



# Flight speed adjustment by three wader species in relation to winds and flock size



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The selection of flight speed (airspeed) in migrating birds depends on multiple internal and external factors, such as wing morphology, weight and winds. Adjustment with respect to side winds to maintain an intended track direction may include a shift in heading direction and/or an increase in airspeed. Compensation for cross-winds cannot always be achieved if visual references are lacking or may not even be beneficial if adaptive wind drift is favourable. Flock size is an additional, although often neglected, factor that could influence the airspeed of birds. Here, we show that responses to cross-winds to achieve compensation differed on a small geographical scale (a few kilometres) in migrating shorebirds, where the availability of topographical features such as coastlines may play an important role for the birds' behaviour. We also show that airspeed was significantly influenced by flock size in three species of shorebirds, increasing with increasing flock size. This is contrary to the prediction based on the hypothesis of energy saving by flight in flock formation, but in agreement with empirical findings for migrating terns. The reason why flock size influences airspeed remains unclear, but we propose a mechanistic explanation based on the largest/heaviest individual(s) determining the speed of the flock. © 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

The collective behaviour of animals when moving in groups, such as swarming insects, schooling fish or bird flocking has long fascinated human observers, but it was not until very recently that scientists started to unravel the underlying mechanisms behind apparent collective motions of animal groups (e.g. [Couzin, 2008](#)). For example, is the direction of movement determined by one or a few individuals (leaders) in the group, or is it the vector sum of all individuals' preferred orientation? Another fundamental aspect is whether the speed of the group is determined by a leader or a compromise of individuals' preferred speeds ([Pettit, Åkos, Vicsek, & Biro, 2015](#))? Many birds migrate in flocks, but the directions and speeds have received relatively little attention. Flocking during migratory flights could arise for various reasons, including reduced predation risk ([Hamilton, 1971](#)), flight economy by formation flight ([Lissaman & Sholleneberger, 1970](#)) or orientation accuracy ([Wallraff, 1978](#)). To stay in a cohesive flock during migratory flights all birds must fly at the same speed, especially when flying in orderly v- or echelon formations. Since individual flight speed may depend on multiple factors ([Hedenström & Ålerstam, 1995](#)), it is likely that the preferred flight speed may differ between members

of a flock. We may therefore ask whether an intrinsic flock-related mechanism exists that operates in addition to other factors to influence the flight speed of bird flocks during migration.

The flight speed observed in birds depends on many internal and external factors, ranging from size, wing morphology, winds and rate of climb to ecological context ([Hedenström & Ålerstam, 1995](#); [Pennycuik, 1978](#)). The response to winds may vary depending on availability of suitable landmarks, such as coastlines or other features in the landscape, allowing birds to not only adjust airspeed to the tail/head and side wind components but also to adjust the heading to compensate for lateral wind drift ([Åkesson, 1993](#); [Ålerstam, 1976, 1979](#); [Green & Ålerstam, 2002](#); [Hedenström & Åkesson, 2016](#)). Even when setting out on over-water flights, migrating birds may compensate for wind drift by using the pattern of the wave scape as visual reference, although full compensation cannot be achieved due to the motion of the waves ([Ålerstam & Pettersson, 1976](#)). The response to winds could also vary along the migration route, where birds may adaptively allow drift when far away from the goal and gradually increase compensation for drift as they approach the goal ([Ålerstam, 1979](#)). Radar studies at different latitudes suggest that such adaptive drift/compensation behaviour may occur in migratory birds ([Green, Ålerstam, Gudmundsson, Hedenström, & Piersma, 2004](#)). More recently it has also become evident that, in addition to other factors, flock size

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may influence flight speed in migrating terns, *Sterna* spp. (Hedenström & Åkesson, 2016). There is also some evidence that flock size affects flight speed in three species of shorebirds (dunlin, *Calidris alpina*, red knot, *Calidris canutus*, and Eurasian oystercatcher, *Haematopus ostralegus*; Noer, 1979), but this study analysed the effect of flock size on ground speed and did not control for potentially confounding factors such as winds, vertical speed and altitude. Here we analysed the influence of multiple factors on flight speed selection in the same shorebird species as analysed by Noer (1979) migrating past the island of Öland in the Baltic Sea. Our main aim was to test the hypothesis that flock size is an independent factor that influences the airspeed of migrating shorebirds simultaneously with other factors. In addition, we tested whether migrating shorebirds compensate for wind drift by adjusting heading and/or airspeed differently with respect to cross-winds at two nearby locations differing in availability of visual landmarks.

