



Patterns and correlates of songbird movements at an ecological barrier during autumn migration assessed using landscape- and regional-scale automated radiotelemetry

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Departure decisions of songbirds at ecological barriers they encounter en route can strongly influence time, energy and survival costs of migration. To date, most field studies of departure decisions and their correlates have used indirect methods and followed migrants at a single stopover site, with limited information on what happens to individuals after they depart from the site. We used an automated radiotelemetry array extending 350 km from southwest Nova Scotia to southern Maine to study the migratory and stopover movements of Northern Waterthrushes *Parkesia noveboracensis*, Red-eyed Vireos *Vireo olivaceus* and Yellow-rumped Warblers *Setophaga coronata* in relation to fuel load and weather at the northeastern edge of the Gulf of Maine. From the 105 radio-transmitters we deployed in southwest Nova Scotia, we recorded 42 landscape-scale stopover flights and 47 migratory flights by 75 individuals. Of the migratory flights, 57% were orientated southwest, a trajectory that, if held, would require individuals to complete a 350–440 km overwater flight. The remaining 43% of migratory flights were orientated northwest, away from the Gulf of Maine, and 15 individuals were confirmed to have detoured around all or a portion of the barrier, as evidenced by their being re-detected over the Bay of Fundy and/or along the coast of Maine between 4 h and 15 days later. Across all individuals, initial fat score had a positive effect on departure probability, especially for individuals that made stopover flights. Among weather variables, tailwind assistance was the best predictor of migratory departures but did not appear to be the main factor determining whether individuals orientated towards or away from the Gulf of Maine. Weather had little effect on departure decisions of individuals that made stopover flights. These differences in the correlates of migratory departures and stopover flights would probably not have been distinguishable had our study been restricted to a local scale. Therefore, our findings highlight the importance of expanding the scale at which departure decisions and the ecology of stopover in general are studied.

Keywords: departure decisions, energetic condition, migratory orientation, stopover, weather.

Most migratory songbirds are capable of making non-stop flights of hundreds to thousands of kilometres (Stutchbury *et al.* 2009, Bairlein *et al.* 2012),

yet they often orientate away from and detour around ecological barriers, such as large bodies of open water or deserts, that they encounter en route to their breeding and wintering sites (Sandberg & Moore 1996, Deutschlander & Muheim 2009, Stutchbury *et al.* 2009, Schmaljohann &

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Naef-Daenzer 2011, Delmore *et al.* 2012). In doing so, migrants may benefit from greater opportunities to locate high-quality stopover sites and reduced costs of energetic shortfalls, navigational errors (Drury & Keith 1962) or unexpected weather events (Butler 2000, Newton 2007). However, detouring around a barrier also increases the distance migrants must travel to reach their ultimate destination, and stopovers in unfamiliar habitat bordering an ecological barrier may be associated with a higher risk of predation (Woodworth *et al.* 2014). Therefore, departure decisions in this ecological context can have important implications for the time, energy and safety costs of migration (Alerstam 2001).

Many factors are known to influence the departure decisions of migrants, including their genetic programming (Berthold 1996), geographical origin (Fitzgerald & Taylor 2008) and age or experience (Ralph 1978, Moore 1984). However, at least at the most immediate level, there is substantial evidence that energetic condition and local weather conditions are highly influential factors. Individuals tend to initiate migration and maintain seasonally appropriate directions across barriers when they have high fuel loads and when weather is favourable for flight, including light and/or following winds, clear skies, little or no precipitation, and high and rising atmospheric pressure (Sandberg & Moore 1996, Dänhardt & Lindström 2001, Deutschlander & Muheim 2009, Goymann *et al.* 2010, Morganti *et al.* 2011, Schmaljohann & Naef-Daenzer 2011, Schmaljohann *et al.* 2011, Smolinsky *et al.* 2013, Smith & McWilliams 2014). When individuals have low fuel loads or encounter poor weather conditions, they are more likely to avoid barriers (Schmaljohann & Naef-Daenzer 2011) or to continue stopover at the same or a nearby stopover site (Alerstam 1978, Åkesson & Hedenström 2000, Åkesson *et al.* 2001, Dänhardt & Lindström 2001).

Although relationships among departure decisions, fuel load and weather have been studied extensively, most studies have used indirect methods and monitored migrants in the immediate area of a single stopover site, with limited information on what happens to individuals after they depart (Sandberg & Moore 1996, Dierschke & Delingat 2001, Schaub *et al.* 2004, 2008, Fitzgerald & Taylor 2008, Calvert *et al.* 2009, Deutschlander & Muheim 2009, Morganti *et al.* 2011, Bulyuk & Tsvey 2013). Consequently, inferences from these studies rely heavily on the assumption that initial

observations accurately reflect subsequent behaviours. For example, it is often assumed that all departures from a stopover site are migratory flights. However, this may not always be the case. As Mills *et al.* (2011) and Taylor *et al.* (2011) showed, many nocturnal departures from stopover sites are not migratory flights but rather local- or landscape-scale relocations within the broader stopover landscape. Such movements may be motivated by entirely different factors than migratory departures (e.g. expanded search for suitable habitat; Alerstam 1978) or could be the result of failed migratory departures (e.g. if conditions experienced aloft are unsuitable for migration; Richardson 1978a, Schmaljohann *et al.* 2011). Therefore, broadening the scale at which stopover is studied is important for improving our understanding of the patterns, causes and consequences of departure decisions and subsequent movement behaviours.

