

MIGRATORY ROUTES AND STOPOVER REGIONS OF EASTERN BREEDING VEERIES
(TURDIDAE: *CATHARUS FUSCESCENS*) AS REVEALED BY ARCHIVAL LIGHT-LEVEL
GEOLOCATORS

by

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A Thesis

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Abstract

Nearctic-Neotropical migrant passerines have experienced population declines presumably largely due to habitat loss and degradation on both the wintering and breeding grounds. Only recently have these declines been attributed in part to the loss of suitable stopover sites available during migration. Stopover sites of high ecological quality are essential along an ecological barrier in order to provide areas for migrants to rest and refuel. The identification and conservation of high quality stopover sites has become a research priority; however, until recent advances in technology it was difficult to identify these sites without quantitative field surveys. Archival light-level geolocators are the only technology that allows ornithologists to recreate the daily positions of small songbirds (<50g) throughout their annual cycle. The focus of the present research was to further our knowledge of the annual movements of the Nearctic-Neotropical migratory species, the Veery (*Catharus fuscescens*), through the use of miniaturized tracking technology. My objectives were to (1) identify important stopover regions used by migrating Veeries, and (2) identify important migratory flyways between the Veery's breeding and wintering grounds. I used kernel density estimations and hot spot analysis to identify important stopover regions used by two distinct eastern breeding populations and compared the results of the different analyses. I identified differences in stopover regions used during migration on the

basis of age, sex, and seasons. I also identified the migratory routes taken by 58 individuals over an eight-year period and found that age and sex did not significantly affect the migratory routes taken during migration; however, I did find that the migratory routes varied greatly between years with respect to the path taken by individuals preparing to cross the Gulf of Mexico. My results highlight the importance of long-term geolocator studies to furthering our understanding of migratory connectivity. Also, through this study, I began establishing a potential framework for the identification of important stopover regions for Nearctic-Neotropical migrants in general. This research will enable conservationists to make more informed decisions regarding the stopover regions to prioritize for protection in future long-term conservation planning efforts.

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List of Abbreviations

ASY	After second-year
SY	Second-year
HY	Hatch-year
KDE	Kernel Density Estimation
Geolocator	Archival light-level geolocator
Neotropical migrant	Nearctic-Neotropical migrant
GIS	Geographic Information Systems
CTA	Contingency Table Analysis

Chapter 1: Introduction

Nearctic-Neotropical (hereafter, Neotropical) migrants are songbirds that spend their wintering season in South America while migrating to North America each year to breed. These long-distance migrants have experienced population declines over the past several decades (Ballard et al. 2003, Lloyd-Evans and Atwood 2004). Historically, these declines have been attributed to detrimental changes in their breeding and wintering grounds (Robbins et al. 1989). More recently, the importance of understanding the migratory routes and stopover locations used have become a research priority (Donovan et al. 2002, Mehlman et al. 2005), as migration is the least understood songbird life history stage (Faaborg et al. 2010).

Urbanization and human development appear to be directly influencing the decline of songbirds. Anthropogenic stressors, such as collisions with man-made obstacles (Crawford and Engstrom 2001), feral cat predation (Erickson et al. 2005), and increased agricultural activity (Murphy 2003) are suggested to be the main factors contributing to the increased mortality rate of Neotropical migrants. These factors are exacerbated during migration while songbirds are at their most vulnerable (Silleet and Holmes 2002). During migration, birds are forced to stop over in urban areas (e.g. city parks, residential gardens, cemeteries, or forest fragments) in order to rest and refuel (Mehlman et al. 2005, Bonter et al. 2009). These areas have been shown to provide critical habitat during migration (Matthews and Rodewald 2010, Seewagen et al. 2010); however, they are threatened by the ever expanding human population.

Although there is ample research about Neotropical migrant songbirds on their breeding grounds, there is a general lack of knowledge regarding their wintering and migratory periods (Faaborg et al. 2010). Understanding the migratory pathways and habitat requirements during

migration is crucial to the conservation of these declining species (Mehlman et al. 2005). However, the identification of ecologically important regions is difficult to achieve because of constantly changing variables (i.e. weather and food availability) that affect the migratory routes and stopover sites used by migrating songbirds (Faaborg et al. 2010).

The Veery (*Catharus fuscescens*) are a medium sized Neotropical migrant. They are a forest-dependent songbird (thrush: Turdidae) that breeds in dense, damp, mostly deciduous woodlands, and winters in South America (Heckscher 2011). Veeries are primarily ground foragers, feeding primarily on insects when breeding and adding fruit in late summer and fall (Heckscher 2017a). The Veery has experienced an overall population decline of 40% since the 1970's (Heckscher 2017a). The primary cause of decline is attributed to the degradation of habitat on their wintering and breeding grounds. Although Veeries are well studied on their breeding grounds, there was limited information available about this species during their migratory and wintering species; therefore the exact cause of population loss is uncertain. The ability to track these songbirds during their annual cycle is required to gain insight into their behavior on their habitat use during migration and on their wintering grounds. Advancement in geolocation technology has provided great insight into this species in decline.

Miniaturized archival light level geolocators (hereafter, geolocators) are currently the only tracking method that can be used to estimate the daily position of small (<50g) migratory songbirds through their annual cycle (Roberto-Charron 2018). In light-level geolocation, coordinates are calculated by astronomical equations using the length of day (latitude) and solar noon (longitude) (Hill and Braun 2001). This process involves the assignment of twilights (e.g. sunset and sunrise times) on a light curve data provided by a geocator, which records ambient

light levels and time. The greatest limitation of this technology is that they are archival, meaning the information does not transmit and the unit must be recovered in order to retrieve the data.

The use of geolocators has enabled ornithologists to fill huge knowledge gaps regarding songbird ecology. However, an inherent shortcoming of geolocation is the effect that shading has on derived location accuracy. Light from the sun rarely reaches the earth without some sort of obstruction, and anything that impacts the light or shades the geolocators can have a negative effect on accuracy. Environmental factors that may obscure the light regime are diverse, but all cause shading events, which can result in erroneous shorter day length (Lisovski et al. 2012). For example, variables like topography and vegetation result in constant shading, which can bias the position estimates by shortening day length, thus delaying/extending perceived twilight times, and subsequently altering the latitude estimates. Alternatively, atmospheric weather conditions and behavior can impact geolocation in a similar way by obstructing the light sensor resulting in changes in the recorded light conditions (Lisovski and Hahn 2012). Time of year can also have major impacts on geolocation as daylight is variable causing erroneous shading similar to vegetation. Latitude error (estimated by day length) varies greatly throughout the year, especially during the solar equinoxes when day lengths are equal making it difficult to estimate an accurate latitude. Recent advances in the methods of geolocator analysis have aimed to fill in the gaps associated with the solar equinox by utilizing the last and next inferred position (Rakhimberdiev et al. 2017) resulting in more reliable results during these events. Understanding the inherent limitations associated with geolocation technology will enable researchers to avoid overanalyzing their results.

This thesis focuses on the migratory patterns and major stopover regions used by a Neotropical migrant songbird species during migration. My objective was to utilize archival

light-level geolocators to gain insight into the migratory spatial patterns of eastern breeding Veeries. From 2009-2018 our research team attached geolocators on a color banded Veery population in northern Delaware, USA. In 2017, we added a color banded Veery population in northwestern Massachusetts, USA. Therefore, the results presented here reveal how intrinsic (age and sex) and extrinsic factors (seasons and years) affect the migratory routes and stopover location of eastern breeding Veeries from two distinct breeding populations. My goal was to provide insight into the migratory behavior of a declining songbird by identifying critical habitat and major flyways used during migration that should be included in future conservation plans.

Chapter II: Migratory Stopover Regions of two Eastern Breeding Populations of Veeries

(*Catharus fuscescens*) using Light-Level Geolocators

2.1 Introduction

Neotropical migrant songbirds can spend up to one-third of their annual cycle in transit between breeding and wintering grounds (Bonter et al. 2009; Mehlman et al. 2005). Migratory periods are when they tend to experience their highest mortality rate (Silllett and Holmes 2002). Most migrants do not make non-stop flights between wintering and breeding grounds; rather, they make multiple stops in order to periodically rest and refuel and many factors can make their migration a risky endeavor (Mehlman et al. 2005). For example, adverse weather conditions, such as hurricanes and tropical storms, is one potential source of mortality due to the intense winds that may blow birds off course or out to sea (Butler 2000). Such conditions can result in a forced stopover in undesirable habitat (Barrow et al. 2005). In addition, large geographical barriers can commonly lead to migratory “fallouts” that commonly result in songbirds arriving in an exhausted or emaciated state (Kneidel 2016). Such conditions will increase a bird’s need to refuel rapidly which in turn can increase exposure to predators (Moore et al. 1990). Therefore, the quality of the stopover sites used during migration is essential to the survival of Neotropical migrants (Moore and Woodrey 1993, Gómez et al. 2015, Bayly et al. 2018). Gómez et al. (2014) found that the rate at which individuals refuel can affect their migratory route and rate of migration. The rate at which a bird completes its spring migration can also affect the overall health of the bird and its ability to successfully reproduce (Moore and Woodrey 1993; Smith and Moore 2005) which in turn can affect fall departure and arrival back in the Neotropics (Heckscher et al. 2017b). Therefore, identification of important migratory stopover regions - where Neotropical migrants repeatedly congregate during migration - is an essential part of any

migratory bird conservation plan (Bonter et al. 2009). However, conservationists have struggled with how to incorporate stopover habitat into the planning process (Mehlman et al. 2005).

A difficult obstacle ornithologists face is determining the link between an individual's breeding grounds and threats that may exist elsewhere during a bird's annual life cycle (Drake et al. 2014, Stanley et al. 2015). The strength of connectivity between breeding grounds, wintering grounds, and migratory routes is known as 'migratory connectivity' (McKinnon et al. 2013a, Fraser et al. 2013, Stanley et al. 2015, Finch et al. 2017). Our knowledge of migratory connectivity of songbirds has been limited due to their small stature and large geographic range in which they traverse (Wilson et al. 2008a, Stanley et al. 2015). The use of isotopic analysis provided researchers with the first major breakthrough into a songbird's migratory connectivity (Hobson and Wassenaar 1997); however, stable isotope analysis is unable to determine small-scale movements (McKinnon and Love 2018) and are restricted to linking individuals to vast geographic regions. Recent efforts have been able to quantify migratory connectivity through tracking technology (Heckscher et al. 2011, Ryder et al. 2011, Stanley et al. 2015, Finch et al. 2017). The results of these studies have answered many important ecological questions that are important for understanding migratory connectivity, thus conserving Neotropical migrants (McKinnon and Love 2018). Understanding migratory connectivity of a species is important in order to predict the response of migrants to environmental change (Taylor and Norris 2010). A major component needed for the conservation of Neotropical migrants is to determine which fall and spring stopover regions have the greatest effect on fitness of migrating birds (Stanley et al. 2015).

Recent advances in miniature tracking devices have allowed researchers to track individual songbirds across the Gulf of Mexico, Caribbean Sea, and through Central America

(Bayly and Gómez 2011, Heckscher et al. 2011, Stanley et al. 2012, Hobson and Kardynal 2015, Kardynal and Hobson 2017). One tracking method includes the use of archival light-level geolocators (hereafter, geolocators). Using geolocators, ornithologists are now able to observe the spatial and temporal migratory movements of individuals during their full annual cycle (Heckscher et al. 2017b). Geolocators have been successfully used to track Neotropical migrants during migration from North America to South America among a variety of different species (Stutchbury et al. 2009, Heckscher et al. 2011, Stanley et al. 2012, Fraser et al. 2012, McKinnon et al. 2013a). A major advantage of geolocators over other tracking devices (e.g., GPS archival tags, Motus Wildlife Tracking System) is that geolocators operate continuously, potentially providing daily location information about individuals across vast regions. As a result, geolocators are particularly useful for assessing the temporal aspects of avian migration (Heckscher et al. 2017b); however, precise location information can be difficult or impossible to obtain (McKinnon et al. 2013b).

The Veery is a forest-dependent Neotropical migrant that spends the boreal winter in South America (Heckscher et al. 2017a). I used Geolocator technology in combination with two spatial analysis techniques to quantify migratory “hotspot” locations of Veeries en route round-trip between the northeastern United States (Delaware and Massachusetts) and South America. Our objectives were to identify regions that were repeatedly visited by transient individuals over a multi-year period (i.e., migratory “hotspots”). Specifically, in order to provide insight into the annual cycle of Veeries, and therefore help assess the conservation and research priorities of this species, I used geolocator technology and spatial models to: (1) identify important spring and fall migratory stopover regions; (2) investigate seasonal-, age-, and sex-dependent differences in the

use of stopover regions. I also discuss the utility of the two spatial models in identifying regions of significant use (Kernel Density and Hotspot analysis).

2.2 Methodology

2.2.1 Study Area and Field Methods

157 geolocators were deployed on two distinct Veery breeding grounds found along the eastern USA. Geolocators were deployed (n=150) (British Antarctic Survey (MK10, MK12, and MK20 [2009-2010], n=43)), Lotek (MK5740C [2011], (n=22)), Migrate Tech (Intigeo-P65C-15 [2012-2017], (n=85)) on Veeries at White Clay Creek State Park, Delaware, USA (39.7382, -75.7598) (Figure 2.1) during the months May- July of 2009-2017. The Delaware study site consisted of hardwood forests of rolling hills and broad floodplains (50 – 105 m elevation) in the Mid-Atlantic Piedmont physiographic province (for more detail, see Heckscher 2004). In May 2017, our team also deployed seven geolocators (Intigeo-P65C2-11 [2017], (n=7) at a breeding site in North Adams, Massachusetts, USA (42.6806, -73.0913) (Figure 2.1). The North Adams, MA, study site is a heterogeneous second growth forest ranging from approximately 240-280 m elevation. The forest has a canopy dominated by Eastern white pine (*Pinus strobus*), American beech (*Fagus granifolia*), Sugar maple (*Acer saccharum*), White ash (*Fraxinus americana*), and Norway maple (*Acer platanoides*) as well as a dense understory comprised primarily of Honeysuckle (*Lonicera spp.*), Multiflora rose (*Rosa multiflora*), and Japanese Barberry (*Berberis thunbergii*).

Our research team captured adult Veeries using mist nets and banded each bird with one United States Geological Survey band and a unique color band combination. Birds were sexed, based on the presence of cloacal protuberance (CP) or brood patch (BP). Birds were then aged to either their second year (SY) or after-second year (ASY) (Pyle 1997), measured their mass with

a digital scale (0.1 g) and acquired standard morphological measurements. Archival light-level geolocators were attached to Veeries using the leg-loop method (Rappole and Tipton 1991) (Figure 2.2). Once outfitted with geolocators, Veeries were released. In the years following deployment, our team systematically searched for returning Veeries that possessed geolocators and set up mist nets in their corresponding territories. This approach was supplemented with passive constant-effort netting. Once the geolocators were recovered, a new unit was often deployed using the aforementioned method and the bird was released. See Heckscher et al. (2011, 2017b) for more detail.

2.2.2 Processing of Geolocator Data

I used the template fit method of estimating locations from light data to infer areas of high use during spring and autumn migration (Rakhimberdiev et al. 2017). Raw light-level data from geolocators were initially downloaded and decompressed using BASTRAK, INTIPROC 2.0, or INTIGeoIF software (Migrate Technology) to derive raw location data for individual Veeries. Raw light level data (.lig/.lux) files were analyzed in R (R Core Team 2018) initially with the TwGeos package (version 0.0-1, (Wotherspoon et al. 2016) and then the FlightR package (version 0.4.6, (Rakhimberdiev et al. 2017)), following the workflow outlined in the supplementary material from Rakhimberdiev et al. (2017). I chose a threshold level of 1.5 to identify sunrises and sunsets using the TwGeos package. The resulting twilights were automatically inspected and potential outliers were flagged using the twilightEdit function in TwGeos. The twilightEdit function was set to observe the eight surrounding twilights and would mark any twilight as an outlier if the time of twilight varied by more than 25 minutes. The potential outliers were then visually inspected and edited/deleted accordingly. The amount of potential outliers varied greatly between geolocators. Outliers are most likely caused by shading

events that occur throughout migration and their occurrences are dependent on the individual (McKinnon and Love 2018).

The geolocator data were calibrated using calibration periods that were visually determined using the `plot_slopes_by_location` function in FlightR (Rakhimberdiev et al. 2017). Veeries were assumed to have remained within their breeding grounds until there was a constant deviation in the estimated slope; therefore, calibration periods were assigned to dates in which the Veeries were known to be on their breeding grounds. Calibration of the geolocator occurs at both the beginning and ending of the track. The start periods began after geolocator deployment and continued until the individual was no longer on the breeding grounds. The ending calibration period was set to occur after the individual was known to arrive on the breeding ground and occurred until the unit was retrieved. Geolocators that did not possess a full annual track were calibrated only using the start calibration period. The benefit of calibrating the geolocator using both the start and end of the track limits the effect that opaqueness may have on the unit over time (Rakhimberdiev et al. 2017). I established a spatial probability mask in which Veeries are most likely to occur during their annual cycle based on their life history. Position estimates were limited to the region between -30° and 43° N and -105° and -40° W, an estimated range that tagged Veeries from the eastern breeding locations would occur based on their natural range (Heckscher et al. 2011, 2017a). The spatial grid was set to allow birds to fly over water; however, location estimates were highly unlikely to occur greater than 50 km away from the coast.

