ABSTRACT

Title of Dissertation: ECOLOGICAL CAUSES AND CONSEQUENCES OF NON-BREEDING MOVEMENTS IN A DECLINING MIGRATORY SONGBIRD, WOOD THRUSH (HYLOCICHLA MUSTELINA)

Calandra Quinn Stanley, Doctor of Philosophy, 2019

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In this dissertation I evaluate the ecological correlates of non-breeding space-use strategies and how these drive within and between season movement dynamics in a declining migratory songbird, wood thrush (*Hylocichla mustelina*). In Chapter 1, I deployed high-resolution GPS transmitters across 5 breeding populations to quantify habitat selection as wood thrush moved across the annual cycle. I found seasonal variation in habitat selection at the regional, landscape and local scales which suggests the factors driving the evolution of habitat selection preferences vary across seasons and environmental conditions. In Chapter 2, I combined radio telemetry and GPS tracking to examine how environmental conditions drove space-use strategies during the non-breeding stationary period. I found evidence that both small- and large-scale movement dynamics were dependent on moisture levels on tropical non-breeding grounds. At small spatial scales, dry conditions drove low food availability, reduced individual body condition and these individuals had larger home ranges. In this same chapter I integrated archival GPS tag data to demonstrate that wood thrush from across the breeding range engaged in permanent large-scale mid-winter shifts in home ranges and, similar to radio-tagged birds, that individuals from wetter, higher quality habitats were more likely to use this strategy. I suggest that the facultative movements are a condition-dependent strategy allowing wood thrush to find alternative habitats as conditions deteriorate across the dry season in their non-breeding grounds. Finally, to determine how food availability may influence timing of spring migration, I performed a food manipulation experiment with captive wood thrush in Chapter 3. I found that food availability and body condition modulated the intensity, but not onset, of migratory restlessness (*Zugunruhe*), an index of migratory disposition in captive birds. These results suggest that non-breeding food limitations could constrain migration preparation in wood thrush. Low food availability also advanced the onset of migratory fattening. I suggest that advancing migratory fattening when food availability is low may provide a mechanism to flexibly adjust migration timing under poor environmental conditions. Together these findings suggest that wood thrush exhibit a diversity of behavioural mechanisms to handle environmental heterogeneity across the annual cycle.

ECOLOGICAL CAUSES AND CONSEQUENCES OF NON-BREEDING MOVEMENTS IN A DECLINING MIGRATORY SONGBIRD, WOOD THRUSH (*HYLOCICHLA MUSTELINA*)

by

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Dedication

To my family,

For all the love

and unwavering support over the years.

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Overview:

Migration, the cyclical large-scale movement of animal populations, is an impressive physiological and navigational feat thought to have evolved in many species as a strategy to inhabit seasonal environments (Milner-Gulland et al. 2011). The large-scale movements of migratory animals split their annual cycle into periods that occur in multiple ecologically and geographically distinct environments that require novel adaptive strategies to negotiate these disparate locations (Åkesson and Hansson 2014). The large-scale movements of migrants, however, also make them more susceptible to environmental change and degradation since they can potentially be affected at any or all of the habitats they occupy across their annual cycle (Lindström et al. 2014).

Recent declines in long-distance migratory songbirds that travel some of the longest known distances between breeding and non-breeding grounds, have brought into focus the need to disentangle the processes regulating these populations across the annual cycle (Faaborg et al. 2010). The largest gaps in our knowledge of the mechanisms mediating these species declines stem from the logistical difficulties in monitoring individuals across the annual cycle and despite migratory songbirds spending only 3-4 months on their breeding grounds, the vast majority of research has focused on this period (Marra et al. 2015). During the non-breeding season, survival is the key vital rate for migrants and the primary ecological drivers for this are food and habitat. However, factors limiting migrants can also act indirectly through non-lethal effects that carry-over to influence survival in subsequent seasons or reproductive success (Marra et al. 1998, Harrison et al. 2011). Determining the key ecological factors limiting demographic characteristics across the non-breeding periods will first require an understanding of the ecological and physiological strategies employed by species during this period, something lacking for the majority of bird species.

The goal of this dissertation was to contribute to a better understanding of the ecological factors driving population dynamics during the non-breeding season of a declining migratory songbird, wood thrush (*Hylocichla mustelina).* To do this I explored the ecological factors driving non-breeding space-use strategies and movement dynamics. I employed both observational and experimental approaches to monitor the behavioural strategies employed by wood thrush in response to environmental heterogeneity both within and across the non-breeding periods. In my first chapter I examined how behavioral strategies vary across periods of the annual cycle by investigating seasonal variation in habitat selection. In the final two chapters I focused on the role of one ecological factor, food availability, and how it potentially influences the movement ecology of wood thrush during the non-breeding stationary period (hereafter winter) and spring migration.

Wood thrush are large (40-50g), omnivorous Neotropical migratory songbirds that breed across eastern North America and winter in Mexico and Central America. Similar to many long-distance Neotropical migratory species, their populations have declined by 60% over the last 50 years (Sauer et al. 2013). Wood thrush are an ideal study system for a study of movement ecology because they are a common forest birds, they engage in multiple non-breeding space-use strategies (Rappole et al.

1989), are large enough to carry a range of tracking devices necessary for monitoring a highly mobile species, and exhibit site fidelity across their breeding and wintering range making it easier to recover archival tracking devices.

Determining how migratory songbirds respond to environmental heterogeneity across the annual cycle will be critical for identifying habitat requirements across each life-history stage, information lacking for most species. In Chapter 1, I deployed high-resolution GPS transmitters across five breeding populations to quantify habitat selection at multiple spatial scale (regional, landscape, local) as wood thrush moved across periods of their annual cycle. For the first time for a migratory songbird I obtained direct evidence from individually tracked birds of seasonal shifts in habitat selection preferences. In general, migratory periods were characterized by greater behavioural flexibility and a shift to more generalist habitat selection. I also employed a novel technique to identify regional habitat selection across populations by quantifying patterns of migratory connectivity between breeding and non-breeding locations. The identification of regional habitat selection and population-specific patterns of habitat use during fall migration and the winter period suggest populations may exhibit different habitat selection preferences. Together these results suggest the factors driving the evolution of habitat selection preferences (e.g. food availability, timing of breeding) vary across seasons but also environmental context and should be considered when assessing habitat suitability for migratory species across the annual cycle.

Food availability has been identified as a key ecological factor contributing to non-breeding season limitation, notably in Neotropical migratory warblers (Sherry et al. 2005, Brown and Sherry 2006a, Smith et al. 2011a). Therefore, in the final two chapters I examined the drivers and consequences of differential winter food availability on the movement behaviour of wood thrush during the winter and spring migratory period. In Chapter 2, I examined how moisture gradients drive food availability and in turn influence space-use strategies during the winter period. By monitoring birds using radio telemetry at a study site in Belize I found evidence of food limitation for non-breeding wood thrush that was driven by patterns of moisture. Dry conditions drove low food availability, low individual body condition and the adoption of larger home ranges. By combining radio telemetry data from our study site in Belize and GPS tracking from Chapter 1, I discovered that a high proportion of wood thrush from across the breeding range engaged in permanent large-scale mid-winter shifts in home ranges. Wood thrush in wetter habitats had a higher probability of engaging in these large-scale facultative movements. I suggest that the facultative movements are a condition-dependent strategy to allow wood thrush to find alternative habitats as conditions deteriorate across the dry season. These results suggest that food availability driven by patterns of moisture influence both small- and large-scale space use strategies for non-breeding wood thrush

In Chapter 3, I evaluated if differential non-breeding food availability could potentially influence the endogenous spring migratory schedules of wood thrush by performing a food manipulation study on a captive population. By holding birds under two feeding treatments (ad libitum or “control” vs. reduced food availability expected to result in a 5% decline in body weight) I found that food availability and body condition modulated the intensity of migratory restlessness (*Zugunruhe*), an index of migratory disposition in captive birds. Low food availability did not influence the onset of *Zugunruhe*, but migratory fattening was advanced. The advancement of migratory fattening when food availability is low may provide a mechanism to flexibly adjust migration timing under poor environmental conditions. These results suggest that non-breeding food limitations could constrain migration preparation in wood thrush and highlights the tricky balancing act faced by wood thrush between optimizing survival during migration and maintaining optimal spring migration schedules.

The results described here and in more detail in the following chapters identify a diversity of behavioral strategies employed by wood thrush to handle environmental heterogeneity during the non-breeding periods. They suggest flexibility in space-use strategies and movement dynamics both across and within seasons as individuals adjust to different life-history stages or environmental conditions. This research also highlights the importance of considering the full annual cycle of migratory songbirds, including seasonal interactions, when investigating factors limiting migratory species. As environmental degradation and climate change proceeds understanding how migratory birds respond to environmental heterogeneity will be increasingly important for the management of declining species. Across the non-breeding range of wood thrush conditions are projected to become increasingly arid and the research presented here suggests that these climate shifts could have important consequences for wood thrush both within the non-breeding periods and potentially into subsequent periods through seasonal interactions in their annual life cycle.

Chapter 1 Year-round habitat selection for a Neotropical migratory songbird using high resolution GPS tags

Abstract

Deciphering how environmental heterogeneity affects population dynamics in migratory species is complicated by the redistribution of individuals in time and space across the annual cycle. Approaches that tackle this problem require information about how migratory species respond to ecological factors across time and space, and how they are linked across migratory periods. Using high spatial resolution GPS tracking of individual male songbirds, we quantified for the first time (1) local and landscape-scale habitat selection across the annual cycle and (2) patterns indicative of regional habitat selection for five populations of wood thrush (*Hylocichla mustelina*) throughout their breeding range. We found that wood thrush exhibited seasonal variation in habitat selection. Across stationary periods, local habitat selection included variables associated with forest habitat, notably, a preference for forest edge habitat. In contrast, during migratory periods wood thrush exhibited greater behavioural flexibility indicative of a more generalist approach to habitat selection. Landscape habitat selection was only identified during the breeding season (average patch size) and could be a result of extensive forest fragmentation in the North American breeding grounds. We also identified individual distribution patterns indicative of regional habitat selection during fall migration and the stationary non-breeding period, but not spring migration. In accordance with patterns of regional habitat selection, we found population-specific patterns in habitat use (e.g. distance to forest edge). Seasonal changes in habitat selection at multiple spatial scales suggest the factors driving habitat selection patterns are aligned with life-history stage and may be dependent on regional differences in landscape composition. These results highlight the importance of a full annual cycle approach to ecological studies that address how migratory species respond to spatial and temporal environmental heterogeneity.

Introduction

The annual cycle for a migratory species is characterized by long-distance movement of individuals between multiple geographically, and often ecologically, disparate locations (Newton 2008, Åkesson and Hansson 2014). In each location, environmental habitat heterogeneity drives individual settlement decisions and habitat selection processes often have individual fitness consequences (Hutto 1985, Mayor et al. 2009). Migratory birds, despite their small size, travel some of the longest distances of any animal (Alerstam et al. 2003). Although empirical studies of habitat selection have been conducted within breeding (Orians and Wittenberger 1991, Mitchell et al. 2001, Lee et al. 2002), migration (Buler et al. 2007, Mccabe and Olsen 2015, Lafleur et al. 2016) and non-breeding stationary periods (Chandler and King 2011, Fraser et al. 2017), few species have been assessed across multiple seasons. Moreover, studies rarely use the same individuals or populations (but see Beatty et al. 2014, Pickens et al. 2017). As such, we know relatively little about the breadth of suitable habitats and how individuals select habitats throughout the annual cycle for migratory birds (Marra et al. 2015, McGarigal et al. 2016).

Adaptive habitat selection has been theorized as a hierarchical decision-making process by which the factors that drive habitat suitability (based on fitness costs and benefits) and the mechanisms for assessing suitability occur at different spatial and temporal scales across the annual cycle (Figure 1.1; Johnson 1980, Wiens 1989, Mayor et al. 2009). At each spatial or temporal scale, the decision making process may involve novel and multiple interacting criteria (e.g., patch size, predation rate) and be constrained by the effects of criteria from higher scales (annual vs diel; Rettie and Messier 2000, Mayor et al. 2009). When considering spatial scales, habitat selection decisions at the broadest scale will shape the species' geographic range and patterns of regional population distribution (hereafter referred to as "regional"; Johnson 1980, Meyer and Thuiller 2006). Hutto (1985) refined this idea for migratory birds and suggested non-habitat factors are expected to drive decisions at the regional scale. For example, an individual's genetically programmed and learned migration route (Hutto 1985), weather (Moore and Aborn 2000, Buler and Moore 2011), or physiological condition (Studds et al. 2008, Rushing et al. 2015) are factors expected to play a role in regional habitat selection. In contrast, as the spatial scale decreases, Hutto (1985) suggested that habitat selection will increasingly be driven by the costs and benefits associated with the habitat itself. At intermediate scales (hereafter referred to as "landscape"), selection drives the choice of a particular habitat type and home range. Finally, at finer spatial scales, selection of habitats within the home range (hereafter referred to as "local") or microhabitat selection is most closely linked to the ultimate factors driving habitat suitability (e.g. food or nesting site availability). Equally important to consider is how the decision-making process changes across temporal scales or levels (Cody 1985, Wiens 1989). For example, factors limiting an individual's fitness can vary between diel and seasonal decisions (scales) or equally across different seasons (levels; Mayor et al. 2009). Therefore, habitat selection may be a hierarchical process that operates across multiple spatial scales ranging from regional to micro-habitat but also across temporal scales.

Over the last thirty years, the multi-scale approach to habitat selection has been incorporated into many ecological studies across a range of vertebrate taxa (Wiens and Milne 1989, Orians and Wittenberger 1991, Rettie and Messier 2000, Grand and Cushman 2003). For instance, Buler et al. (2007) found that factors driving the selection of stopover habitat by migrant songbirds along the Gulf of Mexico differed across multiple spatial scales. At regional spatial scales the most relevant limiting factors driving habitat selection were weather and physiological condition (non-habitat factors) after crossing a large ecological barrier; whereas, at the landscape and microhabitat scale the limiting factor was food (habitat factor). Overall many studies have successfully shown that habitat selection is scale-dependent, largely in terms of spatial scales; however, the inferences that can be drawn from these studies have often been limited due to the low spatiotemporal extent at which they were conducted (McGarigal et al. 2016).

For migratory songbirds, most ecological studies have been conducted during the breeding season (Marra et al. 2015). Although habitat selection studies are increasingly conducted across multiple scales (landscape to microhabitat, seasonal to diel), their scope has been restricted to studies of single seasons on single populations. When habitat use across seasons has been documented, many migratory songbirds, even those considered habitat specialists, appear to show shifts in habitat use during the non-breeding season (Petit 2000, Zuckerberg et al. 2016). This lack of consistency in habitat associations suggests that individuals can maximize their fitness across seasons through behavioural flexibility in their habitat settlement decision-making. (i.e. across life-history stages: nesting vs. re-fueling). However, documenting behavioral flexibility in habitat selection has remained challenging due to the difficulty in tracking small mobile animals across large spatial and temporal scales. Therefore, two large information gaps related to behavioral flexibility in habitat selection need to be addressed: 1) what factors drive habitat selection decisions across seasons for individual birds, and 2) what factors underlying habitat selection vary across the species range?

In migratory species, regional habitat settlement decisions occur seasonally. The practical limitations of sampling across large spatiotemporal scales has prevented studies of regional habitat selection and the ultimate factors (extrinsic vs. intrinsic) and cues (innate vs. learned) driving selection at this scale (Figure 1.1; Moore et al. 1993, Kelly et al. 1999, McGarigal et al. 2016). Migratory connectivity is most commonly used to describe the strength of regional re-distribution of migratory individuals across the annual cycle, but studies of migratory connectivity could also provide important insights into the non-habitat factors that affect regional habitat selection patterns. For example, patterns of migratory connectivity could be used to identify the presence of population-specific regional habitat selection decisions as individuals move across large distance throughout the year. Due to the hierarchical nature of the habitat selection process migratory connectivity can also provide a measure of how regional habitat selection might be expected to constrain settlement decisions at finer spatiotemporal scales. Given that the environment is expected to vary across a species range, better integration of regional scale habitat selection could have important implications for our interpretation of habitat selection patterns across a species range.

Here, we evaluated the spatial and temporal patterns of habitat selection at three spatial scales (local, landscape and regional) and across all seasons (breeding, fall migration, winter and spring migration) of the annual cycle for wood thrush (*Hylocichla mustelina)*, a Neotropical migratory songbird using fine-spatial resolution archival GPS geolocators deployed across five distinct breeding populations. First, to determine how factors driving habitat selection change across seasons, we explored individual variation in habitat selection at the local and landscape scale. Since wood thrush are characterised as forest interior species that are tolerant of forest fragmentation (Evans et al. 2011), we predicted that if habitat selection remains constant across seasons, thrushes will consistently select local and landscape features characteristic of interior forest habitats. In contrast, if habitat selection exhibits seasonal plasticity, we expected habitat selection to differ during migratory periods leading to more generalist habitat selection as birds become more responsive to non-habitat features (e.g. temporal constraints on migration, energetic demands) and have more difficulty accurately assessing the value of unfamiliar habitats. In addition, we predicted that wood thrush will exhibit local and landscape scale habitat selection during stationary (breeding and winter) periods, but selection will shift to landscape scale features during migration, as they provide a quick cue for birds to assess habitat quality (Buler et al. 2007, Beatty et al. 2014).

Second, to test for seasonal changes in regional habitat selection between breeding populations we assessed the strength of migratory connectivity. Based on earlier work on wood thrush migratory connectivity with low resolution tracking devices (Stanley et al. 2015), we predicted the strength of regional habitat selection would vary seasonally. Specifically, strong connectivity during the fall is driven by population specific route (Stanley et al. 2015); these patterns predict regional habitat selection during fall stopover at the Gulf of Mexico. By contrast, from breeding to winter sites, wood thrush show moderate connectivity (Stanley et al. 2015); these patterns suggest weaker patterns of regional habitat selection. Finally, weak connectivity during spring migration is driven by convergence of migratory routes at the Gulf of Mexico; these patterns suggest no regional habitat selection.

Third, if regional habitat selection results in breeding populations remaining geographically isolated across the annual cycle, we predicted populations will diverge in habitat selection at finer spatial scales. Correspondingly, we expected individuals from the same breeding populations to have similar patterns of habitat use during fall migration and the winter period, when regional habitat selection is predicted to occur, but no differences in habitat use between breeding populations during spring migration when regional habitat selection is not predicted to occur.

Methods

Study system

Wood thrush are medium sized, long-distance Neotropical migratory songbirds that breed in deciduous and mixed forests of eastern North America and winter in the broad-leaf and palm forests ranging from southern Mexico to northern Panama (Evans et al. 2011). They are a multi-brooded, omnivorous species that primarily forages on the ground. Wood thrush maintain territories during the winter and breeding season; however, they show extensive flexibility in territorial behavior. Tracking studies have found they engage in regular off-territory forays and can make large scale relocations (1-25 km) throughout stationary periods (Rappole et al. 1989, Lang et al. 2002). Their global population size has declined by 60% since 1966 based on breeding ground surveys (Sauer et al. 2013).

Field Methods and GPS telemetry

To determine spatio-temporal variation in habitat selection across the annual cycle we studied wood thrush from 2014-2015. Archival GPS tags (Model PinPoint-50, 1.8 g, 50 fixes, Lotek Wireless) were deployed on 137 breeding adult male wood thrush over the summer of 2014 and 2015 in Delaware, Indiana, North Carolina, New York and Minnesota (Appendix S1, Supplementary Methods, Table S1.1). The tags provide location estimates for individual birds with an estimated accuracy of 10 meters. GPS tags were recovered by returning to sites the following summer and recapturing individuals. We recovered 23 tags, and retrieved data from 21 tags. Two tags were unresponsive (no data retrieved) and 9 lost antennas sometime after release (partial data recovery). We obtained an average of 26 out of a maximum of 50 points per tag (range: 1-46; Appendix S1, Table S1.2). Most missing fixes, excluding those involving lost antennas, occurred during migratory periods (Appendix S1, Table S1.2). Due to low success of location fixes during migratory periods, annual cycle stages (breeding, fall migration, winter, spring migration) were defined based on the first or last location recorded at stationary stages (i.e. spring migration ends day before first recorded point on breeding grounds). Migratory periods were identified as northward or southward movements over the course of consecutive days (+2 points, 6 - 8 days) and larger than 20km.

Habitat Features:

To quantify the structural characteristics of habitats occupied by wood thrush across the annual cycle we paired location fixes to geospatial habitat data. Location estimates spanned eastern North America and Central America; therefore, we restricted geospatial data to those sources that covered the entire study area (detailed description of satellite imagery in Appendix S1, Table S1.3). At each location fix we examined habitat use characteristics at two spatial scales (local and landscape) using the extract function in the R package *raster* (Hijmans 2016) . Local habitat features represented remotely sensed data interpolated at each point location and included percent tree cover, Enhanced Vegetation Index (EVI), patch size (km^2) and proximity to non-forest (m; detailed description of interpolation methods Appendix S1, Table S1.3). Landscape characteristics represented remotely sensed data interpolated from a buffer of 1 km radius around each point location and included average percent tree cover and average patch size (km^2). A 1 km buffer was used because off-territory forays of wood thrush typically range from 150 m to 1 km (Rappole et al. 1989, Lang et al. 2002). To assess landscape composition, we interpolated data from classified land cover layers using a 5 km buffer (Appendix S1, Table S1.3). A 5 km buffer was used because classified land cover layers suitable for a 1 km buffer were unavailable across our study area, landscape composition was therefore analyzed separately from the other landscape characteristics.

Local and Landscape Habitat Selection

To identify variation in spatio-temporal patterns of habitat selection at the individual level we explored three measures. First, at the landscape scale, we examined diversity in landscape composition across seasons. Second, we quantified the individual repeatability of habitat features at both the landscape and local scales across the stationary (breeding and winter) and migratory periods (fall and spring migration). Finally, to disentangle whether seasonal differences in habitat usage were driven by changes in habitat availability across regions or shifts in factors driving habitat selection, we employed a multi-scale approach to determine habitat selection within a use-availability design.

First, to estimate seasonal diversity in landscape composition for each individual we calculated the Shannon diversity index (Shannon 1948). The index was assessed each season based on landscape composition (the number of classified land cover classes) at each point location used by an individual with the R package *vegan* (Oksanen et al. 2017). High landscape diversity indicates individuals' occupied landscape with multiple habitat types across the season.

Second, for each habitat feature we calculated the repeatability of use among individual birds between stationary and migratory periods. Repeatability quantifies the proportion of between-individual variation from observations relative to the total variation in the population for a repeated measure (Lessells and Boag 1987). Repeatability increases when within-individual variation is low (e.g. individuals chose locations with consistent habitat features) and between-individual variation increases (individuals chose different features). To calculate repeatability we used the r package *rpt* (Stoffel et al. 2017) based on the structure of the best-fit model describing each habitat feature (see Appendix S2).

Third, we constructed discrete-choice models for each season to determine seasonal habitat selection preferences of wood thrush. These models examine the probability of an individual choosing a location based on a choice set of alternative available locations (Cooper and Millspaugh 1999). If habitat features are used disproportionate to their availability, it is assumed they confer a fitness advantage (Manly et al. 2004). If these habitat features change across seasons, we conclude this represents behavioural flexibility in habitat preferences. GPS location fixes were considered as *used* resource units. *Available* resource units were generated by creating a buffer around each *used* resource unit and generating up to 20 random points. Therefore, each *used* resource unit had its own set of *available* units. Due to varying levels of cloud coverage across the study area, number of *available* points ranged from 10 to 20. Consistent parameter estimates can be obtained with as few as four available alternatives (McFadden 1978); however, to account for spatial variation in habitat features we used up to 20 points when possible (Bonnot et al.

2011). For all *used* and *available* points, local and landscape habitat features were extracted as defined in the habitat features section. Fewer location estimates were obtained from each individual during migratory periods (mean number location fixes, migration = 4.3; stationary = 10.25). To account for different numbers of replicate observations during migratory periods, only 4-5 location fixes were used from the stationary periods for each individual (Appendix S1, Table S1.2). Points were subsampled within stationary periods by selecting *used* resource units with the largest distance between them.

A multi-scale approach was used to identify habitat selection patterns that would be ecologically relevant to wood thrush (Wiens 1989, Buler et al. 2007). Since relevant spatial extents were unknown for wood thrush (size of relevant study area), we delineated four spatial extents encompassing distances moved within an individual's territory (0.5 km), during off-territory forays (5km), and during relocation events (15 and 25 km) based on prior information on wood thrush spatial ecology. The spatial extent defined the size of the buffer created around each *used* resource point and served to generate the *available* points for each used point. Bayesian mixed conditional logistic regressions were used to model the probability of a wood thrush choosing a *used* resource unit out of the *available* choice set. The mixed conditional logistic regression was adapted from the methods of Beatty et al. (2014) and a Bayesian framework was employed because comparable mixed conditional logistic regression were not available in existing Maximum Likelihood R packages. We developed a set of candidate models to test alternative hypotheses about the habitat features influencing habitat selection (Appendix S1, Table S1.4). All models, with the exception of the null model, included individual bird as a random variable to account for variation in selection patterns among birds. At the 0.5-km and 5-km spatial extent we evaluated two models (local and null) and at the relocation level (15-km and 25-km) we evaluated four models (local, landscape, full, and null). These models were run for each season for a total of 48 models (12 models x 4 seasons).

Regional Habitat Selection

To identify regional habitat selection, we estimated migratory connectivity between (1) breeding and wintering grounds and (2) breeding and northern Gulf of Mexico stopover sites. We employed two connectivity metrics: (i) the Mantel correlation using the *ade4* package in R (Dray and Dufour 2007) and (ii) the MC metric from the *MigConnectivity* package (Cohen et al. 2018) using orthodromic distances between breeding and winter or stopover sites (detailed methods in Appendix S1). To examine the consistency of annual schedules between breeding populations, we determined the timing of annual events for all individuals (see Appendix S3).

