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Source: The Auk, 135(3) : 547-560

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-18-4.1

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The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 135, 2018, pp. 547–560
DOI: 10.1642/AUK-18-4.1

RESEARCH ARTICLE

Prolonged stopover and consequences of migratory strategy on local-scale movements within a regional songbird staging area

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Submitted January 6, 2018; Accepted February 22, 2018; Published May 9, 2018

ABSTRACT

Geolocator technology has recently demonstrated that many songbird species exhibit prolonged stopovers during migration that may be analogous to the staging behavior typically attributed to shorebirds. Although staging areas can act as ecological bottlenecks, there is little information on how or why songbirds engage in prolonged stopover and whether this behavior differs among individuals. We used automated radio telemetry along the eastern coastline of North America to compare stopover and migration behavior of Blackpoll Warblers (*Setophaga striata*) and Red-eyed Vireos (*Vireo olivaceus*), species that differ markedly in migratory strategy during fall migration. We also tested whether migratory behaviors differed within each species by capture date or breeding origin. Prolonged stopover was more common and longer for Blackpoll Warblers, which suggests that it may be a particularly adaptive behavior for supporting the transatlantic endurance flights they make from the region. Both species made prolonged stopovers that consisted of extended stops at one site, as well as multiple shorter stops within a geographically broad stopover landscape. Later migrants of both species and Blackpoll Warblers from more northwestern origins exhibited migratory traits consistent with a time-minimization strategy.

Keywords: automated telemetry, migration strategy, prolonged stopover, *Setophaga striata*, staging, *Vireo olivaceus*

Parada prolongada y consecuencias de la estrategia migratoria sobre los movimientos a escala local dentro del área regional de descanso de un ave canora

RESUMEN

La tecnología de geo-localización ha demostrado recientemente que muchas especies de aves canoras realizan paradas prolongadas durante la migración que pueden ser análogas al comportamiento de descanso atribuido típicamente a las aves playeras. Aunque las áreas de descanso pueden actuar como cuellos de botella ecológicos, hay poca información sobre cómo o por qué las aves canoras se embarcan en paradas prolongadas, o si este comportamiento difiere entre individuos. Usamos radio telemetría automatizada a lo largo de la línea de costa del este de América del Norte para comparar el comportamiento de parada y migratorio de *Setophaga striata* y *Vireo olivaceus*, especies que se diferencian marcadamente en la estrategia migratoria durante la migración de otoño. También evaluamos si el comportamiento migratorio se diferencia al interior de cada especie según la fecha de captura o el origen del sitio de reproducción. La parada prolongada fue más común y más larga en los individuos de *S. striata*, sugiriendo que puede ser un comportamiento particularmente adaptativo para apoyar los demandantes vuelos transatlánticos que realizan estos individuos desde la región. Ambas especies realizaron paradas prolongadas que consistieron en detenciones extendidas en un sitio, así como múltiples detenciones más cortas dentro de un paisaje de parada geográficamente amplio. Los migrantes tardíos de ambas especies, y los individuos de *S. striata* provenientes de orígenes más hacia el noroeste, mostraron rasgos migratorios consistentes con una estrategia de minimización del tiempo.

Palabras clave: descanso, estrategia migratoria, parada prolongada, *Setophaga striata*, telemetría automatizada, *Vireo olivaceus*

INTRODUCTION

During fall migration, songbirds must balance trade-offs between energetic needs, survival, and progress toward the wintering grounds. Optimal migration theory predicts that birds balance the costs and benefits of different migratory decisions to minimize total time spent on migration, energy expenditure, predation risk, or some combination of these factors (Alerstam and Lindström 1990, Åkesson and Hedenström 2000). Many songbirds minimize migration time by seeking out optimal stopover habitats and accumulating large departure fuel stores rapidly in order to

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fuel long-distance flights (Hedenström 2008), while others minimize risk or energy expenditure by carrying smaller fuel loads, stopping more frequently, and making shorter flights (Bolshakov et al. 2003, Åkesson et al. 2012, Tøttrup et al. 2012). The shorebird literature dubs these tactics "skip" and "hop" strategies, respectively, and outlines an additional strategy in which individuals accumulate extreme fat stores during long staging events to fuel subsequent "jump" flights >1,000 km (Piersma 1987, Warnock 2010). Such a "jump" strategy is in line with a program of time minimization, in that birds quickly depart from low-quality areas to seek highly productive sites where they make prolonged stopovers (Gudmundsson et al. 1991, Warnock 2010).

Although staging activity is typically attributed to shorebirds and waterfowl (Dunne et al. 1982, Newton 2008), numerous geolocator studies have recently reported passerines making stops ranging from 8 to 36 days (Heckscher et al. 2011, Åkesson et al. 2012, Delmore et al. 2012, Tøttrup et al. 2012, Callo et al. 2013, Fraser et al. 2013, Jahn et al. 2013, Kristensen et al. 2013, Renfrew et al. 2013, Wolfe and Johnson 2015, Van Loon et al. 2017) that are analogous in length to staging events. Stops of >7 days surpass the amount of time theoretically expected for migratory refueling under optimality models (Alerstam 1991) and have been classified as "prolonged stopover"—a behavior distinct from typical songbird stopover (McKinnon et al. 2013). Although it is still unclear why songbirds exhibit this behavior, these extended stops may be an adaptive strategy for accumulating large fat stores at food-rich sites to fuel long migratory flights (Tøttrup et al. 2012, Callo et al. 2013), especially just before or after a barrier (Delmore et al. 2012, Fraser et al. 2013, Gómez et al. 2017). Regardless of their purpose, effective conservation requires identifying prolonged stopover areas (McKinnon et al. 2017, Van Loon et al. 2017) and understanding behavioral patterns at these sites, because localized loss of stopover resources can pose an ecological bottleneck (Myers 1983, Buehler and Piersma 2008, Gómez et al. 2017).