2.2.3 Importing to ArcMap

After the FLIGHTR model was performed, the median latitude and longitude of each location estimate for each day were exported to Microsoft Excel (Microsoft Office 2013, Version

15.0.5041.1001) as a comma delimited (.CSV) file (Kardynal and Hobson 2017). All of the FlightR outputs were combined into a single Microsoft Excel spreadsheet in which they were linked to the individual Veeries associated age, sex, and the attachment years of the geolocators from our banding records. This was then exported to ArcMap (ESRI 2018, version 10.6) as a single shapefile and then a Mercator projection was applied to them. The datasets for each individual bird were divided temporally and spatially into four categories autumn, spring, breeding, and wintering data. Autumn data was defined using the mean departure date from the breeding grounds (September 4th) and the mean arrival in South America (October 10th). Spring data was determined by the mean departure from South America (April 15th) and the mean arrival on the breeding grounds (May 3rd). All location estimates within the autumn and spring datasets that were $\geq 7^{\circ}\text{N}$ were removed from these datasets and included as wintering data. The 7°N cut off was chosen because it marks the location due north of the secondary wintering ground used by migratory Veeries (Heckscher et al. 2011). Breeding data encompassed all location estimates that fell between the mean arrival date on the breeding grounds and the mean departure date of the breeding grounds. Breeding data also included all data that was located at the breeding ground location to incorporate the fluctuation in arrival/departure date that occurred. For all Delaware breeding Veeries this included location estimates that were $\leq 39^{\circ}\text{N}$ and for Massachusetts breeding Veeries this included location estimates that fell between $\leq 43^{\circ}\text{N}$. Wintering and breeding data were then omitted from further analysis in order to focus on migratory movements. Location estimates were restricted by latitude in order to address the latitudinal error associated with geolocators and to ensure that the breeding grounds and wintering grounds were excluded from further analyses.

2.2.4 Kernel Density Estimation (KDE)

I used the Kernel Density Estimation tool (KDE) (ESRI 2018, ArcGIS version 10.6) which is typically used to analyze the location estimates from geolocators to derive the wintering and breeding grounds of songbirds (Hallworth et al. 2015). KDE are created using the location estimates derived by the geolocators to reveal areas of high density within the dataset. I calculated a magnitude-per-unit area from location estimates using the kernel density function in ArcMap (ESRI 2018, version 10.6). Stopover locations were estimated and mapped in ArcMap (ESRI 2018, version 10.6) using the kernel density tool (Pillar et al. 2016, Witynski and Bonter 2018). The default settings were used for the KDE except the search radius was set to 150km and the analysis was restricted to land. The data were displayed in ArcMap as polygons (ESRI 2018, version 10.6) displaying the predicted density values of location estimates at intervals of 50%, 60%, 70%, 75%, 80%, 85%, 90%, and 95% (Pillar et al. 2016, Witynski and Bonter 2018).

2.2.5 Optimized Hot Spot Analysis

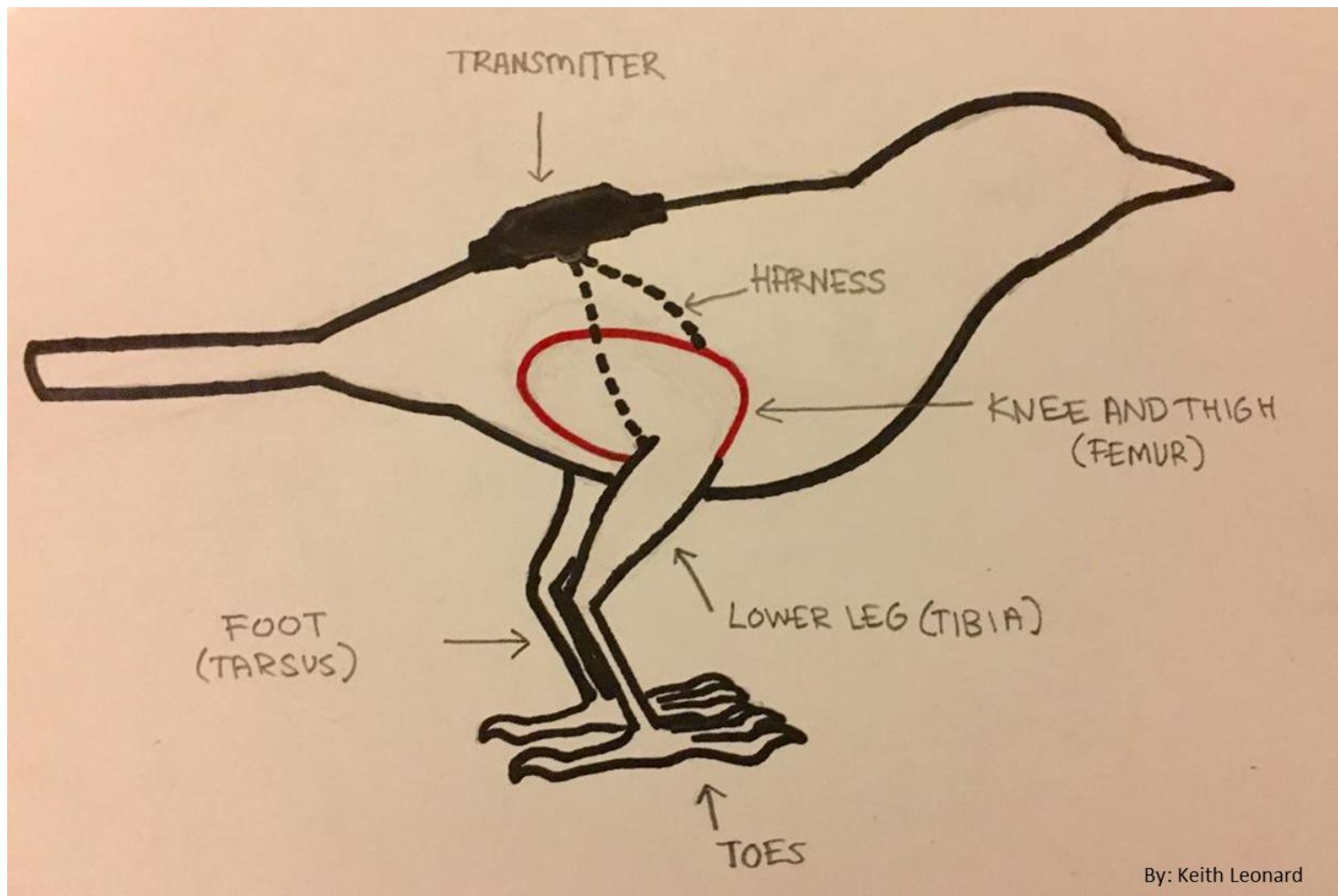
The Optimized Hot spot analysis performs a similar type of analysis, but also incorporates the global average of the data and derives areas that are statistically above/below the average. The optimized hot spot analysis calculates the Getis-Ord G_i^* statistic for each location estimate in the dataset (Ord and Getis 1995). The G_i^* statistic allows for the interpretation of the results to be inherently less subjective, compared to KDE. The statistically significant areas outlined by the G_i^* are areas of importance during migration. I identified statistically significant spatial clusters of high occurrence (hereafter, hot spots) and areas of below average occurrence or avoidance (cold spots) using the optimized hot spot analysis in ArcMap (ESRI 2018, version 10.6). Statistically significant hot spots were points that resulted in a z-score that was ≥ 1.96 ($\alpha = 0.05$). Regions that showed z-score of ≥ 2.58 ($p \leq 0.01$) were assumed to be areas in which

Veeries frequently stopover. The optimized hot spot analysis also identified areas that were used significantly less by Veeries during migration - regions that are revealed to have a z-score ≤ -1.96 were categorized as cold spots ($\alpha = 0.05$). The resultant points from the hot spot analysis were then input into the Empirical Bayesian Kriging tool in ArcGIS (ESRI 2018, version 10.6) which is an interpolation method that accounts for the error in spatial clusters through repeated simulations. The Z-score from the optimized hot spot analysis was used as the value field in the interpolation. The default settings of the Empirical Bayesian Kriging tool were used, except the analysis was restricted to land.

Figure 2.1 – The location of the Veery (*Catharus fuscescens*) breeding sites at White Clay Creek State Park, Delaware, USA (39.7382, -75.7598) and at North Adams, Massachusetts, USA (42.6806, -73.0913). Banding operations occurred from May – July.



Figure 2.2 – A diagram depicting the attachment of archival light-level geolocators on a songbird using the Rappole-Tipton leg loop harness. The dotted line represents the harness which was comprised of waxed nylon string (2009 – 2015) and Stretch Magic® jewelry cord (2016-2018). The total weight of the unit and harness combined cannot exceed $\geq 3\%$ of the individuals body weight.



2.3 Results

2.3.1 Recovery of Geolocators

During the length of this study, our team recovered 59 of the 157 (38%) deployed geolocators. Of the 59, 19 (32%) were from females. Eleven geolocators were recovered from birds that were known to be in their second year (SY) (19%) and 47 from birds aged as after-second year (ASY). Of the 59 geolocators recovered, 12 were recovered from repeat trackers (birds tracked in two separate years) which resulted in two annual cycles of data including two units that had remained on an individual for two consecutive years. One additional bird was tracked for three consecutive years. This resulted in a total of 47 Veeries with recovered units revealing 61 annual trips. During the 2011 (n=8), 2016 (n=1), 2017 (n=1), and 2018 (n=1) seasons there were 11 geolocators recovered that did not record for the full annual cycle. Those geolocators all stopped recording data before April and did not provide us with any spring migration data, but autumn data were used for further analyses. Of the 59 geolocators successfully recovered, I was unable to analyze one of the units recovered from a female that contained 2 years of data. This unit could not be analyzed due to extreme shading events during the calibration period, most likely because of dense vegetation, the individuals nesting behavior, or because the geocator light stalk had fallen below the bird's feathers (Lisovski et al. 2012)

2.3.2 Kernel Density Estimation vs. Hot Spot Analysis

Using all spring and autumn estimates not filtered out by the latitude restriction, I used kernel density estimation (KDE), which revealed areas that have high Veery abundance during migration (Figure 2.3(A)). The KDE showed that most of Florida possessed an overall density > 50%, while there is a small density pocket in north-central Florida that falls between 90-95% along with an area of southwestern Florida that revealed a density between 80-85%. Eastern and

Western Cuba both had a density that is $> 50\%$ and increases to $> 95\%$ approaching the western end of the island. KDE showed that the northeastern part of the Yucatán peninsula possessed a density of 50-80%. The island of Hispaniola had a density within the 50-60% range on the eastern and western parts of the island. The east coast of Costa Rica, Honduras, and Nicaragua had densities $> 50\%$ while there are two areas that reached 90% along the borders of Honduras and Nicaragua as well as the borders of Nicaragua and Costa Rica.

The optimized hot spot analysis elucidated several areas that are statistically significant based on a Z-score ≤ -1.96 or ≥ 1.96 (Figure 2.3(B)). There are two very small areas in northwestern Florida, eastern Hispaniola, and western Cuba that was shown to be areas of interest during migration ($1.96 < z < 2.58$, $0.01 < p < 0.05$). The Yucatán Peninsula falls out as an area of extreme importance ($z \geq 2.58$, $p \geq 0.01$). The eastern coast of Nicaragua was also shown to be a statistically significant area ($z \geq 2.58$, $p \geq 0.01$). This trend of significance extended into Honduras and Costa Rica revealing their importance as well ($1.96 < z < 2.58$, $0.01 < p < 0.05$). The only statistically significant cold spot (i.e., significant low activity) revealed in South America was the area surrounding Lake Maracaibo in western Venezuela and continuing west into northern Columbia ($-1.96 < z < -2.58$, $0.01 < p < 0.05$).

2.3.3 Seasonal effects

2.3.3.1 Autumn Migration

No major stopover regions were identified in North America during fall migration (Fig. 2.4). Western Cuba and the northern tip of the Yucatán Peninsula were important stopover regions ($z > 2.58$, $p > 0.01$). The area ranging from Honduras to Costa Rica appears to be an important migratory bottleneck ($z > 2.58$, $p > 0.01$). The northern coast of Honduras ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$) does not appear to be as important as the Caribbean coast ($z > 2.58$, $p >$

0.01). The island of the Dominican Republic experienced increased Veery activity on the east and western coasts during fall migration ($1.65 < z < 1.96$, $0.06 \leq p < 0.10$), while the eastern side of the island shows significant use ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). Two areas appear to have a lower frequency of stopover activity, central Cuba and several areas surrounding Lake Maracaibo in Colombia ($-1.96 < z \leq -2.58$, $0.01 \leq p < 0.05$).2.3.3.2 Spring Migration

During spring migration, there were no areas found in North America that deviated from the mean density in the study range (Fig. 2.5). The Azuero Peninsula in Panama and a small area along the north-central Venezuela coast were heavily utilized during spring migration ($z > 2.58$, $p > 0.01$). The area surrounding those locations (~150 km) were also statistically significant ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). The Yucatán peninsula is an area of importance during northward migration ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). The Lesser Antilles also appears to be an important migratory corridor ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). Two areas appear to have decreased activity during spring migration, western Hispaniola and the area southwest of Lake Maracaibo in Colombia ($-1.96 < z \leq -2.58$, $0.01 \leq p < 0.05$).

2.3.4 Age Effects

2.3.4.1 After-Second Year Birds

For ASY birds, the west-central coast of Florida north towards the Florida-Georgia line including surrounding areas inland (~ 150 km) were revealed as a potential hot spot ($1.65 < z < 1.96$, $0.06 \leq p < 0.10$; Fig. 2.6). Nicaragua south towards Costa Rica is another significant migratory corridor for ASY birds ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). The Nicoya Peninsula in Costa Rica and a small area in central Nicaragua were also frequently visited ($z > 2.58$, $p > 0.01$). The Eastern portion of Hispaniola was shown to be a significant hot spot for ASY birds ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). Northeastern Mississippi into northwestern Alabama was

shown to be an area that had potentially decreased activity by ASY birds ($-1.96 \leq z < -2.58$, $0.01 < p \leq 0.05$). The only potential cold spot trending towards significance in South America ($-1.96 < z \leq -2.58$, $0.05 \leq p < 0.10$) was surrounding Lake Maracaibo.

2.3.4.2 Second Year Birds

There were no areas revealed in North America in which the incidence of location estimates of SY birds occurred at an above average rate (Fig. 2.7). The majority of the Yucatán Peninsula into Belize was shown to be an area of disproportionate high use ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). The coast of Honduras and central Nicaragua were found to be a potentially important migration corridor ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). The eastern coast of Cuba is an area of interest and experienced increased activity ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). Interior North Carolina, South Carolina and Georgia showed below average activity for SY birds ($-1.96 \leq z < -2.58$, $0.05 \leq p < 0.10$). The southern coast of Mexico bordering the Pacific Ocean was also an area of below average occurrence ($-1.96 < z \leq -2.58$, $0.05 \leq p < 0.10$). 2.3.5 Sex Effects

2.3.5.1 Female Migration

Migrating females congregated in central Florida ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$), particularly along the northwest coast ($z > 2.58$, $p > 0.01$) (Fig. 2.8). Nicaragua and Costa Rica showed significantly high use by females during migration ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$), while the Nicoya Peninsula in Costa Rica and a small area in central Nicaragua were more frequently visited than surrounding areas ($z > 2.58$, $p > 0.01$). Only two areas resulted in potential cold spots: northeastern Mississippi and northwestern Alabama, and the area directly south of Lake Maracaibo in Colombia ($-1.65 < z \leq -1.96$, $0.05 < p \leq 0.10$).

2.3.5.2 Male Migration

Using only location estimates derived from male Veeries no areas in North America occurred in which the incidence of location estimates deviated from average (Fig. 2.9). The majority of the northern Yucatán Peninsula was shown to be an area of very high use ($z > 2.58$, $p > 0.01$). The coast of Honduras and Nicaragua was an area of importance ($z > 2.58$, $p > 0.01$) while inland areas (~300km) were slightly less utilized by migrating males ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). Panama was a migratory corridor for males ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). Western Cuba and the eastern Dominican Republic were also used by male Veeries at an above average rate ($1.96 \leq z < 2.58$, $0.01 < p \leq 0.05$). There was only one area that experienced a significantly lower than average use the area directly west of Lake Maracaibo in Colombia ($-1.96 < z \leq -2.58$, $0.05 < p \leq 0.01$).

