 21$ ).

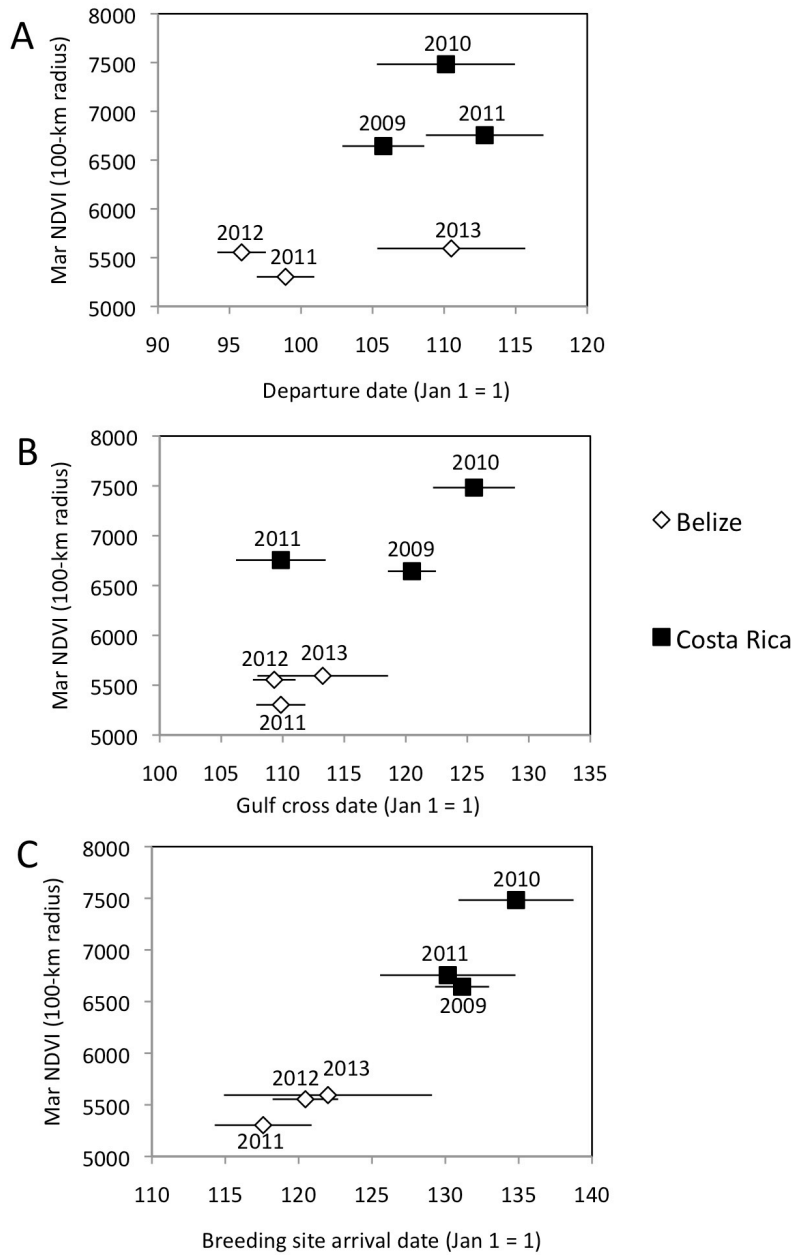


Figure 4-5 March NDVI for two wintering sites in Belize and Costa Rica did not correlate with population-level migration timing, at A) departure from site, B) date crossing the Gulf of Mexico, and C) arrival at breeding sites. March NDVI did predict timing across populations, with birds in wetter sites migrating later.

Table 4-1 Results of general linear models of the effect of March NDVI on individual migration performance for Wood Thrushes from the same breeding site (PA = Pennsylvania) and population-level migration performance at two overwintering sites (BZ = Belize, CR = Costa Rica).

