Articles

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Fall migratory departure decisions and routes of blackpoll warblers *Setophaga striata* and red-eyed vireos *Vireo olivaceus* at a coastal barrier in the Gulf of Maine

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Each year, millions of songbirds concentrate in coastal areas during fall migration. The choices birds make at the coast about stopover habitat use and migratory route can influence both the success of their migratory journey and fitness in subsequent life stages. We made use of a regional-scale automated radio telemetry array to study stopover and migratory flights and migratory routes of blackpoll warblers *Setophaga striata* and red-eyed vireos *Vireo olivaceus* during fall migration in the Gulf of Maine, USA. We focused on differences between species, sexes, age groups, breeding origins, and time of year. Both species made within-stopover relocations (i.e. 'stopover flights') from the coastal capture site. Stopover flights were primarily oriented inland, and were more frequent for blackpolls (87%) than vireos (44%). By studying migratory behavior at a broad spatial scale, we demonstrated that most blackpolls and vireos took coastal and offshore routes through the Gulf of Maine, despite initially relocating inland from the capture site. Though we captured blackpolls and vireos from a broad breeding range, more than 70% of migratory flights from the capture site were oriented for coastal or offshore travel for both species, suggesting that birds actively chose coastal and offshore routes, and were not simply displaced by wind drift. Later vireos oriented offshore more frequently during migratory flights from the coast, indicating that they may be more inclined towards time-minimizing overwater flight routes and thus more exposed to coastal and offshore collision hazards than earlier conspecifics.

Each fall, millions of migrant songbirds concentrate in coastal areas of the eastern US where natural and anthropogenic factors amplify the demands of migration (Buler and Moore 2011). Many songbirds face especially high energy demands and low fuel stores when they reach the eastern coast of the US (Moore et al. 1990, Petit 2000) where they encounter unfamiliar habitats with high competition and predation pressure (Richardson 1978, Åkesson 1993, Ydenberg et al. 2007). Since stopover habitat can influence energetic condition (Moore et al. 1995), the ability to evade predators (McCabe and Olsen 2015a), migration rate (Wikelski et al. 2003, Åkesson et al. 2012), and fitness in subsequent life stages (Runge and Marra 2005, Smith and Moore 2005, Newton 2006, Norris and Taylor 2006), the habitat choices that migrants make in coastal environments may have important fitness consequences.

After landfall, migrant songbirds make landscape-scale stopover flights that are thought to represent short 'within stopover' relocations, rather than a continuation of migration (Mills et al. 2011, Taylor et al. 2011). In coastal regions, many songbirds re-orient inland after landing – a behavior thought to be an adaptive strategy for finding better stopover habitats (Richardson 1978, Lindström and Alerstam 1986, Åkesson et al. 1996, Åkesson 1999). In support of this hypothesis, inland stopover flights in coastal areas are more common for lean individuals (Deutschlander and Muheim 2009, Smolinsky et al. 2013) and in regions with high predation pressure (Woodworth et al. 2014). They also appear to be unrelated to weather conditions (Woodworth et al. 2015). If stopover flights at the coast are an important adaptive strategy for finding better habitats, we would expect these flights to be oriented inland, and to be more common in species with high energetic demands, particularly later in the season when resources are limited. Furthermore, since diet and habitat structure can both influence stopover habitat use (Suomala et al. 2010, Wolfe et al. 2014), we may expect species with different diets and habitat preferences to differ in their propensity to move inland when they reach the coast. Similarly, since females and juveniles are known to be sub-dominant and can be excluded from habitats (Parrish and Sherry 1994, Komar et al. 2005, Rappole 2013, Akresh et al. 2015), then we might also expect the propensity to fly inland to be more frequent for these sex and age classes.

The manner in which migrants negotiate the ecological barrier posed by coastlines can influence the duration, energy expenditure, and risks of migration (Alerstam 2001).

Overwater travel limits feeding and resting opportunities, and can be fatal if poor weather arises, but can be a safe and time-minimizing option if birds have adequate fat stores and favorable weather (Covino and Holberton 2011, Schmaljohann and Naef-Daenzer 2011, Schmaljohann et al. 2011, Smolinsky et al. 2013, Deppe et al. 2015). Detouring around a barrier minimizes the danger of navigational errors, and effects of poor weather or low fuel stores (Butler 2000, Newton 2007) but increases the length of the migratory journey, and as such, overall energy expenditure and exposure to predators and disease (Cimprich et al. 2005, Ydenberg et al. 2007, Hahn et al. 2014).

