

# **Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short- and long-distance migrants**

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## 18    **Abstract**

19    Migrating birds are expected to fly at higher airspeeds when minimizing time rather than energy  
20    costs of their migratory journeys. Spring migration has often been suggested to be more time  
21    selected than autumn migration, because of the advantage of early arrival at breeding sites. We have  
22    earlier demonstrated that nocturnal passerine migrants fly at higher airspeeds during spring  
23    compared to autumn, supporting time-selected spring migration. In this study we test the hypothesis  
24    that seasonal airspeeds are modulated differently between short- and long-distance migrants,  
25    because of a stronger element of time-selection for autumn migration over long distances. In support  
26    of this hypothesis we demonstrate that the seasonal difference in airspeed is significantly larger  
27    (spring airspeed exceeding autumn airspeed by a factor of 1.16 after correcting for the influence of  
28    altitude, wind and climb/descent on airspeed) among short-distance compared to long-distance  
29    (factor 1.12) migrants. This result is based on a large sample of tracking radar data from 3 years at  
30    Falsterbo, South Sweden. Short-distance migrants also tend to fly with more favourable winds during  
31    autumn, indicating relaxed time constraints (being able to afford to wait for favourable winds)  
32    compared to long-distance migrants. These results indicate surprisingly fine-tuned seasonal  
33    modulation of airspeed and responses to wind, associated with behavioural strategies adapted to  
34    different levels of time selection pressures during spring and autumn migration.

35

36    Keywords: Airspeed, Ground speed, Bird migration, Flight speed, Optimal migration, Passerine, Short  
37    distance migrants, Long distance migrants, Spring migration, Autumn migration.

## INTRODUCTION

Many birds migrate faster in spring than in autumn, due to environmental or behavioural factors (La Sorte et al. 2013; Nilsson et al. 2013). The total speed of migration is determined to a large extent by stopover time and there is evidence of more rapid refuelling during spring than during autumn (Nilsson et al. 2013; Seewagen et al. 2013). The other component of the total migration speed is flight speed. By measuring flight speeds under different circumstances we can draw conclusions regarding what factors are important to shape the migratory journey. Theory and empirical data suggest that early arrival at the breeding grounds is of great importance for passerine migrants, as an early arrival brings benefits in the competition for territories, mates and resources (van Noordwijk et al. 1995; McNamara et al. 1998; Newton 2008). Timing of arrival at the winter grounds might be less important, and this could lead to a spring migration dominated by time constraints, and an autumn migration influenced by other selection pressures, such as energy minimization and risk aversion. There are few empirical tests of this, but see for example Conklin et al. (2013).

A bird's airspeed is the speed relative to the air around it, while ground speed is the speed relative to the ground below. Ground speed is therefore the result of the bird's airspeed and the effect of the wind on the bird. Optimal migration theory predicts that birds will migrate at different airspeeds depending on what cost or benefits that are most important for them to optimize (Alerstam and Lindström 1990; Hedenström and Alerstam 1997). Minimizing energy per time gives the slowest airspeed (minimum power airspeed  $V_{mp}$ ), while maximizing the range flown on a given energy reserve gives a higher airspeed (maximum range speed,  $V_{mr}$ ). A still higher airspeed is predicted when minimizing the total duration of migration (minimum time airspeed,  $V_{mt}$ ). When flying at this faster airspeed the bird is using its energy supplies more rapidly, but it also reaches each stopover site sooner. This gives it more time to fuel than if it had been flying at minimal energy speed and results in a shorter total duration of migration (Alerstam and Lindstrom 1990; Alerstam 1991; Hedenström and Alerstam 1995). Minimizing the total duration of migration should not be confused with the

birds' maximal flight speed. The maximum flight speed is faster but much more costly to maintain and is thus associated with the need for prolonged fuelling periods, resulting in a slower total speed of migration. Since it is the arrival order among individuals rather than arrival date that is most important (Kokko 1999), even small differences in migration speed could make a significant difference.

We have previously shown that long distance migrating passerines migrate with higher air speeds during spring than during autumn migration at two distant sites in Sweden (Karlsson et al. 2012). To further investigate this difference between seasons we made detailed flight speed measurements at a third site in Sweden, the Falsterbo Peninsula, where the species composition of the nocturnal passerine migrants was continuously monitored throughout the autumn and spring seasons by the daily captures at the nearby Falsterbo Bird Observatory.

The main objective of this study was to investigate if short- and long-distance migrants (among nocturnal passerine migrants) modulate their airspeed differently between autumn and spring migration. Time restrictions may exert a strong selection pressure on long-distance migrants also during autumn migration when they have to travel at high migration speeds to cover the long distances in a reasonable time. Short-distance migrants on the other hand may afford to travel slowly and be more prone to minimize energy expenditure and predation risks (Alerstam and Lindström 1990) during autumn migration. The importance of time-selection during autumn migration among long-distance migrants may also be manifested by a lower degree of selectivity of favourable wind and weather conditions for the migratory flights when compared to short-distance migrants (see for example Schmaljohann et al. 2012, where a long distance migrant showed more selectivity of winds in autumn than in spring). This was pointed out by Rudebeck (1950) as an explanation for the distinct differences in autumn migratory behaviour between the morphologically similar honey buzzard *Pernis apivorus* and common buzzard *Buteo buteo*. Honey buzzards, which are

long-distance migrants with tropical winter quarters, are much less dependent on thermals and favourable winds for their migratory flights at Falsterbo than common buzzards, presumably because the honey buzzards cannot afford to wait long periods for favourable weather (Rudebeck 1950).

If selection pressure associated with time restrictions differs between short- and long-distance migrants we expect that this will be manifested not only in different responses to weather and winds but also in different seasonal modulation patterns of airspeed. Our hypothesis is that both categories are strongly time-selected during spring migration because of competition for early arrival (see above). We therefore predict that both categories will fly at higher airspeeds (and show a lower degree of wind/weather selectivity) during spring than during autumn migration (Karlsson et al. 2012). During autumn migration we expect time-selection to be relaxed for both categories, but not so much for the long-distance migrants as for the short-distance migrants (see above). Differences in territoriality on the wintering grounds could affect the pattern of time versus energy minimization, however it is unknown whether short and long distance migrants differ in this respect. This leads to the prediction that airspeeds are more reduced during autumn compared to spring migration among short-distance migrants (which are also predicted to be more selective of favourable weather/winds during autumn) compared to long-distance migrants.

