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RESEARCH ARTICLE

Using automated radio telemetry to quantify activity patterns of songbirds during stopover

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ABSTRACT

During migration, birds require stopover habitat to rest and refuel before resuming flight. While long-distance migratory flights represent a large energy investment, stopover accounts for roughly two-thirds of a bird's total energy expenditure during migration. Therefore, birds should minimize energy expenditure while also minimizing time and predation risk during stopover. To understand activity during migration, we recorded activity patterns (i.e. fine-scale movements associated with a range of behaviors) of 3 species, Red-eyed Vireo (*Vireo olivaceus*), Swainson's Thrush (*Catharus ustulatus*), and Wood Thrush (*Hylocichla mustelina*), at a stopover site along the northern coast of the Gulf of Mexico during autumn migration using automated radio telemetry. We found Red-eyed Vireos to be the most active and Swainson's Thrushes the least active. For each species, we used boosted regression trees to investigate associations between activity and factors known to influence bird behavior during stopover. While species differed, day of year and temperature were important predictors of activity for all species. Vireos were active early in the season, under light winds and warmer temperatures, and on evenings when winds were more favorable. Thrushes were more active as the season progressed and when temperatures were cooler. Thrush activity also differed between years, although thrushes increased activity later in the season during all years. Our results illustrate automated radio telemetry as a unique and valuable tool for understanding fine-scale behaviors of birds during stopover.

Keywords: activity, automated radio telemetry, boosted regression tree, *Catharus ustulatus, Hylocichla mustelina,* migration, movement, stopover, *Vireo olivaceus*

Uso de telemetría de radio automatizada para cuantificar los patrones de actividad de aves durante la escala migratoria

RESUMEN

Durante la migración las aves requieren hábitats de escala para descansar y recuperar su energía antes de reanudar el vuelo hacia su destino. Si bien los vuelos migratorios de larga distancia representan una gran inversión en energía, la escala representa aproximadamente dos tercios del gasto total de energía de un ave durante la migración. Por lo tanto, las aves deben minimizar su gasto de energía mientras minimizan el tiempo y la posibilidad de depredación durante su escala. Utilizando sistemas automatizados de telemetría de radio, examinamos patrones de actividad (movimientos a pequeña escala) de tres especies: Vireo ojos rojos (*Vireo olivaceus*), Zorzal de anteojos (*Catharus ustulatus*) y Zorzal moteado (*Hylocichla mustelina*) durante la migración de otoño en un sitio de escala a lo largo de la costa norte del Golfo de México. Los Vireos ojos rojos fueron los más activos, seguidos por el Zorzal moteado y el Zorzal de anteojos. Para cada especie, utilizamos árboles de regresión potenciado para investigar las asociaciones entre la actividad y los factores que influyen en las aves durante la escala. Si bien cada especie difirió, el día del año y la temperatura fueron importantes predictores de actividad para todas las especies. Los Vireos fueron muy activos al inicio de la temporada de migración, bajo condiciones con poco viento y temperaturas cálidas, y por las tardes cuando el viento era favorable. Los Zorzales fueron más activos conforme la temporada fue progresando y cuando las temperaturas fueron más bajas. Aunque cada año los Zorzales aumentó actividad más tarde en la temporada, la actividad de los Zorzales difirió entre años. Nuestros resultados muestran que los sistemas automatizados de telemetría de radio son herramientas valiosas para entender los comportamientos a pequeña escala de las aves durante la escala migratoria.

Palabras clave: actividad, telemetría de radio automatizada, árbol de regresión potenciado, Catharus ustulatus, *Hylocichla mustelina,* migración, movimiento, escala, *Vireo olivaceus*

INTRODUCTION

Long-distance migratory songbirds can invest a large amount of energy in long-distance flights, but they expend more energy per unit time during stopover, because repeated small flights during stopover are more costly (Nudds and Bryant 2000, Wikelski et al. 2003, Bowlin et al. 2005). For birds that cross large geographic features, like the Gulf of Mexico, judicious use of energy is critical, as an individual's quick and successful flight is strongly influenced by its energy reserves (Deppe et al. 2015). However, migrants need to balance energy, time, and predation risk to quickly and safely refuel and continue migrating (see Alerstam and Lindström 1990). A bird's activity during stopover, which is the collective sum of fine-scale movements associated with a range of behaviors, serves as a proxy for energy expenditure (Bäckman et al. 2017).

Activity during stopover is likely influenced by intrinsic (species, body condition, age, sex) and extrinsic (day of year, weather conditions) factors. Species likely vary in their activity because of differences in diet, foraging tactics, flight morphology, and energy needs for crossing geographic barriers (Deppe et al. 2015). Within species, birds preparing to cross geographic barriers may adjust activity based on body condition, previous migration experience (i.e. age), and sex. For example, lean birds show higher movement rates than fat birds prior to departure, especially as food resources decline (Smith and McWilliams 2014). However, lean birds should only increase activity to accumulate fat if foraging is profitable (Graber and Graber 1983, Loria and Moore 1990, Wang and Moore 1993). Less frequent movements of fat birds presumably allow them to conserve energy in preparation for migration. Older, more experienced birds may be less active than their younger counterparts if they are more efficient at gathering resources (Woodrey 2000, Heise and Moore 2003, Moore et al. 2003). Likewise, males may be less active as they tend to gain priority access to resources over females (e.g., Yong et al. 1998, Moore et al. 2003). Finally, activity patterns may also vary across the season as weather conditions, food availability, and pressure to arrive at the winter destination change (Able 1972, Buskirk 1980, Gauthreaux et al. 2005, Smith and McWilliams 2014), reflecting the need to balance energy demands and time constraints.

Local weather conditions can influence birds' activity at stopover sites. Precipitation generally reduces bird activity (Finlay 1976, Richardson 1978, 1990; Smith and McWilliams 2014), and temperature can influence activity in various ways. For example, birds may be more active on warmer days in response to elevated insect activity (e.g., Pinkowski 1977, Lemoine et al. 2014). However, activity also varies by time of day, with morning activity expected to be higher when temperatures are cooler and birds are making up for energy deficits associated with nocturnal inactivity or migration (Titov 1999, Chernetsov 2006). High wind speeds can hinder bird movement directly or indirectly by depressing activity of insect resources (e.g., Møller 2013, Maggini et al. 2015). Songbirds often initiate flights across large geographic features when wind profits, wind support in the direction of flight, are positive (e.g., Schmaljohann and Naef-Daenzer 2011, Shamoun-Baranes and van Gasteren 2011, Woodworth et al. 2015). Songbirds cross the Gulf of Mexico more rapidly and successfully with profitable winds (Deppe et al. 2015). Consequently, if winds are profitable later during the day, birds may adjust their activity toward the end of the day in preparation for southward flight.

Conventional, or manual, radio telemetry has advanced our understanding of fine-scale behaviors at stopover sites, such as habitat selection, movements within habitats or sites, stopover duration, and departure decisions (e.g., Aborn and Moore 2004, Schmaljohann et al. 2013, Schmaljohann and Eikenaar 2017). Nevertheless, many questions remain about the behavioral processes during stopover that can shape migratory pathways, timing, and survival (Cohen et al. 2017). For example, we have a poor understanding of birds' activity patterns across the day during stopover, as well as how activity varies in relation to intrinsic (sex, age, body condition; Seewagen et al. 2010, Smith and McWilliams 2014) or extrinsic (food availability, habitat, predation, weather, or day of year; Cohen et al. 2012, Slager et al. 2015) variables and departure decisions (Smolinsky et al. 2013, Deppe et al. 2015, Schmaljohann and Eikenaar 2017). Additionally, behaviors such as migratory quiescence (period of inactivity that occurs late in the day prior to a species' general departure time from a stopover site) have only recently been described in wild, free-flying birds (Schofield et al. 2018), and we know little about the nature of this behavior or its function.

Although automated radio telemetry systems (ARTS) have typically been used to collect data on broader-scale movements (e.g., Goymann et al. 2010, Smolinsky et al. 2013, Deppe et al. 2015, Sjöberg et al. 2015, Woodworth et al. 2015, Brown and Taylor 2017, Crysler et al. 2016, Zenzal et al. 2018), if they are appropriately positioned at a stopover site and offer adequate spatial coverage they can provide an effective method for studying fine-scale behaviors because they have fewer sampling constraints than manual telemetry. Specifically, ARTS can track movements of multiple individuals continuously over extended periods of time (Ward et al. 2013, 2014; Celis-Murillo et al. 2016, Zúñiga et al. 2016, Schofield et al. 2018). In this study, we used ARTS to explore activity (the sum of all fine-scale movements regardless of type or function) of individuals at a stopover site across the entire daytime period. In doing so we provide a basic framework for how automated telemetry can be used to study individuals' activity during stopover.