## METHODS

We measured flight tracks of migrating shorebirds at southern Öland in the Baltic Sea by using an ornithodolite (Pennycuick, 1982, 1999; Pennycuick, Åkesson, & Hedenström, 2013), which consists of a pair of Vectronix Vector 21 Aero binoculars (7×42 magnification) with three built-in sensors (laser range finder, magnetic compass and elevation angle sensor) mounted on a tripod. When tracking a bird flock, the Vector buttons are pressed and released to store time-stamped recordings of distance, azimuth and elevation angles to a computer file. Each reading of a bird (or flock of birds) is called an 'observation' of the target's timed position in space with the observer in the origin, where a series of two or more observations of the same target is called a 'run'. For each run we calculated mean ground speed, vertical speed and track direction. Wind measurement is necessary to calculate airspeed and heading direction using the triangle of velocities (see Fig. 1; e.g. Alerstam, 2000). A Gill Windsonic anemometer mounted on a 5 m mast in an unobstructed location near the ornithodolite was used to measure wind strength and direction, which transmitted wind readings to the computer at 1 s intervals via a pair of wireless modems (Haccomm UM-96). Wind speeds at altitudes more than 15 m above ground surface were measured by tracking the path of ascending helium-filled balloons with the ornithodolite. Balloons were released at the start and end of each session, and every hour or more often if wind changed noticeably during a session. Each balloon ascent was subsequently analysed to derive the wind profile, consisting of altitudinal segments of wind speed and direction. Depending on flight altitude of the bird(s) being tracked, the anemometer wind was used for low-flying birds (15 m or below), while balloon-tracked winds were used for flight altitudes above 15 m. The ambient air temperature and pressure were recorded at the observer's position using a pocket weather meter (Kestrel 4500NV), and we regularly updated data during a session. Following the completion of a run, data about

species, age, sex, flight mode (continuous flapping, intermittent gliding/flapping, bounding, gliding), flight behaviour (straight, meandering, circling, feeding) and flock size were recorded. For the present data on waders only runs recorded as 'straight flapping flight' were included. If age could not be determined it was noted as 'no age', while if one age group dominated the flock composition the flock was recorded as representative of that age, but a note was made that the flock was composed of mixed age groups. The data were analysed in a custom-written software (Visual Basic), to derive mean airspeed, equivalent airspeed, ground speed, vertical speed, track and heading directions and altitude for each run. Airspeed and heading direction were derived from the mean track, wind speed and wind direction using the triangle of velocities (Fig. 1). Likewise, the tail wind and side wind components of wind along the track direction were derived based on the triangle of velocities. For further details about the ornithodolite system please refer to Pennycuick et al. (2013).

Observations were made at three locations near Ottenby on southern Öland in the Baltic Sea (Fig. 2), where sites B1 and B2 are 1.4 km apart and site A is 6.9 km to the north-northeast of site B1. The migration observed from sites B1 and B2 refers to the same passage of migrants and therefore we combined these observations as one site in the analyses (B). The coastline at site A is oriented along the axis 16°/196°, while the eastern coastline at site B is aligned along the axis 42°/222° and the coastline, consisting of small islands, west of site B1 is aligned as 16°/196°. Fieldwork was carried out in September 2012 at site A, and during July and August in 2013–2016 at sites A and B.

The amount of drift or compensation in relation to winds was estimated according to method 3 in Green and Alerstam (2002), where the magnitude of drift was calculated as

$$b_{\text{track}} = \frac{T_1 - T_2}{\alpha_1 - \alpha_2}, \quad (1)$$

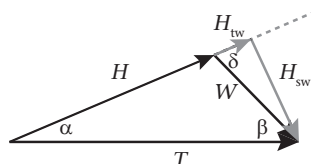
where  $T_1$  and  $T_2$  are track directions for the birds having the wind from left and right with respect to the overall track direction of the whole sample, respectively, with  $H_1$  and  $H_2$  representing the associated heading directions, and  $\alpha_1 = T_1 - H_1$  and  $\alpha_2 = T_2 - H_2$ . A value of  $b_{\text{track}}$  of 0 implies compensation, a value of 1 is full drift, values between 0 and 1 represent partial drift/compensation, while values <0 represent overcompensation and values >1 overdrift (Green & Alerstam, 2002). For graphical illustrations of different drift and compensation scenarios see Chapman et al. (2012).

