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Lynn Schofield
*Eastern Illinois University*

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Daily Activity Patterns in Three Migratory Bird Species at a
Stopover Site on the Northern Coast of the Gulf of Mexico

(TITLE)

BY

Lynn Schofield

**THESIS**

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2015

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# INTRODUCTION

## Background

As a phenomenon that takes place over the span of continents, seasonal avian migrations are notoriously difficult to study. It wasn't until the latter half of the 18th century that people even became aware of these journeys undertaken by billions of birds each year (Collinson 1775, Bowlin et al. 2005). During that era, birds hibernating during the winter at the bottom of muddy ponds seemed just as plausible as migration to some authors (Barrington 1772). With new technologies such as Global Positioning System (GPS; Bouten et al. 2012) and satellite transmitters (Fuller et al. 1995), light-level geolocators (Ekstrom 2004), and stable isotope analyses (Hobson 1999), we now know more than ever about migration at a broad scale. Researchers have finally begun to answer questions about where birds go and the routes they take to get there (Bowlin et al. 2010, Robinson et al. 2010, Thorup et al. 2010). However, there remain significant gaps in our understanding of bird migration, and these gaps are often no longer at the largest scale. What birds are doing at a small scale during stopover is lost in the large scope of most of research using these new technologies. If we hope to gain a complete understanding of complex migratory systems, it is important that every facet of migration receives attention (Gauthreaux 1979). In this paper we use the emerging technology of automated radio telemetry to address the role of small-scale behaviors exhibited by songbirds during migratory stopovers that have rarely been documented in the wild due to the inherent difficulty of studying migratory birds in situ.

Each method historically used to study stopover behaviors has its advantages and disadvantages. Passive observation using shadows passing across the moon or using migratory chip-calls characteristic of many species are only able to elucidate behaviors immediately after departure from a stopover site and suffer from a high probability of observer error (Hebrard 1969). Radar studies allow for a more complete picture of departure timing and behaviors, but operate on a large spatial scale and cannot provide insight into pre-departure behaviors or differentiate individuals or species (Harper 1958, Robinson et al. 2010). Hand telemetry is regularly used to assess stopover behaviors of an individual, but produces low sample sizes, is difficult to use after dark, and requires an enormous amount of effort and the ability to move easily throughout a landscape (Kjos and Cochran 1970, Diehl and Larkin 1998, Bowlin et al. 2005, Schmaljohann 2010). Cage studies provide a continuous picture of avian behavior during stopover, but do not necessarily reflect how a bird might behave in the wild (Agatsuma and Ramenofsky 2006, Ramenofsky et al. 2008). Because the inferences of small-scale migratory behavior that can be drawn using current technology are limited,what we know about migration, as a whole, must be pieced together from numerous studies using a variety of techniques, leaving many migratory behaviors poorly understood.

Although stopover habitats are only used during a small fraction of a bird's life, they still play critical role in the overall survival of an individual. It has been estimated that mortality is at its highest for many species during migration (Sillett and Holmes 2002). Because mortality is known to be high during migration, having places to stop, refuel and to prepare for the next leg of their journey is necessary to mitigate of risk of these long-distance flights (Cohen et al. 2014). To complete the sustained flights necessary for many birds to migrate, individuals need to accumulate significant fat reserves (Tucker 1971, Alerstam and Lindström 1990, Pennycuick 2008). There are many strategies that are used to examine the details of avian behavior at stopover sites, but because individuals are only present for a short period at any given stopover site, passerines migrate almost exclusively at night, and their movements can vary substantially, it is difficult to get a complete picture of what is occurring (Bowlin et al. 2005, Schmaljohann et al. 2010). If we hope to gain insight into the conservation of stopover habitat to improve birds' probability of survival during migration, it is important that we understand the behavioral strategies species use during stopover. Migratory stopovers might be especially important immediately prior to crossing a major barrier such as large bodies of water or deserts. At these staging areas, the behavioral decisions made before crossing might make the difference between success and failure when there are no opportunities to land and refuel.

One method that offers the ability to observe and understand small-scale behaviors during migratory stopover as well as within a multitude of other systems, is automated radio telemetry (Kays et al. 2011, Smolinsky et al. 2013). Automated radio telemetry units (ARUs) are designed to continuously scan and record radio transmissions from radio transmitters attached to a study organism. This technology has already been used to determine the presence and absence of tagged birds during migration (Smolinsky et al. 2013, Woodworth et al. 2014,) and locate tagged birds at a breeding site by triangulating from multiple ARU towers (Ward et al. 2013, Ward et al. 2014). Further, by monitoring fluctuations in the strength of radio signals being received on an ARU and the azimuth from which the transmission was received, it is possible to infer movement of radio-tagged bird (Cochran 2006). Automated radio telemetry has the advantage of being able to continuously monitor many radio-tagged individuals simultaneously over a 24-hour cycle (Kays et al. 2011, Sperry et al. 2013).

Only a handful of studies have begun to explore the potential of ARUs. My work is among the first efforts to explore what we can learn about the daily movement patterns of an animal in the wild and the diel cycles characteristic of a species using ARU technology. The first chapter of this thesis will describe behavior broadly across the entire day and what factors influence movement prior to migratory departure. In the second chapter we use ARU technology to describe for the first time in the wild a behavior known as migratory quiescence, in which birds will greatly reduce their movement and levels of activity just prior to departing from a stopover site.

# CHAPTER I

## A Comparison of Diel Movement Patterns in Three Bird Species at a Stopover Site on the Northern Coast of the Gulf of Mexico

### Abstract

During migration, birds require stopover habitats where they stop en route to rest, refuel, and prepare for the next stage of their migration. For songbirds, many short movements made within a stopover habitat are known to be costlier than a single long migratory flight, as it takes a considerable amount of energy to initiate flight. This indicates that migrating birds should strive to balance the energy expenditure made in movement during stopover and energy gains they might be able to make while active at a stopover site. In this paper we examine the movement levels of three different species (Red-eyed Vireos [*Vireo olivaceous*], Swainson's Thrushes [*Catharus ustulatus*], and Wood Thrushes [*Hylocichla mustelina*]) throughout the day at a fall stopover site in southern Alabama on the coast of the Gulf of Mexico. We used automated radio telemetry to investigate how birds might change their movement patterns based on four variables influential to an individual's energy needs to complete their migration and their foraging abilities: age, fat stores, local wind speed, and wind direction. Our results demonstrate that each species has a unique pattern of movement, that wind direction was the strongest predictor of the proportion of time Red-eyed Vireos and Wood Thrushes spend moving, and that fat is the strongest predictor of movement in Swainson's Thrushes. The degree to which these variables influenced movement, however, was relatively small, and we posit that this might indicate that the habitat at this site is relatively poor and the potential for

energy gain is too low to make altering movement patterns a viable strategy for optimizing energy use and fat gain.

## Introduction

Long-distance migration is estimated to be a period of high mortality (Sillett and Holmes 2002). Sustained flights across geographic features, such as water bodies and deserts, are present in many migratory systems and are considered to be the most dangerous portion of many species' migrations. One notable example of such a feature is the Gulf of Mexico, which hundreds of thousands of birds traverse each year. According to a model describing the limitations of bird flight (Pennycuick 2008), the ability of an individual to complete a long-distance flight (~1000+ km) depends on its energy reserves and the wind conditions it experiences. Fat stores strongly influence the distance a bird can continuously sustain flight, with flight distances increasing as fat stores increase (Tucker 1971, Alerstam and Lindström 1990, Carmi et al. 1992). Wind direction and speed affect the distance a bird can fly and the optimal fat load needed by an individual to migrate most efficiently (Alerstam and Lindström 1990). It has been suggested that for some songbird species, a sufficiently fat bird could potentially complete much of their migration without needing to refuel (Pettersson and Hasselquist 1985). However, a bird with inadequate fat stores, especially when facing poor climatic conditions, is far less likely to successfully complete a long-distance flight. It is well documented that large-scale mortality events can occur when migrating birds are faced with severe weather (Newton 2007). In a recent study focused on birds crossing the Gulf of Mexico from the southern coast of Alabama to the Yucatan Peninsula, the determining factors that predicted an individual's success at completing extended non-stop flights were fat stores, wind direction, and wind speed (Deppe et al. in review).

In addition to intervals of long-distance flight, passerine migration is interspersed with stopover periods, during which migrants rest, refuel, seek refuge from unfavorable weather conditions, and prepare for the next leg of their migration. Individuals in good physical condition will typically remain at a site for only a brief period of time, sometimes less than 24 hours, but individuals in poor condition with diminished fat reserves will generally remain at a stopover site longer than their fatter counterparts (Moore and Kerlinger 1987, Seewagen and Guglielmo 2010, Cohen et al. 2014).

Although stopover is often necessary for migrating passerines, it also presents risks such as predation and unnecessary energy usage (Woodworth et al. 2014). It has been demonstrated that initiating many short flights is more costly than a single long flight, and individuals will expend more energy per unit time during stopover than during a migratory flight itself and that energy expended during stopover accounts for about two-thirds of a bird's total energy usee during migration (Nudds and Bryant 2000, Wikelski et al. 2003, Bowlin et al. 2005). This makes it important that migrating birds conserve energy or successfully feed during the stopover to make such a stop worthwhile (Schmaljohann et al 2013).

Considering the risk inherent in the Gulf of Mexico crossing due to unpredictable weather, the energetic costs of the flight, and the potential energetic costs of low refueling rates during stopover, it is reasonable to assume that birds make economic decisions during stopover as they prepare to continue their migration. An individual moving during stopover expends more energy than it would while still, and increases its risk of failing to recoup the energy stores it expends. Individuals should decide how best to allocate their time to balance the expenditure of energy associated with foraging or predator avoidance with the need to conserve already existing fat stores.

Both the condition of an individual and its immediate environment have been observed to influence movement patterns (Loria and Moore 1991). Loria and Moore (1991) found that leaner Red-eyed Vireos (*Vireo olivaceous*) not only remain at a stopover site longer during spring migration than fatter birds, but also expand their foraging strategies to include more active and costly foraging methods such as hawking for insects or hovering. Although the relationship between fat stores and behavioral decisions is the best described, other factors influential to successful foraging and migratory success include age, wind speed, and wind direction. Age influences foraging efficiency, and young birds tend to be less effective at acquiring food (Heise and Moore 2003). Wind speed influences an individual's energetic expenditures and therefore, its ability to move (Pennycuick 2008). Birds have been show to able to detect wind direction during migration and will adjust migratory flight accordingly and typically maintain the same airspeed regardless of wind direction, indicating that they will necessarily take more time to cover the same ground distance when they are flying against the wind (Larkin 1980).