Although geolocators have revealed prolonged stops for multiple songbird species, understanding of stopover and movement behavior in these staging areas is still limited, since the coarse latitudinal precision of geolocators (~300 km) precludes study of fine-scale behavior (McKinnon et al. 2014, Deppe et al. 2015). Even relatively large landscape-scale stopover movements recorded with automated telemetry (e.g., 250 km; Brown and Taylor 2017) would not be registered with geolocators. Sample-size restrictions of geolocators have also limited the study of how prolonged stopover differs between individuals. However, intraspecific differences in prolonged stopover are likely, given that factors like capture date and breeding latitude can markedly influence stopover duration (Gómez et al. 2017, Van Loon et al. 2017), migration rate (La Sorte et al. 2013, Brown and Taylor 2017), and route choice (Delmore et al. 2012, Fraser et al. 2013). Understanding intraspecific differences is important from a conservation perspective. For instance, sharply declining northern populations of Purple Martins (*Progne subis*) make more extensive prolonged stopovers in the Yucatan Peninsula than more southern conspecifics—highlighting the need for regionally targeted conservation (Van Loon et al. 2017).

We used automated VHF radio telemetry along the eastern coast of North America to study the stopover and regional-scale movements of Red-eyed Vireos (*Vireo olivaceus*; hereafter "vireos") and Blackpoll Warblers (*Setophaga striata*; hereafter "blackpolls"), 2 species that differ in strategy and route during fall migration. Both are long-distance Neotropical migrants that winter in South America. During fall migration, vireos are regularly sited along most of the eastern U.S. coastline (Sullivan et al. 2009). They reach the breeding grounds by either crossing or circumnavigating the Gulf of Mexico (Deppe et al. 2015) and thus represent a short-jump migrant. By contrast, most blackpolls exhibit an extreme jump strategy that involves a 2,500 km transatlantic flight from the eastern coast of the U.S. (DeLuca et al. 2015). Blackpolls are assumed to make long stops in the northeastern United States to amass fat stores for this transatlantic flight, but the duration of these stops is unknown (Warnock 2010). Prolonged stopover has been recorded for both species in the spring (Callo et al. 2013, DeLuca et al. 2015) but not in the fall.

Our first objective was to document whether these species exhibited prolonged stopover (i.e. >7 days; McKinnon et al. 2013) during fall migration in the Gulf of Maine (GOM)—that is, the portion of our study area north of Cape Cod (Figure 1). We also quantified several migration metrics throughout the full extent of the tracking array, including number of stops, total time in stopover, movement rate, and ratio of flight distance per stop. We expected blackpolls to make more prolonged stopovers than vireos—and consequently to exhibit fewer total stops, more total time in stopover, slower movement rates, and a smaller ratio of flight distance per stop. We expected to see evidence of time minimization (i.e. fewer stops, more total time in stopover, faster movement rates, and a greater flight distance per stop) for later migrants that face declining weather conditions and food resources, and individuals from more distant breeding latitudes that have longer migratory journeys and are under greater time constraints. We expected breeding-latitude differences to be more pronounced for blackpolls, which travel to the Atlantic coast from nearby Maritime provinces and breeding grounds as far away as Alaska (Holberton et al. 2015, Leppold 2016).

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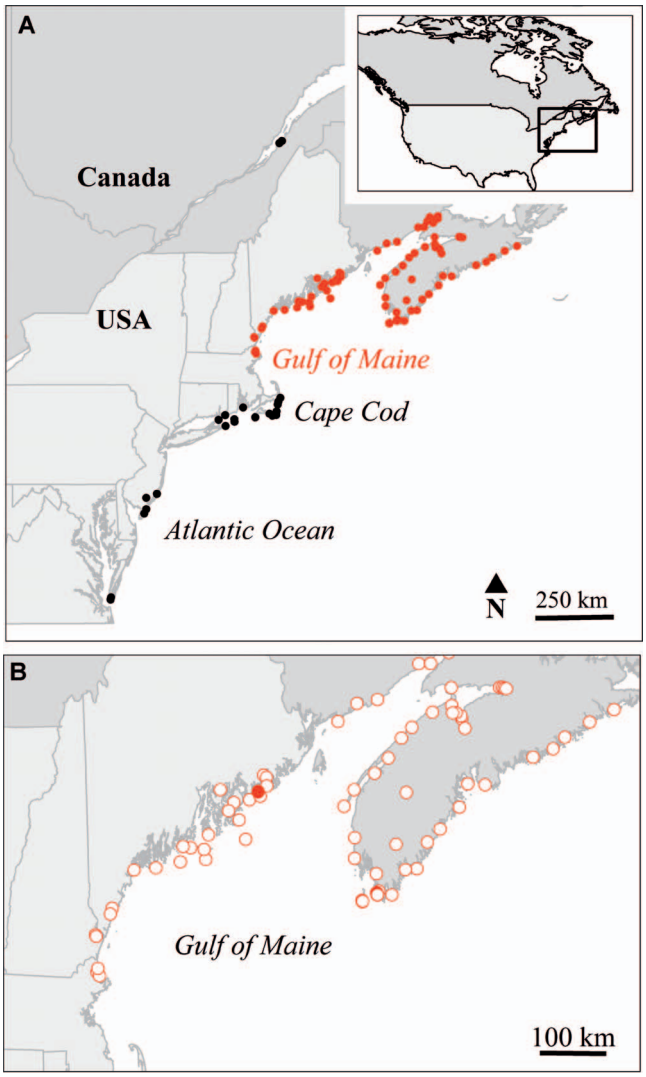


FIGURE 1. (**A**) Map showing locations of automated telemetry array used to track radio-tagged Blackpoll Warblers and Red-eyed Vireos in fall 2014 (points are receiver sites; those in the Gulf of Maine are red). (**B**) Locations of automated telemetry receivers in the Gulf of Maine (unfilled circles) and the capture site (filled circle).