## Statistics

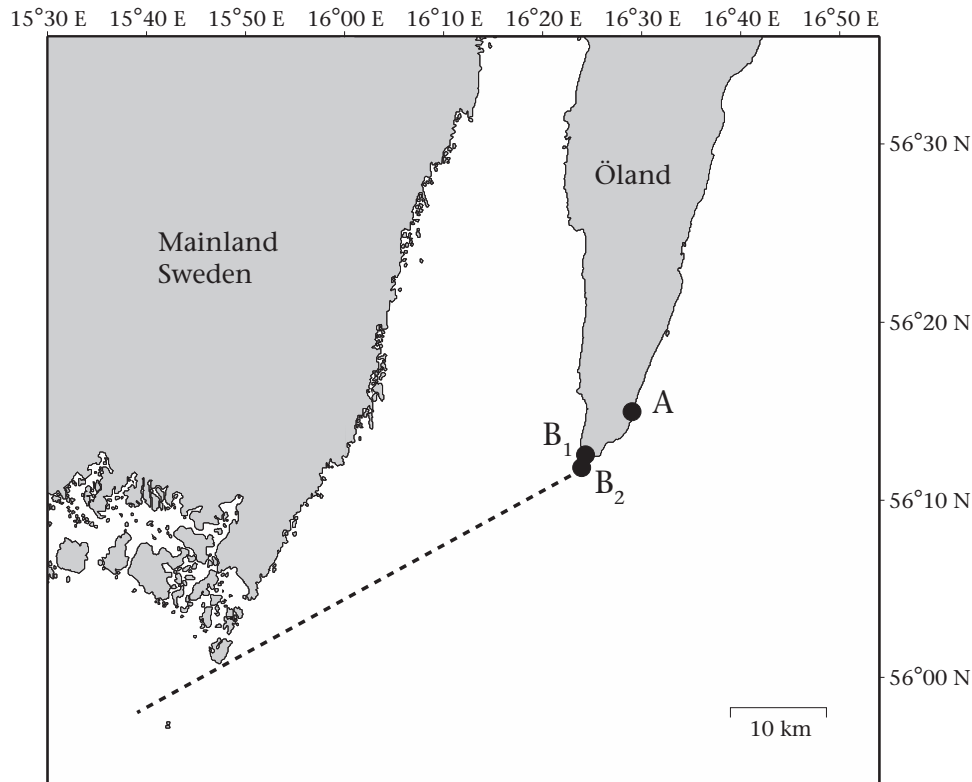
Statistical tests were performed using JMP 12.0 for general linear models (GLM) and Oriana 4 for circular statistics (Batschelet, 1981), respectively. For analyses, we used the run means of speeds and altitude as independent observations. The data of flock sizes were not normally distributed (Shapiro–Wilk normality test:  $P < 0.01$  for all species), and therefore we log<sub>e</sub>-transformed flock size. The GLM was based on which factors, in addition to flock size, are likely candidates to affect airspeed in birds as based on flight mechanical theory (Hedenström, 2003; Pennycuick, 1978).

## Ethical Note

This study comprises observational data of flight tracks in migrating shorebirds at such distances that the birds did not react to the presence of the human observers. Tracks were obtained by using a class 1 eye-safe infrared laser range finder. We did not observe any behavioural signs that would suggest the birds noticed they were being tracked.



**Figure 1.** The triangle of velocities defining the relationship between heading ( $H$ ), wind ( $W$ ) and track ( $T$ ) with the length of the vectors representing the airspeed ( $U$ ), wind speed ( $U_w$ ) and ground speed ( $U_g$ ). The diagram also shows how the tail wind ( $H_{tw}$ ) and side wind ( $H_{sw}$ ) components are calculated according to the heading direction. Tail and side wind components can also be calculated with respect to the track direction using the angle  $\beta$ .



**Figure 2.** The observation sites (A, B<sub>1</sub> and B<sub>2</sub>) on southern Öland in the Baltic. The coastline is oriented along the axis 16°/196° at site A and 42°/222° at site B (B<sub>1</sub> and B<sub>2</sub> combined). Most birds arrive from the northeast during migratory flight, but some take off from stopover sites at nearby lagoons to the northeast of site B<sub>2</sub>. The dotted line shows the direction (242°) to the coast of the biggest island off the southeastern Swedish mainland.

## RESULTS

### *Flock Size and Characteristic Flight Behaviour*

All three species migrated in flock formation (V or echelon), which was most pronounced in the Eurasian oystercatchers. Red knots and dunlins were also observed to fly in cluster-shaped flocks, but the clusters were usually at the front and were followed by a formation segment. When departing from site B, red knots and dunlins typically formed flock formations when climbing to reach their cruising altitude. The largest flock observed was 450 in the Eurasian oystercatcher, while the mean and median flock sizes were much lower (Table 1). The median flock size was very similar at 9–10 individuals for all three species (Table 1).

### *Flight Directions*

At site A the three species showed similar track directions between 185 and 191° (Table 2), which is close to the orientation of the coastline there (196°). The heading directions of 191–201° were also closely aligned with the coastline (Table 2).

All three species made a significant shift in both heading and track directions between site A and B (Table 2). In the Eurasian

oystercatcher the shift in heading was 40° (Watson–Williams test:  $F_{1,78} = 120.3$ ,  $P < 0.001$ ) and the shift in track was 48° (Watson–Williams test:  $F_{1,78} = 147.3$ ,  $P < 0.001$ ), and in the dunlin the shifts in heading and track were 31° (Watson–Williams test:  $F_{1,147} = 94.4$ ,  $P < 0.001$ ) and 41° (Watson–Williams test:  $F_{1,78} = 2.817$ ,  $P < 0.001$ ), respectively. The shifts by red knots were less pronounced and not significant for either heading at 5° (Watson–Williams test:  $F_{1,17} = 0.06$ ,  $P > 0.05$ ) or track at 17° (Watson–Williams test:  $F_{1,17} = 0.613$ ,  $P > 0.05$ ).

### *Wind Compensation*

The close alignment of track directions with the coastline at site A suggests that the birds compensated for lateral wind drift. Dividing the data into groups where wind direction is from the left and right with respect to the overall track direction, respectively, and using equation (1) to calculate the amount of compensation/drift ( $b$ ) revealed that Eurasian oystercatchers showed perfect wind compensation at site A ( $b_{\text{track}} = 0$ ; Table 3), while they showed overdrift at site B ( $b_{\text{track}} = 1.51$ ; Table 3). The compensation for drift at site A is illustrated in Fig. 3, where the heading is clearly shifted into the wind to maintain a constant track direction at 191°. The dunlins showed a partial compensation at both sites A and B, although it was significant at site A only (Table 3). The sample size for the red knot was too low to allow a meaningful drift analysis by subdivision into wind categories.