We used ARTS to track activity patterns of 3 songbird species—Red-eyed Vireo (*Vireo olivaceus*), Swainson's Thrush (*Catharus ustulatus*), and Wood Thrush (*Hylocichla mustelina*)—during their stopover in coastal Alabama prior to crossing the Gulf of Mexico during autumn migration. These species are known to cross the Gulf, are abundant during migration at the study site, and exhibit differences in morphology, foraging strategy, diet, and final wintering destination (Sandberg and Moore 1996, Cimprich et al. 2000, Mack and Yong 2000, Sandberg et al. 2002, Evans et al. 2011). For example, vireos consume more insects during migration than thrushes, which forage primarily on fruit (Parrish 1997), and vireos pass through coastal Alabama earlier in the autumn than thrushes (Woodrey and Moore 1997).

Using data collected by the ARTS, we describe baseline patterns of daily activity and examine intrinsic (species, age, sex, body condition) and extrinsic (precipitation, temperature, wind, year, day of year) factors hypothesized to influence activity during stopover. We also consider how activity patterns are related to an individual's departure direction from the site, which itself is influenced by a combination of energy reserves and weather (Deppe et al. 2015). Understanding daytime activity patterns will provide insight into fine-scale behavioral processes used by individuals in preparation for extended migratory flights (>1,000 km) across large geographic features.

METHODS

Field Methods

Between September 1 and October 31 of 2011–2014 (except October 1–13, 2013, due to the U.S. government shutdown) we captured, banded, radio-tagged, and tracked individuals of 3 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 located in the Bon Secour National Wildlife Refuge (NWR) in Alabama, USA (Figure 1). We operated 29–32 passive nylon mist nets (12.0 × 2.6 m or 6.0 × 2.6 m with 30 mm mesh) every day between ~sunrise and noon (CDT), depending on weather and migrant activity (see table 1 in Zenzal and Moore 2016 for yearly capture effort). Bon Secour NWR is located on the Fort Morgan Peninsula (30.2288°N, 88.0013°W), which is ~20 km in length and 1 km across. The peninsula is dominated by coastal dune scrub and maritime forest (see Zenzal et al. 2013 for a description of the study site).

Once birds were captured and fitted with a USGS aluminum leg band, we affixed radio pulse transmitters to birds' backs, after clipping feathers to leave some stubble at the site of attachment, using eyelash adhesive (Fantasy Lengths; Revlon, New York, New York) and a small amount of cyanoacrylate glue (Loctite, Westlake, Ohio) that would minimally irritate birds' skin. This attachment method allows transmitters to remain adhered for the 4–5 week life span of the transmitter battery, but fall off relatively soon after the transmitter stops functioning (Raim 1978, Smolinsky et al. 2013). We used transmitters from either Lotek (Newmarket, Ontario) or JDJC (Fisher, Illinois). Lotek transmitters ranged in frequency from 163.828 to 166.060 MHz and had pulse widths (i.e. the duration of the radio pulse) of either 22 ± 2 or 28 ± 2 ms. Transmitters from JDJC had a similar frequency range and their pulse widths were either 14 ± 2 or 18 ± 2 ms. Transmitters of both brands weighed 0.68 g for Red-eyed Vireos (~3–5% of tagged bird's total mass) and 0.90 g for thrushes (<4% of tagged bird's mass). We also aged birds as after hatch year or hatch year (based on Pyle 1997), pulled 2 body feathers as well as tail feathers, and assigned a fat score based on a qualitative 0–5 scale of visible fat (Helms and Drury 1960) for all radio-tagged individuals. Birds' fat scores were ultimately categorized as "fat" (score ≥3) or "lean" (score <3). Out of all birds, 65% of Red-eyed Vireos, 51% of Swainson's Thrushes, and 64% of Wood Thrushes were designated as fat, and the remaining birds were lean. Out of all birds that could be reliably aged, 20% of Red-eyed Vireos, 17% of Swainson's Thrushes, and 5% of Wood Thrushes were classified as after hatch year; the remaining individuals were hatch year birds. We determined an individual's sex genetically using the collected feathers (Animal Genetics, Tallahassee, Florida).

We remotely tracked radio-tagged birds using 2 ARTS wherein each automated receiving unit (ARU) was connected to a circular array of 6 Nighthawk brand directional 3-element yagi antennas mounted on a ~10 m tall tower located near the banding station (Figure 1). ARUs were designed and built by JDJC to continuously cycle through a list of preprogrammed frequencies matching those of transmitters attached to focal birds and record the strength (dBm) and pulse widths (ms) of all radio signals received for each frequency (±0.005 MHz). The time needed for ARUs to cycle through all frequencies depended on the number of frequencies programmed into the device but ranged from 1 to 6 min. There was no correlation between day of year and sampling rate ($r^2 = -0.02$, $P = 0.69$, df = 267). Therefore, the probability of detection and subsequent activity estimates were not confounded with capture date.

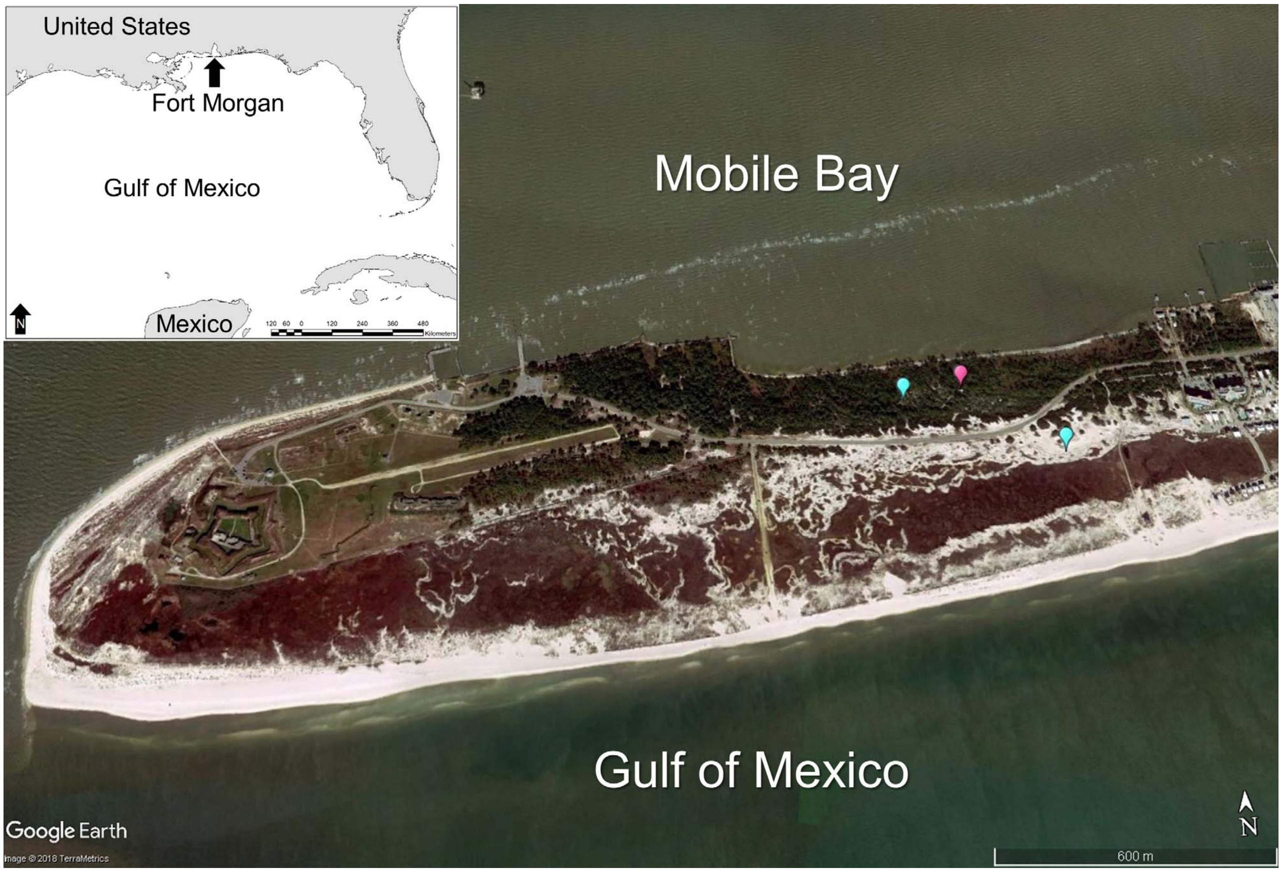

FIGURE 1. Study site in the Bon Secour National Wildlife Refuge on the Fort Morgan Peninsula directly south of Mobile Bay, Alabama. Banding station indicated by pink marker and ARTS indicated by blue markers. Inset: The Fort Morgan Peninsula (indicated by arrow) in relation to the larger Gulf of Mexico system.

ARU Data Interpretation

Because ARUs recorded all radio signals received each cycle that were within the units' frequency range, post-processing was necessary to differentiate ambient electromagnetic noise from radio signals received from the transmitters. We classified positive detections as instances in which there were more than 3 consecutive measurements that satisfied the following criteria: (1) consistent frequency within ±0.003 MHz of the known transmitter frequency, (2) signal minus noise level greater than 10 dBm, and (3) measured pulse width within 2 ms of the manufacturer specifications (Schofield et al. 2018).