We used an automated radiotelemetry array spanning 350 km from southwest Nova Scotia, Canada, to southern Maine, USA, to study the migratory and stopover movements of hatch-year Northern Waterthrushes *Parkesia noveboracensis*, Red-eyed Vireos *Vireo olivaceus* and Yellow-rumped Warblers *Setophaga coronata* in relation to fuel load and weather during autumn migration. Past research in Atlantic Canada has shown that the predominant direction of nocturnal songbird migration is southwest, and passerines following this route commonly cross the Gulf of Maine directly from Nova Scotia to New England, an overwater distance of 350–440 km (Richardson 1972, 1978b). However, considerable variation in migratory and stopover behaviours of migrants in this region has also been observed, suggesting that some migrants, rather than crossing the Gulf of Maine directly, may temporarily relocate to different stopover sites within Nova Scotia or, when they do resume migration, detour around all or parts of the barrier (Richardson 1972, 1978a, 1982, Fitzgerald & Taylor 2008, Calvert *et al.* 2009). With multiple automated radiotelemetry receiving stations in southwest Nova Scotia, on an island in the Bay of Fundy and along the coast of Maine continuously scanning multiple directional antennae, we were able to monitor individuals locally and for many hundreds of kilometres beyond their point of departure. As a result, we were able to separate migratory departures from relocations within the landscape and to infer the proportions of migrants that crossed the Gulf of

Maine directly or that detoured around the barrier, based on the timing and direction of departure flights, as well as subsequent detections of some individuals. We used these data to evaluate effects of fuel load and local weather conditions on departure decisions of individuals that (1) relocated within the landscape prior to continuing migration, (2) initiated migratory flights orientated to the southwest, towards the Gulf of Maine, or (3) initiated migratory flights orientated to the northwest, away from the barrier.

METHODS

Study sites

Individuals were captured and radiotagged on Bon Portage Island (43°28'N, 65°45'W) and at Quinns Falls (43°40'N, 65°28'W) in southwest Nova Scotia (NS), Canada (Fig. 1), in conjunction with annual migration monitoring activities at the Atlantic Bird Observatory (ABO; Crewe *et al.* 2008). Bon Portage Island is approximately 3 km long, 0.25–0.65 km wide, and is situated 3 km from the southwest tip of NS. The north and south ends of the island are dominated by spruce–fir forest, whereas the middle of the island consists of open savannah and coastal wetland. Quinns Falls is situated on the Clyde River approximately 8 km inland and 30 km northeast of Bon Portage Island. Quinns Falls consists primarily of mixed Acadian forest bordered by an expansive bog–fen complex and low-density residential properties. Overall, this landscape shows a transition from boreal at the coastline to Acadian forest farther inland (Neily *et al.* 2011).

Capture and tagging

Individuals were captured using mist-nets from 22 August to 13 October 2010. We recorded the age, un-flattened wing chord (mm), mass (g) and fat score of each individual. Age was determined from species-specific plumage features, moult criteria and extent of skull ossification (Pyle 1997). Individuals were classified as hatch-year (first autumn migration) or after-hatch-year (experienced at least one previous autumn migration). Fat was scored on a categorical index of 0–7 (Kaiser 1993) by visually inspecting subcutaneous fat deposits in the furculum, breast and abdomen. Following measurements, individuals were fitted with a coded radio-transmitter (Avian NanoTag model NTQB-1, Lotek Wireless Inc., Newmarket, ON, Canada) using a figure-of-eight leg loop harness made of biodegradable thread (Rappole & Tipton 1991, see Supporting Information Figure S1 for photograph of a radiotagged Red-eyed Vireo). Transmitters operated at 166.320 MHz (burst interval = 7.2 s) or 166.340 MHz (burst interval = 4.8 s), had an approximate battery life of 21 days and weighed 0.29 g without harness material. Combined weight of the transmitter and harness material was ~ 0.4 g, which was 1.8–3.4% of the body weight of individuals (mean ± se: Northern Waterthrushes = $2.32 \pm 0.04\%$, $n = 24$; Red-eyed Vireos = $2.35 \pm 0.03\%$, $n = 55$; Yellow-rumped Warblers = $3.09 \pm 0.04\%$, $n = 26$). Only hatch-year individuals were tagged because they constituted the bulk of captures in this region in autumn (Ralph 1981, ABO unpublished data). Individuals of all three species were tagged on Bon Portage Island, whereas only Red-eyed Vireos were tagged at Quinns Falls. Most individuals were released

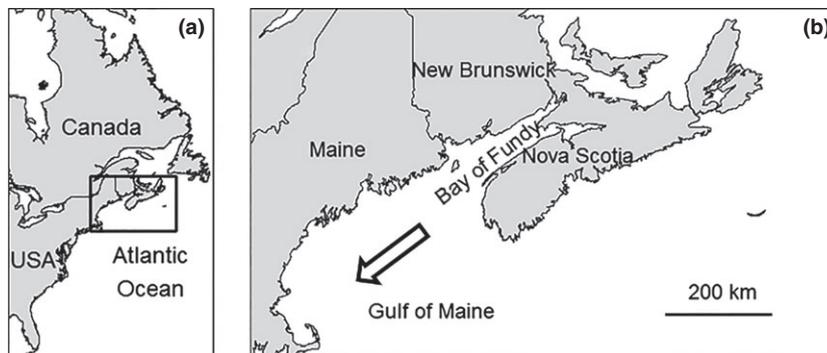


Figure 1. (a) Map showing position of the Gulf of Maine region (inset) in relation to eastern North America. (b) Gulf of Maine region with open arrow showing the predominant southwest direction of autumn nocturnal songbird migration in the region.

within 20 min of capture, with no individuals held for more than 1 h. All handling methods were in accordance with ABO protocols and approved by the Acadia University Animal Care Committee and Environment Canada.