Given the acute stressors that songbirds face in coastal landscapes, even small differences in experience, skill, social status, or selection pressures could cause marked differences between individuals in the choice of migratory route. How individuals balance risk, energy expenditure, and speed at a barrier may differ by sex and capture date, since stopover behavior, fuel deposition rates, and time constraints can vary markedly between sexes and throughout the season (Morris et al. 1994, Rappole 2013, Seewagen et al. 2013, La Sorte et al. 2015). There is also some evidence that route choice can differ by age presumably because of differences in experience and risk management (Crysler et al. 2016). Finally, differences in breeding origin may influence route choice at an ecological barrier due to migratory divides (Delmore et al. 2012) or more compensation for wind drift by individuals from more western populations (Fitzgerald and Taylor 2008). While the effects of weather and fat stores on route choice at an ecological barrier have been well studied (Covino and Holberton 2011, Schmaljohann and Naef-Daenzer 2011, Schmaljohann et al. 2011, Smolinsky et al. 2013, Deppe et al. 2015, Woodworth et al. 2015), the role that age, breeding origin, sex, and capture date play has received less attention. However, intraspecific variation in route choice at ecological barriers has important implications for population dynamics because it can lead to systematic differences in exposure to risk and mortality (Cristol et al. 1999, Mehlman et al. 2005, Longcore and Smith 2013).

We used regional-scale automated VHF radio telemetry to study inland stopover flights and migratory departure flights of blackpoll warblers *Setophaga striata* (hereafter blackpolls) and red-eyed vireos *Vireo olivaceus* (hereafter vireos) from a coastal stopover site in the Gulf of Maine. Our first objective was to characterize the orientation of stopover flights from the coast to determine if they were mainly inland movements. We also tested hypotheses that the probability of stopover flight from the capture site differed by sex, age, capture date or species. Vireos are common along most of the eastern US coast during fall migration (Sullivan et al. 2009), and often circumnavigate rather than cross the Gulf of Mexico (Deppe et al. 2015); however, blackpolls undertake a more energy-demanding migratory strategy that involves doubling their body mass in preparation for extreme trans-oceanic migratory routes (Nisbet et al. 1963, DeLuca et al. 2015). We thus expected vireos to undertake stopover flights less frequently than blackpolls. Our second objective was to characterize migratory routes within the study area to determine whether individuals that initially retreat inland from a coastal barrier subsequently continue migration by inland, coastal, or offshore routes.

Decades of data indicate that some songbirds circumnavigate the Gulf of Maine, while many others traverse this barrier in large overwater flights (Mcclintock et al. 1978, Richardson 1978, Leppold 2016). Our final objective was to investigate the intraspecific factors that influence this decision. We tested the hypotheses that overwater orientation of migratory flight was more likely for later migrants facing increased time constraints and more supportive tailwinds (Smith and McWilliams 2014, La Sorte et al. 2015), males that may benefit more from early arrival on the wintering grounds (Parrish and Sherry 1994), adults that have more experience navigating and assessing if conditions are favorable for overwater passage (Ralph 1978, Moore 1984, McKinnon et al. 2014), and individuals from eastern populations that may exhibit less compensation for wind drift than their more westerly conspecifics (Fitzgerald and Taylor 2008).

Material and methods

Data collection

We captured blackpolls and vireos at the Petit Manan Point section of the Maine Coastal Islands National Wildlife Refuge (Fig. 1) situated on a coastal peninsula in Steuben Maine, United States (44.40846°N, 67.90502°W). The 888 ha refuge is 90% mixed deciduous forest (McCabe and Olsen 2015b) composed of mountain ash *Sorbus americana*, red maple *Acer rubrum*, red *Picea rubens*, black *P. mariana* and white spruce *P. glauca* interspersed with dense fruit-bearing shrubs (McCabe and Olsen 2015a) including alder *Alnus* spp. wild raisin *Viburnum cassinoides*, raspberry *Rubus* spp., bayberry *Myrica* spp., and blueberry barrens *Vaccinium* spp. We captured birds between September 6 and October 13, 2014 using mist-nets located primarily in mixed-forest and shrub habitats. We placed a USGS aluminum band on all individuals, and recorded age, wing and tarsus length, mass, and subcutaneous fat score (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 from a clipped toenail for all radio-tagged individuals for DNA sexing.

We collected feather samples for stable hydrogen isotope (δ^2 H) analysis to serve as a rough proxy for breeding origin. Both species undertake a prebasic molt on the breeding grounds that includes body feathers (Pyle 1997), so during fall migration the δ^2 H ratio of feathers can indicate the relative breeding origin (Wassenaar and Hobson 2001). Following Leppold (2016), we sampled the third retrix on the right for vireos, and upper back feathers between the scapulars from blackpolls to avoid flight interference. Feathers were cleaned and weighed at the Cornell Univ. Stable Isotope Laboratory, and analyzed for δ^2 H on a Thermo Delta V isotope ratio mass spectrometer. The samples were analyzed under a comparative equilibrium method with three calibrated keratin δ^2 H references (CBS, and KHS;Wassenaar and Hobson 2003), and an internal standard run every 10 samples. Isotope corrections were performed using the CBS and KHS standards. We reported all results for nonexchangeable δ^2 H in delta notation of units