### *Airspeed*

Because airspeed selection in birds is probably influenced by many factors (see above), we performed a GLM analysis for each of the three species, with  $\log_e(\text{flock size})$ , altitude, vertical speed, tail

**Table 1**  
Descriptive statistics of flock size for three species of shorebird during autumn migration at Ottenby, southern Baltic, Sweden

Species	N	Mean	SD	Median	Range
Eurasian oystercatcher	80	22.8	58.0	10	1–450
Red knot	19	16.1	33.1	9	2–150
Dunlin	149	17.3	23.0	10	1–200

**Table 2**  
Flight directions of shorebirds at Ottenby, southern Baltic, Sweden.

Species	Site A			Site B		
	Track	Heading	N	Track	Heading	N
Eurasian oystercatcher	191° (7.2)	191° (14.5)	42	239° (24.2)	231° (17.4)	38
Red knot	185° (12.3)	201° (10.9)	8	202° (60.6)	206° (61.2)	11
Dunlin	189° (8.0)	196° (8.5)	70	230° (29.1)	227° (25.7)	79

Mean track, heading and sample size (N) are shown for three species of waders at site A and B (see Fig. 2). The numbers within parentheses are circular standard deviations in degrees.

**Table 3**  
Measures of drift in relation to winds of shorebirds at Ottenby, southern Baltic, Sweden

Species	Site	$b_{\text{track}}$	H left	H right	P
Eurasian oystercatcher	A	0.0005	181° (22)	201° (20)	<0.001
	B	1.52	232° (31)	225° (7)	NS
Dunlin	A	0.36	190° (10)	197° (60)	<0.05
	B	0.26	224° (53)	233 (26)	NS

Calculated magnitude of drift/compensation ( $b_{\text{track}}$ ) is shown for Eurasian oystercatcher and dunlin according to equation (1), together with mean heading and circular deviation for groups with winds coming from the left (H left) and right (H right), respectively, at the sites A and B (see Fig. 2). Numbers within parentheses are sample sizes for each group. The P values refer to a Watson–Williams test (Batschelet, 1981).

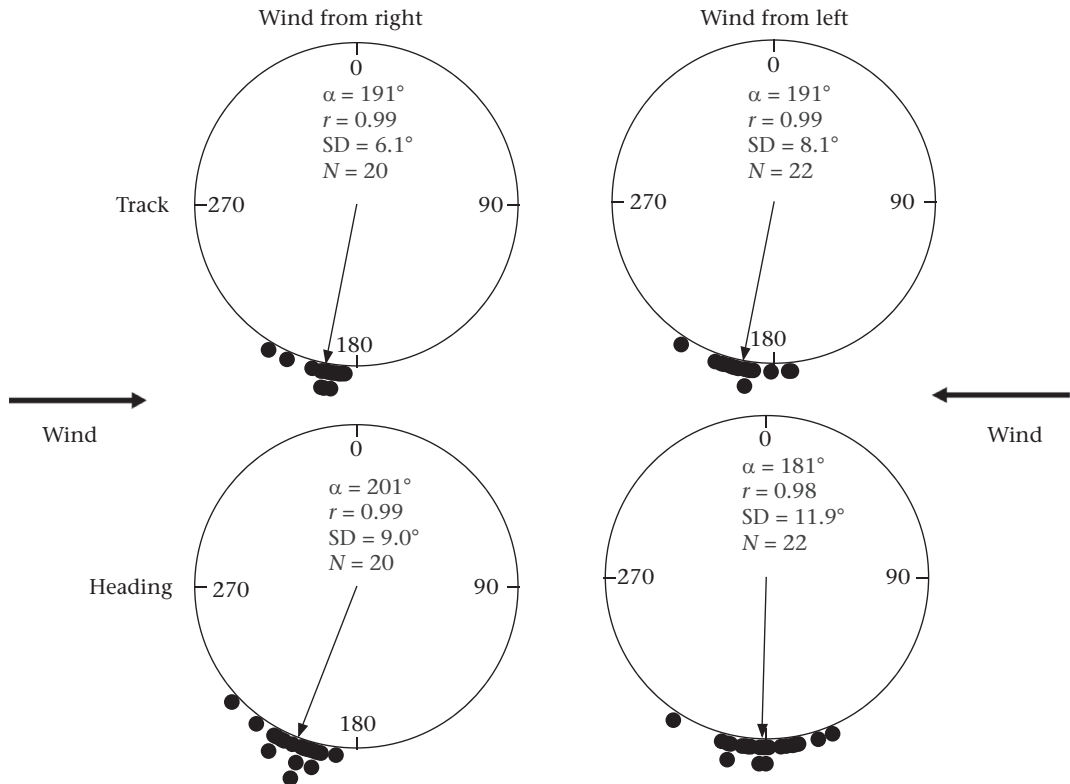
( $H_{\text{tw}}$ ) and side ( $H_{\text{sw}}$ ) wind components as independent variables. For the Eurasian oystercatcher there were significant effects of flock size and vertical speed (Table 4). For the red knot, only flock size showed a significant effect on airspeed, while in the dunlin all the variables included showed significant effects (Table 4). Hence, flock size was the only variable showing significant effect in all three species (Table 4). The relationships between flock size and airspeed are shown in Fig. 4. Nearly identical results were obtained if instead

tail and side wind components in track direction were used. We also combined the data from all three species to perform one analysis with species as random effect, which yielded significant effects of all the factors included (Table 4).

