Behavioral Ecology and Sociobiology (2018) 72:36
https://doi.org/10.1007/s00265-018-2449-y

ORIGINAL ARTICLE

Occurrence of quiescence in free-ranging migratory songbirds

Lynn N. Schofield[1,2] · Jill L. Deppe[1] · Robert H. Diehl[3] · Michael P. Ward[4] · Rachel T. Bolus[3,4,5] · Theodore J. Zenzal Jr[4,6] · Jaclyn Smolinsky[7] · Frank R. Moore[6]

Received: 31 July 2017 / Revised: 19 January 2018 / Accepted: 24 January 2018

Abstract

Quiescence is a period of inactivity that occurs before the onset of migratory activity in nocturnally migrating birds. This behavior has been observed in captive birds in migratory disposition, but its occurrence in free-ranging migratory birds has been documented only anecdotally, and causal factors and function(s), if any, are unknown. In this study, we documented and characterized quiescence in three migratory songbird species (red-eyed vireo [*Vireo olivaceus*], Swainson's thrush [*Catharus ustulatus*], and wood thrush [*Hylocichla mustelina*]) by measuring movement and proportion of time spent inactive prior to departure from a stopover site during fall migration. Individuals of each species displayed a period of inactivity prior to departure which varied from less than 30 min to over 90 min with red-eyed vireos engaged in the longest, most pronounced quiescence. We also examined how quiescence was related to intrinsic and extrinsic factors known to influence the departure of migrating birds, and found some evidence for an effect of age and departure time but no effect of a migrant's energetic condition, departure direction, atmospheric conditions around departure, or day of year on quiescence. Our novel application of an automated radiotelemetry system yielded a large amount of data to characterize quiescence in free-ranging migratory birds, and we provide guidance for future studies to tease apart the various causal factors and function(s) of this migratory behavior.

Significance statement

Quiescence is a poorly understood period of inactivity observed among captive and free-ranging migratory songbirds prior to the onset of nocturnal activity. Our novel use of automated radiotelemetry revealed quiescence among three intercontinental migratory songbirds. It also enabled us to ask how quiescence might be related to intrinsic and extrinsic factors known to influence the departure of migrating birds, and provided an opportunity to explore possible function(s), if any, of this intriguing behavior.

Keywords Quiescence · Migration · Automated radiotelemetry · *Catharus ustulatus* · *Hylocichla mustelina* · *Vireo olivaceus*

Introduction

Migratory quiescence is a period of inactivity that occurs prior to the onset of nocturnal migratory restlessness (*zugunruhe*) (Palmgren 1949; Morton 1967; Agatsuma and Ramenofsky 2006; Ramenofsky et al. 2008) and generally occurs around the time of sunset prior to departure from a stopover site in free-ranging nocturnal migratory birds (Hebrard 1971;

Communicated by W. Wiltschko

✉ Jill L. Deppe
jldeppe@eiu.edu

[1] Department of Biological Sciences, Eastern Illinois University, 600 Lincoln Avenue, Charleston, IL 61920, USA

[2] Institute for Bird Populations, PO Box 1346, Point Reyes Station, CA 94956, USA

[3] U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way Suite 2, Bozeman, MT 59715, USA

[4] Department of Natural Resources and Environmental Sciences, University of Illinois, 1102 S. Goodwin Avenue, Urbana, IL 61801, USA

[5] Department of Biology, Southern Utah University, Cedar City, UT 84720, USA

[6] Department of Biological Sciences, The University of Southern Mississippi, 118 College Drive #5018, Hattiesburg, MS 39406, USA

[7] Department of Entomology and Wildlife Ecology, University of Delaware, 531 S. College Avenue, Newark, DE 19716, USA

Bolshakov 1992; Diehl and Larkin 1998; Cochran et al. 2004). Only a handful of studies have explicitly called attention to quiescence. For example, captive Gambel's white-crowned sparrows (*Zonotrichia leucophrys gamebelii*) displayed a clear reduction in activity in the 1–2 h just prior to migratory restlessness during both spring and fall migration (Morton 1967; Agatsuma and Ramenofsky 2006), and during fall this reduction in activity was significantly greater than other resting periods throughout the day and night (Ramenofsky et al. 2008). Coincident with the quiescent period observed in caged sparrows, Morton (1967) observed that free-ranging flocks of white-crowned sparrows ceased feeding and became inactive prior to sunset before disappearing from the stopover site during spring migration. Likewise, Hebrard (1971) observed that free-ranging intercontinental songbird migrants that had stopped on the Louisiana coast following spring flights across the Gulf of Mexico became inactive around the time of sunset and departed just over an hour later (see also Bolshakov 1992). Kjos and Cochran (1970), who monitored the activity of nocturnally migrating *Catharus* thrushes by radiotelemetry in both spring and fall, reported that diurnal activity, which consisted of intermittent movement interspersed with 5- to 15-min periods of non-movement, ceased about 20 min before sunset. Likewise, when Diehl and Larkin (1998) monitored the movements of radio-tagged *Catharus* thrushes during spring stopover, they observed a variable period of stillness (4–41 min) prior to departure and described the period as quiescence.

Factors that influence quiescence, much less its function(s), if any, are unknown. A period of inactivity (quiescence) may be used to obtain information pertinent to departure, including a birds' internal state (energetic condition, hormone levels), meteorological conditions, directional information, and geographical position in relation to destination (Emlen 1980; Moore 1987; Cochran et al. 2004; Ramenofsky et al. 2008; Chernetsov 2012; Goymann et al. 2017). For example, the calibration of a migrant's magnetic compass with polarized light, which is thought to take place at sunset and sunrise (e.g., Sjöberg and Muheim 2016), is probably most reliably made when the migrant is inactive (Muheim pers. comm.), yet we have no idea how much time is required to make the calibration much less process information about atmospheric conditions. The period prior to departure is also likely when migrants make the metabolic switch between fuel deposition and mobilization of energy stores to prepare for a long-distance flight, including shutting down and emptying their digestive system to achieve better aerodynamic performance during flight (see Piersma 1998). Inactivity also occurs when birds sleep. Typically, diurnal songbird migrants sleep far less during their nocturnal migrations than during non-migratory periods (Fuchs et al. 2006), yet they seem to suffer few of the negative consequences so obvious in sleep-deprived mammals (Rattenborg et al. 2004). Sleep prior to departure may help to offset a sleep debt (see Fuchs et al. 2006), and if periods of sleep are semi-hemispheric (Fuchs et al. 2009), migrants could process directional and atmospheric information at the same time that they gain some sleep (see Rattenborg 2017). Finally, a period of inactivity prior to departure may simply reflect reduced foraging efficiency or increased risk of predation (see Beauchamp 2017) as light levels decline. Of course, these hypothesized explanations for migratory quiescence are not mutually exclusive; a migrant may integrate directional information, weigh internal and external conditions, complete metabolic processing, and rest over the same period of time prior to departure.

In this study, our first objective was to monitor and characterize the activity of free-ranging individuals of three intercontinental migratory songbird species, red-eyed vireo (*Vireo olivaceus*), Swainson's thrush (*Catharus ustulatus*), and wood thrush (*Hylocichla mustelina*), prior to departure from a coastal stopover site in Alabama during fall migration. Our second objective was to examine quiescence of the three species in relation to intrinsic (age and energetic condition) and extrinsic (weather conditions) factors known to influence their departure decisions (Sandberg and Moore 1996; Smolinsky et al. 2013; Deppe et al. 2015) and to reflect on the function(s), if any, of this behavior.

Weather conditions, particularly wind profit (velocity of winds moving in the direction of travel), humidity, and barometric pressure, are important predictors of a bird's decision to initiate a migratory flight across the Gulf of Mexico and its probability of arrival at the Yucatan Peninsula in fall (Deppe et al. 2015). Therefore, weather conditions prior to departure might affect the length of quiescence if that period of time is important in the integration of flight information. Weather favorable for migratory flight may make it easier to process information (shorter quiescence) or, because conditions are conducive to a migratory flight, more time may be taken to integrate information and prepare for flight (longer quiescence). Quiescence may also be influenced by the migrant's energetic status, a key factor in departure decisions (see Deppe et al. 2015). Lean birds are less likely to depart on a migratory flight than fat birds, so they may be less likely to devote time to processing flight information (shorter quiescence), or alternatively more time (longer quiescence) as they weigh the risk of departure with a reduced fuel load. The migrant's context along its migratory route and amount of time remaining in the migratory season influence departure decisions (e.g., Sandberg and Moore 1996; Deppe et al. 2015) and may affect how pertinent information is assessed. For example, a songbird migrant faced with a long flight over inhospitable terrain (e.g., Gulf of Mexico) may weigh more carefully and integrate more slowly flight information (longer quiescent period). Assessment of context in relation to anticipated travel risks likely varies among species. The decision by a red-eyed vireo, for example, to depart over the Gulf of Mexico is more sensitive to intrinsic and extrinsic conditions favorable for that flight than either a Swainson's thrush or wood thrush (Deppe et al. 2015), which might affect the length of time to weigh information and make a departure decision. Finally, the quiescent period may differ with age and migratory experience. Young, less experienced birds of the year may take longer to integrate information and prepare for flight because of their lack of experience (longer quiescence), or for that very reason make a comparatively quick, less informed decisions about departure (shorter quiescence).