Figure 2.3 - Areas of above and below average Veery (*Catharus fuscescens*) use during migration (2009 – 2018) as determined by two different methods. (A) Geolocator derived location estimates displayed as kernel density estimates (KDE) at increasing increments >50% of Veeries during migration. Probability of occurrence increases from orange to red indicating that there is a greater density of location estimates in these areas. (B) Hot spot analysis showing areas of statistical significance based on their corresponding z-score during migration. A significant negative z-score indicates that that location is part of a low-value (below average) cluster (cold spot, z-score < -1.96, $p < 0.05$), whereas a significant positive z-score indicates that the location is part of a high-value (above average) cluster (hot spot, z-score > 1.96, $p < 0.05$). Areas highlighted in dark red are areas with a significantly high z-score while areas in blue have a significant low z-score. Areas in beige have no significance.

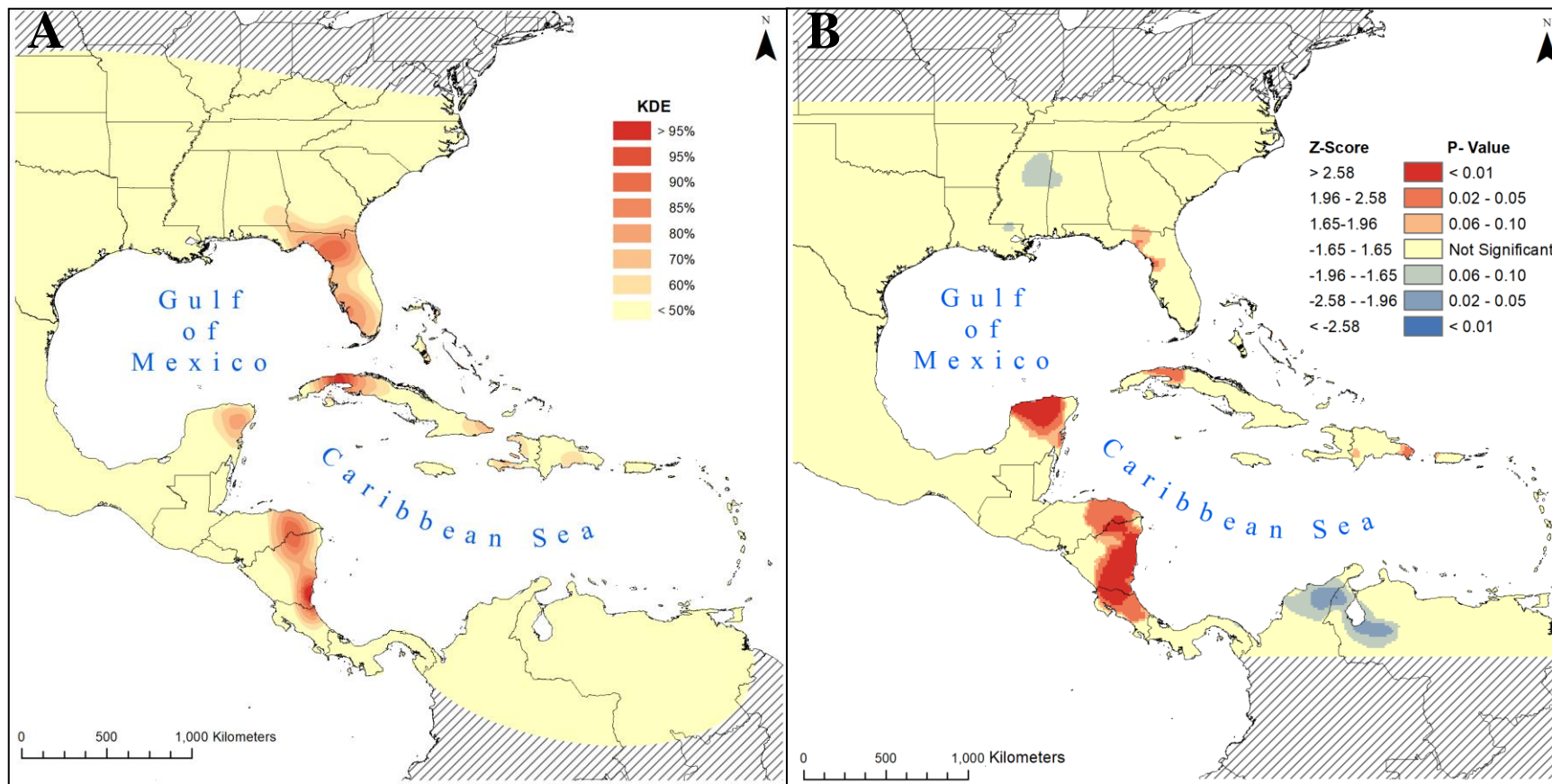


Figure 2.4 - Areas of above and below average Veery (*Catharus fuscescens*) use during autumn migration (2009-2017) as determined by the optimized hot spot analysis. A significant negative z-score indicates that the location is part of a low-value (below average) cluster (“cold spot”, z-score < -1.96 , $p < 0.05$), whereas a significant positive z-score indicates that the location is part of a high-value (above average) cluster (“hot spot”, z-score > 1.96 , $p < 0.05$). Areas highlighted in dark red are areas with a significantly high z-score while areas in blue have a significant low z-score. Areas in beige have no significance.

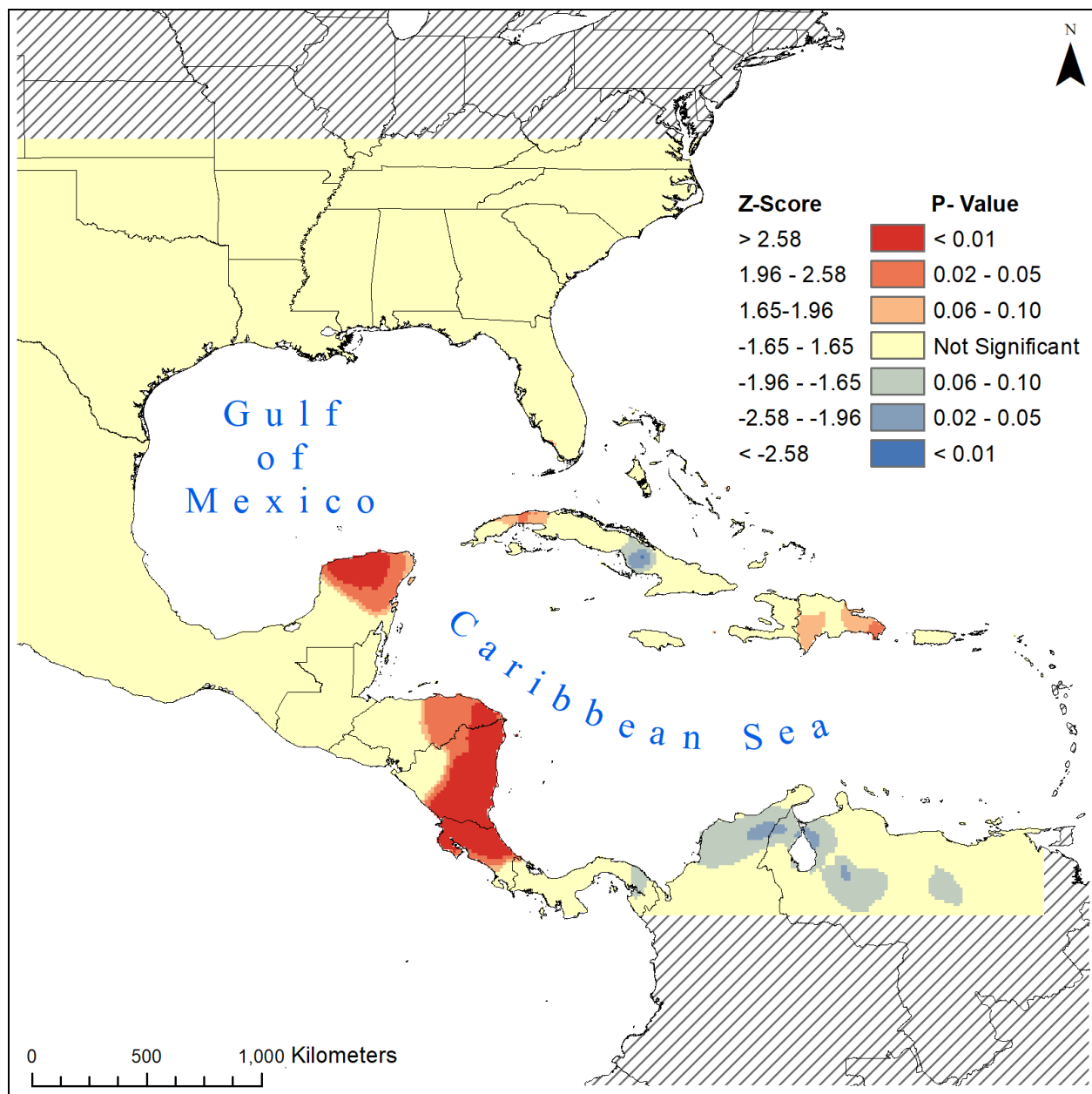


Figure 2.5 - Areas of above and below average Veery (*Catharus fuscescens*) use during spring migration (2010-2018) as determined by the optimized hot spot analysis. A significant negative z-score indicates that the location is part of a low-value (below average) cluster (“cold spot”, z-score < -1.96 , $p < 0.05$), whereas a significant positive z-score indicates that the location is part of a high-value (above average) cluster (“hot spot”, z-score > 1.96 , $p < 0.05$). Areas highlighted in dark red are areas with a significantly high z-score while areas in blue have a significant low z-score. Areas in beige have no significance.

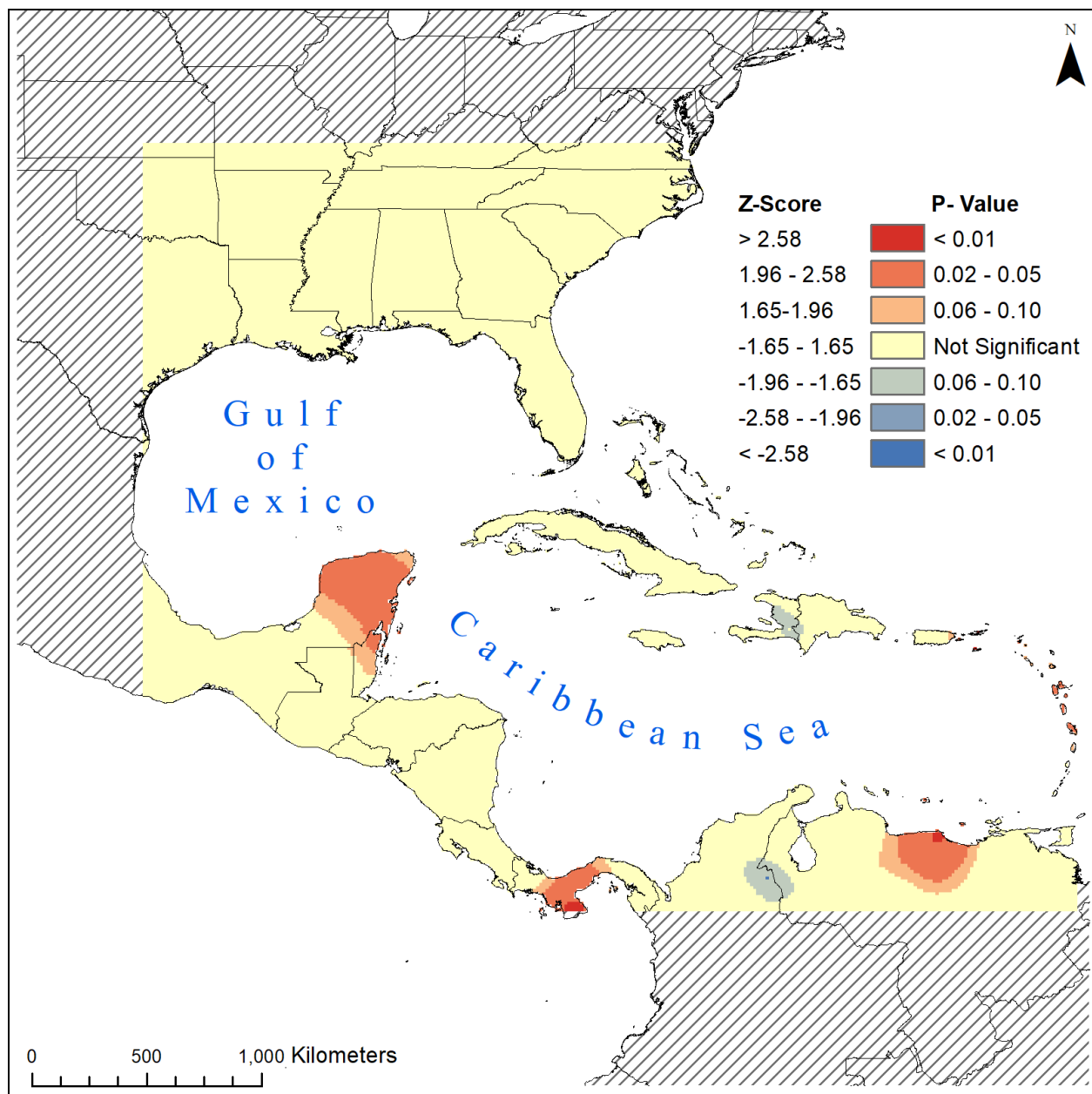


Figure 2.6 - Areas of above and below average ASY Veery (*Catharus fuscescens*) use during migration (2009 – 2018) as determined by the optimized hot spot analysis. A significant negative z-score indicates that the location is part of a low-value (below average) cluster (“cold spot”, z-score < -1.96 , $p < 0.05$), whereas a significant positive z-score indicates that the location is part of a high-value (above average) cluster (“hot spot”, z-score > 1.96 , $p < 0.05$). Areas highlighted in dark red are areas with a significantly high z-score while areas in blue have a significant low z-score. Areas in beige have no significance.

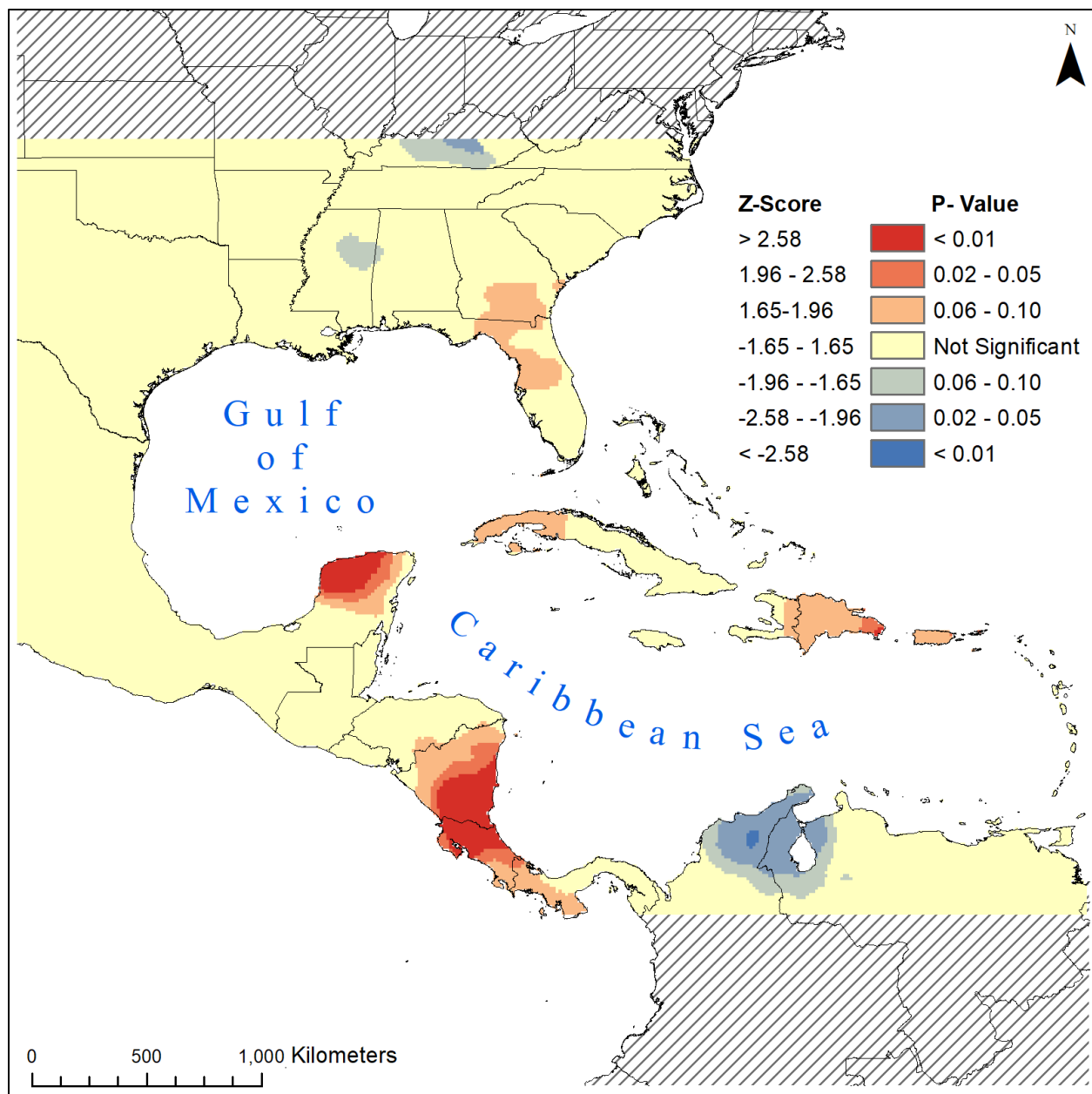


Figure 2.7 - Areas of above and below average SY Veery (*Catharus fuscescens*) use during migration (2009 – 2018) as determined by the optimized hot spot analysis. A significant negative z-score indicates that the location is part of a low-value (below average) cluster (“cold spot”, z-score < -1.96 , $p < 0.05$), whereas a significant positive z-score indicates that the location is part of a high-value (above average) cluster (“hot spot”, z-score > 1.96 , $p < 0.05$). Areas highlighted in dark red are areas with a significantly high z-score while areas in blue have a significant low z-score. Areas in beige have no significance.