To test these predictions we will compare mean airspeeds of short- and long-distance nocturnal passerine migrants between spring and autumn migration, after correcting for the influence of altitude, wind and climb/descent. We will also take into account that mean airspeed may differ between the long- and short-distance migrants because of the differences in species composition. We expect that mean airspeed is at a slightly higher general level for short-distance migrants because of a larger proportion of relatively large-sized passerines, notably thrushes, in this group of migrants (see below), and airspeed is predicted to increase with body size (Pennycuik 2008). After correcting and accounting for all of these factors we will focus on the relative seasonal differences in airspeeds

between the two categories of passerine migrants. We will use a large sample of tracking radar data recorded during three autumn and two spring seasons (2009-2011) at Falsterbo Peninsula in south-western Sweden. We will also investigate if the two categories of migrants tend to fly under more or less favourable wind conditions during the two seasons, according to the above predictions.

## **METHODS**

Falsterbo Peninsula is a migration hot spot at the south-western tip of Sweden where migrants gather, as it is the last stretch of land before the sea crossing to Denmark or Germany. We used a tracking radar at Falsterbo Peninsula (200 kW peak power, 0.25  $\mu$ s pulse duration, 504 Hz pulse repetition frequency, 1.5° pencil beam width, X-band) to track individual targets. Methods were essentially the same as described in Karlsson et al. (2012) for earlier studies, using the same type of radar at Lund (55° 43'N, 13° 12'E) and Abisko (68° 21'N, 18° 49'E), respectively. See also Bäckman and Alerstam (2003) and Henningsson et al. (2009) for more details on the radar data processing. The radar was placed in an open area of the peninsula (55° 24' 50"N, 12° 52' 12"E, antenna 5 m above sea level). The sky was manually scanned for targets that were identified by the operator as bird targets based on the echo signature. Only targets classified as birds and showing a wing beat pattern typical for bounding flight, which is characteristic of passerine migrants, were included in this study (Bruderer et al. 2010). We tracked targets in the altitude span of 100 – 3000 m, mean altitude in the sample included here was 865 m. The radar was usually operated from just before sunset until 3-4 hours after midnight. All tracks included in this study are associated with a wind measurement within 150 meters of the birds' altitude and no more than 2 hours before or after the bird track. Wind measurements were done by releasing helium balloons with reflective foil and tracking them with the radar. To ensure that we only included birds tracked during active migration we excluded birds that were flying in the seasonally inappropriate direction, defined as track directions from 290° to 110° in autumn and from 110° to 290° in spring. Forty observations with airspeeds of <5 m/s or

141 >20 m/s, falling outside the window of expected airspeeds of passerine migrants, were also excluded.

142 The total number of tracks included in this study is 1 858.

143  
144 Equivalent airspeed was calculated by adjusting the airspeed, calculated from measured ground  
145 speed and associated wind measurements, for the difference in air density at different altitudes  
146 according to Pennycuick (2008; eq. 3 in Box 2.3 and eq. 4 in Box 15.3). By doing this, airspeeds were  
147 corrected for the change in air density to reflect the equivalent airspeed at sea level in the  
148 International Standard Atmosphere (Pennycuick 2008, ch. 2.2.1). We did not account for the local  
149 surface variation in barometric pressure, temperature or humidity (Pennycuick 2008, Schmaljohann  
150 and Liechti 2009) as this variation has a negligible effect on the birds' airspeed compared to the  
151 variation in altitude (see above-mentioned equations in Pennycuick 2008). To estimate the possible  
152 bias caused by local surface variation for the seasonal average speeds, we calculated mean  
153 barometric pressure and temperature ( $\pm$  sd) at 22:00 UTC during the nights of radar operation. For  
154 the long-distance migrants they were  $1016 \pm 5$  hPa and  $16.5 \pm 1.4$  °C in autumn and  $1016 \pm 6$  hPa  
155 and  $9.6 \pm 2.0$  °C in spring, and for short-distance migrants  $1022 \pm 5$  hPa and  $12.5 \pm 3.5$  °C in autumn  
156 and  $1020 \pm 4$  hPa and  $5.9 \pm 1.3$  °C in spring. These seasonal differences in local surface barometric  
157 pressure and temperature would have affected equivalent airspeeds by < 1% (with minutely lower  
158 airspeeds expected in spring compared to autumn because of the lower temperatures, making  
159 estimates of airspeed differences in the reverse direction conservative). Also the effect of variation in  
160 humidity is negligible (<<1%) at the moderate and cool temperatures prevailing at temperate  
161 latitudes (Weast 1964). This shows that our results of seasonal differences in airspeeds are clearly  
162 robust with respect to the possible influence of local surface conditions in barometric pressure,  
163 temperature and humidity. To be able to take the effect of wind on airspeed into account, side and  
164 head wind components were calculated in relation to the bird's heading direction.