Methods

Field methods

We captured birds between 2011 and 2014 during the peak of fall songbird migration (1 September to 31 October) at a long-term migration station in the Bon Secour National Wildlife Refuge located on Fort Morgan Peninsula, Alabama, USA (30.2397° N, 87.8199° W). The Fort Morgan Peninsula is a narrow stretch of coastal dune scrub and maritime forest, approximately 42 km in length and averaging about 1 km in width, bordered by Mobile Bay to the north and the Gulf of Mexico to the south (Fig. 1; see Zenzal et al. (2013) for a complete site description).

We studied three species of intercontinental migratory songbirds: red-eyed vireo (2013–2014), Swainson's thrush (2011–2014), and wood thrush (2012–2014). These species are abundant along the northern Gulf coast during fall migration, and have been the focus of research to understand the movement and survival of intercontinental songbird migrants crossing the Gulf of Mexico (e.g., Deppe et al. 2015). We mist-netted, weighed, measured, aged (following Pyle 1997), and banded individuals with aluminum US Geological Survey leg bands. Hatch year birds were engaged in their first fall migration, while after hatch year birds were adults on at least their second fall migration. We assigned each bird a fat class score on a scale ranging from 0 to 5 based on the amount of subcutaneous fat visible in the furcular region and abdomen (Helms and Drury 1960).

We used an automated radiotelemetry system (ARTS) to investigate activity and quiescence in our three focal species. ARTS offer the ability to remotely and continuously track free-ranging birds in their natural environment over extended time periods (Kays et al. 2011; Smolinsky et al. 2013; Ward et al. 2014; Jones et al. 2017). By monitoring temporal fluctuations in the strength of radio signals received by ARTS and the azimuth from which signals originate, it is possible to infer activity of a radio-tagged bird (Ward et al. 2013), allowing quiescence to be examined in a large sample of individuals despite the difficulty of visually observing behavior that typically occurs after dusk (e.g., Louder et al. 2015; Celis-Murillo et al. 2016).

We attached pulsed radiotransmitters to clipped feather stubble on the birds' backs using a non-toxic adhesive (Fantasy Lengths® eyelash adhesive, Revlon®, New York) and a small amount of cyanoacrylate glue (Loctite® Super Glue Gel Control, Düsseldorf, Germany) following the approach outlined by Raim (1978) and modified by Smolinsky et al. (2013). The adhesive approach minimized irritation to birds' skin and allowed transmitters to fall off shortly after the expected battery life of the radio transmitters (approximately 28 days; Raim 1978), which is well beyond the stopover duration of birds included in our study (mean stopover = 1.13 days ± SD 2.73). We used Lotek (Newmarket, Ontario) and JDJC Corp. (Fisher, Illinois) transmitters with frequencies ranging from 163.828 to 166.060 MHz and pulse widths of 28 ± 2 or 22 ± 2 ms (Lotek) and 14 ± 2 or 18 ± 2 ms (JDJC Corp.). We attached 0.68-g Lotek transmitters to red-eyed vireos (~3–5% of tagged bird's mass) and 0.9-g JDJC transmitters to both thrush species (<4% of tagged birds' mass). It was not possible to record data blind because our study involved focal animals in the field.

Once tagged, the signal strength of individual frequencies was recorded using ARTS located near the banding station (30.2288° N, 88.0013° W). Two ARTS, each consisting of a circular array of six three-element Yagi dipole antennas mounted at 60° intervals on top of a 9.2-m tall tower and connected to an automated receiving unit (ARU), were located within 250 m of the banding station (Fig. 1). ARUs were designed and built by JDJC Corp. (Fisher, IL) to continuously scan the frequencies of each deployed transmitter and record their signal strengths, noise levels, pulse widths, and pulse intervals. These metrics were recorded for each transmitter programmed into the ARU once every 2.5–6 min depending on the number of frequencies through which the ARU cycled (see Ward et al. 2014). Because strong signals are needed to estimate activity, birds used in this study likely were within 500 m of the tower. Similar studies of activity patterns estimated detection ranges between 500 and 750 m of ARTS (Ward et al. 2013).

Bird detection and movement estimation from ARUs

Because ARUs continuously record any signal received on each frequency, it was necessary to differentiate positive detections of radio-tagged individuals from ambient electromagnetic noise. To do so, we created algorithms in Python (v2.7) that differentiated positive detections from noise. We defined positive detections as any instance satisfying the following criteria: three or more consecutive readings with a signal-minus-noise level greater than 10 dBm on the specified frequency and with a pulse width within 2 ms of the manufacturer specifications. We manually removed rare instances

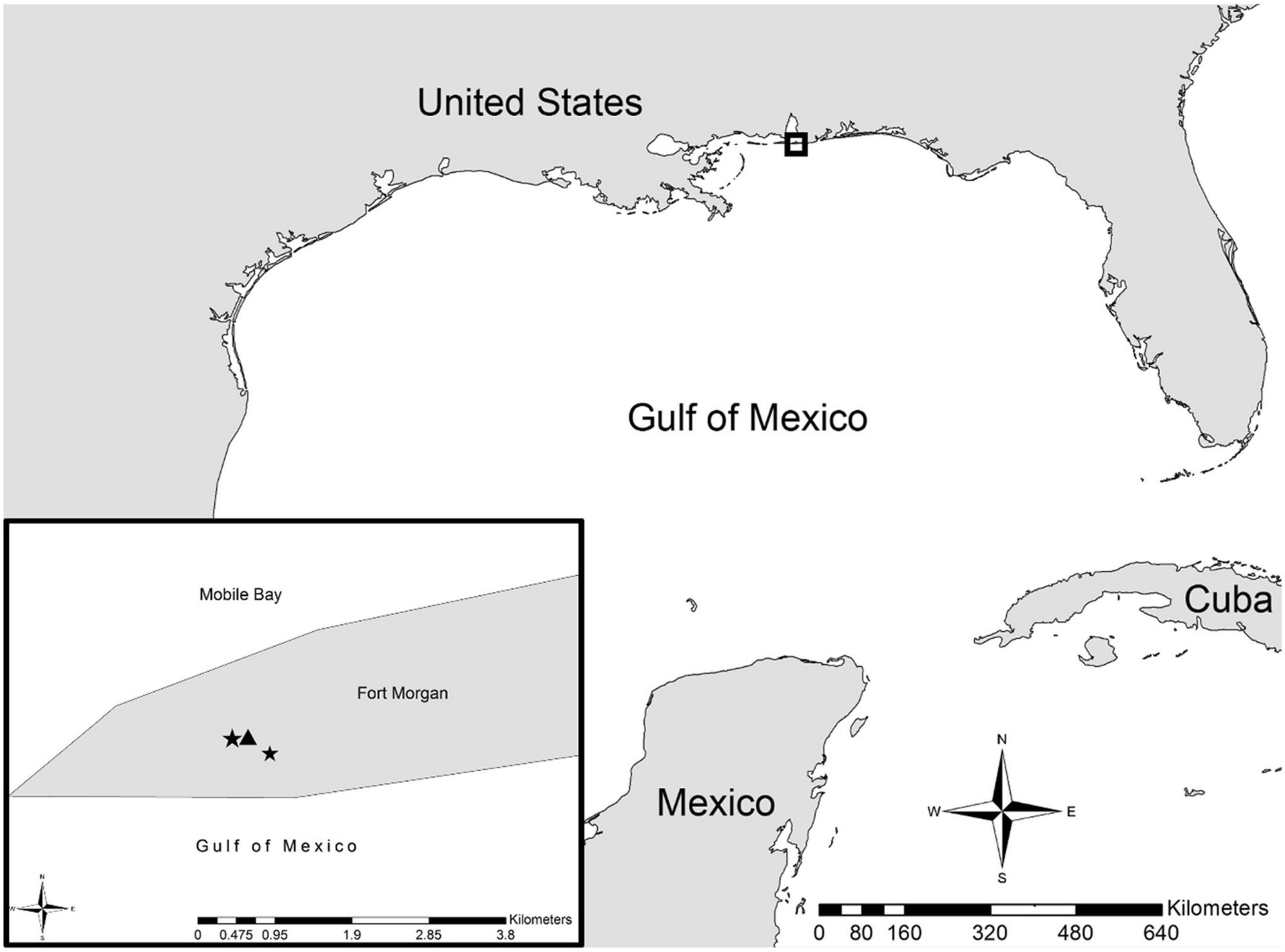

Fig. 1 Gulf of Mexico region, with Fort Morgan Peninsula in Alabama enclosed by a square. *Inset:* Study site (triangle) and automated radio towers (stars) on the Fort Morgan Peninsula, between the northern coast of the Gulf of Mexico and Mobile Bay

where atypically strong detections were being received simultaneously on multiple frequencies from a single direction, regardless of whether a bird could have potentially been present, because such readings were most likely produced by broad-spectrum anthropogenic noise.