Factor	March NDVI*				
	N	Coefficient	t	d.f.	P
Between-individual variation within a breeding population (PA)					
Departure date	21	-0.001 (0.002)	-0.97	2, 18	0.35
Date crossing Gulf	24	0.001 (0.002)	0.85	2, 21	0.40
Arrival at breeding	23	0.0004 (0.0001)	0.30	2, 20	0.77
Spring duration	21	0.002 (0.002)	1.43	2, 18	0.17
Spring speed	21	-0.02 (0.01)	-1.08	2, 18	0.30
Annual variation within two winter populations (BZ and CR)					
Departure date	52	0.0003 (0.001)	0.26	4, 47	0.80
Date crossing Gulf	56	0.0001 (0.0009)	0.14	4, 51	0.89
Arrival at breeding	53	-0.0003 (0.001)	-0.30	4, 48	0.76
Spring duration	50	-0.001 (0.001)	-0.99	4, 45	0.33
Spring speed	46	0.03 (0.02)	1.71	4, 41	0.09

\*For analysis of spring migrations originating from Belize and Costa Rica sites we nested Mar NDVI by site to assess within-population effects of moisture.

## Discussion

We did not detect any carry-over effects of either late season individual body condition or geographic variation in tropical forest moisture on spring migration performance of a Neotropical migratory songbird. Birds in poorer body condition prior to departure from their overwintering site were not more likely to leave later, migrate for more days, or migrate more slowly than birds in better body condition. A drought in the African Sahel

region producing NDVI values <4000 was enough to drastically delay spring migration (by 10-15 days) of two migratory bird species (Tottrup et al. 2012), but we found no effect of low NDVI on individual migration timing for birds from the same breeding population. Birds from the Pennsylvania site experienced a wide range of winter habitat moisture levels in March between 2009-2011, from very dry (NDVI = 4383) to very wet (NDVI = 8022), yet no carry-over effect on spring migration was detected. Also, inter-annual variation in NDVI at two different sites on the wintering grounds did not influence annual differences in migration pace or timing.

Several studies have shown that birds from more wet overwintering habitats (inferred from stable isotope analysis) produce more young (Norris et al. 2004, Rockwell et al. 2012, Saino et al. 2004), an effect mediated by earlier migration timing, such that they arrive at breeding sites earlier. However, an isotope study of Yellow Warblers (*Setophaga petechia*) did not detect any carry-over effects of winter habitat on arrival date or reproductive success in an Arctic-breeding population (Drake et al. 2014), though winter body condition and en-route migration performance was not known. Carry-over effects of winter habitat moisture (assessed by stable isotope analysis) were also undetected in Magnolia Warblers (*Setophaga magnolia*) captured during spring migration (Boone et al. 2010). Recent year-round tracking of a long distance migratory shorebird did not detect any carry-over effects of delayed spring migration on survival or breeding success and suggested that this may be a result of strong selection on endogenous programs for optimal timing of arrival at breeding sites (Senner et al. 2014). It has been shown in Wood Thrushes that individual migration timing is highly repeatable (Stanley et al. 2012), and that consistent sex and age patterns occur (McKinnon et al. 2014) (see Chapter 2). It may

be that in Wood Thrushes, individual-level carry-over effects are masked by strong genetic constraints on migration timing. This is in contrast to spring migration timing in American Redstarts, which shows clear phenotypic plasticity (Studds and Marra 2005). American Redstarts are small (<10g) insectivores that may suffer more pronounced physiological effects of low-quality habitat, compared with Wood Thrushes, which are larger (45-50g) omnivores. Furthermore, territoriality in Wood Thrushes is less exclusive (Rappole et al. 1989), and many individuals appear to shift habitats and home ranges between wet and dry season (see Chapter 3). Comparative research of life history traits in other species that show strong carry-over effects versus those that apparently do not would shed insight into the mechanistic reasons for species differences.

