Seasonal variation in habitat selection for a Neotropical migratory songbird using high-resolution GPS tracking

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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 (10 m) 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 individuals within five populations of wood thrush (Hylocichla mustelina) throughout their breeding range. Wood thrush exhibited seasonal variation in local- and landscape-scale habitat selection. Within stationary periods, wood thrush occupied forested habitats and proximity to forest edge was an important predictor of habitat selection at the local scale. In contrast, during migratory periods wood thrush exhibited greater behavioral 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 response to the extensive forest fragmentation in the North American breeding grounds. We also identified individual population distribution patterns indicative of regional habitat selection during fall migration and winter period, but not spring migration. 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.

Key words: annual cycle; habitat selection; migration; migratory connectivity; tracking; wood thrush.

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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, Akesson and Hansson 2014). In each location, 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 throughout their annual cycle (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 winter (Chandler and King 2011, Fraser et al. 2017) periods, 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 (Fig. 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 nonhabitat 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), and 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, nest predation risk). 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 not only across multiple spatial scales ranging from regional to microhabitat 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, largely in terms of spatial scales (Wiens and Milne 1989, Orians and Wittenberger 1991, Rettie and Messier 2000, Grand and Cushman 2003). However, the scope of this research has often been restricted to studies of single seasons on single populations, limiting the inferences that can be drawn (McGarigal et al. 2016). For migratory songbirds, most ecological studies have been conducted during the breeding season (Marra et al. 2015). 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 nonbreeding season (Petit 2000, Zuckerberg et al. 2016). This lack of consistency in habitat associations suggests that individuals can maximize their fitness across seasons through behavioral flexibility in their habitat settlement decision making (i.e., nesting vs. refueling sites). 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?
Fig. 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.
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 test the hypothesis that factors driving habitat suitability change across seasons, we explored individual variation in habitat selection at the local and landscape scales. Since wood thrush are characterized as forest species that are tolerant of forest fragmentation (Evans et al. 2011), we predicted that if habitat suitability remains constant across seasons, thrushes will consistently select local and landscape feature characteristics of forest habitats. In contrast, if the factors that drive habitat suitability exhibit seasonal variation, we predicted a shift to more generalist habitat selection during migratory periods as nonhabitat features (e.g., temporal constraints on migration, energetic demands) drive the decision-making process and the mechanisms for accurately assessing unfamiliar habitats become difficult for birds. 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 visual cue that can be used in flight to assess habitat quality (Buler et al. 2007, Beatty et al. 2014).

Second, to test for seasonal changes in regional habitat selection among five breeding populations we assessed the strength of migratory connectivity. Migratory connectivity is most commonly used to describe the strength of regional redistribution of migratory individuals across the annual cycle, but here we used it to identify the presence of population-specific regional habitat selection decisions as individuals move large distances throughout the year. 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, we predict regional habitat selection during fall migration driven by population-specific migration routes (Stanley et al. 2015). Wood thrush show moderate connectivity from breeding to winter sites (Stanley et al. 2015), suggesting weaker patterns of regional habitat selection on winter sites. Finally, we predict no regional habitat selection during spring migration due to the convergence of migratory routes at the Gulf of Mexico.

**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 broadleaf and palm forests ranging from southern Mexico to northern Panama (Evans et al. 2011). They are a multibrooded, omnivorous species that primarily forages on the ground. Wood thrush maintain territories during the winter and breeding seasons; 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 (permanent long-distant movements, 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 spatiotemporal variation in habitat selection across the annual cycle, we studied wood thrush from 2014 to 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 summers of 2014 and 2015 across five populations in Delaware, Indiana, North Carolina, New York, and Minnesota (Appendix S1: Table S1). The tags provide location estimates for individual birds with an estimated accuracy of 10 m. Tags were recovered by returning to sites the following summer and recapturing individuals. We recovered 23 tags and retrieved data from 21 tags (Appendix S1: Table S1). Two of the 23 tags were unresponsive (no data retrieved); nine of the 23 lost antennas sometime after release (partial data recovery), and 12 of the 23 were retrieved with antennas intact. We obtained an average of 26 out of a maximum of 50 points per tag (range 1–46;
Appendix S1). Most missing fixes, excluding those involving lost antennas, occurred during migratory periods (Appendix S1: Table S2). 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 (e.g., spring migration ends the day before first recorded point on breeding grounds). Migratory periods were identified as northward or southward movements of at least 20 km over consecutive location fixes (>2 points, 6–8 d).