We inferred temporal movement (activity) using changes in signal strength between each consecutive reading taken by the ARU during which a bird was detected (Ward et al. 2013; Jones et al. 2017). We considered changes in signal strength >2.5 dBm between consecutive ARU readings to be indicative of movement. Otherwise, we considered birds to be stationary. The threshold change in signal strength was chosen as being approximately two standard deviations from the mean change in signal strength recorded between 21:00 and 05:00 CST for birds that did not depart from the study site on a given night (i.e., when birds that had not chosen to initiate migration were likely to be sleeping). This window extended approximately 2.5 h after the average time of sunset September through October and 1.5 h before sunrise. We restricted the presumed interval of nocturnal inactivity to 2.5 h after sunset because most individuals initiated migration within that time period. When calculating the activity level of resting birds, we used only individuals that stayed the entire night to avoid the activity signals of migration. To assure that comparisons of inactivity during quiescence were valid among the three species and not skewed by differences such as transmitter type, the height at which birds tended to perch, or birds' posture while sleeping, we used an ANOVA to assess the difference in average signal change during the nighttime interval among the focal species. The relationship between average signal change and species/transmitter type in our study was non-significant ($F_{2,19} = 1.922$, $p = 0.174$).

While ARUs varied in their sampling rate as described above, ARUs sampled most individuals once every 5 min for the majority of the season. To standardize the sampling rate among birds, we smoothed the change in signal strength data by linearly interpolating the change in signal strength between consecutive samples across the number of minutes between samples, such that we had an estimate of change in signal strength every minute for each individual.

To validate our interpretations of movement based on ARU signal fluctuations, we ground-truthed activity estimations. From October 3 to 15, 2014, we hand-tracked and visually observed 12 radio-tagged birds between the time they were tagged until they departed from the study site. Care was taken to observe the individuals from as far away as possible to reduce the possibility of our presence impacting the activity of the focal animal. During an observation, we categorized birds as either still or active at 1-min 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 1-min observations occurring during a total of 85 individual ARU readings. When compared with direct observations, ARUs assigned activity or non-activity correctly 88% of the time. Using similar methods, 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 transmitter movement using ARU data.

Data analysis

We defined quiescence as the period of inactivity occurring in the 2-h interval prior to the onset of nocturnal activity associated with migratory departure (Ramenofsky et al. 2008). We used a 2-h window to ensure our detection and quantification of the entire quiescent period, as other studies of quiescence have documented that the inactive period prior to departure or migratory restlessness can last up to 120 min (Agatsuma and Ramenofsky 2006). We quantified quiescence in two ways for each bird: (1) the maximum length of consecutive inactivity (i.e., the total number of consecutive minutes prior to initiating departure that no movement was recorded by the ARTS) and (2) the proportion of time the bird was classified as being inactive during the 2-h period prior to departure. We considered both measures of inactivity because they can provide complementary information and are not necessarily correlated; high proportions of inactivity can be characteristic of a single long period of inactivity or multiple shorter bouts of inactivity. For example, a sleeping bird might show both a high proportion and a long duration of inactivity if it engages in a single long nap. On the other hand, a bird trying to acquire information from its environment to make departure decisions may spend a large proportion of the 2-h period being inactive, but short durations of inactivity if the bird periodically moves to new locations in the environment to acquire additional information or achieve a different perspective. When we correlated the two measures of inactivity (proportion and length of inactivity) during quiescence, correlation coefficients ranged from 0.582 for vireos to 0.495 for the two thrush species combined and patterns for the two metrics were similar to one another. For comparisons of inactivity between the 2-h pre-departure period and the rest of the day, we considered both metrics of inactivity as the sampling rate did not vary within a day, or the period over which each individual was tracked.

In our analyses, we only included birds that displayed a clear initiation of migratory departure from the study site, indicated by a rapid loss of signal strength. For some birds, this was preceded by a spike in signal strength (and activity) apparent when birds fly up high prior to departing (Fig. 2; see Smolinsky et al. 2013). Although departure behavior typically occurs in the evening between sunset and civil twilight, we included all birds showing a clear departure in our analyses. We included departure time as a covariate in our analyses to assess potential effects of this variable on quiescence. We excluded birds from our analyses that exhibited a slower, more gradual decline in signal strength, indicative of birds not initiating migration but instead slowly moving outside of the range of the ARTS.

We also explored the behavior of non-departing birds that remained at the site more than 1 day, regardless of their departure pattern from the site, to look for signs of inactivity that may resemble quiescence. We quantified the activity patterns of non-departing birds in a 2-h period prior to the average departure time of each species, which was comparable to our 2-h pre-departure period for birds initiating migratory flights. Few birds remained at the site for > 1 day, and many of those individuals moved in and out of the range of the towers while at the site; consequently, those birds provided insufficient data for quantifying activity patterns. We explored activity of five red-eyed vireos and five Swainson’s thrushes. We had no data for non-departing wood thrushes. We provide only means and SD for non-departing birds because our small sample size did not allow a statistical comparison with departing birds.

Studies of captive white-crowned sparrows (Agatsuma and Ramenofsky 2006; Ramenofsky et al. 2008) revealed that birds in migratory condition spent a greater proportion of time inactive during the 2-h period prior to the onset of nocturnal restlessness (quiescence) than during other fixed observation periods. In our study, we employed iterative Markov chain Monte Carlo simulations similar to those described by Gelman and Rubin (1992) and Downey (2013) to determine if the proportion of time birds spent inactive in the 2 h prior to departing from the study site was distinct from periods of inactivity observed during any 2-h period between sunrise and the 2 h prior to migration. Simulations were chosen to characterize daytime inactivity outside the 2-h period prior to departure rather than randomly selecting 2-h intervals for two reasons: (1) it provides a larger sample in which to compare purported periods of quiescence to same length periods of time during the day, and it (2) avoids comparing autocorrelated background intervals.

We created a program in “R” (version 3.1; R Core Team 2011) to build transition matrices using transition states occurring from 05:00 until the beginning of the 2-h pre-departure

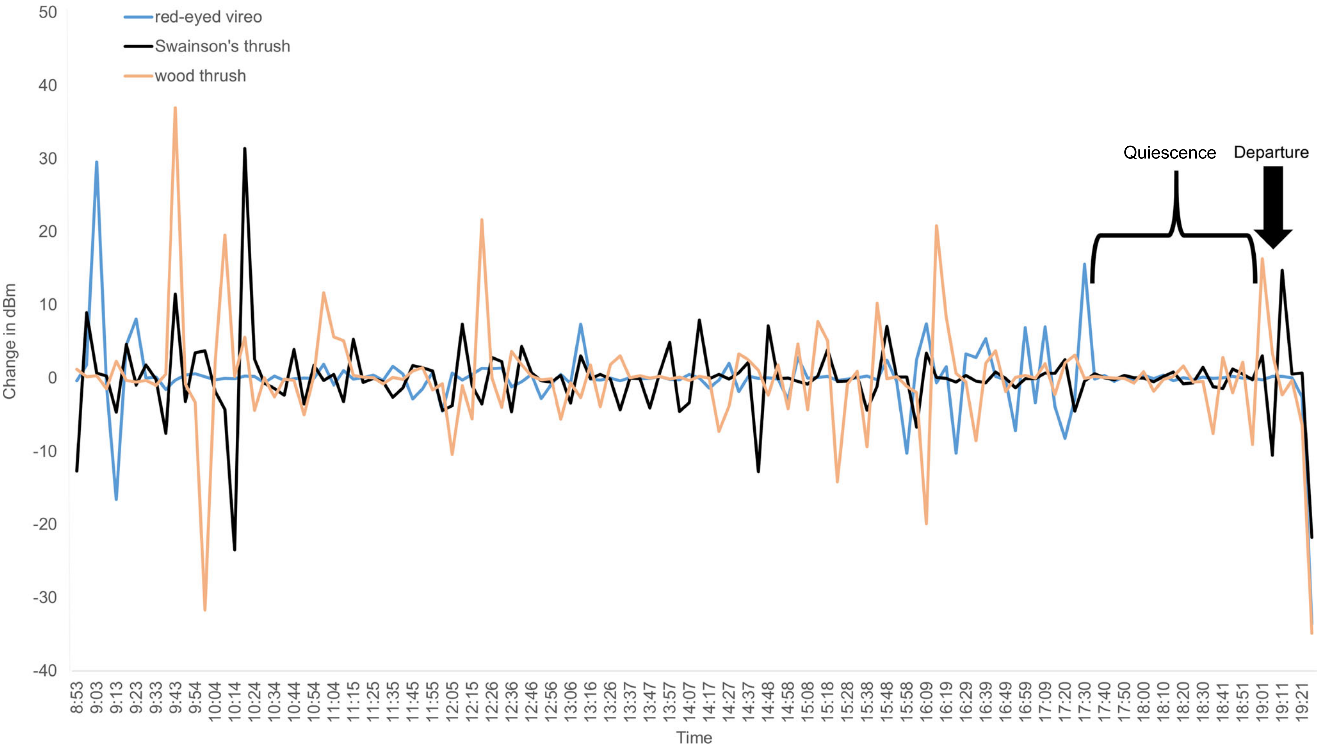

Fig. 2 The activity, quiescence, and departure of a typical red-eyed vireo, Swainson's thrush, and wood thrush that were radio-tagged in the morning and departed that evening based on changes in signal strength from the automated radiotelemetry system

period. We created 9999 simulations of 2-h intervals based on daytime inactivity patterns and determined where the observed proportion of inactivity during the 2-h pre-departure (quiescence) period fell relative to the distribution of simulated data. We used similar simulations to compare the length of inactivity during quiescence with intervals spent inactive occurring randomly throughout the day.

