

Research



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Ecology of tern flight in relation to wind, topography and aerodynamic theory

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Flight is an economical mode of locomotion, because it is both fast and relatively cheap per unit of distance, enabling birds to migrate long distances and obtain food over large areas. The power required to fly follows a U-shaped function in relation to airspeed, from which context dependent 'optimal' flight speeds can be derived. Crosswinds will displace birds away from their intended track unless they make compensatory adjustments of heading and airspeed. We report on flight track measurements in five geometrically similar tern species ranging one magnitude in body mass, from both migration and the breeding season at the island of Öland in the Baltic Sea. When leaving the southern point of Öland, migrating Arctic and common terns made a 60° shift in track direction, probably guided by a distant landmark. Terns adjusted both airspeed and heading in relation to tail and side wind, where coastlines facilitated compensation. Airspeed also depended on ecological context (searching versus not searching for food), and it increased with flock size. Species-specific maximum range speed agreed with predicted speeds from a new aerodynamic theory. Our study shows that the selection of airspeed is a behavioural trait that depended on a complex blend of internal and external factors.

This article is part of the themed issue 'Moving in a moving medium: new perspectives on flight'.

1. Introduction

Even if flapping flight in birds is energetically expensive [1], it is relatively fast and entails an economically favourable mode of locomotion, allowing for seasonal migrations with non-stop flights of 10 000 km and more [2,3]. However, because the power required to fly generally follows a U-shaped function in relation to airspeed [4–7], the flight speed (airspeed) can be selected judiciously by the bird for economical transport [8]. For example, if a bird's objective is to remain airborne for a maximum time, the speed of minimum power (U_{mp}) is advantageous (figure 1), which may occur during sustained song flight displays [9], or when buying time when disoriented during migration [8]. On migration, it is rather the energy cost per unit of (ground) distance covered or the maximum overall migration speed that matter to the bird, objectives that are associated with selecting the maximum range speed (U_{mr}) for energy minimization or the optimal flight speed associated with time-selected migration (U_{mt}) [8]. These latter speeds are typically much faster than U_{mp} (figure 1). Still alternative characteristic flight speeds are associated with food transport to a central place such as a nest or a cache [10], or when searching for food and the encounter rate and detection of cryptic prey/food is speed dependent (figure 1) [8]. Further to this, optimization of flight speed is subject to adjustment in relation to winds, not only by a change in heading direction to compensate for lateral wind drift, but also to adjust the airspeed with respect to head/tail winds to economize transport cost [4,8,11,12]. It should be noted that these problems are faced also by other animals moving in a fluid medium, such as swimmers encountering sea currents [13].

Adjustment with respect to head/tail wind is a direct consequence of a speed decrement and increment due to the wind, respectively, and its effect

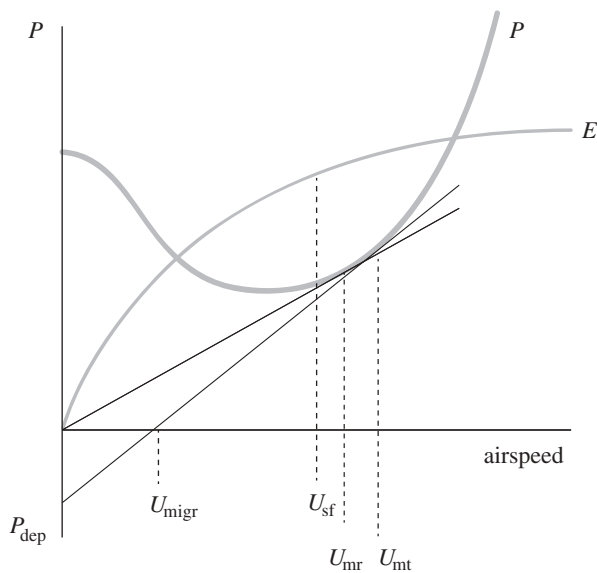


Figure 1. A schematic power curve (P) and a hypothetical function of prey encounter rate (E) in relation to airspeed to illustrate some optimal flight speed in birds. The positive y -axis shows power required to fly (P) and the negative y -axis denotes the rate of energy accumulation at stopovers (P_{dep}). The characteristic (optimal) speeds indicated are the optimal flight speed during food search (U_{sf}), the maximum range speed (U_{mr}), and the optimal flight speed associated with time-minimizing migration (U_{mt}). The overall migration speed (U_{migr}) is the immediate currency of time-minimization migration, and is calculated as $U_{\text{migr}} = U_{\text{mt}} \cdot P_{\text{dep}} / (P + P_{\text{dep}})$; based on [8].

on the ground speed (U_g) in relation to the power curve. In birds that maintain a constant track over ground, which is possible to achieve if birds are following topographical features in the landscape, it can be calculated that in addition to the head/tail wind adjustment, the bird should also adjust its airspeed with respect to the incident side wind [14]. However, this predicted adjustment of airspeed according to side winds, more specifically to the angle between track and heading, has to the best of our knowledge never been observed in birds thus far. Possibly, this depends on the fact that the birds in studies where this predicted effect was tested failed to compensate for wind drift and therefore exhibited partial drift, thus not fulfilling the assumption when this prediction is valid. One possible exception is night migrating common swifts *Apus apus* that did achieve full compensation for wind drift, and did adjust airspeed with respect to the side-wind component (wind component perpendicular to the track direction) [15], but not when analysed according to the predicted criterion (see below) [14].