METHODS

Data Collection

We captured blackpolls and vireos at the 888 ha Petit Manan Point unit of the Maine Coastal Islands National Wildlife Refuge (Figure 1), located on a peninsula in Steuben, Maine, USA (44.40846°N, 67.90502°W). The refuge unit is composed of mixed-deciduous forests containing mountain ash (*Sorbus americana*), red maple (*Acer rubrum*), white spruce (*Picea glauca*), red spruce (*P. rubens*), and black spruce (*P. mariana*), and an extensive shrub component including raspberry (*Rubus* spp.), alder (*Alnus* spp.), wild raisin (*Viburnum cassinoides*), bayberry (*Myrica* spp.), and blueberry (*Vaccinium* spp.).

We captured birds with passive mist nets between September 6 and October 13, 2014. All birds were fitted with a federal band and measured for fat stores (0 = none; 0.5 = trace; 1 = lining furculum; 2 = filling furculum; 3 = mounded in furculum and beginning to cover abdomen; 4 = mounded on breast and sides of abdomen). We collected blood samples for DNA sexing. We collected the third rectrix from vireos, and scapular feathers from blackpolls, for stable hydrogen isotope analysis. We used the stable hydrogen isotope ratio of feathers (δ^2H) as a coarse proxy of the breeding latitude (Wassenaar and Hobson 2001). Although the precision in breeding latitude is coarse (Hobson et al. 2014), this method provides an index of the relative distance that migrants traveled before arriving at our capture site. Feathers were cleaned, weighed, and analyzed for δ^2H at the Cornell University Stable Isotope Laboratory, Ithaca, New York, USA. The comparative equilibrium method was used, and isotopic corrections were performed using the CBS and KHS calibrated keratin δ^2H references (Wassenaar and Hobson 2003). We report all nonexchangeable δ^2H results in the standard delta notation of units per mil (‰), normalized to the Vienna Standard Mean Ocean Water scale (VSMOW; Bowen 2010).

We attached coded VHF radio transmitters (Avian Nano Tag NTQB-2; Lotek Wireless, Newmarket, Canada; 40 days mean battery life) to 49 blackpolls and 47 vireos with leg loop harnesses (Rappole and Tipton 1991). The total mass of the transmitters, including attachment materials (0.29 g), was <3% of body mass for all individuals. The transmitters emitted a signal at 166.38 MHz every 11–15 s, allowing us to identify and track all individuals at once. We tracked the birds using an array of receiver stations within the Motus Wildlife Tracking System (Taylor et al. 2017) that spanned coastal or island locations from Maryland, USA, to northern Nova Scotia, Canada, in 2014 (Figure 1). Receiver stations consisted of 1–6 elevated Yagi antennas and a data logger—either Lotek (http://www.lotek.com) or a handmade SensorGnome (http://www.sensorgnome.org)—that recorded signal strength and GPS-synchronized time for each detected tag pulse. Stations were operational throughout the study and recorded birds that passed within range of the antennas. Previous calibration studies have estimated 12 km detection ranges for birds in flight, and 2 km for grounded birds (Mills et al. 2011, Taylor et al. 2011). We regularly detected simultaneous detections on towers ≤24 km apart, which suggests that we achieved a similar range.

Interpreting Telemetry Data

Movement tracks and behavioral classifications for track segments were previously derived for these data (Smetzer

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et al. 2017). We used graphs of signal strength over time to determine the time of final departure from the capture site for each bird (e.g., Mills et al. 2011: figure 2 in Taylor et al. 2011). Because detection range is limited to 0.5–2 km for birds on the ground (Taylor et al. 2011), we assumed that birds detected at any site beyond the capture site (i.e. in the "external" array) were in flight unless they exhibited a signal at a telemetry station for >3 hr. Indeed, birds were detected at stations in the external array for either relatively brief (<100 min, $n = 326$; mean = 7.3 ± 13.0 min) or long (>180 min, $n = 24$; mean = 116.3 ± 178.7 hr) durations. We thus classified all detections <100 min at a station as flybys, with an arrival time marked by the time stamp of the maximum signal strength recorded at the station (Mitchell et al. 2015). In cases where the first and last detections at a station were >180 min apart, we assumed that birds were detected during arrival and departure flights from a nearby stopover site. In these cases, we assigned arrival and departure time as the first and last detections at the telemetry station.

At each station where a bird was detected, we made a single coarse location estimate, using the point 6 km from the station along the bearing of the antenna that recorded the greatest signal strength (Mitchell et al. 2015). We chose 6 km because it is half the detection range for a bird aloft, and we used the bearing of the antenna with the greatest signal strength because the power received by our directional antennas is maximized along the beam (Friis 1946, Shaw 2013). Finally, we calculated the ground speed for every segment of every bird's movement track and used these movement rates to classify track segments as either "sustained migratory flights" or "slow movements" (Smetzer et al. 2017). There was a clear threshold at 1 m s^{-1} for ground speed, indicating a behavioral difference below this rate. Birds likely stopped during "slow movement" sections of their track; however, we could not pinpoint the exact location of stopovers.

We used the resulting movement tracks to assess whether blackpolls and vireos exhibited prolonged stopovers (i.e. >7 days; McKinnon et al. 2013) specifically within the GOM. We generated 2 metrics to assess prolonged stopover in the GOM. We calculated the total time spent in stopover within the GOM by summing the duration that an individual was detected at the capture site and the duration of all slow-movement track segments that occurred in this portion of the study area. Second, we tallied how many individuals of each species made ≥1 individual stopover in the GOM that exceeded 7 days.

We used the movement tracks to generate a series of metrics that applied to the entire study area and were included in statistical analyses (Table 1). We calculated the total number of stopover bouts in the entire study area for each bird by summing the number of distinct stopovers, including stopover at the capture site, stops at or near telemetry stations, and slow-movement track segments. We summed the duration of all these distinct stops to quantify the total time spent in stopover throughout the entire study area by individual. All stopover values are minimum estimates because we don't know how long birds were at the capture site before we outfitted them with radio transmitters.

