To fly or not to fly depending on winds: shorebird migration in different seasonal wind regimes

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Migratory birds are predicted to adapt their departure to wind, changing their threshold of departure and selectivity of the most favourable winds in relation to the mean, scatter and skewness of the wind regime. The optimal departure behaviour depends also on the importance of time and energy minimization during migration and on the ratio of cost of flight to cost of resting and waiting for more favourable winds. We compared departure and flight activity of shorebirds migrating in contrasting wind regimes during autumn (high probability of wind resistance) and spring (high probability of wind assistance) in southern Scandinavia, using data obtained by radiotelemetry, radar tracking and visual observations. The shorebirds changed their threshold for departure in relation to wind between the two seasons, flying almost exclusively with wind assistance in spring but regularly with wind resistance during autumn. The degree of wind selectivity in relation to the distributions of available wind effects was similar during autumn and spring indicating that reducing time and energy costs for migration was important during both seasons. These results demonstrate that migratory birds change departure behaviour in relation to the prevailing wind regime. It remains unknown whether they change behaviour not only seasonally but also in different zones along the migration route and whether they respond to differences not only in mean wind conditions but also in scatter and skewness between wind regimes. Our study indicates the possible existence of an adaptive flexibility in responses to wind regimes among migratory birds.

Animals moving in air or water are dependent on winds and water currents for their transport efficiency. During migratory movements the motion of the fluid, air or water, provides both important assistance or opposition or produces lateral displacement (drift) which might make orientation difficult. For example, some species of large nocturnal migrating moths show very high selectivity of favourable winds while passerine birds are less selective (Erni et al. 2002; Chapman et al. 2010; Alerstam et al. 2011; Karlsson et al. 2011). Wind affects both travelling speed and cost of transport and several studies have demonstrated that high migratory activity among birds often coincides with favourable winds (e.g. reviewed in Richardson 1978, 1990; Liechti 2006). However, there are important differences in the degree of wind selectivity between different bird species and categories of migrants: some species are highly selective of following winds while others are only weakly selective (Alerstam 1978) or lack any distinct preference for tail wind conditions (Thorup et al. 2006;

Karlsson et al. 2011). Many arctic-breeding shorebirds fly extremely long distances between their breeding areas in the north and stopover and wintering sites further south (e.g. Piersma & Jukema 1990; Gill et al. 2009; Klaassen et al. 2011a) and they predominantly migrate on occasions and at altitudes with favourable winds (Richardson 1979; Gudmundsson 1994; Alerstam & Gudmundsson 1999; Green 2004; Hedenström et al. 2009; Ma et al. 2011). However, in situations/areas where unfavourable winds dominate during the migratory period, migration also occurs in opposing winds (Williams 1985; Alerstam & Gudmundsson 1999). Hence it is of interest to study how arctic shorebirds use winds during their long migratory journeys.

Sweden is situated along one of the major flyways of arctic-breeding shorebirds, the East Atlantic Flyway. Shorebirds breeding in arctic Russia and wintering both in western Africa and western Europe migrate over southern Sweden on their way to and from the southern North Sea where they gather during both autumn and spring to accumulate fat and protein and to moult. Hence, southern Sweden is a suitable area for studying the migratory behaviour of these birds (Gudmundsson 1994; Green 2004).

Winds over southern Scandinavia are predominantly westerly during both spring and autumn (e.g. Supplementary materials in

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Kemp et al. 2010). By way of example, winds during spring and autumn migration periods of shorebirds (see below) during a 10-year period were blowing from the two westerly quadrants on 77% and 71% of the days, respectively. For shorebirds that migrate along an axis about northeast (spring)/southwest (autumn), this means that they can expect to encounter mostly favourable winds during spring and unfavourable ones during autumn.

The objective of this study was to investigate the effects of these contrasting seasonal wind regimes (in relation to the birds' migratory direction) on the shorebirds' responses to and selectivity of winds for their migratory departures and flights. We therefore compared the seasonal relationships (spring versus autumn migration) between wind assistance/resistance and the shorebirds' departure and flight activity using three different approaches: (1) radiotelemetry, (2) tracking radar and (3) visual telescope observations. Specifically, we addressed two main questions. (1) To what degree did the shorebirds differ in their readiness to depart and fly in more or less favourable winds during spring and autumn, under the widely different wind regimes? (2) Did the shorebirds differ in wind selectivity between the two seasons and, if so, was this because they avoided the most unfavourable winds and/or preferred the most favourable winds?

METHODS

Permission to perform this study was given by the Ethical Committee of Lund University (permissions no 14204-06 and 1427-10).

Radiotelemetry

Autumn

Dunlins, *Calidris alpina*, were caught on migration at Ottenby Bird Observatory (56°12′N, 16°24′E), situated on the southernmost point of the island of Öland (southeast Sweden) in the Baltic Sea, using 'Ottenby' walk-in traps (Lindström et al. 2005). Dunlins were captured between 26 July and 13 August 2007 and between 6 August and 11 September 2008. After capture the birds were fitted with small radiotransmitters on their backs (Holohil BD-2, Holohil Systems Ltd., Ontario, Canada, transmitter mass 0.9 g, 1.8% of the average body mass, 2.2% of the lightest bird's weight). In a small area (ca. 1×1 cm) on the rump of the birds the feathers were cut down to 1 cm length. The transmitters were then glued to the clipped feathers with Super Attack glue, with the thin whip antenna protruding backwards over the tail. After the glue had hardened for a few minutes the birds were released at the catching site. By using flat transmitters glued on the rump of the birds any negative aerodynamic effects of the transmitters became negligible (Bowlin et al. 2010) and we did not notice any adverse effects of the transmitters on the birds in this study. The transmitters would have been lost naturally at the next moult. Altogether, 20 birds in 2007 (15 adults, five juveniles) and 25 birds (five adults, 20 juveniles) in 2008 were equipped with radiotransmitters.