If regional habitat selection leads to population-specific habitat selection we expected to see population-specific variation in habitat use patterns (description of *used* habitat features) across the annual cycle. Due to limited sample size, we were unable to assess population-specific habitat selection (the disproportionate use of habitat components). Instead, we described population-specific patterns of local and landscape scale habitat features (characteristics of *used* habitats). To model population-specific habitat use we used a generalized linear model for each habitat feature (local and landscape). The full model included the habitat variable as the response variable, the interaction of season and breeding longitude as fixed effects and individual bird as a random effect.

Statistical Analysis

All analyses were conducted in R 3.4.3 (R Core Team 2017). Bayesian discrete choice models were run with the R package *jagsUI* (Kellner 2017) using the software JAGS 4.3.0 (Appendix S1, Plummer 2003). Generalized mixed effect models were run in the R package *nlme* (Pinheiro et al. 2017) with restricted maximum likelihood estimation. Generalized linear models were run in the R package *stats* (R Core Team 2017). For full model specifications and fit assessment see Appendix S1.

Results

Patterns of Movement

We obtained breeding ground location estimates from 21 birds, fall migration locations from 20 birds, winter locations from 19 birds (1 partial) and spring migration from 18 birds for a total of 554 GPS location fixes across 21 birds (Figure 1.2; Appendix S1, Table S1.2). During the winter period, of the 18 birds tracked across the whole period, 8 individuals engaged in intra-winter movements occupying two or more territories an average of 58.5 ± 20.8 km (± SE, range: 1.5 – 182.3 km) apart (Figure 1.2c). The remaining 10 individuals remained at a single winter territory, moving an average of 0.1 ± 0.09 km between locations from November to April.

Local and Landscape Habitat Selection

The diversity of land cover type occupied by individual wood thrush varied by season ($\chi^2 = 45.92$, df = 3, $p < 0.001$; Figure 1.3). Residual plots for the top model showed deviations from model assumptions so non-parametric Kruskal-Wallis and Dunn Tests with Bonferroni adjustments were used. We did not detect a difference in land cover diversity *within* stationary or migratory periods (Breeding-Winter: $Z = -0.26$, $p = 1.0$), but we did detect a difference in land cover diversity *between* the migratory and stationary periods (Breeding-Fall: $Z = 5.79$, $p < 0.001$; Breeding-Spring: $Z = -3.47$, $p = 0.003$; Winter-Fall: $Z = 5.46$, $p < 0.001$, Winter-Spring: $Z = 3.18$, $p = 0.08$). Within the breeding season the major land cover type used was a matrix of mixed-use agriculture and natural vegetation, while the dominant land cover type on the winter grounds was forest (Figure 1.3). The high diversity of land cover types selected by wood thrush during fall and spring migration included forest, agriculture, agricultural mosaics, wetlands and wooded savannahs.

We quantified the repeatability of selection of habitat features by individual birds as they moved within the stationary and migratory periods. Within the stationary periods, repeatability of local and landscape tree cover, proximity to non-forest and average patch size was moderate ($R > 0.3$; range, $R = 0.327 – 0.483$, Table 1.1). EVI and patch size had low repeatability ($R < 0.3$) during stationary periods. By contrast, all habitat features had very low repeatability estimates, close to zero, within the migratory periods.

Discrete choice models indicated that the habitat features of the resource units (locations) wood thrush selected (compared to what was available) varied across seasons and spatial extent. The top discrete choice model of habitat selection for most spatial extents during the breeding, winter and fall migratory period was the local habitat features model (Figure 1.4; Appendix S1, Table S1.5). The exception was during the breeding season at the 25-km spatial extent, in which the full model (local and landscape habitat features) was the top model. During spring migration, the null model was the top model across all scales, indicating no habitat features measured were important for habitat selection.

On the breeding grounds at all spatial extents, birds selected resource units with high percent tree cover (Figure 1.4). At the smallest spatial extent (0.5 km) birds chose resource units with low EVI values. At the two largest spatial extents (15-km and 25-km), wood thrush selected resource units more proximate to non-forest. Additionally, on the breeding grounds, at the 25-km extent birds selected resource units that were found within landscapes with high average patch size (1-km buffer), but at the local scale, resource units in small forest patches were selected. During fall migration, birds selected resource units with large patch size at the 0.5-km, 5-km and 25-km spatial extent. At the two largest spatial extents (15-km and 25-km) they chose resource units with high EVI values. On wintering grounds, at all spatial extents birds chose resource units with large patch sizes. Birds also chose winter resource units more proximate to non-forest at the 5, 15 and 25-km spatial extent. Additionally, at the 25-km scale birds chose resource units with high tree cover.

Regional Habitat Selection

Between breeding and stationary non-breeding grounds regional habitat selection was present, and migratory connectivity estimates were weak-to-moderate (MC Index =

0.41; $r_M = 0.14$, $p = 0.03$). Regional habitat selection was also present at fall stopovers locations prior to the Gulf of Mexico crossing based on high migratory connectivity estimates (MC index = 0.69; $r_M = 0.69$, $9 < 0.01$) due to breeding populations utilizing region-specific departure points from North America (Figure 1.2b). By contrast, during spring migration, connectivity was low (MC index = 0.28; $r_m = -0.03$, $p = 0.53$) at stopovers after Gulf of Mexico crossing suggesting no regional habitat selection by breeding populations.

There was evidence of population-specific patterns of seasonal habitat use based on two local habitat features (patch size and proximity to non-forest), and one landscape level characteristics (average patch size; Table 1.2 and Appendix S1, Table S1.6). There was no difference in land cover diversity between populations. During the breeding season, eastern populations were found in locations with significantly higher patch size compared to western populations, whereas western populations were found in locations significantly further from non-forest compared to eastern populations (Table 1.2). During fall migration, proximity to non-forest at fall stopover sites was significantly greater for eastern breeding populations compared to western populations. During the non-breeding stationary period, western populations were further from non-forest and were located in landscapes with higher average patch size. There were no significant trends between breeding longitude and habitat features during spring migration. The model of average tree cover included a significant interaction between breeding longitude and season, but the confidence intervals of all trends included zero (Table 1.2).

Discussion

For the first time in a migratory songbird we show direct evidence, from individual birds with high resolution tracking devices, of seasonal shifts in habitat selection across the annual cycle. Most notably individual birds relaxed the degree to which they selected habitat features during migratory periods, suggesting greater behavioural plasticity during migration. We also show evidence of regional habitat selection by using indices of migratory connectivity to assess non-random assortment of five populations across regional geographic scales. As migratory species move through different heterogeneous landscapes they will need to find suitable habitats that meet their needs during different life-history stages. Understanding the factors necessary for persistence will require identifying the breadth of suitable habitats that individuals occupy as they redistribute geographically across the annual cycle (Webster and Marra 2005).

Seasonal Variation in Habitat Selection

This is the first study we are aware of that has documented seasonal variation in habitat selection by tracking the same individual migratory songbird across the entire annual cycle. Fine scale tracking of individual wood thrush revealed variation in habitat selection across periods of the annual cycle. Specifically, by employing a multi-scale approach we determined wood thrush were selective at the local scale and only selective at the landscape scale during the breeding season. The factors that drove habitat selection varied across seasons and spatial extent (size of study area). Habitat selection by migrating wood thrush was less selective, individuals occupied a greater diversity of land cover types than during the stationary periods, and selection focused on local habitat features.

During the stationary non-breeding and breeding periods we found individuals almost exclusively in forested and mixed forest-agriculture landscape. Alternatively, while migrating, wood thrush selected novel land cover types (e.g. agricultural, wood savannah) 36% - 46% of the time. Furthermore, during migration the low repeatability in habitat use indicated that individual birds did not consistently select locations with similar structural attributes. Banding and eBird studies have also suggested greater flexibility in habitat selection for songbirds during the migratory period and changes in foraging behaviour, particularly for fruit-eating species like wood thrush (Yong and Moore 2005, Zuckerberg et al. 2016). Analyses were not conducted on the same individuals or population; however, this study confirms that changes in habitat use during the migration period were due to changes in individual habitat selection across periods. Specifically, unlike the stationary periods, we found fewer predictors of habitat selection during fall migration and no response to habitat features during spring migration, which suggests birds were selecting habitats at random with regards to the features we measured during spring migration.

This shift to be more of a generalist when selecting habitat may be favoured due to the strong selection pressure to minimize time on migration (Hutto 1985, Alerstam and Lindström 1990, Gómez et al. 2017). This is expected to be particularly relevant during spring migration due to intense selective pressure for early arrival on breeding grounds to secure a territory and begin reproduction (Kokko 1999). Migration schedules should therefore ensure optimal arrival dates on breeding grounds, which is consistent with our finding of faster spring migrations and population-specific schedules (Appendix S3, Figure S3.1, Table S3.2). Increased behavioural flexibility during migration may also be an adaptive response to lower migrants' threshold of acceptable habitat to reduce search time for high quality stopover sites (Moore and Aborn 2000). Therefore, if individuals cannot quickly locate high quality habitat they may settle in poorer quality habitats. It has been suggested that compensatory behaviours such as risk-prone foraging strategies (e.g. increased maneuvers or feeding intensity) or shorter stopover duration, may allow birds to maintain migration schedules even when foraging in poorer quality habitats (Yong and Moore 2005, Nilsson et al. 2013). Therefore, during spring migration, at fine spatial and temporal scales food may still be limiting individuals, but at larger spatial scales the timing of migration may be the more limiting factor.

During fall migration, wood thrush selected larger forest fragments and, when examined across large spatial extents (15, 25 km), patches with higher EVI values. In contrast to spring migration, birds were responding to local habitat features, but to a lesser extent compared with the stationary periods. We found fall migration schedules were more variable across individuals and populations and longer in duration (Appendix S3 Figure S3.1, Table S3.2), which suggests individuals may fine tune fall migration to adjust to local conditions *en route* (Balbontín et al. 2009, Stanley et al. 2012). Settlement patterns during migrations are thought to be driven largely by food to meet the energetic demands of migration and this is consistent with the response of birds to EVI, an indicator of primary productivity (Hutto 1985, Buler et al. 2007). Behavioural plasticity between migratory periods could be driven by seasonal difference in environmental conditions linked to food availability. Increased food limitation in the fall, driven by poorer seasonal conditions *en route* or carrying-over from the breeding/moulting period, could lead to increased selection for habitat preferences (Nilsson et al. 2013). In contrast to spring migration, timing of arrival on winter grounds may not be associated with fitness advantages, which could drive differences in behavioural plasticity between seasons (Møller 1994, McKellar et al. 2013b).

Landscape scale habitat selection was only identified during the breeding season across the largest spatial extent. The majority of previous studies have also found that local, and not landscape, habitat features better predicted wood thrush occupancy during both stationary periods (breeding, Lee et al. 2002, Valente and Betts 2018; non-breeding, Graham and Blake 2001). The relevance of landscape variables during the breeding season, but no other season could be driven by several factors. It could be that critical resources unique to the breeding season (e.g. reproduction-related) are influenced at the landscape scale (Hutto 1985). Alternatively, it has been suggested that the impacts of fragmentation are primarily visible when habitat loss across the landscape is high or moderate (fragmentation threshold; Andren 1994, Villard and Metzger 2014). The dominant land cover during the breeding season was mixed forest-agriculture, and there was low forest cover across the landscape (Appendix S2, Table S2.1). In comparison, during the winter period, forest was the dominant land cover and forest cover at the landscape scale was high. Therefore, the higher fragmentation in locations occupied by wood thrush during the breeding season could be driving the greater importance of landscape configuration in our models.

Structural features of the locations occupied by individual wood thrush during the two stationary periods (non-breeding and breeding) showed moderate to high repeatability, once seasonal differences were accounted for. This was particularly notable for distance to edge; individuals that tended to be closer to edge on the breeding grounds also tended to be closer to edge during the non-breeding stationary period. This pattern was not true for patch size or EVI, which showed low repeatability between stationary periods. Overall, three local habitat features - tree cover, patch size and proximity to non-forest - were top predictors of habitat use during both stationary periods however their relevance varied by spatial extent and season. Together these results indicate that factors related to forest structure play a role in habitat selection during the stationary periods and suggests that individual birds may show distinct preferences for particular local and landscape features at different periods of the annual cycle.

Breeding wood thrush settled in landscapes with large forest patches, a pattern that only emerged at the largest spatial extent. Within these landscapes, selection of sites was highly variable (demonstrated by large confidence intervals), but individuals more often settled within small forest fragments and in locations closer to edge habitat with high tree cover. It is well documented that wood thrush inhabit small forest patches across most of their breeding range (Robinson et al. 1995, Burke and Nol 2000, Lee et al. 2002), but occupancy of small forest fragments is usually associated with decreased reproductive success for wood thrush (Donovan et al. 1995, Burke and Nol 2000). Although in some landscapes small fragments can function as source populations (Weinberg and Roth 1998, Fauth 2001). Individuals may be driven into smaller forest fragments due to selection of habitat features associated with small fragments (e.g. high shrub density; Cody 1985). Wood thrush also responded to edge habitat, which would be more common in small fragments and has previously been identified as an important nesting and fledgling habitat for wood thrush (Vega Rivera et al. 1998, Kaiser and Lindell 2007). Alternatively the pattern could be driven by limited high quality forest patches and the displacement of individual to lower quality patches through intraspecific competition (Fretwell and Lucas 1969, Thompson III et al. 2002). Finally, our choice of study plots and deployment location may have also skewed the results towards smaller fragments. Further research measuring fitness components would be better able to dissect which landscape or patch level factors increase the conservation value of small fragments.

In contrast to the breeding grounds, the dominant land cover during the winter period was forest. As predicted, individuals were more likely to settle in large forest patches and locations with high tree cover. However, similar to the breeding grounds, wood thrush disproportionately selected winter locations near edge habitat. Studies of wintering wood thrush suggest they are forest area sensitive but are tolerant of edge (Graham and Blake 2001, Roberts 2011). Fruit is a patchily distributed, ephemeral resource often associated with edge habitats in the tropics (Lindell et al. 2007). Access to fruiting resources could be critical for wintering wood thrush and radio-tracking studies have observed wood thrush making off-territory forays to large fruiting trees (C.Q. Stanley pers. comm.). The observed differences in tree cover and patch size across stationary periods could indicate shifts in the importance of these critical resources. It could also represent trade-offs in preferred habitat features imposed by the hierarchical process of habitat selection in regions with different landscape composition and configuration (Hutto 1985).

Regional Habitat Selection

Due to the hierarchical nature of habitat selection by birds, environmental heterogeneity across a species range will influence which habitat features are limiting populations based on their regional context. Using migratory connectivity, we identified non-random assortment of populations at regional scales between breeding and non-breeding locations, which we interpreted as evidence of regional habitat selection. As predicted based on previous low-resolution tracking studies (Stanley et al. 2015), wood thrush exhibited regional habitat selection on their non-breeding stationary (MC = 0.41) and fall Gulf of Mexico stopover sites (MC = 0.69), but not on their spring Gulf of Mexico stopover sites (MC = 0.28). Weak and moderate levels of migratory connectivity appear to be common in forest-dwelling migratory songbirds (migration, Koleček et al. 2016, Knight et al. 2018; stationary, Gilroy et al. 2016, Finch et al. 2017) which suggests regional habitat selection occurs across many species. Using migratory connectivity to identify patterns of regional habitat selection does not elucidate the factors driving habitat selection at this scale. Hutto (1985) suggested they are largely factors not related to the habitat itself, for example physiological condition influencing regional settlement patterns on the ground (Studds et al. 2008, Rushing et al. 2015). Ultimately identifying what factors drive patterns of regional habitat selection and how flexible they are will have important implications for understanding how populations will be able to respond to changing landscapes.

If regional habitat selection does occur, we could expect to see population-specific patterns of habitat selection at smaller spatial scales. Despite relatively small sample sizes within each breeding population, we identified population specific differences in habitat use patterns during the stationary periods and fall migration, but not spring migration as predicted based on our analysis of regional habitat selection. The habitat features of breeding populations were consistent with regional patterns of forest fragmentation across the United States (higher fragmentation in the mid-west; Riitters et al. 2002); populations in the mid-west were found in smaller forest fragments. A similar trend was also observed during fall migration which was characterized by region-specific migratory routes to the Gulf of Mexico; mid-western population were in locations closer to edge habitat. During spring migration, all populations funneled into the same region of the US after the Gulf of Mexico crossing (eastern Texas to Mississippi) resulting in all populations occupying habitats with similar features. High intra-specific competition at migratory bottlenecks could force individuals into non-optimal habitats and might have contributed to our inability to detect local and landscape habitat selection during spring migration. Due to limited sample size this analysis does not determine if the observed patterns were driven by populations differentially selecting locations based on these structural aspects (disproportionate to their ability) or by differences in the distribution of environmental features across the species range. However, one structural feature, distance to edge, had the same regional pattern across both stationary periods; mid-western populations selected locations further from forest edge. In addition, this structural characteristic had high individual repeatability across both stationary periods. These results hint at the possibility that mid-western populations may have a preference for more interior forest areas. If populations develop unique habitat selection preferences, either learned or innate, ignoring information about regional habitat selection across the annual cycle could obstruct interpretation of habitat selection patterns at lower spatial scale and our understanding of the conservation value of different habitat features across populations.

Conservation Implications

Environmental degradation is causing alterations of the landscapes where most species live. For migratory species that are composed of populations occupying ranges that span continents, deciphering when and where alterations are most impacting species requires considering their full annual cycle ecology (Wilcove and Wikelski 2008, Marra et al. 2015). Here, we found different habitat preferences across periods of the annual cycle, suggesting wood thrush populations will respond differently to changes in habitat composition and configuration during different periods of the annual cycle. For example, relaxation of habitat preferences during migration may be an adaptive trait to facilitate a fast migration, but across rapidly changing landscapes, it could lead to birds occupying unsuitable stopover habitats. Recent work has found high use of human dominated landscapes by migrating songbirds, but whether these represent suitable habitat or ecological traps is not known (La Sorte et al. 2014, Zuckerberg et al. 2016). Developing a better understanding of the vulnerability of migrating wood thrush to landscape changes may be particularly important at spring Gulf of Mexico stopover sites where the entire population of wood thrush appear to spend time during spring migration. Unfortunately, our knowledge of how species respond to environmental heterogeneity in the non-breeding season is lacking, even for well-studied species such as wood thrush (Faaborg et al. 2010). As technologies improve, the increased temporal and spatial resolution of GPS tags will allow researchers to investigate not only how ecological responses of populations and individuals change across the annual cycle but also the factors driving these variations within and across populations and individuals.

Acknowledgements

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Tables

Table 1.1 Repeatability estimates of habitat features used by wood thrush tracked with GPS tags, calculated between stationary (breeding and winter) and migratory periods (fall and spring migration).

	Repeatability					
	Stationary			Migratory		
Habitat Features	n	*R*	p-value	n	*R*	p-value
Patch-level						
Tree Cover (%)	181/186	**0.327**	**<0.0001**	92/51	0.043	0.051
EVI	173/202	**0.128**	**<0.0001**	85/48	0.051	0.274
Patch Size (km^2)	184/214	**0.269**	**<0.0001**	92/59	0.072	0.076
Proximity to Non-Forest (m)	184/163	**0.699**	**<0.0001**	91/55	0.047	0.28
Landscape-level						
Tree Cover 1km (%)	184/212	**0.380**	**<0.0001**	92/52	0.022	0.406
Average Patch Size (km^2)	184/212	**0.379**	**<0.0001**	92/52	0.032	0.329

Notes: Samples sizes (n) are given during stationary period: breeding/winter; migratory period: fall migration/spring migration. Significant effects in boldface.

Table 1.2 Estimated slope of the seasonal trend based on a generalized linear model examining the effects of the interaction between breeding longitude and local and landscape scale habitat features of habitats occupied by wood thrush from 5 breeding populations across the annual cycle. Estimated season-specific trends and 95% confidence intervals.

Model	Season	Estimated Slope	95% CI
Patch Level			
Tree Cover (%)	n/a		
EVI	n/a		
Patch Size (ha)	Breeding	**-344.0**	**3.7, 650.9**
	Fall Migration	-116.4	-218.1, 450.8
	Winter	-276.6	-2.3, 576.1
	Spring Migration	0.3	-381.2, 387.1
Prox. to Non-Forest (m)	Breeding	**-0.082**	**-0.2, -0.009**
	Fall Migration	**0.083**	**0.004, 0.2**
	Winter	**-0.18**	**-0.3, -0.1**
	Spring Migration	0.01	-0.082, 0.10
Landscape level			
Avg. Tree Cover 1 km (%)	Breeding	-0.47	-0.98, 0.10
	Fall Migration	0.0079	-0.57, 0.59
	Winter	0.41	-0.12, 0.95
	Spring Migration	0.20	-0.46, 0.87
Avg. Patch Size 1 km (ha)	Breeding	-68.4	-364.3, 227.3
	Fall Migration	245.6	-75.0, 566.2
	Winter	**-313.4**	**-603.3, -24.2**
	Spring Migration	103.6	-276.7, 483.9
Land Cover 5km	n/a		

Notes: Values in bold have confidence intervals that do not include zero.

Figures

Figures Legend

Figure 1.1. Conceptual hierarchy of the decision-making process of habitat use by a migratory songbird. At higher spatial scales (A) and (B) the process is expected to be largely inflexible and constrained by extrinsic habitat factors. At lower spatial scales (C) and (D) the process likely involves the assessment of the intrinsic factors of the habitat based on cues and exploratory assessment. Different patterns of migratory connectivity are illustrated (A). Strong connectivity (solid lines) occurs when most individuals from one breeding population move to the same nonbreeding locations. Weak connectivity (dashed lines) occurs when individuals from the same breeding population move to different nonbreeding locations.

Figure 1.2. Migratory connectivity of a migratory songbird, the wood thrush, obtained from GPS-tags deployed across 5 breeding populations in the United States. Across maps, colours correspond to breeding location (red = DE, blue = IN, green = MN, purple = NY, orange = NC). (A) Locations (breeding, stopover and winter) and migratory routes of wood thrush (n = 19). Lines connect consecutive location fixes during fall (solid) and spring (dashed) migratory period and do not represent direct path travelled. (B) Stopover locations at the northern coast of the Gulf of Mexico during fall (solid circle, n = 14) and spring (open sqaure, n = 12) migration. (C) Winter locations of wood thrush, shapes denote different individuals. Eight wood thrush occupied two or more winter locations.

Figure 1.3. Seasonal changes in average percent of locations found in each of five land cover class for wood thrush tracked using GPS geolocators from 5 breeding populations across the annual cycle. Land cover classes derived from 5-km buffer around location estimate and include agriculture, mixed agriculture and natural vegetation, forest, wetlands and wooded savannah. For each breeding population, seasonal sample sizes are indicated in the brackets.

Figure 1.4. Parameter estimates and associated 95% credible intervals for the top discrete choice model examining habitat selection patterns of individually tagged wood thrush at multiple spatial scale during a) breeding, b) winter, c) fall migration and d) spring migration. For each period discrete choice models were run at multiple extents: 0.5 km (closed square), 5 km (closed circle), 15 km (open square) and 25 km (closed square). Local habitat features include percent tree cover, Enhanced Vegetation Index (EVI), patch size (km^2) and proximity to non-forest. Landscape habitat features include average percent tree cover and average patch size (km^2). Not all habitat features were present in all top-models.