We determined movement rates throughout the entire study area using the great-circle distance between the banding site and the last location estimate for the individual and the duration between capture and last detection. This metric can be indicative of prolonged stopover activity in the study area, because individuals engaging in prolonged stopovers can exhibit markedly slow movement rates in some portions of their migratory routes (Callo et al. 2013, Fraser et al. 2013). Finally, we calculated 2 metrics that represented flight behavior. The first was the distance of sustained migratory flights recorded between telemetry stations. The second metric —mean distance traveled per stopover bout—represented the ratio of flight to stopover and was the total distance over which we tracked a bird divided by the total number of estimated stops throughout the entire study area.

Statistical Analyses

We established a small set of candidate models for the response variables (Table 1). We included capture date and δ^2H value (as a proxy for breeding latitude) in interspecific models and incorporated quadratic terms when model diagnostics indicated the need. We were interested in comparing the metrics among age groups but didn't have an adequate sample of adults. Preliminary analyses indicated that sex didn't influence any of the response variables, so we excluded this variable. We also excluded fat as a covariate; most birds remained at the capture site for >2 days, indicating that fat didn't represent body condition at departure. However, we included fat stores as a response variable indicating body condition upon arrival at the capture site.

We ran separate models to test whether the response variables differed between the species. We related covariates to the number of stopover bouts using generalized linear models (GLMs) with Poisson error distributions and to total stopover duration using general linear models. We transformed total stopover duration in intraspecific models to improve the normality of residuals and used generalized least squared models with a variance term for species in interspecific models. We employed GLMs with Gamma errors to model movement rate and flight distance per stop because these metrics were greater than zero and right-skewed. We used ordered logistic regression (cumulative link models) to test whether fat stores at the time of capture (0–4) were

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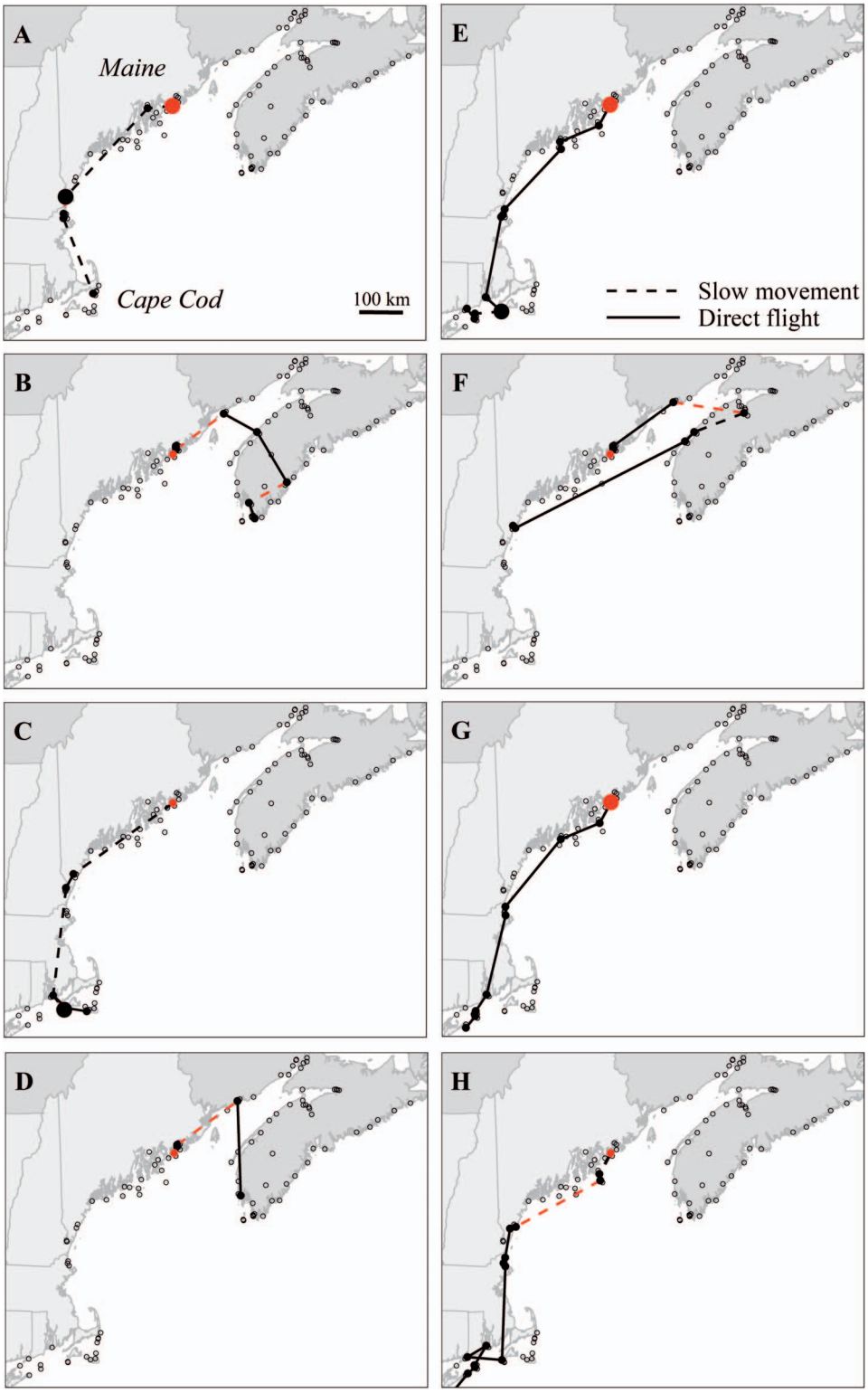


FIGURE 2. Movements of Blackpoll Warblers (**A**–**D**) and Red-eyed Vireos (**E**–**H**) tracked by automated telemetry in fall 2014. The capture site is red. Open circles show automated telemetry towers, and large filled circles show prolonged stopovers at a single location. Dashed lines show slow movements during which birds made a stop, with those in red indicating a prolonged stop of >7 days. For contrast, **G** shows continuous flight following departure from the capture site.

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TABLE 1. Candidate models considered in analyses relating capture date (day), sex, stable isotope values (δ^2H), fat stores, and species to movement metrics as calculated over the entire study area.