One important limitation of our study is that geolocators, by recording migration information passively, result in information only for birds that survive migration. However, this limitation is apparent in other studies that have documented pronounced carry-over effects, such as studies at breeding sites using intrinsic markers (Norris et al. 2004) or remote sensing to infer habitat quality at winter quarters (Saino et al. 2004). We did not detect any significant differences in body condition of birds captured in Belize that returned with geolocators versus those that were not recaptured. However, technology which allows the transmission of migration data remotely, such as satellite transmitters, would illuminate the fates of all the birds tracked, and could clearly identify those individuals which disperse to different winter sites and elude recapturing, versus those that die on migration or at breeding sites.

There are other more subtle types of carry-over effects that have rarely been examined in migratory species, and that could occur in Wood Thrushes. For example, birds



in poor quality habitat may have less access to important micronutrients, such as antioxidants, essential amino acids, or minerals (Harrison et al. 2011); to date, these carry-over effects have rarely or never been studied in the field. Lacking sufficient levels of these resources over the winter could negatively affect breeding success in the following season. In our study, we focused on carry-over effects on spring migration timing, but it would be ideal to follow the same individuals through to breeding to determine if differences in winter conditions correlate with reproductive parameters. However, this would require GPS satellite tags that can transmit the breeding location of a bird that was previously studied and sampled on the wintering grounds, and then monitoring the nesting success of that individual at the given location. For a large sample of wintering birds, the logistics of such a study would be very difficult.

We found that population-level migration timing was earlier at the drier wintering site (Belize), not later as would be expected from individual carry-over effects. This geographic pattern is similar to a pattern documented in five species of migratory songbird in the African-European migration system, where wetter conditions in winter were associated with later departure on migration (Tøttrup et al. 2008). We suggest that in Wood Thrushes this is due to the pattern of leapfrog migration (Stanley et al. 2014). Range-wide tracking revealed relatively strong migratory connectivity and parallel, leapfrog migration in Wood Thrushes, where individuals migrated to wintering sites that were negatively correlated with their breeding latitude (i.e. breed further north, winter further south) and positively correlated with their breeding longitude (i.e. breed further east, winter further east). Most Wood Thrushes wintering at our Costa Rica site bred in the north-eastern U. S., while most Belize birds bred in the south- or central-east U.S. This

resulted in Wood Thrushes overwintering in Costa Rica migrating about 1000km farther than the average Wood Thrush overwintering in Belize (Fig. 4-6). Leapfrog migration may have evolved in this species because individuals that winter at drier latitudes with fewer resources are constrained to migrate shorter distances (Bell 1997, Bell 2005) and breed farther south. The 'disadvantage' of wintering in a relatively dry habitat such as at our Belize study site is compensated for by the fact that these birds can start breeding earlier than birds migrating to the north-eastern U.S. The longer migration of the Costa Rican overwintering Wood Thrush can be supported if the costs are offset by increased resource availability in wetter forest (Bell 2005, Bell 1997). For Wood Thrushes in Costa Rica, the consistently wetter habitat would likely result in better body condition of birds (see Chapter 3) and a greater ability to migrate further distances. A recent study of Wood Thrush connectivity using morphological data found that birds overwintering further south had longer wings (Rushing et al. 2014), indicating that these individuals are more adapted to longer migratory flights (Bowlin and Wikelski 2008).