We tracked the migrants during three autumn and two spring seasons, i.e. between 19<sup>th</sup> of August and 21<sup>th</sup> of October in 2009, 7<sup>th</sup> of April - 26<sup>th</sup> of May and 11<sup>th</sup> of August - 14<sup>th</sup> of September in 2010 and 10<sup>th</sup> of April - 31<sup>th</sup> of May and 24<sup>th</sup> of August – 24<sup>th</sup> of October in 2011. Ringing/banding of migrants has been practiced at the Falsterbo bird observatory since the 1940's (Karlsson 2009). Early in spring and late in autumn, migration passing the Falsterbo peninsula is dominated by short distance migrants such as robins, thrushes and goldcrests. Late spring and early autumn are dominated by long distance migrants such as warblers (Fig. 1; Appendix 1). We have tracked migrants during the full migration season to be able to compare early spring/late autumn with late spring/early autumn, and thereby making a broad comparison between short and long distance migrants. We considered migrants tracked from the start of the autumn season until 9<sup>th</sup> of September and from 25<sup>th</sup> of April until the end of the spring season as belonging to the migration guild of long-distance migrants. Tracks recorded from 10<sup>th</sup> of September until the end of the autumn season and from the start of the spring season until 25<sup>th</sup> of April were thus considered to include mainly short-distance migrants. Even though this division of tracks into long and short distance migration guilds is rough (e.g. the robin does not fit perfectly into the early spring and late autumn categories; Appendix 1), ringing data during the same dates and from the same location as the radar data support these groups (Fig. 1; Appendix 1). The radar sampling periods did not completely cover the whole migration period and numbers of tracks do not reflect population abundances

Birds are expected to change their equivalent airspeed in relation to wind (tail/head-wind and side-wind components) as well as in relation to their vertical speed. Hence, the effects of these variables must be accounted for in order to critically estimate effects of season (spring/autumn) and migration guild (short/long-distance migrants) on airspeed variation. This was tested in a linear mixed model with equivalent airspeed as dependent variable. Season and migration guild were included as fixed factors and side-wind component, head/tail-wind component and vertical speed as covariates. Season X migration guild was included as a fixed interaction. To account for variation between study



periods, year and the interaction between year and season were included as random effects. Analysis was performed in SAS 9.3, using proc mixed with Satterthwaite approximation of denominator df (F test, type 3 method). To test the significance of the random interaction season X year we compared models with the parameter and without by using the  $G^2$  statistic,  $G^2 = -2(\log\text{-likelihood reduced} - \log\text{-likelihood full})$  (Quinn and Keough 2002).

The difference between groundspeed and airspeed was used as a measure of the amount of wind assistance the birds gained. To investigate if the long and short distance migrants encountered very different wind situations during their differential seasonal migration periods we made a summary of surface wind conditions at 18:00 UTC (Swedish metrological and hydrological institute, 2013) over the entire time periods when data was collected (Appendix 2). Furthermore, we summarized mean and scatter of tail/headwind components that prevailed during the time periods associated with migration of mainly short- and long-distance migrants during the autumn and spring study periods (Appendix 2).

## RESULTS

There was a significant difference in mean equivalent airspeed between spring and autumn migration among both short distance ( $t$  test, two-tailed:  $t_{684} = 8.3$ ,  $P < 0.001$ ) and long-distance migrants ( $t$  test, two-tailed:  $t_{782} = 3.0$ ,  $P = 0.003$ ) with spring speeds exceeding those in autumn (Table 1, see also Fig. 2).

Mean airspeeds of the passerine migrants were plotted in relation to date in the spring and autumn seasons (Fig. 3). These diagrams show the transition from the slower, often smaller sized, long distance migrants to the faster, and often larger, short distance migrants in autumn and the other way around in spring. According to ringing data (Appendix 1) the short distance migration guild contains relatively large and fast thrushes but also a large numbers of the smaller and slower flying

European robins, *Erithacus rubecula*. These are most abundant in the beginning of the short distance migrant period in autumn and at the end of it in spring (Appendix 1).

The mixed model (Table 2) confirmed the expected influences of wind components and vertical speed on airspeed. In addition, there were significant effects of season (with airspeeds in spring exceeding those in autumn) and migration guild on airspeed (with short-distance migrants having higher airspeeds than long-distance migrants, as seen in Fig. 2), as well as a significant interaction effect between season and migration guild. Parameter values of the mixed model (Table 2) showed that this significant interaction effect reflected a more pronounced seasonal difference in airspeed among short-distance migrants (model estimates of mean airspeeds at zero wind components and zero vertical speed were 12.44 and 10.69 m/s in spring and autumn, respectively, giving a spring/autumn ratio of 1.16; Table 2) than among long-distance migrants (with corresponding values of 11.72 and 10.49 m/s and a spring/autumn ratio of 1.12; Table 2). The Season X Year interaction was significant according to the log likelihood test ( $G^2 = 6.1$ ,  $df=1$ ,  $p=0.02$ ; variance estimates of random effects : Year = 0, Season X Year = 0.144 and Residual = 5.207) and is therefore included in the model as a random effect.

Subtracting airspeed from the ground speed shows to what extent the birds' resulting flight speed is assisted (positive values of ground speed minus airspeed) or retarded (negative values) by the wind. Wind assistance will of course be beneficial for the birds by reducing both energy and time costs for the migratory flights, while flights into headwinds will be associated with increased energy costs as well as flight times. Comparing the wind effect (difference between ground speed and airspeed) between seasons and migration guild showed that short-distance migrants were flying with on average more favourable winds than long-distance migrants, especially during autumn migration ( $t$  test, two-tailed:  $t_{869} = 17.3$ ,  $P < 0.001$ ; Fig. 4a) while the difference was smaller but still statistically significant during spring migration ( $t$  test, two-tailed:  $t_{552} = 2.2$ ,  $P = 0.025$ ; Fig. 4b). Comparing the

distributions of surface winds (at 18:00 UTC for each day during the study periods) between the two migration guilds, we could see that the wind situations encountered by long distance and short distance migrants did not differ much in either season (Appendix 2), which indicates that the difference in wind effect between migration guilds did not merely reflect a difference in prevailing winds. This was also evident from the theoretically encountered tail/headwind components we calculated (Appendix 2).