We searched for the birds in the stopover area with directional antennas and hand-held portable receivers twice each day to determine when the dunlins had departed from the area. We continued to search for the birds the following 2 days to be sure that the birds had left the area. The area searched ranged from the southern tip of Öland (where the birds were trapped) to a small bay about 3 km north of the catching site. This area includes all suitable stopover areas (grazed shores and sand flats) in the vicinity of Ottenby and the birds were unlikely to move further north out of this area. This assumption is further supported by ringing recoveries 1 day after capture: only one of 24 dunlins was recovered in the northeast sector whereas the others were recovered in

southerly or westerly directions (J. Grönroos, M. Green & T. Alerstam, unpublished data). Hence, birds disappearing from the area had most likely departed on continued migration towards the wintering area. The signals from these transmitters can be registered at a range of up to about 1 km in open areas when the bird is on the ground (J. Grönroos, personal observations). When up in the air reception distance is much longer (see below). We scanned the area during the periods 26 July–20 August 2007 and 6 August–20 September 2008 (i.e. when we had transmitters in the area), in total 65 days. Some dunlins departed on the same days and the total number of 'departure days' was 29. The 'nondeparture days' totalled 36.

Of the 45 birds released with radiotransmitters, we recorded the actual departure of three, while in 42 cases we recorded the time interval when departure must have occurred. Many shorebird species initiate migration some hours before local sunset (Alerstam et al. 1990; Piersma et al. 1990a, b; Gudmundsson 1994), but they may also start migration early in the morning (personal observations). Departure was assumed to take place within 3 h before sunset but if a bird was released/recovered after sunset but then never registered again we assumed it had left the area the next morning.

Migration flight tracks were recorded by measuring the vanishing direction of transmitter signals with a hand-held compass. Birds could be tracked for up to 4 min when departing, during which time they would cover approximately 4 km.

Spring

Bar-tailed godwits, *Limosa lapponica*, were captured on the Dutch island Texel (53°03′N, 04°48′E), with a large wind-driven pull-net, a so called 'wilsternet' (Jukema et al. 2001), between 18 and 29 May 1999–2001 and fitted with radiotransmitters (Holohil BD-2G, Holohil Systems Ltd., Ontario, Canada, transmitter mass 1.75 g, 0.6% of the average body mass, 0.9% of the lightest bird's weight, expected battery lifetime 6 weeks) in the same way as described for dunlins above. A total of 66 birds (17 in 1999, 28 in 2000 and 21 in 2001) were equipped with radiotransmitters. In south Sweden (approximately 600 km northeast of Texel), automatic receiver stations were used to scan for the godwits and to record the signals. The receivers were placed along a 75 km transect running from northwest to southeast, perpendicular to the expected direction of migration (from 55°55′N, 12°50′E to 55°25′N, 13°50′E). Six receiver stations were used in 1999 and 10 in 2000–2001. From data logged by the automatic receiver stations it was possible to decide whether and when a transmitter-carrying bird had passed the transect. The receiver stations were active on 46 days (10 in 1999, 17 in 2000 and 19 in 2001) and during these the timing of passage for 39 birds (59%) was recorded. As several birds passed southern Sweden on the same days, the total number of 'departure days' was 24 and the 'nondeparture days' totalled 22. The godwits were flying nonstop and passed southern Sweden less than 10 h after their departure from the North Sea region. Details of methods and assumptions used for the radiotagged birds are given in Green et al. (2002).

Radar Tracking

Tracks of migrating flocks of shorebirds were recorded at three sites in Scania, South Sweden. Spring-migrating birds were tracked at Lund (55°42′N, 13°12′E) by using a tracking radar (X-band, 200 kW peak power, pulse duration 0.25 μs, pulse repeat frequency 500 Hz, 1.5° pencil beam width), between 17 May and 9 June 1998–2001. Autumn-migrating birds were tracked with mobile tracking radar (X-band, 40 kW peak power, pulse duration 0.3 μs, pulse repeat frequency 1800 Hz, 2.2° pencil beam width) at

Vitemölla at the Baltic Sea coast (55°42′N, 14°12′E) and Björka, in south-central Scania (55°39′N, 13°37′E) between 15 July and 25 September 1982, 1984, 1986, 1989 and 1990. The radars were operated manually and data on the range, elevation and azimuth of the flocks were recorded by a computer. Flocks of shorebirds were tracked for 1–14 min. The range of the radars was about 20 km for large flocks and smaller flocks could be tracked at distances up to 10 km. For a more detailed description of radar tracking in Lund see Green (2004) and at the other localities see Alerstam (1985). Most likely, only a few shorebird species contributed with significant numbers to the late spring passage of flocks over Lund (evening and night passage). These are grey plover, *Pluvialis squatarola*, ringed plover, *Charadrius hiaticula*, red knot, *Calidris canutus*, sanderling, *Calidris alba*, dunlin, bar-tailed godwit and turnstone, *Arenaria interpres*, as supported by visual telescope observations of some of the flocks. During autumn migration (daytime and evening passage) all shorebird flocks were visually identified (by observations with a telescope aligned with the radar beam) and belonged to the species grey plover, ringed plover, red knot, dunlin, little stint *Calidris minuta*, bar-tailed godwit and turnstone. The dunlin was the most abundant species in autumn.

Telescope Tracking

Observations of migrating shorebirds were carried out during the period 26 July to 15 October 2006–2008 at Ottenby Bird Observatory (see above). Observations were made on 36 days. The observation time on each day was not standardized, but 82% of the observations were made between 1730 and 2030 hours (Swedish summer time = GMT + 2 h) and 12% between 0530 and 0830 hours. Migrating flocks were normally located by using $10\times$ binoculars and later tracked in $20-60\times$ telescopes until they vanished from sight. Telescopes were equipped with azimuth scales and were carefully aligned to give geographical compass bearings. The following data were recorded to determine track directions of the birds: (1) the compass bearing ($b_1°$) and (2) estimated horizontal distance (d_1) from the observer to the bird flock when the telescope tracking started, which normally occurred when the flock passed relatively near the observer (mean: 120 m, range 0–600 m); (3) the time of telescope tracking until the flock vanished from sight; and (4) the vanishing bearing ($b_2°$). The flight distance covered by the birds during the time of tracking (d_2) was estimated by assuming that the birds travel with a speed of 16 m/s (Alerstam et al. 2007; M. Green, personal observation) which is a normal flight speed of dunlins (which comprise 95% of the flocks, personal observations). The angle for parallax compensation ($\beta°$) could be calculated from