Following methods discussed in Kays et al. (2011) and Ward et al. (2013, 2014), we inferred movement, and hence activity, based on changes in signal strength between consecutive readings after filtering out noise (mean time between readings was 2.7 min). We considered fluctuations in signal strength $>$2.5 dBm in the interval between consecutive ARU readings to indicate activity; otherwise, we considered birds to be still. We defined the 2.5 dBm threshold based on the variation in signal strength measured during the period when birds were most likely sleeping and thus not active (2100 hours to 0500 hours CDT); this period corresponded to approximately 2.5 hr after dusk until 1.5 hr before sunrise during the months of September and October. When defining our activity threshold, we restricted our analysis to individuals of all species that chose to remain overnight at our study site. The 2.5 dBm represented approximately 2 standard deviations greater than the mean change in signal strength between consecutive readings during that sleeping period (Jones et al. 2017). Large changes in signal strength do not necessarily represent farther movements; birds' movements in the vegetation column or even slight changes in transmitter orientation with respect to ARU antennas can have a large influence on received signal strength, thus it is difficult to relate large changes in signal strength to specific kinds of movement by the bird (Ward et al. 2014).

To ensure 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 mean difference in signal change during the nighttime interval between each focal species. Similar to Kays et al.

(2011), the relationship between mean signal change and species/transmitter type in our study was not significant ($F_{2,19} = 1.922$, $P = 0.174$).

To validate our interpretations of movement based on signal fluctuations recorded by ARTS, we ground-truthed activity estimations. Between October 3 and October 15, 2014, we hand tracked and visually observed 12 radio-tagged Swainson's Thrushes until they departed the study area. Swainson's Thrush was the ideal species to observe because it forages relatively low in the vegetation, hence its movements are more likely to go undetected by the ARTS than those of Red-eyed Vireos that forage high in the vegetation, and they are easy to observe. Swainson's and Wood thrushes have similar behaviors and microhabitats during migration and are suitable surrogates for one another. During each 1-min observation, we categorized birds as either still or active at 1-min intervals. Activity included any turns, hops, and flights. Only observations where the bird could be unambiguously observed were included. We recorded a total of 425 1-min observations corresponding to a total of 85 individual ARU readings. We compared ARU readings to observed activity in the concurrent series of 1-min visual observations. Any movement occurring at the finer observational resolution should also have been detected at the corresponding coarser ARU resolution. ARUs slightly underestimated activity when compared with direct observations, but assigned 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-min interval and the corresponding estimate of percentage of transmitter movement using ARU data.

Given sufficient high-quality data from multiple towers, we used biangulation or triangulation to estimate an individual's departure track and direction following the approach described in Smolinsky et al. (2013). We used Location of a Signal (L.O.A.S) software (Ecological Software Solutions, Sacramento, California) to estimate a series of UTM locations defining the track of each bird, and then we used a locally weighted regression (LOESS) to predict the departure track. When an insufficient number of high-quality locations were available to permit the use of the L.O.A.S–LOESS approach, we estimated birds' vanishing bearings based on data from the strongest tower and used them as estimates of departure direction (Smolinsky et al. 2013). We estimated the accuracy of departure bearings from the 6-antenna towers on the Fort Morgan peninsula to be 2.7° (± 2.4° SD, range 0–13°) via test transmitters at known bearings.

Weather Variables

We obtained weather data for our study site from 2 sources. We collected hourly surface temperature (°C) and wind speed (m s^{-1}) from the Bon Secour NWR weather station (ID: BONA1; 30.252778°N, 87.8125°W). We also used wind speed and direction data from the National Oceanic and Atmospheric Administration's North American Regional Reanalysis (NARR) wind data set (spatial resolution of 32 km and 8 daily measurements; accessed through Env-DATA service of movebank.org; Dodge et al. 2013) to calculate a wind profit index at a 1 km altitude at the study site for the evening of departure. Although raw NARR wind data are available at pressure levels, movebank.org, through which we accessed wind data, calculates the u and v wind components to altitude above sea level so we were able to use a consistent altitude across weather systems. Wind profit was defined here as winds moving in the direction of travel toward the Yucatan Peninsula, in this case winds moving from the north toward the south (Delmore et al. 2012, Deppe et al. 2015; speed [m s^{-1}] of wind toward 180°; see formula for "wind profit" in Liechti 2006).

Data Analyses

We quantified an individual's activity level (i.e. the proportion of ARU readings an individual was active) over each of 3 discrete, biologically relevant periods: morning, midday, and evening (hereafter: diel periods). For consistency, given the length of the day and sunrise and sunset times changed over the course of the season, we defined three 3-hr diel periods in relation to sunrise and sunset. We defined the morning diel period (period 1) as sunrise until 3 hr after sunrise. The midday diel period (2), when birds are typically thought to reduce their movements as the day warms, began 1.5 hr before midday and extended to 1.5 hr after midday (midday was the midpoint between sunrise and sunset). The evening diel period (3) extended from 3 hr before sunset until sunset. For each radio-tagged bird, we calculated the activity level for each 3-hr interval as the number of movements detected divided by the total number of possible movements over the 3-hr period. The total number of possible movements was calculated as the total number of ARU measurements minus those in which electromagnetic noise or poor signal strength might have obscured movements. Due to these external factors, there was variation among individuals in the total number of ARU readings per diel period. To account for variation in the number of possible movements among individuals (mean number of measurements = 66.5 ± 40.1 SD per 3-hr interval), we weighted activity level for each individual such that individuals with fewer readings received less weight in analyses. We calculated the weighted average activity level for each diel period for each species using the weighted mean function in R (version 3.4.2; R Core Team 2017).

We confirmed the independence of our 3 diel periods using a generalized linear mixed model (package lme4;

Bates et al. 2015) with activity level as our response variable, diel period as the predictor variable, and subject as the random effect for each species. In each model the coefficients of the random effect were small, and when taken into consideration with the standard deviation, each measure spanned zero (Red-eyed Vireo: 0.04 ± 0.19; Swainson's Thrush: 0.01 ± 0.12; Wood Thrush: 0.01 ± 0.08). These results suggest that activity level between the 3 periods within individuals were essentially independent. We excluded from the analysis birds ($n = 28$) that stayed at the site >1 day since birds have been found to show differences in activity the day of arrival compared to the day they depart (Paxton et al. 2008, Cohen et al. 2012, Smith and McWilliams 2014, Slager et al. 2015).

We examined migrant activity levels using boosted regression tree (BRT) models (Elith et al. 2008). Given the novelty of using ARTS to understand fine-scale movements and the complexity of the ecological system being examined, the BRT approach allows advantages over more traditional analytical methods to understand linear and nonlinear relationships between response and predictor variables that are not well known. In addition to identifying important predictor variables, the BRT is able to illustrate the functional forms of relationships while considerably limiting the likelihood of over-fitting models to the specific dataset. BRT models generate a relative influence value for each predictor variable (percentages that sum to 100%); higher percentages suggest a stronger association between the response and predictor variables. To generate BRT models, we used R with packages gbm (Ridgeway 2017) and dismo (Hijmans et al. 2017).

We modeled activity level (response variable) with the following predictor variables: diel period (1–3), fat category, age, sex, general departure direction or migratory pathway (southward over water = 90–270° or over land = 271–89°), surface wind speed, surface temperature, wind profit (m s^{-1}) at 1 km above ground, year, and day of year. Hourly surface wind speed and surface temperature were averaged over the 3 hr within each diel period. We calculated the average wind profit over the 3-hr evening period, and only included wind profit during the 3-hr evening period. Prior to analysis we confirmed the absence of multicollinearity using a Spearman's correlation (rho < 0.60) among continuous variables, which can complicate model certainty and interpretation. We also used the transformation $\log(x + 1)$ on the Swainson's Thrush activity level data to better fit a Gaussian distribution; transformations were not necessary for the activity level data of our 2 other focal species.

Following the BRT approach described in Elith et al. (2008), we used a Gaussian distribution, tree complexity of 2 (2-way interactions), bag fraction of 0.5, and a learning rate that ranged between 0.002 and 0.005 to create a minimum of 1,000 trees. We determined which variables to interpret from each model by determining the variables with higher relative influences than possible through chance as described by Müller et al. (2013). To follow this method, we divided the total relative influence (100%) by the total number of predictor variables ($n = 10$), which set the threshold at 10%. Therefore, we considered any variable with a relative influence greater than 10% to have an important association with activity levels. We also interpreted any interaction with an interaction size >0.05.

To better visualize patterns in activity level, we calculated the mean proportion of birds in the radio-tagged population that were active during 5-min intervals across each diel period. We first calculated the proportion of individuals active each minute as the number of individuals active divided by the number of individuals in the radio-tagged population. We then divided each of the diel periods into 5-min bins and calculated the mean proportion of individuals active across the 5 min. We accounted for variation in the number of individuals over time by weighting means by the number of tagged individuals in the population using the weighted mean function in R (version 3.4.2; R Core Team 2017).