Radiotelemetry

The automated telemetry array was in operation from 22 August to 31 October 2010. Towers were positioned at four sites in southwest NS, three locations on Kent Island in the outer Bay of Fundy, and three sites on the coast of Maine (Fig. 2). Each tower stood 8–15 m high and was equipped with an SRX-600 digital telemetry receiver (Lotek Wireless Inc., Newmarket, ON, Canada) and two or four antennae (Fig. 2). Towers in southwest NS and Maine were equipped with nine-element Yagi antennae, whereas towers on Kent Island were equipped with four-element Yagi antennae (Mitchell *et al.* 2012). Receivers were programmed to scan each antenna for 7.8 s on one frequency before switching frequencies. As such, a single frequency was scanned continuously for 31.2 s every other 31.2 s (towers with four antennae) or 15.6 s every other 15.6 s (towers with two antennae). When a signal was detected, receivers logged the digitally coded transmitter ID, time of detection, signal strength and antenna on which the signal was detected. Digital data files containing this information were downloaded from NS towers (except for Seal Island) on a daily basis and from all other towers periodically. After the field season, files were post-processed to ensure that only valid detections were analysed. This involved removing temporally isolated detections of a given tag as these were likely false positives caused by random noise. We also calculated time differences between each detection and its three nearest neighbours. If time differences were not multiples of the tag burst interval (allowing for some error due to clock drift and timestamp precision) then the detection was considered to be a false positive and was removed from the dataset. On average, false positives constituted < 0.8% of all detections for a given bird.

In addition to an automated telemetry array, we also used a handheld SRX-600 receiver with a five-element Yagi antenna to determine the exact locations of individuals close to the capture sites after release, as well as within the broader stopover landscape. This also enabled us to

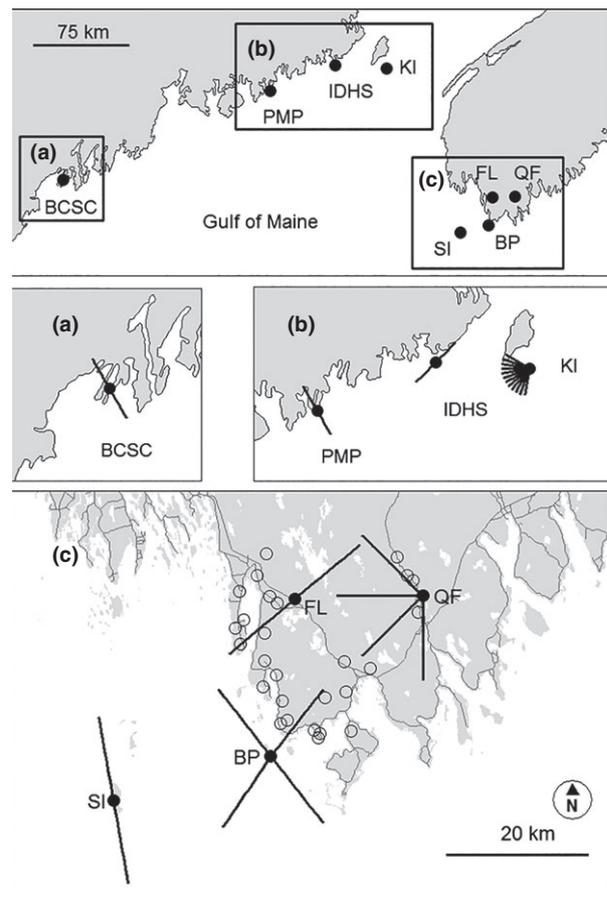


Figure 2. (Top) Map showing the distribution of receiving stations constituting the automated radiotelemetry array used to monitor the movements of three songbird species radiotagged at Quinns Falls (QF) and Bon Portage Island (BP) during autumn migration in southwest Nova Scotia. Telemetry towers were located at Bowdoin Coastal Studies Center (BCSC), Petit Manan Point (PMP) and Inner Double Headshot Island (IDHS) in Maine; Kent Island (KI) in the Bay of Fundy; and Seal Island (SI), French Lake (FL), BP and QF in southwest Nova Scotia. (a–c) With the exception of KI, which was set up for a separate study (Mitchell *et al.* 2012), telemetry towers were equipped with two or four nine-element Yagi antennae. Solid black lines show the orientation and approximate horizontal detection range (12 km) of each antenna. (c) Open circles show positions of scan points from which we searched for tagged individuals that had left their initial capture site.

confirm suspected mortalities and/or tag losses. Individuals were tracked by a single observer until they were sighted or until their signal strength indicated they were within 30 m, at which point their location was recorded using a GPS. Sighting was often not possible because of the density of habitat and because we wanted to avoid disrupting the natural behaviour of individuals. At both

capture sites, individuals were located once or twice each day. When individuals were no longer detected at their capture site, we expanded our ground searches to include a set of fixed scan points throughout the broader stopover landscape (Fig. 2). To maximize detection range, scan points occurred at elevated locations with a clear line of sight. We scanned from each point for 5 min and in approximately 45° intervals on a horizontal plane. If individuals were detected from scan points, we subsequently determined their exact location using the methods described above. In total, we conducted 513 visits to scan points over 44 days, with most visits occurring on days when one or more tagged individuals were detected leaving their capture site the previous night.