$$\beta = \arcsin\left[\frac{d_1}{d_2}\cdot\sin\left(b_1 - b_2\right)\right]$$

The flight direction of the flock is then determined as ($b_2 + \beta$). The angle β will be positive or negative depending on whether the flock passed to the left or right, respectively, of the observer facing the vanishing bearing. To avoid large errors in estimated flight directions we have only included observations with an effective tracking time of at least 1 min. Mean tracking time was 2 min 35 s (maximum 10 min 13 s) and mean absolute angle for parallax compensation was only 2.7° (0°–11°). Estimated flight directions were robust in relation to potential bias caused by the parallax compensation or assumptions about airspeed (16 m/s). Restricting the analyses to include only flight directions with parallax angles less than 2° or changing assumptions about flight speed from 16 to 13 m/s (mean wind effect at Ottenby: −3 m/s) affected mean flight directions by only 0.5° which shows that track direction estimates

are reliable with high accuracy. All shorebird flocks were identified and belonged to the species dunlin, red knot, bar-tailed godwit, sanderling and turnstone.

Wind Data

Wind data for the radiotelemetry in autumn and telescope trackings were obtained from the Swedish Meteorological and Hydrological Institute (SMHI) collected at the local weather station (Ölands Södra Udde). The weather station was located at the site where captures and observations were made and data were collected every hour. The wind direction was given in exact degrees and wind velocity in m/s. Wind data for the radiotelemetry in spring were collected from the European Meteorological Bulletin (EMB, Deutches Wetterdienst; see Green & Piersma 2003 for details). EMB gives wind data from different pressure levels, corresponding to different altitudes, twice a day, 0000 and 1200 GMT (ground-level winds are measured and winds at other pressure levels are calculated). We used wind data from ground level, the 850 hPa level (about 1.5 km altitude) and 700 hPa level (about 3 km altitude). We used departure wind data given for a station in the eastern Wadden Sea for the time closest to estimated departure (based on recorded passage in south Sweden) of our birds with radiotransmitters. We then selected the data from the altitude giving the best wind support, assuming that birds adjusted flight altitude to prevailing winds (see Green & Piersma 2003).

Wind data for radar tracking were collected locally by tracking helium-filled balloons carrying an aluminium foil reflector. Wind profiles were usually measured up to 2000–3000 m altitude.

To calculate the distributions of prevailing winds during the spring and autumn migration periods additional wind data were obtained from the NCEP/NCAR Reanalysis project provided by the NOAA/OAR/ESRL PSD, Boulder, CO, U.S.A. (http://www.ersl.noaa.gov/psd/; Kalnay et al. 1996). These data consist of west–east (u-winds) and south–north (v-winds) wind components, which were combined into single wind vectors (i.e. direction and strength of the wind). Wind data were extracted from the 2.5° grid lying in the middle of the migration corridor between the Wadden Sea and Öland (55°N 12.5°E) at the 925 hPa pressure level, which corresponds to an altitude of about 750 m above sea level (close to the mean altitude of migrating shorebirds recorded in our study). The temporal resolution of these wind data was every 6 h, and we used the mean wind data for each day during the peak spring (20–31 May) and autumn (15 July–31 August) migration periods during a time interval of 10 years (1999–2008).

Hence, we collected wind data from four different sources: the local weather station at Ottenby (radio- and telescope telemetry in autumn), a weather station in the eastern Wadden Sea (radiotelemetry spring), helium-filled balloons released at the sites of the radar (radar tracking autumn and spring) and from the NCEP/NCAR Reanalysis project (mean wind data during peak autumn and spring migration periods).

To estimate the wind effect (ground speed minus airspeed, that is, the wind assistance or resistance that the flying bird would get: positive in following winds and negative in opposed winds) for radio- and telescope-tracked birds, we first calculated the expected ground speed (G) associated with each wind measurement from the relationship:

$$G = \sqrt{A^2 - (W\cdot\sin\alpha)^2} + W\cdot\cos\alpha$$

where A is the airspeed of the birds, W is wind speed and α the angle between wind and track directions (with $\alpha = 0°$ corresponding to tail winds and $\alpha = 180°$ to head winds; cf. Piersma & Jukema 1990; Piersma & van de Sant 1992). For radiotracked

birds we assumed that shorebirds fly with a fixed airspeed of 16 m/s during autumn (Alerstam et al. 2007; M. Green, personal observation) and 17 m/s during spring (see Green & Piersma 2003). We used a flight direction of 63° (northeast; spring) from the Wadden Sea to the southeast coast of Sweden (see Green & Piersma 2003) and 236° (southwest; autumn) for waders departing from Ottenby (mean track direction obtained from telescope tracking). The wind effect was then determined as ground speed minus airspeed $(G - A)$. Expected seasonal distributions of wind effects were calculated with the same assumptions as for radiotracked birds, based on daily wind data from the peak spring and autumn migratory periods. For the autumn distribution of potential wind effect there were seven cases when opposed winds were so strong that the wind effect was <-16 m/s which means that the birds would move backwards (towards $236 - 180 = 56°$) had they departed in these winds to fly along the 236/56° axis. One case where strong winds made it impossible for the birds to fly along this axis was excluded from the autumn wind effect distribution.

For radar-tracked birds airspeeds were calculated by vector subtraction of wind velocity at the altitude at which the birds were flying from the birds' track vector over the ground (track direction and ground speed) and wind effects were calculated by subtracting the calculated airspeed from the measured ground speed. Flight directions and wind effects for the telescope-tracked flocks were calculated assuming that the birds were travelling with a speed of 16 m/s (Alerstam et al. 2007; M. Green, personal observation). Flight directions were used to calculate the wind effect of each flock.

