



## Original Article

# The influence of wind selectivity on migratory behavioral strategies

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Air and water currents affect the timing and energy expenditure of many migratory animals, and therefore selection of favorable currents is important for optimal migratory performance. However, waiting for favorable currents also incurs costs. Here we conduct an optimality analysis to determine how wind selectivity affects 3 migratory currencies: time, energy, and risk. To describe variation in these metrics under varying degrees of selectivity, we constructed an individual-based model to simulate fall migration of passerines across eastern North America, allowing birds to use different thresholds of wind profit as the criterion for daily departure. A gradient of thresholds were tested across a range of realistic wind currents, from initiating flights only on nights when winds were directed in their preferred migratory direction (highly selective), to flying under most wind conditions (low selectivity). Our analysis indicated that relative mortality risk was lowest at intermediate selectivity; energy expended during flight was least for the most selective individuals; and of those that successfully completed migration, time spent on migration was lowest for the least selective birds. We solved for the optimal range of wind selectivity and show that this departure criterion alone can produce a tradeoff between time and energy that has been seen in many other behavioral contexts. While we solved for optima using some conditions specific to eastern North America, we show that variation in wind selectivity at departure can produce migratory behaviors that mimic the classic “time-minimizer” and “energy-minimizer” strategies developed from measurements of wild birds across multiple continents.

**Key words:** birds, individual-based models, migration, optimal migration theory, wind profit, wind selectivity.

## INTRODUCTION

Much of animal behavior can be understood as selection for a preferred outcome among a set of fixed choices. Habitat (Jaenike and Holt 1991), mate (Jennions and Petrie 1997), and prey selection (Pyke et al. 1977) are 3 well-studied cases where individuals and taxa vary both in the absolute value of their preferences and in their willingness to select conditions deviating from this preference (i.e. “selectivity” or “choosiness”). Further, optimal behaviors in these contexts face similar tradeoffs between encountering preferred conditions too infrequently (i.e. high selectivity) and accepting lower quality conditions too readily (i.e. low selectivity). In fact, similar quantitative optimization methods can predict behavioral solutions across contexts as varied as habitat selection, mate choice, foraging behavior, and kin recognition (Reeve 1989; Getty 1995).

The use of optimization approaches to migratory behaviors was pioneered by Pennycuik (1969) and has since been a cornerstone for interpreting flight adaptations and strategies in migrating birds (Alerstam and Lindström 1990). In coining the term “Optimal Migration Theory”, Alerstam and Lindström (1990) aimed to establish relationships between the main behavioral and physiological parameters of migration (resting duration, resting frequency, and flight energy consumption) that minimize the expenditure of total time spent on migration, total energy expended, or mortality risk. Little has been done, however, linking this theory with an understanding of selectivity in preferences for conditions. Here we model the consequences for these 3 currencies as a result of variation in 1 migratory behavior, the degree of selectivity of wind currents, and test for the range of optimal phenotypes that can result from this parameter for passerine songbirds during fall migration along the Atlantic flyway of North America.

Air and water currents can be strong evolutionary selective forces on the movements of migratory animals (Richardson 1990; Srygley and Dudley 2008; Xue et al. 2008; Chapman et al. 2010; Incze et al.

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2010; Alerstam et al. 2011; Kemp et al. 2012; Melià et al. 2013). For instance, currents affect migration speed (Weber and Hedenström 2000; Alerstam et al. 2011), energy expenditure (Liechti 1995), resting (hereafter “stopover”) behavior (Åkesson and Hedenström 2000; McLaren et al. 2012), and migration intensity (Åkesson and Hedenström 2000; Erni et al. 2002; Van Belle et al. 2007; Kemp et al. 2012). Animals that engage in goal-orientated movements, such as migration, can therefore be expected to have evolved behavioral mechanisms for identifying and exploiting favorably directed flows (Chapman et al. 2011). Further, many taxa spend a considerable part of their annual cycle on migration, and it is therefore likely that populations experience significant selection pressures to optimize time, energy, and risk during migration (Alerstam and Lindström 1990; Dingle 1996; Clark and Butler 1999; Weber and Hedenström 2000; Hedenström 2003, 2009; Srygley and Dudley 2008). The ultimate result of these optimization pressures is as a gradient of stable behavioral strategies (Alerstam and Lindström 1990) that use different combinations of the 3 currencies for similar fitness outcomes (Alerstam 1991; Mateos-Rodríguez and Liechti 2011).

The most studied strategy empirically is one that prioritizes minimization of time spent on migration (Dänhardt and Lindström 2001). The advantage of a time-minimizing strategy may be to arrive earlier than competitors to a breeding or wintering site and to decrease the amount of time spent in unknown stopover sites (Weber and Hedenström 2000; Alerstam 2011). Alternatively, a different suite of behaviors can minimize energy spent in flight and on stopover (Liechti 1995; Hedenström and Alerstam 1997). An energy-minimizing strategy has advantages for animals attempting shorter distance migrations that can afford to take shorter movements, stopover more frequently, and carry smaller, more efficient fuel loads (Alerstam 2011). Lastly, an animal’s optimal strategy may be to prioritize risk minimization. Many optimal migration analyses define risk specifically as predation risk (Alerstam 1990; Alerstam and Lindström 1990; Schmaljohann and Dierschke 2005). However, defining risk more broadly as migratory survival (i.e. does a bird complete migration or not) would better reflect classically supported life-history tradeoffs (Stearns 1992; Martin 1995) and capture the suite of correlated behaviors that minimize risk from all mortality factors (e.g. weather, food availability, predation, stopover site selection).

