How birds weather the weather: avian migration in the mid-latitudes

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Can wind help explain seasonal differences in avian migration speed?

4.1 Abstract

A bird's groundspeed is influenced by the wind conditions it encounters. Wind conditions, although variable, are not entirely random. Instead, wind exhibits persistent spatial and temporal dynamics described by the general circulation of the atmosphere. As such, in certain geographical areas wind's assistance (or hindrance) on migratory flight is also persistent, being dependent upon the bird's migratory direction in relation to prevailing wind conditions. We propose that, considering the western migration route of nocturnal migrants through Europe, winds should be more supportive in spring than in autumn. Thus, we expect faster groundspeeds, contributing to faster overall migration speeds, in spring. To test whether winds were more supportive in spring than autumn, we quantified monthly wind conditions within western Europe relative to the seasonal direction of migration using 30 years (1978-2008) of wind data from the NCEP/NCAR Reanalysis dataset. We found that supporting winds were significantly more frequent for spring migration compared to autumn and up to twice as frequent at higher altitudes. We then analyzed three years (2006-2008) of nocturnal migratory groundspeeds measured with radar in the Netherlands which confirmed faster groundspeeds in spring than autumn. This seasonal difference in groundspeed suggests a 16.9% increase in migration speed from autumn to spring. These results stress the importance of considering the specific wind conditions experienced by birds when interpret-

ing migration speed. We provide a simple methodological approach enabling researchers to quantify regional wind conditions for any geographic area and time period of interest.

4.2   Introduction

It is suggested that passerine migration speed is faster in spring than autumn (Berthold, 2001; Newton, 2008). This asymmetry is thought to be driven by 1) evolutionary pressures on migrants (males in particular) to arrive early at the breeding grounds and establish themselves in prime territory (Kokko, 1999), 2) inexperienced juveniles driving down a population's migration speed in autumn (Berthold, 2001; Newton, 2008), and 3) seasonal differences in fuel deposition rate (see Bauchinger and Klaassen, 2005). Empirical evidence of faster total migration speeds in spring than autumn, however, is limited (Fransson, 1995; Yohannes et al., 2009). Though the theoretical driving mechanisms for this seasonal difference in migration speed should hold outside of the Palearctic-Afrotropic system, a recent study on the eastern Siberian stonechat *Saxicola torquata maura* (an inner-Asian migrant) found no significant difference in migration speed between spring and autumn (Raess, 2008). Even within the Palearctic system, Liechti and Bruderer (1995) found that groundspeeds during nocturnal migration over Israel were faster in autumn than in spring due to prevailing wind conditions. It seems likely, then, that other factors may contribute to seasonal (as well as geographic) variation in migration speed (Jenni and Schaub, 2003).

Migration speed (V_{migr}), as described by Hedenström and Alerstam (1998), is determined by three critical components (Equation 4.1): the bird's groundspeed (V_b), its rate of fuel accumulation (P_{dep}), and rate of energy consumption during flight (P_{flight}).

$$V_{migr} = \frac{V_b \cdot P_{dep}}{P_{dep} + P_{flight}} \qquad (4.1)$$

In still-air conditions, V_{migr} is more strongly dependent on variation in P_{dep} than V_b because of the relationship between V_b and P_{flight} (Alerstam, 2003). Wind, however, can alter V_b without any adjustment in P_{flight}. Furthermore, a bird optimizing either energy or time is expected to reduce its airspeed, and hence P_{flight}, in tailwinds and, conversely, increase both in headwinds (Hedenström and Alerstam, 1995).