Data Analysis

Statistical testing was done with SPSS for Windows, version 18.0 (SPSS Inc., Chicago, IL, U.S.A.). The departure behaviour among dunlins migrating from Ottenby during autumn was analysed in a logistic regression model. The dependent variable was departure decision (departure or no departure). We included wind effect and year as well as the interactions in the model, and variables were then removed from the model in a backward stepwise process by excluding nonsignificant $(P > 0.05)$ variables. Paired t tests (two tailed) were used to analyse the difference in wind effect between days of departure and the preceding day for radiotracked dunlins during autumn migration. Differences in wind effect between autumn and spring migration of radio- and radar-tracked waders were tested with t tests. The distribution of wind effects experienced by birds and the seasonal expected distribution of wind effects (over a 10-year period) during peak migration were compared with a chi-square test and the overlap index:

$$\frac{2\sum_i m_i b_i}{\left(\sum_i m_i^2 + \sum_i b_i^2\right)},$$

where m and b are the frequency distributions of wind effects experienced by birds and potential wind effects during the migratory seasons, respectively, in different intervals (i). This overlap index ranges from 0 to 1 (Horn 1966) and provides an estimate of the degree of wind selectivity by the birds, with a small overlap index indicating a high degree of wind selectivity. An overlap index of 1 would indicate that the birds were not selective of winds at all for their migratory flights but departed with the same probability in all wind situations. We tested skewness and differences in scatter and means of the expected autumn and spring distribution of wind effects with normal distribution tests, Levene's tests and t tests. To see whether there were any differences between seasons in proportions of wind occasions used by shorebirds for their flights, we divided wind effect into four categories

Table 1
Average wind effect ± 1 SD at the start of the migratory flight for radiotagged dunlins (autumn) at Ottenby and bar-tailed godwits (spring) at the Wadden Sea

	Wind effect autumn (m/s)	N	Wind effect spring (m/s)	N
Departure days	−0.3±5.1	29	11.7±6.4	24
Nondeparture days	−2.5±4.9	36	6.6±5.9	22
All days	−1.5±5.1	65	9.2±6.6	46

Wind effect is calculated as ground speed minus airspeed. The table shows a comparison between days when radiotagged birds departed (departure days) and when no birds were recorded to depart (nondeparture days).

(quartiles of the wind effect distribution, from unfavourable to favourable winds) and applied two-sample chi-square tests.

RESULTS

Radiotelemetry

Wind effect in autumn

Birds released with radiotransmitters remained in the area between 0 (i.e. the bird migrated on the first evening/morning after being released) and 14 days. Twenty-one birds were never tracked again after release and 19 birds stayed in the area more than 24 h. The wind effect at Ottenby was more favourable on days when radiotracked dunlins departed than on days when no birds departed, although the mean wind effect was negative also on departure days (Table 1). Comparing the distribution of departure and nondeparture days in relation to wind effect and year (Fig. 1) reveals that departure was associated with a slightly better wind effect compared to nondeparture (logistic regression, Table 2). Opposed winds dominated at Ottenby during the study period but there were occasions with following winds (Fig. 2). We compared the wind effect on days of departure with that of the day preceding departure for those birds that stayed for more than 24 h before departing. On days of departure, the wind effect $\pm$ SD was $+1.8 \pm 4.4$ m/s and on the preceding day it was -4.5 ± 4.6 m/s, a statistically significant difference of $+6.3$ m/s (paired t test: $t_{18} = 5.7$, $P < 0.001$). Among radiotracked dunlins, 47% departed with wind assistance (a positive wind effect; Fig. 3b) and the mean wind effect in autumn was negative (Table 3). Rain had no important influence on these departures. None of the 19 birds that stayed for more than 24 h departed on days with rain (>1 mm) and only one bird encountered rain the previous day.

Wind effect in spring

Following winds at the Wadden Sea on days when radiotracked bar-tailed godwits departed were significantly stronger than on days when no birds departed (Table 1; $P = 0.007$; see Green &
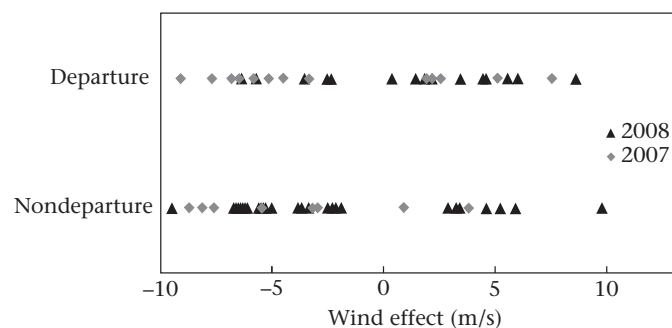

Figure 1. Distribution of wind effect (ground speed minus airspeed) on days when radiotagged dunlins at Ottenby, southern Sweden, departed (departure) and when no birds were recorded to depart (nondeparture) in 2007 and 2008. See also Table 2.

Table 2
Variables included in the logistic regression analysis (final model) of travelling decision in migrating dunlins *Calidris alpina* at Ottenby, southern Sweden

	ß	Wald	df	P
Wind effect	0.12	4.75	1	0.029
Year (2007)	1.39	5.30	1	0.021

Piersma 2003): 95% of the radiotracked bar-tailed godwits departed in following winds (Fig. 4b) and the mean wind effect was positive (Table 3).

Radar Tracking

Wind effect in autumn

Radar registration of migrating wader flocks (all visually identified) comprised 74 different flocks recorded at the two observation sites Vitemölla and Björka. Among radar-tracked shorebirds, 42% passed on occasions with wind assistance (Fig. 3c) and the mean wind effect was negative (Table 3).

Wind effect in spring

A total of 861 radar tracks of migrating shorebirds were recorded at Lund during spring migration. Of these waders, 96% were flying with ground speeds exceeding their airspeed (Fig. 4c) and the mean wind effect for these birds was positive (Table 3).

Telescope Tracking

Altogether, 157 flocks comprising 2702 shorebirds were recorded departing from Ottenby during autumn migration. Of these flocks, 24% departed with wind assistance (Fig. 3d) and the mean wind effect was negative (Table 3).