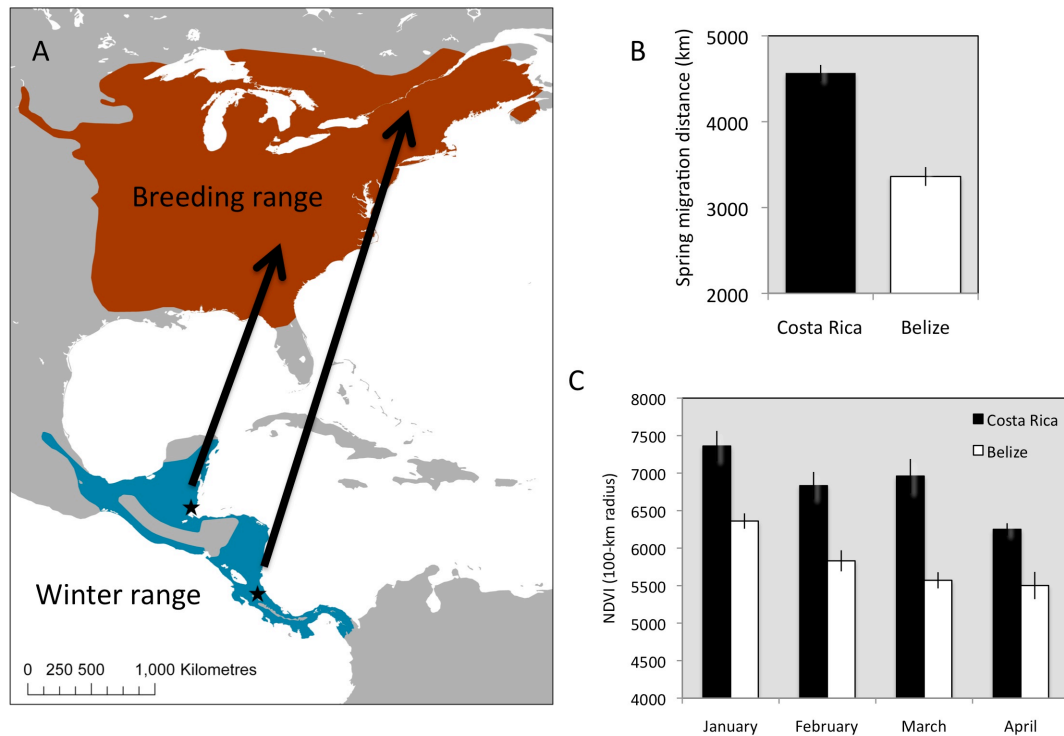


Figure 4-6 Leap-frog migration patterns in Wood Thrushes result in birds from a Costa Rica study site migrating farther than individuals at a Belize study site. A) Map shows breeding and wintering range, with two study sites indicated by stars and arrows indicating general migration destination for birds in spring. B) Migration distance is significantly longer for Costa Rica birds. C) Costa Rica is consistently wetter than Belize, as assessed by monthly NDVI within a 100-km radius of the site, during the overwintering dry season for Wood Thrushes.

Overall our results indicate that carry-over effects of body condition or regional habitat moisture do not affect spring migration timing of Wood Thrushes. Other recent studies in birds have found no or weak support for the influence of winter-grounds carry-over effects on breeding parameters or condition of birds at stopovers (Drake et al. 2014, Drake et al. 2013, Senner et al. 2014, Boone et al. 2010). A recent analysis of 46 species of Afro-Palaearctic migrants found that breeding ground climate was 3.5 times more important for predicting breeding phenology (i.e. laying dates) than winter carry-over

effects (Ockendon et al. 2013). Most Wood Thrushes in this study overwintered during a La Nina ENSO period (all years except 2010, which was a mild El Nino) (National Weather Service 2014, [www.cpc.noaa.gov](http://www.cpc.noaa.gov)), where rainfall on the Caribbean slope of Central America is reduced relative to El Nino years [40], therefore we expected that carry-over effects should be even more likely to occur during the time period of our study than in wetter El Nino years. It is possible that carry-over effects do occur in Wood Thrushes under extreme weather conditions, such as regional droughts, as has been shown for two Afro-Palaeartic migrant songbirds (Tottrup et al. 2012). Such events are predicted to be more common under predicted climate change regimes for Central America (Karmalkar et al. 2011, Hidalgo et al. 2013), and carry-over effects from winter grounds could become more important in future. Range-wide patterns in body condition and habitat moisture should be further explored in the context of migratory connectivity patterns, and life history characteristics, as more migration data becomes available for more species with the further miniaturization of tracking devices.