Both external and internal conditions can influence the amount of risk a bird is willing to expose itself to. In a study investigating optimal time allocation and decision-making in wintering Yellow-eyed Juncos (*Junco phaeonotus*), individuals were more likely to take greater risks in hopes of gathering more food when temperatures were colder and the chance of starvation over the course of the night was higher, however in better conditions, individuals would typically opt for using a stable food source (Caraco et al. 1990). McNamara and Houston (1985) also asserted that behavioral decisions are state dependent and that a bird in poor energetic condition should be more likely to take risks to build energy stores than a bird in good energetic condition.Models described in Alerstam and Lindström (1990) showed that birds optimized the length of their stopover based on their immediate fat stores and the rate of fat deposition possible at a stopover site. Field studies finding that lean birds remain at a stopover site longer than fat birds are possible examples of this kind risk-reward optimization (Moore and Kerlinger 1987, Seewagen and Guglielmo 2010, Cohen et al. 2014); by remaining at a stopover site, a lean individual risks expending more energy than if it migrated, but may bolster its fat stores through successful foraging, increasing its likelihood of successfully migrating.

How birds optimize not just their length of stay, but their energy use during their time at a stopover site is currently unknown. We expect that birds preparing to cross the Gulf of Mexico in the fall will choose to spend a different proportion of their time moving and therefore expending energy, depending on previous migration experience (i.e., age), body condition, and local weather conditions during stopover. Additionally, we expect that movement will vary among species due to different energy needs, diets, migration destinations, and flight abilities. Within species, we predict that fatter birds as well as older, more experienced birds would be more likely to conserve energy and spend more time stationary. We also predict that higher wind speeds and tail winds would result in riskier behaviors, with birds investing more energy into movement.

We tested these hypotheses by using automated radio telemetry to track the movement of Red-eyed Vireos, Swainson's Thrushes (*Catharus ustulatus*), and Wood Thrushes (*Hylocichla mustelina*) throughout the day at a stopover site in coastal Alabama. By examining the decisions made by migratory songbirds during stopover, we hope to understand what conditions are most likely to influence movement. With this information we will gain insight into the behaviors birds employ to energetically prepare for long-distance flights across a geographic barrier.

## Methods

### *Field Methods*

Between September 1 and October 31 2011–2014 we captured, banded, radio-tagged, and tracked individuals of three focal passerine species, Red-eyed Vireo (n = 92), Swainson's Thrush (n = 98), and Wood Thrush (n = 51), at a long-term bird-banding station (established 1993) located on the Bon Secour National Wildlife Refuge in Fort Morgan, Alabama. Bon Secour NWR is located on the Fort Morgan Peninsula (30.2288° N, 88.0013° W), which is about 20 km in length and 1 km across and is dominated by costal scrub dune and maritime forest habitats (Fig. 1). We selected focal species that were known to cross the Gulf of Mexico, were abundant during migration at Bon Secour

NWR, and exhibited differences in flight morphologies and final wintering destinations between species (Yong and Moore 1994, Cimprich and Moore 2000, Mack and Yong 2000, Evans et al. 2011). Once fitted with a USGS aluminum leg band, we affixed radio pulse transmitters to birds' backs using Fantasy Lengths® eyelash adhesive (Revlon, New York, New York) and a small amount of cyanoacrylate glue (Loctite®, Westlake, Ohio) that would irritate birds' skin minimally, stay fast for the 4–5 week life of the transmitter's battery, but fall off relatively soon after the transmitter stopped functioning (Raim 1978, Smolinsky et al. 2013). We used transmitters from either Lotek (Newmarket, Ontario) or JDJC Corp. (Fisher, Illinois). Lotek transmitters ranged in frequencies from 163.828 to 166.060 MHz and had pulse widths (i.e., the duration of the radio pulse) of either 28 ± 2 or 22 ± 2 milliseconds. Transmitters from JDJC Corp. had a similar range of frequencies and their pulse widths were either 14 ± 2 or 18 ± 2 milliseconds. Transmitters of both brands weighed 0.68 grams for Red-eyed Vireos (~3-5 percent of tagged bird's total mass) and 0.9 grams for thrushes (<4% of tagged bird's mass). We also aged, sexed, and assigned a fat score on a qualitative 0-6 scale based on fat visible in the furcular region as described in the Gustafson et al. (2005) for all radio-tagged individuals. Birds' fat scores were then further divided into two categories 'fat' and 'lean'. Lean birds were those birds with fat scores less than 3 and fat birds had scores of 3 or greater (i.e., individuals with at least a half-full furculum).

We remotely tracked radio-tagged birds using an automated radio-telemetry unit (ARU), connected to a circular array of six Nighthawk brand directional yagi antennas mounted on a tower located near the banding station that was ~10 m higher than the surrounding vegetation. ARUs were designed and built by JDJC Corp. to continuously scan radio signals. Specifically, the units cycled through a list of pre-programmed frequencies matching those of study birds and recorded all radio signals (in dBm) being received from each frequency (± 0.005 MHz) and the pulse width of received radio pulses. The cycle speed of the ARU depended on the number of frequencies programmed into the device, but ranged from 3–6 minutes.

*Data Interpretation*

Because the ARU recorded all radio signal received each cycle, a considerable amount of post-processing was necessary to differentiate ambient electro-magnetic noise from signal being received from our transmitters. To do so, we wrote an algorithm in the Python programming language that would identify positive detections of a transmitter by searching through the data for instances where there were more than three consecutive readings that fulfilled the following criteria: 1) had a consistent frequency within 0.003 MHz of the known transmitter, 2) had a signal strength greater than 1000 dBm, and 3) had a pulse length within 3 MHz of that transmitter.

Following methods discussed in Kays et al. (2011) and originally proposed by Cochran (2006), we then inferred movement based on the changes in signal strength detected between consecutive readings on a given frequency. We considered fluctuations in signal strength above a threshold of 250 dBm to indicate movement; otherwise, we considered birds to be still. We based the 250 dBm threshold off of the changes in signal strength we received between 21:00 and 05:00 (all times central standard time) from individuals of all species that chose to remain overnight at our study site, as those birds were most likely to be sleeping. 250 dBm represented approximately two standard deviations greater than the mean change in signal strength during that period. We did not include birds observed by the ARU to depart or return from the site in this calculation because they were certain to have been moving during some portion of the interval. The interval from which this threshold was identified took place approximately two and a half hours after dusk until an hour and a half before sunrise during the months of September and October. The chosen interval extended further beyond dusk than before dawn due to the fact many individuals initiated migration after sunset and so individuals remaining at the site might still have been moving at this time. To assure that comparisons of movement were valid between species and not skewed by differences such as transmitter type, the height at which birds tended to perch, or posture while sleeping, we used an ANOVA to assess the difference in the average signal change during the nighttime interval between each focal species. Similar to another study (Kays et al. 2011), the relationship between average signal change and species/transmitter type in our study was non-significant ($F_{2,19} = 1.922$, $p = 0.174$).

To validate our interpretations of movement based on ARU signal fluctuations, we also ground-truthed activity estimations. Between 3 October and 15 October of 2014 we hand tracked and visually observed all birds radio-tagged during that period ($n = 12$) until they departed the area. During an observation, we categorize birds as either still or active at one-minute intervals. Activity included all turns, hops, and flights. Only observations where the bird could be unambiguously observed were included. We recorded a total of 425 one-minute observations corresponding to a total of 85 individual ARU readings. When compared with direct observations, ARUs assigned activity or non-activity correctly 88% of the time. Kays et al. (2011) also reported a strong correlation between the percentage of time a transmitter was moved by a human subject during a 10-minute interval and the corresponding estimate of transmitter movement using ARU data.

### *Data Analyses*

To assess the level of movement birds exhibited throughout the day, we divided the day into hour-long periods and recorded the rate of movement for each individual (i.e., the percent of ARU observations that the bird was considered to be moving) during each hour. We further divided the day into three discrete, biologically relevant periods: morning, midday, and afternoon. We defined the morning interval as starting at 05:20, the average time of civil twilight (i.e., when the center of the sun is 6 degrees below the horizon), until 09:20. This interval was based off the United States Forest Service recommendations for point count surveys and the time when birds are expected to be most active (Ralph et al. 1995). The midday period extended between 09:20 and 14:20 as the day heated up and birds are typically known to reduce their movement, and afternoon extended between 14:20 and the average time of departure for each species at 19:20 (Chapter 2). We did not include the nighttime interval in statistical tests because few birds remained overnight.

We first assessed whether species and time period were better predictors of hourly movement rates throughout the day than a null model of a constant rate of movement using a generalized linear mixed effects model (GLMM) with a binomial distribution and a logit link function using the 'lme4' package (Bates et al. 2014) in R with species and period considered as fixed effects and individual birds considered a random effect. We selected the best model out of species, time period, and a combination thereof for predicting bird movement rates using Akaike's Information Criterion corrected for small sample size ($AIC_c$; Burnham and Anderson 2002) and assessed the fit of our models using $R^2$ calculated using a technique described by Nakagawa and Schielzeth (2013).

We then assessed which variables best predicted movement rates of each species within the time periods found to be distinct from one another by modeling the effects of intrinsic and weather variables on movement rates using a GLMM function with a binomial distribution and logit link. For each species and time period, we considered two intrinsic variables (fat and age, i.e., hatch year or after hatch year) and extrinsic variables (wind speed (m/sec) and wind direction (classified as being either northerly [i.e. a tail wind] or southerly [i.e. a head wind]). We modeled these intrinsic and weather variables as fixed effects and individual birds as a random effect. We then selected which candidate model best predicted movement in each of these groups using $AIC_c$. We describe the goodness of fit using the previously described $R^2$ function. We then calculated the 95% confidence interval for model averaged regression coefficients (Burnham and Anderson 2002) for each variable using the modavg function from the 'AICcmodavg' package in R (Mazerolle 2015) using all models in that time period as candidate models

We obtained weather data from the National Oceanic and Atmospheric Administration's North American Regional Reanalysis wind data set (spatial resolution of 32 KM, with measurements taken 8 times daily) accessed through movebank.org's Env-DATA service. Because both wind direction (on a 360 degree scale) and wind speed (in meters per second) at the time of departure were correlated with those variables at the time of capture for all individuals (wind speed - adjusted $R^2 = 0.779$, wind direction adjusted $R^2 = 0.619$), we opted to use wind variables at the time of departure to simplify analyses. When we categorized wind direction as headwind or tailwind, that variable rarely changed between a bird's capture time and departure time.

Finally, to visually examine the differences between each species in their distribution of movement throughout the entire twenty-four hour cycle, we calculated the proportion of individual birds that were moving in one-minute intervals. Because ARU observations were made unevenly at rates ranging from once every 3-5 minutes, we linearly interpolated signal strength between measurements to compare individuals with one another.