Response variables	Fat stores	Number of stopover bouts	Total duration of stopovers	Flight distance per stopover	Movement rate
Intraspecific models	Sex δ^2H Day	Sex δ^2H Day	Sex δ^2H Day	Sex δ^2H Day Day * day [a]	Sex δ^2H Day
Interspecific models	Species	Species	Species	Species	Species

[a] Quadratic term improved model residuals and was included only for Red-eyed Vireos.

influenced by the covariates. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank the candidate models in each modeling exercise (Burnham and Anderson 2002). We considered a variable strongly supported if 95% or 99% confidence intervals didn't overlap zero. We report parameter estimates (± SE) for each model within 2 AIC_c of the top model and ΔAIC_c values. Interspecific comparisons are stated as values for vireos in relation to blackpolls. Results are means ± SE unless otherwise noted.

We used principal component analysis on a suite of migration-strategy metrics, including fat stores at capture, total number of stopovers, mean duration of individual stopover bouts, maximum duration of individual stopover bouts, total time spent in stopover, flight distance per stopover, and movement rate to extract the dominant gradients of variation in migration strategy across individuals. We transformed metrics as needed to improve normality, scaled all data to mean = 0 and SD = 1, and report only principal components with loadings >0.4. All analyses were completed in R 3.3.1 (R Core Team 2016); we used the "vegan" package for multivariate analyses (Oksanen et al. 2016).

RESULTS

Three of 49 blackpolls and 6 of 47 vireos were not detected beyond the capture site and didn't exhibit a clear departure flight. These individuals were likely depredated or lost their tag and were excluded from all analyses. All vireos and 74% of blackpolls were juveniles. The δ^2H values ranged from –178‰ to –76‰ for blackpolls and from –112‰ to –57‰ for vireos, with lower δ^2H values indicating a more northern/western breeding area and, thus, a greater distance traveled to the capture site. Based on established feather isoscapes (Bowen et al. 2005, Hobson et al. 2014), these δ^2H values indicate likely breeding origins ranging from the eastern Maritime provinces for both species to as far away as northwestern Canada and possibly Alaska for blackpolls, and as far west as central Quebec, western Ontario, and southeastern Manitoba for vireos. We were unable to calculate movement rate, distance of sustained migratory flights, or flight distance per stop for 6 blackpolls and 4 vireos not re-detected beyond the capture site.

Prolonged Stopover in the Gulf of Maine

Both species exhibited prolonged stopovers in the GOM (Figure 2). The average total stopover duration in the GOM was 14.4 ± 10.5 days for blackpolls and 7.6 ± 4.9 days for vireos. Fifty-nine percent of blackpolls and 35% of vireos made at least one stop in the GOM that exceeded 7 days. Seven vireos and 4 blackpolls stayed at the capture site (i.e. within the 2 km detection range of the banding-station receivers) for >7 days, for a mean duration of 12 days for blackpolls (maximum = 22) and 9 days for vireos (maximum = 12). Four vireos and 2 blackpolls also made prolonged stopovers in Cape Cod, with maximum stays of 20 days and 9 days, respectively (e.g., Figure 2C, 2E).

Stopover Metrics

The number of stopover bouts and total time spent on stopover throughout the entire study region differed significantly between the species, and by breeding origin for blackpolls. We recorded ≥1 stopover bout after departure from the capture site for 83% of blackpolls and 56% of vireos. Individual stopover bouts ranged from <1 day (individuals that departed the evening after they were radio-tagged) to 25 days for blackpolls (5.3 ± 6.3 days), and from <1 day to 14 days for vireos (4.1 ± 3.4). Individual blackpolls made 2.84 ± 1.21 stopover bouts (range: 1–6) and spent 15.1 ± 10.6 days on stopover throughout the study area (range: 0.5–37.9). Individual vireos made 2.0 ± 1.1 stopover bouts (range: 1–5) and spent 8.2 ± 5.5 days in stopover (range: 0.3–20.1). Blackpolls made significantly more stopover bouts (Poisson GLM: $\beta = -0.37 \pm 0.14$, $P = 0.01$; Appendix Table 2) and spent significantly more total time in stopover than vireos (generalized least squares model: $\beta = -2.74 \pm 0.74$, $P < 0.001$; Appendix Table 2). The latter model was >10 AIC_c of the null, indicating high confidence in this result. Blackpolls from more southern breeding origins made significantly more stopover bouts

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(Poisson GLM: $\beta = 0.01 \pm 0.003$, $P = 0.05$; Appendix Table 3) and spent significantly more total time in stopover than their northern conspecifics; however, the null was within 1.40 AIC_c of the top model for number of stopover bouts (general linear model: $\beta = 0.01 \pm 0.01$, $P = 0.04$; Appendix Table 3). We found no compelling evidence that number of stopover bouts or total stopover duration was related to breeding origin or capture date for vireos (Appendix Table 4).

Movement Rates

Movement rates differed significantly between the 2 species and by capture date for vireos, ranging from 0.69 ± 0.63 km day^{-1} for blackpolls ($n = 40$) to 2.09 ± 2.72 km day^{-1} for vireos ($n = 37$), much lower than is typically reported for migratory passerines. Blackpoll movement rates were significantly slower than those of vireos (Gamma GLM: $\beta = 1.10 \pm 0.25$, $P < 0.001$; Appendix Table 3). To understand these results better, we made a post hoc comparison of the geographic distance and time span over which we tracked each species. The distances over which we tracked blackpolls (261.6 ± 222.5 km, range: 0–806.4) and vireos (312.9 ± 316.4 km, range: 0–1,060) were similar (Wilcoxon test: $W = 682.5$, $P = 0.59$). However, we detected blackpolls in the study area for nearly twice as much time (16.3 ± 10.6 days, range: 0.5–38.3) as vireos (8.0 ± 5.7 days, range: 0.4–20.8; Wilcoxon test: $W = 1{,}330$, $P < 0.001$). We found no compelling evidence that movement rate was related to covariates for blackpolls. By contrast, vireos captured later in the season exhibited significantly more rapid movement rates than earlier conspecifics (Gamma GLM: $\beta = -0.05 \pm 0.01$, $P < 0.001$).