Comparison of Wind Effects during Autumn Versus Spring

There were significant differences in wind effect between autumn and spring for both radio- and radar-tracked shorebirds (*t* test: $t_{51} = 7.6$, $P < 0.001$ and $t_{93} = 7.1$, $P < 0.001$, respectively; Table 3). During autumn the shorebirds were migrating in slightly opposed winds while in spring the birds experienced rather strong following winds and this main result was consistent for all three methods of observation (Table 3). Distributions of air and ground speeds for shorebirds that were recorded by tracking radar during autumn and spring migration are illustrated in Fig. 5. Mean air speeds during autumn and spring were 16.7 ± 2.5 m/s and 18.3 ± 3.2 m/s, respectively and mean ground speeds were 15.8 ± 4.2 m/s and 26.8 ± 5.5 m/s, respectively.
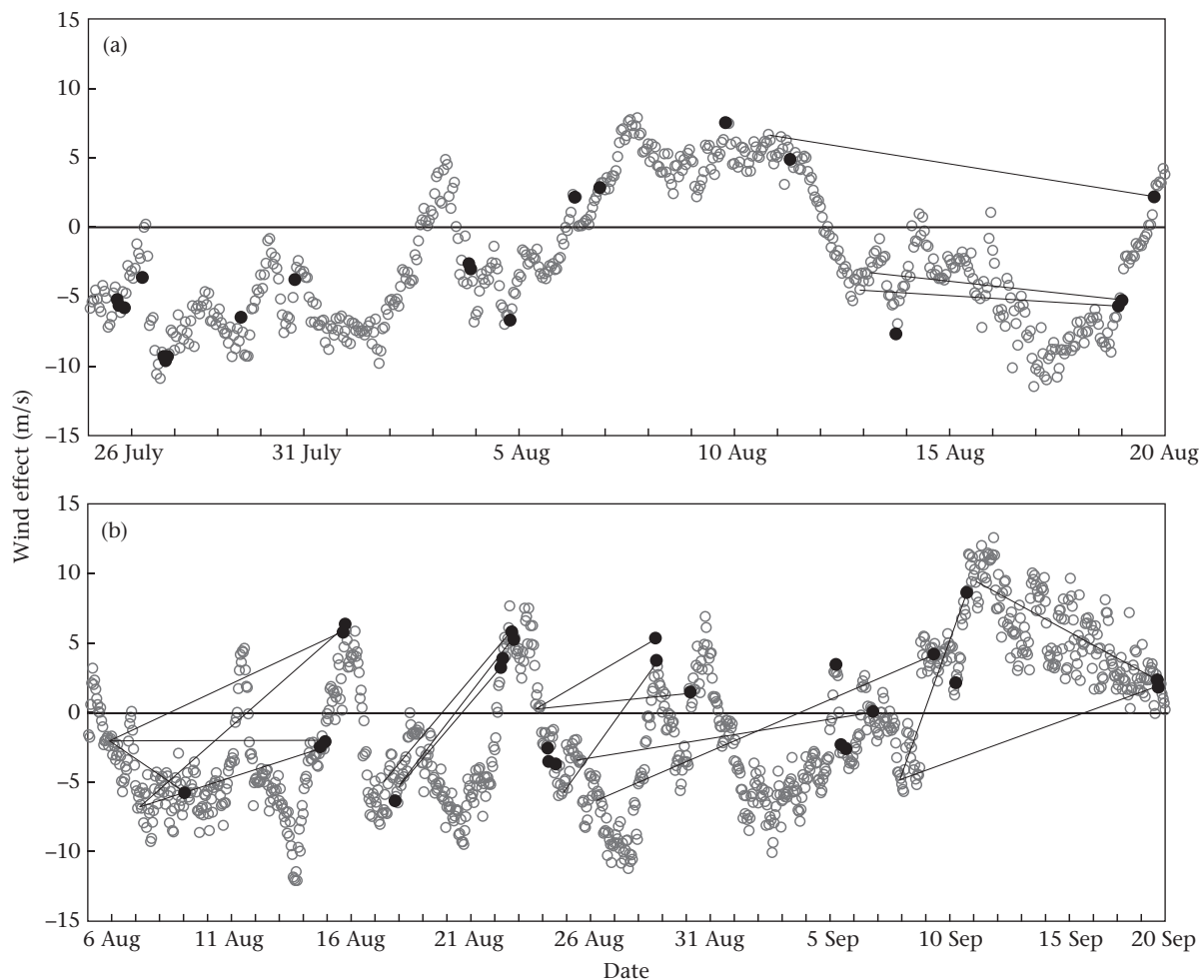

Figure 2. Calculated wind effect (ground speed minus airspeed) for a shorebird migrating from Ottenby, southern Sweden towards the southwest using wind data collected at Ottenby in (a) 2007 and (b) 2008. Wind effect was calculated for every hour during the study period. Negative values describe birds travelling in opposed winds and positive values describe following winds. Filled dots are occasions when radiotagged dunlins left Ottenby and the line from the dots goes back to time of capture (no line if dunlin departed within 24 h after capture).
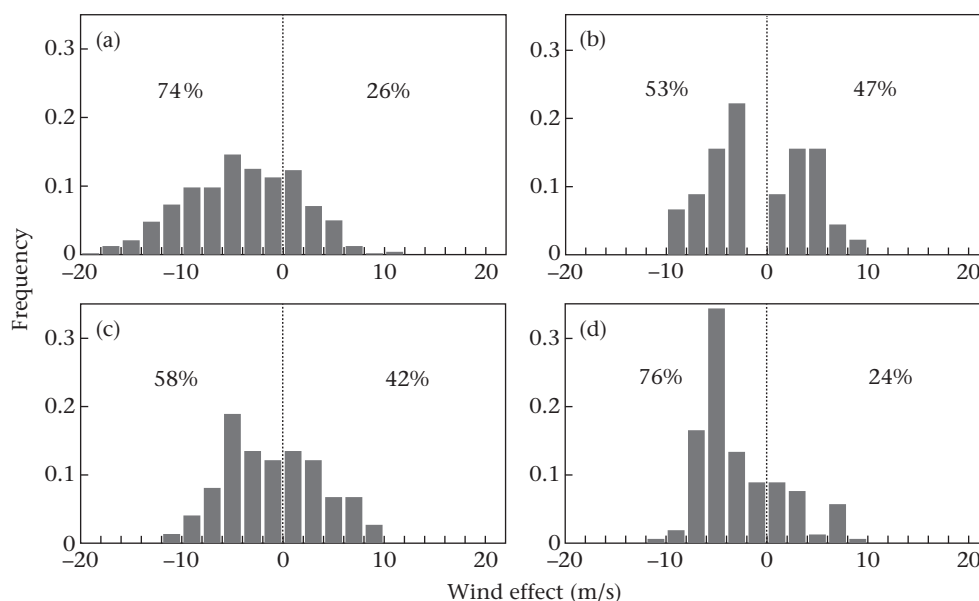
Figure 3. Distributions of wind effects (ground speed minus airspeed) encountered by shorebirds during autumn migration. Bars show the fraction of the total sample size (given in Table 3). (a) Prevailing wind effect during the period of peak autumn migration (15 July–31 August, 1999–2008) for shorebirds migrating between southern Sweden and the Wadden Sea. (b–d) Distribution of wind effect during (b) radiotracking, (c) radar tracking and (d) telescope tracking.