## Results

We examined a total of 92 Red-eyed Vireos, 98 Swainson's Thrushes, and 51 Wood Thrushes. Our models indicated that hourly activity rate was influenced by species and time period ($R^2 = 0.14$; Table 1; Fig. 2). However, afternoon and evening time periods across all species were correlated (*$R^2$* = 0.764), so we considered them to be a single time period in further analyses.

The most predictive model for describing activity in Red-eyed Vireos in the morning period included wind speed as an explanatory variable (Table 2). However, the variable's ability to explain variation in movement was minimal ($R^2$ = 0.01) and the model averaged regression coefficient estimated for wind speed was not significantly different from 0 (95% Confidence Interval = -0.44 – 0.37). The most predictive model for Red-eyed Vireos in the afternoon/evening period was a model that included fat, age, wind speed, and wind direction (Table 2). The variation explained by this model was greater than in the morning ($R^2$ = 0.07). Of the model averaged regression coefficients of variables included in the top ranked model, only wind direction was significantly different from 0 (Fig. 3; Table 3).

In Swainson's Thrushes the most predictive model during the morning period included wind speed and age as explanatory variables ($R^2$ = 0.05; Table 4). Neither the model average regression coefficients estimated for age (95% Confidence Interval = -0.53 – 1.15) or wind speed (95% Confidence Interval = -0.38 – 0.08) was significantly different from 0. The most predictive model for Swainson's Thrushes in the afternoon/evening period was a model that included fat, age, and wind speed ($\mathrm{R}^2$ = 0.06; Table 4). Of the model average regression coefficients for the variables included in the top ranked model, only fat was significantly different from 0 (Fig. 4; Table 5).

The most predictive model for Wood Thrushes in the morning period included wind speed as an explanatory variable ($R^2 = 0.07$; Table 6). The model average regression coefficient estimated for wind speed was not significantly different from 0 (95% Confidence Interval = -0.53 – 0.07). The most predictive model for Wood Thrushes in the afternoon/evening period was a model that included age, wind speed, and wind direction ($R^2 = 0.19$; Table 6). Of the model average regression coefficients for the variables included in the top ranked model, both wind speed and wind direction (Fig. 5) were significantly different from 0 (Table 7).

## Discussion

We observed distinct differences in the proportion of time spent moving between all three species, suggesting that each species made different decisions relating to energy expenditure. Swainson's Thrushes moved the least overall and were observed to have a steady rate of movement that did not change throughout the day; the only discernable variation was a slight peak around the average time of departure. Wood Thrushes displayed greater variation in the percentage of birds moving throughout the day. We also observed an increase in movement near dawn and a slight decline in movement near noon in Wood Thrushes. Red-eyed Vireos moved the most overall and showed a peak in movement around dawn, but their movement levels tapered off well before the average time of departure. Because Red-eyed Vireos are a smaller bird and cannot store as much fat as the thrushes, they would be less likely to have sufficient energy stores remaining from previous stopover intervals and would be more likely to need to forage prior to continuing their migration. They are also primarily insectivores and their foraging strategies are typically more active than those of a thrush (Cimprich et al. 2000).

As we hypothesized, fat and wind variables were influential to the level of movement observed in these species, although the importance of these variables in predicting movement were different for each species. Stopover movement for Red-eyed Vireos and Wood Thrushes were influenced most strongly by wind direction in the afternoon and evening. As we hypothesized, individuals of both species moved more when they experienced a headwind, suggesting that they foraged more when migratory conditions were suboptimal. The difference in movement rates we observed took place in the afternoon and evening, suggesting that individuals altered their behavior only as they prepared for migration. Movement was similar in the morning for both species regardless of wind conditions.

Wind speed, in addition to wind direction, was also an important factor in the movement of Wood Thrushes, which decreased their movement as wind increased. This suggests that the degree of a head wind or tail wind also played a role in a bird's assessment of the favorability of their immediate conditions. Additionally, it is possible that their foraging efficiency or ability to gain fat decreased as wind increased. Because foraging is only energetically viable when there is relatively little energy expenditure, it is most likely that Wood Thrushes in this study might have decided to forego foraging due to the increased energetic cost of short flights in strong wind conditions. It is not clear why wind speed was not influential in Red-eyed Vireos, although it might be possible that the larger body size of Wood Thrushes made them more strongly affected by wind or allowed them to forego foraging more readily than Red-eyed Vireos.

Rather than wind direction, the movement of Swainson's Thrushes was mostly influenced by fat, although fat's influence was small. As we hypothesized, fat birds spent a lesser amount of time moving than lean birds, presumably to better conserve energy. This difference in movement between fat and lean birds took place during midday and afternoon, indicating that birds would initially make similar efforts in search of food or other resources, but only leaner birds would decide on increasing their energy expenditure in preparation for their migration given the resources at hand. Despite fat stores being an important factor in models relating to behavioral optimization and risk assessment in birds, fat was not a strong predictor for movement for Swainson's Thrushes and not a predictor at all for the other two focal species.

It is unclear why wind direction impacted movement in Wood Thrushes and Red-eyed Vireo but not in Swainson's Thrushes. While we would expect the two thrush species to have more similar movement patterns, it was instead the Wood Thrush and Red-eyed Vireo that exhibited similar movement patterns throughout the day (i.e., a peak in the morning followed by a steady or slowly declining movement rate through the rest of the day influenced primarily by wind). The greater differences in movement patterns and decisions related to movement between the two thrush species as compared with the Red-eyed Vireo is surprising considering that Wood Thrushes and Swainson's Thrush are within the same family. The thrushes are considered to be morphologically and behaviorally more similar to each other than to a Red-eyed Vireo. It may indicate that Red-eyed Vireos and Wood Thrushes were making similar behavioral decisions throughout the day based on something other than genetic or morphological traits. With further study of the movement of other species at stopover habitats, it may be possible to assess whether movement patterns are influenced by factors such as a species' foraging behavior, diet, migration distance, wintering habitat, or the plasticity of their migratory routes that we were not able to take into account within the framework of this study.

Fat's lack of influence on movement in Wood Thrushes and Red-eyed Vireos and the minimal influence that it had on movement in Swainson's Thrushes may reflect the quality of Bon Secour NWR as stopover habitat for those species. If the prospect of gaining fat is minimal at a site, then fat and lean birds will both make energy conservation their priority. This could suggest that despite the large number of migratory birds moving through Bon Secour NWR, it is not a high quality habitat in terms of providing opportunities for refueling for Red-eyed Vireos or Wood Thrush and most likely other species as well. Work currently taking place on Swainson's Thrushes during fall migration at Bon Secour NWR found that they do not have fruit DNA in their feces, suggesting they aren't successfully foraging (W. Lewis, pers. comm.). We might not even consider this site to be a true stopover location for some species but instead its function may be more as a staging ground where individuals wait until the correct time of day to continue their migration and traverse the Gulf of Mexico.

Within this and other migratory systems (Smolinsky et al. 2013, Woodworth et al. 2014), it has been observed that birds in poor energetic condition will often opt to return to the north rather than immediately head south, perhaps in search of a more suitable foraging habitat from which to procure resources. We redetected 26% of the birds tagged at Fort Morgan in 2013 passing a single ARU system located ~50 km inland from our banding site,and we relocated 25% of birds tagged in 2014 with two towers located ~50 km and 100 km, respectively,north of the banding site, suggesting that those birds that left to the north were not taking an alternate migratory route but looking for a different place to stopover (Deppe et al. unpublished data). Even if foraging is poor at a site, it does not diminish the importance of potential staging areas where birds initiate flights across large geographic features like Bon Secour NWR. Instead it indicates that making conservation decisions relating to preserving habitat for migratory birds should focus both on areas with high densities of migratory birds and on areas with the most suitable foraging habitats.

The differences in the economic decisions made by each species and the circumstances in which they chose to change their movement highlight the fact that individual species have very different strategies when it comes to migratory behavior, and likely have differing needs during stopover. It further reinforces the difficulty of drawing generalizations about a given species based on the behavior of another. The overall patterns of movement, the assessment of risk, and the tradeoffs between conserving energy and expending energy are likely to vary greatly between species throughout their life histories.

Using ARUs to understand animal movement also has many applications beyond the scope of our study. With further investigation ARUs may prove to be an effective way to compare species and populations occupying differing habitats in differing conditions and to help us make decisions relating not only to questions relating to the preservation of stopover habitat, but also conservation in general. By investigating economic decisions relating to the energy investment, we might be able to understand the factors that birds perceive to be important enough to require altering their behavior.

*Figure 1 – Bon Secour National Wildlife Refuge study site (indicated by thick black dot) located along the northern edge of the Gulf of Mexico just south of Mobile Bay, Alabama.*

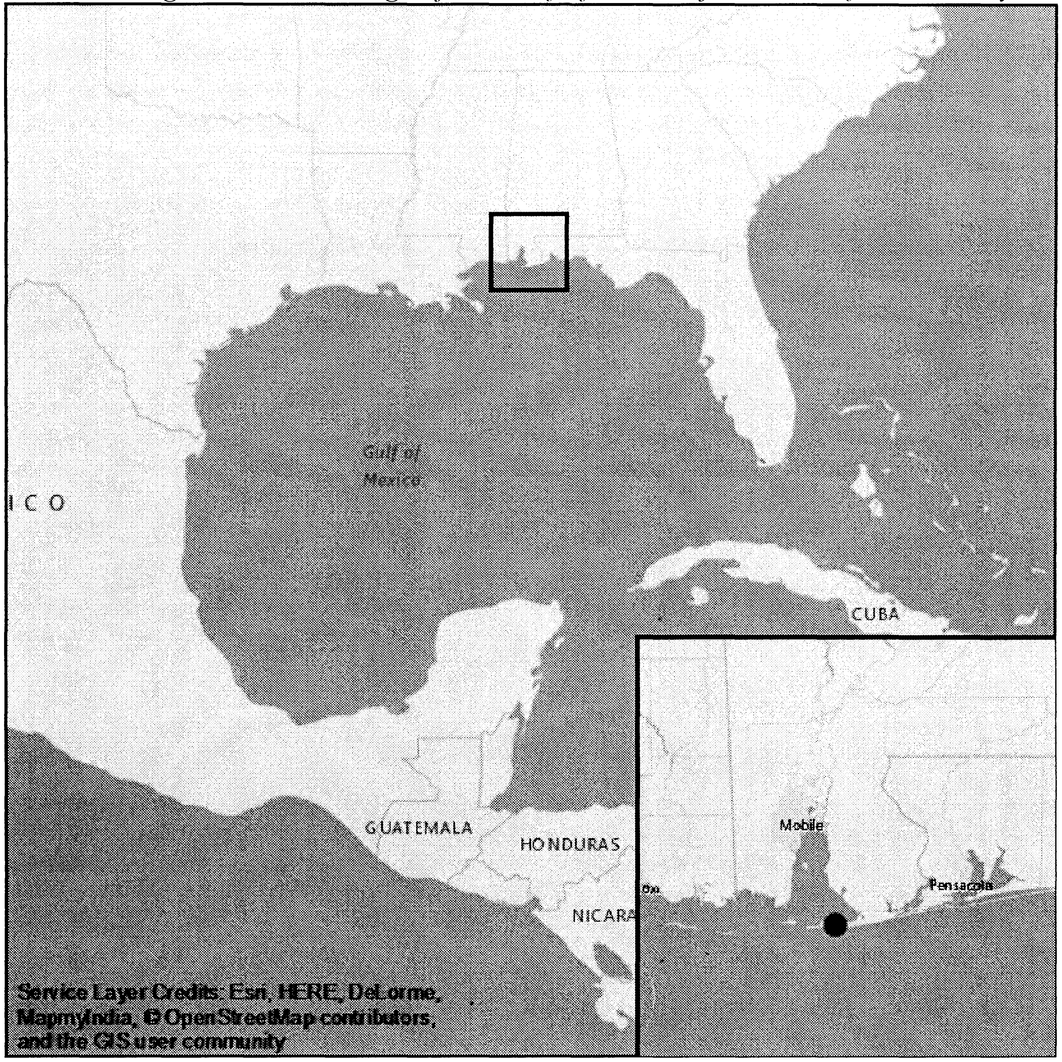


*Figure 2. Proportion of Red-eyed Vireos (a), Swainson's Thrushes (b), and Wood Thrushes (c) moving throughout the day at a stopover site on the Gulf Coast of Alabama from 2011–2014.*