Flight classification

Based on detections from the automated telemetry array (e.g. Fig. 3; Taylor *et al.* 2011) and ground-tracking, flights were classified into three types: 'stopover', 'migratory' or 'ambiguous'. Stopover flights were considered flights (1) in any direction and initiated at any time of day that were followed by an automated or manual re-detection within southwest Nova Scotia at least 1 h after the initial detection and at least 1 km from where the flight began or (2) to the northeast (opposite to expected autumn migratory direction) at any time of day that were not followed by an automated or manual re-detection in southwest Nova Scotia. Migratory flights were flights initiated between the end of civil twilight and the beginning of civil dawn in a seasonally appropriate direction (180°–360°) with either no subsequent manual or automated re-detections in southwest Nova Scotia, or temporary re-detections at a different tower in southwest Nova Scotia within 1 h of departure. Birds temporarily detected by a subsequent tower in southwest Nova Scotia within 1 h of departure were probably flying past the tower, whereas those detected by a subsequent tower in southwest Nova Scotia more than 1 h after departure were probably not in migratory flight because their flight speeds would have been much slower than 10 m/s. Migratory flights orientated between 180° and 270° (inclusive) were further classified as southwest and those orientated between 270° and 360° were classified as northwest. Ambiguous flights were flights that were not followed by a manual

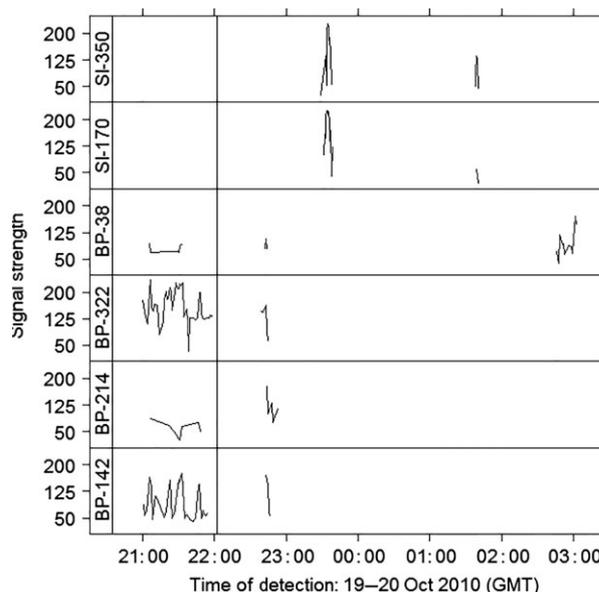


Figure 3. Received signal strength (0–255) by multiple antennae at two automated telemetry receiving stations (Fig. 2) plotted by time for a Yellow-rumped Warbler on 19/20 October 2010. This individual departed Bon Portage Island in a southwest direction within an hour of sunset (vertical black line) and was detected flying past Seal Island in a southwest direction shortly afterwards. Almost 2 h later it was detected flying past Seal Island again, this time towards southwest Nova Scotia, before being re-detected northeast of Bon Portage Island later that night. On the afternoon of 22 October 2010 (not shown here) it was manually re-located on a nearby island (43°32'N, 65°48'W), approximately 8 km north of Bon Portage Island. Later that night it was detected on the northwest antenna of the Bon Portage Island tower departing from a nearby island, but the direction of the departure could not be established and there were no subsequent detections elsewhere. This is an example of an individual that appeared to initiate a migratory flight over the Gulf of Maine before reversing direction and returning to mainland Nova Scotia.

or automated re-detection and whose direction could not be established.

Weather data

Surface wind direction (direction in 10° intervals from which wind was blowing), surface wind speed (km/h), atmospheric pressure (kPa), precipitation (raining or not raining), cloud cover (clear, 10–40%, 50–90%, overcast) and horizontal visibility (km) were measured hourly at the Yarmouth International Airport weather station (43°49'N, 66°05'W; 48 km northwest of Bon Portage Island and 52 km west of Quinns Falls) and accessed from www.climate.weatheroffice.gc.ca.

From surface wind direction and speed we calculated tailwind assistance for flights orientated to the southwest ($\theta_b = 225^\circ$) and northwest ($\theta_b = 315^\circ$) using the following formula: $V_w * \cos((\theta_w + 180^\circ) - \theta_b)$, where V_w is wind speed (km/h), θ_w is wind direction and θ_b is the direction of migration (Sapir *et al.* 2011). For stopover flights, we calculated tailwind assistance for west-orientated migration ($\theta_b = 270^\circ$) because any flight directed to the west could be considered seasonally appropriate (Richardson 1972, 1978b). We explored the use of higher elevation wind data from the North America Regional Reanalysis dataset, which we accessed using the Env-Data system (www.movebank.org) but found wind conditions at two different heights (10 and 30 m) and four different pressure levels (1000, 975, 950, 925 and 900 mb) to be highly correlated (all $r > 0.8$) with one another and with wind conditions from the Yarmouth International Airport weather station. Given these strong correlations, we opted to use only actual measurements of surface wind from Yarmouth.

In addition to tailwind assistance, we also calculated change in atmospheric pressure as the difference in pressure between the time of departure and 24 h prior to departure, and classified this variable as a two-level factor, rising or falling. For all weather variables, we used the value measured closest to the time of departure (i.e. within 30 min). On nights that individuals continued stopover, we used values measured closest to sunset.

Departure decisions in relation to fuel load and local weather conditions

We assessed effects of initial fat score and weather conditions on individual departure decisions using time-dependent Cox proportional hazards models (Gienapp *et al.* 2005, Bauer *et al.* 2008) implemented in the 'survival' package (Therneau 2014) in R 3.0.2 (R Core Team 2014). These models describe the probability of an event occurring over time as a function of a baseline probability (hazard), which can be modified by a set of fixed or time-varying explanatory variables (Gienapp *et al.* 2005). For our analysis, we estimated the probability of a departure (the event) as a function of initial fat score (fixed variable) and weather (time-varying variables). In contrast to most studies, which usually correlate departure decisions to

conditions on departure nights only, this method includes information about weather conditions experienced by individuals on nights they chose not to depart (i.e. continued stopover), which can provide deeper insight into factors shaping departure decisions.

We first examined effects of fat score on departure decisions independent of weather by fitting models for all individuals simultaneously as well as separately for each flight type. In each model we estimated a fixed effect and time-dependent parameter for fat score. We estimated a time-dependent parameter because we only had a single measure of fat score from when individuals were first captured. Given that most individuals spent multiple days in southwest Nova Scotia, their fuel load at departure could have changed substantially since initial capture and therefore the relevance of initial fat score for departure decisions was expected to decrease with time. Because we detected multiple stopover flights for some individuals and a stopover flight followed by a migratory flight for others, we clustered the models for all flights and stopover flights by individual to account for non-independent observations. Clustering by individual was unnecessary for southwest and northwest migratory flights because we only observed one migratory departure for each individual.