DISCUSSION

Flight Directions

There was a clear effect of the topography (coastline) between site A and B on flight directions with a mean 41–48° shift in Eurasian oystercatchers and dunlins, while the shift was less dramatic in red knots. The shift of flight directions was larger than the change in orientation of the coastline in Eurasian oystercatchers and dunlins, which was similar to the shift observed in several species of migrating terns at the same sites (Hedenström & Åkesson, 2016). Departure track directions of Eurasian oystercatchers and dunlins at site B are very close to those of shorebirds observed by Grönroos, Green, and Alerstam (2012) at this site (239°, 230° and 234°, respectively), while the red knots had a mean track direction more to the south (202°). The small differences in heading between the species were not significant, and therefore



**Figure 3.** Track and heading directions for Eurasian oystercatchers migrating at site A (see Fig. 2) with winds coming from the right (seen from the birds' perspective winds from the right are synonymous with westerly winds) and left, respectively. To compensate for winds and maintain a constant track direction the birds shift the heading into the wind.

**Table 4**

Statistical analysis of airspeed in shorebirds in relation to multiple factors at Ottenby, southern Baltic, Sweden

Species	N	Flock size	z	$U_z$	$H_{TW}$	$H_{SW}$
Eurasian oystercatcher	80	0.52***	0.0034	−1.41*	−0.016	0.078
Red knot	19	2.08*	−0.041	1.49	−0.090	0.0045
Dunlin	150	0.69***	−0.010**	−1.30***	−0.23***	0.31**
All	249	0.70***	−0.0054*	−1.44***	0.11**	0.25**

Effect and statistical significance on airspeed ( $U$ ) of flock size, vertical speed ( $U_z$ ), altitude ( $z$ ), tail wind component ( $H_{TW}$ ) and side wind component ( $H_{SW}$ ).  $N$  is sample size. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

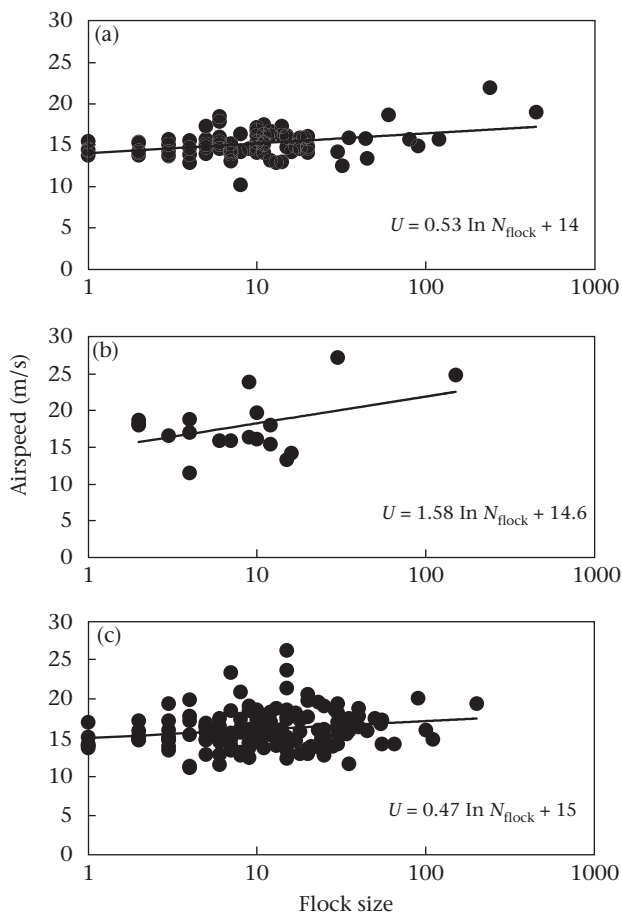
one should not make any far-reaching inferences about them. The direction to the southeast corner of the Swedish mainland coast is  $242^\circ$ , which means that many flocks will miss it unless they change their flight direction when approaching it over sea. The mean track directions of arctic and common terns, *Sterna paradisaea* and *Sterna hirundo*, were  $247^\circ$  and  $258^\circ$ , respectively, suggesting there may be small differences in preferred migration directions between the shorebirds of this study compared with other species observed at the same locations (Hedenström & Åkesson, 2016). The differences between all shorebirds combined versus arctic and common terns combined is statistically significant for both heading and track at site B (Watson–Williams test: heading:  $F_{1,227} = 15.4$ ,  $P < 0.001$ ; track:  $F_{1,227} = 21.1$ ,  $P < 0.001$ ). However, the significance of these differences when it comes to the use of landmarks remains unclear, but suggests there may be species-specific differences in the intended courses to destination areas further away (cf. Grönroos, et al., 2012; Hedenström & Åkesson, 2016).

