Original Article

The effects of wind and fuel stores on stopover departure behavior across a migratory barrier

Bryant C. Dossman,[a,b] Greg W. Mitchell,[c,d] D. Ryan Norris,[e] Philip D. Taylor,[f]
Christopher G. Guglielmo,[c] Stephen N. Matthews,[a] and Paul G. Rodewald[a,b]
[a]School of the Environment and Natural Resources, Terrestrial Wildlife Ecology Lab, The Ohio State University, 2021 Coffey Rd, Columbus, OH 43210, USA, [b]Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Rd, Ithaca, NY 14850, USA, [c]Department of Biology, Advanced Facility for Avian Research, University of Western Ontario, 1393 Western Rd, London, Ontario N6G 1G9, Canada, [d]Wildlife Research Division, National Wildlife Research Center, Environment Canada, Ottawa, Ontario K1H 0H3, Canada, [e]Department of Integrative Biology, University of Guelph, Summerlee Science Complex, Guelph, Ontario N1G 2W1, Canada, [f]Biology Department, Acadia University, 33 Westwood Ave., Wolfville, Nova Scotia B4P 2N5, Canada

During annual migrations between breeding and nonbreeding grounds, billions of land birds encounter migratory barriers *en route*. Although birds are thought to be more selective (i.e., cross under favorable wind conditions) and spend more time refueling at stopover sites when confronted with these barriers, there is no direct evidence to support these hypotheses. Using 2 automated radio-telemetry arrays at stopover sites situated before (south of) and after (north of) a large ecological barrier (Lake Erie), we tracked departure decisions of American redstarts *Setophaga ruticilla* and yellow-rumped (myrtle) warblers *Setophaga coronata coronata* during spring migration. We found evidence that condition, age, and tailwind assistance were all positively correlated with the likelihood of departure. Interestingly, these patterns did not differ between species, with presumably differing migratory tactics, nor across sites, suggesting that during spring migration, migratory songbirds may follow general rules for departure from stopover sites, despite varying ecological and life-history contexts.

Key words: **automated radio-telemetry, Cox Proportional Hazards model, departure decisions, migration, migratory strategies, songbird.**

INTRODUCTION

Each year billions of songbirds migrate thousands of kilometers between their breeding and wintering grounds. In the spring, early arrival to the breeding areas can help individuals secure high-quality territories and mates, ultimately enhancing reproductive success (Norris et al. 2004; Reudink et al. 2009; McKellar et al. 2013). Therefore, migratory songbirds should be attempting to minimize the amount of time spent migrating (Alerstam et al. 2003; McNamara and Houston 2008). However, given their small body sizes and limited fuel storage capacities, migratory passerines must make punctuated stops (stopovers) *en route* to rest and refuel (Blem 1980; Wikelski et al. 2003).

Given that these stopover events increase the duration of migration, selection is hypothesized to act strongly on stopover behavior in order to minimize stopover duration (Alerstam and Lindström 1990). Stopover duration may be increased or decreased to some degree by a suite of intrinsic (condition, sex, and age) and extrinsic factors (suitable weather conditions, date), including the ecological and geographical context in which the stopover site is situated (Dierschke and Delingat 2001; Erni et al. 2002; Goymann et al. 2010; Matthews and Rodewald 2010a). Therefore, intrinsic and extrinsic factors, through their effect on stopover duration, have the capacity to affect individual fitness by influencing migration rate (Drake et al. 2014).

Address correspondence to B.C. Dossman. E-mail: bd342@cornell.edu.

Migratory barriers are landscape features that impede migratory movements (Alerstam and Lindström 1990). For example, studies using weather surveillance radar demonstrate that land birds tend to accumulate along borders of migratory barriers such as the shorelines of the Great Lakes or Gulf of Mexico, indicating some behavioral reluctance toward crossing these barriers (Diehl et al. 2003; Buler and Moore 2011). Given the real or perceived risks associated with crossing a migratory barrier, birds should adopt behaviors that minimize the risk of crossing by refueling sufficiently and timing their departure with favorable atmospheric conditions to minimize cost of transport and increase potential flight range (Schaub 2004; Liechti 2006; Bayly et al. 2012). Thus, departure behaviors associated with migratory barriers may strongly influence the pace and overall duration of migration (Wikelski et al. 2003; Schaub et al. 2008). However, in order to quantify the direct influence that barriers may have on modifying behaviors, simultaneous comparisons of departure decisions prior to and following crossing of a migratory barrier are needed.

In this paper, we utilize 2 automated radio-telemetry arrays at stopover sites located on the south and north shorelines of Lake Erie to evaluate the influence of a migratory barrier (Lake Erie) on spring departure timing of 2 spring migrant passerines, the American redstart *Setophaga ruticilla* (long-distance migrant) and the yellow-rumped warbler *Setophaga coronata coronata* (short-distance migrant; hereafter "myrtle warbler"). First, prior to crossing a migratory barrier, we hypothesized that birds should spend more time on stopover to accumulate greater fuel stores in order to minimize the risks of running out of fuel while crossing the barrier (Alerstam and Lindström 1990; Yong and Moore 1993; Weber et al. 1998). Second, we hypothesized that the daily probability of departure should be more strongly associated with wind assistance prior to crossing Lake Erie than after crossing, again because the risk of running out of fuel is lower post-crossing, but also because the penalty of drifting off course is also reduced post-crossing. Third, we hypothesized that body condition upon arrival should positively related to the daily probability of departure prior to crossing a migratory barrier but

this relationship should be weaker post-crossing because the penalty for running out of fuel would be reduced (Weber et al. 1998; Schaub et al. 2008). Fourth, we hypothesized that redstarts should exhibit riskier departure decisions than myrtle warblers given their relatively longer migration, later date of passage (warmer temperatures and advanced phenology), and likely more temporally constrained migratory schedule (Ellegren 1993; Smith and Moore 2005). Following this hypothesis, we predicted that redstarts would be more likely to leave during unfavorable tailwind conditions and with lower fat loads compared myrtle warblers.