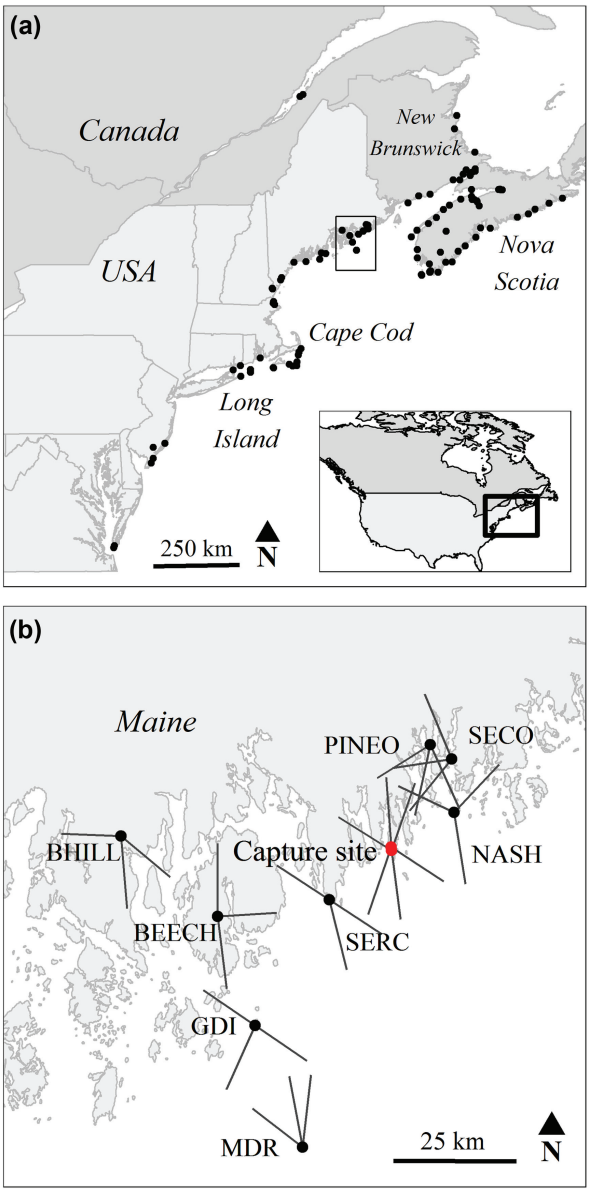

Figure 1. (a) Map of regional automated telemetry stations used to track radio-tagged blackpoll warbler *Setophaga striata* and red-eyed vireo *Vireo olivaceus* in fall 2014. Points represent receiver sites. (b) Automated telemetry receivers surrounding the capture site, shown in red. Solid black lines show the orientation and 12 km approximate detection range for telemetry receivers and their antenna.

per mil (‰), normalized to the Vienna Standard Mean Ocean Water standard scale (Bowen 2010).

We outfitted 49 blackpolls and 47 vireos with coded VHF radio transmitters (Avian NanoTag NTQB—2, Lotek Wireless Inc., Newmarket, ON; 40 d expected tag life). Transmitters and figure-eight leg-loop harness attachments (Rappole and Tipton 1991) were 0.29 g and < 3% of body mass for all individuals. Each radio transmitter emitted a uniquely coded signal at 166.38 MHz every 11–15 s. We tracked birds at the capture site with two automated telemetry stations, each with 3 nine-element Yagi antennas mounted atop an 8-m tower, and a sensorgnome receiver (<www.sensorgnome.org>) that logged a GPS-synchronized time and signal strength for each tag detection. We tracked subsequent movements with an array of coastal and island telemetry stations deployed from Nova Scotia to Maryland within the Motus Wildlife Tracking System (Taylor et al. in 2017; <www.motus.org>; Fig. 1). Previous calibration studies with similar equipment recorded a maximum detection range of 12 km for birds aloft (Mills et al. 2011, Taylor et al. 2011); simultaneous detections on towers situated 24 km apart indicated we achieved a similar range. To eliminate false positives, we only included detection events that contained ≥ 3 bursts of an ID that occurred at multiples of the burst interval for the corresponding tag (Woodworth et al. 2015).

Interpreting telemetry data

Deriving movement tracks

We used graphs of signal strength over time at the two capture-site telemetry stations (hereafter 'banding array') to pinpoint final departure time from the capture site (Mills et al. 2011, Taylor et al. 2011). We assigned departure time from the capture site as the time at which the maximum signal strength was recorded during a final departure flight (Mills et al. 2011). If a clear departure flight was not evident, but a bird was redetected outside the banding array we used the last detection at the banding array as the departure time from the capture site. If an individual did not exhibit a clear departure flight and was not redetected outside the banding array, we excluded it from all subsequent analysis and considered its fate as unknown.

We followed the general procedure of Mitchell et al. (2015) to estimate the spatial midpoint of detections at each tower outside of the capture location because triangulation methods for automated telemetry are not well developed. Birds on the ground can only be detected within 0.5–2 km of a receiver (Taylor et al. 2011), so detections beyond the banding array were predominantly birds in flight. Thus, for all stations outside the banding array we assigned individuals a single location 6 km (half the detection range of a bird in flight) along the bearing of the antenna that recorded the greatest signal strength value. We used the antenna that recorded the strongest signal to determine position relative to a station because power received from a transmitting antenna is maximized along the beam of a receiving directional antenna (Friis 1946, Shaw 2013). The detection power of the antennas we used also drops by 50% within 22.5° of the beams' main axis (PLC1669; <www.arcantenna.com>), and is greatly limited behind the antenna by a high (20 dB) front/back ratio, so the method can reasonably summarize multiple detections at a receiver as a single estimate of mean position. Furthermore, there was no reason localization error would be systematically different between the species, sexes, age groups, or dates across which we compared movement metrics.