We used a General Linear Model (GLM) in "R" (using the default "glm" function; R Core Team 2011) to model the influence of species and year on the proportion of inactivity during the 2-h pre-departure period and length of quiescence. We ran a separate GLM to evaluate the influence of species on departure time. We used *t* tests to determine the significance of all pair-wise comparisons of pre-departure inactivity patterns and departure time between species. To assess if any interspecies differences in pre-departure activity were a function of species' average time of departure, we used a general linear model to quantify the relationship between inactivity (proportion of inactivity and quiescence length) and species' time of departure.

For each species, we used a GLM to examine the relationship between the proportion of inactivity during the 2-h pre-departure period and eight variables. We included three extrinsic weather variables measured at the time of departure: surface wind speed, wind direction, and cloud cover. We considered these weather variables because they are known to influence birds' migration decisions and success in this and other study systems (Able 1972; Deppe et al. 2015). We obtained weather data from the National Centers for Environmental Prediction North American Regional Reanalysis data set (32-km spatial resolution and 8-h temporal resolution; Mesinger et al. 2006) accessed through Movebank.org's Environmental-Data Automated Track Annotation (Env-DATA) system service (Dodge et al. 2013, 2014). We defined wind direction as degrees from north such that north was 0°, south was 180°, and both east and west were 90° in order to account for the circularity of the data. Since birds crossing the Gulf of Mexico are traveling north-south, we expect that this 180° scale is able to capture wind favorability. Cloud cover was defined as percent coverage of the sky by clouds; however, this variable was not included in the wood thrush model due to gaps in cloud cover information on nights when wood thrushes were departing. Our models for each species also included day of year. We pooled data across years because a comparison of quiescence among years was not significant. Additionally, there was no a priori reason to expect a year effect; we expected that any year effect would likely be due to differences in weather, which we included in our models.

We included three intrinsic variables in our GLMs examining the correlates of inactivity: age, subcutaneous fat score recorded at the time of capture, and the direction of departure. We also included departure time (minutes after civil twilight) in species-specific models in order to investigate if the timing of migration departure impacted quiescence. We recorded age as either hatch year (young) or after hatch year (adult) and converted the qualitative 0–5 scale for fat to a binary categorization of fat birds (fat scores > 3) and lean birds (fat scores ≤ 3). A bird's departure direction was the departure direction relative to north, for example, a bird departing as determined by the ARU at 355° would be 5° (scale 1–180). We used Bonferroni adjustment to reduce the likelihood that significant differences were greater than chance when analyzing our three species (adjusted alpha = 0.017). Cohen's d was used when appropriate to assess effect size for comparison between two means.

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

Results

Quiescent period

We quantified the proportion of time spent inactive during the 2-h pre-departure period and the length of inactivity immediately prior to departure for 63 red-eyed vireos, 70 Swainson's thrushes, and 45 wood thrushes (178 total individuals). Red-eyed vireos spent a higher proportion of the 2 h inactive prior to departing the study site (0.84 ± 0.21; this and all following results are shown as mean ± SD) than Swainson's thrushes (0.65 ± 0.24; $t = -4.953$, df = 131, $p < 0.0001$) and wood thrushes (0.60 ± 0.23; $t = -5.624$, df = 106, $p < 0.0001$). Wood thrushes and Swainson's thrushes spent a similar proportion of the 2 h prior to their departure inactive ($t = -1.195$, df = 113, $p = 0.235$). The length of the quiescence period also was significantly longer in red-eyed vireos (95 ± 77 min; $n = 63$) than either Swainson's thrushes (21 ± 34 min; $n = 70$; $t = -8.066$, df = 131, $p < 0.0001$) or wood thrushes (20 ± 29 min; $n = 45$; $t = -7.158$, df = 106, $p < 0.0001$), but did not differ between thrush species ($t = -0.116$, df = 113, $p = 0.908$). Additionally, species differed in their average time of departure. Red-eyed vireos departed significantly earlier following sunset than Swainson's thrushes (red-eyed vireo 35.222 ± 72.48 min after sunset, $n = 63$; Swainson's thrush 74.84 ± 103.10 min after sunset, $n = 70$; $t = 2.537$, df = 131, $p = 0.01$) and wood thrushes (124.28 ± 56.00 min after sunset, $n = 45$; $t = 6.9$, df = 106, $p < 0.001$; Fig. 3), and Swainson's thrushes departed significantly earlier than wood thrushes ($t = -2.947$, df = 113, $p = 0.003$). Considered as a whole, species with shorter quiescent periods left significantly later in the evening of the day of capture ($r^2 = 0.03$, $t = -2.36$, $p = 0.019$).

Quiescence and other periods of daytime inactivity

The Markov chain Monte Carlo simulation analysis revealed that pre-departure inactivity and inactivity during the rest of the day prior to the 2-h pre-departure period varied among the three species ($t < 4.193$, df = 175, $p < 0.001$; Fig. 4) but not among years ($t > 0.478$, $p = 0.384$). Red-eyed vireos showed significant differences in inactivity between the pre-departure period and comparable periods of time during the rest of the day based on our simulations (Fig. 4). They were inactive, on average 47% of the total time prior to the pre-departure period, while the proportion of time inactive increased to 84% during the 2-h pre-departure interval ($p = 0.004$). Furthermore, red-eyed vireos averaged 95 (± 77) consecutive minutes inactive immediately prior to departure, significantly greater than the 6 (± 9) consecutive minutes of inactivity, on average, that characterized simulations of the rest of the day ($p = 0.001$; Fig. 5).

The proportion of time spent inactive did not increase during the pre-departure period for either of the other focal species based on our simulation analysis. Swainson's thrushes were inactive 65% of the time during the 2 h prior to departure and 60% during the rest of the day ($p = 0.375$). Periods of inactivity averaged 21 (± 34) minutes during the pre-departure period compared to 8 (± 14) minutes, on average, for the rest of the day (Fig. 5). Although that difference was not statistically significant ($p = 0.161$), measure of effect size suggests a moderate difference in magnitude between the two time periods (Cohen's $d = 0.50$). Proportion of time spent inactive did not differ between the 2 h before departure (60%) and the rest of the day (52%) for wood thrushes ($p = 0.319$). The average length of time inactive did not differ between the pre-departure period (20 ± 29 min) and the rest of the day (16 ± 15 min) in this species ($p = 0.276$; Fig. 5).

Relationship between quiescence and extrinsic and intrinsic variables

Departure direction, the interaction of wind speed and wind direction, energetic condition (fat scores), cloud cover, and day of year were not significantly related to the proportion of time inactive during the 2-h period prior to departure for any of the three species (Tables 1, 2, and 3). Keep in mind that proportion of inactivity during that window of time may not capture relationships if the effect is more likely in the minutes before flight. The proportion of time spent inactive prior to departure was age-dependent for two species (Fig. 6). Red-eyed vireos showed a significant effect ($p = 0.007$; adjusted alpha = 0.017) in which hatch year birds spent 13% less time inactive (0.81 ± 0.22), on average, prior to departure than after hatch year birds (0.94 ± 0.10; Table 1; Fig. 6). Wood thrush also showed a similar age difference, with hatch year birds spending 12% less time inactive than after hatch year birds prior to departing the site (HY 0.58 ± 0.22 vs. AHY 0.70 ± 0.28, $p = 0.013$, adjusted alpha = 0.017;

Fig. 3 Distribution of departure times relative to sunset for radio-tagged red-eyed vireos, Swainson's thrushes, and wood thrushes whose activity was monitored in relation to quiescence. Means are depicted by red arrows