The timing, magnitude, and direction of local currents can change the optimal solution along all 3 migration-strategy axes. For example, the presence of currents flowing in the animals preferred direction can decrease time and energy expended on migration and reduce risk (Åkesson and Hedenström 2000). However, the magnitude and timing of preferred flow has the potential to affect each axes differently. If the flow is relatively light, compared to the speed of the animal, but consistently in the preferred direction, the animal will spend little time waiting for good conditions (low total migration time). These animals would spend similar amounts of energy but less time on migratory movements compared to individuals experiencing less frequent flows of the same strength in the preferred direction. If preferred flows are few and far between, migration risk becomes greater because optimal conditions may not come often enough to complete migration (Weber and Hedenström 2000) and survival risk on stopover sites also becomes greater.

In many migratory taxa, behavioral plasticity in relation to flow conditions, (i.e. current selectivity), may strongly influence the optimality of migratory behaviors (Liechti and Bruderer 1998; Clark and Butler 1999; Jansen et al. 2007; Schmaljohann and Naef-Daenzer 2011; McLaren et al. 2014). Migratory success should be significantly increased for flying and swimming animals that possess

the ability to adapt to flow conditions compared to those who cannot (Kemp et al. 2005; Gaspar et al. 2006; McLaren et al. 2012; Scholtyssek et al. 2014).

For birds in particular, winds have significant influence on timing and energy expenditures, and therefore the selection of favorable winds at departure is critical for optimal migratory performance (Alerstam 1979, 2011; Horton et al. 2016). Wind assistance can increase flight speed by 30% (Bruderer and Liechti 1998). Thus, by responding adaptively to wind patterns, individuals can decrease the time spent flying and save nearly half the amount of energy required for migration (Bruderer and Liechti 1998). Given the transitory nature of winds, it is reasonable to hypothesize that migrants would benefit from altering their departure probability in relation to current conditions (McLaren et al. 2012, 2014). These responses should be dependent upon which migratory behavioral strategy they employ. For instance, to minimize energetic expenditure on migratory flights, a bird should fly only in the most favorable winds. Selectivity, however, restricts departure opportunities, potentially increasing risk associated with stopover and overall time spent on migration (Alerstam 2011; McLaren et al. 2012).

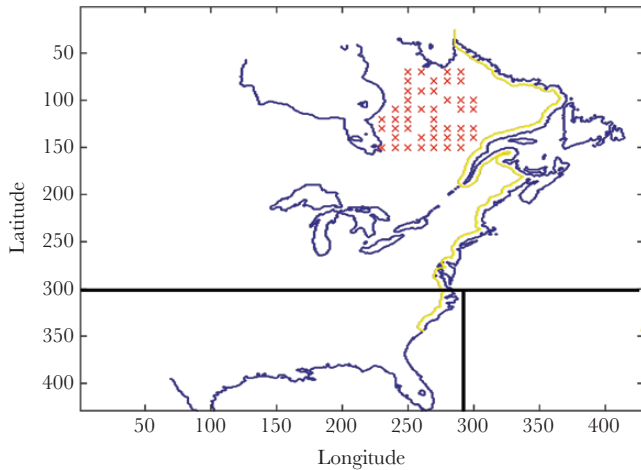
A bird’s decision to depart a stopover site is not simply governed by wind conditions, but rather numerous exogenous and endogenous factors, such as individual refueling rates and fuel loads (Alerstam 2011). A bird’s ability to refuel at stopover is known to influence stopover duration and departure decisions (Alerstam and Hedenström 1998; Moore et al. 2017). The degree to which departure wind selectivity influences the ultimate migratory strategies of wild nocturnal migrants, however, remains unclear. The aim of this study was to evaluate the potential consequences of departure wind selectivity alone on 3 migratory currencies, 1) risk, 2) time, and 3) energy and to determine an optimal range of wind selectivity for first-time (i.e. juvenile) passerine migrants in northeastern North America. We simulated fall migration along the Atlantic flyway using a spatially explicit individual-based model (IBM) and 6 years of wind data. In our analysis, we used a gradient of wind selectivity from initiating flights only when winds were flowing in their preferred direction (highly selective), to flying under most wind conditions (low selectivity). By using a spatially explicit model with realistic wind conditions, our modeling objective was to solve for the range of selectivity that could produce optimal behaviors under a known set of realistic environmental conditions. Optimal behaviors are necessarily environmentally specific, but our more general objective was to test whether it is possible for wind selectivity to explain classic behavioral tradeoffs in time, energy, and risk minimization, which have generally been explained via other biological constraints (e.g. fuel budgets) on multiple continents.

## METHODS

### Model creation

The environment was modeled as a 2-dimensional grid map with a 10 km by 10 km resolution, defined between 57° N to 21° N and 115° W to 42° W (Figure 1). The model grid contained 5 layers: topography, endogenous migratory direction, wind vectors, precipitation, and mean sea-level pressure. The first layer formed the topographical map. Each grid cell of the map was assigned a feature (land, fresh water, or ocean) that altered flight behavior (see below).