Figure 1.1

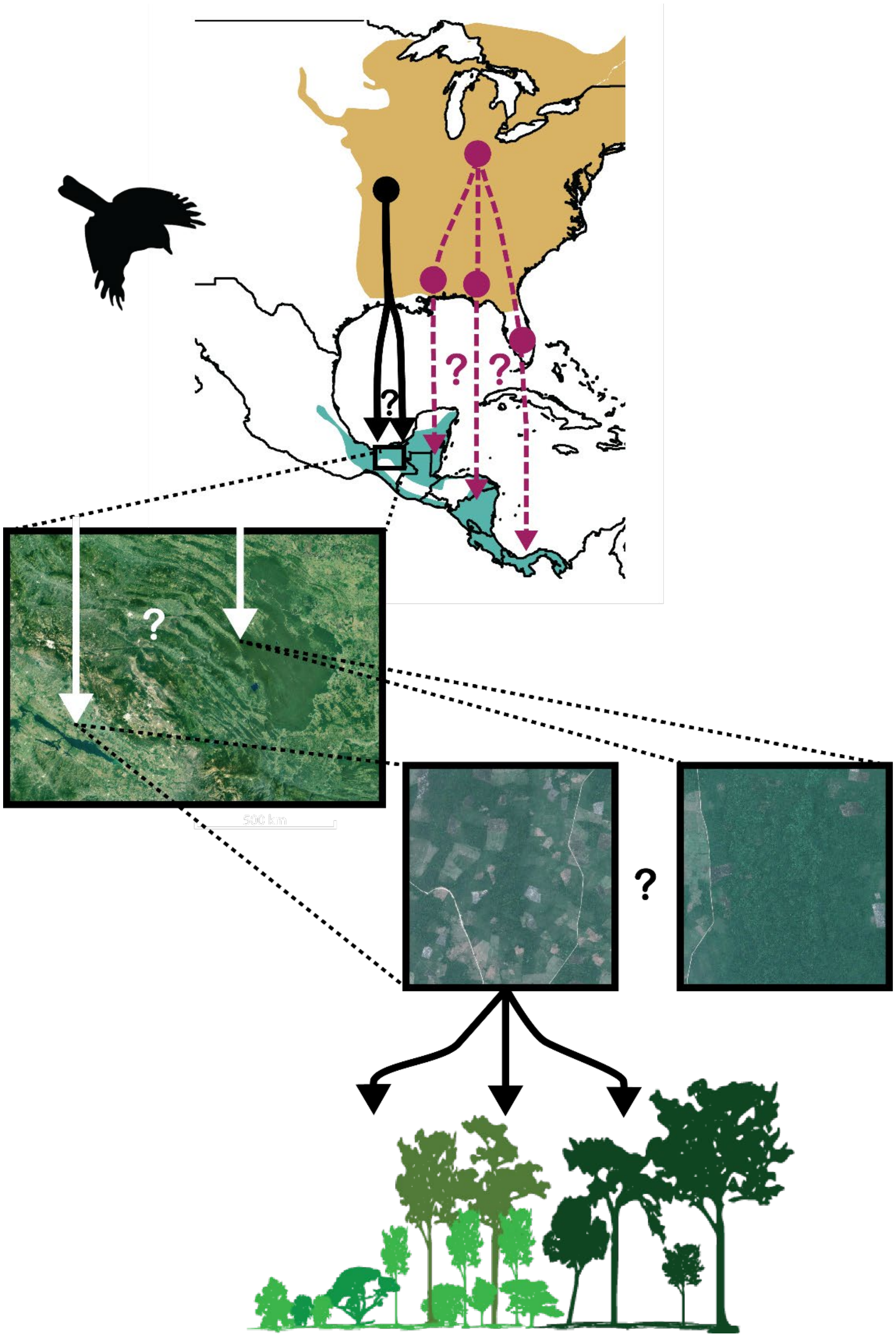


Figure 1.2

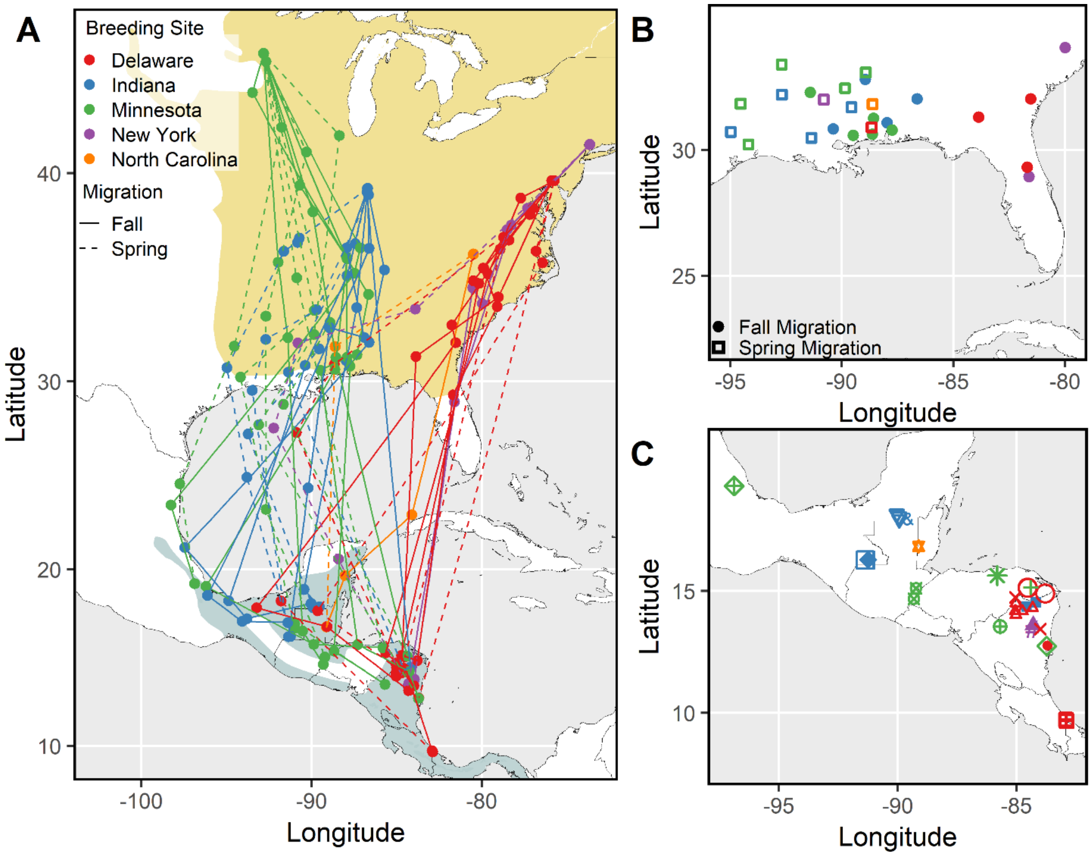

A
Breeding Site
Delaware
Indiana
Minnesota
New York
North Carolina
Migration
Fall
Spring
Latitude
40
30
20
10
Longitude
-100
-90
-80
B
Latitude
30
25
Fall Migration
Spring Migration
-95
-90
-85
-80
Longitude
C
Latitude
15
10
-95
-90
-85
Longitude

Figure 1.3

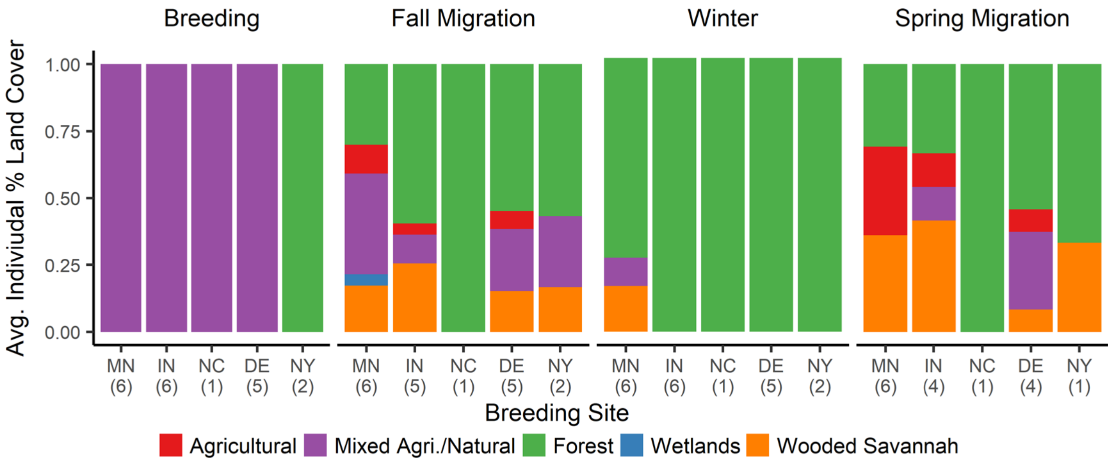
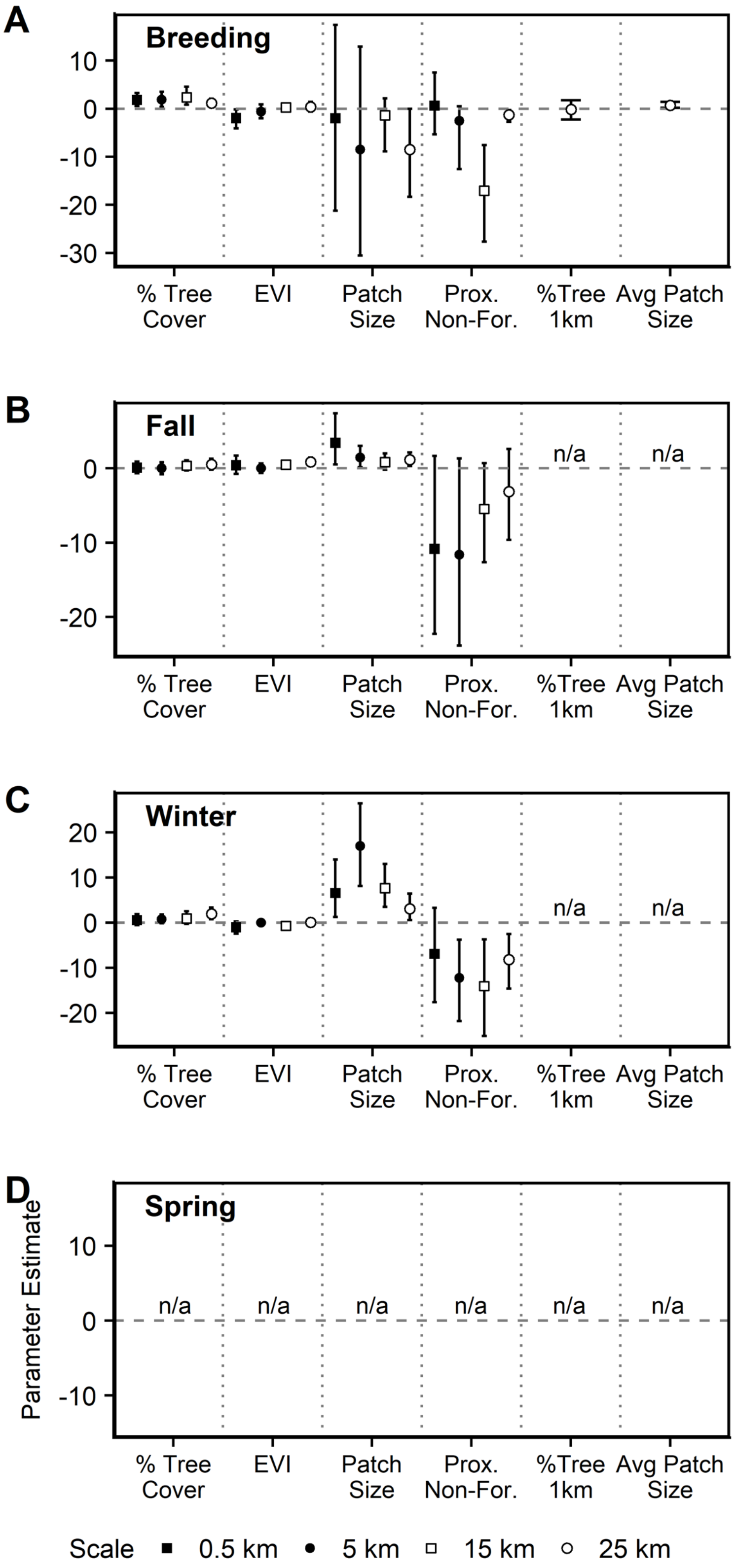

Breeding
Fall Migration
Winter
Spring Migration
Avg. Indiviudal % Land Cover
1.00
0.75
0.50
0.25
0.00
MN (6)
IN (6)
NC (1)
DE (5)
NY (2)
MN (6)
IN (5)
NC (1)
DE (5)
NY (2)
MN (6)
IN (6)
NC (1)
DE (5)
NY (2)
MN (6)
IN (4)
NC (1)
DE (4)
NY (1)
Breeding Site
Agricultural
Mixed Agri./Natural
Forest
Wetlands
Wooded Savannah

Figure 1.4


A
Breeding
10
0
-10
-20
-30
% Tree Cover
EVI
Patch Size
Prox. Non-For.
%Tree 1km
Avg Patch Size
B
Fall
0
-10
-20
n/a
n/a
% Tree Cover
EVI
Patch Size
Prox. Non-For.
%Tree 1km
Avg Patch Size
C
Winter
20
10
0
-10
-20
n/a
n/a
% Tree Cover
EVI
Patch Size
Prox. Non-For.
%Tree 1km
Avg Patch Size
D
Spring
Parameter Estimate
10
0
-10
n/a
n/a
n/a
n/a
n/a
n/a
% Tree Cover
EVI
Patch Size
Prox. Non-For.
%Tree 1km
Avg Patch Size
Scale ■ 0.5 km ● 5 km □ 15 km ○ 25 km

Chapter 2 : Patterns of moisture and food availability during the non-breeding season influence small- and large-scale space use strategies in a migratory songbird

Abstract

Understanding the ecological correlates driving space use strategies in species can be critical for predicting population dynamics; however, such information can be difficult to attain for small mobile species such as migratory songbirds. We combined radio telemetry and high-resolution GPS tracking to examine small- and large-scale space use strategies under different moisture gradients for wood thrush (*Hylocichla mustelina*), a Neotropical migratory songbird. Food availability is often thought to be a key ecological factor dictating space-use patterns in animals and in this study, we explored the role moisture plays in driving food abundance and in turn, space-use strategies at a non-breeding site in Belize across three years. Overall, patterns of moisture on non-breeding home ranges influences food availability and both small- and large-scale movement patterns. Individuals with home ranges in drier habitats experienced lower food abundance, reduced body condition and occupied larger home ranges. Contrary to expectations given previous research, with two types of tracking technologies we discovered wood thrush exhibit low rates of seasonal site persistence across their non-breeding range and that individuals in wetter habitats were more likely to engage in facultative and permanent mid-winter shifts up to 148 km between home ranges. We suggest that these movements may be a condition dependent strategy to enable non-breeding wood thrush to find alternative habitat as food availability declines at the end of the dry season. Given that increased aridity is

predicted across the non-breeding range of wood thrush, future research should delve deeper into understanding how moisture availability impacts within and between season dynamics and ultimately the population dynamics of this declining species.

Introduction

Addressing recent declines in long-distant migratory birds requires an understanding of the processes limiting populations across the annual cycle (Marra et al. 2015). One major gap is the role of ecological factors (e.g., rainfall, predation, food and their interactions) in driving population dynamics while birds are on their tropical nonbreeding ranges (Faaborg et al. 2010). To gain a better understanding of the role of ecological factors it is first necessary to determine the space-use strategies of migrants during the nonbreeding period. It has often been assumed that most species of migratory birds spend their non-breeding season on a single home-range. Evidence is accumulating, however, that suggests they exhibit a broad range of space-use strategies (Heckscher et al. 2015, Koleček et al. 2018). Aside from a few early studies with marked (Moreau 1972, Morton 1980) or radio-telemetered individuals (Rappole et al. 1989), it was not until the advent of modern tracking technologies that researchers have begun to recognize the extent of inter- and intra-specific variation in space-use strategies on the non-breeding range of migratory birds (McKinnon et al. 2013). From facultative short-distance shifts in home ranges (Smith et al. 2011b, Schlaich et al. 2016), to obligate long-distance intra-tropical migrations (Renfrew et al. 2013, Thorup et al. 2017), tracking studies are uncovering a wide range of non-breeding movement behavior from ecologically and socially distinct species (Stutchbury et al. 2016).

Elucidating the ecological factors underlying the diversity of movement strategies has been more limited. Food availability has been identified as a key ecological factor contributing to non-breeding season limitation (Sherry et al. 2005, Brown and Sherry 2006b, Diggs et al. 2011) and winter space use strategies (Zahavi 1971, Brown and Sherry 2008, Smith et al. 2011b). In wintering American Redstarts (*Setophaga ruticilla*), experimental food reductions on individual territories led some individuals to vacate territories and adopt a non-territorial strategy (Cooper et al. 2015). Furthermore, these individuals experienced a reduction in pectoral muscle mass and, on average, a one-week departure delay on spring migration, suggesting food limitation impacted physical condition and ultimately influenced space-use decisions. At larger spatial scales, tracking studies of Palearctic migrants have begun to show that intra-tropical migrations on non-breeding ranges in sub-Saharan Africa follow shifts in proxies of food abundance (e.g. vegetation indices; Trierweiler et al. 2013, Thorup et al. 2017). Therefore, food availability is likely a key factor driving alternative space use strategies; however, the extent to which it dictates space-use dynamics among individuals, populations and species remains poorly resolved.

In much of the tropics differential food availability across habitat types has been shown to be driven largely by gradients in moisture, primarily through its effect on phytophagous insects (Janzen 1973, Wolda 1978, Studds and Marra 2011a). For migratory songbirds in the tropics, this is of particular importance as aridity increases towards the end of the dry season (due to seasonal shifts in rainfall), at the same time birds are preparing for spring migration. For small migratory warblers, non-breeding rainfall can have important consequence for both spring migration phenology and annual survival (McKellar et al. 2013a, Rockwell et al. 2017). Therefore, how migratory birds handle increasingly arid conditions as the non-breeding season progresses and the role this plays in shaping space-use strategies and movement dynamics could have important implications for our understanding of non-breeding ground limitations for migratory birds.

The aim of this study was to explore the ecological correlates of movement behaviour for wood thrush (*Hylocichla mustelina*), a long-distance Neotropical migratory songbird. We tested the hypothesis that moisture indirectly drives food abundance, and this corresponds to space use strategies in wood thrush. Specifically, we tested the prediction that wood thrush in wetter relative to drier sites will (1) occupy smaller home ranges, (2) have access to more fruit and insect resources, (3) maintain better energetic condition, and (4) have higher seasonal site persistence. Using radiotelemetry, we quantified local home ranges for wood thrush as well as moisture levels and food availability on these corresponding areas for individual birds at a non-breeding site in Belize. To explore the influence of patterns of moisture on seasonal site persistence and movement dynamics at larger spatial scales we paired high-resolution GPS tracking data, deployed on 5 breeding populations, to satellite derived indices of wetness. By combining results from field data and remote tracking, we were able to examine the influence of moisture patterns on food availability at both small- and large-spatial scales.

Methods

Study Species

Wood thrush are a large (40-50g), omnivorous Neotropical migratory songbird that breed in the forests of eastern North America and winters primarily in the lowland (up to 500m) tropical forests of Mexico and Central America. Although a common forest songbird, their global population size has declined by 60% since 1966 based on breeding surveys (Sauer et al. 2013). During the non-breeding season wood thrush are solitary and radio-tracking studies have documented two non-breeding space-use strategies. Some individuals maintain flexible territories, while others opportunistically float across territories, a strategy that has been associated with higher mortality (Rappole et al. 1989).

Field Methods:

Research was conducted at two adjacent lowland tropical evergreen forest reserves in the late dry season (mid-January through mid-April) from 2013 to 2015. Both forest reserves were located along the Bladen river at the base of the Maya Mountains in the Toledo District of Belize. The Belize Foundation for Research and Environmental Education consists of 467 ha of secondary forest and early successional scrub habitat due to heavy damage sustained during Hurricane Iris in 2001. The Bladen Nature Reserve consists of 39,270 ha of protected rainforest managed by the Ya'axché Conservation Trust and was less damaged by Hurricane Iris resulting in a mix of secondary and old growth forest in our study area. The area receives an average rainfall of 2500 mm/year and experiences a pronounced dry season that lasts from February-April.

Birds were captured in mist nets using conspecific playback during two sampling periods in order to monitor individuals across the dry season. The first sampling period ran from mid-January until mid-February hereafter "early". We attempted to recapture individuals during a second sampling period in mid-March, hereafter "late". At initial capture, all individuals were marked with a U.S. Geological Service aluminum band and unique color-band combination for identification. Birds were aged by feather characteristics (yearling or adult). Individuals were weighed to the nearest 0.1 g, and morphological measurements taken to estimate body size (unflattened wing chord, tarsus, retrix length and bill length). Visible fat deposits were scored following (Holmes et al. 1989) and pectoral muscles were palpated and scored following Gosler (1991). Blood samples (100-150 μL) were collected from the brachial vein and stored in Queen's lysis buffer for genetic sexing (detailed methods in Appendix S4). Blood and claw samples were also collected for stable isotope analysis (detailed methods in Appendix S4).

Radio-telemetry

To define home-ranges and monitor seasonal site persistence a total of 168 birds were equipped with either a VHS radio transmitters (n = 17, model BD-2, Holohil Systems Ltd., Carp, Ontario, Canada; n = 119, model PipAg393, Lotek Wireless, Newmarket, Ontario, Canada) or coded radio-transmitter (n = 45, model NTQB-4-2, Lotek Wireless). Transmitters were attached using a leg-loop harness constructed of Stretch Magic and secured by crimp beads (Rappole and Tipton 1991). We radio-tracked a total of 98 adults (n = 38 females, n = 50 males, n = 10 unknown) and 78 yearlings (n = 32 females, n = 37 males, n = 9 unknown). Thirteen individuals were tracked in multiple years, and unless otherwise indicated, only their first year of data was included in analyses. Individuals with VHF transmitters were located by homing using a Biotracker receiver (Lotek Wireless) and three-pronged flexible Yagi antenna (Lotek Wireless), individuals with coded tags were located using an SRX receiver (Lotek Wireless). Upon locating a bird, the position was taken with a handheld global positioning system unit (Garmin GPSMap). Location data was collected a maximum of twice per day during either morning and/or evening tracking sessions.

When an individual failed to be detected a systematic search was initiated by walking up to 1 km (minimum 500-m) in all 4 cardinal directions. If the search failed, we would repeat the procedure in the following days and periodically throughout the season (approximately bi-monthly). Individuals were tracked until either (1) the bird departed the site or (2) the transmitter was recovered. Individuals whose transmitters were recovered (e.g. due to mortality, harness failure) were excluded from analyses of seasonal site persistence. Some cases of tag failure or mortality are likely to be included as site departures, however extensive recapture efforts suggest tag failures were rare.

Home-range area was defined as the 95% isopleth of the utilization distribution estimated from an area-corrected kernel density estimator which reduces bias due to small sample sizes (Fleming and Calabrese 2017). We used the *ctmm* package in R (Calabrese et al. 2016) to derive utilization distributions (detailed methods in Appendix S4). We restricted analysis to individuals with 16 or more relocations across the season (n = 53), inspection of confidence intervals indicated area estimates stabilized around 16 locations.

Body Condition

To examine the influence of moisture on body condition we (1) examined the initial condition of individuals in late January and early February and (2) the change in condition of individuals that were recaptured in mid-March. Initial body condition was assessed using a body condition index derived by predicting the lean body mass of each bird based on a regression equation of mass versus unflattened wing chord, tail and tarsus for fat-free birds with a pectoral score of 1 (Strong and Sherry 2000, McKinnon et al. 2015a). Body mass was then compared to the predicted lean body mass based on structural size, and the percent difference was calculated (Predicted Mass – Measured Mass / Predicted Mass). For birds that were successfully recaptured in mid-March we examined change in condition by directly measuring change in mass between the early and late sampling period.

Diet sampling

The influence of moisture on food availability and diet was assessed using two methods: (1) environmental fruit and insect sampling and (2) isotopic analysis. To characterize food availability, fruit and insect surveys were performed at tracking locations selected randomly without replacement for each individual. In 2013, insect and fruit surveys were conducted at 3 and 1 randomly selected tracking locations, respectively. Following 2013 both insect and fruit surveys were performed at 5 randomly selected tracking locations to provide better coverage of wood thrush home ranges. Surveys were performed twice to assess change in food availability across the dry season. Early sampling period surveys were conducted in mid-February on all individuals with a minimum of 8 relocations, late sampling period surveys were conducted in late-March for all individuals that remained on site until the second week of March. Fruit surveys were performed by counting all fleshy fruit in a 5-m radius (ground to canopy). Insect surveys were performed by placing a 0.5 m^2 frame on the ground and performing a 5 min search to identify all arthropods to order and size class (head to abdomen; Strong and Sherry 2000). Due to low site-persistence we focused analysis on surveys obtained for individuals during the first sampling period (n = 44 fruit surveys; n = 43 insect surveys).

To quantify how the proportion of insects in the diet of wood thrush was influenced by moisture we used stable nitrogen isotopes (δ15N) derived from blood and claws as an index of food consumption (versus available food resources; detailed methods in Appendix S4). In general, tissues become more enriched in heavier stable-nitrogen isotopes as their diet includes protein from higher tropic level food items (Hobson 1993, Pearson et al. 2003). Different turnover rates of tissues allow the integration of dietary information over multiple time scales (Bearhop et al. 2002, Bauchinger and McWilliams 2009). Due to the longer turnover rate of claws (half-life = 35 days) relative to whole blood (half-life = 11-16 days) we expect claws to provide an indication of diet integration over a few months, while whole blood provides an integration of diet over several weeks (Pearson et al. 2003, Lourenço et al. 2015).

Patterns of Moisture

Patterns of moisture were quantified using (1) an index of moisture derived from remote sensing imagery and (2) stable-carbon isotopes. To derive an index of moisture from satellite imagery we calculated the wetness metric from the tasseled-cap transformation of Landsat images (Crist and Kauth 1986). This metric has been extensively used in tropical landscapes and reflects soil and canopy moisture (Cohen and Goward 2014). We performed the transformation on bi-monthly 30-m resolution Landsat images obtained from our study area for the period of December to April 2012 to 2015 (detailed methods in Appendix S4). For each image, we extracted the mean wetness metric for each (i) home range and (ii) plot. At each home range and plot we calculated the average and coefficient of variation (CV) of wetness (1) across the dry season and (2) separately across the early (Dec – Feb) and late (Mar-Apr) dry season.

Additionally, we used stable-carbon isotopes from blood and claws as an index of water availability within the habitats utilized by wood thrush (δ13C; detailed methods in Appendix S4). Differences in stable-carbon isotopes are largely driven by photosynthetic pathways in plants, with C3 plants being more depleted than C4 plants, such as grasses. However, within C3 plants, which dominate forested habitats, water-use efficiency also influences δ13C values, with C3 plants becoming more enriched as water availability decreases (Michener and Lajtha 2007, Kohn 2010). Similar to results found in other studies we found that δ13C values correlated well with satellite derived wetness indices (Appendix S5). As with stable-nitrogen isotopes (above), difference in turnover rates between claw and blood tissue allows us to examine changes in environmental conditions over different time windows.

GPS Tracking

To assess seasonal site persistence at a larger spatial scale we examined over-winter location data obtained from archival GPS transmitters (Model PinPoint-50, 1.8 g, 50 fixes, Lotek Wireless) deployed on adult male wood thrush from 5 breeding populations (n = 137; Delaware, Indiana, North Carolina, New York and Minnesota; Appendix S1 Table S1.1). The GPS transmitters provide location estimates every 2 weeks during the winter period for individual birds with an estimated accuracy of 10 meters. We obtained location estimates from 18 individuals across the winter period, with an average of 11 ± 3.9 location estimates per individual (± SD; range 2-17). We defined a dispersal event as any movement greater than 1 km after a stationary period (based on 2 or more locations in the same area) that occurred prior to the commencement of the spring migratory period. Distance between successive points (step length) was calculated using the *move* package in R (Kranstauber et al. 2018). The commencement of the spring migratory period was defined by the departure of the first tracked individual on migration (identified as consistent northward movements over consecutive days). To quantify how moisture patterns influenced seasonal site persistence of individuals equipped with GPS transmitters we derived the wetness metric (see above) from tasseled-cap transformed Landsat images interpolated for each location estimate (detailed methods in Appendix S4).

Data Analysis

To determine the influence of moisture patterns on home range size we constructed generalized mixed effect models. We generated a set of candidate models that reflected *a priori* hypotheses for home range size. We hypothesized that home range size changes with food availability (fruit and insect surveys, δ15N). We also included moisture directly in the model (wetness, δ13C) to account for other potential mechanisms that may influence home range size (e.g. predation). Additionally, we hypothesized that condition (at capture) and dominance hierarchies between sex and age classes would affect home range size. Year was included as a random effect. For both δ13C and δ15N, blood and claw stable-isotope values were highly correlated; therefore, for all response variables separate model sets were constructed including stable-isotope values derived from either blood or claw. Average wetness and the coefficient of variation of wetness was highly correlated in our study site in Belize; therefore, only average wetness was included in model sets.