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## Chapter 5 General Discussion

In this thesis, I applied state-of-the art tracking technology to understand the migration behaviour of a species at risk in Canada (COSEWIC 2012). I conducted the first quantitative review of geolocator tracking in small birds (Ch. 1). I then documented the first-ever spring migrations of naïve juvenile songbirds from start-to-finish (Ch. 2), and conducted the first non-breeding season habitat use study for Wood Thrush (*Hylocichla mustelina*) in Belize (Ch. 3). Finally, I tested for carry-over effects from winter habitat on spring migration performance of Wood Thrushes, from Belize, and across their range (Ch. 4). These studies are part of a larger body of work on Wood Thrushes (see Appendix for abstracts) that includes a study of range-wide migratory connectivity (Stanley et al. 2014), a technical paper on geolocator analysis methods (McKinnon et al. 2013), a note on non-breeding season behaviour of Wood Thrushes in response to playback (Chin et al. 2014), and a test of migration plasticity in Wood Thrushes (Stanley et al. 2012).

### Contribution to understanding of migration

Humans have always been interested in seasonal differences in bird distributions, although it has historically been difficult to study long-distance seasonal migrations of birds (Berthold 2001). Some of the more infamous theories accounting for the disappearance of songbirds from Europe in the winter include Aristotle's idea that swallows bury themselves in the mud of ponds, that small birds ride on the back of large geese, or even that birds migrated to the moon during the temperate winter (Berthold 2001). The actual migratory feats of small birds are hardly less astonishing than even these wild guesses. The

deployment of tracking devices has revolutionized our understanding of the migration of small birds, which despite centuries of bird banding studies, was still so poorly known as to be considered a 'black-box' between stationary breeding and wintering periods. Some of the amazing migration behaviours documented recently include 11,000km non-stop flights by shorebirds between Alaska and New Zealand (Gill et al. 2005), migrations of a 25-g thrush, the Northern Wheatear (*Oenanthe oenanthe*), from Alaska to Africa, travelling over continental Asia (Bairlein et al. 2012), and the revelation, through a combination of geolocator and accelerometer data, that Alpine Swifts (*Tachymarptis melba*) do not ever land (even at night) during their 4-month-stay at their wintering sites in east Africa (Liechti et al. 2013).

In this thesis, I tracked Wood Thrushes on their inaugural spring migrations from winter sites in Belize and Costa Rica (Ch. 2). While our sample size was relatively small, this is the first time juvenile birds have ever been 'followed' northwards to their first breeding sites. We were able to track these birds because of our deployments of geolocators at the winter grounds, where we could capture the first northwards migration. We discovered a strong pattern of age-related delays in timing for juvenile birds. Young birds departed on migration later than adults, and remained delayed throughout the entire migratory journey. In fact, juveniles were increasingly delayed along the way owing to more stopover nights. There are two main theories for why juveniles might be slower and later. First, that they are in poorer condition relative to adults – less able to acquire sufficient resources for migration or out-competed by adults directly. The second (not mutually-exclusive) theory is that there is an age-related shift in endogenous migration programs. Our results support this second theory, as we could find no differences in condition of adults versus juveniles at

a study site in Belize. Furthermore, our related work on migration plasticity showed that adult migration timing was highly repeatable (Stanley et al. 2012), which suggests an age-related switch in migration timing behaviour from late as juveniles to consistently earlier as adults.

This strong genetic control of migration is in contrast to a major body of work on migration of American Redstarts (*Setophaga ruticilla*), where plasticity of timing and performance has been demonstrated (Studds and Marra 2007; Studds and Marra 2011). A broader range of study species, with different life history strategies and habitats would help to tease apart the extent that migration behaviour is plastic. How 'fixed' migration behaviour is likely depends on migration distance, breeding-site habitat or climate, or even phylogenetic history (Berthold 2001). Laboratory studies would also be useful to test if juvenile birds exhibit signs of spring migration preparedness later relative to adults, when access to resources, and photoperiod, are held constant across age classes.