Beyond the banding array, we used the duration of detections at each telemetry station to determine if birds were detected during a single sustained 'flyby' or were detected in flight during arrival and subsequent departure from a nearby stopover site. There was a clear gap in the data such that the time between the first and last detection

at any site was either < 100 min (n = 326; median = 11.9 min; mean = 7.3 ± 13.0 min) or > 180 min (n = 24; median = 44.7 h; mean = 116.3 ± 178.7 h). We thus identified any series of detections at a station < 100 min as a flyby, and assumed a bird stopped near a station if the span between first and last detections was > 180 min. Though 100 min is a lengthy duration given our likely detection range, this interval could occur in strong headwinds, or if a bird flew past a receiver in a highly indirect route during re-orientation, or abandoned migratory flights. Following Mitchell et al. (2015), we used the time of the maximum signal strength recorded at a station to estimate the time of flybys. We used the first and last detections at a site to mark the arrival and departure for series of detections classified as a stopover.

We calculated the movement rate for every segment of every bird's movement track to classify behavior between telemetry stations as a 'sustained migratory flight' or 'slow movement'. Since error in our localization routine can lead to inexact movement rates, particularly where towers were adjacent, we used thresholds in the movement rates to classify behavior, rather than absolute values. There was a clear threshold at 1 m s^{-1}, indicating a behavioral difference above and below this value. All track segments < 1 m s^{-1} were > 177 min in duration, and 97% were > 5 h, indicating that the slow rates calculated for these segments of the movement track were not a function of localization error. Birds likely halted flight at some point during slow track segments; however, since we could not specifically identify the location or duration of stopovers, we classified these segments as 'slow movements'. We categorized track segments with movement rate ≥ 1 as a 'sustained migratory flight', except for a few segments (n = 15; 0.04%) that spanned multiple nights of flight. This classification produced logical results: all segments > 5 m s^{-1} (n = 239) were classified as sustained migratory flights, and this is the lower end of groundspeeds for long-distance migrants (Nilsson et al. 2014).

Departure flights from the capture site

We classified final departure flights from the capture site as 'migratory flights', 'stopover flights', or 'ambiguous'. We only classified departure flights from the capture site. Previous studies have used the timing of flights, the timing and location of subsequent redetections, and flight orientation to differentiate between migratory and stopover flight from a stopover site (Taylor et al. 2011, Woodworth et al. 2014, 2015). Because we had an extensive tracking array with high redetection rates and were specifically interested in comparing the orientation of stopover and migratory flights, whenever possible we only classified 'migratory flights' and 'stopover flights' based on their timing and the movement rates directly following the flights.

We catalogued a departure from the capture site as a migratory flight if a) it occurred between twilight and dawn, b) the track segment immediately following the departure was a sustained migratory flight, and c) the bird did not make a stopover within 50 km of the capture site. We used this last criterion to ensure that any movement rates > 1 m s^{-1} between the capture site and adjacent telemetry stations that may have been inflated due to localization error and/or short flight durations did not result in a migratory flight classification if a bird halted movement near the capture site. We recorded a departure as a stopover flight if we recorded a) a stop within 50 km of the capture site, b) slow movement (i.e. < 1 m s^{-1}) in the track segment immediately after departure, or c) a brief nocturnal redetection at the banding array > 24 h later during a presumed departure from a nearby location. We classified a departure as ambiguous if we did not redetect an individual in the external array and did not have adequate detections to clearly distinguish a departure flight. Six vireos and three blackpolls met these criteria and were excluded from all subsequent analyses.

We used graphs of signal strength over time to classify departure flights (Mills et al. 2011, Taylor et al. 2011) for six vireos and four blackpolls not redetected beyond the banding array. We recorded flights between twilight and dawn that indicated departure from the capture site with a vanishing signal on the 299, 215, 173 or 120° (northwest to southeast) antennas as migratory flights, and flights any time of day on the 357 or 25° antennas as stopover flights (Taylor et al. 2011, Woodworth et al. 2015).

We calculated orientation of migratory flights from the capture site as the great-circle bearing between banding array station that recorded final departure and an individual's first position estimate beyond the banding array. Four birds departed the capture site by migratory flight but were not detected in the external array, so we used graphs of signal strength over time to determine which single antenna best represented their vanishing bearing. We used these graphs to similarly classify flight orientation for birds that departed the capture site on stopover flights because 95% of re-detections after stopover flights occurred > 12 h after departure and were not necessarily representative of departure orientation from the capture site. Since our estimates of flight orientation were coarse, we categorized migratory and stopover flights from the capture site into meaningful behavioral categories of inland (271–90°), coastal (235–270°) or overwater (91–234°) orientation.