To examine effects of local weather conditions on departure decisions we generated a set of candidate models for each flight type comprising all additive combinations of four weather variables: tailwind assistance (km/h), atmospheric pressure (kPa), change in atmospheric pressure (rising or falling) and cloud cover (overcast or not overcast). To account for effects of fat score on departure decisions as well as to facilitate the multi-model selection procedure described below, which requires each explanatory variable to be equally represented in the candidate model set, we stratified on fat score rather than estimating a fixed effect for fat score in each of the models. By specifying a stratification variable, a separate baseline probability function is estimated for each stratum, but coefficients for the other covariates are assumed to be constant across strata. For the stratification variable, we classified individuals with fat scores ≤ 1 as lean and those with fat scores > 2 as fat (Fig. 4).

To evaluate the strength of evidence for each weather variable, we generated cumulative AIC_c

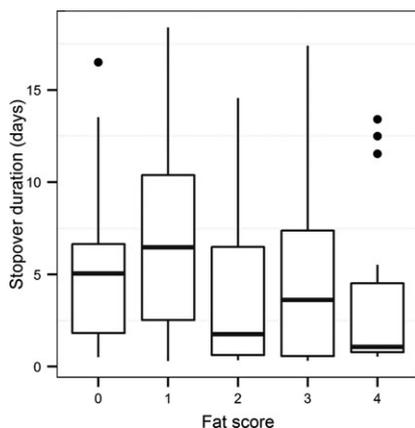


Figure 4. Minimum stopover duration in relation to initial fat score of three songbird species during autumn migration in southwest Nova Scotia.

(Akaike's information criterion corrected for small sample size) weights and model-averaged parameter estimates for each flight type (e.g. Tipton *et al.* 2008). We used model-averaging because there was considerable model selection uncertainty (i.e. the probabilities of several of the best candidate models were similar; Burnham & Anderson 2002, Burnham *et al.* 2011). We excluded precipitation from these models because very few migratory flights orientated to the northwest or stopover flights and no migratory flights to the southwest occurred during rain. We also excluded horizontal visibility because it was consistently highly correlated with other weather variables and few flights occurred when visibility was less than its maximum. Supporting Information Table S1 summarizes the candidate models from which model-averaged parameter estimates were derived for each flight type.

RESULTS

We tagged 24 Northern Waterthrushes, 55 Red-eyed Vireos and 26 Yellow-rumped Warblers between 22 August and 13 October 2010. All Northern Waterthrushes and Yellow-rumped Warblers, and 39 Red-eyed Vireos were tagged on Bon Portage Island, with the remaining 16 Red-eyed Vireos tagged at Quinns Falls. Median tagging dates were 30 August for Northern Waterthrushes, 18 September for Red-eyed Vireos and 7 October for Yellow-rumped Warblers. All individuals had fat scores of 4 or lower and 63% (67/105) were below 3. Individuals were monitored for an

average (± 1 se) of 4.3 ± 0.5 days (range = 0.3–17.4 days, $n = 76$) on Bon Portage Island and 2.4 ± 0.6 days (range = 0.3–6.7 days, $n = 16$) at Quinns Falls. We recovered tags from one Northern Waterthrush and 12 Red-eyed Vireos prior to their leaving Bon Portage Island and from two Red-eyed Vireos after they relocated from the island to mainland Nova Scotia. All tags that we recovered were apparently from individuals that had been killed by raptors (Woodworth *et al.* 2014).

Flight summary

From the 92 individuals that we detected leaving their initial capture site, we recorded 89 non-ambiguous flights (47 migratory flights, 42 stopover flights) by 75 individuals. Of the 47 migratory flights, 57% ($n = 27$) were orientated to the southwest, towards the Gulf of Maine, and 43% ($n = 20$) were orientated to the northwest, away from the Gulf of Maine. Twenty-two per cent (6/27) of those orientated to the southwest and 30% (6/20) of those orientated to the northwest were preceded by stopover flights. Of the 42 stopover flights, 16 were confirmed using handheld receivers and antennae. We were able to infer initial directions for 27 of the stopover flights; 74% (20/27) were orientated away from the Gulf of Maine towards mainland Nova Scotia and 26% (7/27) were orientated towards the Gulf of Maine. Three individuals that made stopover flights were detected flying past Seal Island (~ 20 km offshore; Figs 2 & 3) before returning to the coast.

Migratory flights occurred an average (± 1 se) of 7.3 ± 0.8 days after initial capture (range = 0.3–18.4 days, $n = 47$; Fig. 5), which was on average 4.4 days later than the average stopover flight (2.9 ± 0.5 days after initial capture, range = 0.3–13.4 days, $n = 42$; general linear model of log-transformed stopover durations: $\beta = 3.35 \pm 0.90$, $t_{73} = 3.72$, $P < 0.001$). Migratory flights orientated towards the Gulf of Maine occurred an average (± 1 se) of 8.2 ± 1.0 days after initial capture (range = 0.3–18.4 days, $n = 27$; Fig. 5) compared with 6.0 ± 1.2 days (range = 0.3–15.5 days, $n = 20$; Fig. 5) for flights orientated away from the Gulf ($\beta = 2.15 \pm 1.50$, $t_{45} = 1.44$, $P = 0.15$). More stopover flights (43%, 18/42) were made within 24 h of initial capture than were migratory departures orientated towards the Gulf of Maine (11%, 3/27) or away from the Gulf (25%, 5/20).