The second layer was the endogenous or preferred migratory direction layer. Flight direction for many songbirds, especially juveniles departing on their first migration, is thought to be primarily



**Figure 1**

Map of the eastern United States and Canada illustrating model extent and random starting locations with red X's (i.e. breeding locations of potential migrants). The yellow line indicates a 100 km buffer around the coastline. Endogenous migratory bearing was set to  $135^{\circ}$  for all areas west of the yellow line and  $225^{\circ}$  within the area between the yellow line and the coast, based on empirical observations. Migratory success and the time spent during migration was calculated when birds passed the horizontal black line and were to the west of the vertical black line before December 1<sup>st</sup> without spending longer than 72 h at sea (stringent completion rules) or just when they passed the horizontal black line before December 1<sup>st</sup> (relaxed completion rules).

controlled by an endogenous genetic program that may be modified by experience (Berthold 1990; Pulido 2007; Mitchell et al. 2015). Many North American migration studies have shown that western breeding birds migrate east along the boreal forest (Williams et al. 1977; Dunn et al. 2006; Covino et al. 2015) until reaching the Atlantic coast, after which they alter their heading south following the coastline (Buler and Dawson 2014). Ancestral range expansions post deglaciation (Ruegg and Smith 2002; Ruegg 2007) and/or the prevailing westerly winds in autumn (McCabe et al. 2016) are 2 potential reasons why some birds take this circuitous eastern route during autumn. Migration routes can also follow the morphology of geological features such as coastlines. Coastlines are known to concentrate migrant landbirds (Gauthreaux 1971; Williams et al. 1977; Moore et al. 1995), and this is generally more pronounced juvenile birds that rely on coastlines to navigate during their first migration (Ralph 1971). Hence, in our model we gave birds within grid cells along the coast (100 km buffer around the coastline: Figure 1) an endogenous bearing parallel to the eastern coast at  $225^{\circ}$ . Assuming that our individuals were first-time migrants (i.e. juveniles) allowed us to ignore flight adjustments and navigational means employed by older birds with more experience. Consequently, it also allowed us to examine consequences for variation in wind selectivity during the life stage with the highest mortality and thus the steepest evolutionary selection gradient on migratory behaviors.

We introduced random stochasticity into the birds heading at the start of every flight by randomly choosing a heading from a wrapped normal distribution with an angular deviation of  $30^{\circ}$ , corresponding to a mean vector length,  $r$ , of 0.863 (Erni et al. 2005) and a mean bearing equal to the endogenous direction.

The third, fourth, and fifth layers comprised the weather variables: mean sea-level pressure (MSLP), precipitation, and wind vector data. All weather data is from Climate Forecast System

Reanalysis (CFSR) 3-hourly data from the National Center for Atmospheric Research (NCAR). We used weather data during autumn migration (Aug – Nov) 2008–2013. The CFSR data has a 0.5-degree resolution on a cylindrical equidistant projection. We bilinearly interpolated the weather data to produce a 10 km resolution layer with a Lambert Conformal projection using NCAR command Language. Weather data was also linearly interpolated in time from the original 3-hourly resolution to a 1-hourly resolution, using Matlab (Mathworks 2012).

We used wind profit as a simple proxy for wind selectivity. Wind profit is defined as the distance per second the wind carries the bird towards its intended goal (Erni et al. 2002, 2005). Winds with negative profit values would carry a motionless bird away from its goal, while positive values would carry the bird towards its goal (Erni et al. 2002). At the start of each night, we set the wind profit selectivity thresholds at the surface, such that individuals migrate only if the wind profit was above a given threshold. Once airborne, the birds remained within the 850 mb isobaric pressure level for the remainder of the flight. Even though it has been shown that birds can select flight altitudes based on the location of favorable winds (Mateos-Rodríguez and Liechti 2011), for simplicity we chose 850 mb because it lies within the range of passerine migratory flight altitudes (Gauthreaux et al. 2005; Liechti 2006), and many migration simulation studies have used similar pressure levels successfully (Erni et al. 2005; Kemp et al. 2010; McLaren et al. 2012).

Mean sea-level pressure change was used as a proxy for the passage of a cold front. Rapidly decreasing pressure often signifies stormy weather (i.e. significant rain and winds) and winds from the south in northern latitudes, typically requiring autumn migrants to expend more energy (Gauthreaux 1971; Gauthreaux et al. 2005) or stay grounded. As weather passes, pressure rises, and winds begin to come from the north, fall migration intensity often increases (Richardson 1978). To indicate stormy weather at the location of takeoff, we regressed MSLP at the time of take off to the pressure value from 6 h prior to departure. Thus, birds did not take off when MSLP was low ( $\leq 1009$  mb) and the slope of the regression line was steeply declining ( $< -1.0$  mb h<sup>-1</sup>), indicating rapidly falling pressure. We also prevented birds from taking off when hourly precipitation accumulation values were higher than 2 mm (Schaub et al. 2004). Since our objective was to understand the effects of wind selectivity, and not precipitation and pressure change, on departure behavior, we held the pressure and precipitation rules constant though all simulations, only varying wind profit selectivity thresholds during each run. Therefore, all results presented are due to changes in wind selectivity alone.

Bird airspeed was set to  $10.5$  m s<sup>-1</sup> for all trials, which is well within the range of values observed for small passerine birds (Bloch and Bruderer 1982; Bruderer and Boldt 2001; Erni et al. 2005; Videler 2005). Because we are modeling juvenile autumn migration, birds are set to use vector orientation, an orientation based on a single heading set at departure that disregards drift (McLaren et al. 2014). For simplicity, all migratory flights began at local sunset (Kerlinger and Moore 1989; Alerstam 1990; Fitzgerald and Taylor 2008; Müller et al. 2016). Flight duration followed a series of systematic rules. Flight time per night was set to 6 h (Kerlinger and Moore 1989). At this point, if birds are over land, they rest until nightfall, if not, they compensate for any wind drift by flying directly to the west ( $270^{\circ}$ ) in search of the closest land (Horton et al. 2016; Archibald et al. 2017), landing once they reach the coast. If the birds are unable to find land after 72 hours of continuous flying over the ocean, they perish.