Negative expected wind effects dominated during the autumn migration period (15 July–31 August) for shorebirds migrating between southern Sweden and the Wadden Sea (Fig. 3a). The mean expected wind effect was −4.1 m/s (Table 3) and 74% of the days had negative wind effects. The distribution of wind effect encountered by the shorebirds differed from the expected distribution during the autumn migration period (overlap index: radio = 0.79; radar = 0.91; telescope = 0.78). Dividing the expected wind effect distributions into quartiles, we found that the shorebirds avoided migrating in the quartile of most unfavourable winds (wind effect of −8 m/s or less; chi-square test: radio: $\chi^2_3 = 16.0$, $P = 0.001$; radar: $\chi^2_3 = 9.7$, $P = 0.02$; telescope: $\chi^2_3 = 10.8$, $P = 0.01$; Fig. 3). To see whether the shorebirds were not only avoiding days with strong opposed winds but also selecting days of more favourable winds than expected we removed the quartile of most unfavourable wind effect (days with a wind effect less than −8 m/s) and tested for differential use of winds in the remaining three quartiles. The result showed that the radiotracked birds were selective (chi-square test: $\chi^2_2 = 6.7$, $P = 0.036$): more flocks than expected chose to migrate on days with the most favourable winds, whereas the radar- and telescope-tracked birds did not (chi-square test: radar: $\chi^2_2 = 1.5$, NS; $\chi^2_2 = 0.7$, NS, respectively).

During spring migration (20–31 May) favourable winds often prevailed (Fig. 4a) and the mean wind effect was +3 m/s (Table 3). The wind effect encountered by the shorebirds differed from the distribution of available wind effects during the spring migration period (overlap index: radio = 0.75; radar = 0.77). The shorebirds were avoiding migrating in the quartile of most unfavourable winds (days with negative wind effect; chi-square test: radio: $\chi^2_3 = 33.1$, $P < 0.001$; radar: $\chi^2_3 = 16.7$, $P < 0.001$; Fig. 4). Removing days with negative wind effect and testing for the differential use of winds in the three remaining quartiles showed that the shorebirds were still selective (chi-square test: radio: $\chi^2_2 = 21.1$, $P < 0.001$; radar: $\chi^2_2 = 6.3$, $P = 0.04$), preferring days with the strongest tail wind assistance for their migration.

We found no difference in the proportions of shorebirds in the four different wind effect categories between seasons (two-sample chi-square test: radio: $\chi^2_3 = 5.4$, NS; radar: $\chi^2_3 = 1.2$, NS), indicating

that the birds were as selective during autumn migration as in spring.

We found a large difference in mean expected wind effect between autumn and spring (t test: $t_{597} = 13.1$, $P < 0.001$; Table 3) while the seasonal distributions of wind effect had equal variance (Levene's test: $F_{1,597} = 0.02$, $P = 0.90$) and were normally distributed with no significant skewness.

DISCUSSION

Winds over southern Scandinavia are predominantly westerly during both autumn and spring. During autumn, when shorebirds are migrating from breeding grounds in arctic Russia to stopover sites in the southern North Sea region (towards the southwest), they can expect to encounter mostly unfavourable winds and our results showed that the majority were migrating in opposed winds giving a negative wind effect. During spring, on the other hand, the wind regime provides shorebirds with mostly favourable winds when migrating towards their breeding grounds (northeast) and the birds in our study almost exclusively migrated in following winds.