Unrelated to the location of the stopover site, we also examined hypotheses associated with sex and age. We expected that these factors would play important roles in influencing departure decision rules, with males exhibiting shorter stopover duration than females because male songbirds often display protandry and are under greater selection than females to arrive early at breeding grounds (Morbey et al. 2012). Similarly, given that experience should influence migratory efficiency, for example, older birds might competitively exclude younger birds from high-quality habitats and sites during stopover (Woodrey 2000; Moore et al. 2003; Seewagen et al. 2013), after-second-year (ASY) birds should have shorter stopovers than second-year (SY) birds.

METHODS

Study sites

The pre-crossing study site (hereafter "Ohio") was situated on the south shore of the western Lake Erie basin in northern Ohio, primarily within the Ottawa National Wildlife Refuge, 41°36′56″N, −83°12′58″W, Ottawa County, Ohio. The post-crossing study site (hereafter "Long Point") was located on the north shore of Lake Erie at the Long Point Bird Observatory, 42°34′N, −80°13′W, Ontario, Canada (Figure 1). Both study sites are situated on coastal wetlands and the broader landscape around each site is characterized by a matrix of wetlands and deciduous forest patches, although part of the sand spit at Long Point also has a substantial cottage
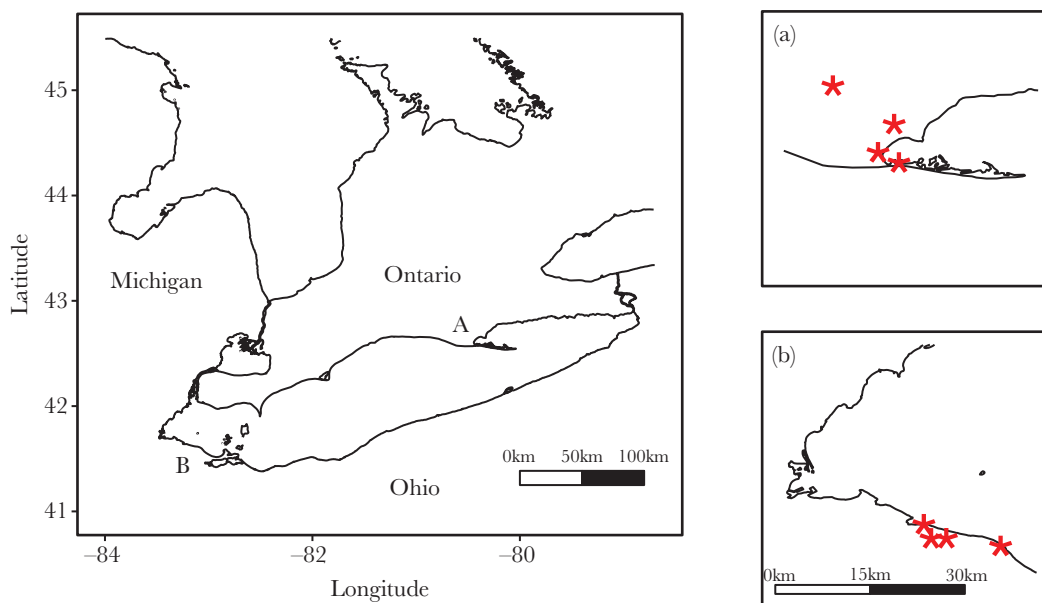

Figure 1
Location of 2 automated radio-telemetry arrays located across Lake Erie. One study site was located north of Lake Erie (post-crossing) at the Long Point Bird Observatory in Long Point, Ontario (a). The second study site was located south of Lake Erie (pre-crossing) at Ottawa National Wildlife Refuge in Oak Harbor, Ohio (b). Red asterisks in figure insets represent individual radio-towers that make up each study site array.

development. Both study sites are also considered important refuges for migratory passerines given the suitable landscape and their proximity to the lakeshore (Ewert et al. 2006; Johnson 2013). Given that emergent aquatic insects are an important component of the diet of avian migrants (MacDade et al. 2011) and that emergent insect abundance is primarily driven by abiotic factors such as weather and limnological characteristics (Merritt and Cummins 1996), we assumed that food availability was similar between sites. This assumption is corroborated by independent studies conducted at Ottawa National Wildlife Refuge (MacDade et al. 2011) and Long Point Bird Observatory (Guglielmo et al. 2005) that show that plasma triglyceride levels (a proxy for refueling rate and therefore habitat quality; Guglielmo et al. 2002) were similar between sites for a closely related species, the Magnolia Warbler *Setophaga magnolia*.