**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 S3). At each location fix, we examined structural characteristics of the habitat used and available to wood thrush 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, index of primary productivity), patch size (ha, connected pixels of >30% tree cover), and proximity to non-forest (m, defined as <30% tree cover; detailed description of interpolation methods in Appendix S1: Table S3). 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 (ha). 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 because classified land cover layers suitable for a 1-km buffer were unavailable across our study area (Appendix S1: Table S3). Landscape composition was therefore analyzed separately from the other landscape characteristics.

**Local and landscape habitat selection**

To identify variation in spatiotemporal patterns of habitat selection at the individual level, we explored three measures. First, at the landscape scale, we examined the consistency of land cover associations for individual birds across seasons. Second, we quantified the repeatability of use of habitat features by individuals at both the landscape and local scales across the stationary (breeding and winter) and migratory (fall and spring migration) periods. 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 characterize consistency in land cover associations we utilized the Shannon diversity index (Shannon 1948) to estimate seasonal diversity in landscape composition for each individual. 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 that individuals showed plasticity in land cover associations and suggests more generalist habitat selection within a 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). 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...
behavioral 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 (detailed methods in Appendices S1, S5). Therefore, each used resource unit had its own set of available units. For all used and available points, local and landscape habitat features were extracted as defined in the habitat features section.

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 (5 km), and during relocation events (15 and 25 km) based on prior information on wood thrush spatial ecology (Rappole et al. 1989, Lang et al. 2002). Off-territory forays have typically been recorded as covering <1 km; however, more recent tracking has found individuals can travel longer distances (Stanley 2019); therefore, we chose a larger spatial extent to account for these movements. 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. The 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 regressions 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 S4). 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- and 5-km spatial extent, we evaluated two models (local and null); and at the relocation level (15 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 × 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 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). We also described population-specific patterns of local- and landscape-scale habitat features (characteristics of used habitats) to determine whether patterns of regional habitat selection corresponded to population-specific patterns of habitat use (see Appendix S4). To examine the consistency of annual schedules between breeding populations, we determined the timing of annual events for all individuals (see Appendix S3).

Statistical analysis
All analyses were conducted in R 3.4.3 (R Core Team 2017). The Bayesian mixed conditional logistic regression models were run with the R package jagsUI (Kellner 2017) using the software JAGS 4.3.0 (Appendix S1, S5; Plummer 2003). Generalized mixed-effects 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 (Fig. 2; Appendix S1: Table S2). During the winter period, of the 18 birds tracked across the whole period, eight individuals engaged in intra-winter movements occupying two or more territories an average of 59 ± 21 km (±SE, range 1.6–180 km) apart (Fig. 2C). The remaining 10 individuals remained at a single winter territory, moving an average of 110 ± 26 m (±SE) between locations from November to April.
Local and landscape habitat selection

The diversity of land cover types occupied by individual wood thrush varied by season ($\chi^2 = 45.9, \text{df} = 3, P < 0.001$; Fig. 3). We detected no 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 $Z = 5.8, P < 0.001$; breeding–spring $Z = -3.5, P = 0.003$; winter–fall $Z = 5.5, P < 0.001$, winter–spring $Z = 3.2, P = 0.08$). 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 (Fig. 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.

