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ORIGINAL ARTICLE

Orientation of shorebirds in relation to wind: both drift and compensation in the same region

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Abstract Migratory movements in air or water are strongly affected by wind and ocean currents and an animal which does not compensate for lateral flow will be drifted from its intended direction of movement. We investigated whether arctic shorebirds during autumn migration in the region of South Sweden and the southern Baltic Sea compensate for wind drift or allow themselves to be drifted when approaching a known goal area under different circumstances (over sea, over land, at low and high altitude) using two different approaches, visual telescope observations and tracking radar. The shorebirds showed clearly different responses to crosswinds along this short section (<200 km) of the migratory journey, from almost full drift when departing over the sea, followed by partial drift and almost full compensation at higher altitudes over land during later stages. Our study demonstrates that shorebirds are also remarkably variable in their response to crosswinds during short sections of their migratory journey. The recorded initial drift close to departure is probably not adaptive but rather a result of constraints in the capacity of the birds to compensate in some situations, e.g. in low-altitude climbing flight over the sea. We found no difference in orientation response to wind between adult and juvenile birds. This study indicates, in addition to adaptive orientation responses to wind, the importance of the non-adaptive wind drift that contributes to increasing the variability of drift/compensation behaviour between places that are separated by only short distances, depending on the local topographic and environmental conditions.

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Zusammenfassung

Orientierung von Watvögeln im Verhältnis zum Wind: sowohl Drift als auch Kompensation in derselben Region

Zugbewegungen in der Luft oder im Wasser sind stark beeinflusst durch Wind oder Meeresströmungen, und ein Tier, das einen seitlichen Versatz nicht ausgleichen kann, wird von seiner angestrebten Bewegungsrichtung abgetrieben. Wir untersuchten, ob arktische Watvögel während des Herbstzugs in Südschweden und der südlichen Ostsee ihren Versatz durch Wind ausgleichen oder es zulassen, abgetrieben zu werden, wenn sie ein bekanntes Zielgebiet unter verschiedenen Bedingungen erreichen können (über See, über Land, in geringer oder großer Höhe). Wir setzten sowohl visuelle Beobachtung mit Teleskopen als auch Radartracking ein. Die Watvögel zeigten deutlich unterschiedliche Reaktionen auf Seitenwinde über diesen kurzen Abschnitt (<200 km) ihrer Zugroute, von fast vollständigem Abtreiben beim Aufbruch über See, gefolgt von einer teilweisen Drift und fast vollständigem Ausgleich der Seitenwinde bei größeren Höhen über Land während späterer Abschnitte. Unsere Untersuchung zeigt, dass Watvögel auch über kurze Abschnitte ihrer Zugroute bemerkenswert variabel sind in ihrer Reaktion auf Seitenwinde. Die festgestellte anfängliche Drift kurz nach dem Abflug ist wahrscheinlich keine Anpassungsleistung, sondern Einschränkung in der Möglichkeit der Vögel zum Ausgleich in bestimmten Situationen geschuldet, zum Beispiel im Steigflug in geringer Höhe über See. Wir fanden keine Unterschiede in der Reaktion auf Seitenwinde zwischen adulten und juvenilen Vögeln. Diese Untersuchung zeigt die Wichtigkeit nicht-adaptiver Wind-Drift, die neben adaptiven Reaktionen auf Seitenwinde die Variabilität des Drift/Kompensations-Verhaltens auch zwischen eng beieinander liegenden Orten beeinflusst.