## DISCUSSION

The results from this study show that nocturnally migrating passerines fly with higher airspeeds in spring than in autumn and that the difference is larger for short distance than for long distance migrants. This provides valuable confirmation that birds fly at generally higher airspeeds during spring compared to autumn (Karlsson et al. 2012; Nilsson et al. 2013). The results for the short- and long-distance migrants at Falsterbo may be compared with the corresponding general linear model (GLM) estimates of mean airspeeds at zero wind components and zero vertical speeds in other studies. In Karlsson et al. 2012, a GLM of nocturnal passerine migrants (mainly long-distance migrants) recorded at Lund showed spring and autumn speeds of 11.48 and 10.29 m/s, respectively with a spring/autumn ratio of 1.12, and at Abisko spring and autumn speeds of 11.19 and 9.39 respectively with a spring/autumn ratio of 1.19 (see Fig. 2). Similar results were found when spring and autumn airspeeds were measured for migratory swifts *Apus apus* (a long-distance non-passerine migrant) showing a spring/autumn model ratio of  $10^{0.049} = 1.12$  (Henningsson et al. 2009). The seasonal differences we found at Falsterbo were thus highly similar to the differences earlier recorded for nocturnal passerine migrants at the other sites in southern (Lund) and northern Sweden (Abisko; Fig. 2; Karlsson et al. 2012) as well as for the swifts (Henningsson et al. 2009). The magnitude of difference in mean airspeed between spring and autumn fits well with the predicted difference between energy minimizing and time minimizing migration (Karlsson et al. 2012).

When comparing short- and long distance migrants we see that the seasonal effect on airspeed was significantly larger in the short distance migrant group (Table 2). The significant difference in spring/autumn airspeed ratio between short- and long-distance migrants, as demonstrated in this study, may be due to a stronger relative reduction in autumn airspeed among the short-distance migrants (according to the hypothesis explained in the introduction) and/or a stronger relative increase in spring airspeed among the short-distance migrants. The main breeding areas for migrants passing Falsterbo seem to be similar for short- and long-distance migrants according to ringing recoveries (Roos 1984; Karlsson 2009) including mainly the southern and central parts of Fennoscandia (see map in Karlsson et al. 2012). This means that there is little reason to expect more sprint migration in one or the other category of migrants (Alerstam 2006). Hence it seems most likely that the enhanced spring/autumn airspeed ratio among short-distance migrants is due to reduced autumn speeds associated with relaxed time pressure during autumn in agreement with our main hypothesis.

Birds with higher body mass require higher airspeeds to fly (Pennycuick 2008). The overall higher airspeed of short-distance migrants compared to long-distance migrants was therefore expected because of larger mean body size of the former category (including many thrushes – see Appendix 1).

The results of this study suggest that migrating birds modulate their airspeed, and also their selectivity of winds for departure on migratory flights, in a fine-tuned way in relation to changes in the selection pressure to reduce time costs for migration. Short- and long-distance migrants differ in this modulation between spring and autumn migration, maybe because the interseasonal difference in importance of time selection differs between the two categories of migrants. Such a fine-tuned modulation of airspeed among migrating birds may seem highly surprising, not least when considering that changes in airspeed from maximal range airspeed ( $V_{mr}$ ) to minimum time airspeed ( $V_{mt}$ ) lead to only small gains in resulting migration speed (Houston 2000; Alerstam 2003; Karlsson et

al. 2012). However, even small time savings in spring may be important, because in many cases it is probably the arrival order among individuals rather than absolute time intervals that are important for the birds' fitness (Kokko 1999; Karlsson et al. 2012).

Many factors may affect seasonal differences in general in airspeed even after accounting for the effects of altitude, wind and vertical flight speed. The birds may differ between seasons with respect to body mass or wing morphology but, as discussed by Karlsson et al. (2012), these factors are not likely to have affected the results for the nocturnal passerine migrants in Sweden. Furthermore, birds may change airspeed with age and there may be a selective loss of individuals in poor condition (possibly associated with relatively slow airspeeds) during the non-breeding season. Depending on condition and situation birds may also increase their airspeed in final sprint flights to their destinations (Alerstam 2006; Karlsson et al. 2012). Airspeed may also be modulated in relation to fuel deposition rate as minimum time airspeed,  $V_{mt}$ , is dependent on energy deposition rate at stopover sites (Alerstam and Lindström 1990; Hedenström and Alerstam 1995). Furthermore, mean airspeeds will also be affected by possible changes in the relative species composition, although we expect species composition within the migration guilds to be broadly the same in autumn and spring. Given these possible sources of variation of airspeed, the hypothesis that birds modulate their airspeed in a fine-tuned way between spring and autumn migration in relation to the degree of interseasonal difference in selection pressure for time minimization, needs to be scrutinized by further challenges and tests.

When the effect of wind is taken into account we find further differences between the short and long distance migrants. Long distance migrants often travelled with airspeeds exceeding ground speeds in autumn, meaning that they were flying in headwinds. Short distance migrants on the other hand had higher ground speeds than airspeeds in both spring and autumn and seem to be benefiting by some wind assistance (Fig. 4). Similar general wind conditions prevailed for the short- and long-distance