Sampling design

Myrtle warblers, a short-distance (Nearctic) migrant and American redstarts, a long-distance (Nearctic-Neotropical) migrant, were captured at both study sites using nine 2.6- × 12-m mist nets (30-mm mesh) between 29 April and the 21 May, 2012. A total of 51 individuals were radio-tagged, including 29 in Ohio (14 myrtle warblers and 15 redstarts) and 22 at Long Point (10 myrtle warblers and 12 redstarts). Tagged myrtle warblers included 3 ASY females, 4 ASY males, 10 SY females, and 6 SY males; redstarts included 8 ASY females, 9 ASY males, 3 SY females, and 7 SY males. Mist nets were checked and captured birds were removed every 20–30 min and held in cloth bags before processing. Netting began at sunrise and continued for 6–8 h each day (weather permitting). Birds were banded with US Geological Survey aluminum leg bands. Morphometric data collected included tarsus length (±0.01 mm), wing chord (±0.5 mm), body mass (±0.01 g), and fat score (0–7; Kaiser 1993). Age and sex were determined using plumage characteristics described in Pyle et al. (1997). We assigned fat scores to classify birds into 2 categories of energetic condition, either lean (fat score ≤ 3) or fat (fat score > 3) (Goymann et al. 2010).

Each bird was tagged with a 0.29-g coded radio-transmitters (Lotek Wireless, Newmarket, Ontario, Canada; NTBQ-1), using a leg-loop harness (Rappole and Tipton 1991). We limited handling time of focal individuals to less than 5 min to minimize stress. Each transmitter was programmed to the same frequency (166.380 mHz; pulse rate: 7.2–7.8 s) and individually coded with a pulse signature. Coded tags are robust to signal bounce and allow digital receivers to continuously monitor up to 512 tags on a single frequency. All birds were released at site of capture. Ohio State University IACUC (#2012A00000043) and the University of Western Ontario Animal Use Subcommittee (#2010–020) approved of all methods conducted in this study.

Automated radio-tracking and telemetry analysis

A digital automated radio-telemetry array was used to passively monitor movement activity of focal birds that were captured, radio-tagged, and released at the study sites. This system consisted of 4 towers per site spaced at intervals that ranged from 3 to 20 km. Each tower was fixed with two to four 5-element and/or 9-element Yagi antennas connected to a SRX 600 (Lotek Wireless) automated receiver with an 8-port switchbox (ASP-8) for sequentially monitoring multiple antennas or a SRX DL (Lotek Wireless) receiver connected to 2 antennas. The 5-element antenna (AF Antronics Inc., Urbana, IL; H-plane 61°, isotropic gain 10.1 dBi, front-to-back

ratio > 20 dB) had broader and shorter sensitivity than the 9-element antenna (Laird Tech., Urbana, IL; H-plane 45°, isotropic gain 11.1 dBi, front-to-back ratio 20 dB), which had narrower and longer sensitivity. Antennas were located approximately 10 m above ground on all towers. The detection range of each tower was approximately 15 km but up to 25 km under ideal conditions with clear line of sight between the radio-tag and antennas (Taylor et al. 2011; Mitchell et al. 2015).

Tag identification, date and time, antenna number, and signal strength (an index from ~20 to 255) were recorded for each received signal. Data collected by the automated telemetry system allowed for continuous and passive monitoring of all deployed radio-tags and given the high temporal resolution of the automated array, we were able to accurately assess departure on all tagged individuals. With this approach, we were able to document the departure timing for all individuals. The timing of departure from stopover was estimated as the time at which signal strength peaked (±8 s), before a rapid decline in signal strength and eventual loss of a detectable signal (c.f. Taylor et al. 2011; Mitchell et al. 2015).

For many migratory passerines, flights from stopover sites may not always represent true migratory flights (i.e., continuation of long-distance migration) but instead represent relocations to new stopover sites within the broader landscape (Mills et al. 2011; Taylor et al. 2011; Sjöberg et al. 2015). These relocation movements tend to occur later in the evening as opposed to migratory departure flights and also occur shortly after arriving at the stopover site (e.g., <48 h after arrival; Mills et al. 2011; Taylor et al. 2011; Sjöberg et al. 2015). Therefore, we included evening departure time in our models to control for potential differences in stopover duration between migratory flights and landscape relocations. Therefore, to account for this, we used evening departure time as a proxy for migratory departure versus landscape relocation type movements given the results of Taylor et al. (2011), where 69% of all migratory movements (*n* = 310 flights) were determined to be "true" departures and according to Mills et al. (2011) occurred within 3 h of sunset contrary to the stopover flights that accord more sporadically and later in the evening. This method accounts for the confounding nature of these movements on our analysis of departure probability but does not directly estimate these relocation type movements.

Meteorological observations

Meteorological data were collected from 2 neighboring, quality assured (NOAA) weather stations: John C. Munro Hamilton International Airport (Hamilton, Ontario, Canada; http://climate.weather.gc.ca/; 75 km NE of Long Point) and the Toledo Express Airport (Toledo, OH; http://cdo.ncdc.noaa.gov; 48 km W of Ottawa National Wildlife Refuge). Hourly weather observations wind speed (m/s) and wind direction (10-degree bins) were obtained for the spring study period (April–June, 2012). Tailwind components were calculated using a simple vector addition model (Safi et al. 2013). This measure simultaneously accounted for wind speed and direction. Tailwind components were derived using the formula $V_w * \cos(\beta)$, where V_w is wind speed and β is the difference between track and wind directions. Tailwind components varied from negative to positive with increasingly negative components representing stronger headwinds and vice versa. We found no evidence that the tailwind conditions varied across sites ($t = 1.472$, $df = 270$, $P = 0.142$), suggesting that birds at both sites were exposed to similar wind conditions.