Statistical Analysis

Each bird was included only once in each model (Table 1) as the data included one final departure from the capture site per bird. We did not explicitly estimate breeding origin from δ^2 H but instead used δ^2 H values to represent a rough index of relative origin/migration distance in models as lower values indicate a more northern/western breeding area (Wassenaar and Hobson 2001; Fig 2). Although fat stores can influence departure and orientation decisions for songbirds (Deutschlander and Muheim 2009, Ktitorov et al. 2010, Covino and Holberton 2011, Schmaljohann and Naef-Daenzer 2011, Deppe et al. 2015), most individuals were quite lean (75% birds < 2 fat score). Furthermore, > 70% of birds remained at the capture site for > 1 d, so fat levels at capture were not necessarily representative of fuel stores at departure. Preliminary analyses indicated that fat did not significantly influence response variables, or differ between species, sexes, or age groups, so we excluded it from analyses.

We used logistic regression (Binomial generalized linear models-glm) to relate species, sex, age, and capture date to the probability of departing the capture site by a stopover or

Table 1. Candidate models considered in analyses relating sex, capture date, stable hydrogen isotope values, age, and species to movement metrics of blackpoll warbler *Setophaga striata* and red-eyed vireo *Vireo olivaceus* radio-tracked in the Gulf of Maine in fall 2014.

Response variables	Stopover vs migratory flight (intraspecific)	Stopover vs migratory flight (interspecific) *	Migratory flight orientation (inland/coastal/offshore) **
Candidate models	sex	species	sex
	day	species + sex	day
	age ***		δ^2 H
	sex + day		sex + day
	sex + age ***		sex + δ^2 H
	day + age ***		
	day + sex + age ***		

Note: day = capture date; δ^2 H = stable hydrogen isotope values (used as a proxy for breeding origin).
*The species differed significantly in mean capture date and δ^2 H value, so we did not include these variables in interspecific models.
**We only had an adequate sample size of migratory departures to run models for red-eyed vireos. Capture date was correlated with δ^2 H for red-eyed vireos, so we did not combine these variables in models.
***Only blackpoll warblers, as all red-eyed vireos were juveniles.

migratory flight. The orientation of migratory and stopover flights were non-normal, so we used Watson-Wheeler tests for homogeneity (Watson 1962, Zar 2010) to examine whether the orientation of stopover and migratory flights from the capture site differed. We only used individuals that were detected in the external array in this comparison (n = 77), as their departure flight classification was not dependent on flight orientation. We used ordered logistic regression (cumulative link models with a logit link) to relate the probability of inland, coastal, or offshore migratory flight orientation from the capture site to sex, δ^2 H values, and capture date.

We used Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson 2002) to rank the candidate logistic and ordered logistic regression models. We reported AICc, Δ AICc, Akaike weight (ωi), and the parameter estimates ± SE for covariates for all models (Supplementary material Appendix 1). We considered a variable as important if the 90% confidence intervals for its parameter estimate did not contain zero across any of the candidate models in which it was considered, and strongly supported if 95 or 99% confidence intervals did not contain zero. To assess model uncertainty, we considered whether the effect of predictor variables (positive or negative) was consistent across candidate models for a given response variable (Cade 2015). We did not model average parameter estimates because our intent was not prediction, and this practice can produce unreliable results since regression coefficients can have different units and interpretations across models that contain different sets of covariates (Cade 2015). We conducted all analyses in the R statistical environment ver. 3.3.1 (R Core Team) using the 'maptools' (Bivand and Lewin-Koh 2015), 'oce' (Kelley and Richards 2015), 'sp' (Bivand et al. 2013) 'rgdal' (Bivand et al. 2015), 'geosphere' (Hijmans 2015) 'circular' (Agostinelli and Lund 2013), and 'ordinal' packages (Christensen 2015).

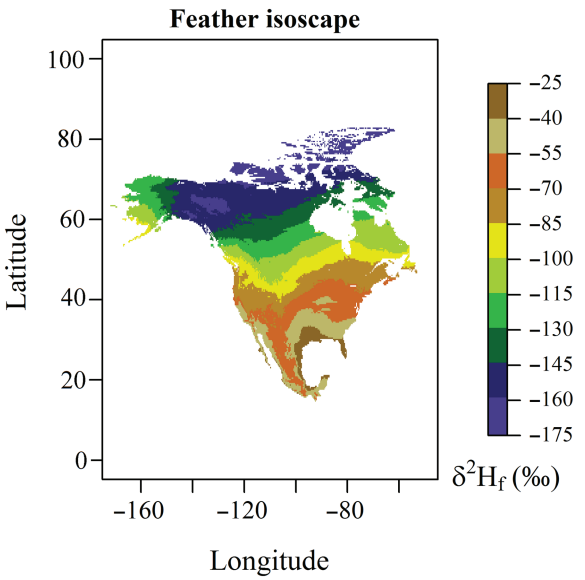

Figure 2. Isotopic regions of North America based on calibration of the stable isotope precipitation map (δ2 Hp) of Bowen et al. (2005) using the algorithm presented in Hobson et al. (2012) for translating δ2 Hp into δ2 H feather values for non-ground-foraging, long-distance migrants. Blackpoll δ2 H values ranged from 177.71 to –76.06‰ and vireo δ2 H values from –111.97 to –57.24‰.

