



Can wind help explain seasonal differences in avian migration speed?

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A bird's ground speed 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 higher ground speeds, contributing to higher 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 ground speeds measured with radar in the Netherlands which confirmed higher ground speeds in spring than autumn. This seasonal difference in ground speed 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 interpreting migration speed. We provide a simple methodological approach enabling researchers to quantify regional wind conditions for any geographic area and time period of interest.

It is suggested that passerine migration speed is higher 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 higher total migration speeds in spring than autumn, however, is limited (Fransson 1995, Johannes 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 ground speeds during nocturnal migration over Israel were higher 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 Ålerstam (1998), is determined by three critical components (Equation 1): the bird's ground speed (V_b), its rate of fuel accumulation (P_{dep}), and rate of energy consumption during flight (P_{flight}).

$$V_{migr} = \frac{V_b P_{dep}}{P_{dep} + P_{flight}} \quad (1)$$

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} (Ålerstam 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 Ålerstam 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 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 (Fig. 1) 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 higher ground speeds (leading to higher migration speeds) in spring than autumn. We test this assumption using radar measurements of ground speed during nocturnal migration over the Netherlands.

Data

Wind data

Gridded wind data from the 850mb 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 Wind profit analysis).

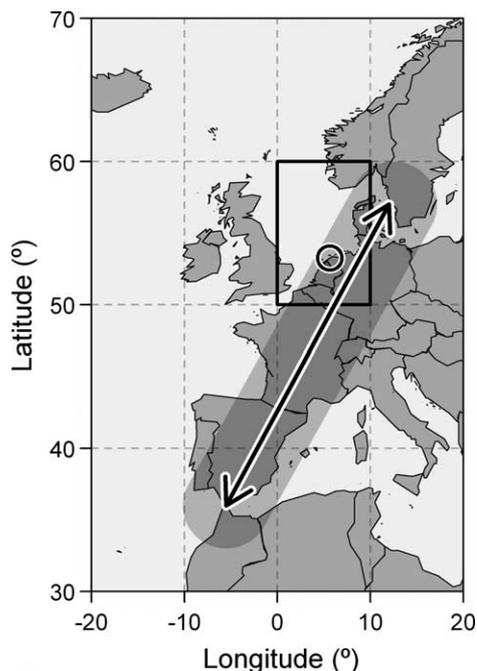


Figure 1. Map of western Europe indicating a generalized migration route and direction of migration for autumn (SW) and spring (NE). The radar measurement location in the Netherlands is circled.

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 925mb and 850mb 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 Flight analysis).

Radar data

Ground speeds 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 ($53^\circ 15' 25''\text{N}$, $5^\circ 37' 12''\text{E}$) operated by the Royal Netherlands Air Force (Buurma 1995). Migration data were collected from 2006–2008, encompassing three spring and three autumn migration seasons. Ground speeds 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 ground speeds (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 ($\alpha < 0.001$).

Analysis

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 (Ihaka and Gentleman 1996). The R-code for wind analysis is available upon request and can easily be implemented for other geographical areas or time periods.

Wind profit analysis

Wind data from the NCEP/NCAR dataset were grouped into $10^\circ \times 10^\circ$ 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 $> 20 \text{ ms}^{-1}$. Seasonal wind summary plots (wind roses) were created for each wind subsection (Fig. 2). Monthly wind summary plots were also created for wind subsections in Europe and Africa (appendix; Fig. A1).

We then performed a quantitative assessment of the monthly and seasonal “profitability” of the wind at 850mb 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 2).