RESULTS

Overall, Red-eyed Vireos were the most active followed by Wood Thrushes and then Swainson's Thrushes. Activity levels of Red-eyed Vireos (Morning: 57.7% ± 21.3 SD, $n = 31$; Midday: 57.7% ± 21.2, $n = 67$; Evening: 62.9% ± 27.7, $n = 66$) were consistently higher than those of Swainson's Thrushes (Morning: 40.2% ± 19.8, $n = 68$; Midday: 33.2% ± 21.5, $n = 81$; Evening: 33.8% ± 23.1, $n = 80$), and both species showed little change in activity levels across the 3 diel periods. Wood Thrush activity levels, on the other hand, varied across the day and in relation to the other 2 species. On average, Wood Thrushes were as active as Red-eyed Vireos in the morning (Wood Thrush: 49.0% ± 15.7, $n = 39$), but reduced their activity in the midday (34.0% ± 19.4, $n = 45$) and evening periods (37.8% ± 19.6, $n = 48$), which was similar to that of Swainson's Thrushes.

Similar to patterns in activity level of individual birds, species differed in the proportion of radio-tagged birds active over any 5-min interval throughout the day (Figure 2). Radio-tagged Red-eyed Vireos had the highest proportion of individuals active (Morning: 0.69 ± 0.17, Midday: 0.64 ± 0.06, Evening: 0.62 ± 0.05), followed by Wood Thrushes (Morning: 0.61 ± 0.14, Midday: 0.41 ± 0.07, Evening: 0.44 ± 0.07) and Swainson's Thrushes (Morning: 0.54 ± 0.08, Midday: 0.44 ± 0.06, Evening: 0.45 ± 0.05). The proportion of Red-eyed Vireos and Wood Thrushes active was highest in the morning (~65% of individuals of both species were active) and decreased in the midday and evening periods, although the reduction in the proportion of individuals active was greater for Wood Thrushes. By

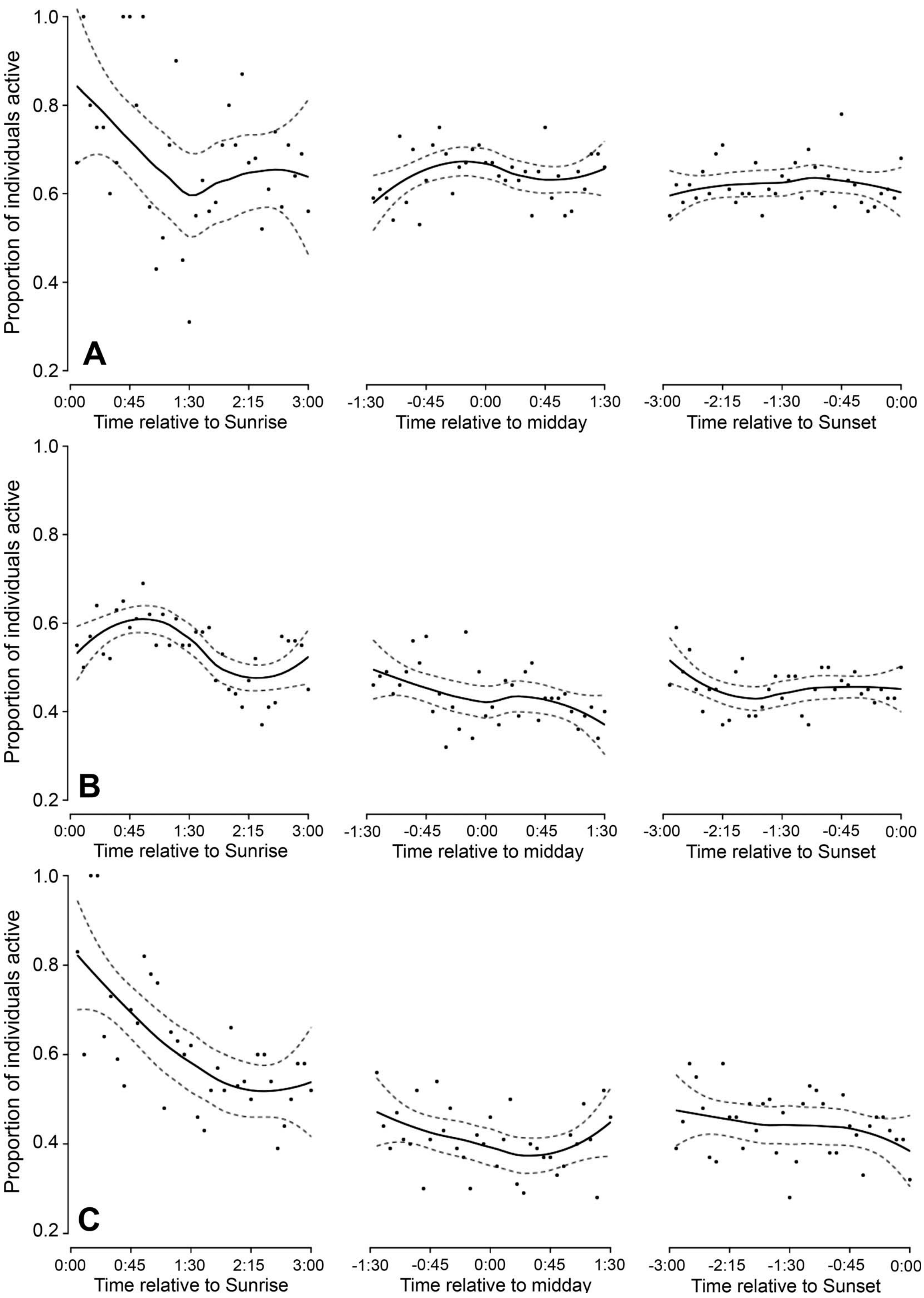

FIGURE 2. Proportion of (**A**) Red-eyed Vireos, (**B**) Swainson's Thrushes, and (**C**) Wood Thrushes active during the 3-hr morning, midday, and evening periods at a stopover site on the Gulf Coast of Alabama from 2011 to 2014. Individuals were considered to be active for a 5-min interval if they were recorded as moving at any point within that period. The solid line represents a locally weighted scatterplot smoothing (lowess) curve (span = 0.9) and the dashed lines represent 95% confidence interval.

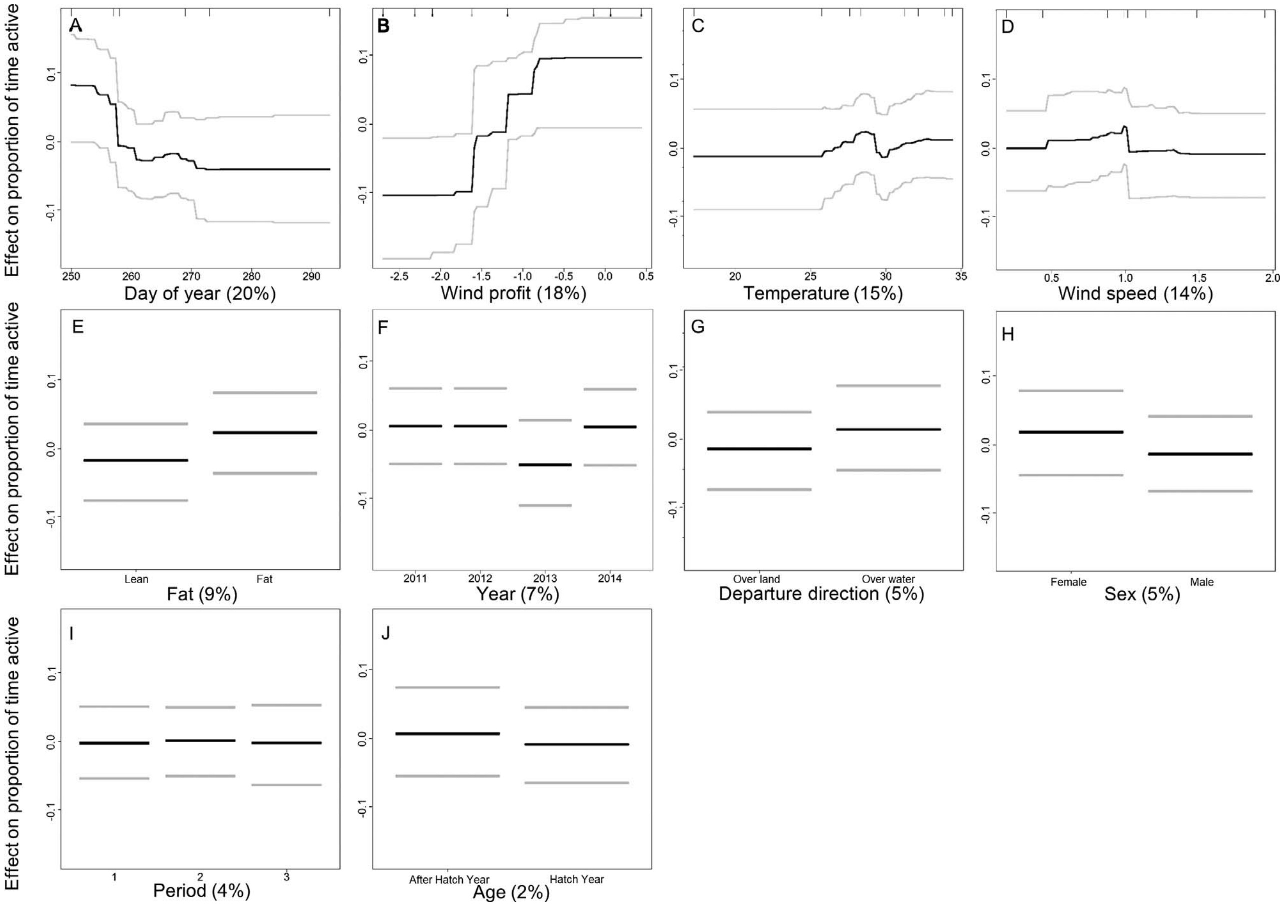

FIGURE 3. Partial dependence plots of variables predicting Red-eyed Vireo activity patterns from the BRT model. Positive values on the *y* axis indicate a positive influence on activity patterns; *y* axes are centered to have a zero mean over the data distribution. The relative influence (%) of each predictor variable is denoted in parentheses. Rug plots inside the top of each plot show the distribution of individuals in percentiles across that variable. Variables with a relative influence >10% (**A–D**) are considered to have an important association with activity (see text).