Earlier studies of arctic-breeding shorebirds demonstrated that these birds preferentially fly in following winds during both autumn and spring (Green 2004 and references therein; Hedenström et al. 2009; Ma et al. 2011), but in our study the majority of birds migrated in opposed winds during autumn which has also been found among nocturnal migrants in central Europe (Erni et al. 2002). Only 26% of the possible migration days in autumn showed following winds (Fig. 3a) and the risk of delayed arrival at stopover and wintering grounds may force the birds to fly also under less favourable wind conditions. One alternative to avoid migrating in unfavourable winds could be to migrate along a different route during autumn compared to spring. For example, many North American shorebirds migrate along different routes during autumn and spring (Richardson 1978; Byrkjedal & Thompson 1998; Gill et al. 2009); probably because they encounter more favourable winds than if they had used the same route in both seasons (but see Ydenberg et al. 2007). However,
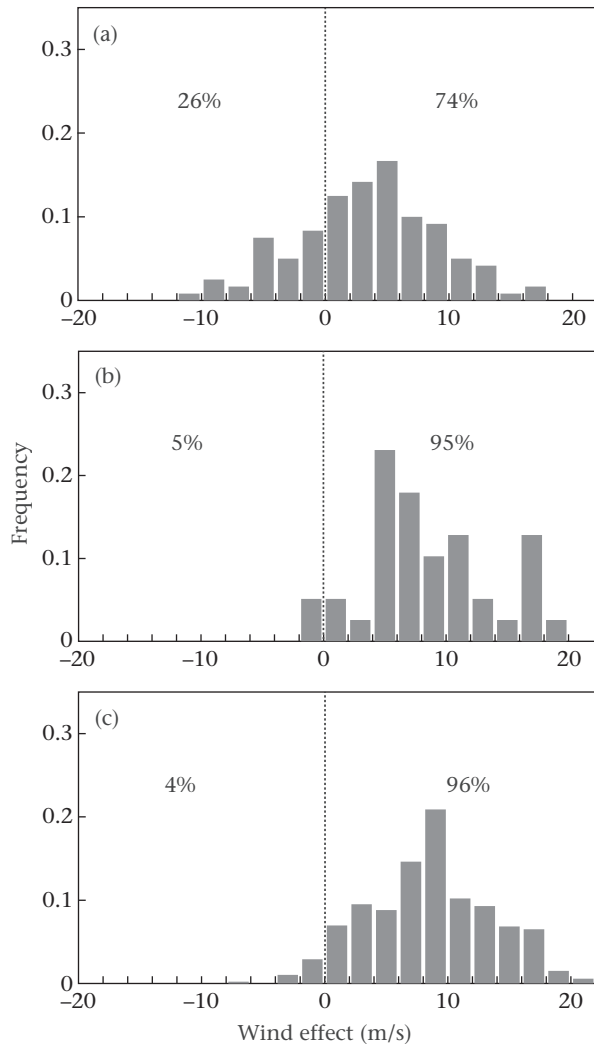
Figure 4. Distributions of wind effects (ground speed minus airspeed) encountered by shorebirds during spring migration. Bars show the fraction of the total sample size (given in Table 3). (a) Prevailing wind effect during the period of peak spring migration (20–31 May, 1999–2008) for shorebirds migrating between the Wadden Sea and southern Sweden. (b–c) Distribution of wind effect during (b) radiotracking and (c) radar tracking.

Figure 5. Distribution of airspeeds and ground speeds for shorebirds recorded by tracking radar during (a) autumn and (b) spring migration. The radar studies were carried out at three sites in Scania, southernmost Sweden. Bars show the fraction of the total sample size (number of flocks is given in Table 3). Grey arrows: mean air speed; black arrows: mean ground speed; see also Table 3.

there are probably no alternative routes with better winds for birds migrating between the Wadden Sea and arctic Russia, forcing them to migrate in head winds during autumn.

Our results show that birds do not have a fixed threshold of wind assistance for their departure on migratory flights, but the same birds depart in very different wind situations during spring and autumn seasons in southern Scandinavia when wind regimes in relation to the birds' migratory direction were very different.

While the shorebirds avoided departure on occasions when there was a negative wind effect in spring, they regularly travelled with negative wind effects during autumn migration. This suggests that migratory birds have an adaptive flexibility in their responses to wind depending on seasonal wind regimes. Given this clear difference in departure behaviour relative to winds between seasons, it seems likely that birds also change their behaviour during the same migratory season (spring or autumn) when travelling long distances across regions or zones with different characteristic wind regimes. It remains to be investigated how fine-tuned and flexible the birds' departure responses relative to winds are. Also, the mechanisms for the birds' flexibility in departure behaviour in relation to wind regime are unknown. It has recently been indicated that the orientation behaviour of migrating birds in relation to wind (drift and compensation behaviour) is more flexible and complex than expected, showing significant variation

Table 3
Expected and observed wind effects ± 1 SD of arctic shorebirds migrating over southern Sweden in autumn and spring

	Wind effect autumn (m/s)		Wind effect spring (m/s)	
	Flock (N)	Day (N)	Flock (N)	Day (N)
Expected		−4.1±5.5 (479)		3.3±5.7 (120)
Observed, radiotracking	−0.9±5.0 (45)	−0.3±5.1 (29)	8.6±5.1 (39)	11.7±6.4 (24)
Observed, radar tracking	−0.9±4.6 (74)	−1.1±4.7 (37)	8.5±5.2 (861)	6.7±5.5 (58)
Observed, telescope tracking	−3.0±4.2 (157)	−2.0±4.4 (36)		

Wind effect is calculated as ground speed minus airspeed. Mean values are shown for both flocks and days (some flocks departed during the same day so the number of days is lower than the number of flocks). Expected wind effects were calculated for each day during the peak spring (20–31 May) and autumn (15 July–31 August) migration periods during a time interval of 10 years (1999–2008).
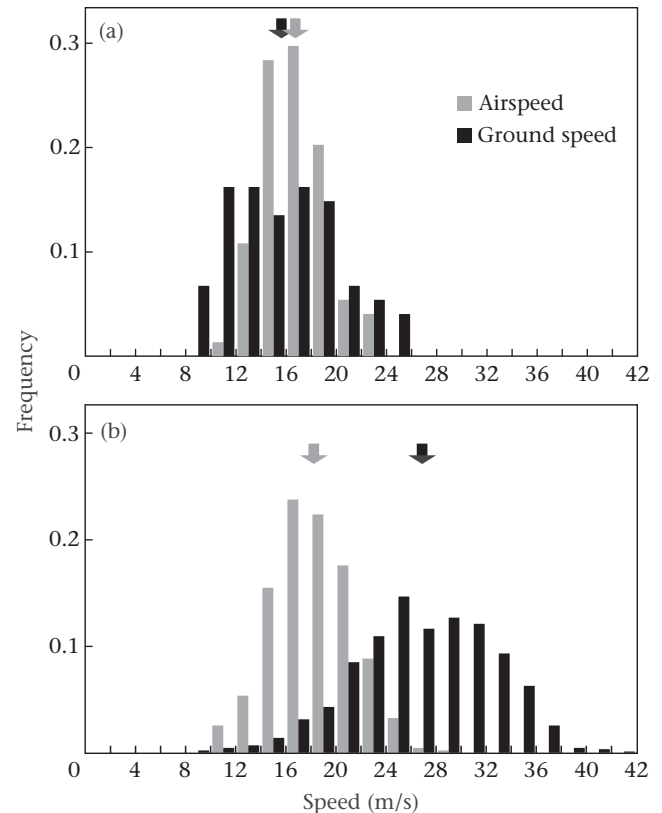
between regions and seasons (Chapman et al. 2011; Klaassen et al. 2011b; J. Grönroos, M. Green & T. Alerstam, unpublished data). A similarly complex adaptive flexibility may hold for the birds' departure behaviour in relation to the wind.