In light of wind's impacts on V_{migr}, it is important to note that wind conditions, while variable, exhibit persistent dynamics described by the general circulation of the atmosphere (Rohli and Vega, 2007). It follows, that winds in
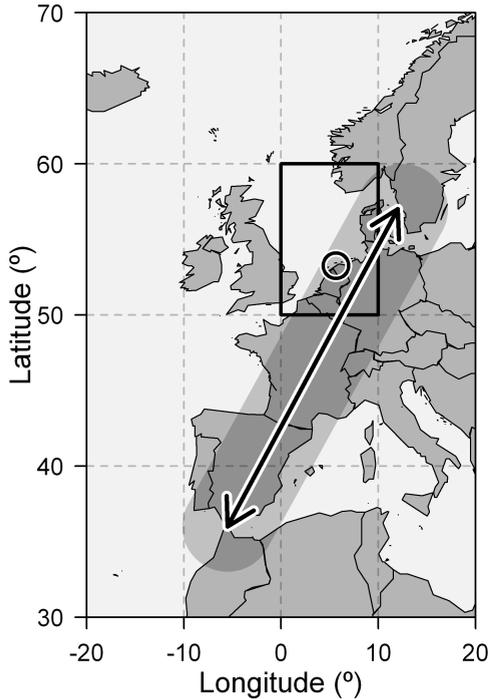
Figure 4.1: Map of western Europe indicating a generalized migration route and direction of migration for autumn (SW) and spring (NE). The radar measurement location in the Netherlands is circled.

certain geographical areas are consistently more (or less) beneficial to migration depending on the preferred direction of migratory movement in relation to prevailing wind conditions (Gauthreaux et al., 2005).

We propose that wind conditions encountered during migration through western Europe (Figure 4.2) are more supportive in spring than autumn. We therefore examine the wind conditions along this route and quantify them in relation to the seasonal direction of migration. Where wind conditions in spring are more beneficial than in autumn, we expect birds to exhibit faster groundspeeds (leading to faster migration speeds) in spring than autumn. We test this assumption using radar measurements of groundspeed during nocturnal migration over the Netherlands.

4.3 Data

4.3.1 Wind data

Gridded wind data from the 850 mb pressure level were obtained from the National Center for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) Reanalysis dataset (Kalnay et al., 1996) at a spatial resolution of 2.5° every six hours for the years 1978-2008 from 30° N

to 70° N and 20° W to 20° E. Surface wind conditions were obtained from the same dataset, but the spatial extent was limited to the area most representative of the radar measurement site in the Netherlands (i.e. 50° N to 60° N and 0° E to 10° E). Wind data (ms^{-1}) were described by the U (east/west) component (east being positive) and V (north/south) component (north being positive); both indicated the direction into which the wind was blowing. These data were used to make a 30-year climatological assessment of wind conditions in western Europe and to calculate wind profit (see Section 4.4.1).

Gridded wind data from the analysis dataset of the European Centre for Medium Range Weather Forecasts (ECMWF) deterministic model were obtained from 2006-2008 for the 925 mb and 850 mb pressure levels at three hour intervals. These data, at a spatial resolution of 0.5° for 2006 and 0.25° thereafter, were used to calculate airspeeds (see Section 4.4.2).

4.3.2   Radar data

Groundspeeds and flight directions were measured every half hour using ten sequential rotations (in ten second intervals) from a long-range medium-power stacked-beam radar in Wier, the Netherlands (53° 15'25"N, 5° 37'12"E) operated by the Royal Netherlands Air Force (Buurma, 1995). Migration data were collected from 2006-2008, encompassing three spring and three autumn migration seasons. Groundspeeds and flight directions were derived from individual tracks across the entire Wier radar area from the two lowest altitude radar beams, covering approximately 100-6000m altitude. These data were used to calculate half-hourly mean groundspeeds (ms^{-1}) per radar beam. This study focused on nocturnal migration and thus only included measurements made between sunset and sunrise.

To ensure that only migratory movements were included in the analysis, a Rayleigh test (Batschelet, 1981) was applied at each time step. Only time steps with a distribution of flight directions sufficiently concentrated to reject the null hypothesis of a uniform distribution were retained ($\alpha < 0.001$).

4.4   Methods

In all comparisons, February, March, April, and May were considered spring. August, September, October, and November were considered autumn. Analyses were conducted and graphics produced using the statistical software package R (R Development Core Team, 2010). The R-code for wind analysis is available upon request and can easily be implemented for other geographical areas or time periods.