The IBM was created in the C programming language. In our simulation birds will initiate migratory flight if, 1) the wind profit is at or above the selectivity threshold, 2) precipitation is below 2 mm at the hour of takeoff, and 3) the MSLP has not declined sharply ( $< -1.0 \text{ mb h}^{-1}$ ) over the past 6 hours. Stopover strategies were not considered in this model, birds only stopped over longer than a day if any of the above conditions were not met for multiple days in a row. We did not consider such strategies for 2 reasons. First, there is not enough empirical evidence as to how long birds stopover in our study region, and the variation in stopover length is most likely species dependent. Second, this approach allows us to quantify variation in stopover length due entirely to the effect of wind selectivity, which is difficult to quantify in the wild where other constraints (e.g. physiological condition) certainly operate.

## IBM simulations

For all simulations the birds started from locations within an area of 8000 km<sup>2</sup> east of the Hudson Bay and west of Newfoundland and Labrador (Figure 1). Breeding birds in this area represent potential migrants heading south during autumn migration within the Atlantic Flyway. To select the starting points we first created a grid of points within the 8000 km<sup>2</sup> area (Figure 1), 1 point every 100 km. We then removed all points that fell within the Hudson Bay or large lakes, and then randomly chose 50 points from the remaining points. Lastly, we removed 5 points that were not located in breeding habitats (i.e. boreal forest habitat types), leaving 45 starting locations. Each starting location was given a random calendar date between 15 August–15 Sept on a random year between 2008 and 2013 to capture variation in weather conditions experienced across the migratory route and among different years.

## Analysis

To understand how wind selectivity at departure may affect migratory behavior, we evaluated 3 variables as proxies of risk, time, and energy for wind profit threshold values between  $-40$  and  $10 \text{ m s}^{-1}$ , in intervals of  $0.5 \text{ m s}^{-1}$ . We conducted 4545 simulations, 1 per wind profit threshold at each of the 45 random starting locations. As a proxy of risk, we counted how many of the 45 simulations failed for each wind profit threshold. Our risk variable does not include risk from predation, a common definition of risk in empirical studies. We considered a migration to have failed if the bird did not make it past  $38^{\circ} 53' \text{N}$  latitude (horizontal black line in Figure 1) by December 1<sup>st</sup>, was far out to sea when it crossed the latitude (further east than  $74^{\circ} 48' \text{W}$ : vertical line in Figure 1), or if it was out to sea over 72 h. To test the sensitivity of our modeling results to these 3 assumptions of risk, we also conducted the entire modeling exercise where a bird only had to cross the latitude threshold at any longitude to be considered successful.

As a proxy of time investment, we used total number of hours spent on migration (including stopover), which is consistent with optimal migration theory (Alerstam and Lindström 1990). For a proxy of energetic investment, we counted the number of hours spent flying. However, energy expended on migration is often considered as the summation of energy spent in flight and during stopover. In empirical migration studies, proxies for energy typically capture a refueling rate during stopover. This is a physiological proxy for energy expended, because time spent in flight is a difficult and expensive metric to acquire empirically, although some studies have calculated it directly (e.g. Wikelski et al. 2003; Schmaljohann et al. 2012). Here we measure energy at a courser level, but with a proxy that is more tightly tied to energetic expenditure in flight

than is typically achieved with empirical measures. Mitchell et al. (2015), after controlling for tailwind, failed to find a difference in airspeed or ground speed among age groups of migrating savannah sparrows (*Passerculus sandwichensis*), which suggests that differences in flight speed are unrelated to differences in frequency or intensity of muscular contraction. If these results are generalizable across passerine songbirds, differences in flight duration can thus act as a reliable proxy for energy expended while in flight. Both time and energy metrics were only calculated for birds that completed migration.

To explore the effects of wind selectivity on our 3 migration currencies, we fit 3 piecewise regression models in the package “segmented” (Muggeo 2008) in Program R (R Core Team 2016) using each currency as a dependent variable and the wind profit selectivity threshold (replicated across starting location and date) as an independent variable. A natural log transformation was used on time to meet linear assumptions. We used piecewise regression to describe the relationship between each currency and wind profit, because in exploratory analysis we found, for all migration variables, there appeared to be 2 different linear relationships with wind profit.

We then standardized all migration variables by subtracting the mean and dividing by the standard deviation. We can thus directly compare the relationships between each variable and wind profit selectivity. We then combined the 3 optimal migration values to create an optimal range of wind selectivity for autumn migrants in northeastern North America and compared these behaviors to those reported from wild populations on multiple continents.

## RESULTS

### IBM simulations

We ran the migration model at each wind profit threshold from 45 starting locations for a total of 4545 migratory tracks using our more stringent migration completion rules. Of the 4545 tracks, 65% failed to reach the finish latitude/longitude or were over the open ocean for more than 72 h (Supplementary Table S1). At wind profit thresholds larger than  $8 \text{ m s}^{-1}$  (highly selective), no bird completed a migration in the time allotted (Supplementary Table S1). Table 1 provides summary statistics for available wind speed, wind direction, and calculated wind profit across all years of the study in our study region.