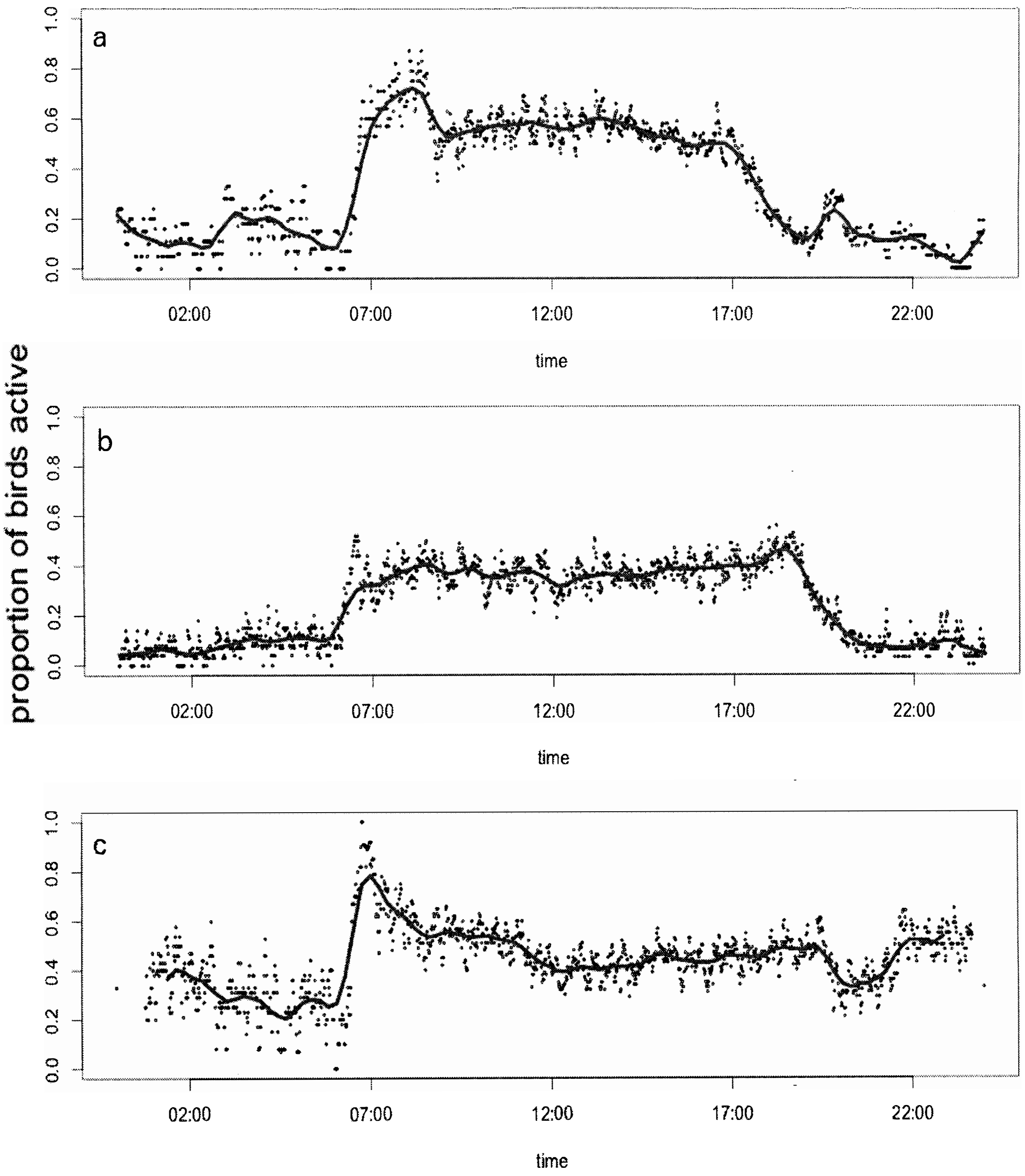


*Figure 3. The impact of wind direction on afternoon and evening movement rates in Red-eyed Vireos at a stopover site on the Gulf Coast of Alabama from 2013–2014.*

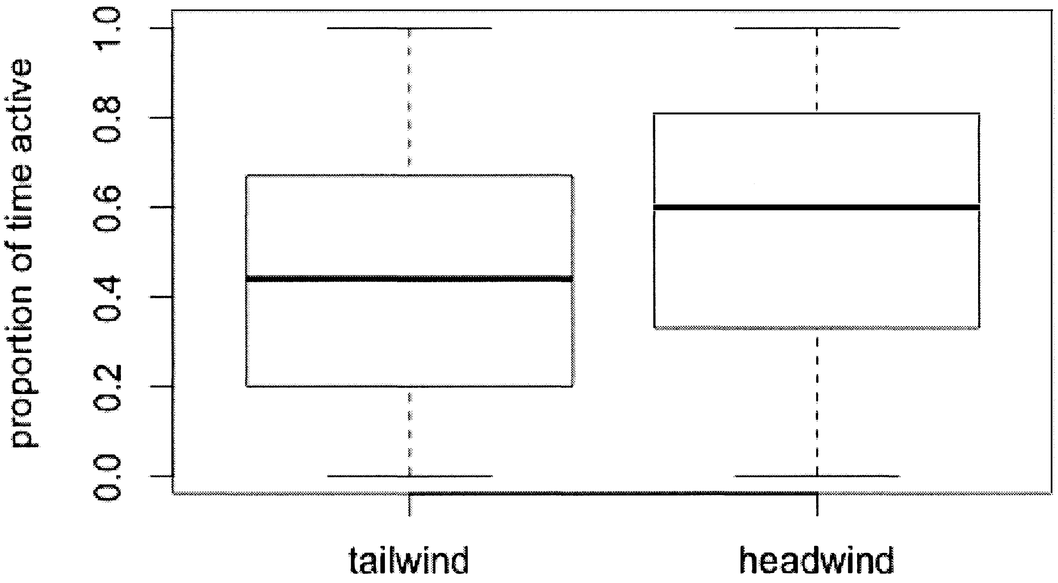


*Figure 4. The impact of fat on afternoon and evening movement rates in Swainson's Thrushes at a stopover site on the Gulf Coast of Alabama from 2011–2014.*

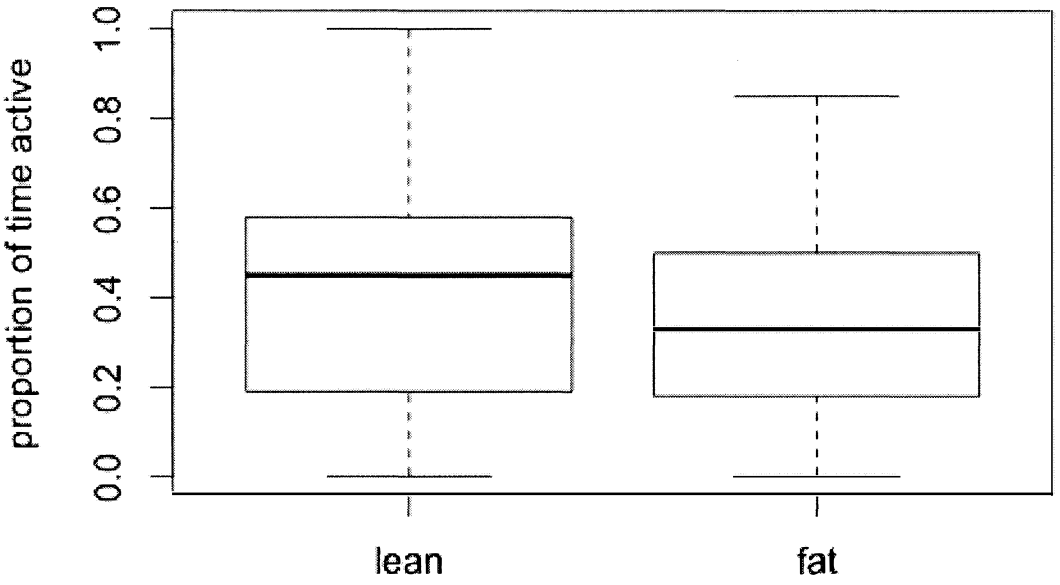


*Figure 5. The impact of wind direction on afternoon and evening movement rates in Wood Thrushes at a stopover site on the Gulf Coast of Alabama from 2012–2014.*