In addition to the ecological objective and winds, flight speed is also influenced by altitude (by air density [11]), climb rate [16] and possibly flock size. Flight in flock formation is expected to alleviate flight cost by reducing the induced drag of individual birds [17,18], which should reduce the characteristic flight speeds U_{mr} and U_{mt} , respectively [19]. However, the few observations available where flight speed was measured in relation to flock size suggest that airspeed increases with increasing flock size [20].

In this paper, we report on flight directions in relation to winds, topography, ecological context and flock size in five related species of terns, ranging one magnitude in body mass but structurally very similar with a wing shape of high aspect ratio. One of the species, the Arctic tern *Sterna paradisaea* shows what currently is known as the longest annual migration

of any species [21,22], while the other species are also long-distance migrants [23,24]. These species search and hunt for fish while flying, suggesting they are well adapted to an aerial lifestyle. Hence, we assume our study species are physiologically and morphologically well equipped to achieve whatever flight speed is optimal in different contexts, and therefore constitute ideal birds for testing some of the optimality predictions of avian flight [25].

2. Material and methods

We measured flight tracks of migrating terns at southern Öland in the Baltic Sea by means of an ornithodolite [26,27], which consists of a pair of Vectronix Vector Aero binoculars (7×42 magnification) with three built-in sensors (a laser range finder, a magnetic compass and an elevation angle sensor) mounted on a tripod. When tracking a bird the Vector buttons are pressed to store time-stamped readings of distance, azimuth and elevation angles directly to a computer file. Each reading of a bird (or flock of birds) is called an 'observation' of the bird's timed position in space with the observer in the origin, and a series of two or more observations of the same target is called a 'run', which is used to calculate mean ground speed, vertical speed and track direction. Wind measurement is necessary to calculate airspeed and heading direction using the triangle of velocities (see the electronic supplementary material, figure S1). We used a Gill Windsonic anemometer mounted on a 5 m mast in an unobstructed location near the ornithodolite, which transmitted the reading to the computer at 1 s intervals via a pair of wireless modems (Haccorn UM-96). Wind speeds at altitudes of more than 15 m above ground surface were measured by tracking the path of released helium-filled balloons with the Vector. 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 later analysed to derive the wind profile, consisting of altitudinal segments of wind speed and direction. Depending on flight altitude of the bird 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. We recorded the ambient air temperature and pressure at the observer's position using a pocket weather meter (Kestrel 4500NV), and updated data regularly during a session. Following the completion of each run, data about species, age, sex, flight mode (continuous flapping, intermittent gliding/flapping, bounding and gliding), flight behaviour (straight, meandering, circling and feeding) and flock size were recorded. For the present data on terns, only runs recorded as 'straight flapping flight' were included. Terns that are searching for food are characteristically flying with their beak pointing downwards, which makes it easy to distinguish food search from other flight activities, where the beak/head is aligned with the body axis. Terns flying with a fish in the beak were noted as 'transport flight', while terns with beak/head aligned with the body axis are referred to as 'neutral flight'. In cases where age could not be determined the age was noted as 'no age', while in cases where one age group dominated the flock composition the flock was recorded as representative of that age. 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. Airspeed and heading direction were derived from the mean track, wind speed and wind direction using the triangle of velocities (see the electronic supplementary material, figure S1). Likewise, the tailwind 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, refer to Pennycuik *et al.* [27].

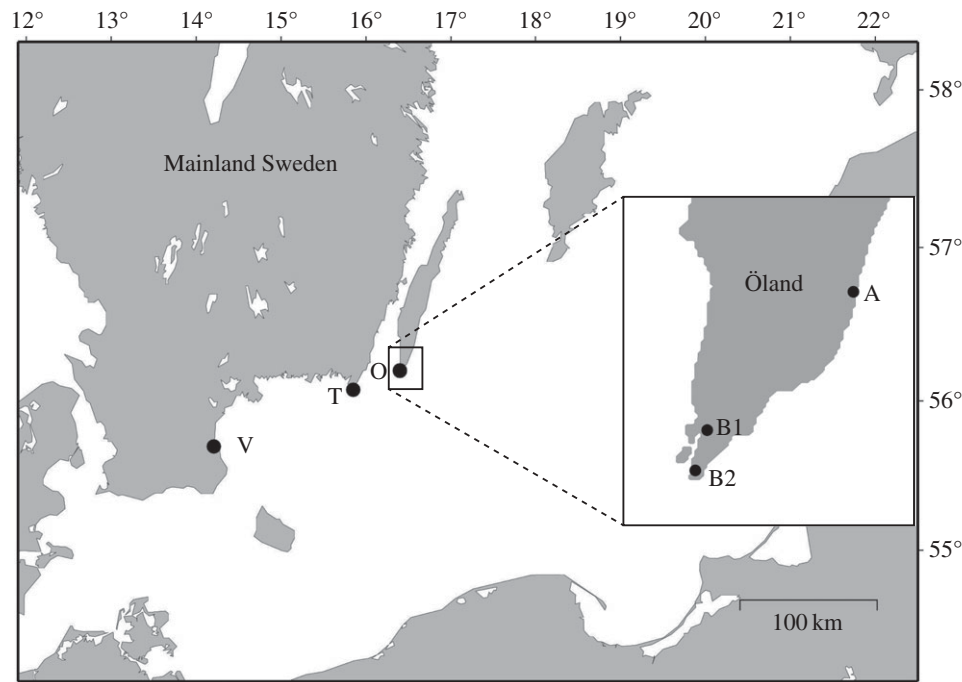


Figure 2. Map over the southern Baltic Sea showing the study sites on Öland as inset with observation sites (A, B1 and B2) used to measure flight performance in terns. Also shown are Torhamn (T) and Vitemölla (V), which are mentioned in the text.