Introduction

Animals that fly or swim are significantly affected by the motion of the fluid—air or water—in which they move, producing lateral displacement (drift) which might cause orientational difficulties. As a consequence, different orientation responses and strategies have evolved to promote efficient movement in flows among different organisms (Chapman et al. 2011). The track of a migrating bird over the ground is the vector sum of its direction and speed through the air (heading and airspeed) plus the direction and speed of the wind (Richardson 1991). Wind speeds are often of similar magnitude as the birds' own airspeeds, thus having a profound effect on orientation as well as flight cost and travelling speed. Flight in crosswinds causes orientational complications, since the bird's track is not the same as its heading. Birds could either keep their headings constant in their preferred migratory directions and be subjected to wind drift, or they could adjust their headings to compensate for the effect of wind, i.e. keep the tracks constant or even overcompensate. Which of these, or any intermediate strategy of partial drift and compensation, will be adaptive depends on wind patterns and distance to the destination (Alerstam 1979). A large number of studies have investigated how birds orient in relation to wind, and cases of full drift, partial drift/partial compensation, complete compensation and overcompensation have been reported (Richardson 1991; Liechti 2006; Chapman et al. 2011). Recent studies have demonstrated that individual birds tracked during their entire migration changed responses to crosswinds between different places and times during their travels, showing a varied repertoire of different drift and compensation behaviours (Klaassen et al. 2011a). The reasons for this variability in orientation response to wind are not fully understood, but it has been suggested that drift and compensation behaviour may differ between species, ages, visibility, areas and environmental circumstances. In shorebirds, both drift and compensation have been demonstrated (e.g. Richardson 1979; Williams et al. 1986; Gudmundsson 1994; Green et al. 2004, and references therein; Klaassen et al. 2011b), and in many cases, these results seem to be in accordance with so-called adaptive drift, where extensive drift is predicted during initial phases of the migratory journey, followed by increased compensation during later stages as the birds are approaching their destinations (Green et al. 2004). This strategy, which is based on the assumptions that birds behave so as to minimise the remaining distance to the goal after each flight step, is optimal in situations where winds are highly variable between different flight steps of the migratory journey or parts of a long non-stop flight (Alerstam 1979).

The objective of this study was to investigate whether migrating arctic shorebirds compensate for wind drift or allow themselves to be drifted when approaching a known goal area under different circumstances (over sea, over land, at low and high altitude). The majority of the shorebirds studied here are migrating from breeding areas in the Russian Arctic towards large-scale staging and/or wintering areas in the North Sea region (Fransson et al. 2008; Grönroos et al. 2012a, b), a journey of 2,000–3,500 km. In this study, we analysed the responses by shorebirds to crosswinds during autumn migration in the region of South Sweden and the southern Baltic Sea at their departure from a short-time stopover area and en route at two sites that were situated 150–200 km downstream from the departure site. These places were all along the final segment of the route between the Arctic and the North Sea region, where the remaining distance to the North Sea region was only 400–1,000 km. On this final segment, winds are expected to be rather constant (e.g. supplementary materials in Kemp et al. 2010; Grönroos et al. 2012a), and we therefore expect complete compensation for wind drift to be most beneficial for the migrants (Alerstam 1979). The studies were conducted at three different sites situated within a distance of 200 km from each other: (1) on an island, where shorebirds depart over the sea; (2) at the coast, where the migrating birds arrive from the sea and continue over land; and (3) at an inland site, where the birds are just passing over. We used two different approaches, visual telescope observations and tracking radar.

Methods

Telescope tracking

Observations of migrating shorebirds were carried out during the period 26 July to 15 October in four years, 2006–2008 and 2011 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 (Fig. 1). Observations were made during 41 days. The observation time each day was not standardised, but 84 % of the observations were made between 1730 and 2030 hours (Swedish summer time = GMT + 2 h) and 16 % between 0530 and 0830 hours. Migrating flocks were

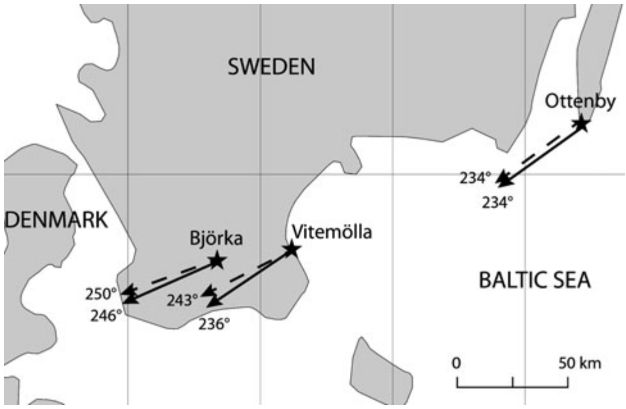

Fig. 1 Mean track (*solid arrows*) and heading (*broken arrows*) directions of shorebirds on autumn migration at three study sites in south Sweden. The map is a Mercator projection

normally located by using 10× binoculars and later tracked in 20–60× telescopes until they vanished from sight. The birds were normally flying at altitudes in the interval between 2 and 50 m above sea level. Telescopes were equipped with azimuth scales and were carefully aligned to give geographic compass bearings. The following data were recorded in order 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—this normally occurred when the flock passed relatively close to the observer; (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, which is a normal flight speed of Dunlin *Calidris alpina* (which comprised 95 % of the flocks, see below). The angle for parallax compensation (ε°) could be calculated from