Flight Behavior

Individuals of both species traversed the study area in multiple short flights rather than in a single, sustained migratory movement (Figure 2); this behavior was more common in blackpolls than in vireos and in earlier vireos than in later conspecifics. The median distance of the recorded sustained migratory flights was 42.73 km (maximum = 275.9) for blackpolls ($n = 40$) and 147.4 km (maximum = 761.2) for vireos ($n = 37$). The ratio of flight distance per stopover was greater for vireos (153.67 ± 150.49 km $stop^{-1}$) than for blackpolls (85.07 ± 72.11 km $stop^{-1}$; Gamma GLM: $\beta = 0.51 \pm 0.21$, $P = 0.02$; Appendix Table 2). We found no compelling evidence that flight distance per stopover was related to covariates for blackpolls (Appendix Table 3). Vireos captured later in the migratory period exhibited significantly higher ratios of flight distances per stopover than earlier conspecifics (Gamma GLM: $\beta = 5.49 \pm 2.12$, $P = 0.01$; Appendix Table 4). The top model also included a negative quadratic term for capture date indicating that the ratio of flight distance per stop increased more rapidly as the season progressed (Gamma GLM: $\beta = -0.01 \pm 0.004$, $P = 0.01$).

Fat Stores

The mean fat score at capture didn't differ significantly between blackpolls (1.27 ± 0.91; range: 0.5–4.0) and vireos (1.26 ± 0.70; range: 0–3; ordered logistic regression: $\beta = 0.28 \pm 0.41$, $P = 0.50$; Appendix Table 2). Blackpolls captured later in the season carried significantly more fat stores than earlier conspecifics (ordered logistic regression: $\beta = 0.32 \pm 0.10$, $P < 0.001$; Appendix Table 3). Vireos from closer breeding origins exhibited significantly greater fat stores than more distant conspecifics (ordered logistic regression: $\beta = 0.06 \pm 0.03$, $P = 0.05$; Appendix Table 4); however, the null was within 1.17 AIC_c of this model.

Principal Component Analysis

A Monte Carlo permutation test indicated that the correlation structure of the first 2 retained principal components was statistically significant ($P < 0.001$). The first principal component (PC1, eigenvalue = 3.1; Figure 3) explained 44% of the variance and was positively related to movement rate (0.49) and negatively correlated with total number of stops (–0.59), total time spent in stopover (–0.97), mean duration of stopovers (–0.82), and maximum duration of stopovers (–0.95). The second principal component (PC2, eigenvalue = 1.6) explained 23% of the variance and was negatively correlated with movement rate (–0.74) and flight distance per stop (–0.93). Thus, PC1 largely represented stopover behavior, and PC2 largely represented movement behavior. Reflecting the overall results from univariate analyses, blackpolls varied more across PC1 (stopover behavior), whereas vireos varied more across PC2 (flight behavior).

DISCUSSION

Using an array of automated radio-telemetry receiving stations, we confirmed long-held predictions that blackpolls exhibit prolonged stopover in the GOM during fall migration (Nisbet et al. 1963, 1995, Nisbet 1970). Our results provide the first evidence of this behavior for Red-eyed Vireos in fall. The stopover durations we observed were consistent with prolonged stopover for Purple Martins in fall (16 ± 9 days; Fraser et al. 2013), Red-eyed Vireos in spring (19 ± 5 days; Callo et al. 2013), and Swainson's Thrushes (*Catharus ustulatus*) in spring (8–29 days) and fall (11–29 days; Delmore et al. 2012). Blackpolls and vireos also exhibited lower movement rates throughout the study area than typically reported for long-distance migrants from banding (60 km day^{-1}; Ellegren 1993) or geolocator studies (68–473 km day^{-1}; Fraser et al. 2013), which suggests that birds were predominantly stopped while in our study area.

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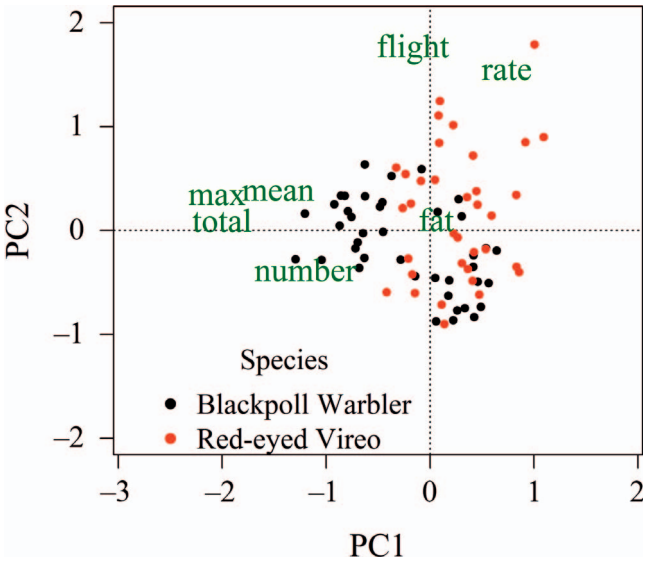


FIGURE 3. Principal component analysis of migration metrics derived from automated radio telemetry conducted on Blackpoll Warblers and Red-eyed Vireos in the Gulf of Main, fall 2014. Migration metrics in green include number of stopovers (number), total time spent in stopover (total), mean and maximum durations of individual stopover bouts (mean and max), fat stores (fat), migration rate (rate), and flight distance per stopover (flight). Variables that are located far from zero along either PC1 or PC2 are important for the respective principal component; thus, PC1 largely represents variation in stopover behavior, and PC2 largely represents variation in flight behavior. Each represents an individual bird, with the location showing its composite score along each principal component.