We examined the influence of moisture levels on food availability and diet by constructing separate mixed effect models with fruit counts, insect counts and δ15N as the response variable. We developed a candidate model set for each response variable based on the predictions that moisture, measured as home-range wetness, will directly influence food availability. We also hypothesized that condition at capture, home range size and dominance relationships between age and sex classes may influence food availability and diet. Fruit and insect counts were log-transformed and fit with a general linear model. For the analysis of δ15N, linear mixed models were constructed. Sampling period was included as a fixed effect and period specific estimates of plot wetness were used. Bird identity was nested within year as a random effect.

To determine the influence of moisture patterns on body condition index during the early sampling period we examined separate linear mixed effect models for isotopes derived from blood and claws. We hypothesized that moisture would indirectly influence body condition through its effect on food availability as measured by stable-nitrogen values. We also included measures of habitat moisture, a satellite-derived wetness metric and stable-carbon values to account for other possible mechanisms in which moisture may influence body condition. We also included sex and age classes to explore the influence of dominance relationships, and year was included as a random effect. For individuals recaptured in the second sampling period we also determined the influence of moisture patterns on weight change between sampling periods. We evaluated the same set of hypotheses as proposed for body condition during the early sampling period. For individuals that remained in our study area until the end of the dry season we also determined how conditions and food availability changed over time. We used a paired-t test to compare mass across sampling periods for recaptured individuals. To assess change in food availability we performed separate Wilcoxon signed-rank tests to compare fruit and insect counts on home ranges.

We modeled seasonal site persistence (time-to-event outcome) using the Cox proportional-hazards regression model (CPH; Cox 1972, Therneau and Grambsch 2000). CPH models allow estimation of the effect of covariates on the hazard of departure (hazard ratio), or risk of departure. CPH models were performed using the *survival* package in R (Therneau 2015). We developed a set of *a priori* models to examine the influence of moisture on seasonal site persistence for radio-tracked birds in Belize. Similar to above, we examined the indirect impact of moisture on food availability as measure by δ15N derived from claws. We also included direct measures of moisture, satellite-derived plot wetness and δ13C derived from claws, to account for other mechanisms driven by moisture levels. We also included condition at capture, age and sex class to explore the influence of dominance hierarchies (Marra 2000). Software to perform random effects CPH models are currently limited and do not provide methods to test model assumptions; therefore, year was included as a fixed effect. For individuals tracked using GPS tags we constructed a more limited candidate set that included wetness, the CV of wetness and winter latitude. For individuals that performed intra-winter movements we also compared wetness and the CV of wetness between locations pre- and post-movements. We tested if wetness or the CV of wetness differed using a paired t-test.

All candidate model sets were ranked using an information theoretic approach by comparing Akaike's information criteria corrected for small sample size using the R package *MUMIn* (Burnham and Anderson 2002, Barton 2017). All models with $\Delta AIC_c \leq 2$ were considered equally plausible. When more than one model was supported, we performed unconditional model averaging to derive coefficient estimates and 95% confidence intervals. Although models ΔAICc up to 4 are also considered well supported (Symonds and Moussalli 2011), the inclusion of more competing models did not yield biologically relevant differences in the final models (based on inspection of confidence intervals) and therefore were not included. All analyses were conducted in R 3.4.3 (R Core Team 2017). Generalized mixed effect models were run in the R package *lme4* (Bates et al. 2015). Linear mixed effects models were run in the R package *nlme* (Pinheiro et al. 2017) with restricted maximum likelihood estimation. General linear models were run in the R package *stats* (R Core Team 2017). All models were assessed for violation of model assumptions by visual inspection of plots of residual versus predicted values and quantile-quantile plots. CPH models were checked for proportional hazards using the *cox.zph()* function in the *survival* package.

Results

The majority of radio-tracked wood thrush (68%; n = 115) departed our study sites in southern Belize prior to the start of the spring migratory period (Julian date range: 25 – 116; Appendix S4 Table S4.1). Despite extensive efforts to relocate individuals, we were unable to locate new home ranges for departed individuals successfully. As the dry season progressed, there were significant changes in environmental conditions on our study site. In general, home-range wetness ($n = 75$, $z = -2.01$, $p = 0.045$) and insect abundance declined ($n = 75$, $z = -2.51$, $p = 0.013$) while fruit abundance increased between our two sampling periods ($n = 78$, $z = -3.30$, $p < 0.001$; Appendix S4, Table S4.1, Figure S4.1). Home range wetness was significantly lower in the 2013 season compared with 2014-2015 ($F_{2,27} = 1270$, $p < 0.001$, $n = 52$; *Bonferroni* adjustment: 2013-2014, $p < 0.001$; 2013-2015, $p < 0.001$; 2014-2015, $p = 1$; Table S4.1) and corresponded to overall lower dry season rainfall across Belize (The World Bank: Climate Change Knowledge Portal: Climatic Research Unit of University of East Anglia).

Home-range Size

For all birds that remained site-persistent until approximately mid-March we obtained sufficient relocations (>16 relocations) to calculate 95% kernel density home-range estimates. Most individuals (n = 44) occupied a contiguous forested area moving an average of 55.8 ± 89.20 m between relocations. However, a number of individuals (n = 9) made regular off-territory forays (up to 2 km away) resulting in less contiguous, larger home ranges. Average home-range size across the three years of this study was 2.3 ± 2.66 ha (±SD, median = 1.35 ha, n = 53; Table S4.1). We found evidence that moisture, as measured by δ13C in blood, influenced home range size (Figure 2.1, Appendix S4 Table S4.2). Individuals with more enriched δ13C (in drier habitats) in their blood, but not claw, occupied larger home ranges (Table 2.1). The model including claw isotopes, which represents diets incorporated over a few months, did not find an effect of δ13C on home range size, but instead found that female and yearling birds were more likely to occupy larger home ranges (Figure 2.1, Table 2.1, Appendix S4 Table S4.1 and Table S4.2).

Food availability and diet

Home range wetness was included in the top model explaining both fruit counts and insect abundance (Figure 2.1; Appendix S4 Table S4.1 and Table S4.3). Individuals with home ranges that were wetter had more fruit ($\beta = 15.66$, 95% CI = 9.97, 21.35) and insects ($\beta = 12.83$, 95% CI = 6.54, 19.13). We also quantified food consumption using stable nitrogen isotopes to assess the proportion of insects versus fruit in individuals' diets. We found evidence that plot wetness and sampling period influenced the proportion of insects consumed in the diet (Figure 2.1, Appendix S4

Table S4.4). Claw δ15N values, which represent stable isotopes incorporated at the timescale of months, were more enriched (higher insect consumption) when study plots were drier (β = -4.66, 95% CI = -8.75, -0.57). Although wetness was included in the top model describing blood δ15N values, which represents stable isotopes incorporated at a weekly time scale, the confidence intervals included zero. The best predictor of blood δ15N values was sampling period, individuals had more depleted δ15N values (fewer insects consumed) during the late sampling period (β = -0.46, 95% CI = -0.72, -0.20).

Body Condition

There was a decline in the body condition of wood thrush across the late dry season, with individuals losing on average 1.4 ± 2.7g (± SD; percent body mass: 2.9 ± 5.83% SD; < 2 months; *t* = 3.23, p = 0.0013). Based on the averaged model including stable isotopes derived from blood, we found evidence of an effect of moisture, diet and an interaction between age and sex class on body condition early in the season (Figure 2.2, Appendix S4 Table S4.1 and Table S4.5). Individuals in wet habitats, as measured by δ13C values in blood, were in better condition (Table 2.2). Body condition was also higher in individuals with enriched δ15N values, indicative of higher insect consumption. Finally, the averaged model predicted body condition would be highest in adult males while lowest in adult females (Figure 2.2a). Similar effects were found in the model that examined claw isotope values (Appendix S4 Table S4.5). Given that blood isotopes have a shorter turnover rate that would better reflect habitats used prior to capture and current body condition we focus on results derived from blood stable isotopes. Change in body mass was negatively related to δ13C signatures in blood but not claw (Figure 2.2d; Appendix S4 Table S4.6). Individuals with depleted δ13C values in blood, characteristic of drier habitats, lost more weight over the sampling period (Table 2.3). For the model that included stable-carbon derived from claw, the confidence intervals for each parameter estimates overlap with zero (Table 2.3).

Seasonal Site Persistence

At the beginning of the spring migratory period (late April), the daily probability of seasonal site persistence was 20.0% (95% CI 0.13 – 0.31; n = 23/92 birds remained on site). We found evidence of an effect of habitat moisture on the probability of site persistence (Figure 2.3; Appendix S4 Table S4.7). Individuals with depleted δ13C in claws, indicative of wetter habitats, had a higher departure probability (β = -1.28, 95% CI = -2.04, -0.51). The probability of departure was also higher in 2015, a relatively wet year (β = 1.43, 95% CI = 0.53, 2.33).

Seasonal site persistence was assessed at a larger spatial scale by examining the winter locations of wood thrush equipped with GPS archival pinpoint tags (Figure 2.4). Overall seasonal site persistence was higher in our GPS tracked sample. At the commencement of the spring migratory period probability of site persistence was 66% (95% CI = 0.44 – 0.97; n = 7/17 individuals) compared with 20.0% (95% CI 0.13 – 0.31) from birds tracked with radio-transmitters from our study site in Belize. The first GPS tracked individual departed its initial home range at the end of February (Appendix S4 Table S4.1). Similar to wood thrush in Belize, site persistence was influenced by both wetness and variability in wetness (Figure 2.3; Appendix S4 Table S4.8), and probability of departure was higher for individuals in wetter habitats (β =

83.52, 95% CI == 12.15, 154.89). In addition, probability of departure was higher for individuals occupying areas with higher variation in wetness (β = 147.33, 95% CI = 8.12, 286.53). On average, individuals that departed initial home ranges moved 48.2 ± 57.8 km (range: 1.3 – 182.3 km; Figure 2.4); whereas, individuals that remained site persistent moved an average of 124 ± 159.5 m (±SD) between relocations (every 2 weeks). There was no difference in the average wetness or variability in wetness of locations occupied by individuals pre- or post-movement (average wetness: $t = 0.68$, p = 0.263; CV wetness: $t = 1.07$, p = 0.168).

Discussion

By combining on the ground field work at a single site with high-resolution tracking data from GPS transmitters we were able to demonstrate that both fine-scale space use strategies and larger scale movement dynamics of non-breeding wood thrush sampled from throughout their breeding range were dependent on patterns of moisture which influenced food availability. At our winter study site in Belize, individuals in drier habitats had lower food resources, were in poorer physical condition and occupied larger home ranges. We also showed that as habitats became more arid across the dry season, insect abundance declined (although fruit abundance increased) and birds in drier habitat lost weight. Overwinter site persistence was low (0.20, 95% CI 0.13 – 0.31), and contrary to expectations, departure probability was higher for birds occupying wetter habitats with higher food availability. GPS tracking confirmed this pattern (regardless of breeding origin) and revealed that individuals can make permanent mid-winter shifts of home ranges and move large distances to settle in new areas (range: 1.3 – 148 km). These results provide evidence that space-use strategies in overwintering wood thrush are flexible, and at least partly driven by fluctuating environmental conditions linked to patterns of moisture.

Mounting evidence points to the importance of food availability as a key non-breeding resource for migratory songbirds and the major driver of individual space-use behavior (Greenberg and Salewski 2005, Sherry et al. 2005, Smith et al. 2011a, McKinnon et al. 2015a). The results presented here support the conclusion that habitat quality is linked to food availability, which is ultimately driven by patterns of moisture. In drier habitats (based on stable-carbon isotope values) with lower fruit and insect abundance, individuals were more likely to occupy larger home-ranges, often using multiple, non-contiguous areas. Previous studies suggest that birds will adopt alternative space use strategies when optimal habitats are saturated to maximize survival under suboptimal conditions or when food resources are unpredictable (Zahavi 1971, Brown and Sherry 2008). Insects are a relatively stable food resource whereas fruit is extinguished more quickly and does not replenish within a season. Wood thrush were often observed making forays (up to 2 km) to large fruiting trees (e.g. *Trophis racemose*), which could explain the increase in home range size for some individuals. However, we found no decrease in the proportion of insects consumed by individuals on larger territories based on stable nitrogen-isotope levels of tissues. Instead, we found that wood thrush consumed larger proportions of insects when plots were drier. Therefore, we suggest that larger home ranges may be an adaptive strategy to compensate for lower insect availability.

Evidence for differential space use by subordinate age and sex classes through behavioral dominance has also been increasing (Marra 2000, Diggs et al. 2011, Catry et al. 2012). Consistent with this, we also found evidence that social dominance influenced space-use strategies in this system. Both females and young birds were more likely to inhabit larger home ranges and had lower body condition suggesting more aggressive adult males may exclude females and young birds from limited high-quality sites. Together, these differences in space use behavior suggest that there is competition for high quality habitats on the non-breeding grounds of wood thrush and less competitive birds are relegated to sub-optimal, drier, habitats where larger home ranges might be required to cope with lower food availability. In American redstarts, sexual habitat segregation due to competitive exclusion by dominant adult males forces subordinate individuals into drier habitats with lower food abundance (Marra 2000). Furthermore, occupancy of suboptimal scrub habitat has been found to carry-over to the breeding season resulting in reproductive consequences for excluded individuals of both sexes (Norris et al. 2004, Reudink et al. 2009). However, the effect of age and sex on home range size was not mirrored in our analysis of stables isotopes derived from blood, which provides information on environmental conditions across more recent time scales. This may indicate that as conditions become drier across plots, which would be better captured by isotopes derived from blood, moisture gradients may become a better predictor of home range size, regardless of age or sex. Given that individuals in drier habitats were in poorer condition and were more likely to lose weight across the dry season, the adoption of a larger home range may not fully compensate for lower food availability under all conditions. Adopting a larger home range, may therefore have consequences for individual performance that could be exacerbated at the end of the dry season when conditions are driest, and individuals need to prepare to migrate back to their breeding grounds.

The permanent mid-winter shifts of home ranges we discovered, in both our study population in Belize and among an independent group of GPS tracked birds from throughout the breeding range of the wood thrush, was unexpected. The fact that we found similar relationships between ecological correlates and space-use behavior with both approaches, however, provides us with confidence in the biological importance of these findings. Prior research on this species have shown that wood thrush can employ a floater or "wanderer" strategy (e.g. expanded home ranges) or large movements (Rappole et al. 1989, Winker et al. 1995). However, these studies were conducted at smaller spatial and temporal scales (transmitter life < 20 days), which makes characterizations of permanent versus temporary departures difficult. Although the probability of departure was high for both study populations, some individuals abstained from movements, suggesting this is not an obligate strategy. Furthermore, individuals that were tracked across multiple years on our Belize study site (n = 17), showed variability in seasonal site persistence across years (e.g. timing, site tenacity). These results suggest that non-breeding movements in wood thrush are a facultative strategy that allow for flexibility in space use among and within individuals. These results contribute to growing evidence that migratory birds engage in a wide array of both short- and long-distance movement behaviors during the non-breeding season that vary across species and populations of migratory songbirds (Stutchbury et al. 2016, Norevik et al. 2018).

Facultative movements recorded from individuals tracked with GPS transmitters suggest that this behavior occurs primarily during the latter part of the non-breeding season (February - April). Wood thrush arrive on their non-breeding range at the end of the wet season (October - November), when insect abundance is high (Janzen and Schoener 1968) and as the dry season progresses insect abundance declines (McKinnon et al. 2015). The timing of facultative movements suggest that the ultimate mechanism driving departure may be deteriorating environmental conditions, driven by declines in moisture (Terrill and Ohmart 1984). This behavior could be akin to the tracking of resources described in altitudinal (Boyle et al. 2010) and intra-tropical migration systems (Thorup et al. 2017, Koleček et al. 2018). For wood thrush, seasonal declines in moisture are more predictable and the scale of movements are smaller and similarly, birds may be initiating movements to search for improved environmental conditions. The broad range of departure dates suggests that individuals were not responding to broad-scale environmental cues (e.g. photoperiod, phenology; Heckscher et al. 2015, Thorup et al. 2017), but may instead be responding to finer-scale changes in habitat suitability. Therefore, facultative movements in wood thrush could be an adaptive response to fine-scale fluctuations in habitat suitability.

Contrary to our predictions, individuals from wetter habitats had a higher probability of engaging in facultative movements. Furthermore, neither sex nor age class influenced the probability of departure. This suggests that facultative movements are not driven by competition avoidance by subordinate individuals (e.g.

competitive release; Smith and Nilsson 1987). Given the evidence that birds in wetter habitats and in better condition were more likely to engage in winter movements, we propose that facultative winter movements in wood thrush may be condition dependent (Ketterson and Nolan 1983). Therefore, as local habitat suitability declines, individuals in poor condition may be constrained from engaging in this putatively risky behavior (e.g. due to low fat or pectoral muscle scores) and may instead try to "ride-out" deteriorating conditions. Given that birds must prepare for spring migration at the end of the dry season, individuals that attempt to "ride-out" conditions may be forced to delay migration preparations should conditions not improve in time. Although we suggest that facultative non-breeding movements by wood thrush are ultimately a response to declining habitat suitability, we found no evidence that individual wood thrush were directly tracking seasonal resources (Thorup et al. 2017) or upgrading to higher quality habitats (Smith et al. 2011b). Based on GPS tracking, there was no difference in the overall average wetness or variability in wetness between locations pre- or post- movements. However, low sample size made it difficult to account for latitudinal and elevation differences among individuals. Furthermore, high cloud coverage in Central America makes time-series of fine-resolution satellite derived data difficult to obtain. Therefore, a large question left unanswered is the proximate mechanism driving timing of movement decisions and settlement in new locations. Additional factors that could drive habitat suitability and influence decision-making of individual birds, including interspecific competition (Stutchbury et al. 2016) or changes in predation risk, should also be considered. Comparing the fitness consequences (e.g. survival, condition, reproductive success) of either strategy will be necessary to better resolve the value of facultative winter movements in wood thrush.

Deciphering the role that seasonal patterns of moisture play for limiting populations of Neotropical migratory songbirds has important implications for the management of these species, as climate models forecast increasingly arid condition on their wintering range (Neelin et al. 2006). In this study, we found that individuals in drier conditions were in lower individual condition and adopted different space-use strategies, the consequences of which are still unclear. At local spatial scales, individuals in drier habitat were more likely to utilize larger home range. Previous research has suggested that wood thrush that occupy larger home ranges face higher mortality rates ("wanderers" *sensu* Rappole et al. 1989). At larger spatial scales, individuals in drier habitats were less likely to depart non-breeding home ranges as conditions deteriorated across the dry season. If facultative movements are an adaptive strategy to avoid deteriorating dry season habitat suitability, this strategy may buffer wood thrush against the predicted increased severity of dry seasons. However, if facultative movements are a condition dependent strategy, then increasingly dry conditions during the non-breeding period could prevent birds from escaping deteriorating conditions as the dry season progresses. Developing a better understanding of the mechanisms driving facultative movements of wood thrush, and perhaps other species of migratory birds, will be essential to understanding the flexibility individuals may need to exhibit to adjust to future climatic shifts.

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Tables

Table 1.1 Model averaged parameter estimates, standard error and unconditional 95% confidence intervals for top generalized mixed effect models for home range size (95% isopleth of utilization distribution) of non-breeding wood thrush in Belize. Separate models were constructed for isotope values derived from claws (n = 37) which provides information on diets over a few months and blood (n = 44) which provides information on diets over a few weeks.

Parameter	Estimate	SE	95% CI
Claw			
Age (yearling)	**-0.30**	**0.11**	**-0.51, -0.09**
Sex (Male)	**0.32**	**0.13**	**0.07, 0.56**
Blood			
Age (yearling)	-0.16	0.09	-0.34, 0.03
Sex (Male)	0.10	0.10	-0.09, 0.30
Condition	1.47	1.05	-0.60, 3.53
δ13C	**-0.13**	**0.06**	**-0.26, -0.01**
δ15N	-0.05	0.06	-0.17, 0.06

Notes: Values in bold have confidence intervals that do not include zero.

Table 1.2 Model averaged parameter estimates, standard error and unconditional 95% confidence intervals for top linear mixed effect models on the body condition index in the early dry season sampling period for non-breeding wood thrush in Belize. Separate models were constructed for isotope values derived from claws (n = 104) which provides information on diets over a few months and blood (n = 112) which provides information on diets over a few weeks.

Parameter	Estimate	SE	95% CI
Claw			
δ13C	**-1.74**	**0.81**	**-3.32, -0.17**
Wetness	-24.68	28.53	-80.59, 31.24
Age (yearling)	2.31	1.72	-1.07, 5.68
Sex (Male)	**3.76**	**1.69**	**0.45, 7.07**
Wetness * δ13C	**38.34**	**17.61**	**3.83, 72.86**
Age (yearling) * Sex (Male)	**-6.33**	**2.37**	**-10.98, -1.69**
δ15N	**1.61**	**0.77**	**0.11, 3.11**
Wetness * δ15N	-19.98	17.05	-53.4, 13.44
Blood			
δ13C	**-2.18**	**0.66**	**-3.48, -0.88**
δ15N	**2.37**	**0.91**	**0.59, 4.15**
Wetness	-7.84	27.46	-61.66, 45.98
Age (yearling)	2.25	1.68	-1.03, 5.54
Sex (Male)	**4.26**	**1.71**	**0.9, 7.62**
Age (yearling) * Sex (Male)	**-5.42**	**2.22**	**-9.77, -1.07**
Wetness * δ15N	-39.93	23.65	-86.29, 6.43
Wetness * δ13C	30.08	17.00	-3.25, 63.41

Notes: Values in bold have confidence intervals that do not include zero.

Table 1.3 Model averaged parameter estimates, standard error and unconditional 95% confidence intervals for top linear mixed effect models describing change in mass between the early and late dry season sampling period for non-breeding wood thrush in Belize. Separate models were constructed for isotope values derived from claws (n = 26) which provides information on diets over a few months and blood (n = 31) which provides information on diets over a few weeks.

Parameter	Estimate	SE	95% CI
Claw			
δ13C	0.68	0.60	-0.5, 1.87
Wetness	14.21	40.86	-65.87, 94.28
Age (yearling)	0.82	1.43	-1.98, 3.63
Sex (Male)	1.22	1.32	-1.37, 3.82
Age (yearling) * Sex (Male)	0.13	1.94	-3.68, 3.94
δ15N	-0.22	0.53	-1.26, 0.81
Blood			
δ13C	**-1.11**	**0.53**	**-2.15, -0.07**
Wetness	2.36	19.16	-35.2, 39.91
Age (yearling)	-0.52	1.42	-3.3, 2.26
Sex (Male)	0.07	1.21	-2.31, 2.45
Age (yearling) * Sex (Male)	1.80	1.91	-1.94, 5.55
δ15N	-0.79	0.45	-1.68, 0.1

Notes: Values in bold have confidence intervals that do not include zero.

Figures

Figure Legend

Figure 2.1. Factors driving home range size (A – C), food availability (D – E) and food consumption (F) for wood thrush during the non-breeding season. Mean (± SE) home range size (ha) for each age (A) and sex (B) class of wood thrush. (C) Positive relationship between home range size and habitat moisture based on stable-carbon values from claws. Stable-carbon values have been scaled; more negative values denote drier habitats. Fruit (D) and insect (E) counts conducted on individual wood thrush home ranges were positively related to satellite-derived home range wetness. Fruit and insect counts were log-transformed and scaled, more positive wetness values denote wetter habitats. (F) Negative relationship between stable-nitrogen levels derived from claws and satellite-derived plot wetness. Stable nitrogen values have been scaled; more positive values denote larger proportions of insects in diet. More negative wetness values denote drier conditions. Asterix denotes significant difference in bar plots. For scatterplots, line denotes the model predicted relationship and shaded area the 95% CI.

Figure 2.2. Factors driving body condition of wood thrush during the non-breeding season in Belize. (A) Body condition index (marginal mean ± 95% CI) during the early dry season by age and sex class. Body condition index (B) and change in mass (D) were negatively related to stable-carbon values in the blood. Stable-carbon value have been scaled, more negative values denote drier habitats. (C) Positive relationship

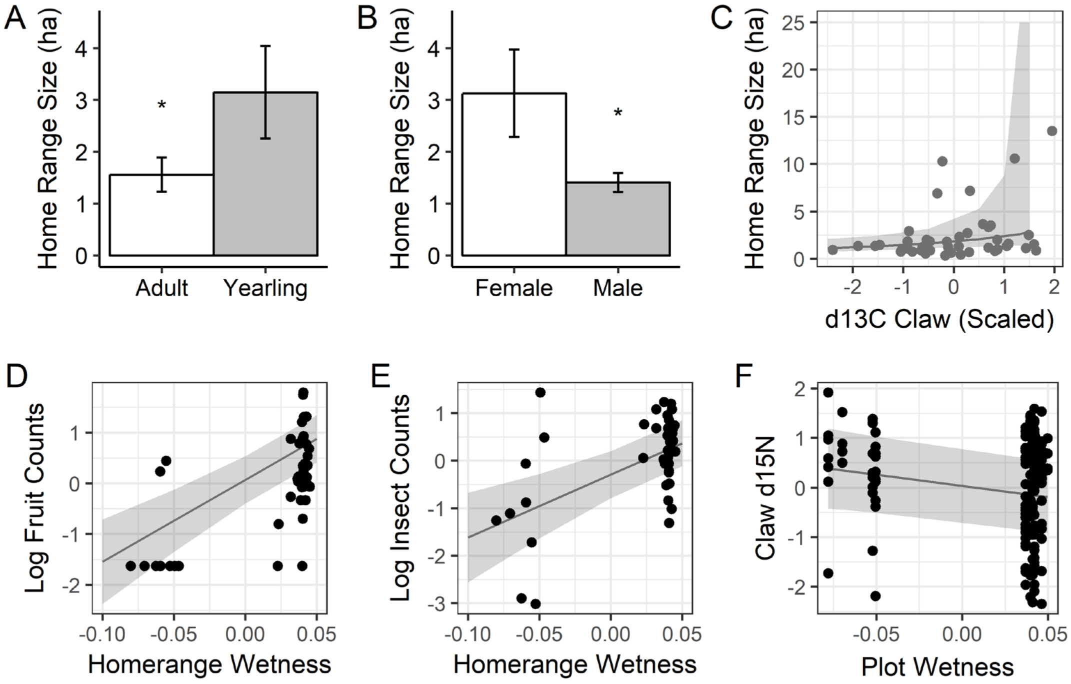
between stable-nitrogen values in blood and body condition index. Stable nitrogen values scaled, more positive values denote larger proportions of insects in diet. For scatterplots, line denotes the model predicted relationship and shaded area the 95% CI.