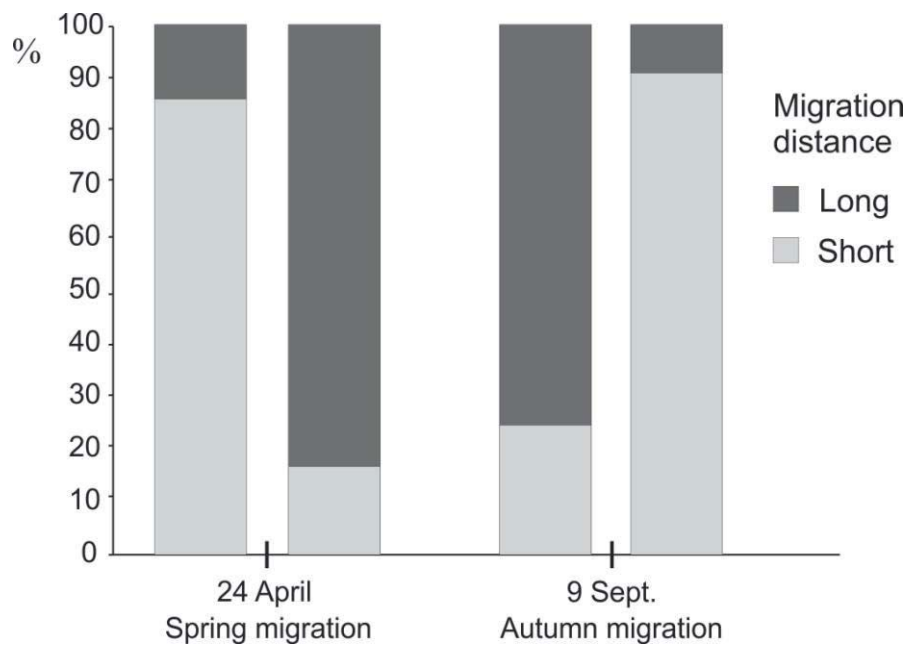
migrants during both autumn and spring (based on comparisons of winds recorded at Falsterbo weather observatory, Swedish Meteorological and Hydrological Institute 2013, between the periods of passage by the short- and long-distance groups of migrants; Appendix 2). This indicates that the differences in wind assistance between these categories were due to differences in selectivity of winds to a higher degree than to different weather conditions during the early and late parts of autumn and spring migration. This is in agreement with our previous studies showing that long distance migrants receive very little wind assistance on average (Karlsson et al. 2011). This is possibly also a sign of increased flexibility among the short distance migrants, being able to wait out good nights while the long distance migrants must fly on a larger proportion of nights, including many with unfavourable winds. Waiting for nights with good wind conditions will save energy, but prolong the migration. Therefore, in a situation with variable wind conditions, wind selectivity is highly beneficial in energy minimizing migration, when the cost of flight transport is minimized, but not to the same degree in time minimizing migration when waiting for the best winds may incur an important time cost (although favourable tailwinds will of course always be preferable) (Alerstam 1979).

At the population level, a large scale study of population occurrences of North American birds over the year found that most populations migrated faster in spring than in autumn, and that the difference in seasonal migration speed increased with increasing migration distance (La Sorte et al. 2013). This is in contrast to our findings that short distance migrants show a larger interseasonal difference in airspeed compared to long distance migrants. However, total migration speed, as measured by La Sorte et al. (2013), is affected by many factors besides the birds' airspeed regulation (Nilsson et al. 2013). It will be an interesting task to investigate how individual speed modulation among different categories of migrants is related to differential total seasonal migration performance at the individual and population levels.

347 **ACKNOWLEDGMENTS**

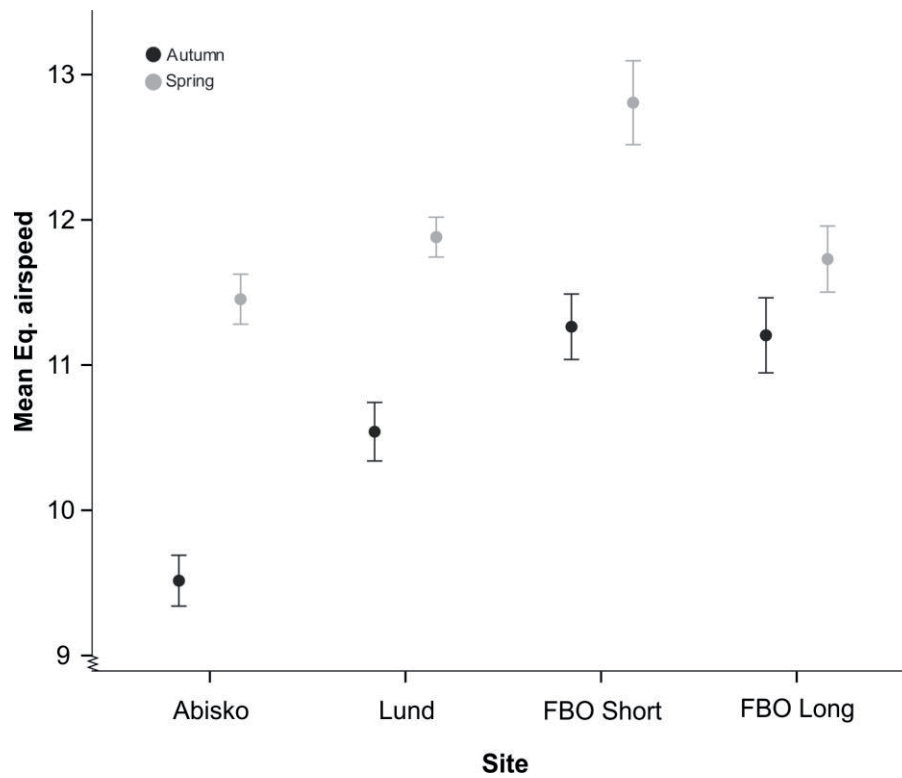
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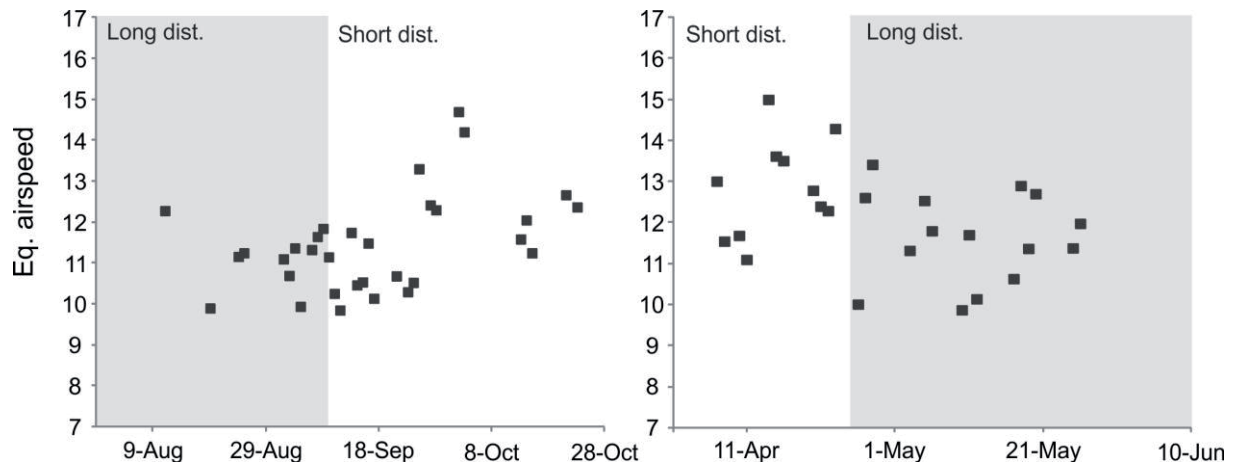