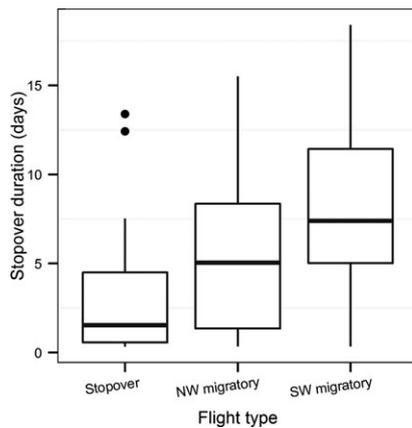


Figure 5. Minimum stopover durations in relation to flight type of three songbird species during autumn migration in southwest Nova Scotia.

All migratory flights, and all except three stopover flights, occurred at night.

After having left southwest Nova Scotia, 15 individuals (12 Red-eyed Vireos, two Yellow-rumped Warblers and one Northern Waterthrush; 16% of all individuals) were re-detected 4 h to 15 days (mean \pm 1 se: 6.1 ± 1.3 days) later and 145–350 km away over Kent Island in the Bay of Fundy and/or along the coast of Maine (see Fig. S1 for the migratory routes of three individuals). Eight individuals were detected at multiple locations outside southwest Nova Scotia, all of which were moving along the coast of Maine in a seasonally appropriate west–southwest direction. Of the 15 individuals that detoured around all or part of the Gulf of Maine, 27% (4/15) were last detected departing southwest Nova Scotia in a northwest direction, 20% (3/15) in a southwest direction and 20% (3/15) were last detected making a stopover flight. Departures of the remaining 33% (5/15) were classified as ambiguous.

Departure decisions in relation to fuel load and local weather conditions

Across all individuals for which we detected a non-ambiguous flight, we found a significant effect of initial fat score on departure probability (Table 1). Departure probability increased with initial fat score ($\beta = 0.29 \pm 0.12$, $P = 0.015$; Table 1) but, as expected, this effect diminished with time ($\beta = -0.03 \pm 0.02$, $P = 0.030$; Table 1). When separate models were fitted for each flight

Table 1. Probability of departure in relation to initial fat score for all flights and each flight separately.

Model	Variable	$\beta \pm se$	P
All flights ($n = 89$)	Fat	0.29 ± 0.12	0.015
	Fat \times time	-0.03 ± 0.02	0.030
Stopover flights ($n = 42$)	Fat	0.39 ± 0.20	0.056
	Fat \times time	-0.01 ± 0.06	0.852
SW migratory flights ($n = 27$)	Fat	0.01 ± 0.32	0.987
	Fat \times time	-0.01 ± 0.03	0.774
NW migratory flights ($n = 20$)	Fat	0.08 ± 0.32	0.807
	Fat \times time	0.01 ± 0.06	0.819

type, the effect of fat score on departure probability was strongest for individuals that made stopover flights, but the effect was in the same direction for birds that made migratory flights (Table 1).

Accounting for effects of initial fat score on departure probability, we found differences among the three flight types with respect to influences of weather on departure decisions. For migratory flights orientated southwest and northwest, tailwind assistance best explained variation in departure probability. Individuals were more likely to depart in the direction of the Gulf of Maine when winds favoured migration to the southwest (mean \pm 1 se: 3.1 ± 1.2 km/h at departure vs. -5.9 ± 0.6 km/h on stopover nights) and away from the Gulf of Maine when winds favoured migration to the northwest (4.9 ± 1.4 km/h at departure vs. -3.7 ± 1.4 km/h on stopover nights). However, despite wind being the most important predictor of migratory departures, a substantial proportion of departures to the southwest and northwest occurred on nights when winds were neutral (i.e. favourable for migration in either direction), favourable for migration in the other direction or unfavourable (Table 2). Moreover, 82% (9/11) of individuals that departed to the southwest in favourable winds and 80% (4/5) of those that departed to the northwest in favourable winds passed up opportunities to depart earlier in stopover when winds were suitable for migration in the other direction.

Following tailwind assistance, southwest departures were most influenced by atmospheric pressure, with individuals being most likely to leave when pressure was high (Table 3). Pressure on departure nights was on average (\pm 1 se) 101.21 ± 0.10 kPa compared with 100.38 ± 0.05 kPa on nights on which

Table 2. Departure directions in relation to wind direction and speed. No flights occurred in winds of > 28 km/h and 91% occurred in winds of < 18 km/h.

Flight orientation	Wind speed (m/s)	Wind direction (favoured flight direction)			
		NW-NE (SW)	SE-SW (NW)	NE-SE/Calm (Either)	SW-NW (Neither)
SW (<i>n</i> = 27)	< 5	0	0	3	0
	5–15	11	1	7	2
	≥ 15	1	1	0	1
	Σ	12 (45)	2 (8)	10 (37)	3 (15)
NW (<i>n</i> = 20)	< 5	1	1	1	1
	5–15	1	2	7	0
	≥ 15	0	3	1	2
	Σ	2 (10)	6 (30)	9 (45)	3 (15)

Table 3. Model-averaged parameter estimates ($\beta \pm se$) and cumulative Akaike weights (Σw_i) for time-dependent proportional hazards models examining the effects of tailwind assistance, atmospheric pressure, change in atmospheric pressure and cloud cover on departure decisions of three songbird species during autumn migration in southwest Nova Scotia. Models describing stopover flights were clustered by individual to account for those for which we observed multiple departures. All models were stratified by fat score to account for any effects of initial fat score on departure probability.