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

The flight direction of the flock is then determined as ($b_2 + \varepsilon$). The angle ε 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 (with maximum 10 min 13 s) and mean angle for parallax compensation was only 2.7° (0°–11°). The sensitivity of estimated flight directions depending on the angle of parallax or assumptions about airspeed (16 m/s) was low. Restricting the analysis to include only flight directions with parallax angles less than 2° or by changing flight speed from 16 to 13 m/s (mean wind effect at Ottenby: −3 m/s) only affected flight directions with 0.5°, which shows that track direction estimates are reliable and with high accuracy. Heading directions were then calculated by subtracting the angle of compensation/drift (α) from the track direction. Alpha (α) was calculated according to the following equation:

$$\alpha = \arcsin(a \sin \beta)$$

where a is the ratio between wind speed and the birds' airspeed (16 m/s), and β is the angle between track and wind direction (Alerstam 1976). All shorebird flocks were identified and were composed of Dunlin, Red Knot *Calidris canutus*, Bar-tailed Godwit *Limosa lapponica*, Grey Plover *Pluvialis squatarola*, Ringed Plover *Charadrius hiaticula*, Turnstone *Arenaria interpres* and Sanderling *Calidris alba*. Eighty-five percent of the flocks were composed of only Dunlin, 10 % were flocks of mixed species including Dunlin (on average 51 % of the individuals in the mixed flocks were Dunlin), and in 5 % of the flocks there were no Dunlin but only other shorebird species. The birds in the flocks were aged (juvenile or adult) when observation conditions allowed.

Radar tracking

Tracks of migrating flocks of shorebirds were recorded at two sites in Scania, South Sweden. Shorebirds were tracked with mobile tracking radar (X-band, 40 kW peak power, pulse duration 0.3 µs, pulse repeat frequency 1,800 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; Fig. 1) between 15 July and 25 September 1982, 1984, 1986, 1989 and 1990. The radar was operated manually, and data about the range, elevation and azimuth of the flocks were recorded by a computer. Flocks of shorebirds were tracked from 1 up to 14 min. The range of the radar was about 15 km for large flocks while smaller flocks could be tracked for up to 10 km. To determine headings (the orientation of the birds' body axis) and airspeeds (the birds' flight speed relative to the surrounding air) of the flocks, wind direction and speed were measured by tracking helium-filled weather balloons carrying an aluminium foil reflector. Heading directions and airspeeds were then 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). For a more detailed description of radar tracking procedures, see Alerstam (1985). All shorebird flocks were visually identified and belonged to the species Dunlin, Bar-tailed Godwit, Grey Plover, Ringed Plover, Red Knot and Turnstone. Fifty-three percent of the flocks were composed of only Dunlin, 3 % were flocks of mixed species including Dunlin (on average 67 % of the individuals in the mixed flocks were Dunlin) and 44 % of the flocks were composed of other shorebird species.

Wind data

Wind data for the telescope trackings were obtained from Swedish Meteorological and Hydrological Institute, (SMHI) collected at the local weather station (Ölands Södra Udde) at Ottenby. The weather station was located at the very site where observations were made, and wind data was collected every hour during the study period (wind was measured at 11 m above sea level). The wind direction was given in exact degrees and wind velocity in m/s. The magnitude of drift/compensation (see below) was robust against different wind speeds corresponding to different flight altitudes. The magnitude of drift did not change much (0.8–1.1; see below) when altering wind speeds (±20 % from the speed at 11 m above sea level) corresponding to birds flying at approximately 2 or 50 m above sea level, according to the wind gradient equation for open and flat land or sea (Sutton 1953), so we used wind speeds collected from the local weather station at 11 m above sea level for our estimates of drift/compensation at Ottenby in the following presentation. Wind data for the radar trackings were collected locally by tracking helium-filled balloons carrying an aluminium foil reflector (wind data were always recorded within 2 h from the tracking of a flock).