The repeatability of habitat features as birds moved within the migratory periods was very low, close to zero. 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, $R = 0.33$–0.48, Table 1). EVI and patch size had low repeatability ($R < 0.3$) during stationary periods.
Discrete choice models indicated that the habitat features of the resource units (locations) wood thrush selected (compared with 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 feature model (Fig. 4; Appendix S1: Table S5). 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 (Fig. 4). At the smallest spatial extent (0.5 km), birds chose resource units with low EVI values. At the two largest spatial extents (15 and 25 km), wood thrush selected resource units proximate to non-forest. Additionally, on the breeding grounds, at the 25-km extent birds selected resource units that were found within
lakes 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-, 5-, and 25-km spatial extent and resource units with high EVI values at the larger spatial extents (15 and 25 km). On wintering grounds, at all spatial extents, birds chose resource units with large patch sizes; at the 5-, 15-, and 25-km spatial extents, birds chose resource units proximate to non-forest; and at the 25-km extent, they chose resource units with high tree cover.

**Regional habitat selection**

The migratory connectivity estimate between breeding and wintering grounds was weak-to-moderate (MC Index = 0.41), indicating regional habitat selection by breeding populations on the wintering grounds. Regional habitat selection was also present at fall stopover locations prior to the Gulf of Mexico crossing based on a high migratory connectivity estimate (MC Index = 0.69) due to breeding populations utilizing region-specific departure points from North America (Fig. 2B). By contrast, during spring migration, connectivity was lower (MC Index = 0.28) at stopovers after the Gulf of Mexico crossing, suggesting no regional habitat selection by breeding populations. As predicted based on our analysis of regional habitat selection, we found evidence of population-specific differences in habitat use patterns during the stationary periods and fall migration, but not spring migration (Appendix S4). Finally, we found evidence that timing of both spring and fall migration was influenced by breeding location, but not winter location (Appendix S3).

**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 behavioral 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 and quality of habitats that individuals occupy as they redistribute geographically across the annual cycle (Webster and Marra 2005).

**Seasonal variation in habitat selection**

Fine-scale tracking of individual wood thrush revealed variation in habitat selection across periods of the annual cycle. By employing a novel multi-scale approach, we determined wood thrush were selective at the local scale across the annual cycle 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 winter 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 behavior, particularly for fruit-eating species such as 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 regard to the habitat features we measured during spring migration.

This shift to be more of a generalist when selecting habitat may be favored 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: Fig. S1, Table S2). Increased behavioral 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 behaviors 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 responded 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 compared with spring migration (Appendix S3: Fig. S1, Table S2), 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
Behavioral plasticity between migratory periods could be driven by seasonal difference in environmental conditions linked to food availability. For example, poor environmental conditions at fall stopover sites or poor physical condition carrying over from the breeding/molting period could drive increased food limitations in the fall and lead to higher selective pressure on habitat suitability. In contrast to spring migration, the higher variability in fall migration schedules also suggests timing of arrival on wintering grounds may not be associated with fitness advantages, which could drive differences in behavioral plasticity between seasons.

Landscape-scale habitat selection was only identified during the breeding season and only 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 (winter, Graham and Blake [2001]; breeding, Lee et al. 2002, Valente and Metzger 2018 but see Fauth et al. [2000]). Therefore, the relevance of landscape variables during only the breeding 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). For example, previous research has found increased nesting success in landscape with higher core forest area and increased rates of nest parasitism and predation in landscapes with higher proportion of developed land cover (Driscolli et al. 2005, Lloyd et al. 2005). 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; Andrén 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 (Fig. 4, Appendix S2: Table S1). 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 (average patch size) in our models.

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. Wood thrush showed a preference for high tree cover and edge habitats during both stationary periods, which has previously been reported for wood thrush (breeding, Vega Rivera et al. [1998], Kaiser and Lindell [2007]; winter, Graham and Blake [2001], Roberts [2011]). Selection of patch size showed contrasting patterns between stationary periods; wood thrush were more likely to settle in smaller forest patches during the breeding season and larger forest patches during the winter season. 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 (but see Weinberg and Roth 1998, Fauth 2001) associated with decreased reproductive success for wood thrush (Donovan et al. 1995, Burke and Nol 2000). Together, these results indicate that factors related to forest structure play a role in habitat selection during the stationary periods. The observed differences in patch size across stationary periods could indicate shifts in the importance of this habitat feature. 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 nonrandom assortment of populations at regional scales between breeding and nonbreeding 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 winter (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 unrelated 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 finer spatial scales. Due to limited sample size, we were unable to perform these analyses. However, we did describe population-specific trends in the use of local- and landscape-scale habitat features (see Appendix S4). As predicted based on our analysis of regional habitat selection, we identified differences in habitat use patterns during the stationary periods and fall migration, but not spring migration. Due to limited sample size, this analysis does not determine whether 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). For example, anthropogenic light pollution has been found to attract nocturnally migrating birds to urban areas (La Sorte et al. 2017, McLaren et al. 2018) and individual tracking data could provide important insight into how artificial light affects the stopover process (Bowlin et al. 2015). 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 nonbreeding 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.