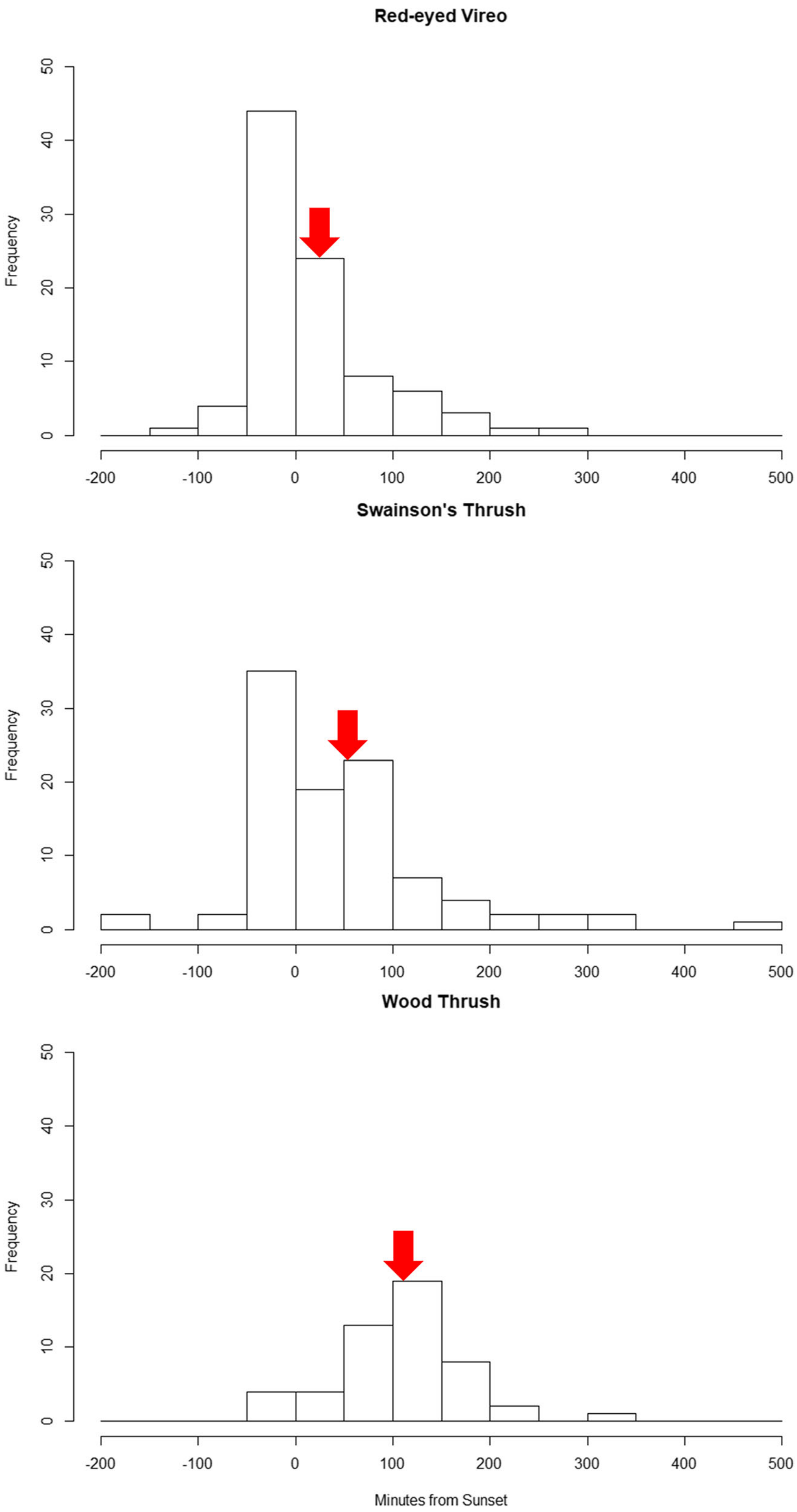

Table 2; see Fig. 6). Swainson's thrush did not show a statistically significant effect of age, although the pattern was similar to the other species (HY 0.63 ± 0.26 vs. AHY 0.69 ± 0.21, $p = 0.816$, Table 3). Swainson's thrush, however, did show a significant positive relationship between proportion of inactivity and departure time ($p = 0.0002$, adjusted alpha = 0.017); birds that left later in the evening spent a greater proportion of time inactive prior to departure.

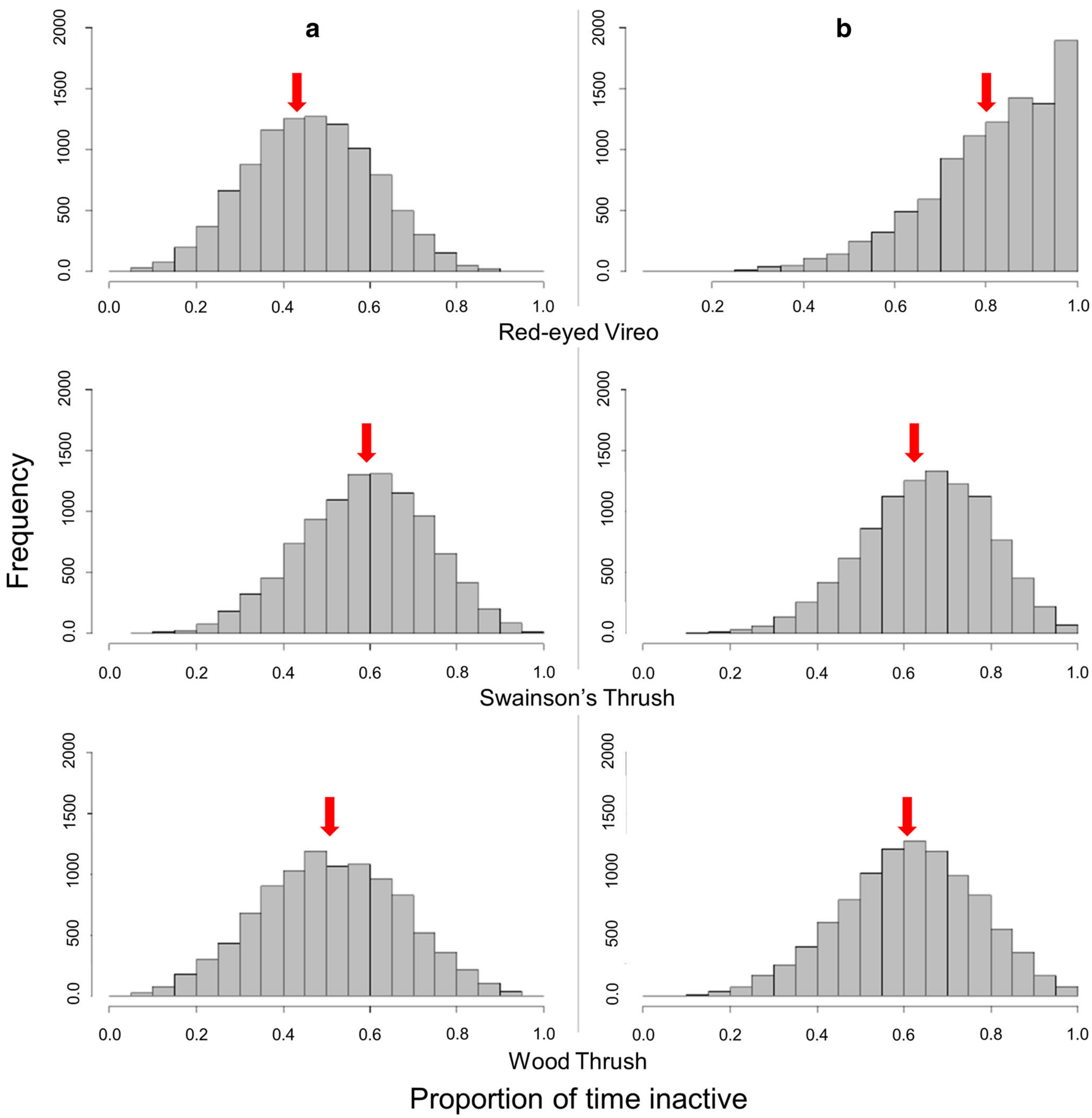

Fig. 4 Distributions of **a** background (daytime) and **b** pre-departure proportions of inactivity based on Markov chain Monte Carlo simulations for the three study species tracked using automated radiotelemetry on the Fort Morgan Peninsula, AL, from 2011 to 2014. Red-eyed vireos showed a significant difference in the proportion of time inactive between the pre-departure and daytime periods ($p = 0.004$) based on the simulations, while the thrush species showed no difference in the proportion of time inactive between the two periods (Swainson's thrush $p = 0.375$, wood thrush $p = 0.319$). Mean simulated proportion of time inactive is indicated by red arrows

Activity patterns of departing and non-departing birds

Non-departing birds showed similar inactivity patterns in the 2-h period prior to the species mean departure time when compared to departing birds in the observed 2-h pre-departure period. Non-departing red-eyed vireos spent an average of 85% of the 2-h interval inactive compared to 84% for departing vireos, and the mean consecutive minutes of inactivity was 102 min for non-departing birds and 95 min for departing birds. Non-departing and departing Swainson's thrushes also were comparable in terms of the mean proportion of time spent inactive (47% for non-departing vs. 65% for departing) and mean consecutive minutes inactive (24 min non-departing vs. 21 min departing).