Our piecewise regressions modeling wind profit as a function of risk ( $R^2 = 0.72$ ), time ( $R^2 = 0.88$ ), or energy ( $R^2 = 0.71$ ) all demonstrated adequate fit. Wind profit selectivity had a significant effect on all 3 variables (Table 2). Breakpoints for risk, energy, and time were 0.5,  $-6$ , and  $-14 \text{ m s}^{-1}$ , respectively (Table 2). Figure 2 illustrates modeled trajectories for 4 wind profit simulations, 1 for each currency's breakpoint, plus the maximum degree of selectivity that included at least 1 successful migration following our more stringent completion rules.

Our analysis indicated that relative risk was lowest at intermediate selectivity and increased at both high and low wind-profit selectivity thresholds. However, the increase in assumed mortality is much more pronounced for wind profit thresholds greater than the minimum risk value (Figure 3a). Of the tracks that successfully completed migration, those with the lowest selectivity spent less overall time on migration but expended more energy in flight (Figure 3b and c), while those with the highest selectivity expended the least amount of energy in flight but spent significantly more time on migration overall while waiting for preferred conditions



**Table 1**

**Summary statistics; mean, median, minimum, and maximum for available wind speed (WS) and wind direction (WD) for each fall season of the study (2008–2013), and for calculated wind profit (WP)**

Year	Mean WS (m s <sup>-1</sup> )	Median WS (m s <sup>-1</sup> )	Minimum WS (m s <sup>-1</sup> )	Maximum WS (m s <sup>-1</sup> )	Mean WD (°)	Median WD (°)	Minimum WD (°)	Maximum WD (°)	Mean WP (m s <sup>-1</sup> )	Median WP (m s <sup>-1</sup> )	Minimum WP (m s <sup>-1</sup> )	Maximum WP (m s <sup>-1</sup> )
2008	8.49	7.89	0	44.30	233.92	257.79	0	360.00	-4.08	-4.37	-22.66	10.44
2009	9.17	8.51	0	48.81	223.71	237.94	0	360.00	-5.70	-5.34	-29.34	10.26
2010	10.03	9.31	0	48.94	240.58	259.27	0	360.00	-5.57	-5.73	-27.87	10.35
2011	9.37	8.50	0	47.16	213.40	226.57	0	360.00	-6.30	-5.72	-38.45	10.30
2012	8.65	8.10	0	48.20	230.81	251.25	0	360.00	-6.41	-5.93	-25.96	10.48
2013	8.57	7.98	0	48.63	224.69	245.34	0	360.00	-4.24	-3.72	-25.89	10.45

Wind profit was only calculated for instances for which birds took flight; therefore, all values are between  $-40$  and  $10.5 \text{ m}^{-1}$

**Table 2**

**Slopes of segments, breakpoint, and 95% confidence intervals for slopes and breakpoint for 3 models explaining the piecewise linear relationships of wind profit (m s<sup>-1</sup>) on risk, time, and energy**

Model	Slopes	95% Confidence Intervals	Breakpoint	95% Confidence Intervals
<b>Risk</b>	-0.27 5.93	(-0.41, -0.12)* (4.74, 7.12)*	0.5	(-1.0, 1.2)
<b>Time</b>	$5.25 \times 10^{-7}$ 0.13	(-0.004, 0.004) (0.11, 0.15)*	-6	(-7.3, -4.8)
<b>Energy</b>	0.57 -2.81	(0.18, 0.96)* (-3.31, -2.31)*	-14	(-16.6, -11.5)

The \* indicates statistically significant segments where  $P \leq 0.05$ .

(Figure 3b and c). For all 3 currencies, variance in the regression to the left of the breakpoint (birds that are less selective of winds) is greater than variance to the right of the breakpoint (birds that are more selective). This is a result of the wider range of wind conditions experienced by less selective birds, which flew under a wider range of conditions due to their lower threshold for migration, relative to more selective birds.

The wind profit threshold that produced the minimum risk was  $0.5 \text{ m s}^{-1}$  (Figure 4). For birds that completed migration, the optimal wind profit threshold was  $-6 \text{ m s}^{-1}$  to minimize time and  $8 \text{ m s}^{-1}$  to minimize energy (Figure 4). By combining these 3 optimal thresholds we came up with an optimal range of wind selectivity for autumn migrants in northeast North America,  $-6$  to  $8 \text{ m s}^{-1}$  (Figure 4). Natural selection for behaviors that minimize any combination of the 3 currencies, including minimization of any 1 currency at the expense of all others, should select for the observation of wind profit thresholds within this range.

## DISCUSSION

We found that birds with less wind selectivity flew on more nights and behaved more like time minimizers, while the most selective birds took longer to complete migration but used less energy in flight. The degree of wind selectivity that produced the greatest proportion of birds that completed migration (i.e. lowest risk) was intermediate to the optima for time and energy (Figures 3 and 4). Alerstam et al. (2011) found similar behavior with long-distance migrants in a flyway other than that modeled here. They found that European songbirds were less selective than originally predicted, relying on self-powered flight in their preferred direction, often with little or no tailwind assistance, and the authors emphasized how