Observations were made at three locations near Ottenby on southern Öland in the Baltic Sea (figure 2), where sites B1 and B2 are 1.4 km apart and site A is 6.9 km to the NNE of site B2. The migration observed from sites B1 and B2 refers to the same passage of migrants and therefore we combined these observations as one site (B). The coastline at site A is oriented along the axis $15.6^\circ/195.6^\circ$, while the eastern coastline at site B is aligned along the axis $42.3^\circ/222.3^\circ$, whereas the alignment of the coastline, consisting of small islands, west of site B1 is aligned as $16.1^\circ/196.1^\circ$. Fieldwork was carried out in September 2012 at site A, and during July and August in 2013–2015 at sites A and B, respectively.

Wing morphology was measured on live captured terns at Ottenby Bird Observatory ($56^\circ 12' \text{N}$, $16^\circ 24' \text{E}$) and a breeding site for Caspian terns *Hydroprogne caspia* in Uppland ($60^\circ 38' \text{N}$, $55^\circ 24' \text{E}$) by taking photographs of the left wing and body with a reference object, with the wing held so that the leading edge is perpendicular with the body axis [28]. Wingspan was measured directly on the live birds or as twice the half span from the wing-tips to the centre-line of the body on photos in a few cases. The two methods gave very similar results (regression slope = 0.98, which is not significantly different from unity, $p > 0.05$, $n = 45$). The wing area includes the area of the body between two wings. Body mass was measured on the same birds using an electronic balance. The body mass and flight-related parameters are presented in the electronic supplementary material, table S1.

The amount of drift or compensation in relation to winds was estimated according to method 3 in Green & Alerstam [29], where the magnitude of drift is calculated as

$$b_{\text{track}} = \frac{T_1 - T_2}{\alpha_1 - \alpha_2}, \quad (2.1)$$

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_{track} of zero implies compensation and a value of unity is full drift, while negative values represent over compensation [29]. For graphical illustrations of different drift and compensation scenarios, refer to Chapman *et al.* [13].

The aerodynamic power required to fly (P_{aero}) is modelled as the product of airspeed (U_a) and total drag D [28] as

$$P_{\text{aero}} = DU_a = (D_{\text{ind}} + D_{\text{pro}} + D_{\text{par}})U_a, \quad (2.2)$$

where the total drag is composed of the three components induced drag (D_{ind}) that arises due to the generation of lift by the wings, profile drag (D_{pro}) that represent the drag of the flapping wings, and parasite drag (D_{par}) that reflects the drag of non-lifting parts of the bird (i.e. mainly the body). For calculation of ecologically relevant characteristic speeds, additional costs for basal metabolic rate and respiration during flight estimates for these costs are usually added to obtain a corresponding 'chemical power curve' [28]. The speed of U_{mp} is obtained by taking the derivative of equation (2.2) with respect to airspeed (U_a) and solving for zero. To calculate characteristic speeds for our study species, we used a recent aerodynamic model [30], which explicitly accounts for flapping flight kinematics of birds and thereby includes more realistic features of powered flight than most previous flight models. An example of the chemical power curve and derived characteristic flight speeds in neutral winds is shown for the Arctic tern in the electronic supplementary material, figure S3, using custom-written Matlab code.

The wind-dependent maximum range speed (U_{mr}) for birds maintaining a constant track is given by the condition

$$\frac{dP}{dU_a} = \frac{P}{U_g} U'_g, \quad (2.3)$$

where P is the 'chemical power curve', U_g is ground speed and $U'_g = 1/\cos\alpha$ when α is the angle between track and heading (see the electronic supplementary material, figure S1) [14]. In situations with a side-wind component the marginal gain of increasing airspeed on ground speed will increase as the angle between track and heading increases, which yields an increased U_a compared with a pure head/tailwind.

Statistical tests were performed using JMP[®] 12.0 for linear mixed models and Oriana[®] 4 for circular statistics, respectively. For analyses, we used the run means of speeds and altitude as independent observations.

3. Results

(a) Characteristic flight behaviour

The data consist of a total of 319 runs divided between the species as: little tern ($n = 36$), Arctic tern ($n = 143$), common tern ($n = 81$), Sandwich tern ($n = 56$) and Caspian tern ($n = 3$). The total time of tracking was 234 min, during which 1959 observations were made, which resulted in an average run duration of 44 s with on average 8.6 s between successive observations. The wind directions were mainly between south and southwest (see the electronic supplementary material, figure S2), with a mean wind strength of 4.8 m s^{-1} (s.d. = 2.4, $n = 319$) and a maximum wind strength of 14.5 m s^{-1} .