Migrating birds, including shorebirds, are thought to reach the east coast of Öland from an overseas crossing of the Baltic Sea (Edelstam, 1972), and are thereafter funnelled along the coast until they reach the southern part of the island, where they change direction. The mainland about 26 km away is usually visible from site B, which probably serves as a cue to the birds to change flight direction at site B.

#### Airspeed and Wind Compensation

Our measurements showed that airspeed is affected by several factors, and this was particularly clear for the dunlin where all variables included in the analysis contributed significantly to the variation in airspeed. This is probably because sample size was largest for the dunlin, but a lack of airspeed adjustment with respect to the tail wind component in Eurasian oystercatchers could likewise be a real phenomenon since the sample size was also rather large in this species. Airspeed adjustment in relation to head/tail winds is found in many studies of migrating birds (see Hedenström, Alerstam, Green, & Gudmundsson, 2002 for a review). The reduction in airspeed when climbing as found for Eurasian oystercatchers and dunlins has been observed also at other sites (Hedenström & Alerstam, 1992; Piersma, Hedenström, & Bruggemann, 1997), and is explained by the need to allocate muscle power to raise the body against gravity and reduce the power required for forward flight by selecting a speed close to the minimum power speed. The multifactorial influence on airspeed in migrating birds implies that these factors should be carefully considered when comparing flight speeds between seasons, sites and flight modes.

The compensation for lateral wind drift varied between the two sites in the Eurasian oystercatcher, where birds showed perfect wind compensation at site A and drift (or even overdrift) at site B. That the amount of drift/compensation varies within short ranges may reflect different opportunities to use topographical features such as coastlines and other landmarks (Grönroos et al., 2012; Richardson, 1990). It is commonly observed that birds flying over water are more susceptible to drift compared to overland flight (Richardson, 1990). Birds may achieve compensation by shifting the heading direction and/or increasing the airspeed. Eurasian oystercatchers compensated by only adjusting heading at site A, while dunlins adjusted both heading and speed (although the shift in heading was not significant at site B). The reason for these differences between the species remain unclear, but it could be related to body size. The heavier Eurasian oystercatcher may have a smaller power margin than the dunlins (difference between power available from the flight muscles and the power required to fly; Hedenström & Alerstam, 1992), which may limit their scope to increase the speed in head or side winds. Grönroos, Green, and Alerstam (2013) were surprised to find different compensation/drift behaviour between sites about 200 km apart in the southern Baltic, including Ottenby, which they interpreted as contrary to regional shifts in adaptive drift/compensation behaviour (cf. Green et al., 2004). Our results show that birds can react differently to cross-winds at sites only a few kilometres apart, suggesting that



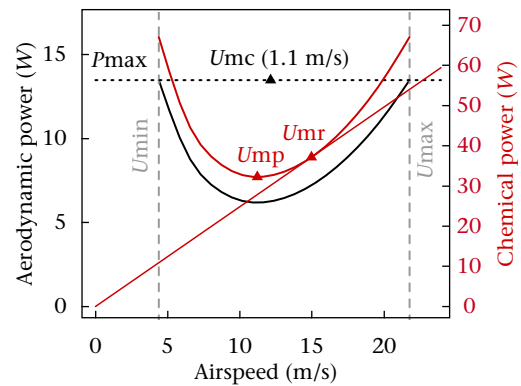
**Figure 4.** The relationship between airspeed (y-axis) and flock size (x-axis, log scale) for (a) Eurasian oystercatcher, (b) red knot and (c) dunlin. Equations are linear regressions between the two variables with flock size  $\log_e$ -transformed.



locally available landscape features and cues play a role in orientation and flight decisions at much smaller scales. At site B the birds leave direct contact with leading lines and set out over open water, where they also lose the opportunity to fully compensate for wind drift due to the slow motion of the wave scape (Alerstam & Pettersson, 1976). Further to this, at site B many dunlins and red knots climb to reach their cruising altitude, which may also prevent them from compensating for wind drift (Alerstam, 1985; Hedenström & Åkesson, 2017).