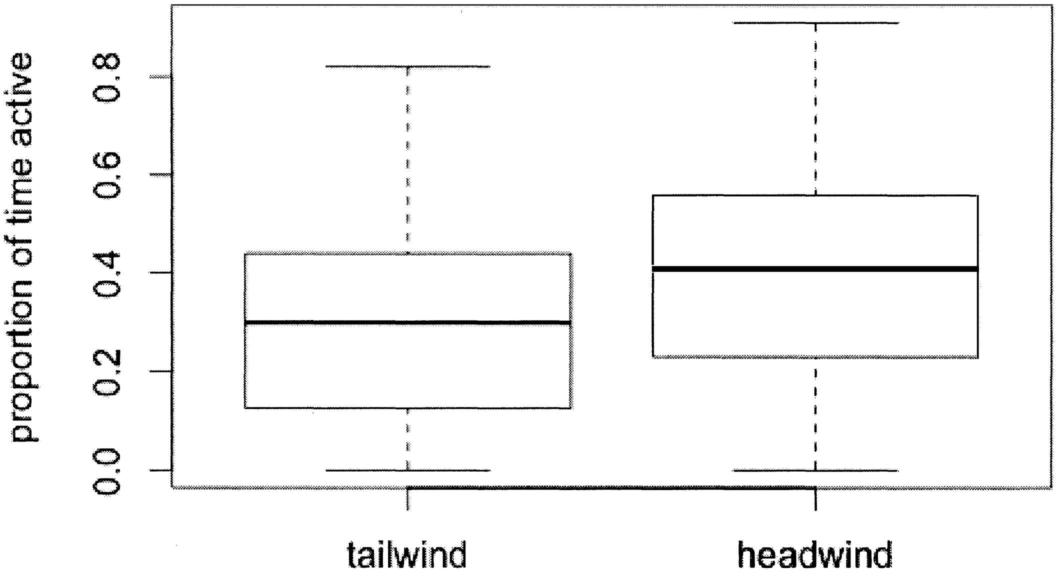


*Table 1. AICc values ofcandidate generalized linear mixed-effect models for hourly movement of three species at a stopover site on the Gulf Coast of Alabama, with Species and Period as fixed effects and individual as a random effect where delta AIC$_c$ is less than 4.*

| Model | K | AICc | Delta AICc | AICc Wt | Cum. Wt | Log Likelihood |
|---|---|---|---|---|---|---|
| Species + Period | 6 | 2832.53 | 0 | 0.71 | 0.71 | -1410.24 |
| Species * Period | 10 | 2834.29 | 1.77 | 0.29 | 1 | -1410.24 |

*Table 2. AICc values of candidate generalized linear mixed-effect models for hourly movement of Red-eyed Vireos in the morning interval and the afternoon and evening interval at a stopover site on the Gulf Coast of Alabama, with Fat, Age, Wind Speed (WS), and Wind Direction (WD) as fixed effects and individual as a random effectwhere delta AICc is less than 4..*

| Model | K | AICc | Delta AICc | AICc Wt | Cum. Wt | Log Likelihood |
|---|---|---|---|---|---|---|
| *Morning* | | | | | | |
| WS | 3 | 74.57 | 0 | 0.28 | 0.28 | -34.02 |
| Age + WS | 4 | 75.23 | 0.66 | 0.2 | 0.47 | -33.17 |
| Fat + WS | 4 | 75.8 | 1.24 | 0.15 | 0.62 | -33.46 |
| Age + WS + WD | 5 | 75.95 | 1.38 | 0.14 | 0.76 | -32.29 |
| Fat + Age + WS | 5 | 76.37 | 1.8 | 0.11 | 0.87 | -32.5 |
| Fat + Age + WS + WD | 6 | 77.6 | 3.03 | 0.06 | 0.93 | -31.82 |
| *Afternoon* | | | | | | |
| Fat + Age + WS + WD | 6 | 326.14 | 0 | 0.51 | 0.51 | -156.89 |
| Age + WS + WD | 5 | 326.5 | 0.36 | 0.43 | 0.94 | -158.12 |

*Table 3. Model averaged estimates and 95% confidence intervals of Fat, Age, Wind Speed (WS), and Wind Direction (WD) for 14 candidate generalized linear mixed-effect models for hourly movement of Red-eyed Vireos in the afternoon at a stopover site on the Gulf Coast of Alabama*

| | | | 95% Confidence Interval | |
|---|---|---|---|---|
| Variable | Regression Estimate | SE | Lower | Upper |
| WS | -0.13 | 0.1 | -0.34 | 0.07 |
| Fat | 0.15 | 0.09 | -0.04 | 0.33 |
| Age (AHY) | 0.21 | 0.29 | -0.37 | 0.79 |
| Headwind | 0.87 | 0.28 | 0.32 | 1.43 |

*Table 4. AICc values of candidate generalized linear mixed-effect models for hourly movement of Swainson's Thrushes in the morning interval and the afternoon and evening intervalat a stopover site on the Gulf Coast of Alabama, with Fat, Age, Wind Speed (WS), and Wind Direction (WD) as fixed effects and individual as a random effectwhere delta AICc is less than 4*

| Model | K | AICc | Delta AICc | AICc Wt | Cum. Wt | Log Likelihood |
|---|---|---|---|---|---|---|
| *Morning* | | | | | | |
| Fat + WS | 4 | 163.52 | 0 | 0.28 | 0.28 | -77.59 |
| WS | 3 | 163.56 | 0.03 | 0.28 | 0.56 | -78.68 |
| Age + WS | 4 | 164.52 | 1 | 0.17 | 0.74 | -78.09 |
| Fat + Age + WS | 5 | 165.48 | 1.95 | 0.11 | 0.84 | -77.48 |
| Age + WS + WD | 5 | 165.76 | 2.24 | 0.09 | 0.94 | -77.62 |
| Fat + Age + WS + WD | 6 | 166.52 | 3 | 0.06 | 1 | -76.89 |
| *Afternoon and Evening* | | | | | | |
| Fat + Age + WS | 5 | 295.08 | 0 | 0.54 | 0.54 | -142.42 |
| Fat + Age + WS + WD | 6 | 296.73 | 1.65 | 0.24 | 0.78 | -142.2 |
| Age + WS | 4 | 298.8 | 3.72 | 0.08 | 0.87 | -145.32 |
| Fat + WS | 4 | 299.16 | 4.08 | 0.07 | 0.94 | -145.5 |

*Table 5. Model averaged estimates and 95% confidence intervals of Fat, Age, and Wind Speed (WS) for 14 candidate generalized linear mixed-effect models for hourly movement of Swainson's Thrushes in the afternoon at a stopover site on the Gulf Coast of Alabama.*

| | | | 95% Confidence Interval | |
|---|---|---|---|---|
| Variable | Regression Estimate | SE | Lower | Upper |
| WS | -0.17 | 0.09 | -0.35 | 0.02 |
| Fat | -0.22 | 0.09 | -0.4 | -0.04 |
| Age (AHY) | 0.24 | 0.36 | -0.46 | 0.95 |

*Table 6. AICc values of candidate generalized linear mixed-effect models for hourly movement of Wood Thrushes in the morning interval and the afternoon and evening interval at a stopover site on the Gulf Coast of Alabama, with Fat, Age, Wind Speed (WS), and Wind Direction (WD) as fixed effects and individual as a random effectwhere delta AICc is less than 4*

| Model | K | AICc | Delta AICc | AICc Wt | Cum. Wt | Log Likelihood |
|---|---|---|---|---|---|---|
| *Morning* | | | | | | |
| WS | 3 | 73.18 | 0 | 0.31 | 0.31 | -33.33 |
| Age + WS + WD | 5 | 73.37 | 0.2 | 0.28 | 0.6 | -31.01 |
| Age + WS | 4 | 74.42 | 1.24 | 0.17 | 0.77 | -32.76 |
| Fat + WS | 4 | 75.51 | 2.33 | 0.1 | 0.86 | -33.31 |
| Fat + Age + WS + WD | 6 | 75.79 | 2.61 | 0.08 | 0.95 | -30.92 |
| Fat + Age + WS | 5 | 76.79 | 3.61 | 0.05 | 1 | -32.71 |
| *Afternoon and Evening* | | | | | | |
| Age + WS + WD | 5 | 141.92 | 0 | 0.74 | 0.74 | -65.68 |
| Fat + Age + WS + WD | 6 | 144.14 | 2.23 | 0.24 | 0.99 | -65.68 |

*Table 7. Model averaged estimates and 95% confidence intervals of Age, Wind Speed (WS), and Wind Direction (WD) for 14 candidate generalized linear mixed-effect models for hourly movement of Wood Thrushes in the afternoon at a stopover site on the Gulf Coast of Alabama.*

| | | | 95% Confidence Interval | |
|---|---|---|---|---|
| Variable | Regression Estimate | SE | Lower | Upper |
| WS | -0.33 | 0.15 | -0.63 | -0.02 |
| Age (AHY) | 0.61 | 0.72 | -0.8 | 2.02 |
| Headwind | 2.05 | 0.61 | 0.86 | 3.23 |

## CHAPTER II

# Migratory Quiescence in Three Bird Species at a Stopover Site on the Northern Coast of the Gulf of Mexico

## Abstract

Migratory quiescence is a behavior characterized by a period of reduced activity occurring before birds depart from a stopover site during migration. It has been documented in captive studies but has not yet been observed in the wild. This study documents and characterizes migratory quiescence at a stopover site along the Gulf Coast in southern Alabama during fall migration in three species of songbirds, Red-eyed Vireo (*Vireo olivaceus*), Swainson's Thrush (*Catharus ustulatus*), and Wood Thrush (*Hylocichla mustelina*). We found that of these three species, only Red-eyed Vireos displayed a period of quiescence prior to migratory departure that differed significantly from other periods of stillness that occurred throughout the day. To investigate the purpose of this behavior, we examined morphological, physiological, and environmental correlates with the quiescent period to gain insight into its function. Only age and surface wind-speed at the time of departing a stopover site were related to quiescence. The purpose of migratory quiescence remains unclear, but our data suggest that some aspect of the physiology of a species (particularly their diet and the need to expel waste prior to initiating migration), and the experience of the individual are the factors most likely to be influencing quiescence.

## Introduction

Songbird migration is typically characterized by a series of long-distance flights interspersed with periods of stopover with only localized movements within a single stopover site. Birds often must stop to build fat stores and prepare for the next stage of their migration to mitigate the risk of long-distance migratory flights (Seewagen and Guglielmo 2010, Cohen et al. 2014). During these stopovers, songbirds need to accumulate significant fat reserves (Pennycuick 2008), especially prior to crossing major geographic barriers such as large bodies of water or deserts. Understanding the full range of behaviors that bird species use during stopovers is important for gaining greater insight into how birds prepare for making these crossings.

Migratory quiescence can be defined as either a period of decreased activity or total inactivity prior to departure from a stopover site often occurring shortly after sunset that is distinctly different from what would be observed during other intervals during the day(Agatsuma and Ramenofsky 2006, Ramenofsky et al. 2008).Only a handful of studies have addressed quiescence, and no study has made an attempt to examine how and why this behavior occurs. Studies focusing on diel activity patterns of captive Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gamebelii*) have noted a clear, significant drop in activity as compared with activity during the rest of the day in the early evening interval prior to migratory restlessness during both spring and fall (Ramenofsky et al. 2008). However, captivity is known to produce some behaviors that are atypical of wild birds (Kjos and Cochran 1970, Moore and Aborn 1996). In the wild, quiescence has only been noted anecdotally (Diehl and Larkin 1998, Agatsuma and

Ramenofsky 2006). In Diehl and Larkin's (1998) telemetry study of migratory birds, they observed a period of inactivity in free-living Swainson's Thrushes (*Catharus ustulatus*)and Gray-cheeked Thrushes (*Catharus minimus*). The observed length of inactivity in this study varied between four and forty-one minutes (*n* = 5), although it was unclear whether these observations of inactivity were biologically meaningful. Without knowledge of a bird's background pattern of activity across an entire day, it is difficult to assess whether these intervals of inactivity are different from the background rate of inactivity that occurs throughout the day. The only other proposed evidence for a quiescent period in free-living birds is observations that passerine birds initiate migration approximately forty-five minutes after sunset, which was interpreted as inactivity between sunset and departure, but the behavior was not directly observed (Hebrard 1969).