Data analysis and statistics

Calculations of mean directions and angular deviations of flight directions and winds were made according to standard circular statistical methods (Batschelet 1981). To evaluate whether or not the birds were compensating for drift, we divided each sample into two groups according to whether winds were from the right or the left of the average flight (track) direction of the whole sample (Green and Alerstam 2002). If the birds compensate for drift, we expect that tracks will be similar for the two groups irrespective of where the winds are coming from, while the headings will differ between the groups, being shifted into the wind (to compensate for the effect of winds, more to the right in winds from the right and vice versa). On the other hand, if the birds are subjected to wind drift, we expect tracks to change with the wind but headings to remain the same, irrespective of what direction the wind is coming from. Differences between flight directions (tracks and headings) in different wind situations were tested with the Watson–Williams test (Batschelet 1981). The relative magnitude of drift and compensation were calculated as follows. We denote mean track directions in winds from the left and right T_L and T_R, respectively, and the corresponding mean heading directions, H_L and H_R. The difference between track and heading is denoted as α, and then α_L will be T_L–H_L and α_R will be T_R–H_R. The estimated magnitude of drift is then:

$$B_{track} = \left(\frac{T_L - T_R}{\alpha_L - \alpha_R}\right)$$

with $B_{track} = 0$ there is no drift and complete compensation; if $B_{track} = 1$, there is full drift and no compensation; when $0 < B_{track} < 1$, there is partial drift and partial compensation; and when $B_{track} > 1$, there is overdrift (Green and Alerstam 2002). The corresponding magnitude of compensation is:

$$B_{heading} = \left(\frac{H_L - H_R}{\alpha_L - \alpha_R}\right)$$

if $B_{heading} = 0$, there is full drift and no compensation ($B_{heading} = B_{track} - 1$); when $B_{heading} = -1$, there is full compensation and no drift; values of $B_{heading}$ between 0 and -1 indicate partial drift and partial compensation; if $B_{heading} < -1$, there is overcompensation; and when $B_{heading} > 0$, there is overdrift (Green and Alerstam 2002).

General linear model (GLM) analyses were performed using the statistical software SPSS v.18.0 (SPSS, Chicago, IL, USA) to test if drift/compensation behaviour differed significantly between sites and age groups. Track and heading directions were used as dependent variables, and for the tests of different wind responses between sites, we used wind (wind from the left and right, fixed factor), site (fixed factor) and the interaction between wind and site as independent variables. Differences in birds' orientation responses to wind between the different sites would be manifested by a significant effect of the interaction wind × site on either track or heading direction. For the tests of a difference in wind response between age groups (data from Ottenby only), we used wind (fixed factor), age (three groups, flocks of adult birds, flocks of juveniles and flocks with mixed adult/juvenile; fixed factor) and the interaction between wind and age as independent variables. Differences in orientation responses to wind between age groups would be indicated by a significant effect of the interaction wind × age on either track or heading direction. We are aware that GLM can provide only approximate tests since directions are not linear but circular data. However, such a test will be robust when directions are highly concentrated around a well-defined mean (the range of directions in all six samples of track and heading directions from the three different sites were within ±25–49° from mean directions; see also Table 1 for angular deviations; Batschelet 1981) and sample sizes are reasonably large, as in our present cases (results with marginal significance must of course be considered with due care).