comparison, the proportion of Swainson's Thrushes that were active remained more constant across all 3 diel periods.

Based on the results from our BRT model (relative influence of predictor variables indicated by percentages), Red-eyed Vireo activity levels were negatively associated with day of year (20%; Figure 3A) but positively associated with wind profit (18%; Figure 3B). The relationship between activity levels and temperature (15%) was more complex; activity levels were greatest when temperatures were 25–30°C and greater than 32°C (Figure 3C). Activity levels were also greatest when wind speeds were <1 m s^{-1} (14%; Figure 3D). All other variables fell below our 10% threshold (Figure 3E–J), and all interactions were ≤ 0.05. The cross-validation correlation and standard error (goodness-of-fit measure) for the model was 0.44 ± 0.08.

Swainson's Thrush activity levels were positively associated with day of year (22%; Figure 4A) and negatively associated with temperature (14%; Figure 4B). Additionally, individuals were least active in 2012 and most active in 2013 (14%; Figure 4C). Individuals departing in an overland direction were more active than those departing over water (12%; Figure 4D). Finally, activity levels were lowest when wind speeds were between ~0.5 and 1.5 m s^{-1} (12%; Figure 4E). All other variables fell below our 10% threshold (Figure 4F–J). The model detected one interaction >0.05, which included day of year and departure direction (Figure 4K). Individuals departing overland were always more active; however, the difference in activity levels between departure direction decreased as the season progressed. The model cross-validation correlation and standard error was 0.32 ± 0.07.

Activity levels in Wood Thrush decreased with temperature (27%; Figure 5A) and increased with day of year (10%; Figure 5D). Activity levels were greatest during 2013 compared to 2012 and 2014 (24%; Figure 5B). Wood Thrush were also most active during the morning period and less active during the midday and evening periods

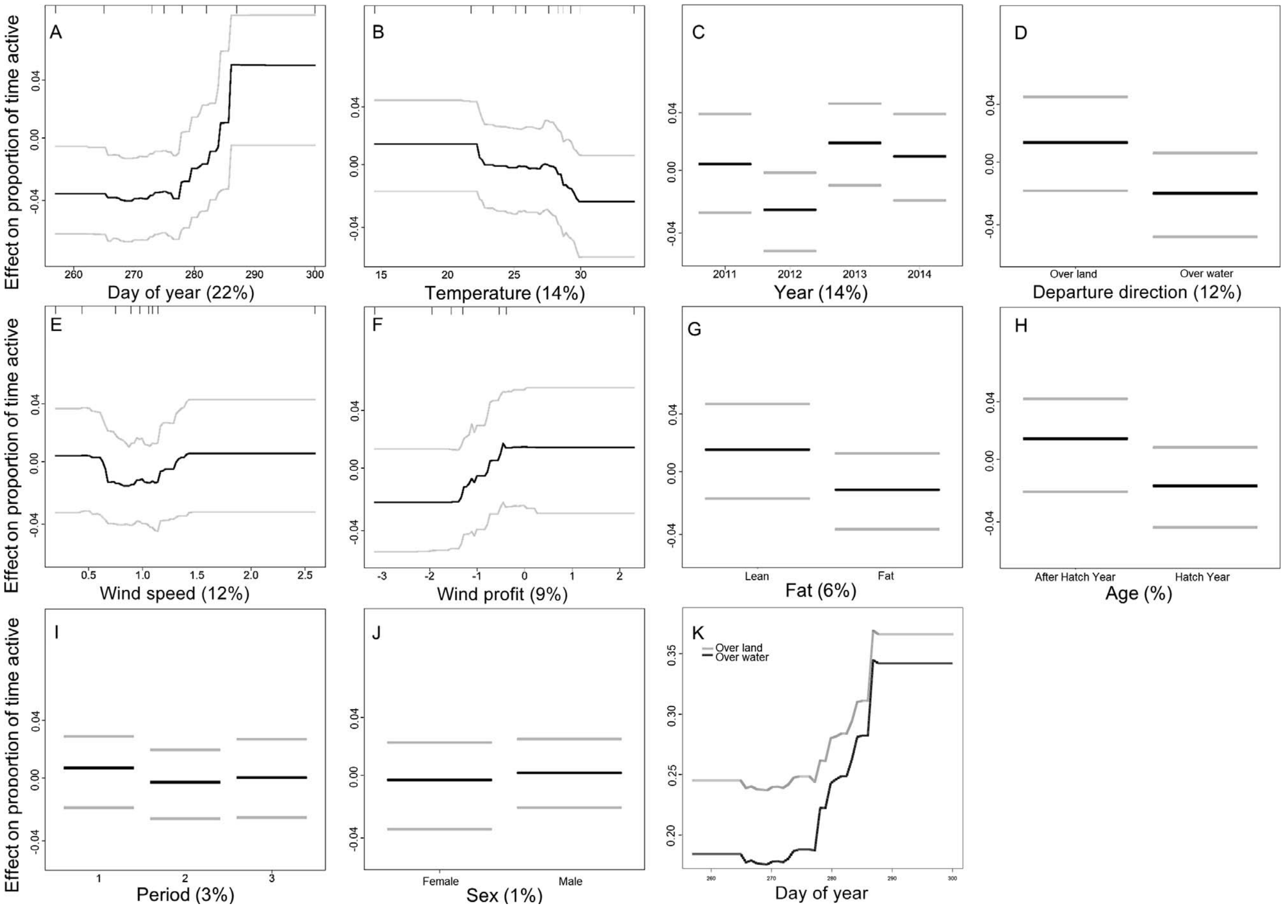

FIGURE 4. Partial dependence plots of variables predicting Swainson's Thrush activity patterns from the BRT model. Positive values on the *y* axis indicate a positive influence on activity patterns; *y* axes are centered to have a zero mean over the data distribution. The relative influence (%) of each predictor variable is denoted in parentheses. Rug plots inside the top of each plot show the distribution of individuals in percentiles across that variable. Variables with a relative influence >10% (**A–E**) are considered to have an important association with activity (see text). (**K**) Interaction between day of year and departure direction.

(19%; Figure 5C). All other variables fell below our 10% threshold (Figures 5E–J). The model detected one interaction >0.05, which included year and period (Figure 5K). The morning period in 2013 showed the highest activity level, while the midday and evening periods of 2012 showed the lowest activity levels. The morning periods in 2012 and 2014 showed the same activity level as the midday and evening periods in 2013. The model cross-validation correlation and standard error was 0.51 ± 0.05.

DISCUSSION

We used ARTS to observe distinct activity patterns at both the individual and population levels of 3 songbird species at a migratory stopover site; Red-eyed Vireos showed the most activity during stopover, followed by Wood Thrushes and then Swainson's Thrushes. The similarity in patterns between activity level and the proportion of individuals active in the radio-tagged population across the day demonstrated consistency in activity behavior among birds within each species. The 3 species also showed differences in their relationships between activity level and extrinsic variables, although temperature and day of year were important predictors of activity for all species. Vireos reduced activity with cooler temperatures and over the course of the season, whereas both thrush species showed increased activity under these same conditions. An increase in activity detected by the ARTS may indicate an increase in foraging movements. Aborn and Moore (2004) found that when birds are actively moving they are typically foraging. Migrants also move in response to predators and to locate shelter, although in some cases these behaviors are related to foraging (e.g., increased foraging activity can make birds more detectable by predators). Therefore, activity differences between species are likely related to variation in availability of food resources (insects and fruit) and species' time of passage through our site.