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Burke, D., and E. Nol. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. Ecological Applications 10:1749–1761.

Chandler, R. B., and D. I. King. 2011. Habitat quality and habitat selection of golden-winged warblers in Costa Rica: an application of hierarchical models for open populations. Journal of Applied Ecology 48:1038–1047.

Cody, M. 1985. An introduction to habitat selection in birds. Pages 3–56 in M. Cody, editor. Habitat selection in birds. Academic Press Inc, Orlando, Florida, USA.

Cohen, E. B., J. A. Hostetler, M. T. Hallworth, C. S. Rushing, T. S. Sillett, and P. P. Marra. 2018. Quantifying the strength of migratory connectivity. Methods in Ecology and Evolution 9:513–524.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife. Ecology 80:566–575.

Donovan, T., R. Lamberson, A. Kimber, F. I. Thompson, and J. Faaborg. 1995. Modeling the effects of habitat fragmentation on source and sink demography of Neotropical migrant birds. Conservation Biology 9:1396–1407.

Driscoll, M. J. L., T. Donovan, A. Howard, and K. K. Fleming. 2005. Determinants of wood thrush nest success: a multi-scale. Model Selection Approach 69:699–709.

Evans, M., E. Gow, R. Roth, M. Johnson, and T. Underwood. 2011. The Birds of North America, version 2.0: wood Thrush (Hylocichla mustelina). Cornell Lab of Ornithology, Ithaca, New York, USA.

Faaborg, J., et al. 2010. Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398–418.

Fauth, P. 2001. Wood Thrush populations are not all sinks in the agricultural midwestern United States. Conservation Biology 15:523–527.

Fauth, P., E. Gustafson, and K. Rabenold. 2000. Using landscape metrics to model source habitat for Neotropical migrants in the midwestern US. Landscape Ecology 15:621–631.

Finch, T., S. J. Butler, A. M. A. Franco, and W. Cresswell. 2017. Low migratory connectivity is common in long-distance migrant birds. Journal of Animal Ecology 86:662–673.

Fraser, K. C., A. Shave, A. Savage, A. Ritchie, K. Bell, J. Siegrist, J. D. Ray, K. Applegate, and M. Pearson. 2017. Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new GPS technology. Journal of Avian Biology 48:339–345.

Gilroy, J. J., J. A. Gill, S. H. M. Butchart, V. R. Jones, and A. M. A. Franco. 2016. Migratory diversity

LITERATURE CITED

Åkesson, S., and L.-A. Hansson, editors. 2014. Animal movement across scales. Oxford University Press, Oxford, UK.

Alerstam, T., A. Hedenstrom, and S. Akesson. 2003. Long-distance migration: evolution and determinants. Oikos 103:247–260.

Alerstam, T., and A. Lindström. 1990. Optimal bird migration: the relative importance of time, energy and safety. Pages 331–351 in E. Gwinner, editor. Bird migration: Physiology and ecophysiology. Springer-Verlag, Berlin, Germany.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355.

Balbontin, J., A. P. Möller, I. G. Hermosell, A. Marzal, M. Reviriego, and F. De Lope. 2009. Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. Journal of Animal Ecology 78:981–989.

Beatty, W. S., E. B. Webb, D. C. Kesler, A. H. Raedeke, L. W. Naylor, and D. D. Humburg. 2014. Landscape effects on mallard habitat selection at multiple spatial scales during the non-breeding period. Landscape Ecology 29:989–1000.