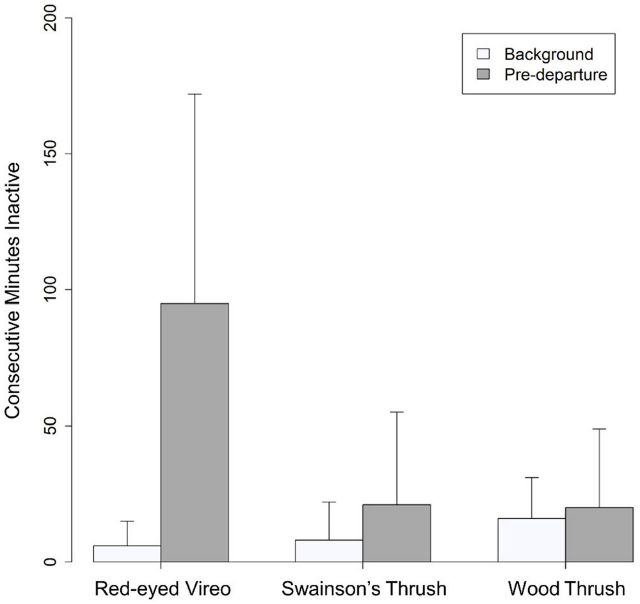

Fig. 5 Mean (+ standard deviation) consecutive minutes spent inactive during the 2-h pre-departure period and background (daytime) period at the Fort Morgan, AL, stopover site for 2011–2014 based on Markov chain Monte Carlo simulations for each species. Red-eyed vireos remained inactive longer in the pre-departure period than the background daytime period ($p = 0.001$). Swainson's thrushes ($p = 0.161$) and wood thrushes ($p = 0.276$) showed no difference in the consecutive number of minutes inactive between the two periods

Discussion

Our study reveals the occurrence of quiescence prior to departure in free-ranging individuals of three intercontinental migratory songbird species, though the quiescent period varied within and among species. Red-eyed vireos engaged in the longest, most pronounced quiescence; they spent a greater proportion of the pre-departure period inactive, and remained inactive for longer periods of time than either of the two thrush species. Moreover, vireos displayed a quiescent period that was proportionally longer than bouts of daytime inactivity. Thrush species were inactive for shorter periods of time during the 2-h pre-departure window, and those periods of inactivity were consistent with those observed during any random 2-h interval throughout the same day.

Table 1 General linear model results for a model with proportion of red-eyed vireo inactivity as the response variable and departure direction, departure time, departure date, cloud cover, age, fat, and the interaction of wind speed and wind direction as the independent variables. Adjusted alpha = 0.017

Variable	Estimate	Std. error	*t*	*p*
Intercept	0.4440	1.2096	0.367	0.7152
Departure direction[a]	0.0661	0.0617	1.072	0.2894
Departure time[b]	0.0010	0.0005	1.853	0.0704
Departure date	0.0007	0.0045	0.162	0.8718
Wind direction[a]	0.0011	0.0017	0.656	0.5151
Wind speed	0.0555	0.0455	1.221	0.2285
Wind dir. * wind sp.	−0.0004	0.0005	−0.852	0.3986
Cloud cover	0.00178	0.0011	1.548	0.1285
Age[c]	−0.1621	0.0579	−2.815	0.0072
Fat[d]	0.0741	0.0892	0.830	0.4106

[a] Degrees from north

[b] Minutes after sunset

[c] Hatch year or after hatch year bird

[d] Fat (fat score > 3) or lean (fat score ≤ 3; Helms and Drury 1960)

Table 2 General linear model results for a model with proportion of wood thrush inactivity as the response variable and departure direction, departure time, departure date, age, fat, and the interaction of wind speed and wind direction as the independent variables. Adjusted alpha = 0.017

Variable	Estimate	Std. error	*t*	*p*
Intercept	2.24E+00	2.84E+00	0.789	0.4408
Departure direction[a]	1.07E−02	9.97E−02	0.107	0.9160
Departure time[b]	−2.60E−03	2.03E−03	−1.281	0.2173
Departure date	−2.94E−03	1.12E−02	−0.264	0.7949
Wind direction[a]	1.32E−04	3.29E−03	0.394	0.6986
Wind speed	1.30E−03	9.88E−04	0.133	0.8955
Wind dir. * wind sp.	−1.81E−07	1.57E−05	−0.011	0.9910
Age[c]	−9.46E−01	3.43E−01	−2.758	0.0134
Fat[d]	1.58E−01	1.19E−01	1.326	0.2023

[a] Degrees from north

[b] Minutes after sunset

[c] Hatch year or after hatch year bird

[d] Fat (fat score > 3) or lean (fat score ≤ 3; Helms and Drury 1960)

Table 3 General linear model results for a model with proportion of Swainson's thrush inactivity as the response variable and departure direction, departure time, departure date, cloud cover, age, fat, and the interaction of wind speed and wind direction as the independent variables. Not enough data on cloud clover later in the year when wood thrushes depart to use in the model. Adjusted alpha = 0.017

Variable	Estimate	Std. error	*t*	*p*
Intercept	2.86E+00	1.03E+00	2.769	0.0079
Departure direction[a]	−3.58E−02	7.24E−02	−0.495	0.6225
Departure time[b]	1.51E−03	3.74E−04	4.084	0.0002
Departure date	−8.98E−03	3.8E−03	−2.364	0.0220
Wind direction[a]	1.31E−03	1.03E−03	1.269	0.2103
Wind speed	−4.49E−05	4.82E−04	−0.093	0.9262
Wind dir. * wind sp.	−1.66E−06	5.42E−06	−0.306	0.7606
Cloud cover	−8.46E−04	5.1E−03	−0.166	0.8688
Age[c]	−1.62E−02	7.58E−02	−0.214	0.8317
Fat[d]	1.26E−01	7.64E−02	1.646	0.1061

[a] Degrees from north

[b] Minutes after sunset

[c] Hatch year or after hatch year bird

[d] Fat (fat score > 3) or lean (fat score ≤ 3; Helms and Drury 1960)

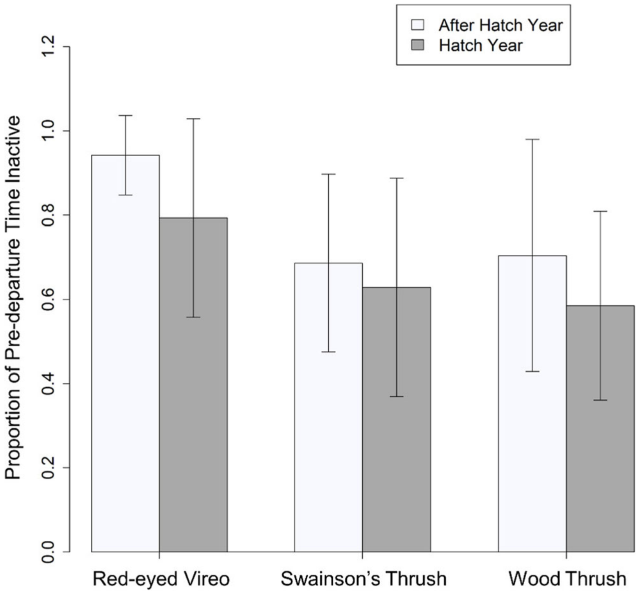

Fig. 6 Mean (± standard deviation) proportion of time spent inactive during the pre-departure interval for after hatch year (adult) and hatch year (young) birds at the Fort Morgan stopover site from 2011 to 2014 for each species. Hatch year birds have yet to complete their first migration, whereas after hatch year birds have completed at least one fall and one spring migration. After hatch year birds were inactive for a significantly greater proportion of time prior to departure for red-eyed vireos ($p = 0.007$, adjusted $p = 0.017$) and wood thrushes ($p = 0.013$, adjusted $p = 0.017$) but not Swainson's thrushes ($p = 0.816$, adjusted $p = 0.017$).

Species differences in quiescence may reflect species-specific decision-making and provide some insight into the function of a bird's activity budget in relation to migration. For example, red-eyed vireos are more sensitive to the interplay of intrinsic and extrinsic conditions favorable for a flight over the Gulf of Mexico than either Swainson's thrushes or wood thrushes (Deppe et al. 2015). A longer quiescence would be consistent with more deliberative weighing of the risks associated with departure. Interestingly, we observed no relationship between quiescence and cloud cover for the species we analyzed, which would likely affect the availability of directional information, nor did we find a relationship between quiescence and wind conditions, which also influence departure decisions in our study system (Deppe et al. 2015; but see Bolus et al. 2017). With respect to orientation, where cloud cover occurs in the sky toward evening may be more important than how much cloud cover, which is what we measured.

Of course, species-specific differences in quiescence may have less to do with the integration of information, and more to do with foraging strategies and preparation for departure at the end of the day. The smaller red-eyed vireo, in principle, will experience a higher fuel deposition rate (Lindström 2003) and might reach optimal departure fuel load sooner than either thrush species (sensu Alerstam and Lindström 1990), which may translate into a longer quiescent period. Moreover, if vireos and the two thrush species differ in the composition of their diet vis-à-vis the ability to process food (see Levey and Karasov 1994; Parrish 1997), time required to digest food, expel waste, turn off digestion, and upregulate physiology for flight may contribute to observed differences in quiescence.

Quiescence in the three species does not appear to reflect the onset of darkness and limited availability of light for foraging and other typical daytime activities. Red-eyed vireos departed between sunset and civil twilight, yet showed little activity during the 2-h pre-departure window despite having sufficient light to remain active. On the other hand, thrushes (especially wood thrushes) left Fort Morgan late in the evening, well beyond civil twilight, and were more active prior to departure than expected if quiescence was driven by light availability. Furthermore, thrushes presumably experience more rapid declines in light levels toward the end of the daylight period than red-eyed vireos, because they are shrub and ground foragers (Yong and Moore 2005). Red-eyed vireos are foliage gleaners that often concentrate in the canopy during stopover (Loria and Moore 1990).