The possible purpose of quiescence remains unknown, and few hypotheses have been proposed to explain why this phenomenon might occur. It has been suggested that birds use the time between sunset and departure to orient themselves in relation to solar or celestial cues or to make other departure decisions (Vleugel 1979, Moore 1987, Thorup and Rabøl 2007, Thorup et al. 2010). If birds are calibrating their internal compass in relation to the setting sun or emerging stars, local light conditions on that day would likely play a part in determining whether or not it occurs. On days when the sun is visible, quiescence would be expected to be relatively uniform in length and other characteristics. The quiescence period may be a physiological requirement, in that it is the time required to excrete excess wastes or to metabolize fat. However, food-limited sparrows, which should require less time for either of these functions, were not observed to vary their quiescence period in comparison to birds with unrestricted access to food in captive studies (Ramenofsky et al. 2008). Were quiescence to play a role in decision making, its duration and intensity could vary greatly and it might be indicative of how prepared a bird is to continue its migration. Wind and weather might also affect a bird's decision-making process and the characteristics of quiescence. In addition, because species differ in flight mechanics, migratory destinations, metabolic needs, departure times from stopover sites, and directions towards which birds will depart (Calvert et al. 2012, Deppe et al. in review), quiescence behavior may also vary among species.

Automated radio telemetry units (ARUs) offer the ability to remotely quantify and more completely understand small-scale behaviors such as quiescence in a continuous manner (Kays et al. 2011, Smolinsky et al. 2013). They also have the advantage of being capable of continuously monitoring many radio-tagged individuals simultaneously (Kays et al. 2011, Sperry et al. 2013). By monitoring fluctuations in the strength of radio signals received by an ARU and the azimuth from which the signal originated, it is possible to infer movement of a radio-tagged bird (Cochran 2006). With this method, quiescence can be readily described in a large sample of individuals despite the difficulty of visually observing a behavior that typically occurs after dusk. Additionally, automated radio telemetry allows comparison of the rate of movement and duration of inactivity directly prior to departure with a species' rate of movement throughout the day, making it possible to put the pre-departure behavior into the context of a bird's movement patterns during other periods of stopover.

This study's main objective was to document the occurrence and nature of the quiescent period during fall migration in three species of migratory songbirds at a stopover site along the northern edge of a major geographic feature (the Gulf of Mexico) prior to crossing. To gain insight into the quiescent period's function, we also examined physiological and environmental correlates: a bird's energy stores at the time of capture, surface wind speed, wind direction, and cloud cover at the time of a bird's departure. We also addressed the role quiescence might play in a bird's departure decisions, namely the direction in which birds depart from the study site.

## Methods:

### *Field Methods*

Between 2011 and 2014, we conducted field work during the peak of autumn songbird migration (1 September to 31 October) at a long-term bird banding stationon the Bon Secour National Wildlife Refuge located on the Fort Morgan Peninsula in Alabama, USA (30.2397° N, 87.8199° W). The Fort Morgan Peninsula is a narrow stretch of coastal scrub dune and maritime forest habitat, approximately 20 km in length and averaging about 1 km in width that is bordered by Mobile Bay to the north and the Gulf of Mexico to the south (Chapter 1, Fig. 1).

We chose three species of trans-gulf migrants: Swainson's Thrush (*n* = 70; 2011–2014), Wood Thrush (*Hylocichla mustelina; n* = 45; 2012–2014) andRed-eyed Vireo (*Vireo olivaceus*; *n* = 63; 2013–2014) as our focal species. These species are abundant at on the Gulf Coast during migration, have diverse flight morphologies with differing wing loadings (i.e., wing surface area to weight ratio) and wing aspect ratios (i.e., wing length to wing width ratio; Yong and Moore 1994), and vary in their wintering locations, preferred habitats and diets (Mack and Yong 2000). We mist-netted, weighed, measured, aged (following Pyle 1997), and fitted individuals with aluminum U.S. Geological Survey leg-bands using standard bird-banding procedures (Gustafson et al. 2005). We assigned a fat class to birds (using a qualitative scale ranging from 0 to 6) based on the amount of subcutaneous fat visible between the furcular region and abdomen (Helms and Drury 1960). We then marked individuals with a radio pulse transmitter by affixing radio tags to an individual's back using the methods and transmitters described in Chapter 1.Once tagged, we recorded the signal strength from individual frequencies with automated radio receiving systems located near the banding station (30.2288° N, 88.0013° W). The radio receiving system consists of a circular array of six three-element Nighthawk brand yagi antennas (described in Chapter 1)

### *Data Interpretation and Movement*

Because ARUs continuously recorded any signal received on each frequency, it was necessary to differentiate positive detections of tagged individuals from ambient electro-magnetic noise. To do so, we created algorithms in Python 2.7 that differentiated positive detections from background noise (Chapter 1).We inferred temporal movement patterns using the fluctuation of signal strength between each consecutive time step in which a bird was detected (Cochran 2006, Chapter 1).

The observations of ARU data differed in their sampling rate with most individuals sampled once every five minutes for the majority of the season, but sampling took place at a rate as high as once every three minutes and as low as once every six minutes depending on the number of frequencies being scanned. To standardize the sampling rate between birds, we smoothed the change in signal strength data by linearly interpolating the change in signal strength between samples across the number of minutes between samples, such that we had an estimate of change in signal strength every minute for each individual.

### *Data Analysis*

We determined the degree of inactivity during the pre-departure period for each bird by comparing its inactivity rate and duration of inactivity with the background rates of inactivity. We defined the inactivity rate as the proportion of time during the two hours prior to initiating departure from the stopover site that a bird was observed by the ARU not to be moving. The duration of inactivity was defined as the total number of minutes prior to the initiation of departure in which no activity was recorded. In our analyses, we only included birds that displayed a clear initiation of migratory-departure behavior from the study site (i.e., a sudden spike in signal strength followed by a rapid tapering-off in signal strength), which occurs when the bird initially flies above the vegetation and then moves away from the ARU (Smolinsky et al. 2013). Although this behavior typically occurs in the evening, all birds showing a clear departure were included in this study. We censored birds that exhibited a slower, more gradual decline in signal strength not preceded by a spike in radio signal, indicative of birds not initiating migration but instead slowly moving outside of the range of the ARUs.

We employed iterative e Chain Monte Carlo simulations similar to those described by Gelman and Rubin (1992) and Downey (2013) to compare movement patterns during the pre-departure period to rates of inactivity observed throughout the day for each species. With this, we determined whether the two-hour pre-departure period was characterized by a greater rate of inactivity and length of inactivity than would occur at other intervals throughout the entirety of the day (Gelman and Rubin 1992, Geyer 1992). We built transition matrices (using a program we designed in ‘R’ version 3.1 [R Development Core Team 2013]) using transition states occurring from 05:00 until the beginning of the two-hour period prior to departure. Nighttime activity was not considered as part of the background activity nor could the typical pre-departure interval be compared between departing and non-departing birds because only 9 birds out of a total of 241 tagged during the course of the study (~4%) remained overnight and many of those never displayed a clear departure. With the daytime background activity, we created 9,999 simulations of two-hour intervals of movement based on these baseline activity patterns and determined where the observed quiescence data fell relative to the distribution of simulated data, although similar patterns could be seen with as few as 19 simulations. Additionally we visually compared the simulated distributions of average rates of background inactivity with simulated distributions of pre-migratory inactivity to add further insight into the differences in movement between background and the quiescent period.

We used a general linear model in 'R' (using the default glm function that comes with the software in package "stats" [R Core Team 2013]) to model the influence of species on the rate of inactivity. Then we used *t*-tests to determine if differences in pre-departure inactivity patterns for each species pair were significant. We examined the relationship between the rates of inactivity in species displaying a clear quiescence period with weather conditions, specifically wind speed (meters per second), wind direction, and cloud cover (percent coverage) using a general linear model. Wind direction was defined as being degrees from north such that north is 0 degrees, south is 180 degrees, and both east and west are 90 degrees in order to account for the circularity of the data. Weather data were obtained from the National Oceanic and Atmospheric Administration's North American Regional Reanalysis wind data set (spatial resolution of 32 KM, with measurements taken 8 times daily) accessed through movebank.org's Env-DATA service.

We also examined the relationship between quiescence and intrinsic factors such as fat (on a qualitative 0-6 scale), age (as either having hatched that year [first year] or as one or more full years old [after first year]), and sex using ANOVA tests. To investigate the influence of the direction of departure (the azimuth from which individuals were last detected from the ARU tower as they left the study site) from the stopover site on quiescence period, we used circular ANOVAs using the 'circular' package in 'R' (Agostinelli and Lund 2013). We considered all results to be significant at $\alpha = 0.05$.

## Results

We examined the length of inactivity prior to migratory departure and the proportion of a pre-departure interval spent inactive in 63 Red-eyed Vireos, 70 Swainson’s Thrushes, and 45 Wood Thrushes. The characteristics of both pre-departure inactivity and background inactivity varied among species examined (Figs. 1a and 1b). Our models indicated the rate of inactivity exhibited by Red-eyed Vireos was greater than in Swainson's Thrushes ($t = -4.953$, $d.f. = 175$, $p < 0.0001$) or Wood Thrushes ($t = -5.624$, $d.f. = 175$, $p < 0.0001$), but Wood Thrushes and Swainson’s Thrushes had a similar level of inactivity ($t = -1.195$, $d.f. = 175$, $p = 0.235$). Similarly, the length of quiescence was significantly greater in Red-eyed Vireos ($\bar{x} = 94$ min) than both Swainson’s Thrushes($\bar{x} = 21$ min; $t = -8.066$ $d.f. = 175$,$p < 0.0001$) and Wood Thrushes ($\bar{x} = 20$; $t = -7.158$, $d.f. = 175$, $p < 0.0001$), whereas there was no difference between thrush species ($t = -0.116$, $d.f. = 175$, $p = 0.908$).