Data deposition

Data available from the Motus Wildlife Tracking System: <http://motus.org/data/downloads>.

Results

We classified the final departure from the capture site as a migratory flight (n = 29) or stopover flight (n = 58) for 46 blackpolls and 41 vireos; the remaining birds with ambiguous departures were not included in analyses. Sixty-three percent of blackpolls and 48% of vireos were female. All vireos and 74% of blackpolls were juveniles. The wide range of stable isotope values for blackpolls (–177.71 to –76.06‰) and vireos (–111.97 to –57.24‰) indicated that we captured birds from a broad geographic breeding area ranging from the Canadian Maritimes and New England for both species, to regions further west (Fig. 2). Blackpolls remained at the capture site for an average of 3.5 ± 3.6 d after capture and vireos for 3.8 ± 2.9 d.

Blackpolls exhibited a significantly greater probability of stopover flight from the capture site (40/46; 87.0%) than vireos (18/41; 43.9%; Binomial glm; Supplementary material Appendix 1 Table A1). However, we found no evidence that

capture date, age, or sex predicted the probability of stopover flight from the capture site for either species (Binomial glm; Supplementary material Appendix 1 Table A2, A3).

We classified 86% of migratory flights (25/29) and 81% of stopover flights (47/58) from the capture site based on departure time and subsequent behavior (i.e. without considering flight orientation). Based on this sample, migratory and stopover flights from the capture site differed significantly in orientation with migratory flights oriented southwest ($n = 25$; $220 \pm 1.4°$) and stopover flights to the north ($n = 47$; $357 \pm 1.2°$; Watson Wheeler test of homogeneity; $W = 21.14$; $p < 0.0001$). We pooled the two species for this comparison because Fisher's exact tests (Agresti 1990), indicated that the proportion of stopover flights oriented for inland, coastal, or offshore flight did not differ between the species ($p = 0.32$; Table 2), nor did the proportion of migratory flights in each directional category ($p = 0.35$). A small percentage of stopover flights from the capture site were notably oriented offshore for blackpolls (10%; 4/40) and vireos (22%; 4/18). These movements were all nocturnal, and may represent abandoned migratory flights that resulted in relocation.

Both species departed on migratory flights with coastal or offshore trajectories more frequently than inland trajectories, and vireos captured later in the season oriented offshore more than earlier conspecifics. We determined orientation for all 29 migratory flights from the capture site and for 91% of the stopover flights (53/58; Table 2). Mean orientation of migratory flights was southwest for blackpolls ($n = 6$; $235 \pm 0.97°$) and south for vireos ($n = 23$; $189 \pm 1.78°$). Eighty-three percent of blackpoll migratory flights from the capture site were oriented for coastal (33%; 2/6) or overwater flight (50%; 3/6). Seventy percent of vireo migratory flights were oriented for coastal (9%; 2/23) or offshore travel (61%; 14/23). We did not have an adequate sample size of blackpoll migratory flights from the capture site to test if orientation varied by sex, age, or capture date. The orientation of vireo migratory flights from the capture site exhibited a significant shift from inland to offshore as the season progressed (ordered logistic regression; Supplementary material Appendix 1 Table A4). We found no evidence that breeding origin or sex influenced the orientation of vireo migratory flights from the capture site.

Both species primarily exhibited a coastal or overwater route through the study area, regardless of how they initially departed the capture site (Fig. 3). Nine percent of blackpolls (4/46) and 7% of vireos (3/41) departed inland from the capture site and were never redetected. We last detected 30% of blackpolls ($n = 14$) at coastal or offshore sites in the central or southern Gulf of Maine, 37% ($n = 17$) in the Cape Cod/ Long Island region where the eastern US coastline protrudes into the Atlantic Ocean, and only 2% ($n = 1$) south of Long Island, suggesting that many individuals moved overwater to and/or from the Long Island area (Fig. 3). Three vireos (7%) were last detected making a migratory flight from the capture site in an overwater orientation, 37% were last detected in south or central Gulf of Maine, 17% in the Cape Cod/Long Island region, and 15% south of Long Island. Eighty-four percent of blackpolls and 83% of vireos that departed the capture site by inland stopover flight were subsequently redetected at coastal or island receivers, indicating that initial inland movement from the coast did not necessarily dictate an inland flight route.

Five individuals of each species traveled in an unexpected migratory direction to Nova Scotia, New Brunswick, or Ontario. Three blackpolls were last detected departing south, and overwater from southeastern Nova Scotia. Three vireos made overwater movements from the capture site to Nova Scotia, and back, while a fourth was last detected departing south, overwater from the New Brunswick coast. The detections were too sparse to determine final flight orientation for the other individuals that travelled to Canada.

Table 2. Stopover flights and migratory departures by orientation for radio-tagged blackpoll warblers *Setophaga striata* and red-eyed vireos *Vireo olivaceus* departing a coastal stopover site in the Gulf of Maine in fall 2014.