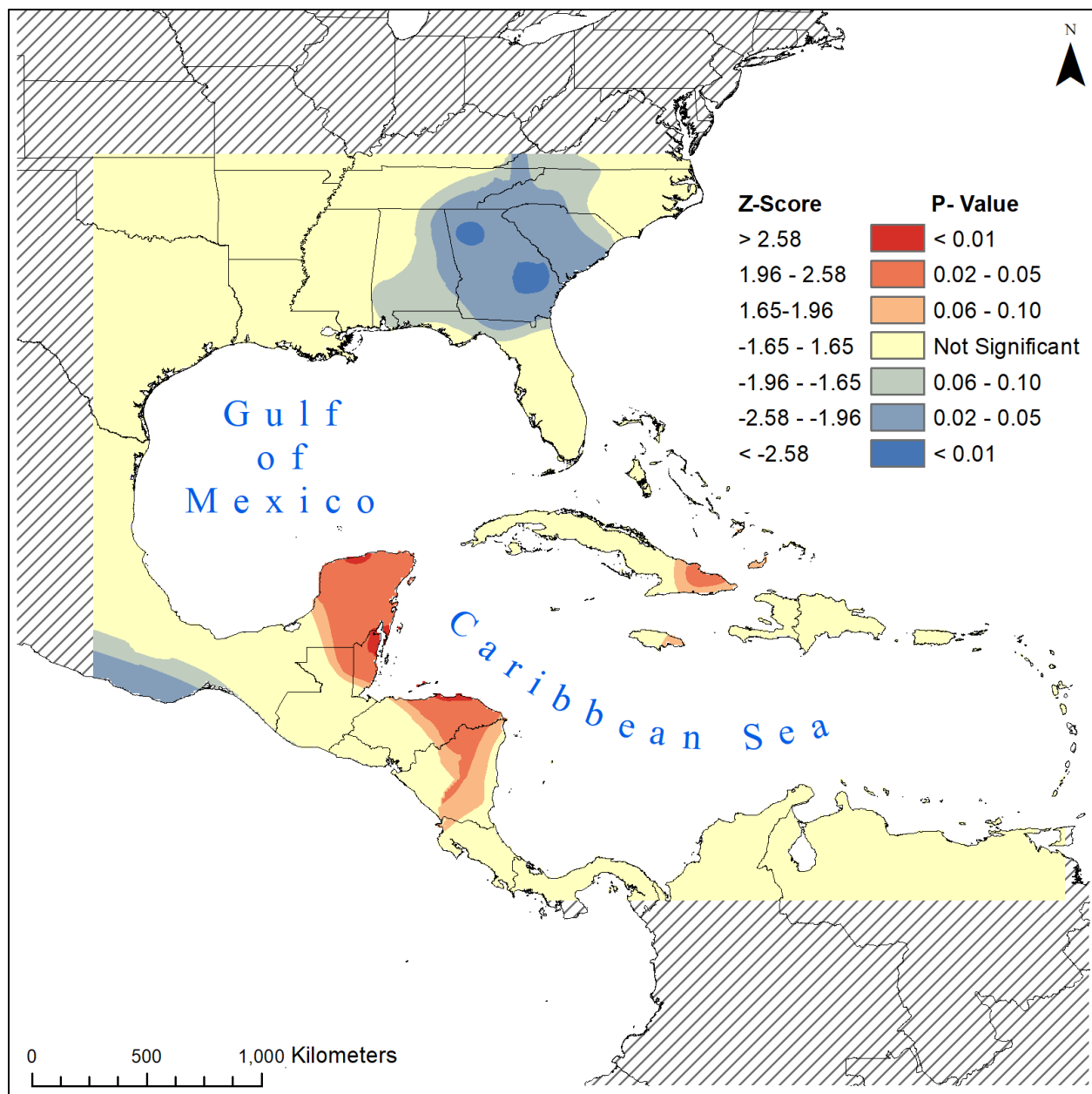


Figure 2.8 - Areas of above and below average female Veery (*Catharus fuscescens*) use during migration (2009 – 2018) as determined by the optimized hot spot analysis. A significant negative z-score indicates that the location is part of a low-value (below average) cluster (“cold spot”, z-score < -1.96 , $p < 0.05$), whereas a significant positive z-score indicates that the location is part of a high-value (above average) cluster (“hot spot”, z-score > 1.96 , $p < 0.05$). Areas highlighted in dark red are areas with a significantly high z-score while areas in blue have a significant low z-score. Areas in beige have no significance.

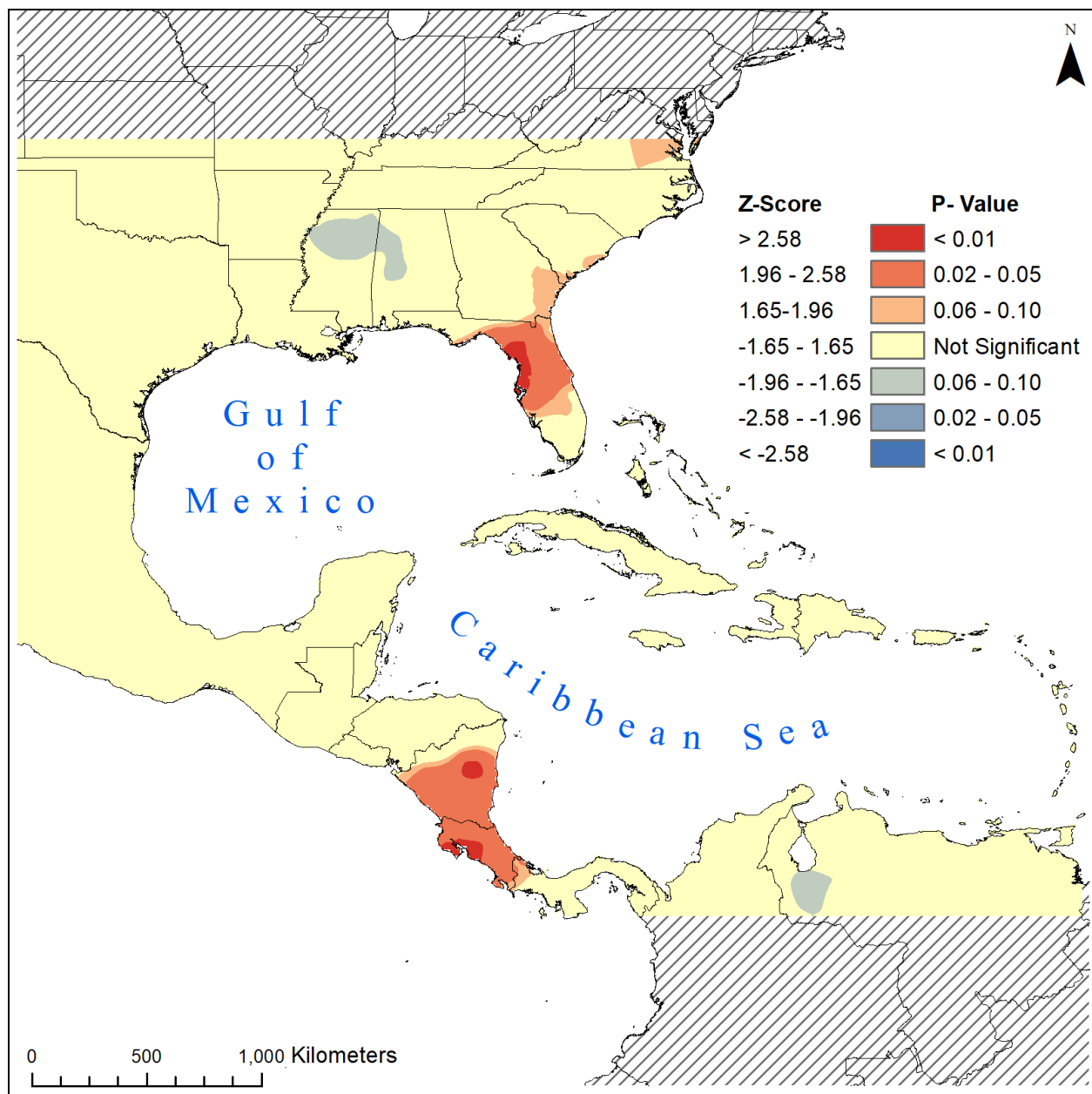
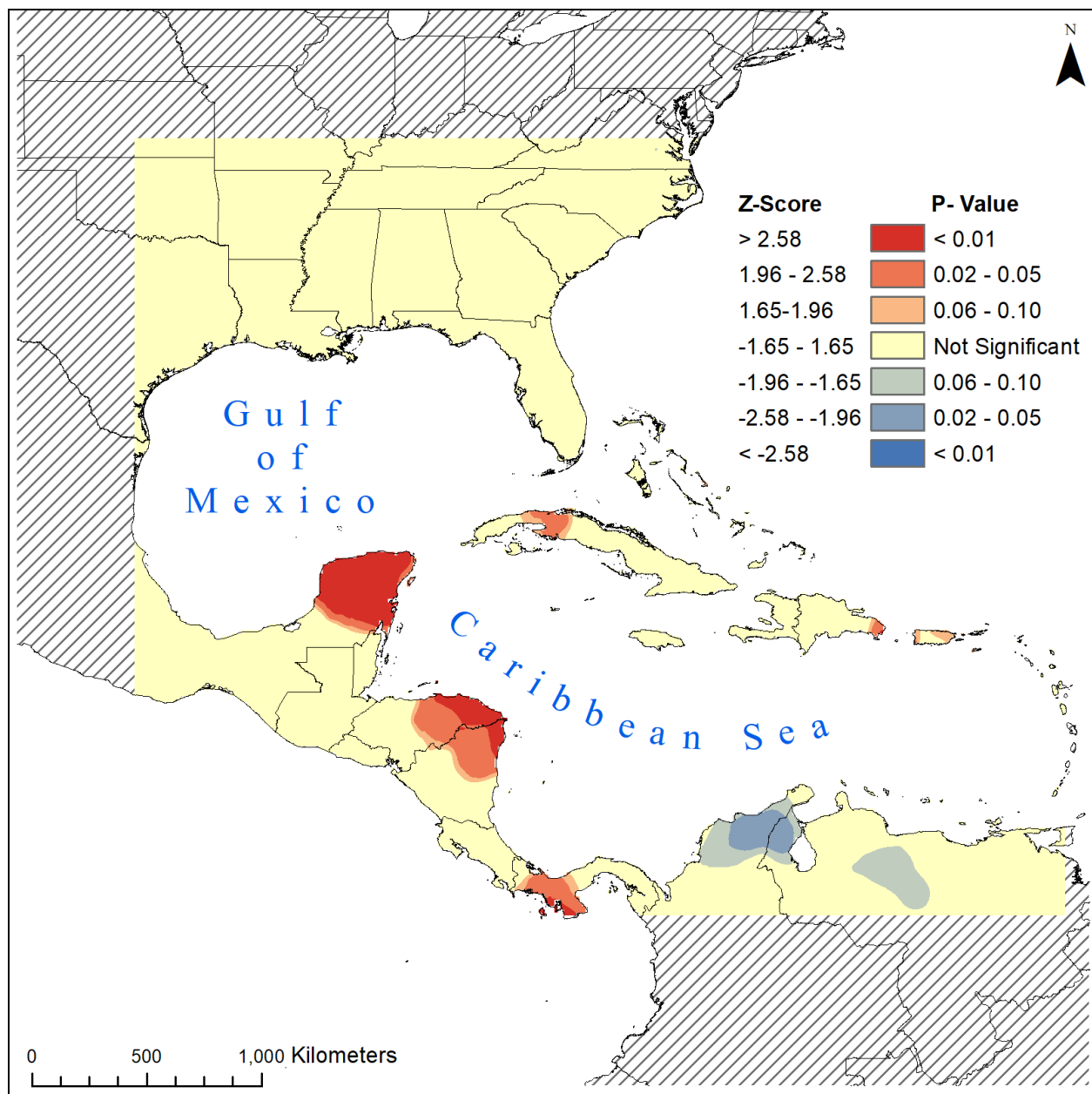


Figure 2.9- Areas of above and below average male Veery (*Catharus fuscescens*) use during migration (2009 – 2018) as determined by the optimized hot spot analysis. A significant negative z-score indicates that the location is part of a low-value (below average) cluster (“cold spot”, z-score < -1.96 , $p < 0.05$), whereas a significant positive z-score indicates that the location is part of a high-value (above average) cluster (“hot spot”, z-score > 1.96 , $p < 0.05$). Areas highlighted in dark red are areas with a significantly high z-score while areas in blue have a significant low z-score. Areas in beige have no significance.



2.4 Discussion

2.4.1 Comparing Kernel Density Estimation to Optimized Hot Spot Analysis

I tracked individual Veeries from two geographically separate breeding populations in eastern North America and used two complementary methods to reveal important migratory stopover regions for this species. Specifically, the hot spot analysis revealed several locations that had a statistically significant deviation from the average density based on their z-score. Similarly, areas revealed to have a greater than 50% density derived by the KDE were assumed areas of increased stopover use and therefore they were considered important concentration areas during migration (Pillar et al. 2016, Witynski and Bonter 2018). Thus, notably, both methods highlight the same general areas as important stopover regions (Figure 2.3). Areas in which there were an increased number of location estimates (hot spots) are assumed to be areas that are ecologically important to Veeries during migration. While areas in which there was an absence of location estimates or very sparse were assumed to be a cold spot or areas that are not optimal for migrating Veeries. The optimized hot spot analysis provided us with the ability to identify regions that deviate significantly from the average occurrence of Veeries during migration. The ability to identify statistically significant hot spots, as well as cold spots, provides us with insight into the regions that are most important for this species and perhaps other Neotropical migrants. The long-term monitoring of the Delaware breeding population and the recent addition of the Massachusetts breeding population may contribute to our understanding of regional migratory behavior of eastern breeding Veeries. Hobson and Kardynal (2017) tracked Veeries from western North America and found that these birds migrated using an ancestral migratory route. Therefore, it is likely the results south of 30°N also apply to western Veery populations.

2.4.2 Stopover Regions

2.4.2.1 *Florida*

The focus of the majority of the migratory bird studies surrounding the Gulf of Mexico have been along the western and central coasts (Lowery Jr 1946, Stevenson 1957, Moore et al. 1990, 2010, Simons et al. 2000) only a few studies have shown the ecological importance of the eastern Gulf Coast (Gutierrez Ramirez 2016, Kneidel 2016, Mancuso 2017). The Apalachicola River Basin has been identified as an important migratory route for Neotropical migrants (Heckscher et al. 2011, Stanley et al. 2012) and our KDE analysis is in support of this, as there appears to be a trend of increased density following the Apalachicola River (Figure 2.3(A)). Contrary to the KDE results, this area was not identified as an important stopover region by the hot spot analysis (Figure 2.3(B)); however, our analyses identified two nearby areas along the western coast of Florida as potentially important stopover regions. Utilizing weather surveillance radars, Lafleur et al. (2016) suggested that areas with dense forests within proximity of the Gulf Coast may provide suitable stopover locations for Neotropical migrants. Both areas identified along coastal Florida coincide with areas that contain wildlife management areas that have intact forests. The hot spot further north encompasses the St. Marks National Wildlife Refuge. This stopover region is also within 200km of the Apalachicola River Basin, which is in the margin of the latitudinal error associated with geolocators (McKinnon et al. 2013a), suggesting that birds within our study may use this region as an important stopover site as previously suggested (Heckscher et al. 2011, Stanley et al. 2012). The area farther south along the coast incorporates Chassahowitzka Wildlife Management Area and the Citrus Wildlife Management Area. Our findings reinforce the initial assertion of Lafleur et al. (2016) who concluded the importance of densely forested areas found along the Gulf coast.