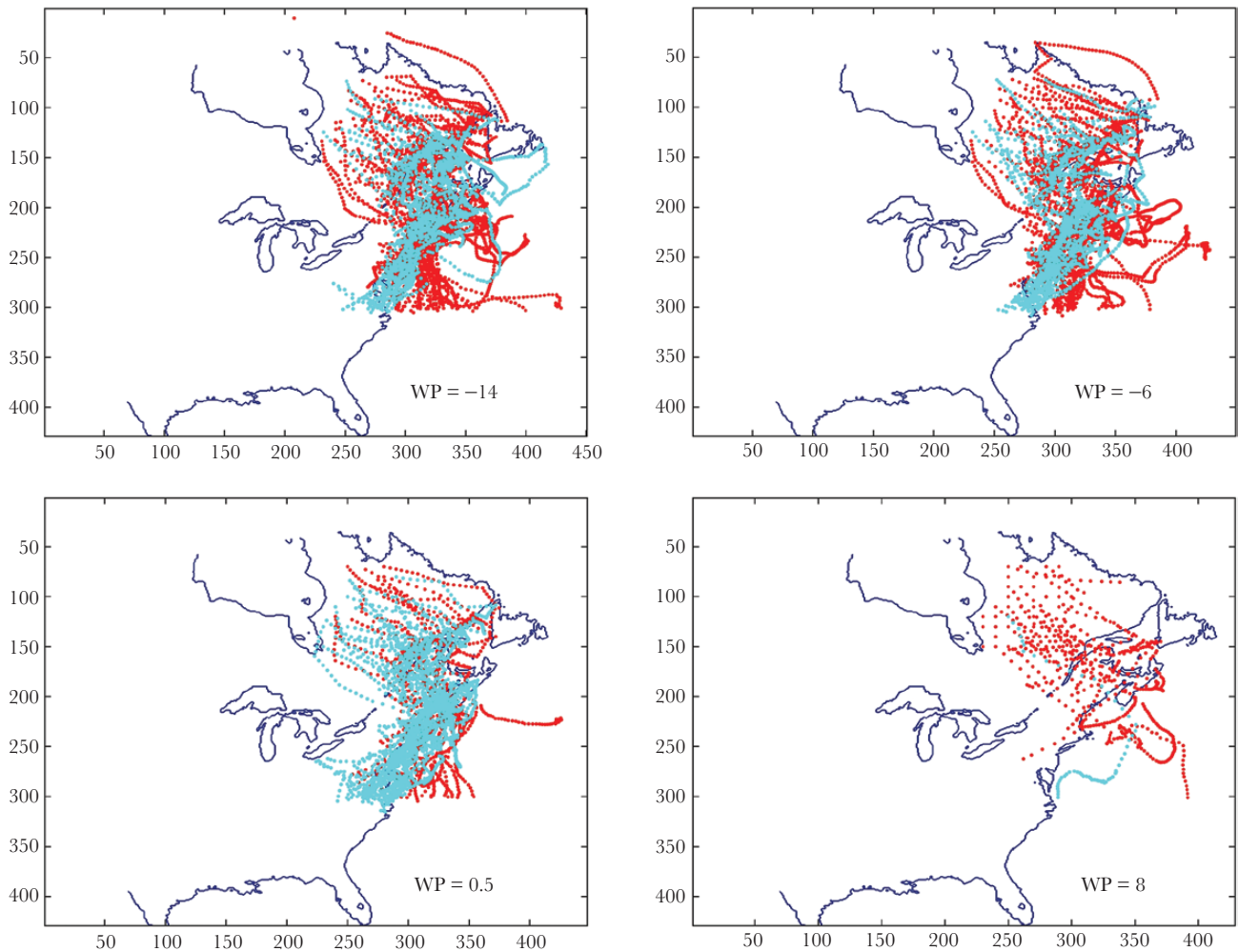
time constraints within the annual routine can necessitate tolerance of non-supportive winds (McLaren et al. 2012; Nilsson et al. 2014).

The optimal value to minimize risk ( $0.5 \text{ m s}^{-1}$ ; Table 2, Figure 3a) was at an intermediate wind profit threshold to the range of those tested (Figures 3 and 4). If birds were too selective, they were more likely to fail to complete migration in the time allotted (before December 1<sup>st</sup>). If birds were not selective enough, they were blown in directions other than their preferred bearing more often.

Unlike risk, time to complete migration showed a rapidly increasing relationship with selectivity for wind profits greater than  $-6 \text{ m s}^{-1}$  (Figures 3 and 4). Our model predicts that pure time minimizers should migrate when wind profit is  $\leq -6 \text{ m s}^{-1}$  (Figure 3c). Any wind profit selectivity  $\leq -6 \text{ m s}^{-1}$  produced similar migration times, however. This is due to increased drift away from the goal for less choosy individuals that compensates on average for the greater percentage of nights spent in migration.

Energetic cost (Figure 3b) was relatively constant, albeit with higher variance, until a migratory threshold of  $-14 \text{ m s}^{-1}$ , beyond which energetic demand decreased steadily with increasing selectivity. Birds to the right of the breakpoint were more likely to experience tailwinds (or conversely, were less likely to experience strong headwinds), and thus were able to cover more distance toward their migratory destination for each hour of flight. Further, less selective birds (that flew under a wider array of conditions) were more likely to end up out at sea, where they were unable to land and thus spent longer in flight each night. These birds were also more likely to engage in reorientation flights (toward land) instead of those directed at their destination. Together, these mechanisms made less selective birds spend more time in flight (expend more energy) than more selective birds. The global minimum for energy, however, occurred at  $8 \text{ m s}^{-1}$ , as no bird that was more selective than this cutoff completed migration under our more stringent rules. This minimum is likely sensitive to our assumptions regarding the length of the migratory period, as birds that could wait longer for more ideal conditions would likely expend even less energy.