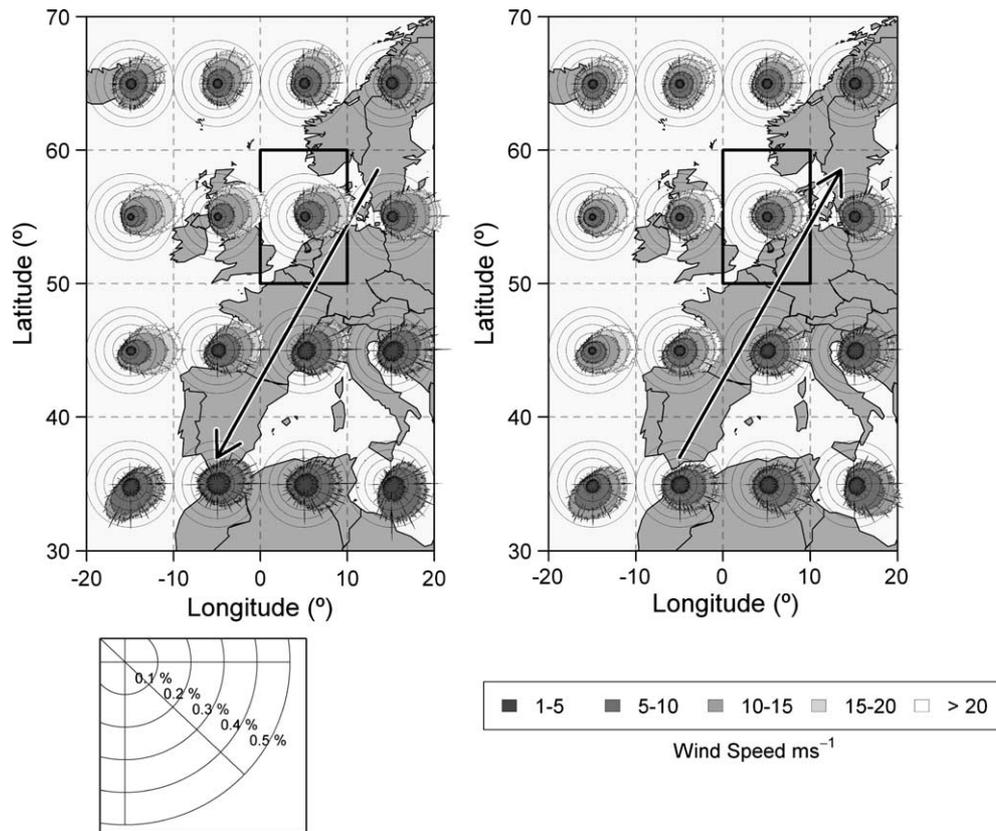


Figure 2. Spring (left) and autumn (right) wind rose maps covering western Europe displaying 30 years (1978-2008) of wind data from the 850mb pressure level. Wind roses indicate the direction into which the wind blows. Total distance from the center indicates the relative frequency of wind in a particular 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 the particular season. Netherlands wind subsection is heavily outlined.

$$WP = V_w \times \cos\theta \quad (2)$$

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).

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 (appendix, Table A1).

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 ground speed 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). We calculated airspeeds through the vector subtraction of the wind components in the ECMWF dataset from the radar-measured ground speeds 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.

Results

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 (Fig. 2). 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 850mb pressure level (Table 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. Wind profit was higher at the surface than at 850mb during autumn and at 850mb, than at the surface, during spring. At the 850mb 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.

Flight speed

Observed ground speeds were significantly higher during spring than autumn ($p < 0.001$; one-sided Mann-Whitney test). Airspeeds, however, were somewhat lower in spring than autumn ($p < 0.001$; one-sided Mann-Whitney test; Table 2). The measured airspeeds indicate that nocturnal migrants in both seasons include a broad range of passerines as well as faster flying migrants such as waders and waterfowl (Bruderer and Boldt 2001).

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 ground speeds measured in Netherlands are 16.9% higher, and 3) mean airspeeds measured in Netherlands are 2.9% lower. Therefore, birds passing through this radar measurement site in spring have higher mean ground

speeds, 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 ground speeds.

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 higher 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 1990 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, lower ground speeds, or some combination of the two, and hence lower migration speeds.

Our study has shown that wind conditions exhibit consistent seasonal and geographic patterns. However, it

Table 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 850 mb pressure level from 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

Table 2. Mean and standard deviation (SD) of air- and ground speeds (ms^{-1}), are shown for spring ($n=3,511,778$) and autumn ($n=3,189,424$).

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

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 higher 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. 2009), 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.

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