4.4.1 Wind profit analysis

Wind data from the NCEP/NCAR dataset were grouped into 10° x 10° subsections (hereafter "wind subsections") to calculate monthly and seasonal frequency distributions of wind speed and direction per wind subsection. Directions were divided into 360 groups (one for each angular degree). Speeds were classified into five ranges of 0-5, 5-10, 10-15, 15-20, and > 20 ms^{-1}. Seasonal wind summary plots (wind roses) were created for each wind subsection for spring(Figure 4.2) and autumn (Figure 4.3). Monthly wind summary plots were also created for wind subsections in Europe and Africa (see Appendix C).

We then performed a quantitative assessment of the monthly and seasonal "profitability" of the wind at 850 mb and the surface for the wind subsection most representative of the radar measurement site in the Netherlands (i.e. 50° N to 60° N and 0° E to 10° E, hereafter "Netherlands wind subsection"), by considering the length of the wind vector along the preferred migratory direction (Equation 4.2).

$$WP = V_W \cos\theta \qquad (4.2)$$

Where wind profit (WP, ms^{-1}) equals wind speed (V_W, ms^{-1}) times the cosine of the angle between wind direction and the preferred migratory direction (θ). This is equivalent to EQ$^{\text{Tailwind}}$ described in section 3.3.1 of Chapter 3.

The preferred autumn migratory direction used to calculate wind profit was 223°. This was the mean of two significant autumn migratory directions in the Netherlands (van Belle et al., 2007) and was similar to the main autumn migratory directions reported for many locations in western Europe – e.g. 220° at a coastal site in southern Spain (Bruderer and Liechti, 1998); 230° for southern Germany and Switzerland (Bruderer et al., 1989); and 225° at Falsterbo in southwestern Sweden (Zehnder et al., 2001). This preferred direction was reversed to 43° for spring.

Spring and autumn wind profit distributions from the 850 mb pressure level were also calculated for other wind subsections in Western Europe using the same methods described above (see Appendix C).

4.4.2 Flight analysis

Weighted probability distributions were calculated, for spring and autumn separately, based on the number of tracks in both beams used to calculate the mean groundspeed at each time step.