**Fig. 1** Percentage of short distance migrants (light grey) and long distance migrants (dark grey) among nocturnal passerine migrants caught early (before 24/4 and 9/9) and late (after 24/4 and 9/9) in spring and autumn, respectively, at Falsterbo Bird Observatory (during the study seasons 2009-2011). Based on capture data in Appendix 1

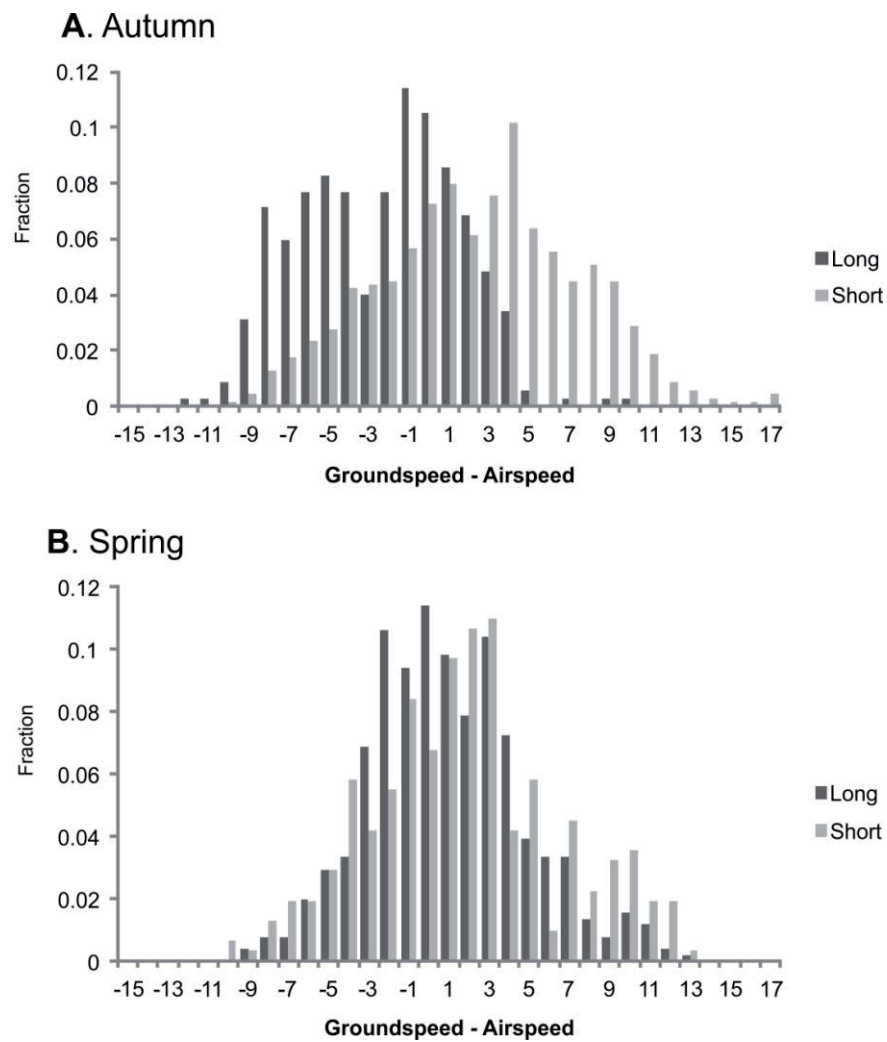




**Fig. 2** Mean equivalent airspeed with 95 % confidence intervals of nocturnal passerine migrants in Abisko and Lund (Karlsson et. al. 2012) and Falsterbo (this study) during autumn (dark grey) and spring (light grey). Falsterbo (FBO) data is divided into short (short) or long distance (long) migrants based on time of passage at Falsterbo



**Fig. 3** Mean equivalent airspeed per calendar day over the autumn and spring season. Grey and white background shows the time period when tracks are assigned to the long distance (long dist.) and short distance (short dist.) migrant guild respectively, according to ringing data. All years (2009, 2010, 2011 in autumn and 2010, 2011 in spring) are combined, days with less than 10 tracks are excluded (80 tracks excluded; total N= 1778)



**Fig. 4** Distribution of difference between ground speed and air speed in (A) autumn and (B) spring. Long distance migrants in dark grey ( $n = 351$  in autumn and  $n = 511$  in spring) and short distance migrants in light grey ( $n = 687$  in autumn and  $n = 309$  in spring)

**Table 1 Mean values and standard deviations of flight speeds and wind conditions for nocturnal passerine migrants at Falsterbo**

		<b>Autumn</b>	<b><i>sd</i></b>	<b>Spring</b>	<b><i>sd</i></b>
<b>Short distance migrants</b>	Eq. Airspeed, m/s	11.26	3.00	12.81	2.58
	Ground speed, m/s	13.69	4.77	14.56	5.20
	GS-AS, m/s	1.95	4.94	1.17	4.76
	Altitude, m	865	461	904	366
	Vertical speed, m/s	0.07	0.68	0.06	0.47
	Side wind comp.	7.05	4.32	5.00	3.55
	Tail/head wind comp.	-1.40	5.87	-0.24	5.06
	<b>N</b>	<b>687</b>		<b>309</b>	
<b>Long distance migrants</b>	Eq. Airspeed, m/s	11.21	2.46	11.73	2.62
	Ground speed, m/s	8.77	3.74	12.70	4.82
	GS-AS, m/s	-2.89	3.87	0.45	3.88
	Altitude, m	797	366	888	356
	Vertical speed, m/s	0.03	0.77	0.25	0.73
	Side wind comp.	4.17	2.77	4.96	2.98
	Tail/head wind comp.	-4.55	3.65	-1.11	4.35
	<b>N</b>	<b>351</b>		<b>511</b>	