### **Contribution to understanding of non-breeding season ecology**

There still exists a major research bias towards the temperate zone in studies of migratory songbirds (Sherry and Holmes 1996), despite the fact that many species spend more than 50% of their life cycle away from their temperate breeding sites (Ch. 1, Table 1-2). The canon of non-breeding site research is dominated by a few study systems (i. e. *Setophaga* warblers) that occupy a relatively small area (the Greater Antilles) and relatively rare mangrove-scrub habitats. I aimed to address part of this bias by studying a humid-forest-dwelling migrant songbird in mainland Central America, and to test if patterns of condition in relation to habitat moisture were a dominant feature of overwintering ecology of this

species, as they have been shown to be in the Greater Antillean mangrove-scrub ecotone (Strong and Sherry 2000; Studds and Marra 2007; Smith et al. 2010).

I found general support for the winter habitat moisture and food limitation as a driver of condition in Wood Thrushes, although I did not detect any differences by habitat type (Ch. 3). Forests used by Wood Thrushes throughout Central America likely vary extensively, and it is possible that the habitats that I studied, although they differed significantly in some ecological measures, were all relatively similar in quality for Wood Thrushes. We expected that body condition would decline over the winter in Wood Thrushes, but that this decline would be less pronounced in better quality habitat. Therefore we were surprised to find an overall decline in body condition of Wood Thrushes from October to April, regardless of habitat type. This result can be explained in the context of the evolution and maintenance of leapfrog migration patterns.

Our connectivity work demonstrated that Wood Thrushes show a broad pattern of parallel, leap-frog connectivity (Berthold 2001), in that birds breeding furthest north and east winter the furthest south and east (Stanley et al. 2014). Birds at my study site in Belize are at the north end of their wintering range, and thus migrate the shortest distances of any Wood Thrushes, primarily to the southeast and southwest of the breeding range. The maintenance and evolution of this pattern is thought to occur when there is a gradient in habitat quality during the non-breeding season (Bell 2005). The costs of migrating farther are mitigated if the habitat is of higher quality than migrating a more short distance. This theory would predict that habitat in Belize, at the north of the winter range, where birds generally migrate short distances, would be of relatively poor quality compared to habitat found further south. Our condition data support this theory.

Patterns of connectivity for most migratory songbirds have not yet been described. In American Redstarts, a general connectivity map produced using stable isotope analysis suggested that birds wintering in the Caribbean travel the shortest distances to their breeding sites (Norris et al. 2006). In contrast, Redstarts wintering in mainland humid forests of Central America travel much further (Norris et al. 2006). It is possible that habitat quality is more limited in the Greater Antilles for redstarts because this region of their wintering range is marginal habitat which only supports relatively short migrations (Bell 2005). Degradation or climate change effects resulting in increased drying in this area may be producing the strong habitat-condition associations documented in many studies (e. g. Studds and Marra 2011). Assessing Wood Thrush condition and resources across a range of latitudes would lend further support to the idea that a leap-frog pattern in migration is being maintained by a gradient in habitat quality from better, wetter habitat in the south to drier, relatively poor quality habitat for Wood Thrushes in the north.

### **Contribution to conservation**

Wood Thrushes throughout their range have declined by 2.2%/year over the last 10 years; in Canada the declines are even more pronounced, at -4.7%/year in the last 10 years (COSEWIC 2012; Sauer et al. 2012). Threats to Wood Thrushes at breeding sites are relatively well-understood, and include habitat fragmentation and degradation, parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Evans et al. 2011), and at least in previous decades, downstream effects of acid rain (Hames et al. 2002). Threats at wintering sites are less well understood, but as a forest-dwelling species Wood Thrush are likely affected by ongoing high rates of deforestation throughout their Central American winter range (Hansen et al. 2013). In this thesis, one of my goals was to provide useful information on

migration demographics and winter habitat quality that could inform population models and conservation management plans for Wood Thrushes.