Figure 2.3. Proportion of wood thrush remaining stationary across the non-breeding period from our study population in Belize and wood thrush tracked using GPS transmitters based on the estimated survival function of a Cox Proportional Hazard model. (A) In Belize, estimated proportion of wood thrush remaining stationary in wet (solid, red line) and dry (dashed, black line) habitats based on stable-carbon values in claws. Enriched δ13C (expressed as first quartile) represents wetter habitats, depleted δ13C (expressed as third quartile) represent dry habitats. (B) Negative effect of habitat moisture as measured by δ13C values in claws on the hazard ratio for departure. The probability of performing a facultative movement increased under wetter conditions, represented by more negative (depleted) δ13C values. (C) For GPS tracked individuals, proportion of wood thrush remaining stationary in wet (solid, red line) and dry (dashed, black line) habitats based on satellite-derived wetness values. Dry values are expressed as the first quartile of wetness values, wet values are expressed as the third quartile of wetness values. (D) Positive effect of habitat moisture as measured by the satellite-derived wetness value on the hazard ratio of departure. The probability of engaging in facultative movements increases with higher wetness values (wetter). (A, C) Line represents estimate of proportion of

stationary individuals from model, shaded area 95% CI. (B, D) Line represent adjusted hazard ratio and shaded area represents 95% CI.

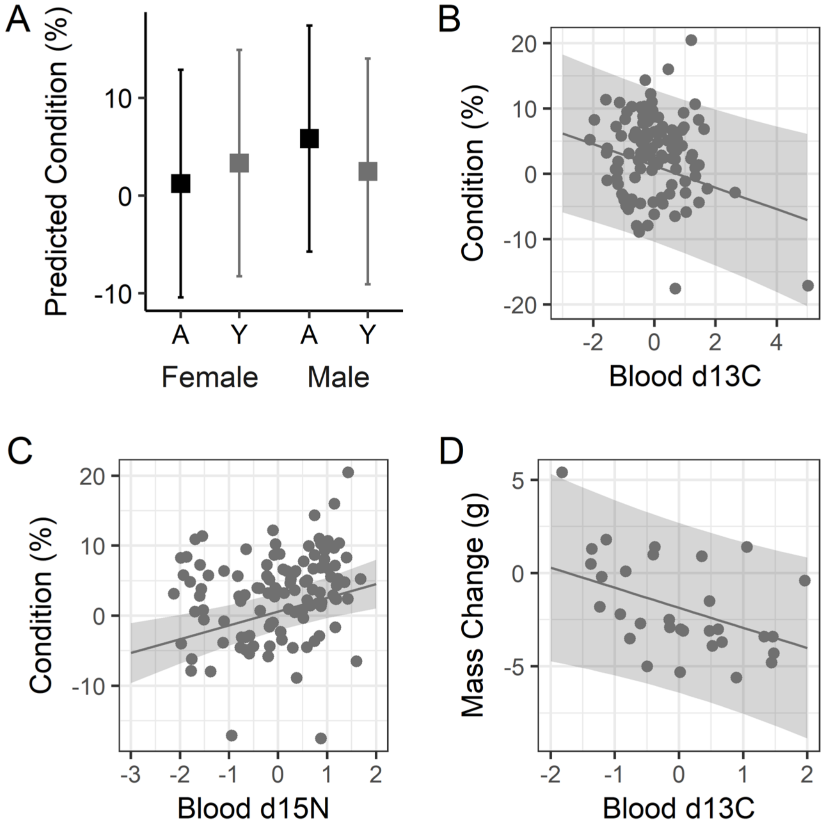
Figure 2.4. (A) Non-breeding locations (bi-monthly) of adult male wood thrush tracked using high-resolution GPS transmitters from 5 breeding populations (n = 17). Circles represents individuals that remained stationary across the non-breeding season. Triangles represent individuals that made non-breeding movements. Different combinations of triangle type (delta vs. inverse) and shades represent unique individuals. (B) Non-breeding movements of 4 individuals in Honduras and Nicaragua, lines connect individual movements. (C) Timing of intra-winter movements for two individuals in Nicaragua.

Figure 2.1



A
Home Range Size (ha)
0
1
2
3
4
*
Adult
Yearling
B
Home Range Size (ha)
0
1
2
3
4
*
Female
Male
C
Home Range Size (ha)
0
5
10
15
20
25
-2
-1
0
1
2
d13C Claw (Scaled)
D
Log Fruit Counts
-2
-1
0
1
-0.10
-0.05
0.00
0.05
Homerange Wetness
E
Log Insect Counts
-3
-2
-1
0
1
-0.10
-0.05
0.00
0.05
Homerange Wetness
F
Claw d15N
-2
-1
0
1
2
-0.05
0.00
0.05
Plot Wetness

Figure 2.2



A
Predicted Condition (%)
10
0
-10
A
Y
A
Y
Female
Male
B
Condition (%)
20
10
0
-10
-20
-2
0
2
4
Blood d13C
C
Condition (%)
20
10
0
-10
-3
-2
-1
0
1
2
Blood d15N
D
Mass Change (g)
5
0
-5
-2
-1
0
1
2
Blood d13C

Figure 2.3

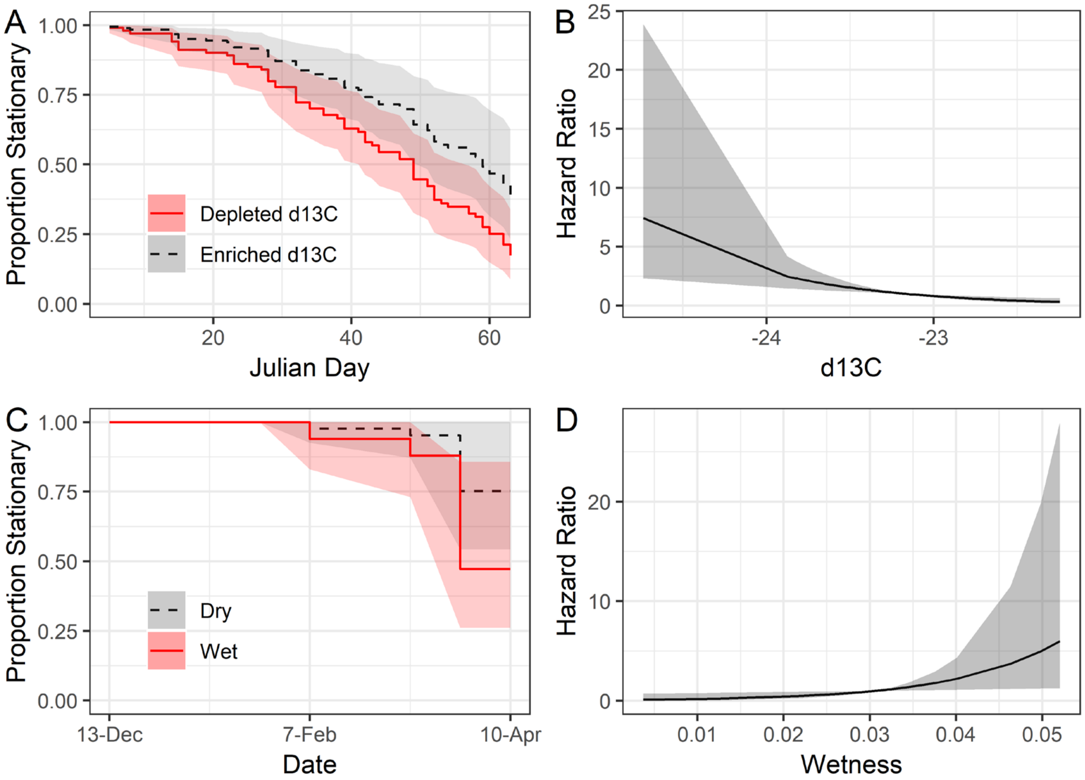
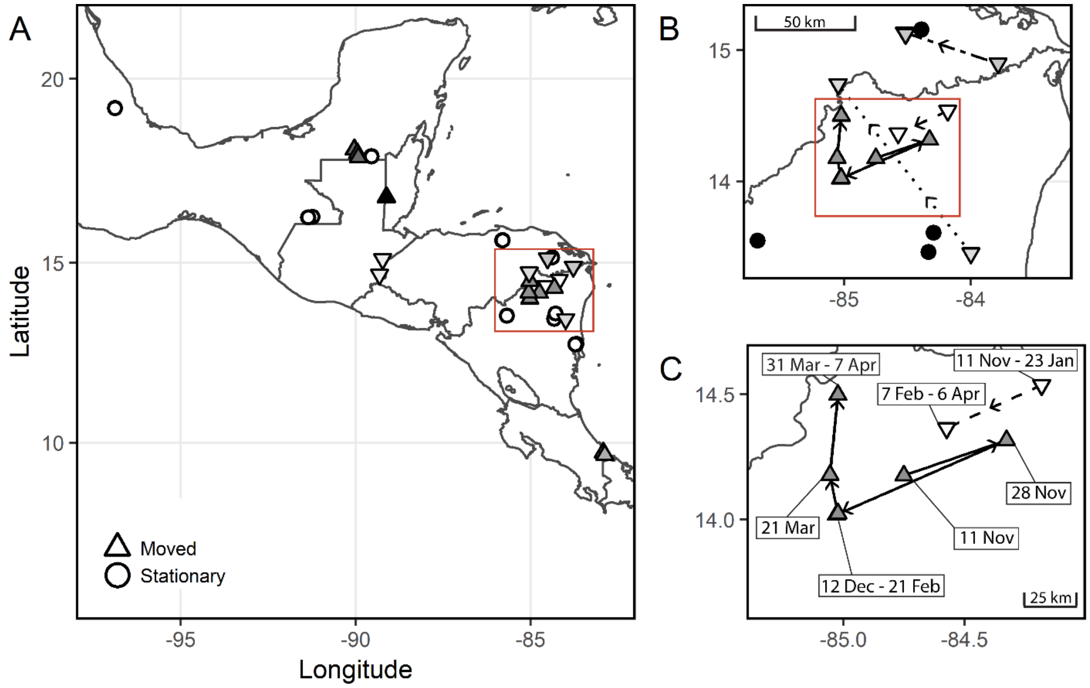

A
1.00
0.75
0.50
0.25
0.00
Proportion Stationary
20
40
60
Julian Day
Depleted d13C
Enriched d13C
B
25
20
15
10
5
0
Hazard Ratio
-24
-23
d13C
C
1.00
0.75
0.50
0.25
0.00
Proportion Stationary
13-Dec
7-Feb
10-Apr
Date
Dry
Wet
D
20
10
0
Hazard Ratio
0.01
0.02
0.03
0.04
0.05
Wetness

Figure 2.4


A
B
C
Latitude
Longitude
20
15
10
-95
-90
-85
Moved
Stationary
50 km
15
14
-85
-84
14.5
14.0
-85.0
-84.5
31 Mar - 7 Apr
11 Nov - 23 Jan
7 Feb - 6 Apr
28 Nov
21 Mar
11 Nov
12 Dec - 21 Feb
25 km

Chapter 3 : Food limitation and the endogenous control of spring migration: a captive experiment with a long-distance migratory bird

Abstract

The onset of spring migratory behavior in birds is thought to be controlled by a rigid endogenous schedule due to the selection pressure to time migration in anticipation of environmental conditions on the breeding grounds. The degree of flexibility for spring departure schedules in response to supplementary environmental cues remains unclear. Recent field studies have suggested an important role of external factors such as weather variation and food availability in modifying the timing of spring departures. Here, we investigated the role of food availability in modifying endogenous spring migratory schedules in a captive population of wild-caught Wood Thrush (*Hylocichla mustelina*) by quantifying nocturnal migratory restlessness (*Zugunruhe)* under two food treatments: ad libitum or "control" food availability expected to maintain body weight vs. reduced food availability expected to result in a 5% decline in body weight. Contrary to predictions, food treatment did not affect the onset of *Zugunruhe*, however, it did advance migratory fattening compared to the control group. Birds with reduced food availability maintained lower fuel loads (% target mass) and decreased *Zugunruhe.* Moreover, fuel load predicted the cumulative magnitude of *Zugunruhe*. These results suggest that food availability may modulate the development of *Zugunruhe*, not its onset, in captive birds adding support to field studies that have demonstrated delayed spring migration departure in physically compromised birds. Fattening when food availability is low may provide a strategy to

escape poor or unpredictable winter environmental conditions regardless of migratory readiness. Our results highlight the challenging trade-off faced by migratory birds between surviving migration and optimally timing arrival on the breeding ground and further solidifies how periods of the annual cycle are linked and the significant role these interacting effects can play in driving the fitness of migratory birds.

Introduction

Migratory species are expected to time their migrations optimally to match the timing of life history events with suitable environmental conditions (Alerstam and Lindström 1990). For migratory birds, this is expected to be particularly important during spring migration because even relatively small differences in the timing of arrival and initiation of nesting on breeding grounds can have profound fitness consequences (Saino et al. 2004, Reudink et al. 2009). To correctly time migration relative to anticipated environmental conditions on northern breeding areas, migratory birds are thought to rely on an endogenous circannual schedule synchronized to photoperiod that acts as a predictable environmental cue (*zeitgeber*; Gwinner 1996, Åkesson et al. 2017). To avoid the risk of mistiming migration, a rigid endogenous schedule would be favoured since additional environmental stimuli on the nonbreeding grounds will have limited or no predictive relevance to current conditions on breeding sites. At the same time, to maximize survival during migration, selection may favor individuals that can flexibly adjust rigid timing mechanisms to respond to current environmental conditions (Helm et al. 2017). For example, spatial (e.g. Latta and Faaborg 2002, Studds and Marra 2008) and temporal (e.g. Studds and Marra 2007, McKinnon et al.

2015) variation in non-breeding habitat suitability have been found to influence individual non-breeding performance. To adjust to these fluctuations in non-breeding conditions, other factors, such as temperature, precipitation and food availability, may impact migration progression by either accelerating or deaccelerating migratory function (Ramenofsky et al. 2012). Mechanistically, precipitation and moisture availability have been shown to control food (arthropod) availability, which limits the physical condition of overwintering American Redstarts (*Setophaga ruticilla*; Studds and Marra 2007). Whether precipitation and food availability act directly as a cue, or, indirectly as a constraint on migration preparation (e.g. migratory fattening) to fine-tuning departure decisions is unknown. Regardless, a quantitative understanding of the role of these factors in influencing the different phases of migration is currently lacking for most species.

The migratory period can be divided into three phases: development, mature expression and arrival *sensu* Cornelius et al. (2013). The developmental phase involves the physiological transition to migratory disposition; mature expression is characterized by consecutive cycles of fuelling and flight; and arrival involves the termination of migratory behaviour and transition to subsequent life history stages. Most of what is known about the proximate mechanisms underlying the timing of migration comes from experiments on captive birds (Gauthreaux, 1996). Under captive situations most obligate migratory species develop fat reserves and exhibit nocturnal restlessness or *Zugunruhe,* typified by periods of wing-whirring, increased perch-hopping, body-turning and other activities. The intensity of these behaviours provide a simple metric to quantify the disposition of captive birds to migrate in the wild (e.g. birds exhibiting lower intensity of *Zugunruhe* have lower migratory disposition). Currently the best understanding of the role of external factors in modifying the onset of migration comes from studies of birds during the mature phase of migration. Studies of free-living individuals have found that departure decisions from stopover sites are influenced by atmospheric, climatic and physiological conditions (Cochran and Wikelski 2005, Fusani et al. 2011) while termination of migration has been linked to climate and availability of food resources (Terrill and Ohmart 1984, Ramenofsky and Wingfield 2017). The role of food availability and physiological condition has been extensively examined due to the importance of acquiring sufficient fat reserves to fuel migration (Bairlein 2003).

Studies examining migrants at stopover locations or by stimulating stopover conditions in captivity (fasting-refueling experiments) have generally found that (1) fasting increased migratory activity and (2) refueling decreased migratory activity (Gwinner et al. 1988, Eikenaar et al. 2014), but that these effects were mediated by physiological condition. Individuals in poor condition (or who had lost large fuel loads) were less likely to leave stopover sites in field studies or displayed lower *Zugunruhe* in captive experiments (Bridge et al. 2010, Fusani et al. 2011). Together these studies suggest that the migration program does show flexibility and supplemental environmental factors can provide spatiotemporally sensitive information to allow fine-tuning of departure decisions based on current behavioural and physiological condition. The degree of flexibility likely varies across species depending on a number of factors including life-history stage (spring vs fall), migratory strategy (facultative vs obligate), and ecological conditions (habitat type, diet).

How supplementary environmental factors influence the development phase of spring migration on the wintering grounds is less well resolved. An emphasis on a rigid endogenous departure schedule was bolstered by early work suggesting a minor role for food availability as a local supplementary cue promoting the development of migratory activity (Berthold 1975, Lofts et al. 2008). However, this work was restricted to fall migratory activity in captive individuals. Far less research has been conducted examining the effects of supplemental environmental factors on spring departure decisions. Recent work investigating the ecology of free-living populations of migratory songbirds on their non-breeding grounds has demonstrated how winter habitat quality, often linked to precipitation, can influence spring departure, shedding new light on how seasonal interactions drive migratory function (Marra et al. 1998, Studds and Marra 2011b, McKinnon et al. 2015b). Collectively, these studies in wild populations suggest that factors, such as food availability, can delay the circannual time program (Helm et al. 2017). On average, these studies observe differences of 3-5 days between years, suggesting flexibility in departure possibly linked to environmental and physical conditions in both observational (Studds and Marra 2011b) and tracking studies (Stanley et al. 2012, Conklin et al. 2013). Therefore, the role supplementary factors play in modulating the rate and magnitude of the development of spring migratory behaviour is unknown. The degree of plasticity is likely a fine balance between the benefits of ensuring optimal timing of arrival at breeding grounds and the ability to flexibly adjust to current conditions to maximize survival while on migration.

To experimentally examine the interaction between the endogenous migratory control program and supplementary factors, such as food availability, we performed a controlled feeding experiment on captive Wood Thrush (*Hylocichla mustelina*) and monitored their spring migratory activity. Specifically, we examined if and how food availability regulates the onset and intensity of *Zugunruhe* and migratory fattening. We predicted that birds on a food-restricted diet would have decreased fuel load, leading to later onset of spring migratory activity and decreased *Zugunruhe* compared to controls with food available *ad libitum*.

Methods

Study System

Wood Thrushes are obligate long-distance Neotropical migratory songbirds that breed in eastern North America and spend the non-breeding season in Central America and Mexico. Tracking studies have revealed some degree of repeatability in spring departure dates for individual Wood Thrush tracked over multiple years, with an average difference of 3 days between years (Stanley et al. 2012). McKinnon et al. (2015b) identified an association between departure dates and dry environmental condition based on coarse resolution remote sensing data (NDVI), but no association with late season body condition. Therefore, the Wood Thrush migratory schedule may show some flexibility in departures dates, but it is unclear whether food availability or some other physical change on the winter grounds drove these differences.

Bird Capture and Maintenance

To investigate the role food availability plays in modifying spring departure dates, adult male Wood Thrush (n = 26) were captured using mist nets in the summer of 2015 on Maryland Department of Natural Resources land units in Carrol, Frederick, Montgomery and Prince Georges counties. Birds were banded, body measurements taken, and transported to the Smithsonian National Zoological Park research facilities where they were housed in individual cages (66 x 36 x 50 cm) kept on a 16L:8D photoperiod and a constant temperature (~26ºC). They were switched to a 12L:12D light cycle to stimulate the overwinter period on 5 March 2016. Birds were maintained on an agar-based mash diet designed to provide 78 kcal and were fed twice per day. The diet consisted of Zulife Softbill Diet (1.8%), Proplan Large Breed Dog (1.8%), fruit and vegetable mix (apple, banana, cantaloupe, papaya, zucchini, blueberries; 15.2%), hard-boiled egg (6.6%), insects (crickets, earthworms, mealworms and waxworms; 25.5%), agar (1.2%) and water (38.3%), and topped with 2 g of live mealworms.

Body Condition

To monitor the experimental treatments, body condition was recorded twice per week in the morning prior to individuals receiving food. Measurements included body mass (nearest 0.1g), and subcutaneous fat deposits. To measure migratory fuel reserves, fuel load was determined using the formula: (body mass – target winter body mass)/target winter body mass. Target winter body mass was estimated for each bird based on their structural size using a regression equation of mass versus metatarsus (to the nearest 0.1 mm) and wing chord (to the nearest 1 mm) generated from a dataset (Chapter 2) for Wood Thrush wintering in Belize with low subcutaneous fat scores (trace or 1 fat; 3 years of data; mass = 18.5 + 0.31(metatarsus) + 1.03(wing chord). Fat deposits were scored by examining the torso visually using a standardized 5-point scoring scale (Holmes et al. 1989).

Nocturnal Activity

To monitor *Zugunruhe*, nocturnal activity was recorded every night using infra-red video cameras (Swann 1080p Digital Video Recorder and Cameras, Model # SWDVK-845008) placed above cages. Each camera recorded the movement of 4 cages simultaneously (Figure 3.1b). Videos were analyzed using BirdOriTrack software (Muheim et al. 2014). Nightly nocturnal activity was calculated as the sum of the total length moved every 30 seconds relative to the length of the cage. Nocturnal activity was calculated from 30 minutes after lights out until 30 minutes prior to lights on.

Experimental design

We randomly assigned 13 birds to the food reduction treatment and 13 birds to the *ad libitum* treatment (Figure 3.1a). The *ad libitum* treatment was designed to maintain target body weight, whereas the food reduction treatment was designed to decrease target body weight by 5%. The food reduction treatment was achieved by reducing the standard diet provided to each bird. The reduction ranged from - 55% to +15%

depending on the individual, but the composition of the diet remained consistent. After three weeks individuals reached the desired body mass for their experimental feeding treatment and were kept on the experimental treatment until the end of the experiment. To promote the transition into migration, the photoperiod was gradually increased over 24 days from 12L:12D to 13L:11D to mimic late-winter pre-migratory daylength in the natural environment (Figure 3.2a). To monitor the development of migratory behaviour we measured: (1) *Zugunruhe* and (2) migratory fattening.

Timing of Migration

To identify periods of *Zugunruhe* changepoint analysis was applied to the time series data of average daily nocturnal activity using the binary segmentation algorithm in the R package *changepoint* (Doren et al. 2017). Changepoint analysis identifies the point in time when the statistical properties (e.g. mean, variance) of a sequence of data changes (Killick and Eckley 2015). We used the “cpt.mean” function which detects changes in the mean of a time series and a cumulative sum test statistic, which does not assume a distribution for the data. To define the *Zugunruhe* period we restricted the number of changepoints to two with a minimum segment length of 20 since we expected *Zugunruhe* periods to be weeks in duration (Doren et al. 2017). Onset and termination of migration were defined as the start and end dates identified by changepoint analysis as periods of elevated nocturnal activity, duration was the number of days between the start and end dates. Birds were excluded from analysis if no changepoint was identified (e.g. consistent low or high nocturnal activity; n = 7), or if changepoints were detected prior to the commencement of the experimental food treatment (n = 3). In total 10 birds were omitted from analyses (5 from each treatment group), resulting in a final sample size of 16 birds (n = 8 per group).

To identify periods of migratory fattening (i.e. the accumulation of fat as an energy reserve for migratory flights) we identified periods of increased fuel load using the same methods as Maggini and Bairlein (2010). In brief, we calculated mean fuel loads in five-day bins and identified periods of 3 consecutive increases or decreases. The third day of the first bin of increase was identified as the onset of migration. The end of migration was calculated by the same method but in reverse direction (3 consecutive decreases, third day of last bin).

Magnitude of Migration

The magnitude of *Zugunruhe* was calculated using a cumulative measure of *Zugunruhe* calculated by measuring the area under the curve formed by taking the average nocturnal activity at each day across the (i) migratory period defined by changepoint analysis and (ii) migratory fattening period. Area under the curve was calculated using linear interpolation with the *auc* function in the R package *MESS* (Ekstrøm 2019).

Statistics

To determine the influence of feeding treatment on body condition we examined fuel load and fat scores at two time periods: prior to migration and across each bird's migratory period based on changepoint analysis of *Zugunruhe* data. For each time period we compared treatment groups using generalized linear models. To examine the effect of feeding treatment on timing and magnitude of migratory behaviour we constructed separate generalized linear models for each timing and magnitude metric (e.g. onset of migratory fattening, average intensity of *Zugunruhe*) to compare treatment groups. To examine how body condition influenced the magnitude of *Zugunruhe* we compared cumulative *Zugunruhe* to average fuel load using generalized linear models.

All analyses were conducted in R 3.4.3 (R Core Team 2017). Generalized linear models were run in the R package *stats* (R Core Team 2017). To assess model fit, each model was compared to a null model using an F-test. All models were assessed for violation of model assumptions by visual inspection of plots of residual versus predicted values and quantile-quantile plots. When necessary to meet model assumptions of normality response variables were transformed and significant outliers were identified using Cook's distance plots (Kutner et al. 2004). One bird was excluded from models of *Zugunruhe* magnitude as an outlier (Cook's distance > 1).