*Mean values and standard deviations of equivalent airspeed, ground speed, ground speed - airspeed (GS-AS), altitude, vertical speed, side wind component and tail/head wind component for nocturnal passerine migration in Falsterbo. Tracks of long or short distance migrants were distinguished according to the time of passage at Falsterbo (see text and Appendix 1)*

387 **Table 2 Results from mixed model analysis of equivalent airspeed: regression**  
388 **estimates, test data and significance**

Parameter	Regr. Estimate (m/s)	Std. Error	95% Confidence Interval		df denom (df num=1)	F	Sig.
			Lower Bound	Upper Bound			
Intercept	11.72	0.30	10.84	12.61	-	-	0.000
Autumn	-1.23	0.39	-2.37	-0.10	2.98	16.07	0.028
Spring	-	-	.	.	.	.	.
Short Distance	0.72	0.17	0.40	1.04	1851	15.33	0.000
Long Distance	-	-	.	.	.	.	.
Sidewind Component	0.09	0.02	0.06	0.12	1850	37.44	0.000
Tailwind Component	-0.05	0.01	-0.07	-0.02	1824	17.69	0.000
Vertical speed	-2.01	0.08	-2.16	-1.85	1851	656.51	0.000
Autumn X Short Dist.	-0.52	0.23	-0.98	-0.07	1851	5.17	0.023
Autumn X Long Dist.	-	-	.	.	.	.	.
Spring X Short Dist.	-	-	.	.	.	.	.
Spring X Long Dist.	-	-	.	.	.	.	.

389 *Dependent variable is equivalent airspeed. Season and migration guild are fixed factors, side-wind*  
390 *component, tail/head wind component and vertical speed are covariates. Interactions were season X*  
391 *migration guild (fixed) and year X season (random). For variance estimates of random factors, see*  
392 *results*

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## Appendix 1

Capture data for long- and short-distance migrant passerine species at Falsterbo during early and late radar study periods in autumn and spring 2009-2011

### Autumn capture data

			2009		2010		2011		Total	
Species		Mig. Distance	Early	Late	Early	Late	Early	Late	Early	Late
Chiffchaff	<i>Phylloscopus collybita</i>	Short	2	157	21	1	5	307	28	465
Blackbird	<i>Turdus merula</i>	Short	3	38	0	1	1	27	4	66
Goldcrest	<i>Regulus regulus</i>	Short	0	430	1	2	0	233	1	665
Euro. Robin	<i>Erithacus rubecula</i>	Short	20	2031	537	79	99	1283	656	3393
Redwing	<i>Turdus iliacus</i>	Short	0	19	0	0	0	25	0	44
Song Thrush	<i>Turdus philomelos</i>	Short	0	155	3	1	1	293	4	449
Other short dist. mig.		Short	1	3	1	0	0	1	2	4
<b>Total</b>			<b>26</b>	<b>2833</b>	<b>563</b>	<b>84</b>	<b>106</b>	<b>2169</b>	<b>695</b>	<b>5086</b>
Wood Warbler	<i>Phylloscopus sibilatrix</i>	Long	3	0	33	0	3	1	39	1
Icterine Warbler	<i>Hippolais icterina</i>	Long	7	0	30	1	10	0	47	1
Willow warbler	<i>Phylloscopus trochilus</i>	Long	177	41	611	45	371	80	1159	166
Redstart	<i>Phoenicurus phoenicurus</i>	Long	51	30	101	20	91	71	243	121
Eura. Reed Warbler	<i>Acrocephalus scirpaceus</i>	Long	4	0	28	1	6	4	38	5
Eura. Blackcap	<i>Sylvia atricapilla</i>	Long	19	51	98	22	37	59	154	132
Garden Warbler	<i>Sylvia borin</i>	Long	35	18	201	17	38	10	274	45
Whitethroat	<i>Sylvia communis</i>	Long	30	4	45	4	12	3	87	11
Lesser Whitethroat	<i>Sylvia curruca</i>	Long	7	9	48	5	13	8	68	22
Other long dist. mig.		Long	3	2	16	1	2	3	21	6
<b>Total</b>			<b>336</b>	<b>155</b>	<b>1211</b>	<b>116</b>	<b>583</b>	<b>239</b>	<b>2130</b>	<b>510</b>
% short distance migrants			7	95	32	42	15	90	25	91
% long distance migrants			93	5	68	58	85	10	75	9

Autumn capture data from Falsterbo bird observatory during the study periods, 19/8 to 21/10 in 2009, 11/8-14/9 in 2010 and 24/8-24/10 in 2011. Captures are divided into "early", before 10/9, and "late", after (and including) 10/9, and the percentages in each category are given (Falsterbo Bird Observatory, 2013). Species of nocturnal passerine migrants are divided into two categories – short-distance migrants with winter quarters in Europe and the Mediterranean region and long-distance migrants with winter quarters in Africa south of Sahara