2.4.2.2 The Yucatán Peninsula

The Yucatán Peninsula is thought to be an extremely important stopover region for Neotropical migrants (Gauthreaux et al. 1999, 2006, Bayly et al. 2018). This is partly because, for southbound trans-Gulf migrants facing adverse weather conditions, the Yucatán Peninsula is often the first available landfall (Gauthreaux et al. 1999, Deppe et al. 2015, Cohen et al. 2017). Geolocator data from three different breeding populations of Veery have now shown birds using the northern portion of the Yucatán Peninsula during migration (Heckscher et al. 2011, Hobson and Kardynal 2015, Kardynal and Hobson 2017). In addition to the evidence provided by geolocator data, the occurrence of Veeries in the Yucatán peninsula has been revealed by a collection of museum specimens (Macouzet and Escalante-Pliego 2013). Cumulatively, these studies demonstrate the overall importance of this region, not only to our breeding populations of Veeries, but also for Neotropical migrants in general.

2.4.2.3 Northern Central America (Nicaragua and Honduras)

Parker (1994) proposed that the area from northern Honduras towards northwestern Nicaragua was crucial to the successful migration of Neotropical migrants. The KDE and hot spot analysis corroborated this assertion for migrating Veeries, suggesting that this region is important for Neotropical migrants. This conclusion is further supported by additional studies that claimed the Caribbean facing slopes of the Nicaragua and Honduras region possess a high density of migrants compared to nearby areas (Welton et al. 2012, Callo et al. 2013).

2.4.2.4 Cuba

Cuba has been hypothesized to be an area of ecological importance for migrating land birds (Bayly et al. 2018). However, most analyses of the ecological importance of Cuba have been done by incorporating remote sensing technologies (Cohen et al. 2017). Brenner et al.

(2016) conducted a threat analysis incorporating several anthropogenic and environmental factors across the Gulf of Mexico region. That analysis concluded that the least disturbed area in Cuba was found along the western coast (Wildlife Conservation Society - WCS 2005), which aligns with the location highlighted by our study as an important stopover region. Other studies utilizing geolocators have identified Cuba as a stopover site for migrating Veeries (Heckscher et al. 2011, Hobson and Kardynal 2015, Kardynal and Hobson 2017). Due to recent collaborations with Cuban scientists, ornithologists are beginning to learn the true ecological value that Cuba provides for Neotropical migrants (Boom 2012). Analyses have identified the area of western Cuba as an important stopover region, which has also been identified as an important stopover site for other Neotropical migrants (González et al. 2006, Brenner et al. 2016).

2.4.2.5 Southern Central America (Costa Rica and Panama)

Our study identified the Caribbean coast of Costa Rica as a critical stopover region during the migration of Veeries. It is hypothesized that lower Central America acts as a migratory bottleneck for land dwelling Neotropical migrants, and birds that make landfall in northern Central America likely continue through Central America funneling through the Darién Gap of Panama and Colombia (Bayly et al. 2018). A study by Wilson et al. (2008b) at a stopover site in Costa Rica, confirmed high densities of Swainson's Thrush (*Catharus ustulatus*) during migration; however, that study reported a low recapture rate (~2%) suggesting birds did not stopover. These findings were corroborated by a different study by Wilson et al. (2008a) that concluded that the fat reserves carried by Swainson's Thrush at the same study location were well above the amount needed to continue their migration. These results suggest that Costa Rica and Panama should be categorized as a "bottleneck" (c.f. Bayly et al. 2018) for Neotropical Migrants. However, our findings identified only Costa Rica as an area of importance during

migration, although there is a small region that was approaching significance around the Gulf of Montijo, suggesting that Panama is also a migratory bottleneck (c.f. Bayly et al. 2018; Mehlman et al. 2005). Rogers and Odum (1966) hypothesized that Panama was an essential stopover region during migration because of the emaciated state of the birds arriving there during migration; however, it has been shown that birds facing inclement weather during migration stopover with depleted fuel supplies (Kneidel 2016). These findings suggest that Neotropical migrants may utilize the surrounding regions such as: Honduras (Johnson and Winker 2008), Nicaragua (Callo et al. 2013), or northern Colombia (Bayly et al. 2012) as major refueling sites depending on the timing of migration.

2.4.2.6 Hispaniola

Studies focusing on the stopover behavior of Neotropical migrants within Hispaniola are extremely rare (Bayly et al. 2018). The occurrence of Veeries on the Dominican Republic was confirmed by the North American Breeding Bird Survey (BBS), which assessed population trends of Neotropical migrants during migration (Robbins et al. 1989). Our study emphasized the southwestern and the eastern coast of the Dominican Republic as important stopover regions for migrating Veeries. The areas that are highlighted by our analysis encompass four protected areas in the Dominican Republic that are known to have high avian biodiversity: Laguna de Cabral Scientific Reserve, Del Este National Park, Sierra de Bahoruco National Park, and Jaragua National Park (Latta 2005). During the boreal winter, the protected areas mentioned above have been shown to host a wide array of Neotropical migrants (Wunderle and Waide 1993, Latta et al. 1999, Latta 2005).

2.4.2.7 Northern Venezuela

During spring migration there is a statistically significant hot spot located in north central Venezuela along the Caribbean Sea coast (Figure 2.5). This region encompasses El Avila and Guatopo National Parks, and appears to be an important launching point for northbound Veeries preparing to cross the Caribbean Sea. This region most likely provides northbound Veeries with an essential stopover region to gain an adequate fuel load before encountering their first migratory barrier. This launching point enables the individuals to take different routes while undergoing their spring migration. From this important stopover region, Veeries may navigate through the Antilles, Cuba, Central America, or the Yucatán Peninsula before traversing the Gulf of Mexico (c.f. Heckscher et al. 2011, Hobson and Kardynal 2015, Kardynal and Hobson 2017). This area may give Veeries flexibility in deciding which route north will be ideal perhaps dependent upon weather patterns at the time. This may explain why this area is a migratory hotspot prior to northbound migration across the Caribbean Sea and Gulf of Mexico.

2.4.3 Cold Spots

Cold spots may be caused by a variety of environmental factors. Factors such as urbanization, xeric environments, and increased elevation may be responsible for the avoidance of this area. The area surrounding Lake Maracaibo was an area that consistently had significantly below average occurrence of migrating Veeries except for SY birds (Figure 2.7). Cordillera de Mérida and the Cordillera Oriental, two major mountain ranges found in this area, were revealed as the most significant cold spots in the study area. Both of the cold spots increase in significance while approaching the highest peaks of the mountain ranges (>5,000 meters elevation), suggesting that the Veeries are avoiding traversing areas of high elevation. This hypothesis is supported from the findings of Gómez (2015) in which they concluded that species richness

during migration was lower at higher elevations >2000 meters than at lower elevations < 500 meters. Within a two-year study in the Sierra Nevada de Santa Marta, only two Veeries were observed, and both were sighted at the lowest elevation range (Gómez et al. 2015). This trend continues into North America in which some of the cold spots (Figure 2.7) can be explained by the presence of the high elevations in the Appalachian Mountains. Other areas of below average use that were revealed in North America, such as northeastern Mississippi, appear to correlate with increased urbanization and decreased forest density. Veeries have been known to gravitate towards forested areas on their breeding grounds (Heckscher et al. 2017a). Little is known about their habitat requirements during migration. Neotropical migrants appear to avoid urban areas while selecting breeding grounds (Pennington et al. 2008), but are assumed to stopover in urban areas that are perceived to have a high amount of tree cover while en route (Petit 2000).

Although small urban areas have been found to be beneficial to migrating birds (Mehlman et al. 2005, Bonter et al. 2009), these fragmented stretches of forests may increase their vulnerability to predators as well increase their likelihood of flying into manmade structures (Crawford and Engstrom 2001, Erickson et al. 2005).

2.4.4 Seasonal Effect

Geolocator technologies have shown that Neotropical migrants take varying routes during spring and fall migration (Bayly and Gómez 2011, Delmore et al. 2012, Stanley et al. 2012, Cohen et al. 2017, Kramer et al. 2017). During the spring migration birds are more likely to fly directly over the Gulf of Mexico (Stanley et al. 2012), which may reflect the urgency for the individual to arrive on their breeding ground. Early arrival of males to their breeding site increases their chances of securing high quality territory (Aebischer et al. 1996, Lozano et al. 1996, Kokko 1999, Smith and Moore 2005), thus increasing their chances of attracting a high

quality mate resulting in greater success while rearing offspring (Rowe et al. 1994, Lozano et al. 1996). Although females have been shown to arrive at the breeding grounds later than males (Seewagen et al. 2013, Heckscher et al. 2017b), the arrival time may also benefit their reproductive success (Smith and Moore 2005). The early arrival of females provides them with more opportunities to choose a mate or territory compared to the females that arrive later in the season (Bensch and Hasselquist 1992). Females who arrive early have been known to experience higher breeding success (Rowe et al. 1994) and have the ability to reneest if the first fails (Bensch and Hasselquist 1992). The reproductive advantages of arriving at the breeding grounds may explain the variations observed between fall and spring stopover regions. An accelerated spring migration has been documented for Veeries in multiple studies (Heckscher et al. 2011, Hobson and Kardynal 2015, Kardynal and Hobson 2017) and is corroborated by this study. During the fall migration, Veeries appear to favor a more Caribbean based (i.e. island hopping) route (Hobson and Kardynal 2015), suggesting that they do not have the same sense of urgency as they do during spring migration. Weather may be the leading cause of the variation in seasonal stopover locations and may be associated with the individuals' ability to avoid increased tropical storm activity and adjust their migratory route accordingly (Heckscher 2018). The Yucatán peninsula appears to be an area of importance for Neotropical migrants for the fall and the spring. This is most likely because it is the last piece of land that northbound migrants will see before they cross the Gulf of Mexico and conversely for southbound migrants it is the first land opportunity for landfall after crossing the Gulf. The Yucatán peninsula is the only major stopover site found in this study that is used during both fall and spring migration. There are substantial differences between fall and spring stopover locations in Northern Central America for Neotropical migrants (Bayly and Gómez 2011). Panama was identified as an important

stopover region for northbound Veeries, which align with other *Catharus* species that also utilize Panama during spring migration (Delmore et al. 2012). The long stopovers in this region could function as important refueling sites prior to crossing the Gulf of Mexico (Bayly et al. 2012, Delmore et al. 2012). The strategy is slightly different during the fall migration in which *Catharus* species have been found to use stopover locations further south in Honduras (Delmore et al. 2012).

2.4.5 Age Effect

The higher abundance of younger birds present along coastal environments is known as the “coastal effect” (Ralph 1981). This phenomena is further explained by Woodrey and Moore (1997) as they concluded that ASY birds typically stopped farther inland than SY birds that primarily stopped along the coast. These findings were in support of Leberman and Clench (1972) who hypothesized that migratory routes would vary depending on the age class of the birds in questions. Due to the spatial error associated with geolocators, it is not possible to assess if this trend is present within this study.

A fall migratory study focused on coastal Alabama assessed the age dependent effect of the birds’ fat load, stopover length, and rate of mass change for Neotropical migrants and concluded that adults typically carried more fat than younger birds, therefore they were better prepared energetically to cross the Gulf of Mexico (Woodrey and Moore 1997). This is most likely the result of an adult bird’s ability to gain energy quickly, which possibly allows for a different migration strategy taken by the inexperienced younger birds (Wunderle 1991). It has been shown that the rate at which an individual refuels can affect the rate in which migration is completed (Gómez, et al. 2014). A higher rate of migration by ASY birds may also be responsible for the use and timing of arrival at stopover regions (González-Prieto et al. 2011).

Our study revealed a greater amount of potentially important stopover regions during the migration of SY birds (Figure 2.7) than their older counterparts (Figure 2.6), this is most likely due to their inexperience replenishing fuel supplies (Woodrey and Moore 1997) and their lack of experience with the challenges faced during migration (Németh et al. 2017). Older songbirds are more experienced and are believed to benefit from previous migrations, and are expected to respond differently to adverse conditions while migrating (Mitchell et al. 2015). The experience of older birds may affect their migratory strategy in a different way: younger birds are hypothesized to navigate primarily based on instincts, while older birds incorporate their experiences of past migrations and knowledge of major geographic features (Németh et al. 2017). This may be a possible explanation for the age related differences found between the stopover regions. When ASY birds are blown off of their intended trajectory they can potentially reorient themselves more efficiently than SY birds. This is hypothesized to occur because ASY birds possess knowledge of the landscapes from previous migrations, while SY birds have to return to a location that is familiar to them in order to gain their bearings (Németh et al. 2017). This may potentially explain the increased use of stopover sites during migration by younger birds (Rguibi-Idrissi et al. 2003).

2.4.6 Sex Effect

Due to the lack of sexual dimorphism between male and female Veeries, it is impossible to distinguish the sex of birds captured at stopover sites during migration without genetic testing (Pyle 1997). This logistical constraint results in limited knowledge of how sex influences the use of stopover locations. However, some insight may be derived from the ecological pressures related to breeding success (Heckscher et al. 2017). For instance, males are likely under additional pressure to arrive on the breeding ground earlier to secure high quality territory

(Aebischer et al. 1996, Lozano et al. 1996, Kokko 1999, Heckscher et al. 2017b). Males have been known to restore fuel supplies at a faster rate, resulting in less time spent at stopover sites, increasing the overall rate of spring migration (Newton 2006, Seewagen et al. 2013). This ecological “time crunch” may explain the results of my analyses, which indicated no significant hot spots in North America for north-bound male Veeries (Figure 2.9). Hot spot locations were derived from areas where occurrence was higher than normal, based on both the number of individuals that used the area and the length of time the individuals remained there. Thus, the lack of identified hot spot locations may indicate that males are indeed spending less time at fewer stopover sites. Males may be forgoing longer rest and refueling stops, prioritizing early arrival on their breeding grounds in order to increase their overall fitness (Kokko 1999). In contrast, females appear to make more deliberate stops during their spring migration northward, utilizing particular areas such as Florida (Figure 2.8). While males may suffer a loss in reproductive fitness if they arrive late to their breeding ground, Females are less constrained by this intrinsic pressure.

2.4.7 Comparison of Kernel Density Estimation and Optimized Hot Spot Analysis

The areas that are revealed through the clustering analyses are regions that have an increased presence of location estimates. KDE are commonly used on point data to smooth out the information and make it more aesthetically pleasing and understandable to the viewer, especially when the points cover a large portion of the map. When this analysis is performed for this purpose, it provides the individual with the density value in a given cell. The KDE will reveal clustering within the dataset, but does not reveal whether this clustering could be due to chance; therefore, KDE does not provide the user with a literal interpretation, rather a qualitative interpretation (Mitchell 1999). Hot spot analysis gives us the ability to reveal statistically

distinct areas within the data and provides the user with more meaning in the results and the conclusions than could be drawn from KDE alone. As the extent of analysis becomes larger, spatial patterns and trends become more difficult to observe by visual inspection alone. Therefore, a different method must be applied to observe trends at a larger scale (Harris et al. 2017). The G_i^* allows us to be able to compare the results of one hot spot analysis to another other based on the resulting z-score whereas the KDE output cannot be easily standardized or compared due to changing density from one dataset to the next. The hot spot analysis and KDE revealed the same major stopover regions; however, the hot spot analysis was used for further analyses and comparisons because of the statistical power and standardization it provides.

2.5.8 Conclusion

Identifying Veery hot spot regions is important in determining the connectivity of their annual cycle and potentially allows us to better understand population declines (Fraser et al. 2012). The location of these hot spots provides us with greater insight into the important stopover regions for transient Neotropical migrants. Using geolocators in conjunction with spatial analysis tools, such as the optimized hot spot analysis, researchers are potentially able to identify important migratory stopover regions. I identified several areas that are of great importance to migratory Veeries, and these areas are likely also important to several other species of Neotropical Migrants. The areas identified in my study that corroborate the results from migratory banding studies should be declared areas of ecological importance and should be considered a conservation priority. As methods to identify migratory hot spot regions continue to advance, ornithologists will gain a better understanding of which areas are important for conservation, and the levels of connectivity among breeding, migratory, and wintering regions. The identification of stopover regions will allow ornithologists to incorporate remote sensing

data, which may be able to provide a potential explanation into the repeated use of stopover sites. Having a comprehension of why these stopover regions are used more heavily, than other regions, may allow conservationists to identify specific natural areas for preservation. This individual-based tracking analysis allows the examination of potential age and sex effects, as well as year effects, and can be applied to multiple species of Neotropical migrants in the future (Heckscher et al. 2017). It has the potential to be an important methodology in order to gain insight into the behavioral and physiological constraints that songbirds face during migration. Here I demonstrated the usefulness of the hot spot Analysis as an approach for evaluating potential stopover sites used during migration.