Results

Summary statistics of flight directions and winds for the different sites are shown in Table 1, and mean track and

Table 1 Flight directions and winds for migrating shorebirds during autumn at three different sites in South Sweden, based on visual telescope tracking at Ottenby and on radar tracking at Vitemölla and Björka

Site	Track ± a.d. (°)	Heading ± a.d. (°)	Wind direction ± a.d. (°)	Wind speed ± s.d. (m/s)	Flight altitude median (m)	*n*
Ottenby	234 ± 16	234 ± 13	228 ± 65	5.2 ± 2.0	N.a.	176
Vitemölla	236 ± 20	243 ± 17	267 ± 92	6.5 ± 3.0	607	41
Björka	246 ± 22	250 ± 25	345 ± 81	7.2 ± 2.7	621	33

Average flight (track and heading) and wind directions (refer to the direction from where the wind is blowing) of each sample are shown together with angular deviations (*a.d.*). Mean flight directions at the different sites are also shown on the map in Fig. 1. The Ottenby material mainly refers to birds flying at low altitudes in the range 0.5–100 m

N.a. Not applicable

heading directions at the three sites are illustrated in Fig. 1. In all cases, the migratory movements were concentrated with relatively small scatter (angular deviations ranging between 13 and 25°).

Significant differences between track directions in winds from left and right of the overall mean direction of the sample were recorded at Ottenby and Vitemölla but not in Björka (Fig. 2; Table 2). The differences in track and/or heading directions between birds flying in winds from the left and right (Fig. 2; Table 2) indicate full drift at Ottenby, partial drift in Vitemölla and almost full compensation in Björka. The results from the general linear model (GLM) analysis of the effect of wind and site on track and heading directions are presented in Table 3. There was a significant effect of site and wind on both track and heading directions, indicating that the shorebirds had different track and heading directions at the different sites (Fig. 1). The interaction between site and wind was highly significant for heading but not track direction. This shows that the birds changed heading differently in relation to wind at the different sites, confirming that their drift/compensation behaviour differed clearly between the sites (Table 2). We conducted pairwise GLM tests of the effect of the interaction between site and wind for heading and found that the difference was highly significant between Ottenby and Vitemölla ($F_{1,213} = 6.9$, $P = 0.009$) and Ottenby and Björka ($F_{1,205} = 11.3$, $P = 0.001$) but not between Vitemölla and Björka ($F_{1,70} = 0.8$, $P = 0.36$).

The samples of track and heading directions of birds departing from Ottenby did not indicate any difference in drift/compensation behaviour between adult and juvenile birds (Table 4). The results indicated extensive drift among all age groups, although a significant drift effect was recorded only for adult birds (small sample size of juvenile and mixed flocks). The GLM analyses of track and heading directions confirmed that there was no significant difference in orientation response to wind between the age groups (interaction wind × age: $F_{2,152} = 1.5$, $P = 0.23$; $F_{2,152} = 0.8$, $P = 0.44$).

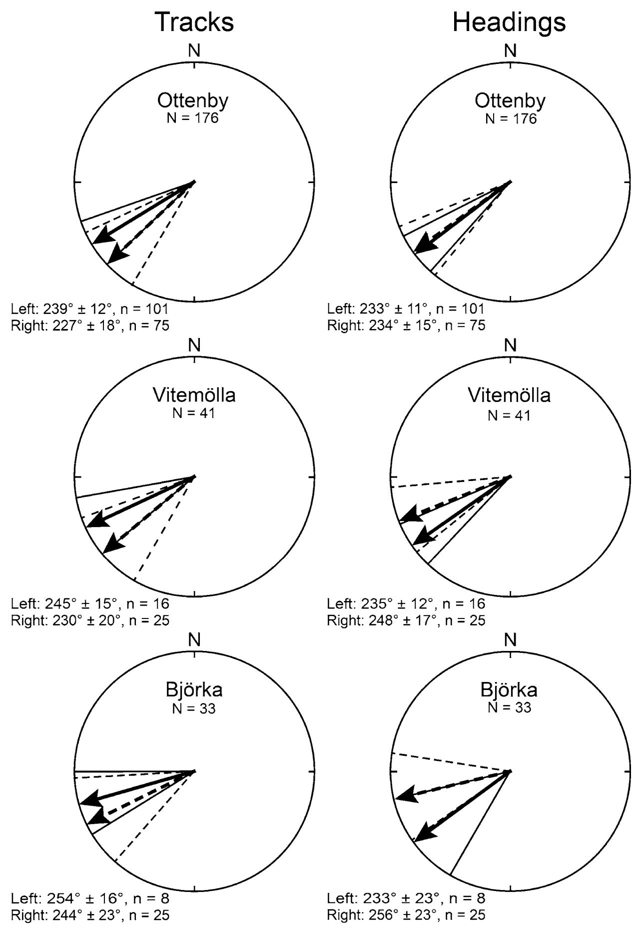

Fig. 2 Average flight directions, tracks and headings, in winds from the left (*unbroken bold arrows*) and right (*broken bold arrows*) of the mean direction of the total sample. Angular deviations are shown with *unbroken lines* for flight directions in winds from the left and *broken lines* for flight directions in winds from the right. *N* values give the total sample sizes (see also Table 2). Mean directions ± angular deviations for each group are given below each panel