Weather variable	Parameter	SW migratory flight	NW migratory flight	Stopover flight
Tailwind assistance	$\beta \pm se$	0.12 ± 0.05	0.07 ± 0.04	0.00 ± 0.16
	Σw_i	0.96	0.61	0.28
Pressure	$\beta \pm se$	1.37 ± 0.55	0.49 ± 0.47	0.86 ± 0.26
	Σw_i	0.94	0.39	0.89
Δ pressure (falling)	$\beta \pm se$	0.83 ± 1.03	0.16 ± 0.68	0.47 ± 0.39
	Σw_i	0.37	0.28	0.40
Cloud cover (not overcast)	$\beta \pm se$	-1.49 ± 0.94	1.12 ± 0.71	-0.43 ± 0.37
	Σw_i	0.64	0.57	0.39

individuals continued stopover. Although we excluded precipitation from the statistical models, it had a strong influence on departure decisions because no migratory flights to the southwest occurred in rain. Individuals were also more likely to depart when skies were clear (20/27; 74%), horizontal visibility was at a maximum (26/27; 96%) and pressure was rising (23/27; 85%), but these variables were less influential than wind and atmospheric pressure (Table 3).

For departures to the northwest, cloud cover was the most important predictor of departure after tailwind assistance, with departures more likely under overcast skies (Table 3). Of the 88 total stopover nights experienced by individuals that departed to the northwest, skies were only overcast on 42% of nights, yet 60% of departures occurred in overcast conditions. Departures to the northwest were also more likely to occur on nights of high pressure (101.2 ± 0.2 kPa at departure vs. 100.8 ± 0.1 kPa on stopover nights), when pressure was rising (12/20; 60%),

with maximum visibility (16/20; 80%) and with no rain (17/20; 85%). However, a greater proportion of flights to the northwest were initiated in poor conditions compared with flights to the southwest.

Atmospheric pressure was the most important predictor of stopover flights. Individuals were more likely to initiate stopover flights when pressure was high (101.0 ± 0.1 kPa at departure vs. 100.4 ± 0.1 kPa on stopover nights). However, unlike migratory flights, wind had the weakest influence on stopover flights of all weather variables considered (Table 3). Mean tailwind assistance for flights to the west was on average ($\pm 1 se$) -3.6 ± 1.3 km/h on nights individuals made stopover flights and -7.1 ± 1.4 km/h on nights they continued stopover. Most stopover flights occurred on nights of rising pressure (31/41; 76%), clear skies (28/41; 68%), maximum visibility (31/41; 76%) and no rain (37/41; 90%), but similar to migratory flights to the northwest, a greater proportion of stopover flights were made in poor

conditions than were migratory flights to the southwest.

DISCUSSION

Recent work has shown that the scale of stopover among migratory songbirds may be greater than previously thought, with important implications for our understanding of patterns, causes and consequences of departure decisions and of migratory behaviours in general (Taylor *et al.* 2011). With an array of automated radiotelemetry receiving stations spanning 350 km around the Gulf of Maine, from southwest Nova Scotia to southern Maine, we were able to monitor directly the migratory and stopover movements of three songbird species over a broad range of spatial and temporal scales. In doing so, we found that a high proportion of departures from our study sites (47% of non-ambiguous flights) comprised individuals making landscape-scale stopover flights prior to continuing migration. When we detected 'true' migratory departures, we were able to distinguish between those orientated towards the Gulf of Maine and those orientated away from this barrier, and subsequently confirmed directly that some individuals detoured around the barrier. Given important differences in the costs and benefits of different strategies for negotiating an ecological barrier during migration and that we also found differences in factors influencing departure decisions of migrants making these different movements, our results reinforce the importance of expanding the scale at which departure decisions and the ecology of stopover are studied (Taylor *et al.* 2011).

Although birds are capable of crossing large ecological barriers during migration, there is growing evidence that many migrants opt to circumvent these barriers when possible (Sandberg & Moore 1996, Deutschlander & Muheim 2009, Stutchbury *et al.* 2009, Schmaljohann & Naef-Daenzer 2011, Delmore *et al.* 2012). The same appears to be true of the Gulf of Maine, where 43% of migratory departures we observed from southwest Nova Scotia were orientated to the northwest, suggesting that individuals initiating these flights detoured around at least part of the Gulf of Maine, and 16% of individuals were directly confirmed to have detoured around this barrier. In Atlantic Canada, migrants that congregate along the coast during autumn migration are predominantly inexperienced, first-time migrants

(the 'coastal effect'; Ralph 1971, 1981) from a mixture of populations of different geographical origin (Dunn *et al.* 2006, Fitzgerald & Taylor 2008). For some, southwest Nova Scotia and the Gulf of Maine may not represent the usual migration route. Rather, birds may end up in this region due to navigational errors (Drury & Keith 1962) or eastward displacement by broad- or regional-scale wind patterns (McLaren *et al.* 2006), both of which may be especially likely to affect first-time migrants. As such, individuals may migrate to the west and northwest to correct for displacement and to 're-calibrate' their original migratory route (Baird & Nisbet 1960, Moore 1990, Fitzgerald & Taylor 2008). Alternatively, for others, especially those originating from populations further east in Nova Scotia and Newfoundland, the Gulf of Maine probably forms part of their usual migration route (Richardson 1978b) and detours may be chosen as an alternate strategy for negotiating the barrier. For naïve, first-time migrants as we studied here, avoiding the hazards of overwater flight and extended stopovers in coastal areas where the risk of predation can be high relative to further inland may often be the better strategy for some species (Woodworth *et al.* 2014).