Chapter III: Variation in Migratory Routes of Eastern Breeding Veeries (*Catharus fuscescens*) Revealed by Light-Level Geolocators

3.1 Introduction

Migratory connectivity of Neotropical migrant songbirds has been described as the link between an individual's breeding and wintering ground; however, the zone between those areas is known as an ecological "black box" because little is known about their migratory behavior (Delmore et al. 2012). The mechanisms used by small passerines to migrate and orient during their migration is poorly understood and may involve trade-offs among multiple biotic and abiotic factors (Hobson and Kardynal 2015). Migratory routes of Neotropical migrants are influenced by ecological barriers during their annual cycle (Hallworth et al. 2015). Neotropical migrants have developed different strategies in order to overcome these obstacles resulting in distinct routes observed. Some migrants fly directly over the Gulf of Mexico, successfully crossing the obstacle in one long flight (Lowery Jr 1946, Stevenson 1957, Gauthreaux Jr 1971). This strategy can be very hazardous for the birds because the flight across the Gulf of Mexico is very energetically demanding, and there are no available stopover locations over open water. Therefore, Neotropical migrants traversing the Gulf of Mexico must have an adequate fuel supply in order to sustain continuous flight or rest and refuel at stopover sites along the way (Moore et al. 1990, Mehlman et al. 2005).

Despite these hazardous obstacles faced during migration, most birds return to the same breeding territories each year (McKinnon et al. 2013a). Identifying the typical paths taken during migration is essential to the successful conservation of these long distance migrants (Hallworth et al. 2015). Determining the amount of plasticity in migration allows researchers to understand how well these birds respond to environmental stress, and how populations might respond to

additional stressors in the future. Obtaining data of repeat migratory journeys of Neotropical migrants may provide us with important insights into their capabilities to respond to adverse weather conditions (Stanley et al. 2012). These types of data are difficult to acquire due to the geographic scales in which they occur and the logistical challenges associated with repeat tracking of small passerines (Hallworth et al. 2015). Furthermore, by combining results from multiple geographic regions ornithologists may be able to grasp a better understanding of migratory connectivity (Webster et al. 2002, Cormier et al. 2013, Fraser et al. 2013).

Gathering information about the migratory patterns of Neotropical migrants is extremely difficult due to their small stature and rapid movement their annual cycle (Smith and Moore 2005). During migration, Neotropical migrants are constantly in transit, either to or from their breeding grounds, and rarely spend a prolonged period of time in one location (Mehlman et al. 2005). These factors make gaining insight into an individual's migratory behaviors extremely difficult using mistnets and other traditional mark-recapture techniques. Due to the ineffectiveness of traditional methods, ornithologists have begun utilizing more complex methods in order to understand the behaviors undertaken by Neotropical migrants. There have been several technological advances that have made the tracking of Neotropical migrants possible. Development in miniaturized tracking technology - such as archival light-level geolocators, automated radio telemetry, and archival GPS loggers - is progressing at a fast pace (Rakhimberdiev et al. 2017). Geolocators provide researchers with cost effective means to reconstruct detailed migratory routes of individual songbirds during migration (Delmore et al. 2012).

Our research team began studying the migratory patterns of a population of Veeries at two breeding sites in the eastern USA, utilizing geolocation technology to track individual

Veeries. The Veery is a Nearctic-Neotropical, trans-hemispheric, migratory thrush, that breeds in northern temperate and boreal forests of North America and overwinters in Amazonia (Heckscher et al. 2017a). The objective of this study was to look for variation in the migratory routes of individuals based on the population's (1) age, (2) sex, (3) year of migration, and, (4) seasonal migration.

3.2 Methods

3.3 ArcMap Analyses

Geolocators from the Massachusetts and Delaware breeding sites were deployed/retrieved following pre-determined protocol (refer to section 2.2.1). The geolocators were then analyzed and the data exported into ArcMap (ESRI 2018, version 10.6) abiding by the methods previously established (refer to section 2.2.3). Before the migratory routes were identified I removed all location estimates that occurred > 150 km from coastal areas, which are believed to be outliers (n=63 events, Kramer et al. 2017). All location estimates that were within 150 km of the coast were moved to the closest body of land (cf. Heckscher et al. 2011) using the snapping tool in ArcMap (n=1555 events, ESRI 2018, version 10.6). Location estimates that are located over the ocean are assumed to be erroneous due to the lack of suitable stopover habitats available. The data were broken up into four seasons, according to the previously mentioned methods (refer to section 2.2.3) while wintering data were omitted in order to focus on migratory movements. The “Split By Attributes” tool in ArcMap was employed to sort the dataset according to the bird's unique color combination and the year the unit was retrieved. The spring datasets for each individual bird included the last location estimate in South America and included all location estimates between South America and the breeding site in northern Delaware. Autumn datasets were split using the same premise - they included all points between

the breeding site and the first location estimate in South America. I estimated migratory routes by linking single points or clusters of points together chronologically (Kramer et al. 2017) utilizing the “Point To Line” tool in ArcMap (ESRI 2018, version 10.6) to portray a straight line interpretation of the route taken. These methods provided us with the shortest migratory distance possible, and it is accepted that the individuals may actually travel farther than this estimation (Kramer et al. 2017). The estimated migratory routes are to be interpreted as general migratory trajectories, and not as the precise route travelled.

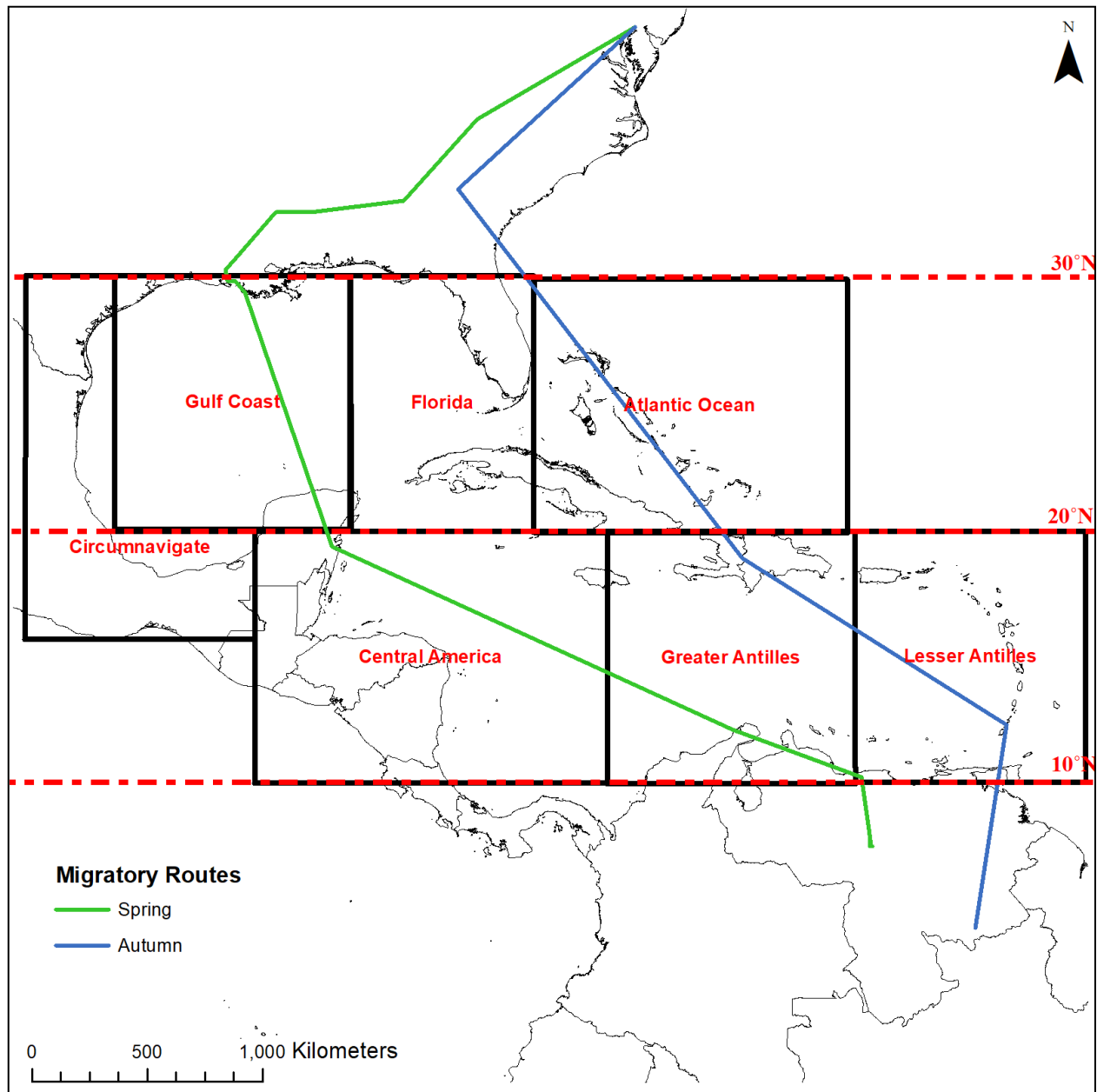
3.4 Analysis of Migratory Routes

I established seven migratory pathways around the Gulf of Mexico based on major geographic features in those areas. Those pathways included: Lesser Antilles, Greater Antilles, Central America, perimeter the Gulf of Mexico (Circumnavigate), Gulf Coast, Florida, and the Atlantic Ocean (Figure 3.1). All established regions fell between the 10°N and 30°N latitude markers. The 10°N marker was chosen because it represents the area in which the Veeries would be departing/arriving in South America during their migration. The 20°N marker was chosen because it encompasses the area that Veeries use while preparing to cross the Gulf of Mexico and the first land they will encounter after completing the journey. Similarly, the 30°N marker encompasses the area that the Veeries will use while preparing for their southbound journey across the Gulf of Mexico and the region that they will use after crossing the Gulf of Mexico after their northbound journey. The established migratory pathways were used to objectively identify the routes individual Veeries used while migrating across the Gulf of Mexico Individual spring and autumn migratory routes were analyzed separately from one another. Using the “Select By Location” tool in ArcMap (ESRI 2018, version 10.6) each routes wasbroken up into two segments depending on which established migratory pathway was used to cross the 20°N

and which regions used to cross the 30°N. A contingency table analysis (CTA) was employed to determine if there were any interactions between the routes taken and the variables such as: age, sex, and year. The significance level for all contingency table analyses were set at $\alpha < 0.05$. The results for the CTA, looking at the interactions between route taken and year, may not yield reliable results due to a small sample size. The analysis was performed as an exploratory analyses to see if there was a trend and whether additional analyses were warranted.

Figure 3.1 – Migratory pathways identified based on major geographic features between 10°N and 30°N. The estimated routes derived by archival light-level geolocators (blue and green routes) were categorized based on these predetermined pathways. During spring migration (green

route) the migratory route were identified by which geographic region the bird was in while crossing the 20°N and 30°N. The migratory routes for autumn (blue route) were identified at the same crossings.



3.3 Results

3.3.1 Geolocator Recovery Rate

Throughout the 2010-2018 breeding periods, 55 geolocators were recovered from the Delaware breeding site. The overall rate of geolocator recovery during this span of time was 36%; however, the recovery rate varied greatly among years (Figure 3.2). Geolocators from the Massachusetts site were recovered during the 2018 breeding season only: four units were recovered (57%). The total number of units recovered from both breeding sites was 59 (37%). Of those units recovered, 11 were from SY birds, 47 from ASY birds, 39 from males and 19 from females. Although the same 58 units were used for the spring analysis, 11 units stopped recording before the onset of spring migration. As a result, these geolocators could not be used for further analysis for the 2011(n=8), 2015(n=1), 2016(n=1) and 2017(n=1) spring migrations. There was also one unit that could not be used for further analysis (refer to section 2.3.1)

3.3.2 Migratory routes

3.3.2.1 Autumn 20 °N

The estimated routes were broken up into four distinct routes based on the geographical region used while migrating across the 20°N. The geographic regions used for analyses were: Lesser Antilles, Greater Antilles, Central America, and Circumnavigation (Figure 3.1). In total, I assigned 58 migration events to these routes, of those migration events, 19 traveled through Greater Antilles, 38 through Central America, one through the Lesser Antilles, and none took a circumnavigation route (Figure 3.3). The routes taken were independent of age ($\chi^2 = 1.7$, $df = 2$, $p = 0.43$), sex ($\chi^2 = 10.7$, $df = 2$, $p = 0.47$), and year ($\chi^2 = 17.6$, $df = 16$, $p = 0.35$).

3.3.2.2 Autumn 30 °N

The migratory pathways were broken up into four distinct routes based on geographical features across 30°N. The routes were split into three groups as follows: Circumnavigate, Gulf Coast, Florida, and the Atlantic Ocean (Figure 3.1). In total, I assigned 58 migration events to these routes, of those migration events, 8 traveled through the Gulf Coast, 30 through Florida, and 20 through the Atlantic Ocean (Figure 3.4). The routes taken were independent of age ($\chi^2=3.8$, $df=2$, $p=0.15$) and sex ($\chi^2=0.8$, $df=2$, $p=0.67$) on routes taken. However, there was a significant relationship between the year and the route taken ($\chi^2=41.1$, $df=16$, $p<0.01$).

3.3.3.3 Spring 20 °N

The migratory routes were again broken up into four distinct paths based on the geographical features used while migrating across 20°N: Lesser Antilles, Central America, Greater Antilles, and Circumnavigate (Figure 3.1). In total I assigned 47 migration events to these routes, of those migration events, 13 traveled through Greater Antilles, 27 through Central America, 6 through the Lesser Antilles, and one individual took the circumnavigate route (Figure 3.5). The routes taken were independent of age ($\chi^2=0.9$ $df=3$, $p=0.82$), sex ($\chi^2=0.8$, $df=3$, $p=0.85$), and year ($\chi^2=24$, $df=18$, $p=0.15$).

3.3.3.4 Spring 30 °N

The migratory pathways were broken up into four distinct routes based on geographical features across 30°N. The routes were split into three groups as follows: Circumnavigate, Gulf Coast, Florida, and the Atlantic Ocean (Figure 3.1). In total, I assigned 47 migration events to these routes, of those migration events 15 traveled through the Gulf Coast, 20 through Florida, and 12 across the Atlantic Ocean (Figure 3.6). The routes taken were independent of age ($\chi^2=0.8$, $df=2$, $p=.66$), sex ($\chi^2=0.1$, $df=2$, $p=0.97$), and year ($\chi^2=18.4$, $df=12$, $p=0.11$).

Figure 3.2 – Yearly recovery rate of geolocators from Delaware Veery (*Catharus fuscescens*) breeding site. The number of geolocators recovered is represented above each column. An asterisk (*) represents years in which geolocators did not record for the full annual cycle. As a result, spring migration could not be derived from the units during the following years: 2012 (n=8), 2016 (n=1), 2017 (n=1) and 2018 (n=1).

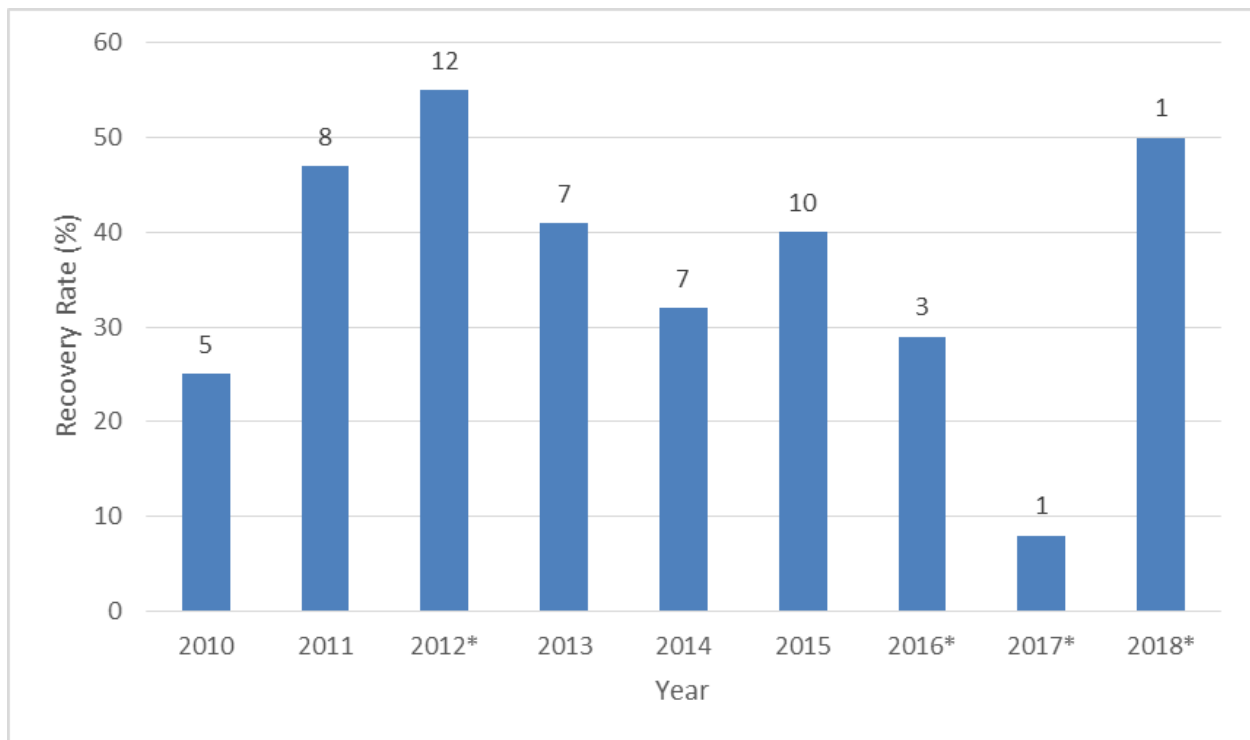


Figure 3.3 - Migratory pathways used by individual Veeries (*Catharus fuscescens*) while crossing 20°N latitude during their autumn migration (2009-2017). The number above each column represents the number of geolocators used for the analysis. Contingency table analysis revealed that the routes taken were independent of age, sex, and year.