Summary statistics of characteristic data about flock size and flight performance by age and behavioural categories are presented in the electronic supplementary material, table S2. Migrating Arctic and common terns typically flew singly or in small flocks of on average six to seven individuals, and even fewer individuals in little, Sandwich and Caspian terns. The maximum flock size on migration was 70 individuals in the Arctic tern. Birds involved in local flights during the breeding season most often moved singly or in small parties. Flight altitudes were generally low during food search and migration, with a maximum altitude of 218 m recorded in a flock of migrating Arctic terns. Because flight altitudes were generally low, so were climb rates, typically very close to zero (see the electronic supplementary material, table S2 for details).

(b) Migration directions

The overall migratory flight track directions were not found to be significantly different between age groups (adults versus first year) in neither the Arctic tern (site A: Watson's $U^2 = 0.033$, $p > 0.5$, d.f. = (8, 42); site B: Watson's $U^2 = 0.156$, $p > 0.05$, d.f. = (6, 37)) nor the common tern (site A: Watson's $U^2 = 0.127$, $p > 0.5$, d.f. = (23, 24); site B: Watson's $U^2 = 0.109$, $p > 0.2$, d.f. = (5, 10)). For the Sandwich terns and little tern, there were not enough data to allow a comparison between age groups, and the Caspian tern is not included in these analyses due to only three runs measured. Therefore, the age groups were combined for each species. There were no significant difference in track directions between the species at site A (Watson–Williams F -test, $F_{4,26} = 1.496$, $p = 0.207$), but there was a significant difference in track directions at site B (Watson–Williams F -test, $F_{3,103} = 3.555$, $p = 0.017$). At site A, the mean track direction for all species, excluding Caspian tern, was 195° with small deviations from this in species-specific means (figure 3). The overall track direction was aligned with the coastline at 195.6° at site A. At site B, all species shifted their track direction by on average 53° (31–61; figure 3), to become oriented between SW and WSW. This shift was significant in the Arctic tern (Watson's $U^2 = 1.863$, $p < 0.001$, d.f. = (50, 67)) and the common tern (Watson's $U^2 = 1.149$, $p < 0.001$, d.f. = (31, 47)), but not significant in the Sandwich tern *Sterna sandwichensis* (too few observations at site B) and the little tern *Sterna albifrons* (Watson's $U^2 = 0.044$, $p > 0.05$, d.f. = (5, 5)). The same results were obtained for shifts in heading directions between sites A versus B. The shifts in track direction of 56° and 61° in Arctic and common terns, respectively, were more than the actual shift of coastline orientation of 27° between sites A and B. When approaching the southern point of Öland (site B) many Arctic and common terns make a short cut across the point towards WSW rather than flying

around the southernmost point by following the coastline. The direction from site B to the southeastern point, Torhamn, of mainland Sweden (figure 2) is 242° . At a distance of 43 km, this point is visible from site B in good weather conditions, and it is likely that the birds aim for this point or the mainland north of it when departing from southern Öland. However, as is apparent from figure 3, the circular distributions show a higher degree of variation in track directions at site B compared with A. Especially in the Arctic tern, there are a few tracks clustering near south (figure 3), suggesting some birds may cross the Baltic without touching the Swedish mainland coast.

(c) Wind compensation

If a bird's objective is to maintain a certain track over ground, it must adjust the heading direction with respect to crosswinds. The analysis of wind drift is associated with potential pitfalls [26], but one robust method is to compare shifts in heading and track directions between groups where the wind is from the left and right, respectively. For Arctic and common terns at site A, we divided the data according to the mean track direction, where one group had winds coming from the left (i.e. wind directions less than the mean track direction in south-bound migration, i.e. mainly from the east sector) and right (wind direction above the mean track direction, i.e. from the west sector). There was no significant difference in track direction between winds from left versus right in the Arctic tern (figure 4; Watson's $U^2 = 0.099$, $p > 0.2$, d.f. = (18, 24)), while heading directions differed significantly (figure 4; Watson's $U^2 = 0.537$, $p < 0.001$, d.f. = (18, 24)). A similar result was obtained for the common tern for track (figure 4; Watson's $U^2 = 0.113$, $p < 0.2$, d.f. = (9, 38)) and heading (figure 4; Watson's $U^2 = 0.526$, $p < 0.001$, d.f. = (9, 38)). The subdivision in left and right wind direction categories at site B gave highly unbalanced numbers of runs in the two groups, which rendered further analysis not meaningful.

The amount of drift using equation (2.1) yielded $b_{\text{track}} = 0.29$ for the Arctic tern at site A, suggesting a small amount of partial drift. For the common tern $b_{\text{track}} = -0.39$, which implicates a degree of overcompensation (figure 4).