I found that juvenile birds spend ~50% longer on spring migration relative to adults (Ch. 2). This implies that threats to habitat at stopover sites could have a bigger impact on juvenile birds than on adults. In Wood Thrushes, population trends at breeding sites are related to recruitment of juveniles (Saracco and Desante 2008). Mapping out specific migration routes and high quality stopover sites for different breeding populations of Wood Thrush would be an important step to increase the survival rate of juvenile Wood Thrushes on migration, and thus improve recruitment into breeding populations. The geolocators that I used in this thesis do not provide enough fine-scale detail of migration routes and stopovers to allow identification of specific stopover sites. However, new archival GPS tags can be programmed to record up to 50 locations to within 10-m, and these tags are now small enough to be safely carried by Wood Thrushes. Programming tags to record locations during the month of April and into early May, when most Wood Thrushes are migrating (Ch. 2, Ch. 4), would allow precise locations of stopovers to be mapped and conservation measures to be directed to those sites where habitat is at risk or sites connected to breeding populations that are declining the most.

My work on winter habitat quality has important implications for Wood Thrushes in the context of projected climate change effects on Central American forests. Climate modelling predicts decreased rainfall and more frequent severe droughts, especially in the northern part of Central America (i. e. Belize) (Hidalgo et al. 2013). I found that habitats in Belize are already relatively low quality for Wood Thrushes (Ch. 3) (although this does not carry-over to affect their migration, Ch. 4). If this area experiences more pronounced dry

seasons over the coming decades and more frequent droughts, forests in this area could begin to cause increased rates of mortality in winter or carry-over negatively to affect spring migration or breeding success. My work suggests that more southern wintering sites, such as those in Costa Rica, could be more buffered from effects of drying, as the habitat there is relatively high quality and is expected to experience less severe drying than the northern part of Central America. Conservation of remaining intact forests in the northern part of Central America, including in Belize, southern Mexico, Guatemala and Honduras, is of critical importance for Wood Thrushes.

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## **Appendix A: Abstracts and citations of related and collaborative work**

The following manuscripts were indirectly part of this thesis, and or collaborative projects using data collected during this project. A brief note under each citation outlines the author's contribution to each manuscript.

**1) Stanley, C. Q., E. A. McKinnon, K. C. Fraser, M. P. MacPherson, G. Casbourn, L. Friesen, P. P. Marra, C. E. Studds, T. B. Ryder, N. Diggs, and B. J. Stutchbury. 2014. Connectivity of Wood Thrush breeding, wintering, and migration sites based on range-wide tracking. *Conservation Biology Early Online* pp 1-11. DOI:10.1111/cobi.12352**

Contribution: EAM was joint first-author and corresponding author, contributed substantially to writing, analysis, and data collection.

Many migratory animals are experiencing rapid population declines, but migration data with the geographic scope and resolution to quantify the complex network of movements between breeding and non-breeding regions are often lacking. Determining the most frequently used migration routes and non-breeding regions for a species is critical for understanding population dynamics and making effective conservation decisions. We tracked the migration of individual Wood Thrushes (*Hylocichla mustelina*) ( $n = 102$ ) from across their range with light-level geolocators and, for the first time, quantified migration routes and wintering regions for distinct breeding populations. We identified regional and species-level migratory connectivity networks for this declining songbird by combining our tracking results with range-wide breeding abundance estimates and forest cover data. More than 50% of the species occupied the eastern wintering range (Honduras to Costa Rica), a region that includes only one-third of all wintering habitat and that is undergoing intensive deforestation. We estimated that half of all Wood Thrushes in North

America migrate south through Florida in fall, while in spring approximately 73% funnel northwards through a narrow span along the central U.S. Gulf Coast (88-93°W). Identifying migratory networks is a critical step for conservation of songbirds and we demonstrated with Wood Thrushes how it can highlight conservation hotspots for regional populations and species as a whole.

**2) McKinnon, E. A., C. Q. Stanley, K. C. Fraser, M. MacPherson, G. Casbourn, P. P. Marra, C. E. Studds, N. Diggs, and B. J. M. Stutchbury. 2013. Estimating geolocator accuracy for a migratory songbird using live ground-truthing in tropical forest. *Animal Migration* 1:31-38.**

Contribution: EAM was corresponding author, wrote manuscript, conducted analyses and fieldwork.