Among Swainson's thrushes, however, individuals that departed later in the evening spent a greater proportion of time inactive, keeping in mind that the species overall engaged in short inactivity periods. Given evidence documenting sleep deprivation in migratory songbirds that forage during the day and migrate at night (Fuchs et al. 2006, 2009), it is possible that the greater amount of inactivity for later departing thrushes could be a result of individuals taking a short nap before departing. It could also be that Swainson's thrushes leaving later in the night are on the cusp of deciding whether to take off and may be using that time to weigh their options.

Age appears to affect the length of quiescence. Both vireo and wood thrush adults spent significantly more time inactive prior to departure than young birds, but the age difference was not significant in Swainson's thrush. This pattern may reflect age-dependent differences in migration strategy, orientation capabilities, or both. Adults may devote more time to assessing alternative departure strategies and/or processing more information specific to their spatio-temporal position on the migratory journey, whereas young, less experienced birds on their first migration may simply rely on their endogenous time-direction program (Berthold 1996). Another, unrelated factor may contribute to an age-dependent result: adult migrants enjoy greater foraging success (e.g., Heise and Moore 2003; see also Woodrey and Moore 1997), so they may meet energetic demands sooner than younger, less experienced birds who may continue actively foraging later in the day.

Findings from our exploration of inactivity patterns of individuals that stayed at the site > 1 day suggest that non-departing birds behave comparably to departing birds during the 2-h period prior to expected departure. The apparent lack of differences between non-departing and departing birds is unclear, although if confirmed by other studies, it does not preclude the notion that birds use this time to prepare for departure and/or process information. Birds that do not depart may simply decide to remain at the site after processing information necessary to prepare for departure. Additionally, these findings raise the question of how migratory quiescence is defined. Previous studies define quiescence specifically as a period of inactivity prior to the departure of free-flying birds from a stopover site or the onset of *zugunruhe* in caged birds (e.g., Morton 1967; Hebrard 1971; Diehl and Larkin 1998; Ramenofsky et al. 2008), implying that it is uniquely expressed on departure nights. Perhaps quiescence should be more broadly defined as a daily inactive period toward the end of the day in nocturnally migrating species during stopover. However, we emphasize that these findings need to be considered cautiously because of our small sample size. Future studies of activity patterns conducted at sites where birds are likely to stopover for multiple days are necessary to confirm this pattern and better inform our understanding of quiescence behavior in migrating birds.

Although our novel use of automated radiotelemetry provides evidence of quiescent behavior in free-ranging migratory songbirds and our analysis hints at possible function(s), the spatial and temporal scales over which movement could be monitored may have made it difficult to tease apart the relative contribution of different intrinsic and extrinsic factors to quiescence. While the ARTS provided a large amount of data on many individuals, activity was determined via changes in signal strength over a few minutes rather than recording continuous signals as was the case in the earlier observations of Kjos and Cochran (1970) and Diehl and Larkin (1998). The advent of new software-based receivers, such as Motus (Taylor et al. 2017), may allow for a more rapid sampling of the activity of multiple individuals. The broad distribution of Motus towers, which can be fitted with up to eight antennas to provide higher spatial resolution data, may provide an opportunity to examine activity (i.e., quiescence behavior) in many different contexts, such as fall and spring, coastal and inland, and position of birds relative to their wintering or breeding destinations, as well as additional species.

Migratory birds surely become inactive prior to departure for several reasons, and our study reveals the nuanced nature of that quiescence and the need to more closely track movements in an experimental framework. Two general approaches could be used to identify the causal factors regulating quiescence and test hypotheses regarding its function. First, the experience or condition of migrants could be manipulated during stopover prior to release, and then free-ranging behavior monitored during the pre-departure period. For example, investigators have controlled access to directional information known to be important to migratory orientation (e.g., pattern of polarized light and magnetic cues), and then monitored departure direction using radiotelemetry (Cochran et al. 2004; Chernetsov et al. 2011; Schmaljohann et al. 2013). Similarly, Smith and McWilliams (2014) manipulated diet to adjust fuel loads during stopover, and evaluated their effect on movement behavior and departure decisions of radio-tagged hermit thrushes (*Catharus guttatus*). Using such an approach, future studies could experimentally manipulate migratory orientation cues, hormone levels (e.g., ghrelin), type and availability of food resources, fuel loads, and sleep deprivation. In addition to monitoring activity rates and durations, collection of data on expulsion of waste products and apparent sleeping behavior would provide further data to test particular hypotheses regarding the function of quiescence. Second, the experience or condition of captive migrants in migratory disposition could be manipulated, and activity evaluated in a controlled cage setting (Agatsuma and Ramenofsky 2006; Ramenofsky et al. 2008). For example, the function of the hormone ghrelin has been shown experimentally to suppress food intake and increase *zugunruhe* in songbirds (Goymann et al. 2017). Manipulations of ghrelin or other hormones and a detailed characterization of their movement prior to migratory departure would provide insight into physiological mechanisms regulating quiescence. Early orientation-activity cage designs (Emlen and Emlen 1966) did not permit investigators to observe detailed behavior of the birds, so little was gained about the actual behavior of birds while they are exhibiting migratory restlessness and making directional choices. Video-tracking programs (e.g., Muheim et al. 2014) now exist for extracting time-resolved, positional data of caged birds in migratory condition (e.g., Pakhomov and Chernetsov 2014). There remain many questions associated with the function of quiescence, and using automated radiotelemetry in an experimental context during both spring and fall migration may improve our understanding of this interesting behavior.

Acknowledgments We thank our numerous field technicians at the University of Southern Mississippi (USM) Fort Morgan Peninsula Banding Station for their work and dedication as well as the USM radio tower crews and members of the USM Migratory Bird Research Group. We appreciate the Bon Secour National Wildlife Refuge for providing permission to conduct work on their property. We also thank Sarah Davidson and Rolf Weinzierl from Movebank.org, who assisted us in accessing atmospheric data. We thank Eben Paxton and two anonymous reviewers, who provided comments that substantially improved the quality of our paper. James Novak, Eric Bollinger, and Sean Peterson provided valuable feedback on the research and comments on earlier drafts. This work was supported by the National Science Foundation (IOS Award nos. 1146832, 1147096, and 1147022), National Geographic Society Committee on Research and Exploration (Award no. 8971-11), Eastern Illinois University (Research and Creative Activity Awards to JLD and LNS), University of Illinois Urbana-Champaign, and University of Southern Mississippi. TJZ was supported by a National Science Foundation GK-12 Program Award (no. 0947944). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

Compliance with ethical standards

Ethical approval All research activities involving animals were approved by the University of Southern Mississippi Institutional Animal Care and Use Committee (protocol no. 11092210), US Geological Survey Bird Banding Laboratory (permit no. 21221), and Bon Secour National Wildlife Refuge.

Conflict of interest The authors declare that they have no conflict of interest.

References

Able KP (1972) Fall migration in coastal Louisiana and the evolution of migration patterns in the Gulf region. Wilson Bull 84:231–242

Agatsuma R, Ramenofsky M (2006) Migratory behaviour of captive white-crowned sparrows, *Zonotrichia leucophrys gambelii*, differs during autumn and spring migration. Behaviour 143(10):1219–1240. https://doi.org/10.1163/156853906778691586

Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E (ed) Bird migration. Springer, Berlin, pp 331–351. https://doi.org/10.1007/978-3-642-74542-3_22

Beauchamp G (2017) Does sun glare increase antipredator behavior in prey? J Avian Biol 48(4):591–595. https://doi.org/10.1111/jav.01154

Berthold P (1996) Control of bird migration. Chapman and Hall, London

Bolshakov CV (1992) Evening movements and the start of nocturnal migratory flight in the fieldfare (*Turdus pilaris*): preliminary results. Proc Zool Inst 247:18–42 [Russian with English summary]

Bolus R, Diehl R, Moore FR, Deppe J, Ward M, Smolinsky J, Zenzal TJ Jr (2017) Swainson's thrushes do not show strong wind selectivity prior to crossing the Gulf of Mexico. Sci Rep 7(1):14280. https://doi.org/10.1038/s41598-017-14668-3

Celis-Murillo A, Benson TJ, Sosa-Lopez JR, Ward MP (2016) Nocturnal songs in a diurnal passerine: attracting mates or repelling intruders? Anim Behav 118:105–114. https://doi.org/10.1016/j.anbehav.2016.04.023

Chernetsov N (2012) Passerine migration: stopovers and flight. Springer, Berlin. https://doi.org/10.1007/978-3-642-29020-6

Chernetsov N, Kishkinev D, Kosarev V, Bolshakov C V (2011) Not all songbirds calibrate their magnetic compass from twilight cues: a telemetry study. J Exp Biol 214:2540–2543

Cochran WW, Mouritsen H, Wikelski M (2004) Migrating songbirds recalibrate their magnetic compass daily from twilight cues. Science 304:405–408