(d) Airspeed in relation to multiple factors

The airspeed was measured during both local flights in the breeding season for three of the species and during migration for five species of terns. The data broken down into age and flight behavioural categories are shown as means for flock size, airspeed (U_a), ground speed (U_g), vertical speed (U_z) altitude (z) in the electronic supplementary material, table S2. First, we tested for the effects of different factors for each species separately, including local flights during breeding and migration. The different factors included were behaviour (migratory flight, non-migratory local flight), flight mode (searching for food, transporting food or flight denoted 'neutral flight' that is neither food search nor food transport), age (adult, juvenile), altitude, vertical speed, flock size (entered as \log_e -transformed flock size), tailwind and side-wind components. The outcome of these analyses is summarized in table 1, where significant variables are indicated. Statistical details from the mixed models are given in the electronic supplement material, tables S3–S6. In the Arctic tern, the species with the biggest sample, there were significant effects of six variables so that migratory airspeed is higher than for local flights, food search is slower than

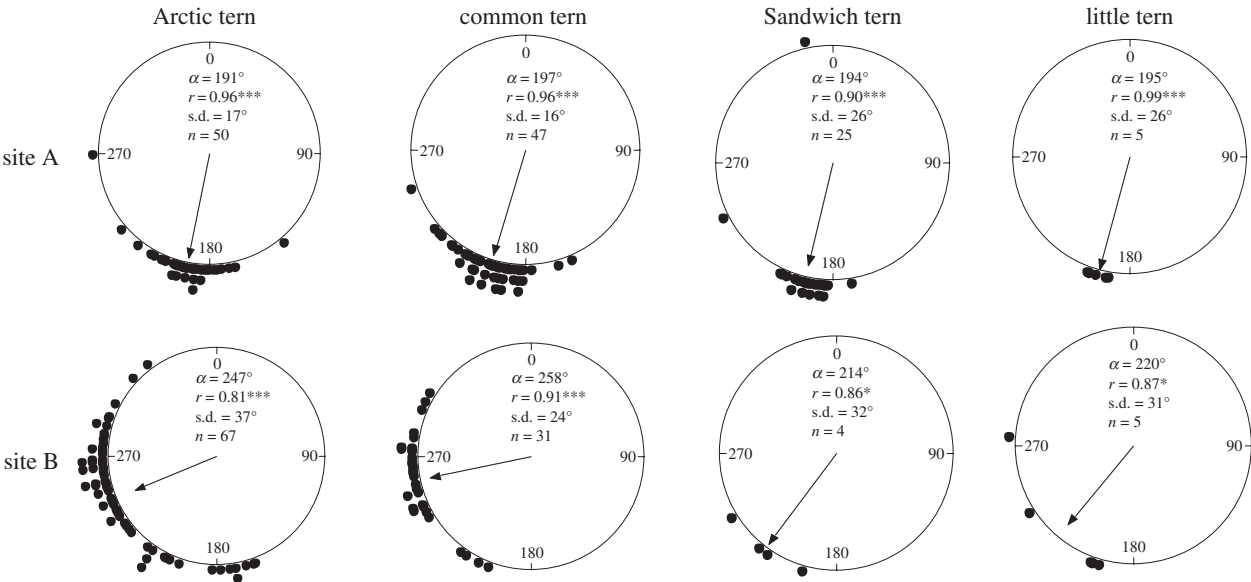


Figure 3. Circular distributions of migratory flight track directions in four species of terns in four species of terns at site A (a) and site B (b). The arrows show the mean track directions (α), vector length (r), and in addition angular deviation (s.d.) and sample size (n) are given for each diagram. Statistical significance refers to a Rayleigh test (* $p < 0.05$, *** $p < 0.001$).

Table 1. The result of linear mixed models with airspeed as dependent variable and age (adult and juvenile), behaviour (migrating and not migrating), flight mode (food search, not searching food transport), altitude, vertical speed, the log_e of flock size, tailwind component and side-wind component as independent factors. Factors with a significant ($p < 0.05$) effect are marked with 'x', and full statistical details are given in the electronic supplementary material, tables S3–S6. n is sample size.

species	n	age	behaviour	flight mode	z	U_z	flock size	T_{comp}	S_{comp}
<i>Sterna albifrons</i>	36			x	x				
<i>Sterna paradisaea</i>	143	x	x	x			x	x	x
<i>Sterna hirundo</i>	82		n.a.	x			x	x	
<i>Sterna sandwichensis</i>	56			x				x	

food transport and 'neutral' flight, juveniles fly slower than adults, airspeed increases with increasing flock size, airspeed is reduced with increasing tailwind component and increases with increasing side-wind component (table 1; electronic supplementary material, table S4). For the other species, two or three variables had a significant effect on airspeed (table 1), which could partly be due to lower sample size than for the Arctic tern. The prediction of side-wind compensation according to equation (2.3) was tested for migrating Arctic terns, where we can expect that either maximum range speed (U_{mr}) or the speed associated with time-selected migration (U_{mt}), which are speeds for which the prediction was derived [14], will show effects. A mixed model analysis of the influence of tailwind component and $1/\cos\alpha$, where α is angle between track and heading, with age, flight mode and flock size as random effects, only yielded a significant effect of the tailwind component (T_{comp} : $F_{1,102} = 53.3$, $p < 0.0001$; $1/\cos\alpha$: $F_{1,95} = 1.02$, $p > 0.315$). However, repeating the analysis, but with the perpendicular side-wind component replaced for $1/\cos\alpha$ resulted in significant effects for both tailwind and side-wind components (T_{comp} : $F_{1,106} = 49.0$, $p < 0.0001$; S_{comp} : $F_{1,112} = 5.57$, $p = 0.02$).