### Flock Size

Our measurements of flight speeds revealed that airspeed was influenced by flock size, which was a significant factor in all three species studied. That flock size could influence flight speed in the same set of shorebird species was suggested by Noer (1979), but he analysed the effect of flock size in relation to ground speed without controlling for other factors. That airspeed is positively related to flock size has also been reported for migrating terns, *Sterna* spp. (Hedenström & Åkesson, 2016). On theoretical grounds, it has been predicted that birds flying in a flock formation could exploit the upwash generated outside the wing tip of the bird flying in front and thereby reduce the induced drag (Wieselsberger, 1914). Measurements have shown that pelicans, *Pelecanus onocrotalus*, lowered their heart rate (proxy for flight metabolism) and extended their glide phases when flying in formation (Weimerskirch, Martin, Clerquin, Alexandre, & Jiraskova, 2001). However, the expected response to lowering the individual power required to fly by reducing induced drag is to reduce airspeed (Hummel, 1983), which is contrary to most empirical findings (this study; Hedenström & Åkesson, 2016). A study of formation flying bald ibises, *Geronticus eremita*, suggested that the birds phased their wing beats as if exploiting the wing tip vortices from one another (Portugal et al., 2014), but whether or how much these birds reduced their flight cost was not studied. Flight in cluster-shaped flocks is more likely to increase flight costs compared to solo flight (Usherwood, Stavrou, Lowe, Roskilly, & Wilson, 2011). Why birds appear to increase airspeed in relation to flock size is not clear, but there could be several reasons. One potential explanation is that if birds maintain their flight effort (muscle work rate) at a preset level, a reduced power required to fly could lead to an increased characteristic speed. This would, however, lead to individually different optima for flock members depending on weight, morphology and flock position, and would be likely to lead to flock disorder. Body mass is a major determinant of flight speed (Pennycuik, 1975). For statistical reasons, there will be a positive correlation between the heaviest individual of a flock and flock size. The expected relation between airspeed and flock size will emerge if one assumes a body mass distribution (mean  $\pm$  SD) for a flock and simulates flocks of different size, from which the heaviest individual is used to calculate a flight speed that is assigned to the flock. If flock individuals choose to fly at their individual optimal airspeed (such as maximum range speed or the optimal speed associated with time-selected migration; Hedenström & Alerstam, 1995), then a pattern like that observed will emerge with the heaviest flock members determining the speed and lighter individuals flying somewhat faster than their own optimum speed to stay in the flock (Hedenström, 2003). To determine whether this is the case in real bird flocks, however, will be a challenge, but using time-resolved GPS loggers on flocks composed of individuals whose mass and morphology is known could be one way forward (cf. Usherwood et al., 2011). In this context, it could be of interest to consider the cost of increasing the flight speed by 2–3 m/s above the preferred (optimal) speed. As an example, we calculated the cost of increasing the speed by 2.6 m/s, representing a Eurasian oystercatcher flying



**Figure 5.** Power required to fly in relation to airspeed calculated for a bird of dimensions representing a Eurasian oystercatcher (body mass 0.544 kg, wing span 0.852 m and wing area 0.0873 m<sup>2</sup>; Pennycuik, 1999), using the model by Klein Heerenbrink et al. (2015). The lower curve is the aerodynamic power required to fly (left hand y-axis) and the upper (red) curve is the estimated chemical (metabolic) power (right hand y-axis). The horizontal dashed line represents the maximum power ( $P_{max}$ ) available from flight muscles, which determines the minimum speed ( $U_{min}$ ) and maximum speed ( $U_{max}$ ). The characteristic speeds are minimum power speed ( $U_{mp}$  = 11.22 m/s) and maximum range speed ( $U_{mr}$  = 14.97 m/s) and the speed of maximum climb rate ( $U_{mc}$  = 12.14 m/s to yield a climb rate of 1.1 m/s).

singly or in a large flock (see Fig. 4a), using an aerodynamic model for vertebrate flight (Klein Heerenbrink, Johansson, & Hedenström, 2015). The resulting power–speed relationship for a Eurasian oystercatcher is shown in Fig. 5, from which it can be derived that increasing the maximum range speed (14.97 m/s) by 2.6 m/s results in an increased power required to fly of 23%, while the cost of transport (energy cost per unit distance) increases by 5%. Even this superficially small increase in cost of transport by flying sub-optimally may still be of ecological significance in a migration context. It also remains to be clarified whether birds whose formation flight probably leads to a cost reduction, such as pelicans (Weimerskirch et al., 2001), adjust airspeed adaptively by reducing it as a function of flock size (as predicted from aerodynamic theory) or whether they increase speed as other birds do.

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### References

- Åkesson, S. (1993). Coastal migration and wind drift compensation in nocturnal passerine migrants. *Ornis Scandinavica*, 24, 87–94.
- Alerstam, T. (1976). *Bird migration in relation to wind and topography* [Ph.D. thesis]. Lund, Sweden: Lund University.
- Alerstam, T. (1979). Wind as selective agent in bird migration. *Ornis Scandinavica*, 10, 76–93.
- Alerstam, T. (1985). Strategies of migratory flight, illustrated by Arctic and common terns *Sterna paradisaea* and *Sterna hirundo*. *Contributions in Marine Science, Supplement*, 27, 580–603.
- Alerstam, T. (2000). Bird migration performance on the basis of flight mechanics and trigonometry. In P. Domenici, & R. W. Blake (Eds.), *Biomechanics in animal behaviour* (pp. 105–124). Oxford, U.K.: BIOS Scientific Publishers.