Bowlin, M. S., D. A. Enstrom, B. J. Murphy, E. Plaza, P. Jurich, and J. Cochran. 2015. Unexplained altitude changes in a migrating thrush: long-flight altitude data from radio-telemetry. Auk 132:808–816.

Buler, J. J., and F. R. Moore. 2011. Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. Journal of Ornithology 152:101–112.

Buler, J. J., F. R. Moore, and S. Woltmann. 2007. A multi-scale examination of stopover habitat use by birds. Ecology 88:1789–1802.
predicts population declines in birds. Ecology Letters 19:308–317.

Gómez, C., N. J. Bayly, D. R. Norris, S. A. Mackenzie, K. V. Rosenberg, P. D. Taylor, K. A. Hobson, and C. Daniel Cadena. 2017. Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. Scientific Reports 7:1–11.

Graham, C. H., and J. G. Blake. 2001. Influence of patch- and landscape-level factors on bird assemblages in a fragmented tropical landscape. Ecological Applications 11:1709–1721.

Grand, J., and S. A. Cushman. 2003. A multi-scale analysis of species-environment relationships: breeding birds in a pitch pine–scrub oak (Pinus rigida–Quercus ilicifolia) community. Biological Conservation 112:307–317.

Hijmans, R. 2016. raster: geographic Data Analysis and Modeling. https://cran.r-project.org/package=raster

Hutto, R. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455–476 in M. Cody, editor. Habitat selection in birds. Academic Press Inc, Orlando, Florida, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kaiser, S. A., and C. A. Lindell. 2007. Effects of distance to edge and edge type on nestling growth and nest survival in the wood thrush. Condor 109:288–303.

Kellner, K. 2017. jagsUI: a Wrapper Around “rjags” to Streamline “JAGS” Analyses. https://cran.r-project.org/package=jagsUI

Knight, S. M., et al. 2018. Constructing and evaluating a continent-wide migratory songbird network across the annual cycle. Ecological Monographs 88:445–460.

Kokko, H. 1999. Competition for early arrival in migratory birds. Journal of Animal Ecology 68:940–950.

Koleček, J., et al. 2016. Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. Journal of Avian Biology 47:756–767.

La Sorte, F. A., D. Fink, J. J. Buler, A. Farnsworth, and S. A. Cabrera-Cruz. 2017. Seasonal associations with urban light pollution for nocturnally migrating bird populations. Global Change Biology 23:4609–4619.

La Sorte, F. A., M. W. Tingley, and A. H. Hutto. 2014. The role of urban and agricultural areas during avian migration: an assessment of within-year temporal turnover. Global Ecology and Biogeography 23:1225–1234.

Lafleur, J. M., J. J. Buler, and F. R. Moore. 2016. Geographic position and landscape composition explain regional patterns of migrating landbird distributions during spring stopover along the northern coast of the Gulf of Mexico. Landscape Ecology 31:1697–1709.

Lang, J. D., L. A. Powell, D. G. Krementz, and M. J. Conroy. 2002. Wood thrush movements and habitat use: effects of forest management for red-cockaded woodpeckers. The Auk 119:109–124.

Lee, M., L. Fahrig, K. Freemark, and D. J. Currie. 2002. Importance of patch scale vs landscape scale on selected forest birds. Oikos 96:110–118.

Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Lloyd, P., T. Martin, and R. Redmond. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications 15:1504–1514.

Manly, B. F., L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2004. Resource selection by animals. Second edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. A call for full annual cycle research in animal ecology. Biology Letters 11:20150552.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

Mccabe, J. D., and B. J. Olsen. 2015. Landscape-scale habitat availability, and not local geography, predicts migratory landbird stopover across the Gulf of Maine. Journal of Avian Biology 46:395–405.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

McLaren, J. D., J. J. Buler, T. Schreckengost, J. A. Smolinsky, M. Boone, E. Emiel van Loon, D. K. Dawson, and E. L. Walters. 2018. Artificial light at night confounds broad-scale habitat use by migrating birds. Ecology Letters 21:356–364.