Deppe JL, Ward MP, Bolus RT, Diehl RH, Celis-Murillo A, Zenzal TJ Jr, Moore FR, Benson TJ, Smolinsky JA, Schofield LN, Enstrom DA, Paxton EH, Bohrer G, Beveroth TA, Raim A, Obringer RL, Delaney D, Cochran WW (2015) Negotiating the Gulf of Mexico: fat, weather and date affect migratory songbirds' departure decisions, routes, and crossing times. Proc Natl Acad Sci U S A 112(46):E6331–E6338. https://doi.org/10.1073/pnas.1503381112

Diehl RH, Larkin RP (1998) Wingbeat frequency of two Catharus thrushes during nocturnal migration. Auk 115(3):591–601. https://doi.org/10.2307/4089408

Dodge S, Bohrer G, Weinzierl R, Davidson SC, Kays R, Douglas D, Cruz S, Han J, Brandes D, Wikelski M (2013) The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. Mov Ecol 1(1):3. https://doi.org/10.1186/2051-3933-1-3

Dodge S, Bohrer G, Bildstein K et al (2014) Environmental drivers of variability in the movement ecology of turkey vultures (*Cathartes aura*) in North and South America. Philos T Roy Soc B 369:1471–2970

Downey A (2013) Think Bayes. O'reilly Media, Sebastopol

Emlen S (1980) Decision making by nocturnal bird migrants: the integration of multiple cues. In: Nohring R (ed) Acta XVII International Ornithological Congress. Deutsche Ornithologen-Gesellschaft, Berlin, pp 553–560

Emlen ST, Emlen JT (1966) A technique for recording orientation of captive birds. Auk 83:361–367

Fuchs T, Haney A, Jechura TJ, Moore FR, Bingman V (2006) Daytime naps in night-migrating birds: behavioural adaptation to seasonal sleep deprivation in the Swainson's thrush, *Catharus ustulatus*. Anim Behav 72(4):951–958. https://doi.org/10.1016/j.anbehav.2006.03.008

Fuchs T, Maury M, Moore FR, Bingman V (2009) Daytime micro-naps in a nocturnal migrants: an EEG analysis. Biol Lett 5(1):77–80. https://doi.org/10.1098/rsbl.2008.0405

Gelman A, Rubin DB (1992) Inference from interative simulation using multiple sequences. Stat Sci 7(4):457–511. https://doi.org/10.1214/ss/1177011136

Goymann W, Lupi S, Kaiya H, Cardinale M, Fusani L (2017) Ghrelin regulates migratory decisions in birds. Proc Natl Acad Sci USA 114:1946–1951. https://doi.org/10.1073/pnas.1619565114

Hebrard JJ (1971) The nightly initiation of passerine migrant in spring: a direct visual study. Ibis 113:8–18

Heise CD, Moore FR (2003) Age-related differences in foraging efficiency, molt, and fat deposition of gray catbirds prior to autumn migration. Condor 105(3):496–504. https://doi.org/10.1650/7183

Helms CW, Drury WH (1960) Winter and migratory weight and fat field studies on some North American buntings. Bird Band 31(1):1–40. https://doi.org/10.2307/4510793

Jones TM, Ward MP, Benson TJ, Brawn JD (2017) Variation in nestling body condition and wing development predict cause-specific mortality in fledgling dickcissels. J Avian Biol 48(3):439–447. https://doi.org/10.1111/jav.01143

Kays R, Tilak S, Crofoot M, Fountain T, Obando D, Ortega A, Wikelski M (2011) Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. Comput J 54(12):1931–1948. https://doi.org/10.1093/comjnl/bxr072

Kjos CG, Cochran WW (1970) Activity of migrant thrushes as determined by radio-telemetry. Wilson Bull 82:225–226

Levey DJ, Karasov WH (1994) Gut passage of insects by European starlings and a comparison with other species. Auk 111(2):478–481. https://doi.org/10.2307/4088614

Lindström Å (2003) Fuel deposition rates in migrating birds: causes, constraints, and consequences. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin, pp 307–320. https://doi.org/10.1007/978-3-662-05957-9_21

Loria DE, Moore FR (1990) Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. Behav Ecol Sociobiol 1(1):24–25. https://doi.org/10.1093/beheco/1.1.24

Louder MIM, Ward MP, Schelsky WM, Hauber ME, Hoover JP (2015) Out on their own: a test of adult-assisted dispersal in fledgling brood parasites reveals solitary departures from hosts. Anim Behav 110:29–37. https://doi.org/10.1016/j.anbehav.2015.09.009

Mesinger F, DiMego G, Kalnay E et al (2006) North American regional reanalysis. Bull Am Meteorol Soc 87:343–360

Moore FR (1987) Sunset and the orientation behavior of migrating birds. Biol Rev 62(1):65–86. https://doi.org/10.1111/j.1469-185X.1987.tb00626.x

Morton ML (1967) Diurnal feeding patterns in white-crowned sparrows *Zonotrichia leucophyrs gambelii*. Condor 69(5):491–512. https://doi.org/10.2307/1366149

Muheim R, Henshaw I, Sjöberg S, Deutschlander ME (2014) BirdOriTrack: a new video-tracking program for orientation research with migratory birds. J Field Ornithol 85:91–105

Pakhomov A, Chernetsov N (2014) Early evening activity of migratory Garden Warbler Sylvia borin: compass calibration activity? J Ornithol 155:621–630

Palmgren P (1949) On the diurnal rhythm of activity and sleep in birds. Ibis 91:561–575

Parrish JD (1997) Patterns of frugivory and energetic condition in Neotropical landbirds during autumn migration. Condor 99(3): 681–697. https://doi.org/10.2307/1370480

Piersma T (1998) Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight? J Avian Biol 29(4):511–520. https://doi.org/10.2307/3677170

Pyle P (1997) Identification guide to north American birds. Slate Creek Press, Bolinas

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna http://www.R-project.org

Raim A (1978) A radio transmitter attachment for small passerine birds. Bird Band 49(4):326–332. https://doi.org/10.2307/4512391

Ramenofsky M, Agatsuma R, Ramfar T (2008) Environmental conditions affect the behavior of captive, migratory white-crowned sparrows. Condor 110:658–671

Rattenborg NC (2017) Sleeping on the wing. Interface Focus 7(1): 20160082. https://doi.org/10.1098/rsfs.2016.0082

Rattenborg NC, Mandt BH, Obermeyer WH, Winsauer PJ, Huber R, Wikelski M, Benca RM (2004) Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). PLoS Biol 2(7):e212. https://doi.org/10.1371/journal.pbio.0020212

Sandberg R, Moore FR (1996) Migratory orientatation of red-eyed vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. Behav Ecol Sociobiol 39(1):1–10. https://doi.org/10.1007/s002650050261

Schmaljohann H, Rautenberg T, Muheim R, Naef-Daenzer B, Bairlein F (2013) Response of a freeflying songbird to an experimental shift of the light polarization pattern around sunset. J Exp Biol 216:1381–1387

Smith AD, McWilliams S (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. Behav Ecol 25:1423–1435. https://doi.org/10.1093/beheco/aru148

Sjöberg S, Muheim R (2016) A new view on an old debate: type of cue-conflict manipulation and availability of stars can explain the discrepancies between cue-calibration experiments with migratory songbirds. Front Behav Neuosci 10:29

Smolinsky J, Diehl RH, Radzio T, Delaney DK, Moore FR (2013) Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. Behav Ecol Sociobiol 67(12):2041–2051. https://doi.org/10.1007/s00265-013-1614-6

Taylor PD, Crewe TL, Mackenzie SA, Lepage D, Aubry Y, Crysler Z, Finney G, Francis CM, Guglielmo CG, Hamilton DJ, Holberton RL, Loring PH, Mitchell GW, Norris DR, Paquet J, Ronconi RA, Smetzer JR, Smith PA, Welch LJ, Woodworth BK (2017) The motus wildlife tracking system: a collaborative research network to enhance the understanding of wildlife movement. Avian Cons and Ecol 12(1):8. https://doi.org/10.5751/ACE-00953-120108

Ward MP, Sperry JH, Weatherhead PJ (2013) Evaluation of automated eadio telemetry for quantifying movements and home ranges of snakes. J Herpetol 47(2):337–345. https://doi.org/10.1670/12-018

Ward MP, Alessi M, Benson TJ, Chiavacci SJ (2014) The active nightlife of diurnal birds: extraterritorial forays and nocturnal activity patterns. Anim Behav 88:175–184. https://doi.org/10.1016/j.anbehav.2013.11.024

Woodrey M, Moore FR (1997) Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. Auk 114(4):695–707. https://doi.org/10.2307/4089289

Yong W, Moore FR (2005) Long-distance bird migrants adjust their foraging behavior in relation to energy stores. Acta Zool Sin 51:12–23

Zenzal TJ Jr, Fish AC, Jones TM, Ospina EA, Moore FR (2013) Observations of mortality and anti-predator behavior of ruby-throated hummingbirds (*Archilocus colubris*) during migratory stopover. Southeast Nat 12(4):N21–N25. https://doi.org/10.1656/058.012.0416