(e) Predicted and observed migratory flight speeds
Predicted flight speed from flight mechanical theory refers to a single bird flying in neutral wind conditions [25,27].

Because the airspeed in the wild depends on multiple factors as shown here, an appropriate comparison with predictions from flight mechanics should refer to the intercept of the statistical model. We therefore derived these speeds for our five study species as shown in table 2; hence for this analysis also the Caspian tern was included because it extends the size range of species even though we only have three measurements. We also calculated the characteristic speeds of minimum power and maximum range according to the flapping flight model by Klein Heerenbrink *et al.* [30], as shown in table 2. There was a high correlation between observed airspeed and predicted maximum range speed on migration (figure 5), with a slope of observed versus predicted U_{mr} of 0.92 ($t = 6.42$, $p = 0.0077$, $n = 5$), which did not differ from unity ($t = 0.56$, $p > 0.62$, $n = 5$). With Caspian tern excluded, the slope between observed airspeed and predicted U_{mr} was 1.44 ($t = 4.92$, $p = 0.039$, $n = 4$), which again is not significantly different from a slope of unity ($t = 1.5$, $p > 0.27$, $n = 5$). However, it should be kept in mind that statistical power is low with such low sample sizes (figure 5).

Characteristic flight speeds are expected to scale with body mass as $\propto m^{1/6}$ in a series of geometrically similar (isometric) birds [4]. The five tern species of this study can be considered to be close to geometric similarity by the lack of significant scaling exponent of aspect ratio on body mass ($AR = 12.5m^{0.006}$, $t = 0.20$, $p = 0.8567$, $n = 5$). Using our standardized migratory airspeeds (table 2), the scaling of airspeed on body mass is

Table 2. Predicted minimum power (U_{mp}), maximum range (U_{mr}) and observed (U_{obs}) migratory flight speed derived as the intercept using significant factors in a mixed linear model in five species of adult terns. n is sample size.

species	n	mass (kg)	aspect ratio	U_{mp} ($m\ s^{-1}$) ^a	U_{mr} ($m\ s^{-1}$) ^a	U_{obs} ($m\ s^{-1}$)
<i>Sterna albifrons</i>	10	0.051	13.3	6.7	9.6	9.8
<i>Sterna paradisaea</i>	118	0.122	12.2	6.8	9.8	9.8
<i>Sterna hirundo</i>	81	0.133	11.8	7.0	10.0	10.8
<i>Sterna sandwichensis</i>	30	0.242	13.2	8.2	11.5	12.6
<i>Hydroprogne caspia</i>	3	0.662	12.6	10.7	14.6	14.5

^aModel assumptions: air density = $1.255\ kg\ m^{-3}$, kinematic viscosity of air = $1.5 \times 10^{-6}\ m^2\ s^{-1}$, basal metabolic rate = $3.79\ m^{0.723}\ W$, energy conversion efficiency = 0.23, stroke plane angle = 0° , $C_{Dpro0} = 2.66/\sqrt{\text{Re}_c}$, $C_{Dpro2} = 0.03$, $C_{Dpar} = 0.1$, body frontal area = $0.00813m^{2/3}$ and wingbeat frequency = $m^{3/8}g^{1/2}b^{-23/24}S^{-1/3}\rho^{-3/8}\ Hz$, where m is body mass (kg), g is acceleration due to gravity, b is wingspan, S is wing area and ρ is air density. See the studies of Alerstam [25] and Pennycuik *et al.* [27] for further information.

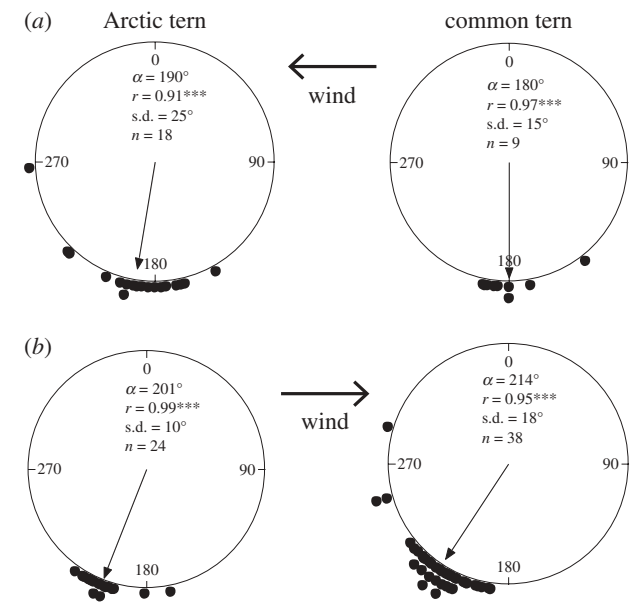


Figure 4. The mean heading directions of Arctic and common terns at site A (figure 2) under conditions of wind coming from the left (a) with respect to mean track direction for the whole sample (all winds) and from the right (b). The arrows show the mean heading direction (α) and vector length (r), and in addition angular deviation (s.d.) and sample size (n) are given for each diagram. Statistical significances refer to a Rayleigh test (* $p < 0.05$, *** $p < 0.001$).