Among individuals, we found strong evidence for local weather conditions influencing migratory departure decisions. Individuals that began migratory flights chose nights with tailwind assistance. However, departures to the northwest were more likely to occur when skies were overcast, whereas departures to the southwest were more likely when skies were clear. This difference suggests that availability of celestial navigational cues may have played a role in determining whether individuals departed to the northwest and around the Gulf of Maine rather than to the southwest and across the barrier. With regard to other weather variables, most departures occurred in suitable conditions but a greater proportion of northwest flights occurred in rain and reduced visibility than did southwest flights. Collectively, these results suggest that weather may have had more of an influence on departure decisions of individuals that attempted to cross the barrier directly than individuals that detoured around it. Similarly, Schmaljohann and Naef-Daenzer (2011) found that Northern Wheatears *Oenanthe oenanthe* were more likely to orientate towards the North Sea in suitable weather and towards the nearby mainland when weather was poor. In a separate study of the

same species, Dierschke and Delingat (2001) found that the relative importance of weather at departure was greater for members of the subspecies that undertake a long-distance, trans-oceanic flight to their breeding grounds than for members of the Scandinavian subspecies that undertake a much shorter barrier crossing. However, because favourable winds for northwest migration in Nova Scotia are often correlated with deteriorating weather conditions (Richardson 1978a), the fact that in our study more departures to the northwest occurred in poor weather compared with those to the southwest may have been due to these individuals selecting strongly for tailwind assistance.

Although tailwind assistance was the most important weather variable influencing departure decisions of individuals making migratory flights, departure direction did not always coincide with wind direction, and individuals often did not take advantage of nights earlier in stopover when winds were favourable for migration in the opposite direction. Both of these results suggest that wind was not the only factor (or perhaps not even the primary factor) determining whether individuals attempted to cross the Gulf of Maine directly or detoured around it. Although we found only weak evidence for an effect of initial fat score on migratory departure probability, the amount of fuel individuals were carrying at the time of departure could have played an important role in their decision to cross or detour around the Gulf of Maine (Sandberg & Moore 1996, Deutschlander & Muheim 2009, Schmaljohann & Naef-Daenzer 2011, Smolinsky *et al.* 2013). We could not test this hypothesis because most migratory departures we observed occurred after individuals had spent multiple days in southwest Nova Scotia and our only measure of fuel load came from when they were first captured. Given that the energetic state of migrants during stopover is dynamic, correlating their condition at capture to decisions they make at the time of departure could be misleading. Future work involving more dynamic measures of migrant condition and refuelling performance (e.g. plasma metabolites; Jenni-Eiermann & Jenni 1994, Guglielmo *et al.* 2005, Covino & Holberton 2011) will help to resolve this issue.

In addition to the many individuals that orientated away from and detoured around the Gulf of Maine, 46% of individuals we detected leaving their initial stopover site made one or more

stopover flights prior to continuing migration, with 48% (20/42) of these landscape-scale flights occurring within 24 h of initial capture. In a mark-recapture analysis, Calvert *et al.* (2009) found that the annual proportion of migrants that departed from Bon Portage Island within 24 h of capture ranged from 24% to 96%. Although individuals that depart from a stopover site on the first available night are often assumed to have continued migrating, the frequency and timing of stopover flights we observed suggests that many 'transients' are actually relocating within the landscape and not continuing migration immediately.

The initial departure directions of individuals that made stopover flights may provide insight into the purpose of these movements. The majority of stopover flights we observed were orientated inland, away from the Gulf of Maine, immediately upon takeoff, and they tended to occur on nights when weather, especially wind, was unfavourable for migration. Both of these results suggest that individuals had already decided to relocate inland prior to takeoff. Such flights may allow migrants to find habitat that provides better conditions for refuelling or predator avoidance while waiting for the next period of favourable weather for migration (Alerstam 1978, Lindström & Alerstam 1986, Åkesson *et al.* 1996, Calvert *et al.* 2009, Woodworth *et al.* 2014). However, we also observed stopover flights that appeared to be the result of a decision made after takeoff. For example, one individual was detected flying past Seal Island, 25 km offshore to the southwest, and then reversing direction and returning to southwest Nova Scotia on the same night. Two other individuals flew past Seal Island and were re-detected in southwest Nova Scotia on a subsequent night. Such flights may have been exploratory flights used to test flight conditions aloft (Richardson 1990, Schmaljohann *et al.* 2011), migratory departures that were aborted in response to external conditions experienced after departure (Richardson 1978a), or internal decisions reflecting uncertain knowledge of the extent of the sea barrier (Bruderer & Liechti 1998). However, whether the three reversing flights we observed were a response to weather is not immediately apparent. Two flights were on the same night when tailwind assistance for southwest migration was strongly negative (-13.93 m/s) 30 min prior to departure but improved to only weakly negative 30 min (-2.96 m/s) and 90 min (-1.04 m/s)

after departure. There was no wind on the night of the third flight and all three flights occurred on nights when there was no precipitation and skies were partly clear.

Overall, this study highlights the importance of studying stopover behaviour and migratory departure decisions at an appropriate (broad) landscape scale, and the value of using similar broad-scale networks of automated tracking systems. Until recently, satellite and GPS transmitters were the only technologies that could provide detailed information on migratory decisions of individual birds, but cost and size limit these to relatively large species of birds and often small sample sizes (e.g. Green *et al.* 2002, Thorup *et al.* 2003, Gill *et al.* 2009). Light-level geolocators provide valuable insight on long-distance movements of smaller birds but are only effective for individuals that can be reliably recaptured at a later time and they lack sufficient precision to study stopover behaviour (e.g. Fudickar *et al.* 2012, Lisovski *et al.* 2012). In contrast, automated networks of radiotelemetry receivers allow the tracking of thousands of individuals at the same time without the need for recapture. Recent development of low-cost receivers has led to deployment of a large network of towers covering significant portions of eastern Canada and the northeastern United States (www.motus-wts.org), and we can thus anticipate an influx of new information on the migratory strategies of small birds in the near future.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. (a–c) Maps showing the migration routes of three individuals around the Gulf of Maine. (d) Photo of a radiotagged, hatch-year Red-eyed Vireo.

Table S1. Summary of candidate time-dependent proportional hazards models relating departure decisions to local weather conditions.