Discussion

We were surprised to find that the shorebirds showed clearly different responses to crosswinds along this short section (<200 km) of the migratory journey, from almost

Table 2 The magnitude of drift and compensation (calculated according to Green and Alerstam 2002) as estimated from the comparison between flight directions in winds from the left and right (see text and Fig. 2)

Site	Magnitude of drift B_{track}	Magnitude of compensation $B_{heading}$	Recorded behaviour
Ottenby	0.90***	−0.10 ns	Full drift/partial drift
Vitemölla	0.52*	−0.48**	Partial drift
Björka	0.30 ns	−0.70*	Full compensation/ partial drift

When the magnitude of drift (B_{track}) equals 1 there is full drift and when it is 0 there is full compensation; intermediate values indicate partial drift. Similarly, when the magnitude of compensation ($B_{heading}$) equals −1 there is full compensation and when it is 0 there is full drift; intermediate values indicate partial compensation. If B_{track} is significantly different from 0, full compensation can be rejected. If $B_{heading}$ is significantly different from 0, full drift can be rejected

Levels of significance for tests of difference between average direction in winds from the left and right (see text): $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Statistical testing was done using the Watson–Williams test (Batschelet 1981)

Table 3 Results from general linear models (GLM) with track and heading directions as dependent variables and with site, wind and site × wind as independent variables

	Track			Heading		
	df	*F*	*P*	*df*	*F*	*P*
Site	2	10.0	<0.001	2	7.8	<0.001
Wind	1	17.0	<0.001	1	21.8	<0.001
Site × wind	2	0.1	<0.871	2	7.3	<0.001
Error	244			244		

full drift during departure over the sea at Ottenby followed by partial drift and almost full compensation at higher altitudes over land during later stages (Table 2). This difference in drift/compensation between sites is clearly seen from the changing difference in heading directions between winds from the left and right (Fig. 2). While mean headings in winds from the left and right (H_L and H_R, respectively) were very similar at Ottenby (no compensation), there was a distinct difference between H_L and H_R (13°) at Vitemölla (partial compensation) and an even more pronounced difference (23°) at Björka (almost full compensation).

The fact that mean heading directions with winds from the left (H_L) remained almost the same at the different sites (233–235°; Fig. 2) could be attributed to a change in mean orientation towards the right between the successive sites (Grönroos et al. 2012b) that occurred independently of (but in combination with) the different drift/compensation behaviour at the different sites.

Table 4 The magnitude of drift and compensation in different age groups of shorebirds migrating from Ottenby during autumn

Age	Magnitude of drift B_{track}	Magnitude of compensation $B_{heading}$	*n*
Adult	0.82*	−0.18 ns	105
Juvenile	0.91 ns	−0.09 ns	19
Mixed flocks	0.63 ns	−0.37 ns	34

Magnitude of drift and compensation have been calculated according to Green and Alerstam (2002). When the magnitude of drift (B_{track}) equals 1 there is full drift and when it is 0 there is full compensation; intermediate values indicate partial drift. Similarly, when the magnitude of compensation ($B_{heading}$) equals −1 there is full compensation and when it is 0 there is full drift; intermediate values indicate partial compensation. If B_{track} is significantly different from 0, full compensation can be rejected. If $B_{heading}$ is significantly different from 0, full drift can be rejected

Levels of significance for tests of difference between average direction in winds from the left and right (see text): $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Statistical testing was done using the Watson–Williams test (Batschelet 1981)

Both drift and compensation have been reported among migrating shorebirds (e.g. Richardson 1979; Williams et al. 1986; Gudmundsson 1994; Green et al. 2004, and references therein; Klaassen et al. 2011b). After analysing several datasets on migrating arctic shorebirds, Green et al. (2004) suggested that these birds use adaptive drift strategies with extensive drift during the initial part of the migratory journey, followed by an increasing degree of compensation during later stages as the birds are approaching their destinations.