Wind conditions at time of migratory departure were taken as the average for the hour preceding departure of each radio-tagged bird.

Weather conditions on days when a bird did not depart were calculated similarly but "departure time" was taken as the median-departure hour of all focal birds (21:00) (Matthews and Rodewald 2010b). This allowed us to estimate differences in weather conditions between days on which birds departed and versus days when birds did not depart.

Statistical design

We modeled stopover duration under a survival-time analysis framework to assess the factors that influenced stopover duration and the probability of departure. Extended Cox Proportional Hazards (CPH) models (semiparametric survival models) allowed us to explicitly determine how the "risk" of departure varied with time-independent and time-dependent endogenous and exogenous factors (see Therneau and Grambsch 2000 for more details on CPH models). The advantages associated with working within a CPH framework is that it permits inclusion of time-dependent variables such as weather. Higher "risk" can be translated in this context to higher probability of departure and shorter stopover durations because the "risk" of a bird departing a stopover site is high. Similarly, lower "risk" of departure can be associated with lower probability of departure and longer stopover durations. As such, "risk" of departure will be referred hereafter as probability of departure.

Given our hypotheses, we developed 5 *a priori* models based on known theoretical concepts and experimental evidence describing the factors that influence stopover duration and the probability of departure. We ranked competing models associated with our hypotheses using an information theoretic approach (Anderson et al. 2000; Burnham et al. 2010). Our top models were assessed by comparing corrected Akaike information criterion (AIC$_c$; AIC adjusted for small sample sizes) values and discriminating against those models with >2 units from the top-ranked model. We included species, sex, fat status (lean or fat), age, and evening departure time (hours from sunset) as endogenous predictors in every model except the Null. Departure time was included to control for the possibility of landscape scale relocations that might obscure results and has been shown to relate positively evening departure time (Mills et al. 2011). In order to assess the influence of migratory barriers and available wind conditions on the probability of departure, we also included site (Ohio or Long Point) and tailwind component as exogenous predictors in all the models except for the Null model. Thus, the "Additive Model" included Species + Sex + Age + Fat Status + Julian Date + Departure Time + Site + Tailwind. The second model we fit was the "Site Interaction" model (Species + Sex + Age + Julian Date + Departure Time + Fat Status*Site + Tailwind*Site), which included all factors within the additive model, but assumed that these patterns varied according to site. Similarly, the third model we fit was a "Species Interaction Model" (Species + Sex + Age + Julian Date + Departure Time + Fat Status*Species + Tailwind*Species), where we included a species interaction term and assumed that these patterns varied by species. The fourth model we fit was the "Full Model" (Species + Sex + Age + Julian Date + Departure Time + Fat Status*Species*Site + Tailwind*Species*Site), which included fat status and tailwind along with the aforementioned 2-way and 3-way interactions that included both site and species. The fifth model we fit was the null. The importance of model covariates in the top-ranked model was assessed with 95% confidence intervals (CIs).

RESULTS

The "Additive Model" was the top-ranked model describing departure behavior (Table 1). However, the species and site interaction

models were reasonably close (3.02 and 3.80 ΔAIC$_c$ units, respectively) to the top model considering small sample sizes (Table 1). Minimum stopover duration for redstarts averaged 3.99 ± 2.24 days (regardless of site), substantially shorter than for myrtle warblers (6.96 ± 2.98 days). However, we found no difference in the daily probability of departure between redstarts and myrtle warblers (Figure 2b; hazard ratio [HR$_{Species}$] = 3.1, 95% CI = 0.5, 21.4) when considering Julian date (HR$_{Julian Date}$ = 1.07, 95% CI = 0.93, 1.24). For both species, age was also strongly associated to daily departure probability with ASY birds exhibiting a 2.4 times greater daily probability of departure than SY birds (Figure 2c; HR$_{Age}$= 2.4, 95% CI = 1.1, 5.1). Fat status was positively associated with the daily probability of departure, with fat birds being 6.4 times more likely to depart than lean birds (Figure 2d; HR$_{Fat Status}$ = HR: 6.4, 95% CI = 2.2, 18.5). Tailwind component was positively related to daily probability of departure (Figure 3; HR$_{Tailwind}$ = 1.03, 95% CI = 1.00, 1.06). The daily probability of departure increased with hours since sunset (HR$_{Departure Time}$ = 1.4, 95% CI = 1.1, 1.8).

Table 1

AIC model selection analysis of stopover departure behavior of 2 migratory songbirds (American redstart and yellow-rumped (myrtle) warbler) at 2 sites across a migratory barrier

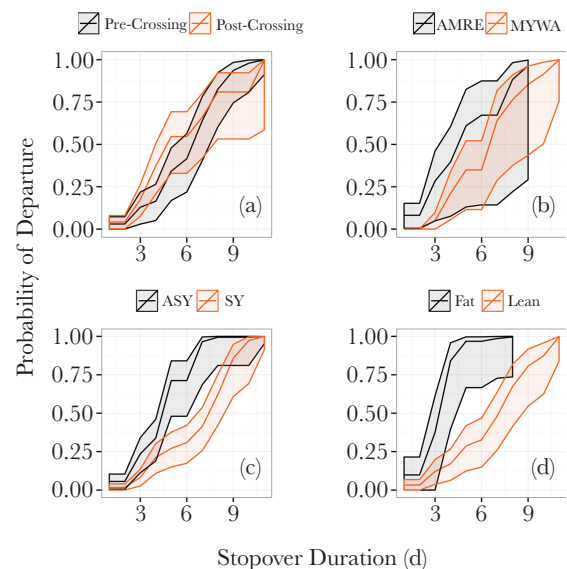| Model	AIC$_c$	ΔAIC	Log likelihood	Wi	K
Additive model	264.77	0.00	−124.10	0.73	8
Site interaction model	267.80	3.02	−123.46	0.16	10
Species interaction model	268.57	3.80	−123.85	0.11	10
Full model	277.48	12.70	−122.77	0.00	15
Null model	304.82	40.04	−152.41	0.00	0