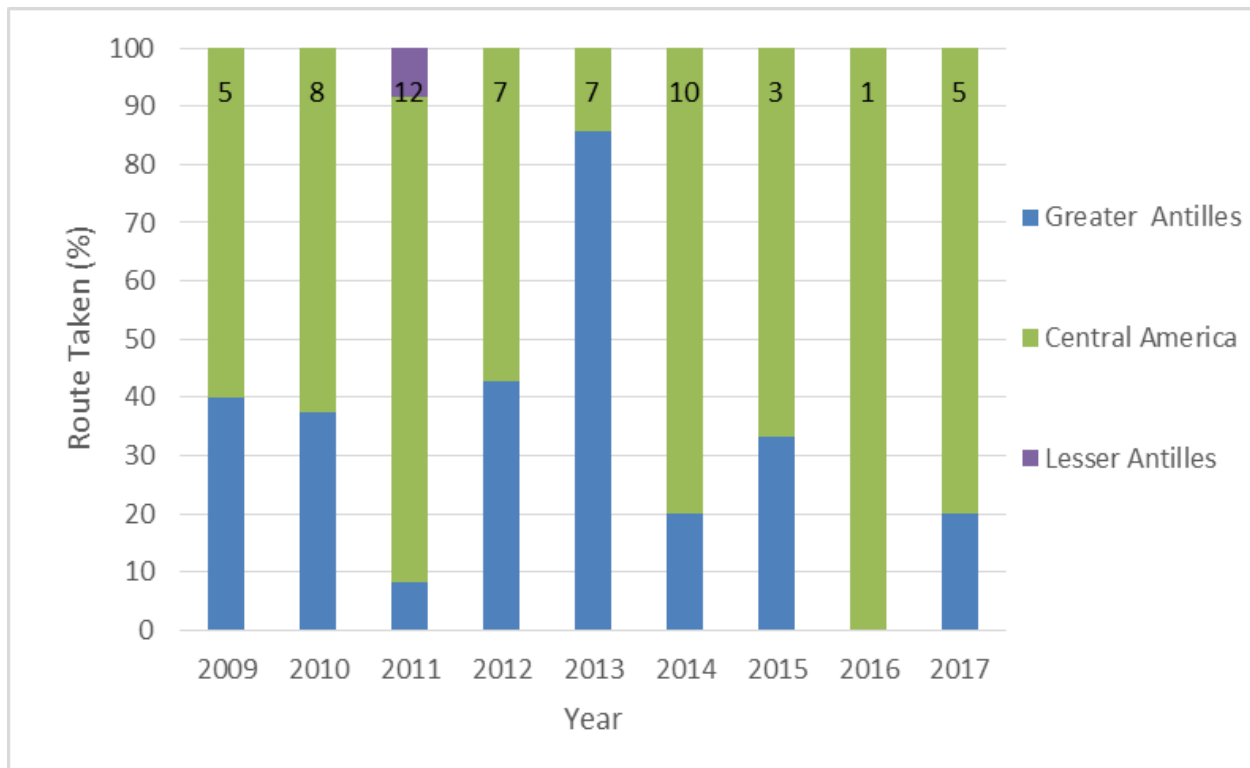


Figure 3.4 - Migratory pathways used by individual Veeries (*Catharus fuscescens*) while crossing 30°N latitude during their autumn migration (2009-2017). The number above each column represents the number of geolocators used for the analysis. Contingency table analysis revealed that the routes taken were independent of age and sex. However, there appears to be a relationship between the year and the route taken.

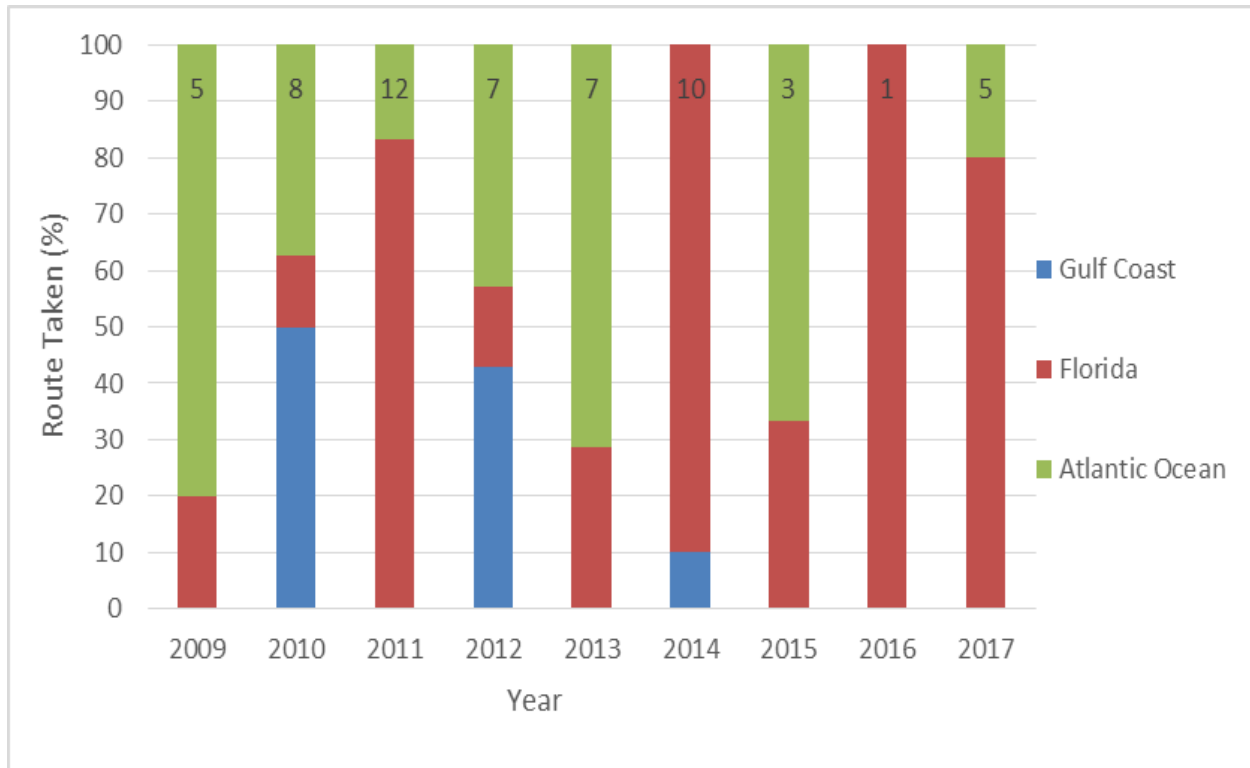


Figure 3.5 - Migratory pathways used by individual Veeries (*Catharus fuscescens*) while crossing 20°N latitude marker during their spring migration during (2010-2018). The number above each column represents the number of geolocators used for the analysis. Contingency table analysis revealed that the routes taken were independent of age, sex, and year.

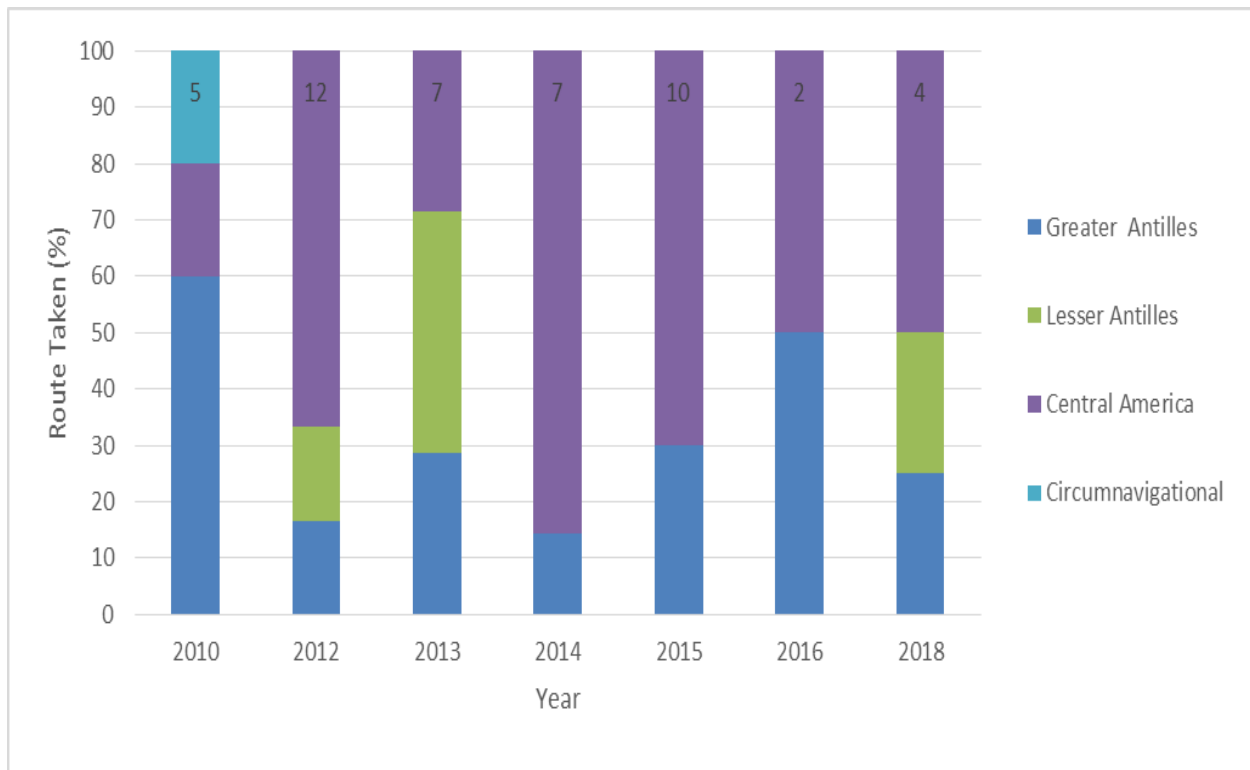
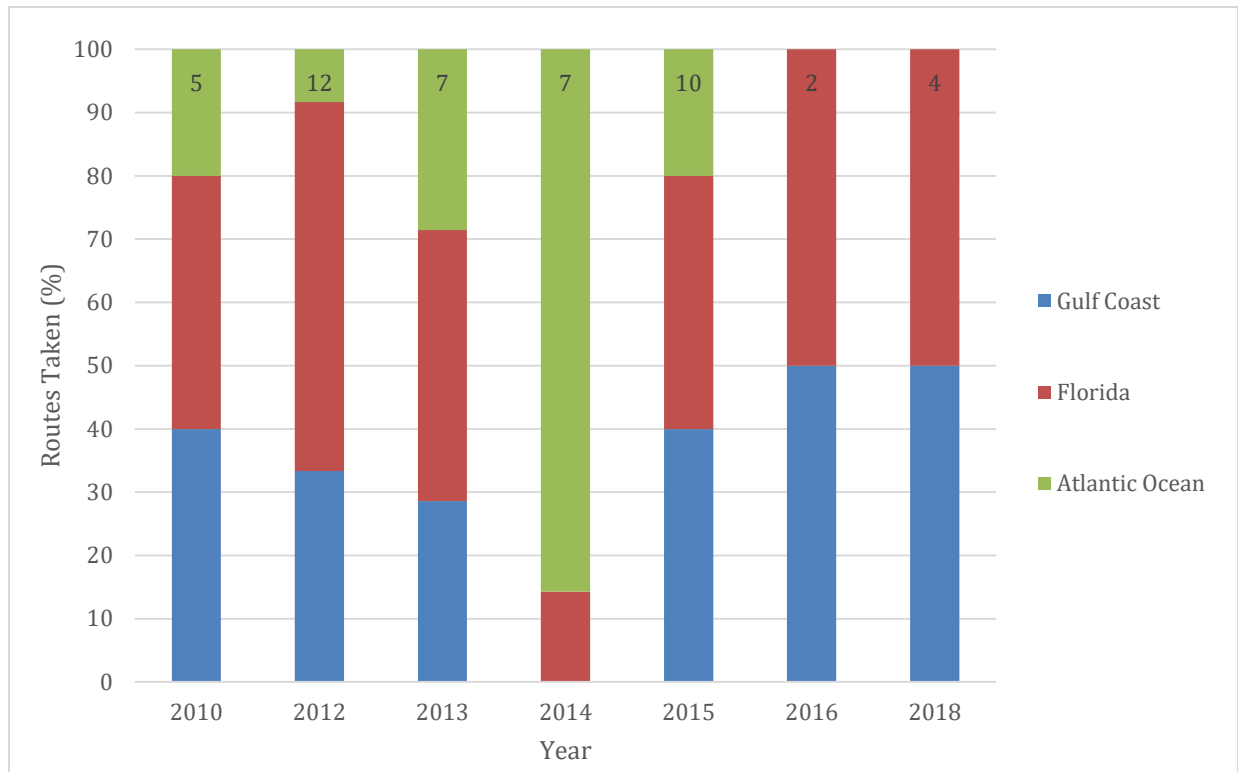


Figure 3.6 - Migratory pathways used by individual Veeries (*Catharus fuscescens*) while crossing 30°N latitude during their spring migration (2010 – 2018). The number above each column represents the number of geolocators used for the analysis. Contingency table analysis revealed that the routes taken were independent of age, sex, and year.



3.4 Discussion

3.4.1 Age and Sex Effect

My study did not show any effect of sex or age on migratory routes suggesting that intrinsic factors may not influence the migratory routes taken by the Veery population. The majority of geolocator studies to date have been primarily comprised of adult (ASY) male birds (McKinnon and Love 2018, Smetzer and King 2018). The modest sample size of SY birds (n=11) and females (n=19) enabled the ability to look for variation in routes among different age and sex classes. Although it was originally hypothesized that there is a sex effect during the spring migration due to the males' preference for arriving at the breeding ground earlier to secure a high quality breeding territory (Aebischer et al. 1996, Lozano et al. 1996, Kokko 1999, Heckscher et al. 2017b), I did not observe a sex-dependent effect on migratory pathways.

I hypothesized that there would be a difference in migratory routes based on age class because younger birds that have not yet performed this migration are believed to rely on intrinsic variables while older birds may incorporate experience, thus altering the migratory routes taken (McKinnon et al. 2014). However, age does not appear to have had a significant effect on the use of migratory pathways within the two eastern breeding populations. The lack of a difference could be because geolocators were not deployed on hatch-year (HY) birds. This means that this study did not have a true "naïve" cohort of migrants to compare to experienced ASY birds, as the SY birds have already completed the entire migration once before the attachment of the geolocators and may have already gained an adequate amount of experience (Németh et al. 2017). These findings support the work of Smolinsky et al. (2013), who found that there were no differences between the departure directions in regard to wind direction in ASY birds compared to that of SY birds, suggesting that SY birds already possess enough knowledge about migration

that there would be no age dependent effect between the two age classes. McKinnon et al. (2014) also did not detect any age related difference in routes between birds on their first spring migration and on SY birds. Although biotic factors like age, sex, and wing load (McKinnon et al. 2014, Deppe et al. 2015) have not been found to directly dictate the migratory pathways, it has been suggested that the extrinsic factors (e.g. weather and food availability) have the greatest influence on migratory pathways (Smolinsky et al. 2013, Deppe et al. 2015).

3.4.2 Year Effect

I did not possess a large enough sample size to make statistical inferences about the relationship between routes taken and year. However my exploratory analyses suggests that there may be relationship between route taken and year, but there is no statistical support of this. My study showed that there may be a relationship between the year and the path taken by individuals preparing to cross the Gulf of Mexico during fall migration (Figure 3.4). For individuals preparing to traverse the Gulf of Mexico during spring migration, there may also be a relationship between year and path taken (Figure 3.5). Although my exploratory statistics did not yield significance for this analysis, I believe that there may have been a relationship between route taken and year if geolocator malfunction had not occurred during some spring migrations (n=11). Geolocators did not record a full annual cycle due to battery failure before the individuals initiated spring migration in that year. The variation in migratory pathways taken while traversing the Gulf of Mexico can most likely be explained by the difference in meteorological conditions (Arizaga et al. 2011) and the individual's fat load (Smolinsky et al. 2013). Traversing the Gulf of Mexico has been acknowledged as a major geographic barrier for Neotropical migrants (Buler et al. 2007, 2017, Delmore et al. 2012, Lafleur et al. 2016); however, it has been suggested that the degree to which it serves as a barrier is dependent on

local weather conditions at the time of departure (Clipp 2018). Weather conditions such as wind, rain and clouds may impact departure decisions resulting in a longer stopover (Åkesson and Hedenström 2000, Arizaga et al. 2011, Smolinsky et al. 2013). Therefore, the majority of birds attempting to cross a major barrier choose to do so under favorable weather conditions (Smolinsky et al. 2013). Long distance migrants preparing to cross major barriers typically rely on additional support through tail winds before departing (Erni et al. 2005). Winds that occur while individuals are traversing the Gulf of Mexico have been known to blow birds off course (Smolinsky et al. 2013) while adverse weather conditions impact their departure decisions (Butler 2000). These findings suggest that weather may play a major role in altering the migratory pathways of migrating Veeries. The impact that weather has on the timing and migratory pathways may explain why there was a relationship between year and the point of departure before crossing the Gulf of Mexico.