$U_a = 15.3m^{0.17}$ ($t = 5.11$, $p = 0.0181$, $n = 5$). This is indeed very close to the expected exponent of $1/6$ (≈ 0.167). Also with the Caspian tern excluded, the scaling of airspeed on body mass yields a relationship close to that expected for isometrically scaled birds as $U_a = 14.8m^{0.15}$ ($t = 2.08$, $p = 0.173$, $n = 4$), but in this case it is not significant.

4. Discussion

(a) Migratory flight directions

There was a clear shift by about 60° in flight track direction in the Arctic and common terns as they approached the southern point of Öland arriving from the coast further to the north, where the track direction was nearly aligned with the coastline. The scatter of track directions increased as the terns departed from the island of Öland, perhaps a result of a funnelling

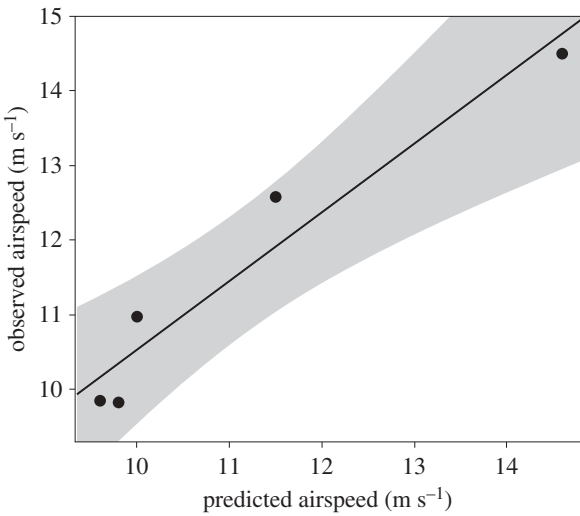


Figure 5. The relationship between observed and predicted airspeed in five species of tern, where airspeed represents the intercept from mixed linear models including significant factors contributing to the variation during migratory flight. The slope of the regression line is 0.92 ($t = 6.42$, $p = 0.0077$). Based on data shown in table 2.

effect by the coast as terns arrive from the north and northeast, followed by a ‘release’ of this constraint when confronted by the open sea beyond the south point. The shift of flight direction follows the shift in coastline alignment between site A and site B (figure 2), but the track directions of the Arctic and (56°) common terns (61°) shifted more than that of the coastline (27°). Many flocks crossed the southern part of the Öland about 1 km further to the north from the point (see the electronic supplementary material, figure S4), perhaps because they could already see the coast of the Swedish mainland. In good weather conditions, which prevailed during the study period, the mainland is readily visible by the human eye at ground level, and so for birds this should also be the case. The direction from Ottenby (site B2) to the southeast corner of the Swedish mainland (Torhamn, figure 2) is 242° , close to the mean track direction of Arctic and common terns. On average, the terns actually aim somewhat north of this point, probably because this is the closest and visible part of the mainland. Shorebirds departing on autumn migration from Ottenby keep a somewhat different mean track direction at about 234° [31], which would make them miss the point at Torhamn. This suggests inherently different preferred routes among different species, presumably

aiming for different stopover sites along the route when compared with the terns of this study.

A radar study of migrating Arctic and common terns at Vitemölla on the east coast of Scania (figure 2; [25]), reports that birds arrive from the northeast over the sea at low altitude and when approaching the coastline they start climbing with more vigorous wingbeats and cross the coastline at altitudes of 1000 m and above [25]. Mean track direction (235° , angular deviation = 25°) was about 20° more to the south at Vitemölla compared with Ottenby (note that species were not separated at the Vitemölla study), while scatter was similar between the sites (angular deviation = 25° at Vitemölla, and 37° for Arctic and 24° for common terns at Ottenby). The observed difference in mean track direction again suggests that flight directions are influenced by local topography, something that has been observed also in Arctic terns departing from the Antarctic Peninsula on spring migration [32] and in shorebirds leaving Iceland in the spring [33]. That local topographical landmarks such as coastlines and peninsulas affect migrating birds flying at low altitudes has been observed at other sites for passerines [34], but such landscape features may also affect flight directions in migrants at higher altitudes [35].

On autumn migration Arctic terns from populations on Greenland, Iceland and The Netherlands are initially bound for a first stopover area north of the Azores in the North Atlantic [21,22]. The loxodromic (rhumb line, i.e. constant compass course) direction from Ottenby to this area is 254° (orthodromic or great circle direction is 265°), and so it seems likely that the population passing the Baltic is also aiming for this area as a first goal area on their epic migration to the Antarctic.

(b) Wind drift

To compensate for wind drift a bird needs a visual frame of reference, unless another sense than vision is used for navigation. Unlike some insects, birds seem unable to determine wind direction based on fine-scale anisotropic turbulence [36]. Typically, topographical features in the landscape such as coastlines, islands, the wavescape or clouds are considered important for flight guidance [37]. We found near complete compensation in the Arctic tern and overcompensation in the common tern at site A. Overcompensation could occur as a correction back to the intended track following an episode of drift, which may have occurred during a previous sea crossing [38]. Overcompensation is often considered as a means of reaching the final migratory goal, while it could also occur in birds that aim for an intermediate goal on a long-distance migration. The wavescape moves at a certain speed, which prevents full compensation for wind drift if used as frame of reference by the birds [39]. The small degree of partial drift as observed in the Arctic tern could likewise be attributed to failure to achieve complete compensation if the wavescape is used for orientation, even if the coastline was within sight to the birds.