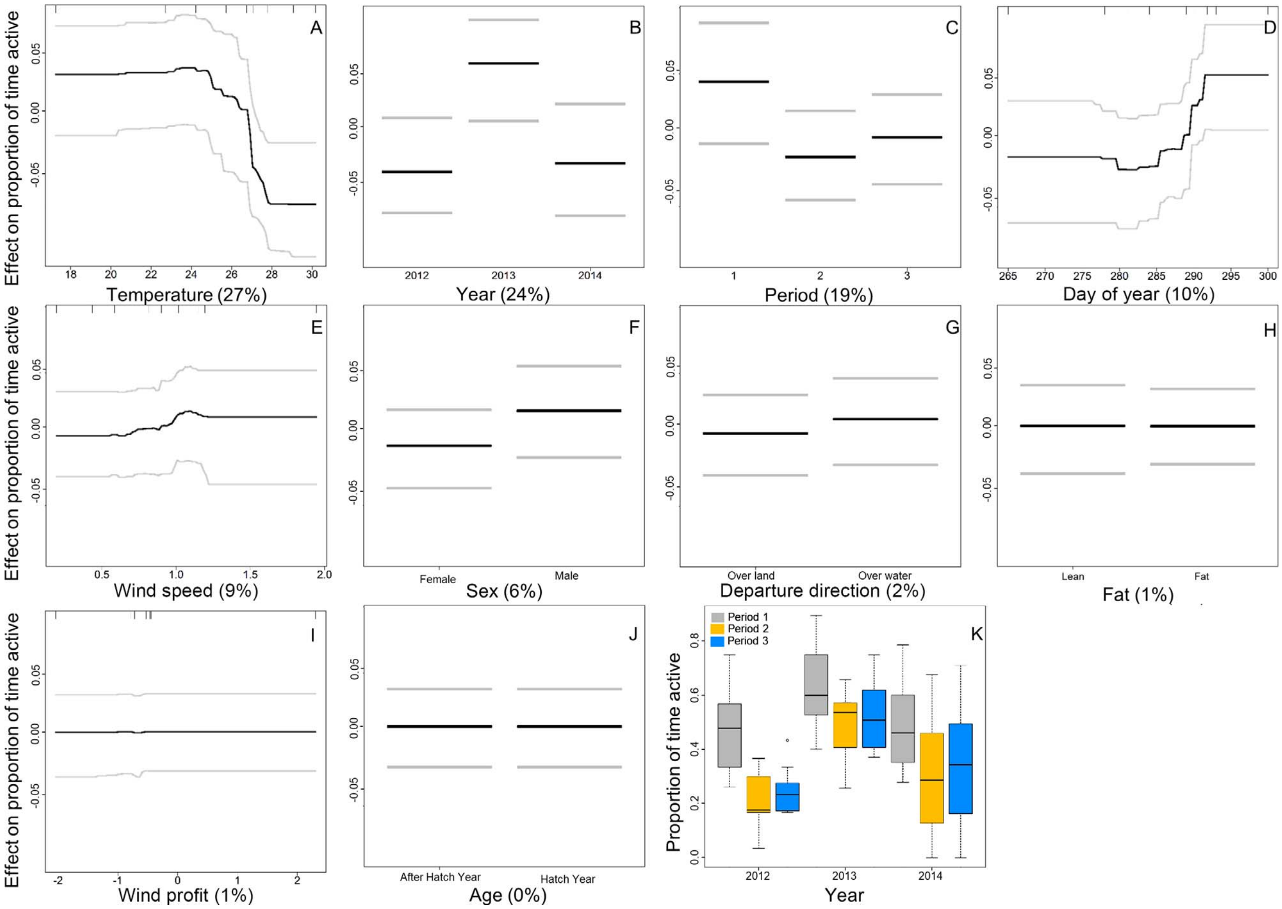

FIGURE 5. Partial dependence plots of variables predicting Wood Thrush activity patterns from the BRT model. Positive values on the *y* axis indicate a positive influence on activity patterns; *y* axes are centered to have a zero mean over the data distribution. The relative influence (%) of each predictor variable is denoted in parentheses. Rug plots inside the top of each plot show the distribution of individuals in percentiles across that variable. Variables with a relative influence >10% (**A–D**) are considered to have an important association with activity (see text). (**K**) Interaction between year and diel period.

Red-eyed Vireo activity levels declined over the season and were generally higher under warmer temperatures and calmer winds, all of which are likely linked to the availability of their food resources. The Red-eyed Vireo is omnivorous during migration, supplementing its insectivorous diet with fruit (Parrish 1997). Insect activity, especially that of some aerial insects, increases with warmer temperatures and calmer winds (Pinkowski 1977, Møller 2013, Lemoine et al. 2014, Maggini et al. 2015) such that vireos increase activity as their insect prey become more active and available. However, under cool temperatures and strong winds, they likely consume more fruit, which requires less movement and energy expenditure. Bird movement is also directly hindered by strong winds (Møller 2013). Temperature and insect abundances both decrease as autumn progresses, consistent with declines in vireo activity as well as abundance. The elevated activity of vireos during evening periods when wind profit was favorable for migrating across the Gulf (i.e. availability of tailwinds) is not surprising as vireos only attempt to cross the Gulf under particularly favorable tailwinds (Deppe et al. 2015). Possibly, birds increase activity during this time to improve fuel loads immediately prior to departure or to explore conditions aloft to assess suitability for departure.

In contrast to vireos, activity levels of Swainson's and Wood Thrush differed between years and increased as the season progressed and temperatures cooled. These patterns may reflect, in part, the availability of their main food resource (fruit) during autumn migration. As food resources decline over the season, coinciding with lower temperatures, thrushes may have to move around more in search of food or make longer movements (Smith and McWilliams 2014). Additionally, activity of both thrush species was highest in 2013 and lower in 2012, which may also reflect differences in food availability, although additional research is necessary to test hypotheses about the influence of food availability on activity patterns. The relationships between thrush activity, day of year, and temperature can also be explained by cold fronts that occur later in the season, coinciding with the passage of thrushes through our study area (Able 1972, Buskirk 1980, Gauthreaux et al. 2005). Furthermore, both thrush species are territorial on their wintering grounds (Mack and Yong 2000, Evans et al. 2011), which may increase pressure to migrate south and contribute to elevated activity levels later in the autumn, whereas vireos do not appear to be territorial during the wintering period (Cimprich et al. 2000).

In addition to increasing activity later in the season, Wood Thrushes were most active in the morning and much less active in the midday and evening periods. This difference in activity patterns across the 3 diel periods was most pronounced in 2012. The Fort Morgan Peninsula appears to be a resource-poor site, where 2 of our focal species have been documented to either lose mass (e.g., Swainson's Thrush and juvenile Red-eyed Vireos) or gain miniscule amounts of mass (e.g., adult Red-eyed Vireos) over the course of a day (Woodrey and Moore 1997). Additionally, 89% of birds in our radio-tagged population stayed at our site for less than a day, consistent with short stopovers observed in other food-poor sites (e.g., Graber and Graber 1983, Schaub et al. 2008). Low food availability may contribute to variation in activity of Wood Thrushes during the day. Given the low availability of food, after locating fruiting resources in the morning, Wood Thrushes may attend to those resources throughout the day rather than forage in other areas that may prove less "fruitful." Alternatively, if morning explorations are unsuccessful, birds may switch to an energy conservation strategy for the remainder of the day prior to departure (Graber and Graber 1983). We encourage more research to assess temporal variation (annual, seasonal, and diel) in food availability and corresponding activity patterns.

Swainson's Thrushes departing southward over water had lower activity rates compared to their overland counterparts, likely reflecting efforts to conserve energy reserves needed to cross the Gulf. Bäckman et al. (2017) recorded similar reductions in activity of Red-backed Shrikes (*Lanius collurio*) prior to crossing the Sahara and Arabian deserts. The higher activity levels of Swainson's Thrushes during light winds than strong winds may be related to an individual's preparation and/or readiness for departure. For example, birds may become more active under calmer winds, which facilitate foraging and other movements (Maggini et al. 2015). Additionally, under calm winds Swainson's Thrushes may become more active as they explore and assess conditions for departure.

Fat stores are known to be an important factor in determining whether individuals attempt to cross the Gulf and are ultimately successful (Deppe et al. 2015). Unexpectedly, fat was not an important variable for predicting individuals' activity patterns as observed in other studies (e.g., Smith and McWilliams 2014). We sampled lean and fat birds in roughly the same proportions, so this result is likely not an artifact of sampling bias. We expected lean individuals to be more active as they attempt to accumulate fat (Loria and Moore 1990, Wang and Moore 1993, Cohen et al. 2012), whereas fat birds should be less active to conserve energy. We suspect that fat was not a strong predictor of individual activity rates in our study because of the food-limited nature of the Fort Morgan Peninsula relative to other sites (Woodrey and Moore 1997). For example, if food availability does not allow lean birds to replenish fat, then they should conserve energy and depart shortly after arrival (Graber and Graber 1983, Schaub et al. 2008), similar to fat birds. The demand for foraging is also mediated by other factors such as wind profit (which may influence the urge to prepare for migration), departure direction (i.e. whether an individual chooses to cross the Gulf of Mexico or migrate over land), and temperature. We encourage additional research to examine the relationship between fat and activity; for example, track birds with different levels of fat on the same day (similar wind profit, temperature, and day of the year) or experimentally manipulate fat levels (Smith and McWilliams 2014).