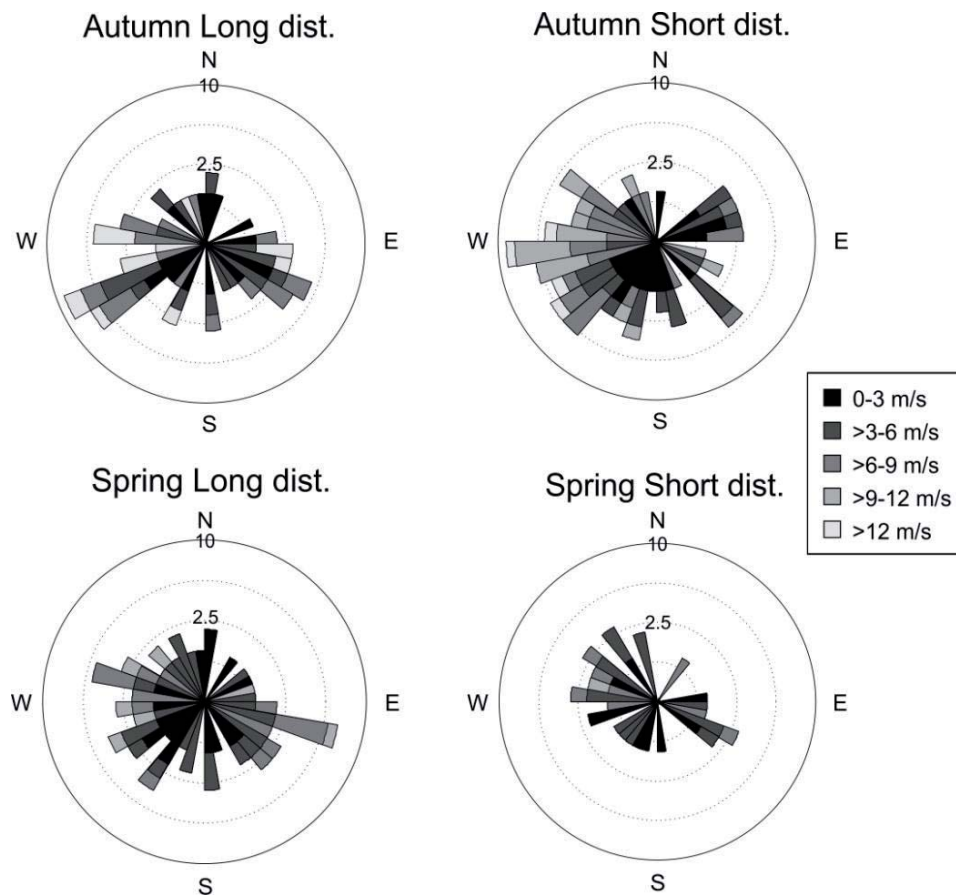
## Spring capture data

			2010		2011		Total	
Species		Mig. Distance	Early	Late	Early	Late	Early	Late
Chiffchaff	<i>Phylloscopus collybita</i>	Short	30	47	52	82	82	129
Blackbird	<i>Turdus merula</i>	Short	17	19	5	11	22	30
Goldcrest	<i>Regulus regulus</i>	Short	4	1	10	6	14	7
Euro. Robin	<i>Erithacus rubecula</i>	Short	326	238	706	208	1032	446
Redwing	<i>Turdus iliacus</i>	Short	4	0	2	0	6	0
Song Thrush	<i>Turdus philomelos</i>	Short	11	5	17	16	28	21
Other short dist. mig.		Short	0	1	0	5	0	6
<b>Total</b>			<b>392</b>	<b>311</b>	<b>792</b>	<b>328</b>	<b>1184</b>	<b>639</b>
Wood Warbler	<i>Phylloscopus sibilatrix</i>	Long	0	0	1	4	1	4
Icterine Warbler	<i>Hippolais icterina</i>	Long	0	16	0	20	0	36
Willow warbler	<i>Phylloscopus trochilus</i>	Long	26	1310	137	1093	163	2403
Redstart	<i>Phoenicurus phoenicurus</i>	Long	2	210	18	104	20	314
Eura. Reed Warbler	<i>Acrocephalus scirpaceus</i>	Long	0	8	0	8	0	16
Eura. Blackcap	<i>Sylvia atricapilla</i>	Long	1	54	15	118	16	172
Garden Warbler	<i>Sylvia borin</i>	Long	0	76	0	23	0	99
Whitethroat	<i>Sylvia communis</i>	Long	0	56	0	66	0	122
Lesser Whitethroat	<i>Sylvia curruca</i>	Long	0	49	0	99	0	148
Other long dist. mig.		Long	0	14	0	6	0	20
<b>Total</b>			<b>29</b>	<b>1793</b>	<b>171</b>	<b>1541</b>	<b>200</b>	<b>3334</b>
<b>% short distance migrants</b>			93	15	82	18	86	16
<b>% long distance migrants</b>			7	85	18	82	14	84

Spring capture data from Falsterbo bird observatory during the study periods, 7/4 -26/5 in 2010 and 10/4-31/5 in 2011. Captures are divided into “early”, before 25/4, and “late”, after (and including) 25/4, and the percentages in each category are given (Falsterbo Bird Observatory, 2013.) Species of nocturnal passerine migrants are divided into two categories – short-distance migrants with winter quarters in Europe and the Mediterranean region and long-distance migrants with winter quarters in Africa south of Sahara

## Appendix 2

**Wind conditions prevailing during the radar study periods for long- and short-distance passerine migration at Falsterbo 2009-2011.**



Circular histogram of wind directions (bars) and wind speeds (m/s, grey scale) of the study period at ground level, 18:00 UTC (Swedish meteorological and hydrological institute, 2013). The area of the wedges represents the frequency, see numbers in the circles. Wind direction is from which direction the wind is blowing

## Theoretical wind components

		Dates	Side wind comp.	SD	Tail/head wind comp.	SD	N
<b>Autumn</b>	<b>Long dist.</b>	19/8-9/9 2009, 11/8-9/9 2010, 24/8-9/9 2011	5.48	3.72	-1.64	3.55	68
	<b>Short dist.</b>	10/9-21/10 2009, 10/9-14/9 2010, 10/9-24/10 2011	5.77	3.72	-1.42	4.00	92
<b>Spring</b>	<b>Long dist.</b>	25/4-26/5 2010, 25/4-31/5 2011	4.55	3.09	0.72	2.91	68
	<b>Short dist.</b>	7/4-24/4 2010, 10/4-24/4 2011	4.21	2.58	-0.36	2.79	33

*Wind components prevailing during the radar study periods for long- and short-distance passerine migration at Falsterbo 2009-2011. Mean side wind and head/tail wind components and standard deviations were calculated for a bird with fixed heading (0° in spring and 180° in autumn) using surface wind at 18:00 UTC in Falsterbo. N, number of nights. Wind measurements from the Swedish Meteorological and Hydrological Institute, <http://www.smhi.se/klimatdata/meteorologi/dataserier-2.1102>*