Meyer, C. B., and W. Thuiller. 2006. Accuracy of resource selection functions across spatial scales. Diversity & Distributions 12:288–297.

Mitchell, M. S., R. A. Lancia, and J. A. Gerwin. 2001. Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. Ecological Applications 11:1692–1708.

Moore, F., and D. Aborn. 2000. Mechanisms of en route habitat selection: how do migrants make
habitat decisions during stopover? Studies in Avian Biology 20:34–42.

Newton, I. 2008. The migration ecology of birds. Academic Press/Elsevier, Amsterdam, The Netherlands.

Nilsson, C., R. H. G. Klaassen, and T. Alerstam. 2013. Differences in speed and duration of bird migration between spring and autumn. American Naturalist 181:837–845.

Oksanen, J., et al. 2017. vegan: community Ecology Package. https://cran.r-project.org/package=vegan

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 1–10 in K. Hornik, F. Leisch, and A. Zeileis, editors. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, Vienna, Austria, March 20–22, 2003. R Foundation for Statistical Computing, Vienna, Austria.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R C Team. 2017. nlme: linear and Nonlinear Mixed Effects Models. https://CRAN.R-project.org/package=nlme

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 1–10 in K. Hornik, F. Leisch, and A. Zeileis, editors. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, Vienna, Austria, March 20–22, 2003. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rappole, J. H., M. A. Ramos, and K. Winker. 1989. Wintering wood thrush movements and mortality in southern Veracruz. Auk: Ornithological Advances 106:402–410.

Retie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466–478.

Roberts, D. L. 2011. Conservation value of forest fragments for wood thrush (Hylocichla mustelina) in Costa Rica’s caribbean lowlands. Latin American Journal of Conservation 2:8–17.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

Rushing, C. S., M. R. Dudash, C. E. Studds, and P. P. Marra. 2015. Annual variation in long-distance dispersal driven by breeding and non-breeding season climatic conditions in a migratory bird. Ecography 38:1006–1014.

Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski. 2013. The North American Breeding Bird Survey 1966–2011: summary analysis and species accounts. North American Fauna 79:1–32.

Shannon, C. E. 1948. A mathematical theory of communication. Bell System Technical Journal 27:379–423.

Stanley, C. Q., et al. 2015. Connectivity of wood thrush breeding, wintering, and migration sites based on range-wide tracking. Conservation Biology 29:164–174.

Stanley, C. Q. 2019. Ecological causes and consequences of non-breeding movements in a declining migratory songbird, Wood Thrush (Hylocichla mustelina). Dissertation. University of Maryland, College Park, Maryland, USA.

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

Stoffel, M. A., S. Nakagawa, and H. Schielzeth. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution 8:1639–1644.

Studds, C. E., T. K. Kyser, and P. P. Marra. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. Proceedings of the National Academy of Sciences of the United States of America 105:2929–2933.

Valente, J. J., and M. G. Betts. 2018. Response to fragmentation by avian communities is mediated by species traits. Diversity and Distributions 1–13.

Vega Rivera, J., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood thrush postfledging movements and habitat use in Northern Virginia. Condor 100:69–78.

Villard, M. A., and J. P. Metzger. 2014. Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology 51:309–318.

Webster, M. S., and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199–209 in R. Greenberg and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA.

Weinberg, H., and R. Roth. 1998. Forest area and habitat quality for nesting Wood Thrushes. Auk 115:879–889.
Wiens, J. A. 1989. Spatial Scaling in Ecology. Functional Ecology 3:385.
Wiens, J. A., and B. T. Milne. 1989. Scaling of ‘landscapes’ in landscape ecology, or, landscape ecology from a beetle’s perspective. Landscape Ecology 3:87–96.
Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biology 6:1361–1364.
Yong, W., and F. R. Moore. 2005. Long-distance bird migrants adjust their foraging behavior in relation to energy stores. Acta Zoologica Sinica 51:12–23.
Zuckerberg, B., D. Fink, F. A. La Sorte, W. M. Hochachka, and S. Kelling. 2016. Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. Diversity and Distributions 22:717–730.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3421/full