ARTS and Fine-scale Data

Automated radio telemetry is typically used to understand animal movement over broad spatial scales (e.g., Goymann et al. 2010, Smolinsky et al. 2013, Brown and Taylor 2015, Deppe et al. 2015, Sjöberg et al. 2015, Woodworth et al. 2015, Smetzer et al. 2017); however, as we have demonstrated, ARTS can also be used to infer finer-scale behaviors. Our study offers an example of how automated telemetry can quantify activity patterns to gain insight into birds' energy expenditure during stopover and prior to negotiating a large geographic feature. There is great potential to use automated telemetry to study fine-scale behaviors of individuals at stopover sites. For example, automated telemetry using the Motus system (Taylor et al. 2017) has been used to identify the onset and end of diel activity during stopover (Morbey et al. 2018). Automated tracking concurrent with detailed field observations of foraging, predator avoidance, search for shelter, and the co-occurrence of such movements would clarify our understanding of energy expenditure and help explain the activity patterns we describe here.

Conventional telemetry has advanced our understanding of fine-scale movements during stopover (e.g., Fransson et al. 2008, Schmaljohann and Naef-Daenzer 2011, Cohen et al. 2012, Schmaljohann et al. 2013, Smith and McWilliams 2014, Slager et al. 2015), but owing to the high level of field effort required to manually track birds, our ability to study activity patterns is limited. Studies employing conventional telemetry are restricted by (1) the relatively small number of individuals that can be tracked during a season, (2) the limited ability to track individuals simultaneously, (3) incomplete diel sampling (e.g., disproportionate sampling early in the day), and (4) limited ability to track individuals spatially at stopover sites. Data loggers equipped with accelerometers also capture animal activity but typically require recapture of the animal to retrieve the data. Automated telemetry systems overcome these limitations. The Motus system allows many birds to be simultaneously tracked at high sampling rates (Taylor et al. 2017). With the increased use and spatial extent of the Motus array, activity patterns can be examined across wide areas. More frequent sampling rates using software receivers (e.g., sensorgnomes) and digitally coded tags could improve temporal resolution of activity data, although electromagnetic noise (i.e. signal-to-noise ratio) and other obstructions are still a concern. For automated tracking technology to accurately detect movement of individuals and estimate activity rates, receiving systems should monitor the environment in 360° using multi-antenna arrays (with antennas positioned at equal angles to one another), otherwise movements will be under-detected in a portion of the environment. However, with few antennas simple detection of initiation and termination of diel activity is possible (Morbey et al. 2018).

Useful applications of automated telemetry systems include studies of animal activity in habitats known to vary in wider geographic context, availability of food resources, anthropogenic impact, abundance of natural or introduced predators, and severity of weather. While tracking technology has advanced our understanding of long-distance movements and is shedding light on issues such as migratory connectivity, there remains much to learn about fine-scale behaviors during stopover and other less-vagile phases of the avian life cycle. Automated radio telemetry can be a powerful tool to further advance our understanding of these behaviors gained from years of conventional telemetry.

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Data deposit: The datasets collected and analyzed during the current study are available from the corresponding author on reasonable request.

LITERATURE CITED

Able, K. P. (1972). Fall migration in coastal Louisiana and the evolution of migration patterns in the Gulf Region. The Wilson Bulletin 84:231–242.

Aborn, D. A., and F. R. Moore (2004). Activity budgets of Summer Tanagers during spring migratory stopover. The Wilson Bulletin 116:64–68.

Alerstam, T., and Å. Lindström (1990). Optimal bird migration: The relative importance of time, energy, and safety. In Bird Migration: Physiology and Ecophysiology (E. Gwinner, Editor). Springer, Berlin. pp. 331–351.

Bäckman, J., A. Andersson, T. Alerstam, L. Pedersen, S. Sjöberg, K. Thorup, and A. P. Tøttrup (2017). Activity and migratory flights of individual free-flying songbirds throughout the annual cycle: Method and first case study. Journal of Avian Biology 48:309–319.

Bates, D., M. Maechler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bowlin, M. S., W. W. Cochran, and M. C. Wikelski (2005). Biotelemetry of New World thrushes during migration: Physiology, energetics and orientation in the wild. Integrative and Comparative Biology 45:295–304.

Brown, J. M., and P. D. Taylor (2015). Adult and hatch-year Blackpoll Warblers exhibit radically different regional scale movements during post-fledging dispersal. Biology Letters 11:20150593.

Brown, J. M., and P. D. Taylor (2017). Migratory Blackpoll Warblers (*Setophaga striata*) make regional-scale movements that are not oriented toward their migratory goal during fall. Movement Ecology 5:15.

Buskirk, W. H. (1980). Influence of meteorological patterns and trans-gulf migration on the calendars of latitudinal migrants. In Migrant Birds in the Neotropics: Ecology, Distribution, and Conservation (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington, DC, USA. pp. 485–491.

Celis-Murillo, A., T. J. Benson, J. R. Sosa-Lopez, and M. P. Ward (2016). Nocturnal songs in a diurnal passerine: Attracting mates or repelling intruders? Animal Behavior 118:105–114.

Chernetsov, N. (2006). Habitat selection by nocturnal passerine migrants en route: Mechanisms and results. Journal of Ornithology 47:185–191.

Cimprich, D. A., F. R. Moore, and M. P. Guilfoyle (2000). Red-eyed Vireo (*Vireo olivaceus*). In The Birds of North America (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.527

Cimprich, D. A., M. S. Woodrey, and F. R. Moore (2005). Passerine migrants respond to variation in predation risk during stopover. Animal Behavior 69:1174–1179.

Cohen, E. B., W. C. Barrow, J. J. Buler, J. L. Deppe, A. Farnsworth, P. P. Marra, S. R. McWilliams, D. W. Mehlman, R. R. Wilson, M. S. Woodrey, and F. R. Moore (2017). How do en route events around the Gulf of Mexico influence migratory landbird populations? The Condor: Ornithological Applications 119: 327–343.

Cohen, E. B., F. R. Moore, and R. A. Fischer (2012). Experimental evidence for the interplay of exogenous and endogenous factors on the movement ecology of a migrating songbird. PLOS One 7:e41818.

Crysler, Z. J., R. A. Ronconi, and P. D. Taylor (2016). Differential fall migratory routes of adult and juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*). Movement Ecology 4:3.

Delmore, K. E., J. W. Fox, and D. E. Irwin (2012). Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proceedings of the Royal Society B: Biological Sciences 279: 4582–4589.

Deppe, J. L., M. P. Ward, R. T. Bolus, R. H. Diehl, A. Celis-Murillo, T. J. Zenzal, F. R. Moore, T. J. Benson, J. A. Smolinsky, L. N. Schofield, D. A. Enstrom, et al. (2015). Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. Proceedings of the National Academy of Sciences USA 112:E6331–E6338.

Dodge, S., G. Bohrer, R. Weinzierl, S. C. Davidson, R. Kays, D. Douglas, S. Cruz, J. Han, D. Brandes, and M. Wikelski (2013). The environmental-data automated track annotation (Env-DATA) system: Linking animal tracks with environmental data. Movement Ecology 1:3.

Elith, J., J. R. Leathwick, and T. Hastie (2008). A working guide to boosted regression trees. Journal of Animal Ecology 77:802–813.

Evans, M., E. Gow, R. R. Roth, M. S. Johnson, and T. J. Underwood (2011). Wood Thrush (*Hylocichla mustelina*). In The Birds of North America (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.246

Finlay, J. C. (1976). Some effects of weather on Purple Martin activity. The Auk 93:231–244.

Fransson, T., C. Barboutis, R. Mellroth, and T. Akriotis (2008). When and where to fuel before crossing the Sahara desert – Extended stopover and migratory fuelling in first-year garden warblers *Sylvia borin*. Journal of Avian Biology 39:133–138.

Gauthreaux, S. A., J. E. Michi, and C. G. Belser (2005). The temporal and spatial structure of the atmosphere and the evolution of bird migration. In Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA. pp. 222–234.

Goymann, W., F. Spina, A. Ferri, and L. Fusani (2010). Body fat influences departure from stopover sites in migratory birds: Evidence from whole-island telemetry. Biological Letters 6: 478–481.

Graber, J. W., and R. R. Graber (1983). Feeding rates of warblers in spring. The Condor 85:139–150.

Heise, C. D., and F. R. Moore (2003). Age-related differences in foraging efficiency, molt, and fat deposition of Gray Catbirds prior to autumn migration. The Condor 105:496–504.

Helms, C. W., and W. H. Drury (1960). Winter and migratory weight and fat field studies on some North American buntings. Bird-Banding 31:1–40.

Hijmans, A. R. J., S. Phillips, J. Leathwick, J. Elith, and M. R. J. Hijmans (2017). Package "dismo." Circles 9(1).