Figure 2

Probability of departure between (a) pre-crossing (black, Ohio) and post-crossing (orange, Long Point) a migratory barrier, (b) between species, American redstart (AMRE, black) and yellow-rumped (myrtle) warbler (MYWA, orange), (c) between age classes, ASY (black) and SY (orange), and (d) between fat birds (black) and lean birds (orange). An extended Cox Proportional Hazards model that included site, species, sex, age, fat score, Julian date, and tailwind component significantly predicted the likelihood of departure (Wald test = 40.75, df = 8, $P \ll 0.001$, n_{Events} = 50). Shaded regions represent 95% log-log confidence bands for each respective group.
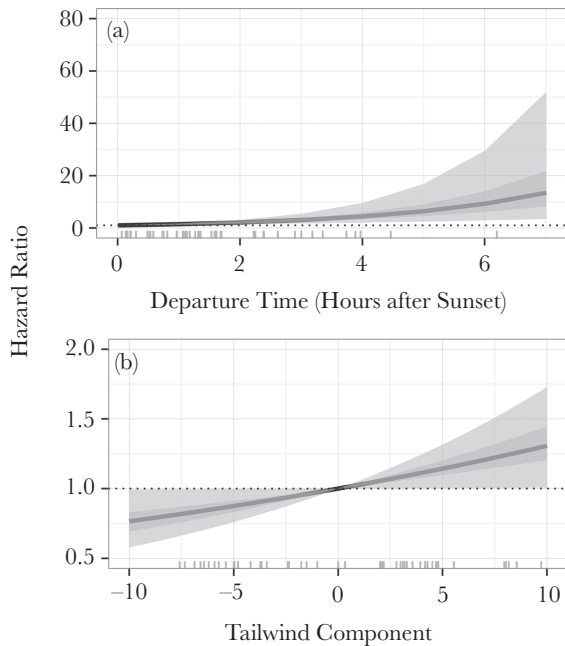
Figure 3
The effect of departure time (top) and tailwind component (bottom) on the HR for departure simulated across varying tailwind conditions. The daily probability of departure increased with increasing tailwind component 1 h prior to departure ($HR_{Tailwind}$ = 1.03, 95% CI = 1.00, 1.06). It was also positively related to nighttime departure timing (hours after sunset) with bird departing later exhibiting shorter stopover durations ($HR_{Departure Time}$ = 1.4, 95% CI = 1.1, 1.8). Dark line represents the mean and dark grey shaded region represent 50% CI and light grey represents 95% CI.

After controlling for fat status and availability of suitable tailwinds for migration, we found no difference in daily departure probability between sites (Figure 2a; HR_{Site} = 1.7, 95% CI = 0.88, 3.38). Further, we found no evidence for interactions between fat status or wind conditions with either species or sites (Table 1).

DISCUSSION

Stopover departure decisions are the key factors that determine overall pace of migration (Jenni and Schaub 2003; Wikelski et al. 2003; Schaub et al. 2008). Risk-averse decisions, such as delaying departure to acquire larger fuel stores or waiting for favorable tail winds at the edge of an ecological barrier, may have a large effect on overall migration rate (Alerstam and Lindström 1990; Alerstam 2001; Jenni and Schaub 2003). This is particularly important during spring migration, when early arrival at the breeding grounds often results in higher reproductive success (Norris et al. 2004; Smith and Moore 2005; Reudink et al. 2009; Cooper et al. 2011).

Given the actual (or perceived) risks associated with crossing Lake Erie, we expected that birds at the Ohio stopover site would adopt more risk-averse migration tactics relative to those occupying Long Point. Through the use of a novel automated telemetry array, we determined which factors are most influential in shaping departure decisions in the context of a migratory barrier, and the extent to which these relationships are structured by species-specific differences in migratory life histories. Contrary to our expectations, we did not find any evidence for differences in departure tailwind conditions and fat loads attributed to site (pre-crossing vs. post-crossing)

nor species (long-distance vs. short-distance migrants). This may have been because the extent of the barrier was relatively small (width of direct crossing from Ohio site = 50–60 km) and may not serve as an appreciable barrier to migration. Although radar studies in the Great Lakes have shown that birds accumulate along shorelines (Diehl et al. 2003), suggesting that migrants are hesitant to cross Lake Erie. However, given the relatively small barrier, penalties associated with suboptimal departure decisions are likely not as severe or are easily mitigated. Alternative routes around Lake Erie may be another reason why no differences were found in stopover behavior pre- and post-crossing. If birds circumnavigate the Lake to avoid direct open water crossing, then they may be better able to accommodate varying environmental conditions and optimize departure behavior in light of alternative route choices (Sjöberg et al. 2015). Therefore, we hypothesize that departure decisions could be contingent on the severity of the barrier (i.e., length/width of crossing) with substantially large barriers imposing greater selection pressure on departure decisions because alternative routes are less feasible (Alerstam 2001). Further study comparing stopover behavior along barriers of varying sizes is needed to test this hypothesis.