By optimizing risk, time, and energy, we derived an optimal range of wind selectivity,  $-6$  to  $8 \text{ m s}^{-1}$ , for autumn migrants along the Atlantic flyway of North America (Figure 4). Birds that only departed when winds were more favorable than this range did not complete migration because winds with ample assistance do not exist in the region frequently enough. Conversely, birds departing when wind profits were lower than this range spent too many nights being carried away from their destination to complete migration before the end of the season. Risk optimization has little effect on the optimal selectivity range; the optimal wind profit value is approximately halfway between the time and energy optima (Figure 4). Taxa compromising between time and energy optima,



**Figure 2**

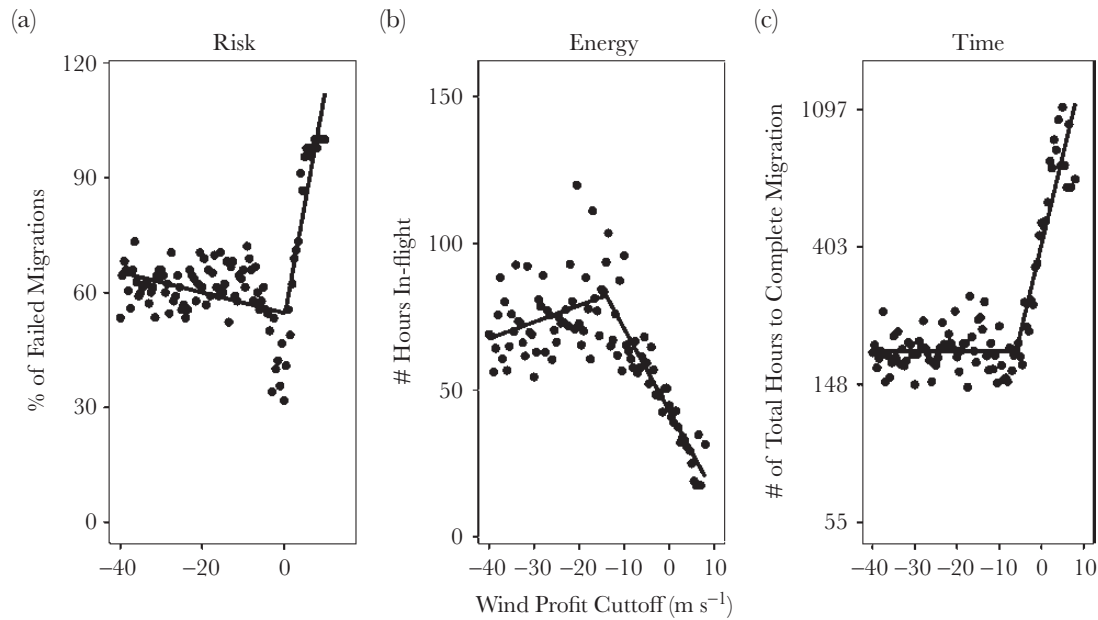
Output from 4 simulations for each currency's breakpoint and the maximum wind profit threshold (WP) investigated. Red tracks are birds that did not complete the migration due to either not crossing the benchmark latitude or longitude before December 1<sup>st</sup>, or due to more than 72 h spent out at sea. Cyan tracks indicate birds that successfully completed their migration.

therefore, might show similar departure wind selectivity to those optimizing exclusively for risk. If these results are generalizable, this could explain why empirical evidence for time-minimizing strategies (Lindström and Alerstam 1992), energy-minimizing strategies (Dänhardt and Lindström 2001), and compromises between the 2 strategies (Alerstam and Lindström 1990) have been reported, while no species we know of have been suggested to follow a purely risk-minimizing strategy (but see Mitchell et al. 2015).

Our reported behavioral optima are partially determined by the range of wind conditions and coastal orientation of the North American Atlantic flyway. The optimal wind selectivities we suggest, however, are similar to those seen in other flyways. According to our model, birds minimizing either risk or energy at the expense of the other 2 currencies should only migrate in conditions with positive wind profits (risk optimum threshold =  $0.5 \text{ m s}^{-1}$ ; energy optimum threshold =  $8 \text{ m s}^{-1}$ ). A radar study in central Europe found that migratory intensity, however, increased at wind profits of  $-7 \text{ m s}^{-1}$  and greater (Enri et al. 2002). This threshold is very similar to our optimum for time minimization ( $-6 \text{ m s}^{-1}$ ). Further, our model suggests that such an empirical result would only occur for taxa that are at least partially prioritizing time minimization, and indeed, time minimization has been reported in far more songbird

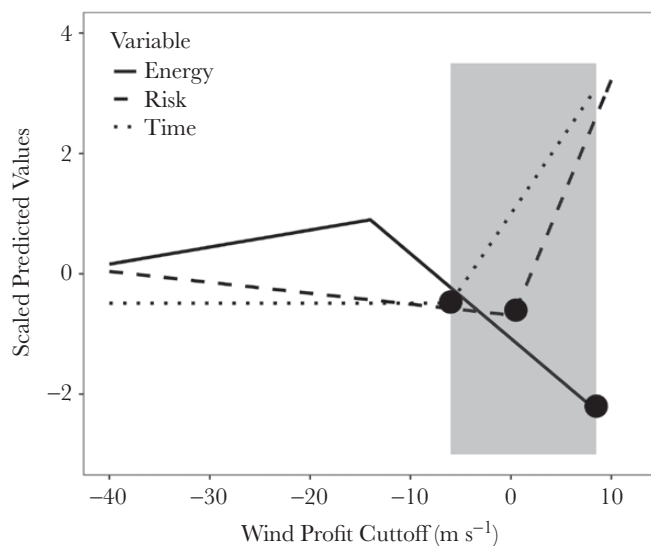
taxa in Europe than has energy or risk minimization (Alerstam et al. 2011). While this does not demonstrate that the optima are the same among flyways, time minimizers should generally be less selective of departure conditions than risk or energy minimizers, and the optimal degree of selectivity we report for time minimization matches that shown by time minimizers in at least one other flyway. Further work is necessary to determine how similar these optima might be in other flyways.