That we sampled almost entirely hatch-year birds may partly explain some of the long stopover durations we observed. Adults select tailwinds more effectively (Mitchell et al. 2015), refuel faster (Seewagen et al. 2013), make fewer and shorter stopovers (Crysler et al. 2016), and migrate more rapidly than juveniles (Ellegren 1993). However, it is unlikely that age is the primary cause of prolonged stopovers in our study, given that adults comprise nearly every instance of prolonged stopovers documented to date in geolocator studies. Our study is one of the first—to our knowledge—to document prolonged stopover for hatch-year birds on their first migration.

Our interspecific models provide indirect support for the hypothesis that prolonged stopovers may be an adaptive strategy for accumulating large fat stores to fuel long migratory flights. Nearly twice as many blackpolls exhibited stops of >7 days in the GOM than vireos. Within the entire study area, blackpolls spent nearly twice as much time in stopover and exhibited slower movement than vireos. These patterns likely reflect interspecific differences in subsequent movement—specifically, blackpolls' need to accrue large fuel stores to support transatlantic flights from the coast. Consistent with this, blackpolls deposit more fat than congeners in the fall (Nisbet et al. 1963), often nearly doubling their mass. Longer stopovers may be necessary for completing the time-consuming physiological changes that precede endurance flights, such as increases in digestive capacity, subsequent reabsorption of digestive organs, and increases in flight muscles (Piersma and Gill 1998, Karasov and Pinshow 2000). However, diet may also drive some of the interspecific differences we observed. Vireos are more frugivorous during the fall migratory period than blackpolls (Parrish 1997, Smith and McWilliams 2010). A frugivore's greater capacity for rapid fat mobilization (Bairlein and Gwinner 1994, Smith et al. 2007) could aid vireos in making shorter, less frequent stops and longer flights between stops.

To date, it has been assumed that passerines are relatively stationary during prolonged stopovers, occupying a single location. However, prolonged stopovers have principally been recorded with geolocators, with too coarse a resolution to assess this assumption. In line with the traditional definition of prolonged stopover, we recorded birds making protracted stops at one location; however, many individuals that remained in the GOM for >7 days exhibited landscape-scale movements (Figure 2). These results suggest that prolonged stops may occur over a range of scales, from a single site to a regional-scale stopover landscape, and may involve landscape-scale relocations.

Although some of the landscape-scale relocations we observed may be the result of abandoned migratory flights, many could represent birds refining their habitat choices—even during prolonged stopovers. Long-distance migrants prefer stopover sites with high refueling opportunities and cover from predators (McCabe and Olsen 2015), particularly for extended stops (Warnock 2010). However, finding high-quality sites often involves fine-tuning habitat choices after initial landing (Aborn and Moore 1997, Chernetsov 2005, 2006, Taylor et al. 2011). Adult blackpolls—despite greater experience—are known to make landscape-scale nondirected flights more than juveniles, which suggests that these movements indeed have an adaptive benefit (Brown and Taylor 2017). It is therefore fitting that blackpolls—with a presumably greater selective pressure for finding high-quality stopover sites—made more stopovers than vireos and shorter flights per stopover bout, indicating more landscape-scale relocation.

Collectively, these results suggest that migration strategy may be scale dependent. Within an overall program of prolonged stopover and time minimization, songbirds may exhibit a short-term hop strategy of energy minimization while seeking optimal stopover habitats. Although time-

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consuming, relocating to more ideal stopover sites before accruing large fat stores could allow birds to minimize energy expenditure during flight (Alerstam and Lindström 1990, Hedenström and Alerstam 1992) and reduce risk through greater predator evasion (Kullberg et al. 1996). A short-term energy- and risk-minimizing strategy could be particularly important in coastal areas where predators are concentrated (Åkesson 1993, Ydenberg et al. 2007). Moreover, the physiological changes required for hyperphagia and extreme fat storage take significant time and energy (Newton 2008, Rappole 2013), so short movements in search of optimum habitats may ultimately save time and energy.

This strategy of energy and risk minimization appeared to be less pronounced for northwestern populations of blackpolls that exhibited fewer stopovers. This suggests less exploratory movements and may represent a willingness to "settle" for riskier foraging conditions, as has been documented in migrants that travel large distances (Metcalfe and Furness 1984, Pomeroy et al. 2008, McCabe and Olsen 2015). In contrast to our expectation, and patterns seen for other species (e.g., Purple Marin; Van Loon et al. 2017), blackpolls from more distant breeding latitudes spent less time on stopover. This could reflect lower predator vigilance, as is common in energetically stressed birds (Lima 1998, Cimprich and Moore 2006).

The seasonal increase in migration rate that we documented in vireos has been seen in several other long-distance migrants and indicates that later migrants may prioritize time more than earlier conspecifics (Ellegren 1993, Fransson 1995, Gómez et al. 2017). Indeed, later conspecifics of these vireos also departed from the capture site in an overwater trajectory more frequently, indicating a time-minimizing tendency for more direct travel (Smetzer et al. 2017). That later vireos exhibited greater flight distances per stop is consistent with previous findings that later blackpolls also made fewer tortuous landscape-scale flights than earlier conspecifics (Brown and Taylor 2017). This pattern of time minimization in later migrants can arise from a corresponding seasonal increase in directed movement, flight speeds, availability and/or selection of supportive tailwinds, decisions to engage in flight for a greater portion of the night, or a combination of these factors (Alerstam and Lindström 1990, Ellegren 1993).

Consistent with the findings of previous work (Nisbet et al. 1963, Morris et al. 2016), later blackpolls in our sample carried greater fat stores than earlier conspecifics. Rapidly accruing and carrying large fuel stores can increase energetic costs (Alerstam and Lindström 1990, Hedenström and Alerstam 1997) and predation risks (Hedenström and Alerstam 1992, Kullberg et al. 1996) but may be an optimal choice for later migrants facing declining food stores, temperatures, and day lengths (Schaub and Jenni 2000, La Sorte et al. 2015). A seasonal increase in fat stores can result from seasonal intensification of fuel deposition rates (Schaub and Jenni 2000, Dänhardt and Lindström 2001) and tailwinds (Koch et al. 2006, Pena-Ortiz et al. 2013). Later blackpolls didn't make longer flights per stopover, so it is unlikely that they had larger fuel stores because they burned less fuel during arrival. However, vireos showed a seasonal increase in flight distance per stop, indicating that later birds may have carried less fat because they arrived via longer flights.