While species could not be identified directly from this radar, species groups could be inferred from measured airspeeds (Bruderer and Boldt, 2001).
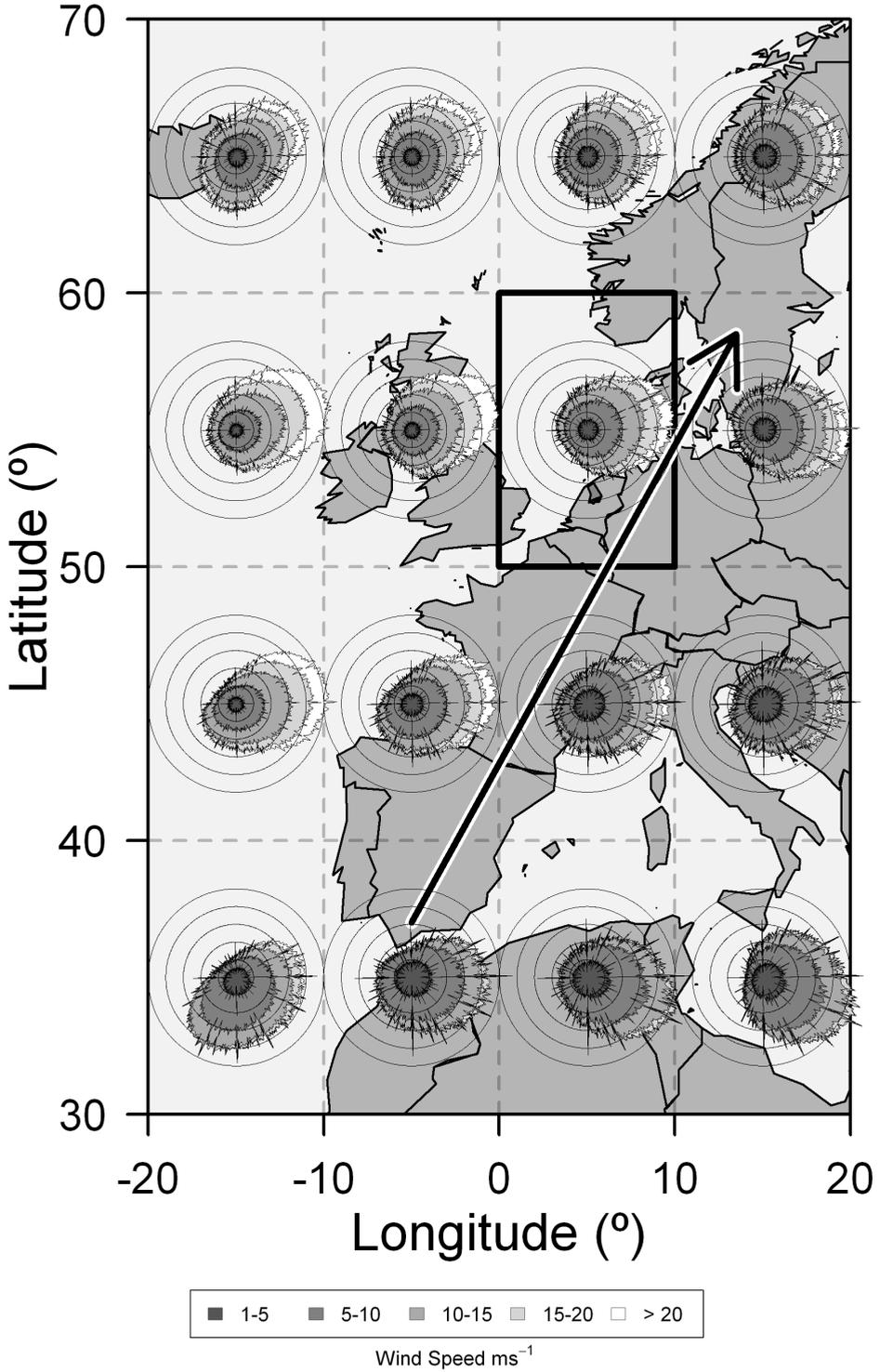
Figure 4.2 (previous page): Spring wind rose maps covering western Europe displaying 30 years (1978-2008) of wind data from the 850 mb pressure level. Wind roses indicate the direction into which the wind blows. Total distance from the center indicates the relative frequency of wind in a particular direction, while shades describe the relative frequencies of the different wind speed ranges (ms^{-1}) in that direction. Concentric circles indicate relative frequency in increments of 0.1%; with the outer circle indicating 0.5% relative frequency. Large arrows in the background indicate the general direction of migration for spring. The Netherlands wind subsection is heavily outlined.

We calculated airspeeds through the vector subtraction of the wind components in the ECMWF dataset from the radar-measured groundspeeds according to Shamoun-Baranes et al. (2007). These ECMWF wind data were linearly interpolated in space and time to match the center of the radar and the time of each measurement. Airspeeds were calculated in the upper beam using wind data from the 850 mb pressure level and in the lower beam using data from the 925 mb pressure level.

4.5   Results

4.5.1   Wind conditions

A qualitative examination of the seasonal wind rose maps showed that wind conditions were more supportive of the northeasterly movement of spring migration and frequently and forcefully opposed to the southwesterly movement of autumn migration (Figures 4.2 and 4.3). There appeared a great deal of intra-seasonal variability between adjacent wind subsections (particularly latitudinally). Wind speeds were consistently highest between 50° N and 60° N, although speeds at all latitudes decreased farther inland. Winds south of 40° N in both seasons were weaker in speed and more variable in directionality than winds north of 40° N.