Only Red-eyed Vireos had a clearly defined difference in inactivity between the observed quiescent period and simulations based on transition matrices built using background rates of inactivity (Fig.2). Additionally, only Red-eyed Vireos differed in their distribution of inactivity rates between simulations based on background movement and those based on pre-departure movement (Fig.3). During the quiescent period, inactivity rose from an average of 46.9% of total time spent inactive during the daytime interval to 84.3% of time spent inactive during the two hours prior to departure ($p = 0.0039$). Similarly, Red-eyed Vireos spent a mean of 94 consecutive minutes inactive prior to departure, significantly higher than average of six consecutive minutes of inactivity occurring in simulations based on their daylight activity transition pattern ($p = 0.0002$).

Swainson's Thrushes did not significantly show a quiescence period. There was no difference between the proportion of time they spent inactive during the two hours prior to departure (65.0%) and the background rate of inactivity (60.2%; $p$ =0.375). Additionally, the average number of consecutive minutes Swainson's Thrushes spent inactive prior to initiating migration (21 min) was not different from the number of minutes spent inactive during random simulations (8 min; $p$ =0.161).

Wood Thrushes also did not display migratory quiescence. They spent 59.6% of their time inactive prior to departure compared with 51.8% of the time inactive during the rest of the day ($p$ = 0.319). The amount of time inactive prior to initiation of migration for Wood Thrushes (20 minutes) was similar to the simulated average length of inactivity (16 minutes; $p$ = 0.276).

Wind direction was not found to significantly influence the quiescence rate ($t$ = 0.299*d.f.*= 54, $p$ = 0.766). Wind speed, regardless of wind direction, significantly influenced the proportion of time Red-eyed Vireos spent inactive during quiescence ($t$= 2.096, *d.f.* = 54, $p$ = 0.0408) with higher wind speeds resulting in a greater amount of inactivity (Fig. 4). However, the effect size was relatively small (adjusted $R^2$ 0.0453). There was also no relationship between either departure direction ($p$ = 0.778, Fig. 5) or fat (F$0.017_{1,60}p$ = 0.896) and quiescence. However, age was significantly related to the proportion of time spent inactive prior to departing from the stopover site ($F_{1,61}$ = 8.066., *p* = 0.00612, Fig. 6) with first-year birds spending 10% less time on average inactive prior to departure.

## Discussion

We observed a distinct quiescence period in Red-eyed Vireos at Bon Secour NWR prior to departing from the study site. However, neither Swainson's Thrushes nor Wood Thrushes displayed a period of decreased activity prior to departing from the study site.One explanation for the existence of a quiescent period is that it functions as a time for birds to calibrate their internal compass with the setting sun and orient themselves in preparation for continuing their migration (Moore 1987). Although birds have been shown to use solar cues in navigation (Armstrong et al. 2013), it is not clear that quiescence is related to how birds orientation with the sun. Were Red-eyed Vireos using quiescence for calibrating their internal compass, we would expect to observe a significant relationship between cloud cover and quiescence, which we did not. The average time of departure is also variable in Red-eyed Vireos, extending up to several hours past civil twilight (i.e., when the center of the sun is 6 degrees below the horizon), suggesting that the quiescent period is not related to time of sunset.

We did not find evidence to support the hypothesis that quiescence functions in decision-making. Decisions a migratory bird might make as it prepares to depart across a large barrier such as the Gulf of Mexico include 1) whether to depart or to remain foraging at the same stopover site and 2) in which direction to depart. Only a very small percentage of birds remained at the stopover site; in this system most Red-eyed Vireos departed the same day as they were captured. It therefore seems unlikely that the variation in quiescence for Red-eyed Vireos is related to the decision to continue their migration. Departure directions were highly variable in Red-eyed Vireos, with birds often moving north rather than south (Fig. 5; Sandberg and Moore 1996), but there was no relationship between the departure direction and quiescence. In other studies fat storeswere observed to be the single greatest factor in the direction of departure chosen by a bird (Smolinsky et al. 2013, Deppe et al. in review), and also influenced a tagged bird's probability of being encountered on the other side of the Gulf of Mexico along the Yucatan Peninsula within this study system (Deppe et al. in review). However, fat was not related to quiescence in this study. The relationship between age and quiescence suggests that individual experience (i.e., awareness of the upcoming effort required to traverse the Gulf of Mexico) could play a role in this behavior. This might suggest that a decision is possibly being made in relation to how birds choose to allocate their resources just prior to leaving the stopover site.

The hypothesis that quiescence is a time when birds are assessing their surroundings and waiting for an appropriate time to depart is partially supported by our data. Birds departing later in the evening tended to have a somewhat longer quiescent period, indicating that these birds might have been remaining still until certain conditions occurred or until the point at which waiting was no longer viable. Wind conditions that birds are experiencing are likely to influence their assessment of their surroundings, and our findings showed quiescence to be slightly longer on evenings with higher surface wind speeds, potentially indicating that Red-eyed Vireos were waiting for wind speeds to moderate as the evening progressed before continuing migration, regardless of the direction. The relationship between quiescence and wind speed or timing of departure could indicate birds are waiting for winds to calm, but since the great majority still ultimately depart and the range of departure times is relatively narrow (interquartile range of 29 minutes), it seems counterintuitive that it would be advantageous for a bird to gamble its time on a sudden change in wind conditions. The small effect size of wind on quiescence also calls into question how much wind speed is really influencing a bird's pre-departure behavior.

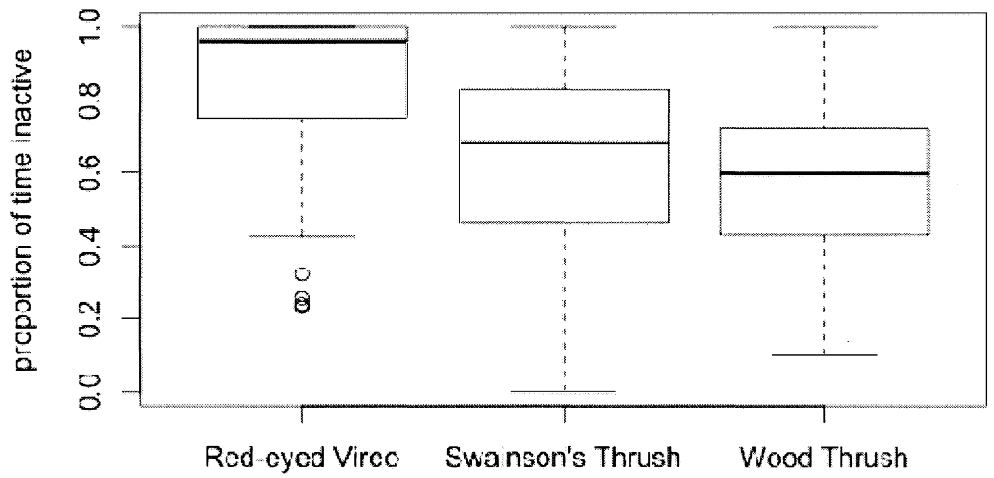
Because quiescence is a phenomenon that is most strongly correlated with species, it seems likely that the purpose of quiescence has more to do with the biology of a species than the conditions experienced by any given individual. As such, the final hypothesis that we propose for the function of quiescence is that it is a time for individuals to digest food and expel waste prior to initiating departure. Since thrushes are primarily frugivorous during the fall, it takes very little time for them to eliminate waste (Mack and Yong 2000). Red-eyed Vireos, on the other hand, have a more generalist diet during migration and a larger proportion of their diet is composed of arthropods (Cimprich et al. 2000). This diet could require more time to digest. There would also be diminishing returns when foraging for insects as the day progresses making it more beneficial to cease activity during the latter part of the day than to keep actively searching for food. This hypothesis is further supported by the fact that the few captive studies to have observed quiescence period have focused on seed-eating White-crowned Sparrows (Ramenofsy et al. 2008 and 2012), which would also require a relatively long time to digest their meals.

This is also supported by the fact that adult Red-eyed Vireos, which are presumably more efficient foragers and more capable of being selective in terms of food choice tend to spend more time inactive prior to departing the stopover site than do younger birds. It has also been shown that individuals of some species may delay migration if they consumed an insufficient amount of protein during stopover (Aamidor et al. 2011). However, in cage studies it has also been noted that the rate of inactivity during the evening prior to initiating migratory activity does not apparently vary in response to a marginally restricted food intake, suggesting that if quiescence is related to digestion it is perhaps influenced more by diet type than by overall food intake.

Although an experimental approach would be needed to determine the exact function of migratory quiescence, this study has documented the existence of quiescence behavior in wild Red-eyed Vireos and a distinct contrast in pre-departure behavior between Red-eyed Vireos and two thrush species. Techniques that take advantage of ARU technology have great potential for aiding our understanding of small-scale behaviors such as quiescence that have, up until now, been prohibitively difficult to study in the wild. Although recent research related to migration has focused largely on assessing migratory connectivity and the migratory routes selected by birds, fine scale questions remain important (Gauthreaux 1979, Bowlin et al 2010). ARU technology might be one of the best ways to understand behaviors at a fine scale for a wide variety of species in the wild and, most importantly, may help us obtain a more complete understanding of migratory systems as a whole and to compare how different species respond to the challenges of migration.

*Figure 1. The observed proportion of time spent inactive during the two-hour interval prior to departing from a stopover site on the Gulf Coast of Alabama (a) and the simulated proportion of time spent inactive during the rest of the day (b) for three study species from 2011–2014.*

1a



1b

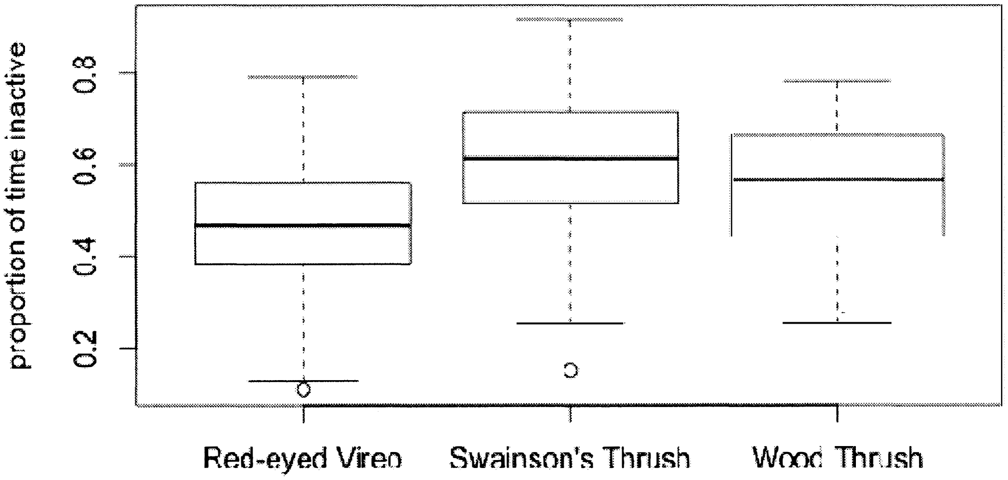


*Figure 2. Proportion of time inactive pre-departure as compared with the proportion of time spent inactive during simulated two-hour intervals based on activity patterns throughout the entire day for three study species on the Gulf Coast of Alabama from 2011–2014.*