Could the pattern of drift and compensation found in our study be attributed to adaptive drift strategies? If we consider the whole migratory journey from breeding areas in the Arctic Russia to staging areas in the North Sea region, a mean distance of approximately 3,500 km, the final leg from Ottenby to the destination (500–1,000 km) is more to be considered as part of the final approach to the goal area, when we should expect winds to remain rather constant and, consequently, complete compensation to be the most favourable behaviour (Alerstam 1979). Furthermore, we studied the birds along a rather short part of their migratory journey (less than 200 km, corresponding to only a few hours' flight), and changes from drift to compensation behaviour are not predicted to occur so abruptly according to the strategy of adaptive drift.

Are there other explanations for the pattern of drift and compensation in our study? One possibility is that the birds allow themselves to be drifted when departing over the sea at Ottenby, because in that way their ground speed will be higher and they will pass more rapidly over the open sea. If this was an important aspect, we would expect the shorebirds to allow themselves to be drifted mainly by crosswinds from the left, when they would quickly reach coastal regions of mainland Sweden, but not by crosswinds from the right when they would be drifted out over wider sea expanses (Fig. 1). However, the birds departing from Ottenby seemed to be drifted to a similar degree by winds from both left and right (Fig. 2). Still another possibility is that the two sites, Vitemölla and Björka, were passed by only a subset of migrants with specific track directions compared to a larger cohort of migrants passing Ottenby. This could lead to a spurious pattern of compensation at the two former sites. However, this is contradicted by the fact that the scatter of track directions was not smaller at these two sites compared to Ottenby (Table 1), making this possibility unlikely.

Drift could also occur as a result of constraints in the capacity of birds to compensate, e.g. because of lack of visual landmark features that can be used as reference cues for determining the resulting track direction (Alerstam and Pettersson 1976; Green 2001). This has been termed non-adaptive drift. Shorebirds departing from Ottenby flew out over the open sea, and in this situation it may be possible to compensate only partially if the birds are using the seascape (wave pattern) as a reference (Alerstam and Pettersson 1976). Also, the majority of flocks flew at very low altitudes (just above the water surface), and then it might not be possible to use the seascape at all as a reference. Some flocks ascended during departure, and in this situation it might also be difficult to compensate for wind drift because of the changing altitude. Later, when approaching the coast of Scania (Vitemölla), the birds might have the possibility to compensate when flying at higher altitudes in level flight and having visual access to the seascape or landmarks as reference cues (Alerstam and Pettersson 1976; Richardson 1991). Further inland (Björka), they have the capacity to compensate fully due to visual landmarks, and the birds in our study did in fact compensate to a high degree at this site. Another explanation for the drift at Ottenby could be that birds just after departure allow themselves to be drifted while sensing the winds and locating their cruising flight altitude. Such full drift during migratory departure and climbing flight was also recorded for Arctic and Common Terns in the southern Baltic region (Alerstam 1985).

We found no difference in wind drift between adult and juvenile birds departing from Ottenby (Table 4). If the capacity to compensate is something that birds have to learn, e.g. by means of an acquired map (navigation) sense, non-adaptive drift should be more obvious in young inexperienced migrants than in older birds. This has been demonstrated in raptors where juvenile birds during their first migration drifted fully while adult birds compensated to a higher degree (Thorup et al. 2003). But if the birds at Ottenby are unable to correct for wind drift, then we would not expect to find any difference between the age groups.

Our study demonstrates that shorebirds are remarkably variable in their response to crosswinds including during short sections of their migratory journey. This is in accordance with recent studies demonstrating that birds use a much more varied repertoire of behavioural responses to wind than previously assumed (Klaassen et al. 2011a; Grönroos et al. 2012a). This study indicates, in addition to adaptive orientation responses to wind, the importance of the non-adaptive wind drift that contributes to increasing the variability of drift/compensation behaviour between places that are separated by only short distances, depending on the local topographic and environmental conditions.

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