Our model includes a few assumptions that warrant discussion. First, our proxy for energy investment excludes energy spent while on stopover. Second, our estimates of risk are biased high for some taxa because our definitions of failure do not capture how some taxa are known to migrate over the open ocean (DeLuca et al. 2015; Bairlein et al. 2012; Ouwehand and Both 2016). To illustrate that our overall conclusions are robust to these failure assumptions, we modeled an additional scenario in which the birds that crossed the goal latitude but remained out to sea were considered successful (Supplementary Figure S1). By relaxing the assumption of failure, we estimated a lower failure rate (26% vs. 65% for the more stringent rules), indicating failure rate is very sensitive to these assumptions. However, the optimal thresholds for all 3 currencies were similar and the general patterns of the relationship for all



**Figure 3**

The relationships between wind profit on (a) risk (percent of failed migrations), (b) energy (number of hours in flight), and (c) time (number of hours to complete migration). The dots represent the mean model outputs across all 45 starting locations and the lines were parameterized using piecewise regression.



**Figure 4**

Scaled predicted values for models explaining the effect of wind profit thresholds ( $\text{m s}^{-1}$ ) on 3 migratory variables. Black dots represent the optimal wind profit threshold for each migratory currency. If optimizing only energy, birds should only fly when wind profits are above  $8 \text{ m s}^{-1}$ . Time optimizers should fly when wind profits are above  $-6 \text{ m s}^{-1}$  and to optimize solely for risk, birds should migrate with a wind profit threshold of  $0.5 \text{ m s}^{-1}$ . The gray rectangle is the range of optimum migratory selectivity if multiple strategies are being used.

migratory behavior metrics and wind profit threshold remained the same. Allowing birds to remain at sea longer and complete migration successfully at any distance from land did, however, decrease the slope of the relationship between risk and wind profit thresholds to the left of the optimum. Relaxation of these rules, while predicting a similar optimal value for risk, caused fewer birds to be lost due to wind drift (Supplementary Figure S1A). Importantly,

however, it did not greatly alter the relationship between survival and wind profit threshold above the risk minimum (Supplementary Table S2). Waiting longer for preferred conditions resulted in similarly increased risk of running out of time under both modeling scenarios.

We also note that our model simplified a number of parameters that might affect our optima. First, although our assumption that birds orient along the coast within 100 km of the ocean (see Figure 1) is based on ample empirical observations (see methods) and our inclusion of orientation stochasticity should prevent our results from being sensitive to small changes in assumed orientation, we have no empirical evidence to describe avian perception of what constitutes the coast (i.e. how wide our buffer should be). Further modeling should test the sensitivity of this assumption. Likewise, we ignored endogenous factors that might alter departure (e.g. individual condition) and the ability of birds to alter altitude to offset suboptimal wind conditions, something which has been widely reported (Stoddard et al. 1983; Gauthreaux 1991; Bruderer et al. 1995; Liechti 2006; Mateos-Rodríguez and Liechti 2011; Kemp et al. 2012). Shamoun-Baranes and van Gasteren (2011), however, found that pressure level (i.e. altitude) only had a minor effect on the proportion of successful trajectories in a modeling study.

Despite an understanding that reality is undoubtedly more complicated than what we have modeled here, we were able to mimic tradeoffs between time and energy using only variation in wind selectivity, lending support for the potential importance of wind selectivity as a significant driving force in the evolution of migratory behavioral strategies. Furthermore, the tradeoff between waiting too long for preferred conditions and accepting conditions that are disadvantageous has been reported in a number of other behavioral paradigms (e.g. prey selection and mate choice; Reeve 1989; Getty 1995) and appears to be a viable mechanism behind animal migratory behaviors as well. While improvements in our model would undoubtedly improve the specific predictive optima of our simulation, our broad results appear at least partially insensitive to some of our assumptions, and we predict that the relative

effect of wind selectivity on tradeoffs among time, energy, and risk optimization are likely similar in a broad range of realistic climates. This prediction, however, remains untested. Of the 3 currencies, the risk optimum is most likely to change with an improved model, as it relies more heavily on appropriate modeling of over-water behavior. This optimum, however, did not affect the range of optimal wind selectivity we report here.

In general, we expect that natural selection on wind selectivity can influence the impacts of total migration time, energy expenditure, and mortality risk on individual fitness during migration, yet the relative importance of these pressures should vary among species, regions, seasons, and phases of migration (Kemp et al. 2013). We show here that it is possible to reproduce classic behavioral tradeoffs in migratory behaviors by considering only the selection of the wind “habitat” in which migration occurs. These results underscore the potential importance of individual variance in selection (i.e. “choosiness”) for producing optimal behaviors in a way that has been similarly shown in foraging ecology (Pyke et al. 1977), mate choice (Jennions and Petrie 1997), and habitat selection (Jaenike and Holt 1991).

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <https://academic.oup.com/beheco/>.

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