When comparing the distribution of wind effects encountered by the shorebirds with the expected distribution (mean wind effect during peak autumn and spring migration period over 10 years), we found large similarities in wind selectivity between autumn and spring as indicated by the similar overlap indices between distributions of available wind effects and wind effects for the migratory flights during the two seasons. During both seasons the birds were avoiding migrating in the quartile of most unfavourable winds (wind effect of −8 m/s or less in autumn; wind effect of 0 m/s or less in spring). Furthermore, they were selecting similar proportions of the remaining three quartiles, favouring the quartile with the best winds during both seasons. Thus, the shorebirds chose to migrate on days with better winds than expected during both autumn and spring.

Migratory birds are expected to adapt their wind selectivity (i.e. proportion of the wind effect distribution potentially used for migratory flights) depending on the trade-off between benefits associated with departing only on occasions with the most favourable wind effects and the costs of waiting and postponing departure until these occasions occur (Alerstam 1979; Weber et al. 1998; Thorup et al. 2006). If the optimality criterion is to minimize energy costs for the migratory flights alone (assuming that the birds are not pressed for time and that it is not very important if energy costs for existence metabolism are paid during waiting periods on migration or after arrival at the migratory destinations), it is predicted that birds should be very tolerant of long waiting periods and not depart until they can obtain the very best wind assistance for their flights. Hence, in this case they are expected to show the highest degree of wind selectivity (Alerstam 1979). This did not seem to apply to the shorebirds in this study, which showed rather large overlap indices between the distributions of wind effects during their flights and wind effects available during the migration periods, indicating a significant but modest level of wind selectivity.

However, for migrants that are adapted to minimize the total duration of the migratory journey or the total energy consumption for migration (including not only energy cost for flight but also metabolic costs for existence/stopover during the migration period) the degree of wind selectivity should be less pronounced. These conditions are likely to apply to migrants that benefit from early arrival to their destinations and from having a surplus of energy resources at their arrival after migration.

During spring, arctic shorebirds have to arrive early at their breeding grounds in order to breed within a limited period of time during the short arctic summer. Furthermore, arriving in good condition during spring is also important. Arriving at the breeding grounds with stores of fat and protein remaining (Morrison & Davidson 1990; Morrison et al. 2005; Tulp et al. 2009) will enhance survival in the arctic when the weather is cold and unpredictable and food resources scarce (Morrison et al. 2007). Arriving in good condition is also important for breeding success (Piersma 1987; Davidson & Evans 1988; Morrison & Hobson 2004; Morrison et al. 2005). However, long-distance migrants may be time stressed not only during spring but all year round since they have to allocate time for moult as well as migration and breeding in their annual cycle, and these events do not normally overlap (Buehler & Piersma 2008). The further a bird migrates the higher the proportion of the year it has to spend on migration and less time is available for breeding, moult and winter survival, so time is important also during southward migration. During autumn, shorebirds have to arrive at their staging areas in time to fatten up

and moult before continuing further south. There is evidence that a slower moult may improve the quality of the feathers grown and durable primaries may be particularly important for the survival of long-distance migrants (Serra 2001). Another advantage of arriving at staging sites early during autumn is to exploit food resources before they are depleted (Schneider & Harrington 1981; Zwarts et al. 1992). In the Wadden Sea, prey density declines from July to September (van Gils et al. 2005) highlighting the importance of a timely arrival. Predator densities (mainly peregrines, *Falco peregrinus*, but also other raptors) increase during autumn owing to their southbound migration (Ydenberg et al. 2007) and during moult and migratory fattening the shorebirds are more vulnerable to predators because of a reduction in flight performance (Hedenström 2003; Dietz et al. 2007). So, by arriving early at autumn staging sites the shorebirds have time to moult and/or put on fat at a time when food resources are plenty and predator numbers are low.

The optimal degree of wind selectivity for migrants that are adapted to minimize the total duration of the migratory journey or the total energy consumption for migration will depend on (1) the scatter and (2) the skew of the wind effect distribution as well as on (3) the ratio of energy consumption during flight to that during waiting/resting (Alerstam 1979; Weber et al. 1998; Thorup et al. 2006). Although the mean wind effect was dramatically different between spring and autumn, the scatter and skewness of the wind effect distributions were very similar during spring and autumn (no significant difference in scatter and no significant skewness; Table 3, Figs 3a, 4a). This means that one would not expect these factors to cause any seasonal difference in wind selectivity. A higher ratio of energy consumption during flight relative to rest (waiting) is predicted to be associated with a higher degree of wind selectivity (Thorup et al. 2006). This follows from the fact that a high level of flight power will increase the importance of reducing migratory flight time by selecting occasions with the best wind assistance, while high energy costs during waiting/resting (e.g. at lower temperatures) will make the birds less prone to wait for the best wind conditions. We have little reason to believe that waiting/resting costs differ between spring and autumn, but it seems likely that the flight power is higher in spring because the shorebirds fly with larger fuel loads during spring compared to autumn (e.g. Goede et al. 1990; Helseth et al. 2005). This would promote higher wind selectivity in spring, but our results showed only a slight and nonsignificant tendency in that direction.

Arctic shorebirds and probably other migratory birds have an adaptive flexibility in their responses to wind depending on the prevailing wind regimes and regularly depart with wind resistance in situations with predominantly unfavourable winds. Shorebirds are selective of favourable (or less unfavourable) winds during both autumn and spring indicating that savings in total time and energy costs for migration are important during both seasons. In terms of wind selectivity shorebirds seem to be intermediate between passerines (poorly selective; e.g. Alerstam et al. 2011) on the one hand and noctuid moths (highly selective; e.g. Chapman et al. 2010) on the other.

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