	Blackpoll warblers		Red-eyed vireos	
Orientation	Stopover flights	Migratory flights	Stopover flights	Migratory flights
Inland (91–269°)	31	1	12	7
Coastal (235–270°)	1	2	1	2
Offshore (90–234°)	4	3	4	14
Unknown	4	0	1	0
Total	40	6	18	23

Note: Unknown represents departures for which we could not determine flight orientation.

Discussion

Though coastal stopover flights are assumed to represent an adaptive behavior for finding alternative stopover habitats inland (Richardson 1978, Lindström and Alerstam 1986, Åkesson et al. 1996, Åkesson 1999), direct study of this behavior has only recently been possible (Woodworth et al. 2014, 2015). By using a regional-scale telemetry array to classify behavior and movement rates after departure, we characterized most final departures from the capture site as stopover or migratory flights independent of their orientation, and thus could successfully compare the direction of stopover and migratory flights. Birds seldom made stopover flights from the capture site that were oriented for coastal or offshore flight, even though the Schoodic peninsula < 20 km to the southwest of the capture site is an easily visible target for landscape-scale stopover movements in a seasonally appropriate direction. That stopover flights were primarily oriented inland, and migratory flights for coastal or offshore travel lends further support to the hypothesis that stopover flights at a coastal barrier represent birds seeking alternate habitats inland.

Blackpolls made more inland stopover flights than vireos, providing indirect support for our hypothesis that this behavior may be advantageous for species with high energetic demands. Most blackpolls depart for wintering sites from the northeastern coast of North America on multi-day trans-Atlantic flights (DeLuca et al. 2015) that require extensive fat deposition (Nisbet et al. 1963). In contrast, vireos are regularly sighted along the eastern US coastline during migration (Sullivan et al. 2009), and often circumnavigate rather than cross the Gulf of Mexico (Deppe et al. 2015), suggesting a less energy-demanding migratory strategy compared to

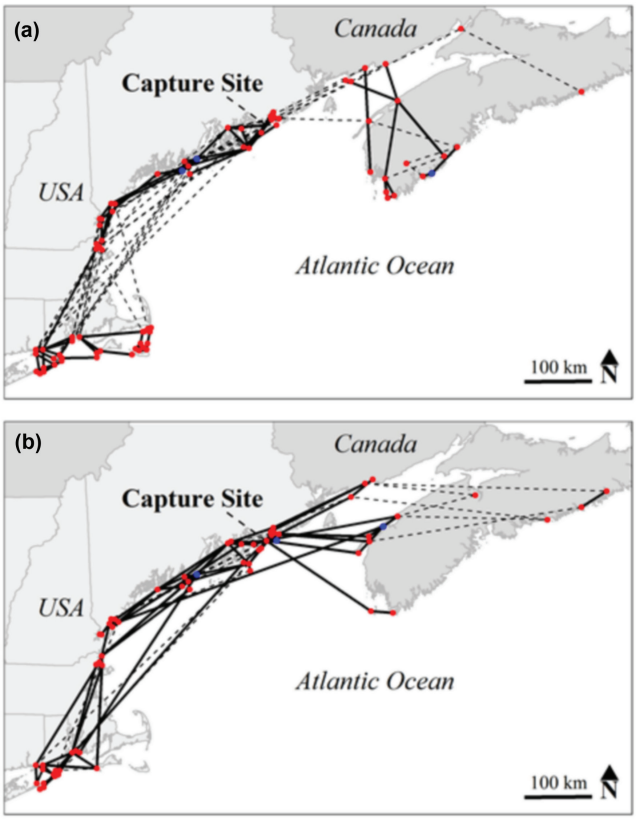

Figure 3. Map of (a) blackpoll warbler *Setophaga striata* and (b) red-eyed vireo *Vireo olivaceus* migratory routes observed by automated telemetry, in fall 2014 for the northern portion of the study area where most detections occurred. Direct flights are shown with solid lines, and likely represent actual flight paths. Slower movements are shown with dashed lines and may not represent actual routes. Estimated locations at receiver stations are shown in red and locations of observed stopovers at a telemetry station are blue.

blackpolls. We therefore speculate that the selection pressure and fitness consequences of finding prime stopover habitat for refueling and evading predators may be more important for blackpolls. Further analysis comparing more species would help test this hypothesis, as many other traits that differ between blackpolls and vireos that could have contributed to the interspecific differences we observed.

It is possible, for instance, that differences in diet and habitat preference also contributed to the behavioral differences that we observed between blackpolls and vireos. As we saw for vireos, some species occupy small geographic areas during stopover (Paxton et al. 2008, Ktitorov et al. 2010). In contrast, others may make large stopover movements (Chernetsov 2006, Taylor et al. 2011), or move fairly continuously throughout stopover (Aborn and Moore 1997, Chernetsov 2005). Food availability and habitat structure both influence stopover habitat use (Buler et al. 2007, Mudrzynski and Norment 2013, McCabe and Olsen 2015a, b), and thus the degree to which migrants relocate during stopover to fine-tune habitat selection (Chernetsov 2006). Fruit availability plays a principal role for highly frugivorous species, and vegetation structure for more omnivorous migrants (Wolfe et al. 2014). During migration, vireos are highly frugivorous (Parrish 1997, Smith and McWilliams 2010), and strongly associated with deciduous and mixed-deciduous forests, dense hardwood understory (Moore and Simons 1992, Suomala et al. 2010), and abundant fruits (McCabe and Olsen 2015a). The capture site contained all these habitat attributes, and likely provided excellent stopover resources for vireos. In contrast, blackpolls are more omnivorous than vireos during migration (Parrish 1997) and are associated with montane or spruce-fir forests habitats (Rimmer and McFarland 2000, DeLuca et al. 2013) that were not plentiful at the capture site. By departing inland, where coniferous forests are more abundant (McWilliams et al. 2005), blackpolls were likely able to find more suitable stopover habitats.