Our results contribute to growing evidence that fuel loads and wind conditions are the 2 most important factors determining departure timing from stopover sites (Erni et al. 2005; Liechti 2006; Goymann et al. 2010; Kemp et al. 2010; Safi et al. 2013; Sjöberg et al. 2015) yet we found no evidence of these relationships to vary pre- and post-crossing of Lake Erie as hypothesized. We found that birds arriving with larger fuel loads had shorter stopover durations. This is likely because fat is the primary fuel used to power migratory flight in passerines but also because a large amount of fat is catabolized for thermoregulation during stopover when nighttime temperatures are low (Jenni and Jenni-Eiermann 1998; Jenni and Schaub 2003; Wikelski et al. 2003; McWilliams et al. 2004). We found that birds were more likely to depart on days with tailwinds, which would result in an overall energy savings provided by the wind support (Liechti 2006; Bowlin and Wikelski 2008; Mitchell et al. 2015; Sjöberg et al. 2015) and less compensation for potential wind drift (Sjöberg et al. 2015). These energy savings ultimately have profound implications for the extent and speed of migration following departure (Schmaljohann et al. 2013; Drake et al. 2014; Sjöberg et al. 2015), thereby facilitating optimal arrival timing on the breeding grounds (Drent et al. 2003).

Of the endogenous predictor variables, we found that age significantly influenced daily probability of departure, with ASY birds exhibiting greater likelihood of departure on a given day than SY birds. Experience has been implicated in influencing the speed of fuel deposition (Alerstam and Lindström 1990; Heise and Moore 2003); however, Seewagen et al. (2013) demonstrated, using plasma metabolites, that refueling efficiency did not differ between age classes in migratory passerines during fall. If age does not account for differences in refueling efficiency and therefore stopover duration, then another potential driver of differences in stopover duration between age classes could be owing to navigational proficiency (Mitchell et al. 2015). Adult birds with prior migration experience may have an understanding of regional geography (e.g., stopover areas, barriers) along the migratory route. However, SY birds undertaking their first spring migration are not likely aware of regional opportunities for stopover and therefore may hedge stopover durations to facilitate uncertain future stopover opportunities. Therefore, differences in stopover duration in relation to age may be

because navigational experience allows adults to modulate stopover duration with the future expectations of available stopover sites.

Surprisingly, males exhibited the same daily probability of departure as females. Although departure probability might be expected to differ between sexes given selection for early arrival of males, we argue that selection should favor differences in migratory timing and not necessarily stopover duration (e.g., departure probability). Given the risks associated with shortening stopover duration (e.g., inadequate refueling, suboptimal departure conditions), males may achieve flexibility in arrival timing by shifting their migratory phenology earlier than females (Maggini and Bairlein 2012; Mitchell et al. 2012a,b; Mitchell et al. 2015), which has been shown in these species and many migratory passerines in general. This would enable males to maintain stopover durations similar to those of females yet promote optimal timing of arrival on the breeding grounds through advancement in migratory phenology. On the other hand, Seewagen et al. (2013) found evidence that males refuel more quickly than females under some conditions. More information is needed to understand the mechanisms underlying protandry, and whether these mechanisms vary under different environmental conditions (Morbey et al. 2012).

We sought to determine how species with different migratory strategies differed in the factors that influence departure decisions with respect to ecological context. Migratory distance should play a role in influencing migration speed (Alerstam and Lindström 1990; Weber et al. 1998; Alerstam 2001; Erni et al. 2002; Hedenström 2008) because longer migration imposes greater temporal constraints on the annual routines of migrants (McNamara and Houston 2008; La Sorte et al. 2013). Specifically, we expected that myrtle warblers (a short-distance migrant) should exhibit different departure decisions with respect to daily probability of departure as well as the wind conditions individuals choose to depart under, relative to American redstarts (a long-distance migrant). Contrary to this, we found no difference in the departure behavior between species. Perhaps differences in migratory distance between each of our study species are not great enough to impart different selective forces on departure decisions. Therefore, differences in departure behavior might only be expected between very different species (with very different migratory schedules and migratory distances) and in general many migratory birds should follow generalist type departure decision rules that are further refined by exogenous and endogenous cues (Erni et al. 2002; Hedenström 2008). Alternatively, differences in migratory speed may still exist but may do so in different portions of migration because the constraints on migratory speed likely differ across the migratory period. For example, La Sorte et al. (2013), using *ebird* citizen science data, demonstrated that overall migration distance correlated positively with migratory speed and population-level rates of migration decelerated towards the breeding grounds indicating that migratory speeds tend to slow over the course of migration. However, given the difficulties in tracking small migratory birds across migration, this pattern has yet to be demonstrated at the individual level. However, future technological innovations in tracking technology and rapid expansion of the MOTUS (motus-wts.org) automated radio-telemetry array will enable researchers to track small-bodied migrants test whether the constraints on migration change throughout migratory period.