Conservation Implications

Our evidence that the GOM serves as a prolonged stopover site has important conservation implications. Stopover resources can influence migratory pace (Wikelski et al. 2003, Åkesson et al. 2012), energetic condition (Moore et al. 1995), and condition in subsequent life stages (Smith and Moore 2005, Norris and Taylor 2006). Stopover areas that support large concentrations of birds in making flights over ecological barriers are particularly important and represent ecological bottlenecks where localized habitat loss can have population-level consequences (Myers 1983, Warnock 2010). Blackpolls may be particularly vulnerable to localized habitat loss as they make large overwater flights from the region. Furthermore, as our isotope results show, loss of these stopover sites could affect much of their breeding population. Blackpolls have already experienced a global population decline of 92% in the past 40 yr and are projected to decline by another 50% within the next 16 yr if current trends continue (Rosenberg et al. 2016). Protecting GOM stopover areas may therefore be an important conservation priority for this species. Other declining species, like the Connecticut Warbler (*Oporornis agilis*), also make transatlantic flights from the eastern U.S. coastline, which highlights the potential importance of this region for supporting the successful migration of other songbirds (McKinnon et al. 2017).

That some individuals made short, frequent movements in the region is also notable because flight behavior can influence the degree to which birds are exposed to collision hazards like communication towers and wind turbines (Drewitt and Langston 2006, Langston 2013). These structures can pose a significant threat to migrant songbirds, particularly during takeoffs, landings, and short flights (Crawford and Engstrom 2001, Hüppop et al. 2006, Longcore et al. 2012). In turn, predictable differences in behavior—as observed in the present study—can lead to systematic differences in risk and possible implications for population dynamics (Cristol et al. 1999, Mehlman et al. 2005, Longcore and Smith 2013).

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ACKNOWLEDGMENTS

We thank A. Leppold, J. Reese, J. Feura, T. Duclos, J. Ruebesam, M. Akresh, and B. Bailey aided in the field. P. Taylor, B. Woodworth, J. Brzustowski, N. Pau, K. O'Brien, L. Welch, S. Williams, J. Fortier, C. Familiaris, and the College of the Atlantic for logistical support; and W. DeLuca for valuable reviews that greatly enhanced the manuscript.

Funding statement: This study was funded by the U.S. Fish and Wildlife Service, the USDA Forest Service, and the National Science Foundation–sponsored IGERT: Offshore Wind Energy, Engineering, Environmental Science, and Policy (grant no. 1068864).

Ethics statement: This work was executed in accordance with proper Institutional Animal Care and Use (IACUC) protocols and permits, including University of Massachusetts IACUC protocol no. 2013-0019 and U.S. Federal Bird Banding Permit no. 23140.

Author contributions: J.R.S. conceived the research idea, developed the methods, collected and analyzed the data, and wrote the paper. D.I.K. supervised research and contributed materials, resources, and funding.

Data deposits: The data that supported the analyses in this paper are available at http://www.motus-wts.org

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APPENDIX

APPENDIX TABLE 2. Results of models comparing migration metrics between Blackpoll Warblers and Red-eyed Vireos (REVI) tracked by automated telemetry in the Gulf of Maine in fall 2014. Models with ΔAIC_c values ≤ 2 are shown. Parameter estimates are in relation to Blackpoll Warblers, and those with 95% (**) and 99% (***) confidence intervals that exclude zero are marked.

Response variable	Models	Species (REVI)	ΔAIC_c
Number of stopovers	Species	−0.37 ± 0.14**	0.00
Total stopover duration	Species	−2.74 ± 0.74***	0.00
Flight distance per stopover	Species	0.51 ± 0.21**	0.00
Migration rate	Species	1.10 ± 0.25***	0.00
Fat at capture	Null		0.00
	Species	0.28 ± 0.41	1.85

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APPENDIX TABLE 3. Models relating migratory response variables to capture date (Day) and stable isotope values (δ^2H) of Blackpoll Warblers tracked by automated telemetry in the Gulf of Maine in fall 2014. Models with ΔAIC_c values ≤ 2 are shown. Parameter estimates with 95% (**) and 99% (***) confidence intervals that exclude zero are marked.

Response variable	Models	Day	δ^2H	ΔAIC_c
Number of stopovers	δ^2H		0.01 ± 0.003**	0.00
	Null			1.40
Total stopover duration	δ^2H		0.01 ± 0.01**	0.00
Flight distance per stopover	Null			0.00
	Day	−0.04 ± 0.04		1.54
	δ^2H		−0.01 ± 0.01	1.58
Movement rate	Null			0.00
	δ^2H		−0.01 ± 0.01	1.53
Fat at capture	Day	0.32 ± 0.10 ***		0.00

APPENDIX TABLE 4. Models relating migratory response variables to capture date (Day) and stable isotope values (δ^2H) of Red-eyed Vireos tracked by automated telemetry in the Gulf of Maine in fall 2014. Models with ΔAIC_c values ≤ 2 are shown. Parameter estimates with 95% (**) and 99% (***) confidence intervals that exclude zero are marked.

Response variable	Models	Day	Day^2	δ^2H	ΔAIC_c
Number of stopovers	Null				0.00
	Day	−0.03 ± 0.02			0.21
	Sex				1.60
Total stopover duration	Null				0.00
	Sex				1.23
	Day	−0.05 ± 0.06			1.31
	δ^2H			−0.02 ± 0.03	1.88
Flight distance per stopover	Day + day^2	5.49 ± 2.13**	−0.01 ± 0.004**		0.00
Movement rate	Day	−0.05 ± 0.01***			0.00
Fat at capture	δ^2H			0.06 ± 0.03**	0.00
	Null				1.17

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