Predation pressure is also thought to play a strong role in motivating inland stopover flights because predators are highly concentrated along coastlines (Richardson 1978, Åkesson 1993, Ydenberg et al. 2007, Woodworth et al. 2014). Though re-detection rates indicate that mortality was relatively high at the capture site ($<14\%$ for blackpolls, $<19\%$ for vireos) we do not know the extent to which predation influenced inland movement in our study.

In contrast to our hypothesis, migratory flight orientation was not related to δ^2 H, and most individuals oriented for coastal or offshore flight regardless of breeding origin, suggesting that the blackpolls and vireos we sampled were actively selecting coastal and offshore routes. Many migrants are assumed to occupy coastal and offshore areas mainly due to navigational errors or wind displacement (Drury and Keith 1962, Ralph 1978). Consequently, individuals from western breeding areas may re-orient inland to regain their intended migratory route (Fitzgerald and Taylor 2008). In contrast to this expectation, $<10\%$ of blackpolls disappeared inland,

even though our sample was not exclusively birds from eastern breeding ranges. Furthermore, we found no relationship between stable isotope value and departure orientation for vireos, though our sample contained individuals from different portions of the breeding range.

That vireos were more likely to orient offshore during migratory departure as the season progressed provides support for our hypothesis that an overwater route may be more strategic later in the fall. Seasonal changes in food resources and raptor abundance along the coast (Ydenberg et al. 2007, Smith and McWilliams 2014) may make a longer coastal route less favorable later in the season, while increased time constraints may cause the time-saving benefits of overwater travel to outweigh the risk of navigational errors and unexpected storms. The favorable tailwinds that appear to support overwater flight at an ecological barrier (Shamoun-Baranes et al. 2010, Deppe et al. 2015) also tend to increase throughout the fall (La Sorte et al. 2015). The offshore flight orientation we observed for later vireos may therefore be an adaptive advantage for time minimization that is supported by seasonal changes in wind condition.

Conservation Implications

The tendency for vireos and blackpolls to follow coastal and offshore routes is of conservation interest because these behaviors can increase exposure to hazards like wind turbines or communication towers that cause sporadic mass mortality events (Crawford and Engstrom 2001, Manville 2009, Longcore et al. 2012, Loss et al. 2013). Man-made structures are of particular concern in coastal and offshore areas where turbines are typically larger (Loss et al. 2013), flight altitudes are significantly lower (Drewitt and Langston 2006, Hüppop et al. 2006, Petterson 2011, Hill et al. 2014), and songbirds are attracted to lights more frequently during poor weather (Hüppop et al. 2006, Manville 2009). The flights that both species made to Canada may also increase exposure to collision hazards because 'reverse migrations' involve traversing landscapes repeatedly (Hüppop et al. 2006), often at lower flight altitudes (Bruderer and Liechti 1998, Komenda-Zehnder et al. 2002, Nilsson and Sjöberg 2015).

Conclusion

Our work highlights the importance of studying migration, and conserving stopover resources at a large spatial scale. Without the use of a large regional array, we may not have been able to compare the orientation of stopover and migratory flights from the capture site, determine that most individuals took coastal or offshore routes despite making an initial inland departure, or detect birds making large-scale movements to the north and east after their initial departure from the capture site. Similarly, only by studying migration at a large spatial scale, could we confirm that most vireos remained at the capture site until migratory departure, and demonstrate that the dense coastal scrub and deciduous forests at the capture site likely provided valuable stopover resources for this species. These findings reinforce the importance of maintaining stopover habitats with mature fruiting shrubs for more frugivorous migrants (Smith and McWilliams 2010, Mudrzynski and Norment 2013), particularly in the Gulf of Maine where frugivorous species from across the boreal region concentrate in the fall (Leppold and Mulvihill 2011, Leppold 2016). The regional array also revealed that most blackpoll departures were inland stopover flights, not true migratory departures. This underscores the importance of conserving stopover habitats at a broad spatial scale, and implicates inland habitats as more favorable for blackpoll fat deposition. Though we were unable to specifically measure the scale of inland movements or habitat choices of blackpolls that relocated inland, our results suggest that a dense array of receivers just inland from the coast may help to elucidate the stopover needs of this rapidly declining species (Rosenberg et al. 2016).

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Supplementary material (Appendix JAV-01450 at <www.avianbiology.org/appendix/jav-01450>). Appendix 1.