Results

Body Condition

Prior to the start of food treatments there were no differences in fuel load or fat scores between treatment groups (Fuel load: $F_{1,16} = -0.0554$, $p = 0.114$; Fat: $F_{1,16} = -0.0542$, $p = 0.896$). Food reduction decreased condition compared to the control group (Table 3.1). At the beginning of the experimental trial, prior to the development of *Zugunruhe,* fuel loads were lower in the reduction food treatment, but not significantly. ($F_{1,13} = -0.04106$, $p = 0.0566$). There was no difference in fat scores

($F_{1,13} = -0.171$, $p = 0.646$). Once migratory condition began all birds put on fat deposits and gained weight, irrespective of treatment. During *Zugunruhe* expression, food reduction birds exhibited significantly lowered fuel loads ($F_{1,15} = -0.147$, $p = 0.0030$) and fat scores ($F_{1,15} = -1.030$, $p = 0.0353$) compared to the control birds.

Timing of Migration

Birds began developing migratory disposition (either migration fattening or *Zugunruhe*) between 1 to 6 weeks after the start of the experimental feeding treatments (Julian dates range: 67 to 107; Figure 3.2). Feeding treatment had no effect on the start or end day of *Zugunruhe* (start: $F_{1,14} = 0.0443$, $p = 0.446$; end: $F_{1,14} = -0.0446$, $p = 0.287$). Food restriction advanced the start of migratory fattening by 2-3 days ($F_{1,16} = -3.097$, $p = 0.0276$; Figure 3.2) but had no effect on the termination day of migratory fattening ($F_{1,14} = -0.0446$, $p = 0.287$). Overall there was a broader range in onset of *Zugunruhe* (72 days, range = 67 to 145) compared with migratory fattening (9 days, range = 98 to 107). Most individuals began exhibiting *Zugunruhe* prior to migratory fattening; however, four individuals (Food reduction: n = 3; Control: n = 1) did not exhibit *Zugunruhe* until after migratory fattening. Six individuals began developing *Zugunruhe* prior to the increase in photoperiod, three from each treatment group.

Magnitude of Migration

Across the migratory period, food restricted birds exhibited lower cumulative *Zugunruhe,* although it was not significant ($F_{1,14} = -9.812$, $p = 0.\ 0796$; Figure 3.3). Across the migratory fattening period, food restriction significantly decreased cumulative *Zugunruhe* ($F_{1,14} = 0.0381$, $p = 0.0502$). Fuel load had a significant positive effect on cumulative *Zugunruhe* across the migratory period ($F_{1,14} = 80.182$, $p = 0.0415$) and the effect approached significance across the migratory fattening period ($F_{1,14} = -0.260$, $p = 0.0558$; Figure 3.4).

Discussion

To ensure optimal timing of reproduction, long-distance migratory songbirds have been thought to rely on a rigid genetically controlled spring migration schedule to ensure timely departure from wintering grounds (Berthold et al. 2003). The degree of flexibility to fine tune timing of winter departure, based on supplementary environmental factors such as food availability, remains poorly resolved but could represent an important strategy for ensuring successful completion of migration. Here we found that reduced food availability lowers migratory body condition and decreases a cumulative measure of *Zugunruhe*. However, we did not identify differences in the timing of expression of *Zugunruhe* between diets, but instead found that onset of migratory fattening was advanced in individuals on reduced diets. Our study provides the first direct evidence that food availability modulates the development and intensity of spring migratory behaviour in an obligate long-distance migratory songbird.

Food availability is expected to be an important supplementary factor because the development of mature migratory capabilities relies on the accumulation of fuel stores (Ramenofsky et al. 2012, Cornelius et al. 2013). Despite the role of fat stores in fueling migration, early studies on captive migrants did not consistently find an effect of food restriction on migratory behaviour in captive birds. More recent research examining later phases of migration (mature expression) have found that fuel load and/or amount of fuel lost is a good predictor of intensity of *Zugunruhe* (Fusani et al. 2011, Eikenaar et al. 2014). In this study, by challenging individuals as they developed migratory disposition, we similarly observed inhibition of *Zugunruhe* as birds attempted to accumulate fat reserves on a reduced diet and positive effects of fuel load on *Zugunruhe*. If intensity of *Zugunruhe* represent the disposition of a bird to depart on migration, we interpret the inhibition of cumulative *Zugunruhe* to suggest that low food availability on the non-breeding grounds will slow progression of migration development and possibly delay departure on migration. These results suggest that inter-annual variation in spring departure schedules, as observed in American Redstarts (Studds and Marra 2011b) and Wood Thrush (Stanley et al. 2012) by monitoring or tracking the same individuals across years, could be explained by differences in food availability on wintering territories. Flexibility to adjust the timing program based on non-breeding ground condition could therefore provide an important mechanism to handle variability in habitat suitability and maximize survival on migration. However, if birds are not able to correct for delays (e.g. faster migration; McKinnon et al. 2015b), events on the wintering grounds would likely carry-over to influence timing of subsequent life-history stages and reproductive success (Marra et al. 1998, Reudink et al. 2009).

Contrary to expectations, we found food reduction advanced onset of migratory fattening an average of 3 days. Attempts to prevent migratory fattening were unsuccessful and accumulation of migratory fat reserves occurred in the food reduction group, likely through increased food utilization efficiency and not hyperphagia as birds did not have access to extra food (Bairlein 2003). During fall migration, intermittent fasting similarly advanced fall migratory fattening in garden warblers (*Sylvia borin*; Totzke et al. 2000). The advancement of migratory fattening could be a strategy to buffer birds against unpredictable environmental conditions ahead of migration. For example, increased fat reserves has been predicted and observed in prior experiments as a form of insurance during periods of temporary nutritional stress (McNamara and Houston 1990, Gosler 1996). Alternatively, low food availability, resulting in a negative energy balance, may also provide a supplemental cue to the migratory fattening program and serves to accelerate fuel accumulation. If birds require a threshold fuel load for departure, advancing migratory fattening could afford additional time to accumulate sufficient fat reserves. An interesting possibility might be advanced based on findings from tracking studies that revealed that Wood Thrush engage in facultative movements during the winter period (Chapter 2). Accelerating migratory development could therefore provide individuals the opportunity to locate staging areas more suitable for migration preparation prior to spring departures. Since low food availability inhibits the intensity of *Zugunruhe,* the ability to advance migratory fattening may provide a mechanism to avoid delays in the spring migratory program by advancing preparation for departures.

The rigidity of spring migration schedules is often espoused due to (1) the fitness consequences associated with mistiming arrival on the breeding grounds and (2) the lack of relevant environmental factors on non-breeding areas to predict breeding conditions. However, a growing body of work suggests that obligate migrants show facultative components with their migrations, particular during later phases of migration (Ramenofsky et al. 2012). For example, in extreme sub-alpine conditions, Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*) arrive on breeding sites when snow still blankets the ground (Ramenofsky and Wingfield 2017). To balance the reproductive advantage of early arrival with the survival challenge of cold temperate breeding grounds, should conditions deteriorate, individuals are thought to engage in facultative irruptive flights by extending the migratory state until conditions improve. Additionally, during fall migration, both short- and long-distance migrants have been shown to redevelop migratory disposition at the end of migration, sometimes extending well into the winter period, if environmental or social conditions deteriorate (Berthold 1978, Terrill and Ohmart 1984). The results presented here suggest that onset of spring migration may also display a facultative aspect most often associated with later phases of migration. This may be particularly relevant for species with unpredictable late-winter environmental conditions. For example, many Neotropical migratory birds prepare for spring migration at the end of the tropical dry season which vary in severity depending on yearly rainfall (Studds and Marra 2011b). Being able to advance migration preparation in dry years could prevent delays from influencing subsequent activities through seasonal interactions.

The hypothesis that lower food availability would delay onset of *Zugunruhe* was not supported by the present study, which suggests the temporal control of *Zugunruhe* onset and migratory fattening are independent. In general, there was a separation between migratory fattening and onset of *Zugunruhe* and more variation in onset of *Zugunruhe* (range = 107 days) compared with migratory fattening (range = 9 days). This separation has been found in other studies and it is thought that these processes evolved independently (Berthold 1975, Lofts et al. 2008) and may be in part attributable to each bird's genetically determined endogenous circannual schedule (Helm et al. 2017).

The unnatural conditions the birds were housed in may have additionally contributed to this variation (unnatural photoperiod, proximity of birds to one another, missing environmental factors; Calisi and Bentley 2009). It is unclear whether migration departure is best represented by onset of *Zugunruhe* or a threshold intensity of *Zugunruhe*. In general, the intensity of *Zugunruhe* corresponds well to departure decisions in wild counterparts (Alerstam and Lindström 1990, Eikenaar et al. 2014). In a recent tracking study of European Blackbirds (*Turdus merula*), a short-distant migrant, individuals did not shift diel activity patterns until night of departure (Zúñiga et al. 2016). Therefore, whether onset of *Zugunruhe* versus achieving a threshold intensity of *Zugunruhe* represents a departure decision in captive settings remains unclear. Tentatively, these results could be interpreted to suggest that development of *Zugunruhe* may be less (or not) responsive to food availability, compared with onset of migratory fattening, but disposition to depart as measured through intensity of activity is dampened by low food availability.

This study provides novel quantitative evidence that support the hypothesis that low food availability during spring migration development could reduce cumulative *Zugunruhe* and can advance migratory fattening in captive Wood Thrush.

Therefore, the availability of food on wintering territories prior to spring migration could play a role in modulating the spring migratory program. Low food availability could therefore delay spring migration schedules, if birds are not able to develop sufficient fuel reserves, as an adaptive strategy to maximize survival during the migration period. These results support prior studies of wild populations of wintering songbirds which have found an association between winter habitat quality, spring departure dates and reproductive success (Rockwell et al. 2012, Saino et al. 2017). For example, field studies have shown that American Redstarts wintering in low quality habitat and in poor physical condition depart later on spring migration, resulting in more variable arrival timing on breeding grounds and reduced breeding success (Marra et al. 1998, Reudink et al. 2009). When individuals are experimentally upgraded to higher quality non-breeding habitats and improve their physical condition, they advance departure dates on spring migration compared to controls in lower quality habitat (Studds and Marra 2005). Results from studies on American Redstarts suggest that birds modify departure timing depending on non-breeding environmental conditions and the physical condition of the birds themselves. Together, this work also highlights the tricky timing challenge faced by migratory songbirds between migration survival and optimal breeding ground arrival. The advancement of spring migration fattening observed here could represent an important strategy to allow Wood Thrush to flexibly adjust migration timing when faced with unfavourable environmental conditions ahead of spring migration.

The interaction of individuals with their environment can be difficult to monitor in highly mobile species; therefore, controlled experiments like ours isolate the potential roles and interactions among behaviour, food availability and timing of spring migration. Flexibility in response to supplemental factors could have important implications for how well migratory birds adjust to climatic variation in the future (Åkesson et al. 2017). As climate change increases and tropical deforestation proceeds, the wintering grounds of Wood Thrush and many Neotropical-Nearctic migrants are expected to experience increasingly severe dry seasons, which are predicted to decrease food availability for wintering birds (Neelin et al. 2006). The ability to modulate spring migration programs and advance migratory fattening could provide Wood Thrush flexibility to respond to changing environmental conditions before migration departure is delayed. However, advancements in migratory fattening may ultimately be limited if advancements in the other programs (i.e. *Zugunruhe*) associated with the vernal migratory stage are not equally plastic.

Acknowledgements

We thank Adrienne Dale, Kevin Bennett, Justin Saunders, Rebecca Zurlo for assistance with the collection and husbandry of the Wood Thrush collection. We would also like to thank all the FONZ and University of Maryland volunteers, as well as the National Zoological Park staff who aided with animal husbandry, most notably Elizabeth Fisher, Erin Kendrick, Mike Maslanka, Eric Slovak, Debra Talbot, Jordana Todd, and Jennifer Wall.

Tables

Table 1.1 Mean fuel load and fat scores between individuals in *Ad Libitum* and Reduction groups prior to migration and during migration. Migratory period was defined for each individual based on the onset of migratory restlessness. Values in bold denote a significant difference ($p < 0.05$) and a tilde (~) a difference that approaches significance ($p < 0.06$) between the Ad Libitum and Reduction feeding treatments.

		Ad Libitum		Reduction
	n	Mean ± SE	n	Mean ± SE
Fuel Load				
Pre-migration	7	0.0457 ±0.0138	7	~ 0.00466 ± 0.0137
Migration	8	**0.155 ± 0.024**	8	**0.00738 ± 0.0332**
Fat Scores				
Pre-migration	7	1.47 ± 0.288	7	1.30 ± 0.220
Migration	8	**2.82 ±0.766**	8	**1.79 ± 0.350**

Figures

Figure Legend

Figure 3.1. (A) Experimental protocol: birds were randomly assigned to one of two feeding treatments *Ad Libitum* or Reduction (n = 13 each) and maintained at a constant 12L:12D to mimic tropical winter conditions. After 3 weeks, birds were exposed to a changing photoperiod with daily shifts to longer light periods to photostimulate birds and mimic spring migratory conditions. (B) Image of cage and video camera set up. Each infra-red camera recorded activity from four cages simultaneously.

Figure 3.2. Timing of spring migration by feeding treatment. (A) Shows the change in daylength across the experimental period. (B) and (C) boxplots show the start and end day of migration based on (B) changepoint analysis and (C) migratory fattening. Asterix represents significant ($p < 0.05$) differences between feeding treatment.

Figure 3.3. Cumulative intensity of *Zugunruhe* by feeding treatment compared across the migratory period defined by changepoint analysis and the migratory fattening period. Asterix represents significant ($p < 0.05$) differences between feeding treatment and a tilde (~) a difference that approaches significance ($p < 0.08$).

Figure 3.4. Effect of mean fuel load across the migratory period on cumulative *Zugunruhe* during the migratory period defined by (A) changepoint analysis and (B)

migratory fattening. Treatment groups shown as reference (filled: Reduction, open: *Ad Libitum*).

Figure 3.1

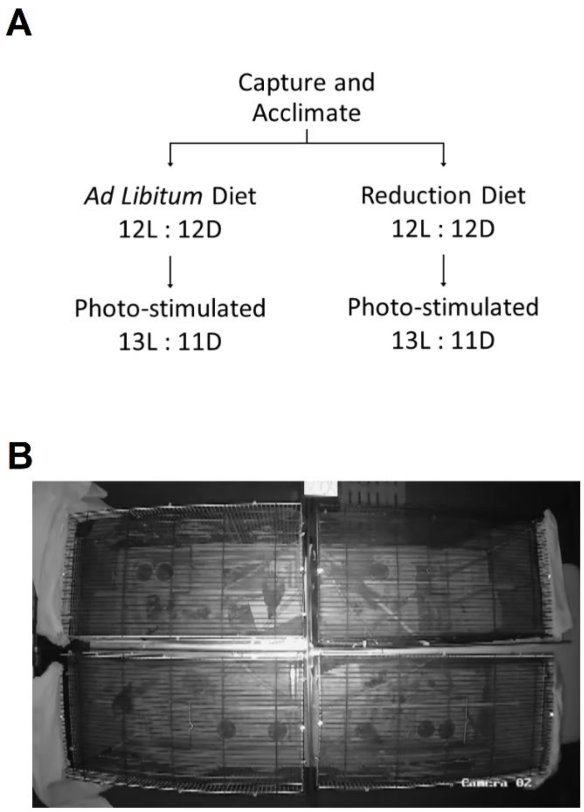

A
Capture and Acclimate
Ad Libitum Diet
12L : 12D
Reduction Diet
12L : 12D
Photo-stimulated
13L : 11D
Photo-stimulated
13L : 11D
B
Camera 02

Figure 3.2

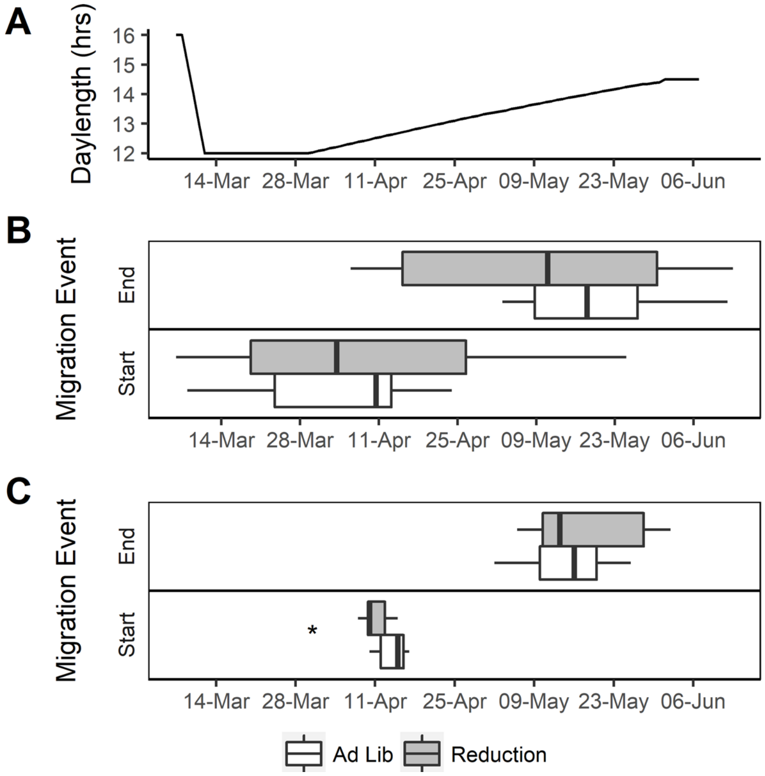
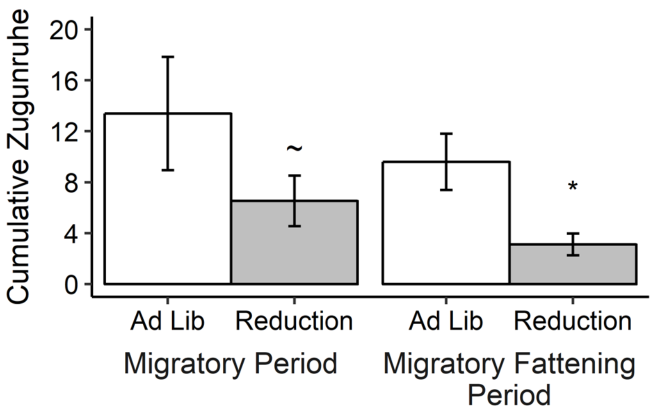
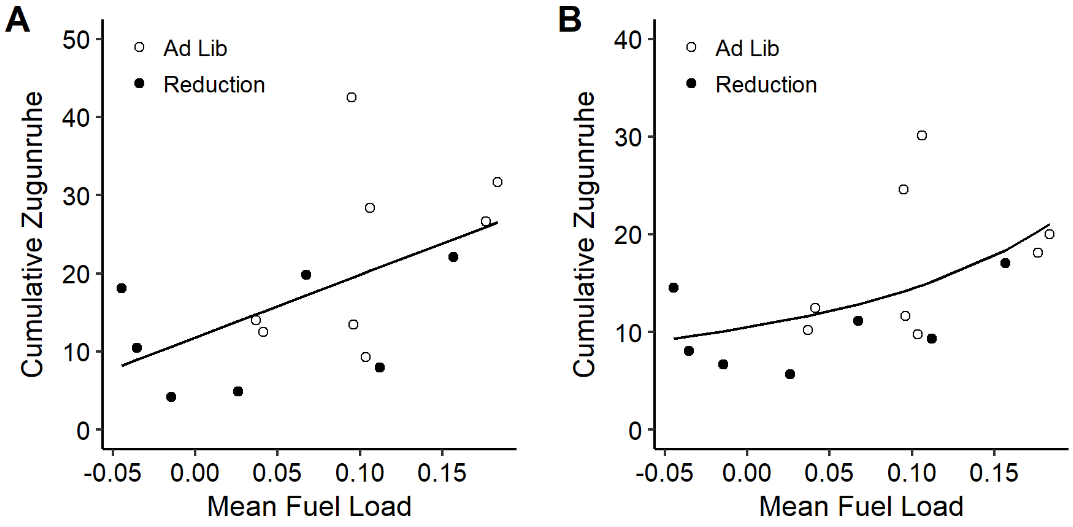

A
Daylength (hrs)
16
15
14
13
12
14-Mar
28-Mar
11-Apr
25-Apr
09-May
23-May
06-Jun
B
Migration Event
End
Start
14-Mar
28-Mar
11-Apr
25-Apr
09-May
23-May
06-Jun
C
Migration Event
End
Start
*
14-Mar
28-Mar
11-Apr
25-Apr
09-May
23-May
06-Jun
Ad Lib
Reduction

Figure 3.3



Cumulative Zugunruhe
20
16
12
8
4
0
~
*
Ad Lib
Reduction
Ad Lib
Reduction
Migratory Period
Migratory Fattening Period

Figure 3.4


A
B
Ad Lib
Reduction
Cumulative Zugunruhe
Mean Fuel Load
0
10
20
30
40
50
-0.05
0.00
0.05
0.10
0.15

Appendices

Appendix S1

Supplement to Chapter 1:
Supplementary Methods
Supplementary Tables S1-S8

Supplementary Methods

Geolocator Deployment and Programming

Individual wood thrush were captured using mist-nets and a song playback. Upon capture identification bands were placed on their legs (one aluminum United States Geological Service band and up to three plastic color bands in unique combinations) and standard body measurements taken (mass, fat score, tarsus, wing, bill size). GPS tags were attached using a backpack leg-loop harness (<5% of birds body mass; Rappole and Tipton 1991). We preferentially tagged adult males because they have higher site fidelity and to reduce confounding variables due to age and sex specific migratory schedules (Stanley et al. 2012). Recapture rates were variable among sites, the average recapture rate for tagged individuals was 0.16 ± 0.10% (±SD), which approached significantly lower levels than the recapture rate of untagged males (0.24 ± 0.14%, $t_{paired} = -1.73$, df = 8, p-value = 0.06). No significant difference in the mass of birds between deployment and retrieval of tags was detected (t = 0.73, df = 16, p = 0.81).

To maximize the number of location fixes per season, GPS tags were programmed to obtain fixes every 2 weeks during stationary periods, every 4 days during fall migration and every 3 days during spring migration. Fixes were obtained at midnight EST during stationary periods (roosting birds have higher probability of communication with satellites) and at noon EST during migratory periods to capture stopover locations (not migratory flights). Location data was downloaded from tags using PinPoint Host Software (Lotek Wireless Inc., Version 2.12.3.4).

Migratory Connectivity Indices

Two connectivity metrics were used to assess migratory connectivity. We calculated the Mantel correlation (rM) using the *ade4* package in R (Dray and Dufour 2007, Besag et al. 2016). Pairwise orthodromic distances between breeding and winter or stopover sites were calculated using the *geosphere* package in R (Hijmans 2017). We estimate P-values based on 9,999 random permutations of the sets of sites. The second index was the MC metric from the R package *MigConnectivity* (Cohen et al. 2018). For the MC metric, breeding regions were assigned based on Rushing et al. (2016) delineation of natural breeding populations for wood thrush; winter and stopover regions followed Stanley et al. (2015) assignments. The distance matrix was generated using the same methods as above. Relative breeding abundance for each population was derived from Rushing et al. (2016) population level estimates of abundance based on standardized survey routes (Breeding Bird Surveys). For both connectivity indices, values close to 1 indicate birds close together during the breeding season remain close together in the subsequent season (winter or stopover location). This suggests high migratory connectivity and low population mixing. Value close to 0 indicate low migratory connectivity and high population mixing.

Model Specifications and Fit Assessment

For Bayesian mixed conditional logistic regression we assumed individual level coefficients for all predictors were normally distributed. Vague gaussian priors were used with for all population level coefficients ($\beta_i \sim N(0,0.01)$). Three separate Markov Chain Monte Carlo (MCMC) were run for each model with 200,000 iterations, 100,000 burn-in, 50 thinning. Convergence was assessed using Brooks–Gelman–Rubin statistic (rhat < 1.1; Gelman et al. 2004) and by visual inspection of trace plots of population and individual level coefficients. To assess model fit a Bayesian P-value approach was employed (Gelman et al. 1996, Valente and Betts 2018). At each iteration in the chain (MCMC) a discrepancy statistic (D) was calculated as the sum of square differences between each observed data point and the expected value based on the fitted model. D was compared to a discrepancy statistic (D_{sim}) calculated in the same method based on a simulated data set (drawn from the posterior distribution of the fitted model). The p-value represented the proportion of time $D > D_{sim}$. Extreme Bayesian p-values (0.05 < p-value > 0.95) indicate the model is inadequate. Models were ranked based on deviance information criterion (DIC) and we assumed models > 5 ΔDIC had substantial differences in model fit (Thomas et al. 2006). The mean population level parameter estimates and their 95% credible intervals were inspected and those that did not overlap zero were interpreted as being important predictors in habitat selection models. All predictor variables were centered and standardized to improve convergence.

To identify the top models for generalized linear and mixed effect models, candidate models included a fully specified global model, a null model and all biologically relevant combination of factors. Competing models were evaluated using AIC_c in the R package *MUMln* (Barton 2017). All models < 2 ΔAIC were considered competitive and 95% confidence were inspected. If confidence intervals of additional parameters in competing models included zero and did not change the log-likelihood estimates they were discarded (Arnold 2010). If more than one model was supported we performed unconditional model averaging of estimates and 95% confidence intervals in the package *MUMIn* (Barton 2017). Estimated marginal means and estimated trends were calculated using the R package *emmeans* (Lenth 2018). All models were assessed for violation of model assumptions by visual inspection of plots of residual versus predicted values and quantile-quantile plots.

Supplementary Tables

Table S1.1 Number of geolocators deployed and retrieved by deployment location. Recapture rates of individual that did not receive GPS tags provided for comparison.