We found a positive relationship between departure probability and departure timing (hours since sunset). This suggests that birds leaving later in the evening were at the capture site for shorter periods of time. Given that they likely did not have time to adequately fuel, we interpret these shorter stopover durations as landscape relocations. Mills et al. (2011) and Taylor et al. (2011) demonstrated

similar patterns where departures later in the evening were not actually migratory movements but were relocations within the broader landscape. They hypothesized that these relocations likely facilitated the sampling of new habitat patches within the broader stopover landscape and are more likely to occur at night because they can explore novel environments safely from predators. Further, given the importance of refueling during migration, daytime hours are more optimally spent foraging than exploring new habitats (Mills et al. 2011). Here, we utilize departure timing (hours after sunset) as an approach to account for these movements and their confounding nature but must emphasize that this approach does not directly estimate them. To unequivocally determine whether a movement is a "true" migratory one, rather than stopover relocation would require substantial hand tracking outside of the study area (40^2 km) in the surrounding landscape, or the use of an expansive automated telemetry array like MOTUS (motus-wts.org) to track individuals throughout migration thereby accurately defining whether an individual has continued its migration or simply relocating to another stopover site. Future studies, utilizing a combination of these approaches, should seek to evaluate what drives the prevalence of these stopover relocations and its implications on true stopover duration. Ultimately, had we not controlled for hour of departure, we may have underestimated departure probability and thus stopover duration in our study biasing our interpretation of the drivers of stopover departure (Taylor et al. 2011).

In summary, our results provide novel insights into some of the theoretical underpinnings of optimal avian migration in response to ecological context and migratory life history. This is the first study to directly analyze the effect that a migratory barrier has on the departure decisions with comparisons made pre- and post-crossing and builds upon previous studies that have investigated the migratory behavior around ecological barriers (Alerstam 2001; Buler and Moore 2011; Sjöberg et al. 2015). Although previous radar studies have purported that Lake Erie serves as a barrier to migration, we found that this is not the case with respect to stopover departure decisions relating to stopover duration and timing, fuel loads, and selection of supporting winds. Additionally, we further corroborate the role that wind and fuel play in determining stopover departure and suggest that conservation approaches should prioritize creating or maintaining high-quality stopover habitat, which would allow migrants to refuel quickly and efficiently.

FUNDING

and Use Committee and the University of Western Ontario's Institute for Animal Care.

Conflict of Interest: The authors declare that they have no conflicts of interest.

Handling editor: David Stephens

REFERENCES

Alerstam T. 2001. Detours in bird migration. J Theor Biol. 209:319–331.

Alerstam T, Hedenström A, Åkesson S. 2003. Long-distance migration: evolution and determinants. Oikos. 103:247–260.

Alerstam T, Lindström Å. 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E, editor. Bird migration. Berlin (Germany): Springer. p. 331–351.

Anderson DR, Burnham KP, Thompson WL. 2000. Null hypothesis testing: problems, prevalence, and an alternative. J Wildl Manage. 64:912–923.

Bayly NJ, Atkinson PW, Rumsey SJR. 2012. Fueling for the Sahara crossing: variation in site use and the onset and rate of spring mass gain by 38 Palearctic migrants in the western Sahel. J Ornithol. 153:931–945.

Blem C. 1980. The energetics of migration. *In:* Gauthreaux SA, *editor.* Animal migration, orientation and navigation. Orlando (FL): Academic Press. *p.* 175–224.

Bowlin MS, Wikelski M. 2008. Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. PLoS One. 3(5):e2154.

Buler JJ, Moore FR. 2011. Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. J Ornithol. 152:101–112.

Burnham KP, Anderson DR, Huyvaert KP. 2010. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol. 65:23–35.

Cooper NW, Murphy MT, Redmond LJ, Dolan AC. 2011. Reproductive correlates of spring arrival date in the Eastern Kingbird *Tyrannus tyrannus*. J Ornithol. 152:143–152.

Diehl RH, Larkin RP, Black JE, Moore FR. 2003. Radar observations of bird migration over the Great Lakes. Auk. 120:278–290.

Dierschke V, Delingat J. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behav Ecol Sociobiol. 50:535–545.

Drake A, Rock CA, Quinlan SP, Martin M, Green DJ. 2014. Wind speed during migration influences the survival, timing of breeding, and productivity of a neotropical migrant, *Setophaga petechia*. PLoS ONE. 9(5):e97152.

Drent R, Both C, Green M, Madsen J, Piersma T. 2003. Pay-offs and penalties of competing migratory schedules. Oikos. 103:274–292.

Ellegren H. 1993. Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. Ornis Scand. 24:220–228.

Erni B, Liechti F, Bruderer B. 2002. Stopover strategies in passerine bird migration: a simulation study. J Theor Biol. 219:479–493.

Erni B, Liechti F, Bruderer B. 2005. The role of wind in passerine autumn migration between Europe and Africa. Behav Ecol. 16:732–740.

Ewert DN, Soulliere GJ, Macleod RD, Shieldcastle MC, Rodewald PG, Fujimura E, Shieldcastle J, Gates RJ. 2006. Migratory bird stopover site attributes in the western Lake Erie basin. Ann Arbor. 1001:48103.

Goymann W, Spina F, Ferri A, Fusani L. 2010. Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. Biol Lett. 6:478–481.

Guglielmo CG, Cerasale DJ, Eldermire C. 2005. A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiol Biochem Zool. 78:116–125.

Guglielmo CG, O'Hara PD, Williams TD. 2002. Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living western sandpipers (*Calidris mauri*). Auk. 119:437–445.

Hedenström A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Phil Trans Roy Soc B Biol Sci. 363(1490):287–299.

Heise CD, Moore FR. 2003. Age-related differences in foraging efficiency, molt, and fat deposition of Gray Catbirds prior to autumn migration. Condor. 105:496–504.