A quantitative assessment of wind profit between the two seasons within the Netherlands wind subsection was performed for both the surface and 850 mb pressure level (Table 4.1). Winds were significantly more profitable ($P < 0.001$; one-sided Mann-Whitney test) in spring (n=372,800) than autumn (n=378,200) at both levels. The percentage of wind profit values greater than zero, describing the percentage of observations in which wind had some component in the direction of migration, showed that beneficial winds were also more frequent in spring compared to autumn. Furthermore, the mean of wind profit values greater than zero was higher in spring than in autumn; thus winds in the direction of migration were stronger in spring than autumn.
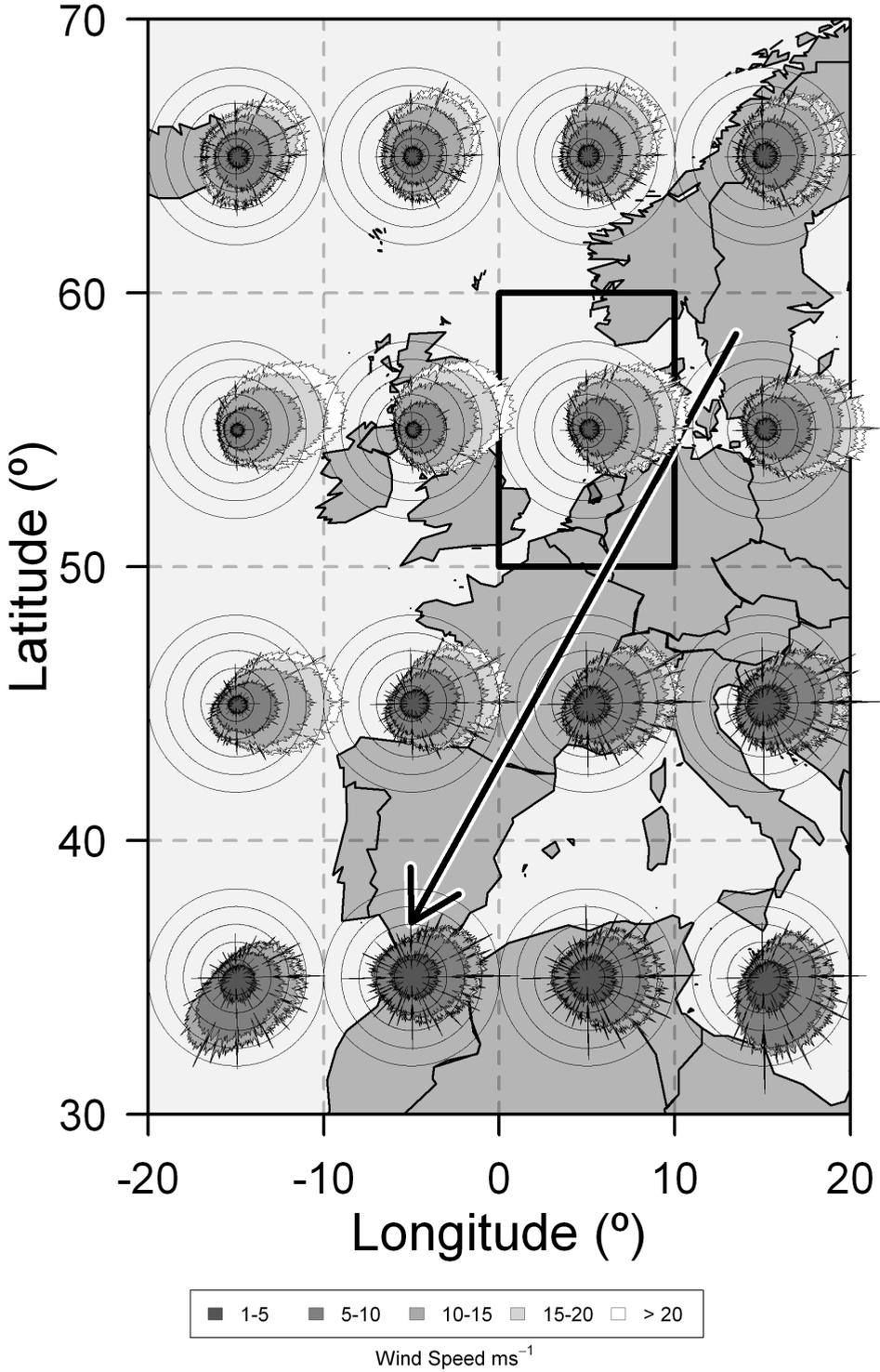
Figure 4.3 (previous page): Autumn wind rose maps covering western Europe displaying 30 years (1978-2008) of wind data from the 850 mb pressure level. Wind roses indicate the direction into which the wind blows. Total distance from the center indicates the relative frequency of wind in a particular direction, while shades describe the relative frequencies of the different wind speed ranges (ms^{-1}) in that direction. Concentric circles indicate relative frequency in increments of 0.1%; with the outer circle indicating 0.5% relative frequency. Large arrows in the background indicate the general direction of migration for autumn. The Netherlands wind subsection is heavily outlined.