Location	Coordinates	Year Deploy.	Tag Retrieval Rate	Recapture Rate[a]	Local Partners
Delaware	39.7°N, -75.7°W	2014	5/17	n/a[b]	University of Delaware
Indiana	39.9°N, -86.7°W	2014	5/24	7/65 (7/43)	Department of Defense
		2015	2/20	9/45(7/33)	
New York	41.3°N, -73.6°W	2014	0/5	2/4 (1/3)	Bedford Audubon Society
	41.3°N, -73.7°W	2014	2[c]/12	6/28 (5/17)	
	41.3°N, -73.7°W	2014	1/5	2/4 (2/4)	
North Carolina	36.2°N, -80.3°W	2014	0/5	1/8 (1/4)	Forsyth Audubon Society
	36.3°N, -80.5°W	2014	2/16	2/18 (2/12)	
Minnesota	45.1°N, -92.8°W	2014	6/18	4/14 (1/4)	National Park Service
	44.7°N, -93.0W	2014	1/7	0/2 (0/2)	

[a] Males in bracket

[b] Birds were target netted and therefore few individuals did not receive GPS tags

[c] One additional bird re-sighted but tag not retrieved

Table S1.2 Samples statistics for habitat use and discrete choice models used to examine patterns of habitat use and selection of wood thrush across the annual cycle. Percentage of missing location estimates not attributed to lost antenna.

Season	% Missing Locations	# Birds	# Points/Bird		Discrete Choice Models	
			n ± SD	Range	n ± SD	Range
Breeding	30.0	20*	9.2 ± 4.2	5 - 22	5 ± 0	5 - 5
Fall Migration	46.7	20	4.7 ± 1.7	1 – 7	4.7 ± 1.7	1 - 7
Winter	18.0	19	11.3 ± 3.9	2 – 17	4.8 ± 0.7	2 - 5
Spring Migration	49.0	16	3.8 ± 2.3	1 – 8	3.8 ± 2.3	1 -8

Notes: * One additional bird had a single location fix on the breeding ground for a total of 21 individuals but was omitted from analyses.

Table S1.3 Source of local and landscape scale habitat features derived for habitat use and discrete choice models of habitat

Habitat Features	Unit	Scale	Dataset/Product	Description
Local-level				
Enhanced Vegetation Index	n/a	250-m	MODIS Land Terra Vegetation Indices 16-Day L3 Global 250m[a]	Inverse-distance-weighted interpolation at point-estimate of pixels representing EVI
Tree Cover	% area	30-m	Landsat 2012 Tree Cover Continuous Fields[b]	Bilinear interpolation at point-estimate of pixels representing % tree cover.
Distance to Non-Forest	m	30-m	Landsat 2012 Tree Cover Continuous Fields[b]	Proximity to nearest pixel of non-forest (< 30% area of tree cover)
Patch Size	ha	30-m	Landsat 2012 Tree Cover Continuous Fields[b]	Area of horizontally or vertically connected pixels of forest (> 30% area of tree cover) where point-estimate located. If point-estimate found in non-forest value is 0.
Landscape-level				
Average Tree Cover	% area	30-m	Landsat 2012 Tree Cover Continuous Fields[b]	Average value of % tree cover pixels located within a 1-km buffer of point-estimate
Average Patch Size	ha	30-m	Landsat 2012 Tree Cover Continuous Fields[b]	Average area of all forest patches (see above) located within a 1-km buffer of point estimate.
Forest Loss	ha	30-m	Landsat 2000 – 2014 Forest Cover Change[c,d]	Average of forest loss pixels located within a 1-km buffer of point-estimate.
Land Cover Diversity	n/a	0.083°	MODIS Land Cover: 2001 – 2012[e]	Calculated Shannon Index of Diversity based on the proportion of land cover classes within a 5-km buffer of point-estimate.

[a] Retrieved from Env-DATA Track Annotation Service (Dodge et al. 2013).

[b] Retrieved from Global Land Cover Facility (www.landcover.org; Sexton et al. 2013).

[c] Retrieved from Global Land Cover Facility (Sexton et al. 2013).

[d] Data downloaded using R package *gfcanalysis* (Zvoleff 2015).

[e] Retrieved from Global Land Cover Facility (www.landcover.org; Friedl et al. 2010, Channan et al. 2014)

Table S1.4 Candidate model sets to assess alternative hypotheses for seasonal habitat selection from individually tracked wood thrush. Model set run separately for each season (fall, spring, breeding and winter). All models included individual as a random factor, with the exception of the null model, to account for difference in selection patterns across birds.

	Hypothesis	Model
Null	The null model assumed probability of use equal to random expectations (1 / # choice sets). If consistently chosen it would suggest geospatial data not adequate to predict habitat selection.	n/a
Local	The local model would be appropriate if resources units were selected based on local habitat features only.	% Tree Cover + EVI + Patch Size + Proximity to Non-Forest
Landscape[1]	The landscape model would be appropriate if resources units were selected based on landscape habitat features.	% Tree Cover 1Km + Average Patch Size 1km
Full[1]	The full model would be appropriate if resource units were selected for both local and landscape habitat features	% Tree Cover + EVI + Patch Size + Proximity to Non-Forest +% Tree Cover 1Km + Average Patch Size 1km

[1] Only run for 15 km and 25 km spatial extent

Table S1.5 Delta deviance information criteria (ΔDIC) model selection for discrete choice models that examined habitat selection of male wood thrushes from 5 breeding population across the annual cycle. For each spatial extent and season, a candidate set of models were run, the parameters included in each model found in Table S1.4. All models < 5 ΔDIC were considered competitive.

	Spatial Extent			
Season	0.5 km	5 km	15 km	25 km
Breeding				
Null	219.26	336.29	295.51	109.47
Patch	**0.00**	**0.00**	**0.00**	101.58
Landscape	n/a	n/a	227.78	48.37
Patch + Landscape	n/a	n/a	*4.86	**0.00**
Fall				
Null	185.19	195.12	80.45	65.41
Patch	**0.00**	**0.00**	**0.00**	**0.00**
Landscape	n/a	n/a	82.78	63.66
Patch + Landscape	n/a	n/a	*3.12	6.25
Spring				
Null	**0.00**	**0.00**	**0.00**	**0.00**
Patch	23.15	14.48	13.46	72.14
Landscape	n/a	n/a	*4.41	6.59
Patch + Landscape	n/a	n/a	19.36	70.29
Winter				
Null	157.48	205.43	130.52	103.22
Patch	**0.00**	**0.00**	**0.00**	**0.00**
Landscape	n/a	n/a	104.02	70.17
Patch + Landscape	n/a	n/a	*1.23	9.16

Notes: Bolded values indicate top models. Asterix indicate models with ΔDIC < 5, which have the same parameter estimates with 95% credible intervals that do not cross zero as the top model.

Table S1.6 $\mathrm{AIC_c}$ model selection for generalized linear models of seasonal and population differences in habitat features for male wood thrush from 5 breeding populations. All models included random intercept for individuals and models < 2 ΔAICc were considered competitive.

Model	n	Variables	df	Log-likelihood	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$
Patch Level						
Tree Cover (%)	510	Season	6	-1977.47	3967.11	0.00
		Breed. Long. + Season	7	-1978.16	3970.55	3.43
		Breed. Long. * Season	10	-1975.85	3972.15	5.03
		Null	3	-2014.45	4034.95	67.84
		Breed. Long.	4	-2015.08	4038.24	71.13
EVI	508	Season	6	506.16	-1000.14	0.00
		Breed. Long. + Season	7	502.17	-990.11	10.04
		Null	3	490.28	-974.51	25.63
		Breed. Long.	4	485.64	-963.19	36.95
		Breed. Long. * Season	10	488.48	-956.52	43.62
Patch Size (ha)	549	Breed. Long. * Season	10	-8122.12	16264.65	0.00
		Breed. Long. + Season	7	-8156.41	16327.02	62.37
		Season	6	-8168.41	16348.98	84.33
		Breed. Long.	4	-8357.81	16723.69	459.04
		Null	3	-8369.47	16744.99	480.34
Prox. to Non-Forest (m)	493	Breed. Long. * Season	10	-959.64	1939.73	0.00
		Season	6	-990.66	1993.50	53.77
		Breed. Long. + Season	7	-991.50	1997.24	57.51
		Null	3	-1030.54	2067.13	127.41
		Breed. Long.	4	-1031.45	2070.98	131.25
Landscape level						
Avg. Tree Cover 1 km (%)	540	Breed. Long. * Season	10	-2084.52	4189.46	0.00
		Season	6	-2095.97	4204.09	14.63
		Breed. Long. + Season	7	-2096.48	4207.18	17.72
		Null	3	-2228.84	4463.73	274.27
		Breed. Long.	4	-2229.33	4466.74	277.28
Avg. Patch Size 1 km (ha)	540	Breed. Long. * Season	10	-7949.99	15920.40	0.00
		Breed. Long. + Season	7	-7993.79	16001.78	81.38
		Season	6	-8004.39	16020.93	100.53
		Breed. Long.	4	-8054.86	16117.79	197.39
		Null	3	-8065.45	16136.95	216.54
Land Cover						
Land Cover 5km		Season	6	-26.15	65.54	0.00
		Breed. Long. + Season	7	-30.41	76.50	10.96
		Breed. Long. * Season	10	-39.35	102.13	36.60
		Null	3	-55.71	117.76	52.23

Appendix S2: Seasonal Changes in Habitat Features

Supplement to Chapter 1

To better interpret habitat selection patterns (i.e. the behavioural decision making process) we investigated how habitat-use patterns changed across the annual cycle (Jones 2001). We paired location fixes to geospatial habitat data (detailed description of methods in Appendix S1, Table S1.3) to determine how habitat features (local and landscape) of locations occupied by wood thrush changed across the annual cycle. A generalized linear model was performed for each habitat characteristic (local and landscape), the full model included the habitat variable as the response variable, the interaction of season and breeding longitude as fixed effects and individual as a random effect. The best-fit model for each habitat features was used to calculate the repeatability in use of habitat features.

The characteristics of habitats occupied by wood thrush varied significantly between seasons for all local and landscape habitat features. Marginal means of most habitat features (local and landscape) were highest during the winter period (Table S2.1), indicative of more forested and productive habitats (high EVI). Most habitat features had the lowest marginal mean values during the migratory periods and there was no significant difference in marginal mean values between migratory periods (Table S2.1).

Table S2.1 Estimated marginal means and 95% confidence intervals of the effect of season on local and landscape level (1 km radius) environmental characteristics of habitats occupied by wood thrush across the annual cycle.

	Patch-level Characteristics							
	Tree Cover (%)		EVI		Patch Size (km^2)		Prox. to Non-Forest (m)	
Season	Means	95% CI	Means	95% CI	Means	95% CI	Means	95% CI
Breeding	56.2^{a}	53.1 – 59.3	0.52^{a}	0.52 – 0.54	$*1972^{a}$	0 – 4220	$*99.2^{a}$	57.8 – 170.3
Fall Migration	55.3^{ab}	51.7 – 58.8	0.46^{b}	0.46 – 0.48	8738^{b}	6025.5 – 11270.4	$*19.7^{c}$	10.8 – 35.8
Winter	63.5^{c}	60.4 – 66.7	0.53^{c}	0.53 – 0.55	17714^{c}	15498.9 – 19929.2	$*38.0^{b}$	21.8 – 66.4
Spring Migration	50.4^{b}	46.1 – 54.7	0.48^{ab}	0.48 – 0.51	6141^{ab}	3305.5– 8977.1	10.2^{c}	5.2 – 19.9

	Landscape-level Characteristics			
	Tree Cover 1km (%)		Avg. Patch Size (km^2)	
Season	Means	95% CI	Means	95% CI
Breeding	39.5^{a}	35.5 – 43.5	33045^{a}	30876.3 – 35233.9
Fall Migration	48.1^{b}	43.7 – 52.4	29123^{b}	26697.2 – 31548.8
Winter	60.3^{c}	56.3 – 64.2	$*28489^{b}$	26346.9 – 30631.7
Spring Migration	43.2^{ab}	38.3 – 48.1	27378^{b}	24583.2 – 30174.2

Notes: Letters denote values that are significantly different from each other using Tukey's adjustments for multiple comparisons. Asterix indicates a significant interaction with breeding longitude.

Appendix S3: Population-specific annual schedules

Supplement to Chapter 1

To examine the consistency of annual schedules between breeding populations, the timing of annual events was determined for all individuals. Due to low success of location fixes during migratory periods, annual cycle stages were defined based on the first or last location recorded at stationary stages (i.e. spring migration ends day before first recorded point on breeding grounds). Migratory periods were identified as northward or southward movements over the course of consecutive days (+2 points, 6 - 8 days) and larger than 20km. To determine if population-specific annual schedule were present we examined the timing of migratory events across breeding populations using generalized linear model. The full model included, timing event (start, end, duration, rate, day of gulf cross) as the response variable and breeding latitude, breeding longitude and winter longitude as fixed effects. Winter arrival dates could not be reliably assigned for some individuals due to low frequency of location fixes (bimonthly fixes) at arrival. Therefore, analysis of the fall migration period was restricted to departure from breeding grounds to departure from Gulf of Mexico.

We found evidence that timing of both spring and fall migration were influenced by breeding location, but not winter location (Figure S3.1; Table S3.1). Breeding latitude and longitude had a negative effect on fall migration departure, more northern and eastern populations departed earlier on fall migration (Table S3.2). There was no evidence that latitude or longitude of breeding and winter location influenced date of arrival at the Gulf of Mexico during fall migration or the number of days on route to the Gulf of Mexico (mean ± SE = 26.7 ± 10.9 days). During spring migration, winter departure date, arrival at the Gulf of Mexico and breeding arrival date were positively predicted by breeding latitude, indicating southern breeding populations had an earlier migration schedule than northern populations (Table S3.2). There was no evidence that breeding longitude or winter location influenced spring migration departure or arrival dates (Table S3.2). Spring migration duration (mean ± SE = 12.2 ± 5.6 days) and speed were not influenced by breeding and winter location (Table S3.2).

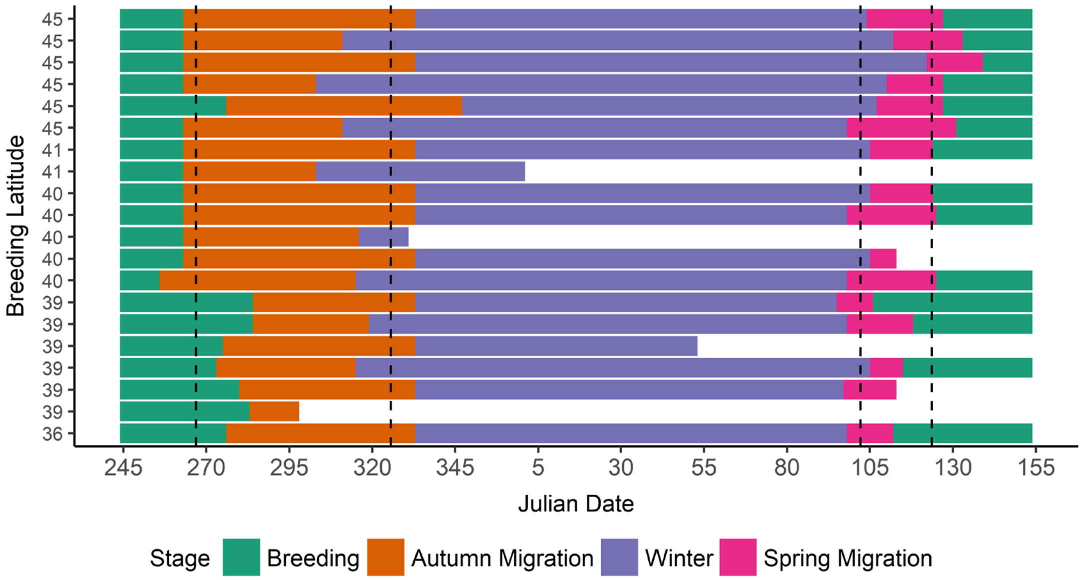
Table S3.1AICc model selection results for generalized linear models evaluating the influence of breeding and winter location on migration timing events of male wood thrush from 5 breeding populations. All models < 2 ΔAICc were considered competitive.

Model	n	Variables	df	Log-likelihood	AIC_c	ΔAIC_c
Fall Migration						
Breeding Departure	20	Breed. Lat. + Breed. Long.	4	-62.18	135.22	0.00
		Breed. Lat. + Breed. Long. + W Lat.	5	-62.00	138.62	3.40
		Null	2	-67.54	139.84	4.62
		Breed. Lat.	3	-66.43	140.47	5.25
Gulf Coast Arrival	13	Null	2	-38.50	82.33	0.00
		W Lat.	3	-38.07	85.14	2.80
		Breed. Long. + W Lat.	4	-37.85	89.42	7.09
		Breed. Lat. + Breed. Long. + W Lat.	5	-36.70	93.39	11.06
Duration to Gulf	13	Null	2	-43.84	93.00	0.00
		W Lat.	3	-42.31	93.62	0.61
		Breed. Long. + W Lat.	4	-42.29	98.28	5.28
		Breed. Lat. + Breed. Long. + W Lat.	5	-42.24	104.48	11.48
Spring Migration						
Winter Departure	16	Breed. Lat.	3	-48.84	105.69	0.00
		Breed. Lat. + Breed. Long.	4	-48.57	108.77	3.08
		Breed. Lat. + Breed. Long. + W Lat.	5	-48.01	112.01	6.33
		Null	2	-53.57	112.07	6.38
Gulf Coast Arrival	12	Breed. Lat.	3	-35.10	79.20	0.00
		Breed. Lat. + Breed. Long.	4	-34.93	83.57	4.37
		Null	2	-41.04	87.41	8.21
		Breed. Lat. + Breed. Long. + W Lat.	5	-34.89	89.78	10.58
Breeding Arrival	14	Breed. Lat. + Breed. Long.	4	-38.91	90.26	0.00
		Breed. Lat.	3	-41.74	91.88	1.62
		Breed. Lat. + Breed. Long. + W Lat.	5	-38.86	95.22	4.96
		Null	2	-49.20	103.49	13.23
Duration	14	W Lat.	3	-40.99	90.38	0.00
		Null	2	-43.41	91.91	1.52
		Breed. Lat. + W Lat.	4	-40.00	92.44	2.05
		Breed. Lat. + Breed. Long. + W Lat.	5	-39.57	96.64	6.26
Speed	14	Null	2	-67.94	140.98	0.00
		W Lat.	3	-67.11	142.61	1.63
		Breed. Long. + W Lat.	4	-66.60	145.64	4.67
		Breed. Lat. + Breed. Long. + W Lat.	5	-66.43	150.37	9.39

Table S3.2 Model averaged parameter estimates and unconditional 95% confidence intervals for top linear models examining the influence of breeding location (latitude and longitude) and winter location (latitude and longitude) on migration timing events of male wood thrush from 5 breeding populations.

Model	Variable	Estimate	95% CI
Fall Migration			
Breeding Departure	Intercept	5.70	5.53 – 5.88
	Breeding latitude	-0.0094	-0.004 - -0.0044
	Breeding longitude	-0.0032	-.0052 - -0.0013
Gulf Coast Arrival	Null		
Duration to Gulf	Null		
Spring Migration			
Winter Departure	Intercept	3.99	3.62 – 4.36
	Breeding latitude	0.015	0.0064 – 0.024
Gulf Coast Arrival	Intercept	29.50	-7.43 – 66.44
	Breeding latitude	1.86	0.97 – 2.75
Breeding Arrival	Intercept	37.92	-0.49 – 76.34
	Breeding latitude	2.80	1.39 – 4.21
	Breeding longitude	0.36	-0.60 – 0.95
Duration	Null		
Speed	Null		

Figure S3.1 Spatiotemproal organization of the annual cycle of five breeding populations of wood thrush tracked using GPS tags (n = 20). Each horizontal bar represents an individual and colours represent different stages of the annual cycle. Dashed vertical lines represent mean start and end date of fall and spring migration, respectively.



Appendix S4

Supplement to Chapter 2:
Supplementary Methods
Supplementary Tables S1-S7
Supplementary Figure S1

Supplementary Methods

Genetic Sexing

Genomic DNA was extracted from whole blood (~50 μl) stored in Queen's lysis buffer using the BioSprint 96 Tissue DNA Kit (Qiagen, Valencia, CA). Sex was determined by amplifying genomic DNA (2 μl) using highly conserved P2 and P8 primers (Griffiths et al. 1998) in a 11 μl polymerase chain reaction. PCR products were size-sorted on an Applied Biosystems 3130 Genetic Analyzer (ABI, Foster City, CA) run with GeneScan 500 base pair ROX internal size standard (ABI). Samples were scored using Genemapper v.4.1 (ABI). Both sexes carry a CHD-*Z* gene (~380 bp long), only the females carry the CHD-*W* gene (~400 bp long).

Home Range Analysis

To derive utilization distributions, location data for each individual was first fit to three continuous-time movement models using the *ctmm* package in R (Calabrese et al. 2016). The first model was considered a null model assuming independent and identically distributed data (IID, equivalent to traditional kernel density estimators). The second model fit locations to a Brownian motion model with restricted space-use (Ornstein-Uhlenbeck). The final model represented an extension of the second model and introduced both correlated velocities and restricted space-use (Ornstein-Uhlenbeck Foraging). Models were ranked using the Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002) and the top model was used to fit the Autocorrelated Kernel Density Estimate. The best-fit model for the majority of individuals (n = 31) was the IID, followed by the Ornstein-Uhlenbeck Foraging (n = 13) and Ornstein-Uhlenbeck model (n = 9).

Stable-isotope analysis

Whole blood samples were kept frozen until they were oven dried at ~100° for 24 hours. Blood was powdered and approximately 0.5 mg weighed and packaged in a tin capsule. Claw samples were cleaned in 2:1 choloroform:methanol solution and air dried in a fume hood for 24 hours. Approximately 0.5g of claw was cut from the distal end of the claw, weighed and packaged in tin capsules. All samples were analyzed at the Smithsonian OUSS/MCI Stable Isotope Mass Spectrometry Laboratory (Suitland, MD). Samples were crushed and combusted on a Costech Elemental Analyzer and introduced to a Thermo Delta V Advantage mass spectrometer through a Thermo Conflo IV. For every 10-12 samples a set of standards were run that included Costech Acetanilide and Urea-UIN31 calibrated to USGS40 (L-glutamic acid) and USGS41 (L-glutamic acid). Isotope values were corrected using a 2-point linear correction on the calibrated standards. δ13C and δ15N values were reproducible to ±0.2‰.

Remote Sensing

To assess pattern of moisture at our study site in Belize and for GPS tracked individuals we derived the wetness metric based on the tasseled-cap transformation of 30-m resolution Landsat imagery (Crist and Kauth 1986). At our study site in Belize we derived the wetness metric for each plot and home range and for GPS-tracked individuals we derived the wetness metric for each relocation. A plot level index of wetness was derived in order to perform analyses that included individuals that departed our study site before sufficient relocations were accumulated to estimate home range area. Landsat images are available on a bi-monthly basis from locations across the globe. Level-1 Landsat images were obtained from our study areas in Belize from December to April 2013 to 2015 and for GPS-tracked birds from December to April 2014-2016 from the USGS database EarthExplorer (Landsat 7 +ETM in 2013, Landsat 8 OLI from 2014 to 2016). Differences in spectral responses between Landsat sensors have been found, however comparisons of vegetation indices derived from across Landsat sensors suggest a high continuity across sensor types, particularly for band-transformation derived vegetation indices such as the tasseled cap transformation (Li et al. 2013, She et al. 2015).

All image processing was performed in R. In brief, digital numbers were converted to top-of-atmosphere reflectance using the *radCor* function in *RStoolbox* (cit) and the Quality Assessment band was used to create a cloud mask. The *tasseledCap* function in *RStoolbox* was used to derive the wetness metric. In Belize, for each image, we extracted the mean wetness metric across each (i) individual home range and (ii) plot, as defined by a 1-km radius at the centroid of tracking locations using the *extract* function in the R package *raster* (cite). We excluded values derived from home ranges that were masked > 90% by contamination (over 50% of values were excluded). For GPS transmitters, we extracted mean wetness from each point using bilinear interpolation in the *raster* package. For birds that made intra-winter movements, only locations prior to the first movement were included. In some instances, multiple tiles covered locations, to account for this we took the average wetness value for every two-week period.

Supplementary Tables

Table S4.1 Summary statistics for population and environmental condition variables collected from non-breeding wood thrush (a) radio tracked in Belize from 2013 to 2015 and (b) monitored with GPS tags across the non-breeding range.

Variables	Mean (± SE)			
	Year			Average/ Overall
	2013	2014	2015	
(a) Belize Radio tracking				
Population				
Age Ratio (Adult:Yearling)	36:30	24:23	29:16	86:69
Sex Ratio (Male:Female:Unk)	23:29:14	15:30:2	23:20:2	58:72:17
Body Condition Index	2.8 ± 0.64	3.7 ± 0.83	1.7 ± 0.97	2.7 ± 0.48
Home Range Size (ha)	1.6 ± 0.20	1.6 ± 0.45	3.4 ± 0.76	2.3 ± 0.37
Departure Dates (Julian date)	79 ± 2.5	67 ± 2.7	65 ± 3.0	72 ± 1.6
Environmental Condition				
Fruit Counts	39.5 ± 19.97	104.1 ± 21.80	51.0 ± 7.89	55.4 ± 10.46
Insect Counts	8.72 ± 0.77	14.9 ± 0.70	16.6 ± 0.62	12.6 ± 0.50
δ15N Claws	9.3 ± 0.15	8.6 ± 0.15	8.8 ± 0.16	8.9 ± 0.09
δ15N Blood	10.3 ± 0.12	9.7 ± 0.16	9.8 ± 0.16	9.9 ± 0.09
Home range Wetness	-0.06 ± 0.002	0.04 ± 0.001	0.04 ± 0.0008	0.01± 0.006
Plot Wetness	-0.06 ± 0.001	0.04 ± 0.003	0.04 ± 0.002	0.008 ± 0.0219
δ13C Claws	-23.0 ± 0.06	-23.4 ± 0.04	-23.1 ± 0.05	-23.2 ± 0.03
δ13C Blood	-24.9 ± 0.09	-25.1 ± 0.06	-24.9 ± 0.06	-25.0 ± 0.04
(b) GPS tracking				
Departure Dates (Julian Week)				15 ± 0.5
Wetness				0.03 ± 0.003

Table S4.2 AIC_c model selection for generalized mixed effect models describing home range size (95% isopleth of utilization distribution) of non-breeding wood thrush in Belize. Age (yearling or adult), sex (male or female), stable-carbon values derived from claws or blood and mean satellite-derived wetness, fruit counts and insect counts for each home range were included as fixed effects. All models included a random intercept for year and models < 2 ΔAICc were considered competitive. Separate models were constructed for isotope values derived from claws (n = 37) which provides information on diets over a few months and blood (n = 44) which provides information on diets over a few weeks.