Miniaturized light-level geolocators allow year-round tracking of small migratory birds, but most studies use calibration only at breeding sites to estimate geographic positions. Ground-truthing of positions in tropical habitat is needed to determine how accurate breeding site calibrations (i.e. sun elevations) are for estimating location of winter sites. We tested the accuracy of geographic assignments using geolocator data collected from Wood Thrushes (*Hylocichla mustelina*) in Central America. For a given light threshold, sun elevation angle was higher in the tropics than at breeding sites and also varied significantly at tropical winter sites between wet (Oct- Dec) and dry (Jan-Mar) seasons. However, estimation of Wood Thrush territory latitude did not differ significantly when using breeding or tropical dry season sun elevation. Average error in assignment to tropical sites was  $365 \pm 97$  km ( $0.2-4.4^\circ$ ) in latitude. To obtain the best latitude estimates in the tropics with geolocators, we recommend using locations during the dry season where sun elevations are closer to those measured at breeding sites. We emphasize the importance of longitude in assigning forest birds to unknown sites; longitude estimates for Wood Thrushes in the tropics were, on average, within  $66 \pm 13$  km (0-

0.6°) of actual longitude. Latitude estimates were more accurate ( $180 \pm 48$  km) when assigning birds to breeding sites using deployments of geolocators in the tropics. Studies of species that are territorial in winter could collect more accurate migratory connectivity data by deploying geolocators at tropical wintering sites.

**3) Chin, S., E. A. McKinnon, K. C. Fraser, J. Rotenberg, and B. J. M. Stutchbury. 2014. No sex bias in Wood Thrushes (*Hylocichla mustelina*) captured by using audio playback during the non-breeding season. *Wilson Journal of Ornithology* 126(3):599-605.**

Contribution: First author SC was a lab volunteer who worked with EAM for two summers doing genetic sexing. Project design and fieldwork conducted by EAM. Co-written by EAM and SC.

Conservation of migratory songbird species requires information on abundance and survival over the annual cycle, including from overwintering sites. Broadcasting recorded calls or songs (playback) often increases detections or capture rates of birds, and can improve estimates of abundance or survival. Wood Thrushes overwintering in Belize regularly respond to broadcasted conspecific vocalizations (songs); however, it is unknown if song attracts a specific age, sex, or size class of birds. Our goal was to determine if the use of playback resulted in sex, age, or size-biases in captures of Wood Thrushes, relative to captures without playback, at a non-breeding site in Belize, Central America. We predicted that birds responding to playback would be: (1) male, (2) adults, and (3) larger than birds caught without playback, owing to social dominance of larger adult males over juveniles and females. Surprisingly, we found no significant difference in sex or age ratio, or body size of birds captured with or without playback. It may be that predicted patterns of social dominance are not apparent in non-breeding Wood Thrushes, or that song playback does not elicit responses related to local social dominance. Regardless of the mechanism, we conclude that the use of song playback during the non-breeding season does not bias captures of Wood Thrushes by sex, age, or body size, and when

used with caution, can be an effective tool for studies on the species' wintering grounds.

**4) Stanley, C. Q., MacPherson, M., K. C. Fraser, E. A. McKinnon, and B. J. M. Stutchbury. 2012. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. PLOS ONE 7(7): e40688.**

Contribution: EAM edited manuscript, helped with analyses and collected data.

Tracking repeat migratory journeys of individual animals is required to assess phenotypic plasticity of individual migration behaviour in space and time. We used light-level geolocators to track the long-distance journeys of migratory songbirds (wood thrush, *Hylocichla mustelina*), and, for the first time, repeat journeys of individuals. We compare between- and within individual variation in migration to examine flexibility of timing and route in spring and autumn. Date of departure from wintering sites in Central America, along with sex and age factors, explained most of the variation (71%) in arrival date at North American breeding sites. Spring migration showed high within-individual repeatability in timing, but not in route. In particular, spring departure dates of individuals were highly repeatable, with a mean difference between years of just 3 days. Autumn migration timing and routes were not repeatable. Our results provide novel evidence of low phenotypic plasticity in timing of spring migration, which may limit the ability of individuals to adjust migration schedules in response to climate change.