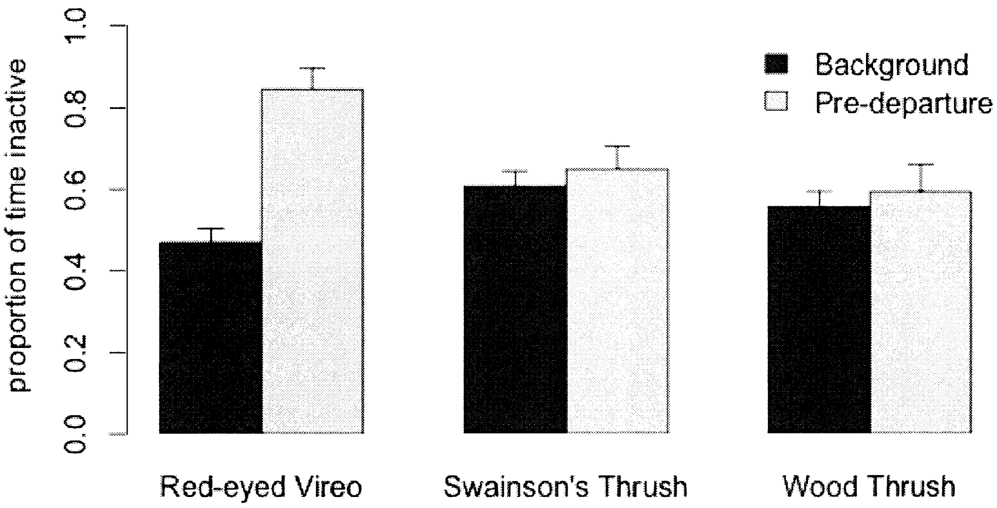


*Figure 3. Simulated distribution of background inactivity rates (a) and simulated distribution of rates of pre-departure inactivity (b) based on automated radio-telemetry unit measurements for three study species on the Gulf Coast of Alabama from 2011–2014.*

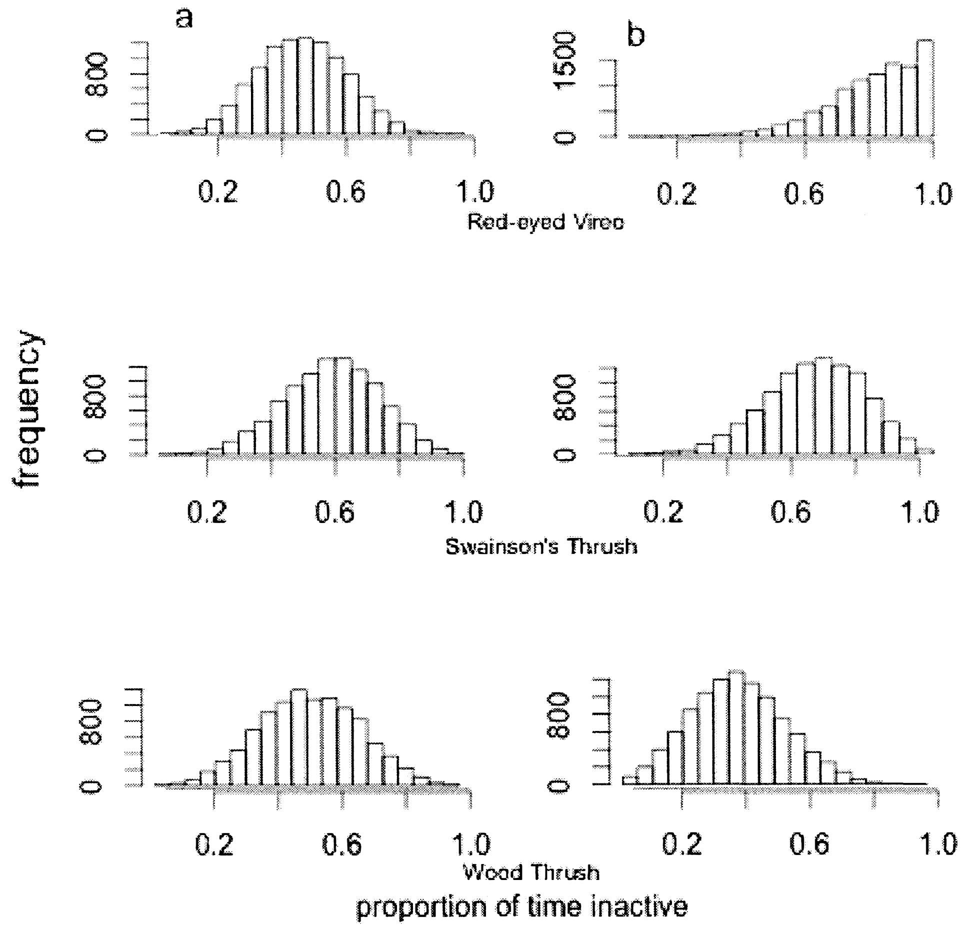


*Figure 4. The log number of consecutive minutes of inactivity prior to initiating departure from the stopover site versus sea surface wind speed at the time of departure for three study species on the Gulf Coast Alabama from 2011–2014.*

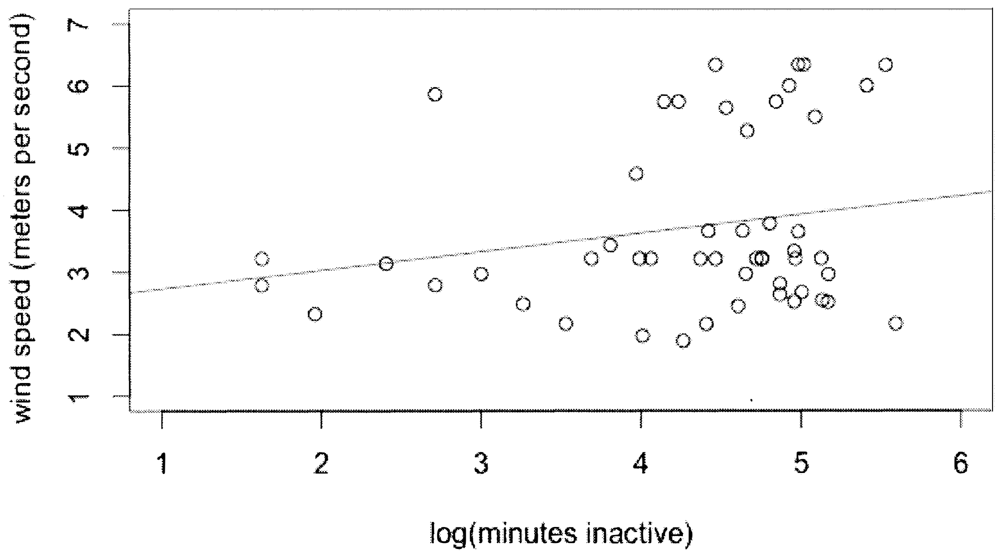


*Figure 5. The proportion of time Red-eyed Vireos spent inactive (radial axis) during the two-hour interval prior to initiating migration in relation to the compass direction of departure from the Gulf Coast of Alabama from 2013–2014.*

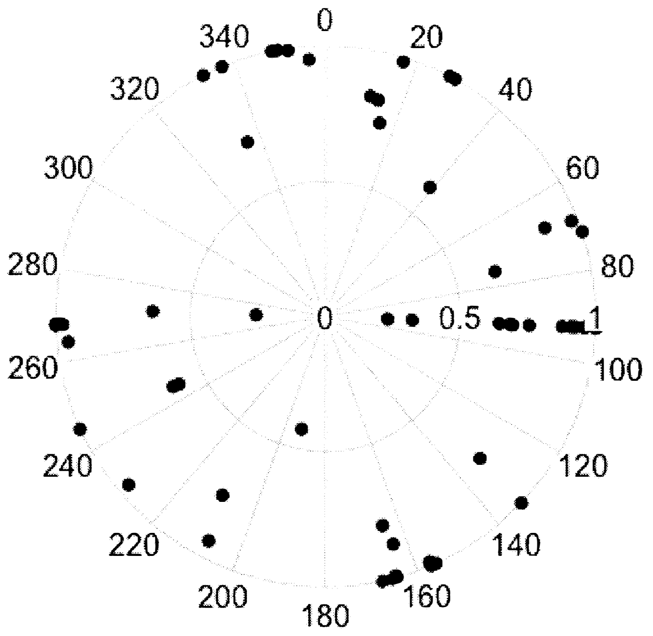
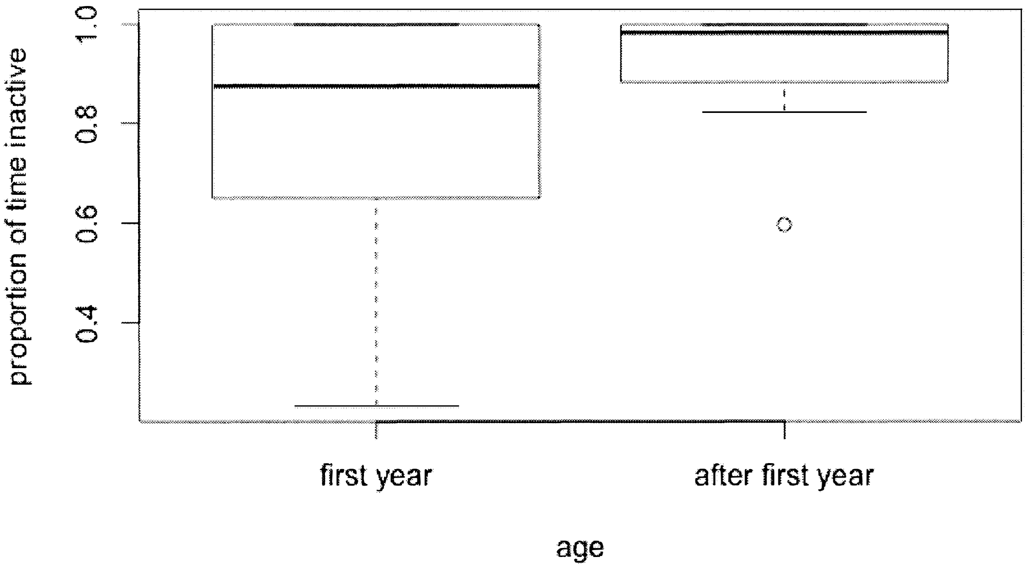


*Figure 6. The proportion of time spent inactive during the pre-departure interval in first year Red-eyed Vireos (that have yet to complete their first migration) and after first year Red-eyed Vireos (that have completed their migration at least once) at a migratory stopover site on the Gulf Coast of Alabama from 2013–2014.*



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