Model	df	Log-likelihood	AIC_c	ΔAIC_c
Claw				
Age + Sex	5	-58.90	129.74	0.00
Age * Sex	6	-58.57	131.93	2.19
Age + Sex + δ13C + Condition	7	-57.34	132.54	2.80
Age + Sex + FruitCounts + InsectCounts	7	-57.63	133.13	3.38
Age + Sex + Wetness + Condition	7	-57.97	133.81	4.07
Age + Sex + δ13C + δ15N	7	-58.02	133.91	4.17
Age + Sex + FruitCounts + InsectCounts + Condition	8	-57.56	136.26	6.51
FruitCounts + InsectCounts	5	-64.49	140.93	11.18
Null	3	-67.41	141.54	11.79
Wetness	4	-67.14	143.53	13.79
Condition	4	-67.26	143.77	14.03
Wetness + Condition	5	-67.04	146.02	16.28
δ13C + Condition	5	-67.24	146.42	16.68
Blood				
Age + Sex + δ13C + Condition	7	-73.85	164.81	0.00
δ13C + Condition	5	-76.92	165.42	0.62
Age + Sex + δ13C + δ15N	7	-74.45	166.00	1.20
Age + Sex	5	-77.51	166.60	1.79
Age * Sex	6	-76.84	167.96	3.15
FruitCounts + InsectCounts	5	-78.28	168.14	3.33
Null	3	-81.00	168.60	3.79
Age + Sex + FruitCounts + InsectCounts	7	-76.32	169.74	4.94
Wetness	4	-80.78	170.59	5.78
Condition	4	-81.00	171.02	6.21
Age + Sex + Wetness + Condition	7	-77.35	171.81	7.01
Age + Sex + FruitCounts + InsectCounts + Condition	8	-76.23	172.57	7.76
Wetness + Condition	5	-80.77	173.12	8.31

Table S4.3 AICc model selection for general linear models evaluating variation in fruit (n = 44) and insect (n = 43) counts conducted on non-breeding home ranges of wood thrush during the early dry season sampling period (mid-February) in Belize. Age (yearling or adult), sex (male or female), mean satellite-derived wetness of home range and home range size (area of 95% isopleth of utilization distribution) were included as fixed effects. Models < 2 ΔAICc were considered competitive.

Model	df	Log-likelihood	AIC_c	ΔAIC_c
Fruit Counts				
Wetness	3	-50.34	107.28	0.00
Age * Sex + Wetness + Area	7	-46.43	109.96	2.68
Age + Sex + Wetness	5	-49.82	111.21	3.93
Age + Sex + Wetness + Area	6	-49.32	112.91	5.63
Null	2	-61.93	128.15	20.87
Area	3	-61.86	130.32	23.04
Age + Sex	4	-60.78	130.58	23.30
Age * Sex	5	-59.74	131.07	23.79
Age + Sex + Area	5	-60.75	133.07	25.79
Insect Counts				
Wetness	3	-53.44	113.49	0.00
Age + Sex + Wetness	5	-52.54	116.70	3.21
Age + Sex + Wetness + Area	6	-51.66	117.65	4.15
Age * Sex + Wetness + Area	7	-51.56	120.31	6.82
Null	2	-60.51	125.32	11.83
Area	3	-60.43	127.47	13.98
Age + Sex	4	-60.07	129.19	15.70
Age + Sex + Area	5	-59.86	131.35	17.86
Age * Sex	5	-60.06	131.74	18.25

Table S4.4 AICc model selection for linear mixed effect models evaluating variation in δ15N values in the blood or claws of non-breeding wood thrush in Belize across the dry season. δ15N values provide a proxy for proportion of insects consumed. Age (yearling or adult), sex (male or female), mean satellite-derived wetness of plots, δ13C (proxy for habitat moisture) and sampling period (early or late) were included as fixed effects. All models included a random intercept for bird identity nested within year and models < 2 ΔAICc were considered competitive. Separate models were constructed for isotope values derived from claws (n = 148) which provides information on diets over a few months and blood (n = 165) which provides information on diets over a few weeks.

Model	df	Log-likelihood	AIC_c	ΔAIC_c
Claws				
Wetness * Period	6	-185.30	383.20	0.00
Wetness + Period	5	-186.93	384.28	1.08
Age + Sex + Wetness + Period	7	-186.21	387.22	4.02
Wetness + δ13C + Period	6	-187.43	387.46	4.26
Age * Sex + Wetness + Period	8	-186.18	389.39	6.19
Age + Sex + Wetness * Period + δ13C	9	-185.12	389.55	6.35
Age + Sex + Wetness + δ13C + Period	8	-186.74	390.52	7.32
Null	3	-190.85	392.12	8.92
δ13C + Period	5	-186.68	392.66	9.46
Age * Sex + Wetness + δ13C + Period	9	-189.35	393.49	10.29
Age + Sex + δ13C + Period	7	-192.45	397.49	14.29
Blood				
Wetness * Period	6	-213.87	440.27	0.00
Wetness + Period	5	-215.92	442.21	1.94
Wetness + δ13C + Period	6	-214.95	442.44	2.16
δ13C + Period	5	-217.56	445.49	5.22
Age + Sex + Wetness * Period + δ13C	9	-214.03	447.22	6.95
Age + Sex + Wetness + Period	7	-216.94	448.59	8.32
Age + Sex + Wetness + δ13C + Period	8	-215.96	448.83	8.56
Age + Sex + δ13C + Period	7	-218.27	451.25	10.98
Age * Sex + Wetness + Period	8	-217.17	451.26	10.98
Age * Sex + Wetness + δ13C + Period	9	-216.20	451.55	11.28
Null	3	-222.74	451.62	11.35

Table S4.5 AICc model selection for general linear mixed effect models evaluating variation in the body condition index of non-breeding wood thrush during the early dry season sampling period (mid-January – mid-February) in Belize. Age (yearling or adult), sex (male or female), mean satellite-derived wetness of plots and δ13C (proxy for habitat moisture) and δ15N (proxy for proportion of insects) values were included as fixed effects. Separate models were run including isotope values derived from either claws (n = 104) which provides information on diets over a few months and blood (n = 112) which provides information on diets over a few weeks. Year was included as a random effect and models < 2 ΔAICc were considered competitive.

Model	df	Log-likelihood	AIC_c	ΔAIC_c
Claw				
Age * Sex + Wetness * δ13C	9	-316.41	652.74	0.00
Age * Sex + Wetness * δ15N	9	-317.29	654.50	1.76
Age * Sex + Wetness + δ13C + δ15N	9	-320.25	660.41	7.67
Age * Sex + Wetness + δ15N	8	-321.74	660.99	8.25
Age * Sex + Wetness + δ13C	8	-322.52	662.55	9.81
Age * Sex	6	-327.64	668.14	15.40
Age * Sex + δ13C	7	-326.63	668.43	15.70
Null	3	-335.59	677.42	24.69
Blood				
Age * Sex + Wetness + δ13C + δ15N	9	-339.57	698.90	0.00
Age * Sex + Wetness * δ15N	9	-339.79	699.35	0.45
Age * Sex + Wetness * δ13C	9	-340.38	700.52	1.62
Age * Sex + Wetness + δ15N	8	-345.31	708.03	9.12
Age * Sex + Wetness + δ13C	8	-345.67	708.73	9.83
Age * Sex + δ13C	7	-350.05	715.18	16.28
Age * Sex	6	-352.93	718.66	19.76
Null	3	-360.15	726.53	27.63

Table S4.6 AICc model selection for general linear mixed effect models evaluating differences in weight change of non-breeding wood thrush across our early (mid-January – mid-February) and late sampling period (mid-March) in Belize. Age (yearling or adult), sex (male or female), mean satellite-derived wetness of plots and δ13C (proxy for habitat moisture) and δ15N (proxy for proportion of insects) value were included as fixed effects. Separate models were run including isotope values derived from either claws (n = 26) which provides information on diets over a few months and blood (n = 31) which provides information on diets over a few weeks. Year was included as a random effect and models < 2 ΔAICc were considered competitive.

Model	df	Log-likelihood	AIC_c	ΔAIC_c
Claw				
Age * Sex + Wetness + δ13C	8	-48.41	121.29	0.00
Age * Sex + Wetness + δ15N	8	-49.16	122.79	1.50
Null	3	-58.16	123.41	2.12
Age * Sex	6	-53.82	124.06	2.77
Age * Sex + Wetness + δ13C + δ15N	9	-48.19	125.62	4.33
Age * Sex + δ13C	7	-53.01	126.24	4.95
Age * Sex + δ15N	7	-53.48	127.19	5.90
Blood				
Age * Sex + Wetness + δ13C	8	-59.57	141.69	0.00
Age * Sex + Wetness + δ13C + δ15N	9	-57.93	142.43	0.74
Age * Sex + Wetness + δ15N	8	-60.22	142.99	1.30
Age * Sex + δ13C	7	-63.07	145.00	3.31
Null	3	-69.80	146.49	4.80
Age * Sex + δ15N	7	-64.15	147.17	5.48
Age * Sex	6	-66.16	147.81	6.12

Table S4.7 AICc model selection for Cox proportional hazard models evaluating site persistence of non-breeding wood thrush in Belize. Age (yearling or adult), sex (male or female), early season body condition index, mean satellite-derived wetness of plots, δ13C (proxy for habitat moisture) and δ15N (proxy for proportion of insects) isotopic signatures and year were included as fixed effects. Separate models were run including isotope values derived from either claws (n = 91) which provides information on diets over a few months and blood (n = 101) which provides information on diets over a few weeks. Year was included as a random effect and models < 2 ΔAICc were considered competitive.

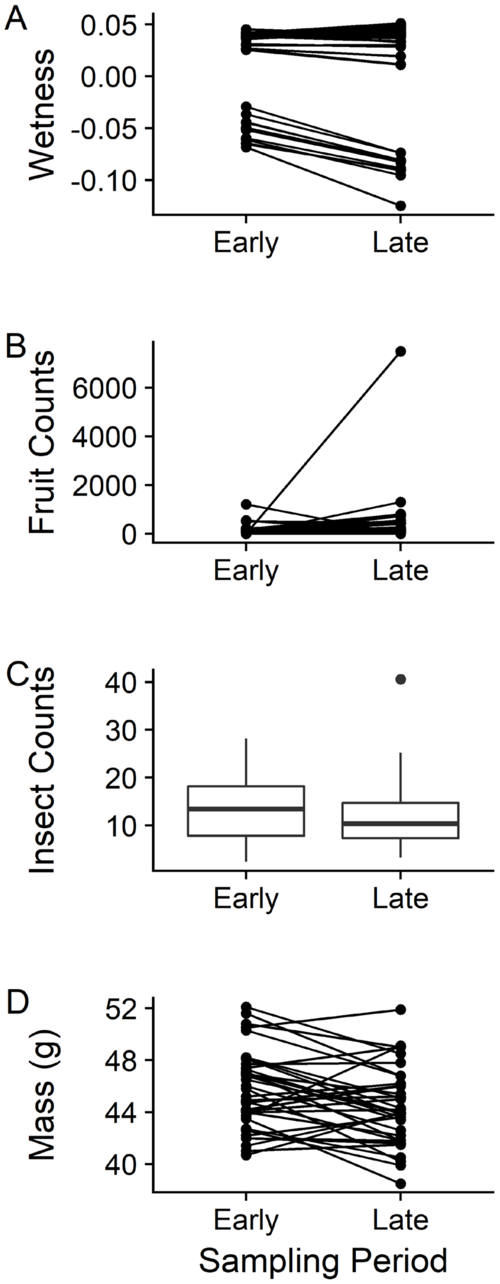
Model	df	Log-likelihood	AIC$_c$	ΔAIC$_c$
Claw				
δ13C + δ15N + Condition + Year	5	-271.90	554.72	0.00
δ13C + δ15N + Year	4	-273.70	556.00	1.28
Age + Sex + δ13C + δ15N + Condition + Year	7	-271.23	558.21	3.49
Age * Sex + δ13C + δ15N + Condition + Year	8	-270.92	560.13	5.41
Age + Sex + δ13C + Wetness + Condition + Year	7	-272.32	560.38	5.66
Age + Sex + δ13C + δ15N + Wetness + Condition + Year	8	-271.18	560.65	5.93
Age + Sex + δ13C * Wetness + Condition + Year	8	-271.21	560.70	5.98
Wetness + Year	3	-278.13	562.61	7.90
Age * Sex + δ13C + δ15N + Wetness + Condition + Year	9	-270.87	562.65	7.93
Condition + Year	3	-278.22	562.79	8.08
Age + Sex + Wetness + Year	5	-277.70	566.32	11.60
Null	0	-284.85	569.70	14.98
Blood				
Condition + Year	3	-306.53	619.38	0.00
Wetness + Year	3	-306.60	619.53	0.15
δ13C + δ15N + Year	4	-306.39	621.34	1.95
δ13C + δ15N + Condition + Year	5	-306.03	622.90	3.51
Age + Sex + Wetness + Year	5	-306.41	623.66	4.28
Null	0	-313.57	627.14	7.76
Age + Sex + δ13C + δ15N + Condition + Year	7	-305.77	627.16	7.77
Age + Sex + δ13C + Wetness + Condition + Year	7	-306.02	627.65	8.27
Age + Sex + δ13C + δ15N + Wetness + Condition + Year	8	-305.68	629.47	10.09
Age * Sex + δ13C + δ15N + Condition + Year	8	-305.77	629.65	10.27
Age + Sex + δ13C * Wetness + Condition + Year	8	-306.01	630.14	10.76
Age * Sex + δ13C + δ15N + Wetness + Condition + Year	9	-305.68	632.04	12.66

Table S4.8 AICc model selection for Cox proportional hazard models evaluating site persistence of non-breeding adult male wood thrush tracked using GPS transmitters from 5 breeding populations (n = 16). Satellite-derived wetness and coefficient of variation of wetness values interpolated from location estimates and winter latitude were included as fixed effects. Models < 2 ΔAICc were considered competitive.

Model	df	Log-likelihood	AIC_c	ΔAIC_c
Wetness	1	-15.76	34.33	0.00
Wetness + cvWetness	2	-13.96	34.92	0.59
Null	0	- 18.40	36.80	2.47
cvWetness	1	-17.46	37.73	3.40
Latitude	1	-17.48	37.76	3.44
Wetness + Latitude	2	-15.63	38.26	3.94
cvWetness + Latitude	2	-16.77	40.55	6.22

Supplementary Figures

Figure S4.1 Change in environmental (A – C) and body condition (D) for non-breeding wood thrush in Belize between early and late dry season sampling points. (A) Decrease in satellite-derived home range wetness between the early (December – February) and late (March – April) dry season. Increase in (B) fruit counts and decrease in (C) insect counts performed on wood thrush home ranges between early (mid-February) and late (end of March) sampling periods. Decrease in mass (D) of wood thrush capture during the early (mid-January to mid-February) and late (mid-March) sampling periods.



Appendix S5: Relationship between stable carbon isotopes and satellite wetness

Stable isotopes have been extensively used in ecological studies because stable isotope ratios in the tissues of animals reflect that of their supporting food web (Hobson 2011). For stable-carbon isotopes differences in the photosynthetic pathways and water-use efficiency in plants drive variation in stable-carbon isotopic signatures which can be used to identify habitat occupancy (Michener and Lajtha 2007, Kohn 2010). C3 plants incorporate less ^{13}C during photosynthesis compared with C4 and CAM plants, leading to more depleted δ13C values in their tissues. Furthermore, within C3 plants water-use efficiency also influences δ13C values and plant tissue becomes become more enriched as water availability decreases. C3 plants are the dominant plants in forested habitats and can therefore be used to infer an index of habitat moisture across the home range of individual birds (Smith et al. 2011b).

To establish that stable-carbon values at our study site in Belize reflect moisture gradients across habitats we examined the factors that drove variation in stable-carbon values. We developed a candidate model set that reflected *a priori* hypotheses for variation in δ13C values. We hypothesized the moisture, as measured by satellite-derived wetness metric, would drive variation in δ13C values. We also hypothesized that dominance relationships between age and sex classes may influence habitat occupancy and therefore δ13C values. Stable-nitrogen values were included in the model because differences in the proportion of insects consumed has also been found to influence stable carbon values (Pearson et al. 2003). Finally, period was included in the analysis as a fixed effect because we expected moisture to decline as the dry season progressed. Separate models were run to include plot wetness or home range wetness as a fixed effect. Bird identity nested within year as a random effect.

As predicted, we found evidence that stable-carbon values reflected habitat moisture as measured by the satellite-derived wetness metric (Figure S5.1, Table S5.1 and Table S5.2). Wetness measured at the plot level negatively influenced stable-carbon values in both blood (β = -5.98, 95% CI = -10.69, -1.27) and claws (β = -7.15, 95% CI = -11.85, -2.45; Table S5.3). As plot wetness decreased, δ13C became more enriched (positive) in the tissues of wood thrush. The sampling period also influenced stable-carbon values in blood (β = -0.54, 95% CI = -0.85, -0.22). δ13C values became more depleted during the late sampling period. Separate models were constructed including individuals with known home ranges, although home range wetness was included in the top model with stable isotopes derived from blood and claw (Table S5.2) the confidence intervals crossed zero (Table S5.3). Models including home range wetness had a smaller sample size compared to models using plot wetness which may have contributed to differences in parameter estimates. Overall, these results suggest, that similar to other studies examining habitat occupancy in migratory songbirds (Marra et al. 1998, Drake et al. 2013), stable-carbon values in the tissues of wood thrush can be used to reflect habitat moisture.

Table S5.1 AICc model selection for generalized mixed effect models describing variation in stable-carbon values of non-breeding wood thrush in Belize across two different plots. Age (yearling or adult), sex (male or female), mean satellite-derived wetness of plots, δ15N (proxy for proportion of insects consumed) and sampling period (early or late) were included as fixed effects. Separate models were run including isotope values derived from either claw (n = 147) which provides information on diets over a few months and blood (n = 164) which provides information on diets over a few weeks. All models included a random intercept for bird identity nested within year and models < 2 ΔAICc were considered competitive.

Model	df	Log-likelihood	AIC_c	ΔAIC_c
Claw				
Wetness * Period	6	-191.90	396.39	0.00
Wetness + Period	5	-193.91	398.25	1.86
Wetness + δ15N + Period	6	-193.82	400.24	3.85
Age + Sex + Wetness + Period	7	-195.30	405.40	9.00
Age + Sex + Wetness + δ15N + Period	8	-195.36	407.75	11.35
Age * Period + Sex * Period + Wetness	9	-195.81	410.92	14.53
δ15N + Period	5	-200.50	411.42	15.03
Age * Period + Sex * Period + Wetness * Period + δ15N	11	-193.79	411.53	15.14
Age * Period + Sex * Period + Wetness + δ15N	10	-195.83	413.27	16.88
Null	3	-203.97	414.10	17.71
Age + Sex + δ15N + Period	7	-202.00	418.81	22.42
Blood				
Wetness * Period	6	-215.19	442.91	0.00
Wetness + δ15N + Period	6	-215.89	444.32	1.41
Age * Period + Sex * Period + Wetness * Period + δ15N	11	-210.39	444.51	1.60
Wetness + Period	5	-217.65	445.67	2.75
Age * Period + Sex * Period + Wetness + δ15N	10	-213.09	447.62	4.70
Age * Period + Sex * Period + Wetness	9	-215.18	449.52	6.61
Age + Sex + Wetness + δ15N + Period	8	-217.43	451.78	8.86
δ15N + Period	5	-220.72	451.82	8.91
Age + Sex + Wetness + Period	7	-219.17	453.05	10.14
Age + Sex + δ15N + Period	7	-222.24	459.19	16.27
Null	3	-229.93	466.01	23.10

Table S5.2 AICc model selection for generalized mixed effect models describing variation in stable-carbon values of non-breeding wood thrush in Belize with known home ranges. Age (yearling or adult), sex (male or female), mean satellite-derived wetness of home ranges, δ15N (proxy for proportion of insects consumed) and sampling period were included as fixed effects. Separate models were run including isotope values derived from either claw (n = 97) which provides information on diets over a few months and blood (n = 110) which provides information on diets over a few weeks. All models included a random intercept for bird identity nested within year and models < 2 ΔAICc were considered competitive.

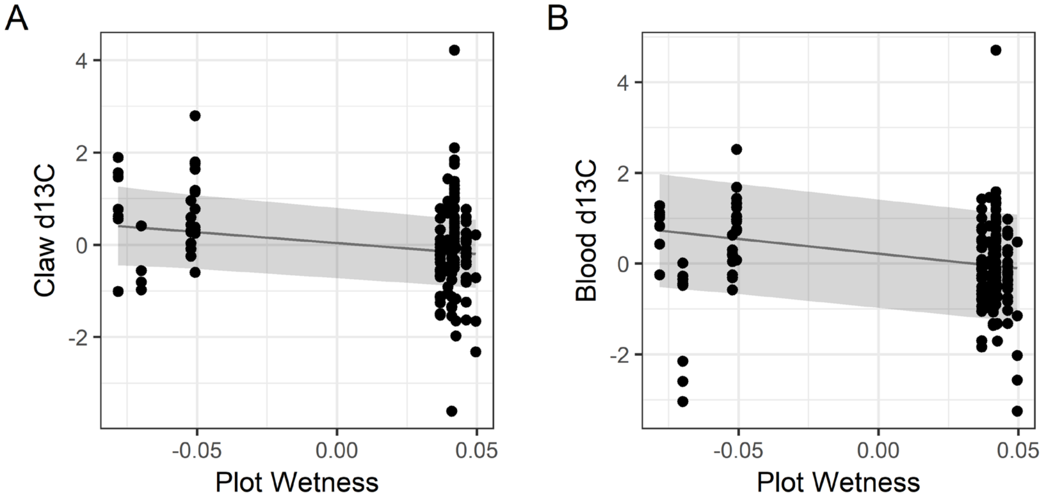
Model	df	Log-likelihood	AIC_c	ΔAIC_c
Claw				
Wetness * Period	6	-127.23	267.39	0.00
Wetness + δ15N + Period	6	-128.30	269.53	2.14
Wetness + Period	5	-129.65	269.97	2.58
δ15N + Period	5	-131.46	273.57	6.18
Age + Sex + Wetness + δ15N + Period	8	-128.60	274.83	7.44
Age + Sex + Wetness + Period	7	-130.17	275.60	8.21
Age * Period + Sex * Period + Wetness * Period + δ15N	11	-125.73	276.57	9.18
Age * Period + Sex * Period + Wetness + δ15N	10	-128.18	278.91	11.52
Age + Sex + δ15N + Period	7	-132.09	279.44	12.04
Age * Period + Sex * Period + Wetness	9	-129.88	279.84	12.44
Null	3	-137.01	280.27	12.88
Blood				
Wetness * Period	6	-143.93	300.68	0.00
Age * Period + Sex * Period + Wetness * Period + δ15N	11	-138.14	300.97	0.29
Wetness + δ15N + Period	6	-144.87	302.55	1.88
Wetness + Period	5	-146.84	304.26	3.58
Age * Period + Sex * Period + Wetness + δ15N	10	-141.27	304.76	4.09
δ15N + Period	5	-147.61	305.79	5.11
Age * Period + Sex * Period + Wetness	9	-143.76	307.32	6.64
Age + Sex + Wetness + δ15N + Period	8	-145.37	308.17	7.49
Age + Sex + Wetness + Period	7	-147.53	310.16	9.48
Age + Sex + δ15N + Period	7	-148.48	312.07	11.39
Null	3	-155.19	316.61	15.93

Table S5.3 Model averaged parameter estimates, standard error and unconditional 95% confidence intervals for top linear mixed effect models describing variation in stable-carbon values across the non-breeding season for wood thrush in Belize. Separate models were constructed for isotope values derived from claw which provides information on diets over a few months and blood which provides information on diets over a few weeks. Separate models were also constructed for wetness measured across plots (claws, n = 147; blood, n = 164) or home ranges (claw, n = 97; blood, n = 110).

Parameter	Estimate	SE	95% CI
Plot			
Claw			
Wetness	**-7.15**	**2.40**	**-11.85, -2.45**
Period	**-0.54**	**0.16**	**-0.85, -0.22**
Wetness * Period	0.29	3.12	-4.98, 5.4
Blood			
Wetness	**-5.98**	**2.40**	**-10.69, -1.27**
Period	-0.52	0.38	-1.26, 0.22
Wetness * Period	3.02	3.06	-3.53, 8.04
δ15N	0.20	0.08	-0.13, 0.33
Age (yearling)	0.00	0.16	-0.15, 0.15
Sex (Male)	0.17	0.17	-0.17, 0.25
Age (yearling) * Period	-0.75	0.31	-0.86, 0.51
Sex (Male) * Period	-0.66	0.30	-0.77, 0.46
Home range			
Claw			
Wetness	-5.45	3.61	-13.00, 2.10
Period	-0.69	0.22	-1.15, -0.24
Wetness * Period	-0.01	4.54	-9.52, 9.50
Blood			
Wetness	-5.44	3.26	-11.82, 0.94
Period	-0.46	0.46	-1.36, 0.44
Wetness * Period	4.78	4.32	-4.53, 12.43
δ15N	0.26	0.10	-0.14, 0.43
Age (yearling)	-0.10	0.21	-0.31, 0.24
Sex (Male)	0.13	0.20	-0.22, 0.32
Age (yearling) * Period	-0.72	0.39	-1.12, 0.56
Sex (Male) * Period	-0.72	0.40	-1.12, 0.56

Notes: Values in bold have confidence intervals that do not include zero.

Figure S5.1 Factors driving stable-carbon value in wood thrush across the non-breeding season in Belize. Negative relationship between satellite-derived wetness on plots and stable-carbon values from (A) claws and (B) blood. More negative wetness values denote drier conditions. Line denotes the predicted relationship and shaded area the 95% CI.



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