Jenni L, Jenni-Eiermann S. 1998. Fuel supply and metabolic constraints in migrating birds. J Avian Biol. 29:521–528.

Jenni L, Schaub M. 2003. Behavioural and physiological reactions to environmental variation in bird migration: a review. In: Berthold P, Gwinner E, Sonnenschein E, editors. Avian migration. Berlin (Germany): Springer. p. 155–171.

Johnson PL. 2013. Migratory stopover of songbirds in the Western Lake Erie Basin [thesis]. [Columbus (OH)]: The Ohio State University.

Kaiser A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. J Field Ornithol. 64:246–255.

Kemp MU, Shamoun Baranes J, Van Gasteren H, Bouten W, Van Loon EE. 2010. Can wind help explain seasonal differences in avian migration speed? J Avian Biol. 41:672–677.

La Sorte FA, Fink D, Hochachka WM, DeLong JP, Kelling S. 2013. Population-level scaling of avian migration speed with body size and migration distance for powered fliers. Ecology. 94:1839–1847.

Liechti F. 2006. Birds: blowin' by the wind? J Ornithol. 147:202–211.

MacDade LS, Rodewald PG, Hatch KA. 2011. Contribution of emergent aquatic insects to refueling in spring migrant songbirds. Auk. 128:127–137.

Maggini I, Bairlein F. 2012. Innate sex differences in the timing of spring migration in a songbird. PLoS ONE. 7(2):e31271.

Matthews SN, Rodewald PG. 2010a. Movement behaviour of a forest songbird in an urbanized landscape: the relative importance of patch-level effects and body condition during migratory stopover. Landscape Ecol. 25:955–965.

Matthews SN, Rodewald PG. 2010b. Urban forest patches and stopover duration of migratory Swainson's thrushes. Condor. 112:96–104.

McKellar AE, Marra PP, Ratcliffe LM. 2013. Starting over: experimental effects of breeding delay on reproductive success in early-arriving male American redstarts. J Avian Biol. 44:495–503.

McNamara JM, Houston AI. 2008. Optimal annual routines: behaviour in the context of physiology and ecology. Phil Trans Roy Soc B Biol Sci. 363(1490):301–319.

McWilliams SR, Guglielmo C, Pierce B, Klaassen M. 2004. Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. J Avian Biol. 35:377–393.

Merritt RW, Cummins KW. 1996. An introduction to the aquatic insects of North America. Chicago (IL): Kendall Hunt.

Mills AM, Thurber BG, Mackenzie SA, Taylor PD. 2011. Passerines use nocturnal flights for landscape-scale movements during migration stopover. Condor. 113:597–607.

Mitchell GW, Newman AE, Wikelski M, Ryan Norris D. 2012a. Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. J Anim Ecol. 81:1024–1033.

Mitchell GW, Wheelwright NT, Guglielmo CG, Norris DR. 2012b. Short- and long-term costs of reproduction in a migratory songbird. Ibis. 154:325–337.

Mitchell GW, Woodworth BK, Taylor PD, Norris DR. 2015. Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Mov Ecol. 3(1):19.

Moore FR, Mabey S, Woodrey M. 2003. Priority access to food in migratory birds: age, sex, and motivational asymmetries. In: Berthold P, Gwinner E, Sonnenschein E, editors. Avian migration. Berlin (Germany): Springer. p. 281–292.

Morbey YE, Coppack T, Pulido F. 2012. Adaptive hypotheses for protandry in arrival to breeding areas: a review of models and empirical tests. J Ornithol. 153:207–215.

Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc Roy Soc Lond B Biol Sci. 271:59–64.

Pyle P, Howell SN, DeSante DF, Yunick DF, Gustafson M. 1997. Identification guide to North American birds. Bolinas (CA): Slate Creek Press.

Rappole JH, Tipton AR. 1991. New harness design for attachment of radio transmitters to small passerines. J Field Ornithol. 62(3):335–337.

Reudink MW, Marra PP, Kyser TK, Boag PT, Langin KM, Ratcliffe LM. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proc Roy Soc B Biol Sci. 276:1619–1626.

Safi K, Kranstauber B, Weinzierl R, Griffin L, Rees EC, Cabot D, Cruz S, Proaño C, Takekawa JY, Newman SH, et al. 2013. Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. Mov Ecol. 1:4.

Schaub M. 2004. Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. Anim Behav. 67:229–237.

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

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

Seewagen CL, Guglielmo CG, Morbey YE. 2013. Stopover refueling rate underlies protandry and seasonal variation in migration timing of songbirds. Behav Ecol. 24:634–642.

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

Smith RJ, Moore FR. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behav Ecol Sociobiol. 57:231–239.

Taylor PD, Mackenzie SA, Thurber BG, Calvert AM, Mills AM, McGuire LP, Guglielmo CG. 2011. Landscape movements of migratory birds and bats reveal an expanded scale of stopover. PLoS One. 6:e27054.

Therneau TM, Grambsch PM. 2000. Modeling survival data: extending the Cox model. New York: Springer New York.

Weber TP, Ens BJ, Houston AI. 1998. Optimal avian migration: a dynamic model of fuel stores and site use. Evol Ecol. 12:377–401.

Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP, Visser GH. 2003. Avian metabolism: costs of migration in free-flying songbirds. Nature. 423:704.

Woodrey MS. 2000. Age-dependent aspects of stopover biology of passerine migrants. Stud Avian Biol. 20:43–52.

Yong W, Moore FR. 1993. Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico. Condor. 95:934–943.