Alternatively, a bird's subcutaneous fat deposits can be a contributing factor to stopover duration (Goymann et al. 2010). Therefore, the variation in migratory pathways may be explained by the individuals' fuel load which have been found to impact a bird's departure decisions (Arizaga et al. 2008, 2011). An individual's fuel load is determined by food availability (e.g., fruits and insects) which may be linked to the timing of migration (Renfrew et al. 2013, La Sorte et al. 2014, Wolfe et al. 2014). Climate conditions affect the timing of food availability. A correlation between arthropod biomass and the timing of migration suggests that annual food availability is an important determinant in departure (Studds and Marra 2011). Birds that possess a higher fuel load are better suited for migration and are more likely to depart from a stopover site the following night if weather conditions are suitable (Arizaga et al. 2008). Smolinsky et al. (2013) observed that Swainson's Thrush that arrived at the stopover site with

adequate fat began migrating across the Gulf of Mexico the following night if favorable weather conditions were present, while lean individuals oriented themselves in the opposite direction presumably to relocate and refuel at a more inland stopover location. Fuel deposition rate is a crucial factor that not only affects the ability of the individual to replenish depleted fuel supplies, but also impacts their migration strategies (Dänhardt and Lindström 2001). The overall quality of a stopover site can influence the food availability, thus the fuel deposition rate, which can cause individuals to prolong stopover at this location or seek an alternative location with better fuel availability (Mehlman et al. 2005). While an individual that does not have an adequate fuel supply will undoubtedly delay migration, an individual that has a sufficient fuel supply will also delay their departure until more favorable weather conditions develop (Arizaga et al. 2011). Deppe et al. (2015) concluded that songbirds encountering the Gulf of Mexico overcome the potential risk of crossing the Gulf of Mexico by departing during favorable weather conditions. The possession of larger fat reserves act as a buffer if they encounter adverse weather conditions while enduring the ~1000 km flight (Deppe et al. 2015, Clipp 2018). Birds typically will not continue with migration if they do not possess an adequate fuel supply or if weather conditions aren't ideal. Birds preparing to cross a barrier, require a minimum fat supply to fuel their migration and birds that do not depart with favorable wind conditions have an increased mortality rate (Schmaljohann and Naef-Daenzer 2011). The energetic condition of the individual is an important factor in depicting the migratory pathways taken; however, it appears that weather may have a larger impact on the yearly migratory patterns.

3.4.3 Future research needs

While there may be a significant difference in migratory routes of individuals preparing to cross the Gulf of Mexico among years, the scope of this study does not allow for conclusions

on why such differences occur. I hypothesize that a year effect would be primarily due to extrinsic factors (Arizaga et al. 2011, Smolinsky et al. 2013, Deppe et al. 2015, Clipp 2018) which vary greatly between years. Veeries from the Delaware breeding population have been shown to alter their nesting behavior and presumably depart from their breeding grounds early in years that have a propensity for high tropical storm activity (Heckscher 2017b, 2018). If Veeries are in fact capable of detecting adverse weather conditions on their projected route then they would likely adjust their route or stopover accordingly to avoid inclement weather. Adverse weather may lead to an increased mortality rate during migration (Deppe et al. 2015). In order to grasp a better explanation for the proposed year effect, I recommend future studies compare the estimated migratory routes provided by the geolocators to existing weather data. Hurricane tracts and/or surface winds found throughout the Gulf of Mexico that were present during migration may provide insight into potential impacts on migratory routes. Observing any potential impacts that surface wind direction and magnitude have on the migratory pathways taken may explain the variation that occurs between years. Comparing how previous hurricane tracts may have influenced the migratory routes of a given year may provide insight into the migratory pathways and further coincide with the findings of Heckscher (2018). Having a greater understanding about why a Neotropical Migrant undertakes a particular pathway during migration will potentially grant ornithologists insight into why these populations are experiencing declines.

Figure 3.7 - Migratory routes used by individual Veeries (*Catharus fuscescens*) (n=58 birds) during their autumn migration from their North American breeding site to South America.

Migratory routes are grouped according to the year the migration occurred.

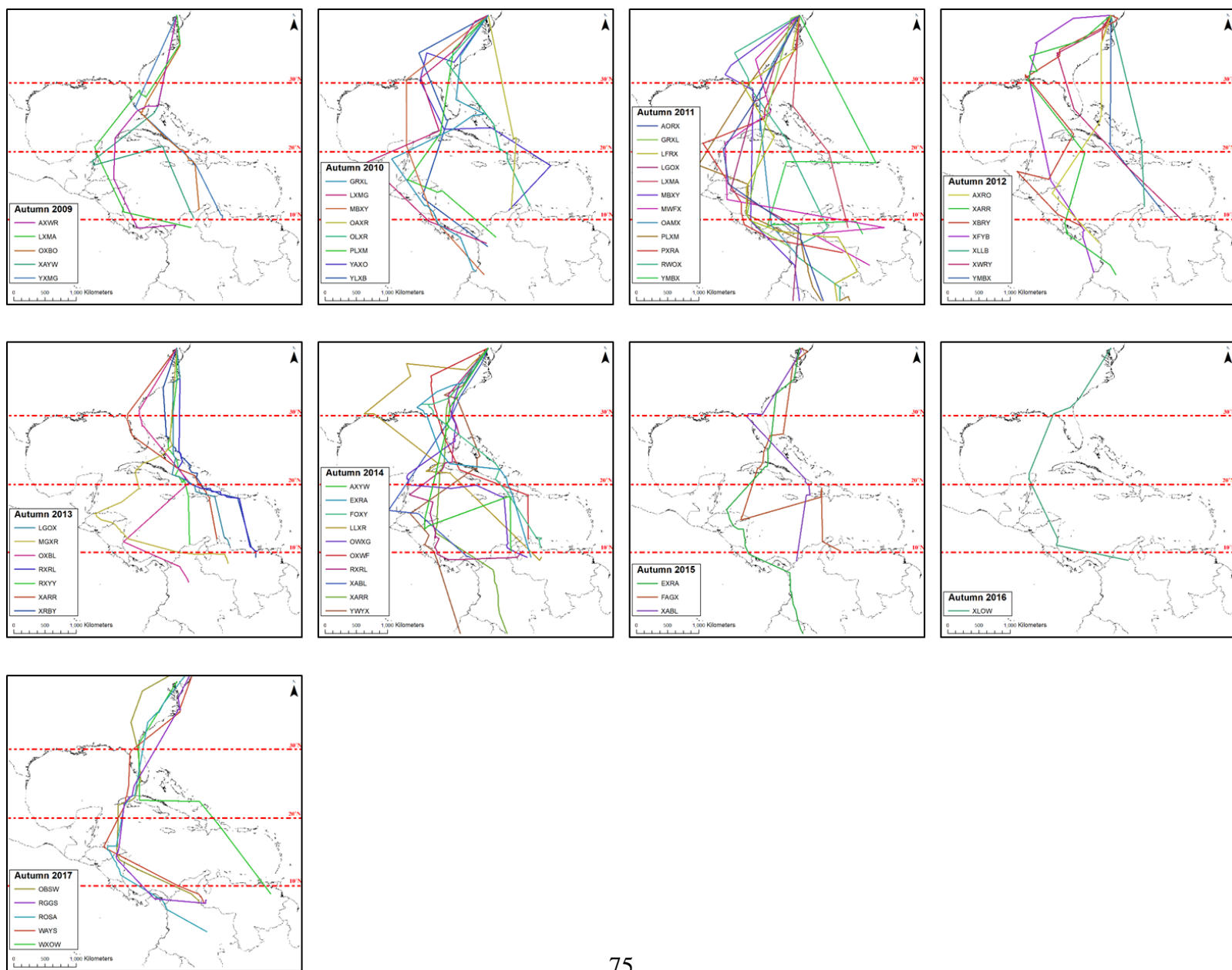
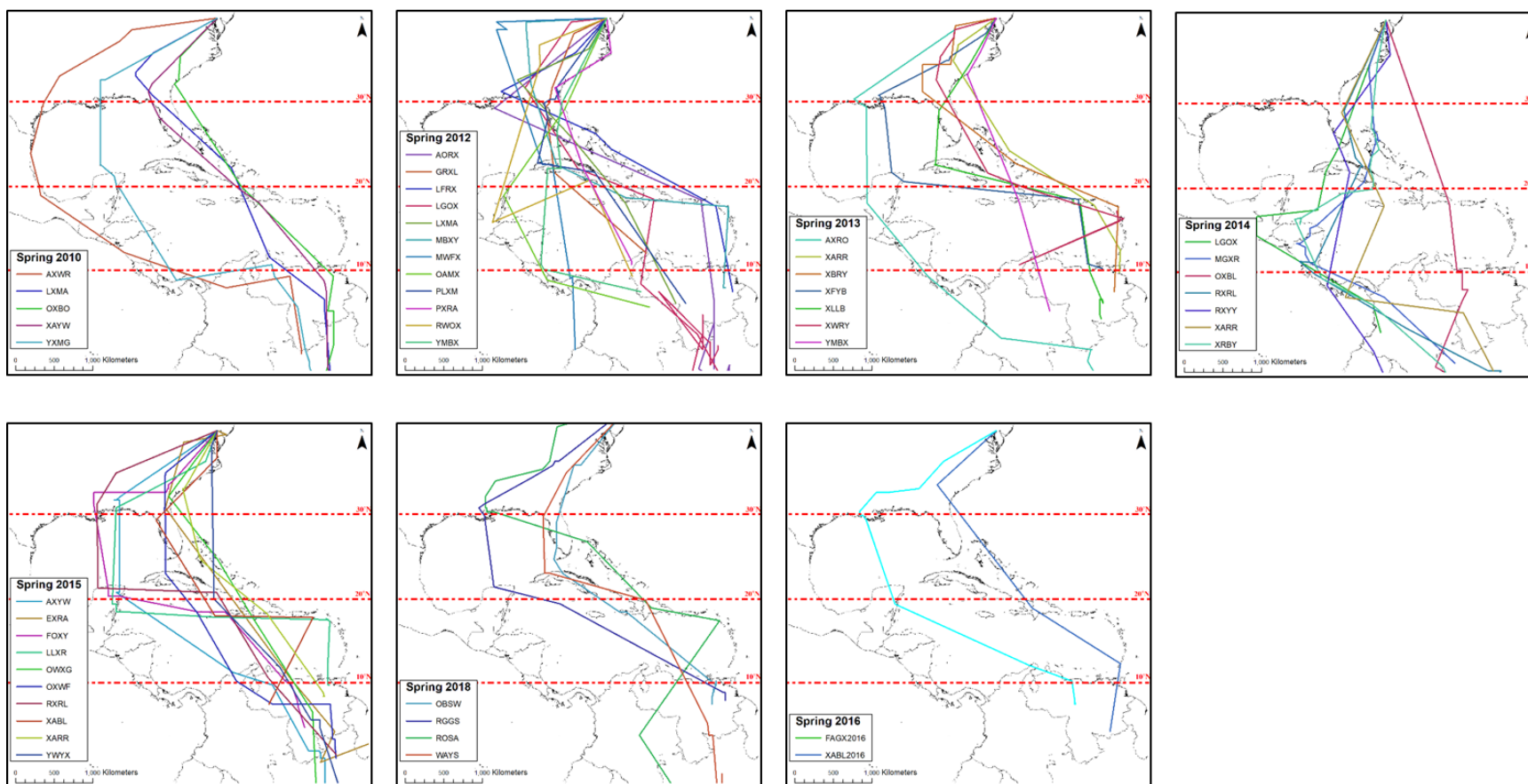


Figure 3.7 - Migratory routes used by individual Veeries (*Catharus fuscescens*) (n=47 birds) during their northbound migration from South America to their breeding grounds in North America. Migratory routes are grouped according to the year the migration occurred.



Chapter IV: Conclusions

Many songbirds, especially long distance migrants, are experiencing population declines from causes that are largely unclear (Sauer et al. 2013). Ornithologists are now well aware that conservation efforts must take into consideration the habitat needed throughout the full annual cycle: wintering, breeding, and migration. Use of geolocators provides an opportunity to further the understanding of songbird ecology by shedding light on the “black box” of songbird migration. Geolocators provide researchers with a number of advantages over other methods, as they are lightweight, cost effective, and can track individuals year-round (Rakhimberdiev et al. 2015). Through this technology we are discovering migratory corridors that were not previously known. Despite the widespread interest in quantifying migratory connectivity, few studies have a large enough geographic scope and sample size to actually show migratory trends (McKinnon and Love 2018). Most studies have focused on the attachment of geolocators to ASY males from a single breeding population. While this provides essential insight into songbird ecology, the scope of these studies are limited geographically and demographically, making it difficult to address migratory connectivity.

While my study does not definitely assess the migratory connectivity of eastern breeding populations, it does introduce a novel tool that researchers can use to better identify conservation areas. Through the use of spatial analysis tools coupled with avian tracking technology I have improved upon the current use of KDE to derive stopover regions and have shown that the hot spot analysis not only identified the same areas, but provides the user with statistical significance. The use of these improved methods will allow conservationists to more confidently extrapolate important areas needed for migration.

Through this analysis I was able to identify several important stopover regions that are heavily used during spring and autumn migration. The protection of the identified stopover regions are essential for the conservation of Veeries, and potentially migratory songbirds in general. Due to the large sample size and diverse demographic data present in this thesis, I was able to visualize the different stopover regions used by the different sexes and age classes. The next step in this process is to evaluate these stopover sites and attempt to identify the environmental factors on which Veeries rely during migration. Due to the vast extent of these regions the only way these areas can be evaluated efficiently is through the use of remote sensing technology. The use of remote sensing technology will allow us to quantify the environmental factors (e.g. elevation, forest density, land use, fresh water availability, and urban development) of the stopover sites and see which factors have the greatest influence on stopover site use. The breakdown of these stopover sites will provide conservationists with greater insight into the stopover site requirements needed to complete migration.

Although my research focused on the migratory periods of Veeries and does not directly address migratory connectivity, it does further the understanding of a well-studied breeding population and sheds light on the ecology of this declining species in general. The Delaware Veery breeding population is a color-banded population that has been monitored since 1998 (Heckscher 2007), and through this long-term study we have greatly advanced the understanding of Veery ecology throughout their annual cycle. As with most songbirds, the majority of the research has been focused on understanding their breeding ecology (Heckscher 2004, 2007, Halley and Heckscher 2012, 2013, Heckscher et al. 2014). Initial geolocator studies on this population provided us with the first insight into the migratory behavior of Veeries by identifying the true wintering range of Veeries (Heckscher et al. 2011) as well as the existence of

an intratropical migration on their wintering grounds (Heckscher et al. 2015). Recent studies have focused on the temporal aspects of migration, correlating reproductive biology with subsequent migratory behavior (Heckscher et al. 2017b), and relating breeding phenology with tropical storm activity (Heckscher 2018). My research aimed to fill the largest gap remaining in the understanding of the migratory connectivity of Veeries: their migratory behavior stopover sites and migration pathways. To my knowledge, this is the most complete dataset of any geolocator study to date. In addition to the collection of data from all demographics of a population, this thesis includes geolocator data for an eight year period from a single population; however, caution should be taken while trying to infer migratory connectivity from a single breeding population (Wellbrock et al. 2017). Finch et al. (2017) suggested in a recent meta-analysis of tracking data that strong migratory connectivity among songbirds might be quite rare. Therefore, in order to better gauge the migratory connectivity of Veeries this long-term study should be continued in collaboration with the Massachusetts breeding population and perhaps other locations.

Migratory connectivity is comprised of two components: mixing of individuals from across different populations, and the spread of individuals throughout their range (Finch et al. 2017). The challenge in determining migratory connectivity is that the nonbreeding and breeding areas of a population need to be identified (Webster et al. 2002). In order to achieve this task researchers must improve their collaboration efforts, thus increasing their geographic scope and sample size (McKinnon and Love 2018). While my research provides important new information on route selection for two populations of Veeries from across the eastern breeding range, to continue to address knowledge gaps on the migration connectivity and the population decline of this species, I recommend future research be conducted on quantifying the migratory

connectivity of the Veery between breeding and overwintering sites. Future research on the migratory connectivity of the species could provide insight into where the declines of this species occur.

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