Table 4.1: Seasonal and monthly mean and standard deviation (SD) of wind profit values (ms^{-1}), the percentage of wind profit values greater than zero (%> 0), and the mean of wind profit values greater than zero (mean> 0) are shown using 30 years (1978-2008) of wind data from the surface and 850mb pressure level from the Netherlands wind subsection.

	Surface				850 mb			
	Mean	SD	%> 0	Mean> 0	Mean	SD	%> 0	Mean> 0
Spring	1.4	6.1	57.1	5.5	2.9	7.9	62.3	7.7
Autumn	-2.3	5.6	34.6	3.7	-4.4	7.4	28.5	4.3
February	2.5	6.9	63.0	6.7	3.7	9.3	62.7	9.3
March	2.5	6.3	64.2	6.2	4.1	8.2	67.5	8.5
April	0.4	5.5	52.2	4.6	1.8	7.2	58.4	6.6
May	0.1	5.1	49.4	4.3	2.2	6.5	60.3	6.3
August	-1.6	4.6	37.7	3.0	-3.5	5.8	28.1	3.2
September	-2.0	5.4	35.9	3.6	-4.0	7.0	29.2	4.3
October	-2.8	6.0	32.4	3.8	-5.5	7.9	25.4	4.3
November	-2.9	6.3	32.5	4.1	-4.6	8.7	31.3	5.3

Wind profit was greater at the surface than at 850 mb during autumn and at 850 mb, than at the surface, during spring. At the 850 mb pressure level, profitable winds were more than twice as frequent in spring than autumn. While there was considerable variation within a season, no autumn month displayed more beneficial winds than a spring month.

4.5.2 Flight speed

Observed groundspeeds were significantly faster during spring than autumn ($P < 0.001$; one-sided Mann-Whitney test). Airspeeds, however, were somewhat slower in spring than autumn ($P < 0.001$; one-sided Mann-Whitney test; Table 4.2). The measured airspeeds indicate that nocturnal migrants in both

Table 4.2: Mean and standard deviation (SD) of air- and groundspeeds (ms^{-1}), are shown for spring (n=3,511,778) and autumn (n=3,189,424)

	Spring		Autumn	
	Mean	SD	Mean	SD
Groundspeed	22.1	5.5	18.9	3.7
Airspeed	13.6	3.6	14.0	4.7

seasons include a broad range of passerines as well as faster flying migrants such as waders and waterfowl (Bruderer and Boldt, 2001).

4.6   Discussion

Our study has shown that, in spring compared to autumn: 1) wind conditions along the western migration route through Europe are more supportive of migration, 2) mean groundspeeds measured in Netherlands are 16.9% faster, and 3) mean airspeeds measured in Netherlands are 2.9% slower. Therefore, birds passing through this radar measurement site in spring have faster mean groundspeeds, with no more fuel expenditure, than birds passing through in autumn. All other things being equal, this suggests an increase of at least 16.9% in migration speed through the Netherlands in spring compared to autumn due to the effect of wind on groundspeeds.