Jones, T. M., M. P. Ward, and J. D. Brawn (2017). Variation in nestling body condition and wing development predict cause-specific mortality in fledgling dickcissels. Journal of Avian Biology 48:439–447.

Kays, R., S. Tilak, M. Crofoot, T. Fountain, D. Obando, A. Ortega, F. Kuemmeth, J. Mandel, G. Swenson, T. Lambert, B. Hirsch, and M. Wikelski (2011). Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. Computer Journal 54:1931–1948.

Lemoine, N. P., D. E. Burkepile, and J. D. Parker (2014). Variable effects of temperature on insect herbivory. PeerJ 2:e376.

Liechti, F. (2006). Birds: Blowin' by the wind? Journal of Ornithology 147:202–211.

Loria, D. E., and F. R. Moore (1990). Energy demands of migration on Red-eyed Vireos, *Vireo olivaceus*. Behavioral Ecology 1:24–35.

Mack, D. E., and W. Yong. (2000). Swainson's Thrush (*Catharus ustulatus*). In The Birds of North America (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.540

Maggini, I., F. Hama, D. Robson, H. R. Idrissi, F. Bairlein, and G. Gargallo (2015). Foraging behavior of three species of songbirds during stopover in southeastern Morocco during spring migration. Journal of Field Ornithology 86:266–276.

Møller, A. P. (2013). Long-term trends in wind speed, insect abundance and ecology of an insectivorous bird. Ecosphere 4:1–11.

Moore, F. R., S. Mabey, and M. S. Woodrey (2003). Priority access to food in migratory birds: Age, sex, and motivational asymmetries. In Avian Migration (P. Berthod, E. Gwinner, and E. Sonnenschein, Editors). Springer, Berlin. pp. 281–292.

Morbey, Y. E., C. G. Guglielmo, P. D. Taylor, I. Maggini, J. Deakin, S. A. Mackenzie, J. M. Brown, and L. Zhao (2018). Evaluation of sex differences in the stopover behavior and postdeparture movements of wood-warblers. Behavioral Ecology 29:117–127.

Müller, D., P. J. Leitão, and T. Sikor (2013). Comparing the determinants of cropland abandonment in Albania and Romania using boosted regression trees. Agricultural Systems 117:66–77.

Nudds, R. L., and D. M. Bryant (2000). The energetic cost of short flights in birds. The Journal of Experimental Biology 203: 1561–1572.

Parrish, J. D. (1997). Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. The Condor 99:681–697.

Paxton, K. L., C. Van Riper III, and C. O'Brien (2008). Movement patterns and stopover ecology of Wilson's Warblers during spring migration on the lower Colorado River in southwestern Arizona. The Condor 110:672–681.

Pinkowski, B. C. (1977). Foraging behavior of the Eastern Bluebird. The Wilson Bulletin 89:404–414.

Pyle, P. (1997). Identification Guide to North American Birds, Part 1: Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA, USA.

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

Raim, A. (1978). A radio transmitter attachment for small passerine birds. Bird-Banding 49:326–332.

Richardson, W. J. (1978). Timing and amount of bird migration in relation to weather: A review. Oikos 30:224–272.

Richardson, W. J. (1990). Timing of bird migration in relation to weather: Updated review. In Bird Migration (E. Gwinner, Editor). Springer, Berlin. pp. 78–101.

Ridgeway, G. (2017). Package 'gbm.' The R Project for Statistical Computing.

Sandberg, R., and F. R. Moore (1996). Fat stores and arrival on the breeding grounds: Reproductive consequences for passerine migrants. Oikos 77:577–581.

Sandberg, R., F. R. Moore, J. Bäckman, and M. Lohmus (2002). Orientation of nocturnally migrating Swainson's Thrush at dawn and dusk: Importance of energetic condition and geomagnetic cues. The Auk 119:201–219.

Schaub, M., L. Jenni, and F. Bairlein (2008). Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19:657–666.

Schmaljohann, H., and C. Eikenaar (2017). How do energy stores and changes in these affect departure decisions by migratory birds? A critical view on stopover ecology studies and some future perspectives. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 203:411–429.

Schmaljohann, H., and B. Naef-Daenzer (2011). Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. Journal of Animal Ecology 80:1115–1122.

Schmaljohann, H., F. Korner-Nievergelt, B. Naef-Daenzer, R. Nagel, I. Maggini, M. Bulte, and F. Bairlein (2013). Stopover optimization in a long-distance migrant: The role of fuel load and nocturnal take-off time in Alaskan Northern Wheatears (*Oenanthe oenanthe*). Frontiers in Zoology 10:26.

Schofield, L. N., J. L. Deppe, R. H. Diehl, M. P. Ward, R. T. Bolus, T. J. Zenzal, J. Smolinsky, and F. R. Moore (2018). Occurrence of quiescence in free-ranging migratory songbirds. Behavioral Ecology and Sociobiology 72:36.

Seewagen, C. L., E. J. Slayton, and C. G. Guglielmo (2010). Passerine migrant stopover duration and spatial behaviour at an urban stopover site. Acta Oecologica 36:484–492.

Shamoun-Baranes, J., and H. van Gasteren (2011). Atmospheric conditions facilitate mass migration events across the North Sea. Animal Behavior 81:691–704.

Sjöberg, S., T. Alerstam, S. Åkesson, A. Schulz, A. Weidauer, T. Coppack, and R. Muheim (2015). Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. Animal Behaviour 104:59–68.

Slager, D. L., P. G. Rodewald, and P. J. Heglund (2015). Experimental effects of habitat type on the movement ecology and stopover duration of spring migrant Northern Waterthrushes (*Parkesia noveboracensis*). Behavioral Ecology and Sociobiology 69:1809–1819.

Smetzer, J. R., D. I. King, and P. D. Taylor (2017). Fall migratory departure decisions and routes of Blackpoll Warblers *Setophaga striata* and Red-eyed Vireos *Vireo olivaceus* at a coastal barrier in the Gulf of Maine. Journal of Avian Biology 48:1451–1461.

Smith, A. D., and S. R. McWilliams (2014). What to do when stopping over: Behavioral decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions. Behavioral Ecology 25:1423–1435.

Smolinsky, J. A., R. H. Diehl, T. A. Radzio, D. K. Delaney, and F. R. Moore (2013). Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. Behavioral Ecology and Sociobiology 67:2041–2051.

Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. Holberton, et al. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:8.

Titov, N. (1999). Fat level and temporal pattern of diurnal movements of Robins (*Erithacus rubecula*) at an autumn stopover site. Avian Ecology and Behaviour 2:89–99.

Wang, Y., and F. R. Moore (1993). Relation between migratory activity and energetic condition among thrushes (Turdinae). The Condor 95:934–943.

Ward, M. P., M. Alessi, T. J. Benson, and S. J. Chiavacci (2014). The active nightlife of diurnal birds: Extraterritorial forays and nocturnal activity patterns. Animal Behaviour 88:175–184.

Ward, M. P., J. H. Sperry, and P. J. Weatherhead (2013). Evaluation of automated radio telemetry for quantifying movements and home ranges of snakes. Journal of Herpetology 47:337–345.

Wikelski, M., E. M. Tarlow, A. Raim, R. H. Diehl, R. P. Larkin, and G. H. Visser (2003). Avian metabolism: Costs of migration in free-flying songbirds. Nature 423(6941):704.

Woodrey, M. S. (2000). Age-dependent aspects of stopover biology of passerine migrants. In Stopover Ecology of Nearctic–Neotropical Landbird Migrants: Habitat Relations and Conservation Implications (F. R. Moore, Editor). Studies in Avian Biology 20:43–52.

Woodrey, M. S., and F. R. Moore (1997). Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. The Auk 114:695–707.

Woodworth, B. K., G. W. Mitchell, D. R. Norris, C. M. Francis, and P. D. Taylor (2015). Patterns and correlates of songbird movements at an ecological barrier during autumn migration assessed using landscape- and regional-scale automated radiotelemetry. Ibis 157:326–339.

Yong, W., D. M. Finch, F. R. Moore, and J. F. Kelly (1998). Stopover ecology and habitat use of migratory Wilson's Warblers. The Auk 115:829–842.

Zenzal, T. J., and F. R. Moore (2016). Stopover biology of Ruby-throated Hummingbirds (*Archilochus colubris*) during autumn migration. The Auk: Ornithological Advances 133:237–250.

Zenzal, T. J., A. C. Fish, T. M. Jones, E. A. Ospina, and F. R. Moore (2013). Observations of predation and anti-predator behavior of Ruby-throated Hummingbirds during migratory stopover. Southeastern Naturalist 12:21–26.

Zenzal, T. J., F. R. Moore, R. H. Diehl, M. P. Ward, and J. L. Deppe (2018). Migratory hummingbirds make their own rules: The decision to resume migration along a barrier. Animal Behaviour 137:215–224.

Zúñiga, D., J. Falconer, A. M. Fudickar, W. Jensen, A. Schmidt, M. Wikelski, and J. Partecke (2016). Abrupt switch to migratory night flight in a wild migratory songbird. Scientific Reports 6: 34207.