- Alerstam, T., & Pettersson, S. G. (1976). Do birds use waves for orientation when migrating across the sea? *Nature*, 259, 205–207.
- Batschelet, E. (1981). *Circular statistics in biology*. London, U.K.: Academic Press.
- Chapman, J. W., Klaassen, R. H. G., Drake, V. A., Fossette, S., Hays, G. C., Metcalfe, J. D., et al. (2011). Animal orientation strategies for movement in flows. *Current Biology*, 21, R861–R870.
- Couzin, I. D. (2008). Collective cognition in animal groups. *Trends in Cognitive Sciences*, 13, 36–43.
- Edelstam, C. (1972). The visible migration of birds at Ottenby, Sweden. *Vår Fågelvärld Supplement*, 7, 1–360.
- Green, M., & Alerstam, T. (2002). The problem of estimating wind drift in migrating birds. *Journal of Theoretical Biology*, 218, 485–496.
- Green, M., Alerstam, T., Gudmundsson, G. A., Hedenström, A., & Piersma, T. (2004). Do arctic waders use adaptive wind drift? *Journal of Avian Biology*, 35, 305–315.
- Grönroos, J., Green, M., & Alerstam, T. (2012). Fine-scaled orientation changes in migrating shorebirds. *Ardea*, 100, 45–53.
- Grönroos, J., Green, M., & Alerstam, T. (2013). Orientation of shorebirds in relation to wind: Both drift and compensation in the same region. *Journal of Ornithology*, 154, 385–392.
- Hamilton, W. D. (1971). Geometry of the selfish herd. *Journal of Theoretical Biology*, 31, 295–311.
- Hedenström, A. (2003). Twenty-three testable predictions about bird flight. In E. Gwinner (Ed.), *Avian migration* (pp. 563–582). Berlin, Germany: Springer.
- Hedenström, A., & Åkesson, S. (2016). Ecology of tern flight in relation to wind, topography and aerodynamic theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 20150396.
- Hedenström, A., & Åkesson, S. (2017). Adaptive airspeed adjustment and compensation for wind drift in the common swift: differences between day and night. *Animal Behaviour*, 127, 117–123.
- Hedenström, A., & Alerstam, T. (1992). Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *Journal of Experimental Biology*, 164, 19–38.
- Hedenström, A., & Alerstam, T. (1995). Optimal flight speed of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 348, 471–487.
- Hedenström, A., Alerstam, T., Green, M., & Gudmundsson, G. A. (2002). Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. *Behavioural Ecology and Sociobiology*, 52, 308–317.
- Hummel, D. (1983). Aerodynamic aspects of formation flight in birds. *Journal of Theoretical Biology*, 104, 321–347.
- Klein Heerenbrink, M., Johansson, L. C., & Hedenström, A. (2015). Power of the wingbeat: Modelling the effects of flapping wings in vertebrate flight. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 471, 20140952.
- Lissaman, P. B. S., & Shollenberger, C. (1970). Formation flight in birds. *Science*, 168, 1003–1005.
- Noer, H. (1979). Speeds of migrating waders Charadriidae. *Dansk Ornitologisk Forening Tidsskrift*, 73, 215–224.
- Pennycuik, C. J. (1975). Mechanics of flight. In D. S. Farner, J. R. King, & K. C. Parkes (Eds.), *Avian biology* (Vol. 5, pp. 1–75). New York, NY: Academic Press.
- Pennycuik, C. J. (1978). Fifteen testable predictions about bird flight. *Oikos*, 30, 165–176.
- Pennycuik, C. J. (1982). The ornithodolite: an instrument for collecting large samples of bird speed measurements. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 300, 61–73.
- Pennycuik, C. J. (1999). *Measuring birds' wings for flight performance calculations* (2nd ed.). Bristol, U.K.: Boundary Layer Publications.
- Pennycuik, C. J., Åkesson, S., & Hedenström, A. (2013). Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. *Journal of the Royal Society Interface*, 10, 20130419.
- Pettit, B., Ákos, Z., Vicsek, T., & Biro, D. (2015). Speed determines leadership and leadership determines learning during pigeon flocking. *Current Biology*, 25, 3132–3137.
- Piersma, T., Hedenström, A., & Brüggemann, J. H. (1997). Climb and flight speeds of shorebirds embarking on an intercontinental flight; do they achieve the predicted optimal behavior? *Ibis*, 139, 299–304.
- Portugal, S. J., Hubel, T. Y., Fritz, J., Heese, S., Trobe, D., Voelkl, B., et al. (2014). Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature*, 505, 399–402.
- Richardson, W. J. (1990). Wind and orientation of migrating birds: A review. *Experientia*, 46, 416–425.
- Usherwood, J. R., Stavrou, M., Lowe, J. C., Roskilly, K., & Wilson, A. (2011). Flying in a flock comes at a cost in pigeons. *Nature*, 474, 494–497.
- Wallraff, H. G. (1978). Social interactions involved in migratory orientation of birds: Possible contribution of field studies. *Oikos*, 30, 401–404.
- Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P., & Jiraskova, S. (2001). Energy saving in flight formation. *Nature*, 413, 697–698.
- Wieselsberger, C. (1914). Beitrag zur Erklärung des Winkelfluges Einiger Zogvögel. *Zeitschrift für Flugtechnik und Motorluftschiffahrt*, 5, 225–229.