Recent positive trends in the frequency of favorable winds in spring have been associated with earlier spring arrival of song thrushes in the southeast Baltic region (Sinelschikova et al., 2007) which may in turn reflect faster migration speeds. In recent years, the relationship between climate change and migration phenology has received a great deal of attention (Forchhammer et al., 2002; Cotton, 2003; Jonzén et al., 2006), yet the potential role of wind conditions has rarely been studied in this context.

Gauthreaux et al. (2005), showed that prevailing wind patterns also favor migratory movement in spring more than autumn in North America. The authors described a "go-with-the-prevailing-flow" strategy in spring compared to a "sit-and-wait-for-favorable-winds" strategy in autumn. As studies on the timing of migration in relation to weather suggest, birds tend to migrate more readily in profitable rather than prohibitive wind conditions in both seasons (Richardson, 1990a, and references therein). Thus, if birds employ the "sit-and-wait-for-favorable-winds" strategy in both seasons, in our study area they would migrate more frequently in spring (appearing to "go-with-the-prevailing-flow"), and less often in autumn.

Newton (2008) suggests that migration can be delayed for days or weeks

at a time due to unfavorable weather conditions. Weber and Hedenström (2000) theorize that, if wind conditions are correlated in time, it is optimal for a bird to wait for better wind conditions (even when they are energetically prepared to migrate) unless the probability that the unfavorable winds will persist is close to one. Our study shows that the frequency of beneficial winds (and therefore the time a bird may have to wait for beneficial winds) can differ dramatically by season, direction of migration, and geographic location. Therefore, in areas with frequently prohibitive winds, birds must either remain longer at a stopover waiting for conditions to improve or depart in suboptimal conditions resulting in greater energy expenditure, slower groundspeeds, or some combination of the two, and hence slower migration speeds.

Our study has shown that wind conditions exhibit consistent seasonal and geographic patterns. However, it is not clear whether birds are aware of these patterns and, if so, to what extent. Do birds have an idea of the frequency of favorable winds within a particular region, and is that foreknowledge applied in their stopover, refueling, and route-selection strategies (i.e. can areas with consistently unfavorable winds be considered a kind of ecological barrier)? More experienced migrants may even learn to anticipate the frequency of beneficial winds in a particular area and adjust the rigidity of their wind selection criteria and/or compensation strategy accordingly.

This raises interesting questions regarding detours from more direct migratory routes and the use of alternative migratory routes between spring and autumn (i.e. loop migration). Alerstam (2001) describes detours circumventing ecological barriers which are still energetically optimal and demonstrates that wind conditions influence the optimality of a particular route (Alerstam, 1979). Because of wind's influence on optimal routes and its persistent nature, areas with frequently prohibitive winds may be viewed as a type of ecological barrier.

In conclusion, consideration of the wind conditions relative to migration is important for a better interpretation of migration speed. We provide a simple methodology to quantify regional wind conditions for any geographic area and time period of interest. While wind is only one of several internal and external factors influencing migration speed, it may help explain part of the variability observed between and within regions, species, seasons, and years. For example, Fransson (1995) reported faster migration speeds in spring than in autumn. The lesser whitethroat, though migrating SE in autumn and expected to encounter more beneficial winds, still flew faster in spring. Yet, the seasonal difference in migration speed was smaller than in the other species, suggesting both seasonal and wind effects. Reanalysis of results such as these and new studies are needed to help clarify wind's importance relative to other

factors. Individual-based simulation models (Erni et al., 2005; Vrugt et al., 2007), in combination with advances in tracking technologies (Robinson et al., 2010), could improve our understanding of the interactions between influential variables, as they allow us to consider specific environmental and physiological details relating to a particular migratory individual.

Acknowledgments