In general, birds are expected to allow wind drift when far from the goal and compensate or overcompensate as they approach the final destination, a strategy known as adaptive drift [40]. Radar observations of Arctic breeding shorebirds at different locations along the migration route are in general agreement with this hypothesis [41]. Arctic terns on passage in the Baltic Sea can definitely be considered as being far from their final goal, but they probably have more nearby intermediate goals along their route, such as the Swedish mainland

coast and the North Atlantic stopover area used by other populations [21,22]. When passing Vitemölla, Arctic and common terns exhibited full wind drift when climbing inland, which may be due to sensory difficulties to achieve compensation during this flight behaviour [25]. Shorebirds may show quite different responses to wind drift between relatively close locations, such as wind drift over the sea at Ottenby, partial drift at Vitemölla and full compensation when passing inland [42]. Taken together, our results on terns and previous observations on shorebirds show that response to wind drift is complex, probably depending on timing and availability of a useful frame of reference. Exactly how vision is involved to control heading direction and flight speed is not known, but some use of optic flow seems likely [43]. There is certainly room for the design of new experiments to unravel sensory capacities and constraints to detect and correct for crosswinds in birds.

(c) Airspeed

A bird's selection of airspeed is a complex behavioural decision that depends on several factors. The most important factors emerging from the present data on tern flight speeds are effects of ecological context, winds and flock size. Airspeed also differed between the species, which mainly depends on body mass and wing morphology as explained by flight mechanical theory. Terns that look out for food, characteristically with the beak pointing earthwards, fly more slowly than those transporting prey or not engaged in food search. Also during migration terns are often seen searching for and capturing fish, which also reduces airspeed compared with those not fishing. Surprisingly, vertical speed had no significant effect on airspeed in the present data, but vertical speeds were generally very low. In terns climbing at high rates (1.4 m s^{-1}), the airspeed is reduced as a result of this [25]. The uncorrected observed airspeeds in Arctic and common terns on passage migration at Öland are similar to those measured at Vitemölla [25] and on northbound migration at the Antarctic Peninsula [32].

Airspeed is adjusted according to head and/or tailwinds when measured as the tailwind component, which has been found in several other studies of migrating birds [44]. The predicted effect of the angle between track and heading (equation (2.3)) did not emerge as a significant factor for the Arctic tern. One could argue that since the Arctic terns did not show complete compensation for wind drift, the basis for the prediction is violated, but on the other hand the magnitude of the drift was low. It therefore appears unlikely that birds pay attention to this factor when selecting airspeed. By contrast, airspeed is adjusted in relation to the side-wind component, which in addition to the angle between track and wind directions also includes the wind speed. A similar adjustment of airspeed to the side-wind component has also been observed in nocturnally migrating common swifts and European shags *Phalacrocorax aristotelis* during local flights [15,45]. If ignored, wind drift will increase with increasing side-wind component, and so by increasing the airspeed some compensation is achieved even without changing the heading direction.

Flock size had a significant effect on airspeed, which has been observed in a few species of shorebirds [20], and hinted at for Arctic and common terns [25]. With the present result, we may conclude that flock size is a determinant of airspeed

at least in Arctic and common terns. Observed airspeeds above predicted maximum range speed in previous studies of Arctic and common terns [25,32] is probably due to disregard of the effect of flock size. If birds save energy from flying in flock formation the prediction is a lowering of airspeed in relation to single flight [8]. The observed effect of flock size was, however, opposite to the prediction from energy saving in formation flight. Even if large species may obtain aerodynamic benefit from formation flight [18,46], such a benefit is unlikely in our terns that most often formed quite loose flocks with large inter-individual distances, although tight formations did also occur on migration. A potential mechanistic explanation for the observed effect of flock size on airspeed could result from the increased likelihood of inclusion of heavy individuals in flocks of increasing numbers from random sampling from a source population. If the flock flight speed is mainly determined by the heaviest individual(s) the observed pattern would emerge [47]. Individually consistent flight speed was found to be an important factor for determining leadership structure and flock flight speed in homing pigeons [48]. Whether similar dynamics determine leadership and flock flight speed also in migrating birds remains an open question, but they certainly could have a similar effect as in homing pigeons be they determined by dominance structures or body size [47].

The body mass scaling of airspeed showed a close agreement with that predicted from flight theory. In similar analyses of broader samples of species, the scaling exponents were lower than predicted [27,49], which most probably is explained by the departure from shape isometry among the species analysed in those studies. When birds are isometrically scaled, as in the present study, the predicted body mass scaling between species is near $1/6$ as predicted by theory.

With an average flight speed of 12 m s^{-1} , an Arctic tern would travel for about 1040 km d^{-1} , while observed autumn migration speed is $330\text{--}420 \text{ km d}^{-1}$ [21,22]. This implies that Arctic terns would travel for about 36% of the time and spend the remaining time at stopovers, which is a higher proportion of flight time than the $1/8$ (12.5%) expected for small birds [50], suggesting the terns adopt a fly-and-forage strategy at least during parts of their migration. This is evident from observations during their passage at Öland, where terns frequently were observed searching for and capturing fish while on migration.

5. Concluding remarks

Our analysis of tern flight demonstrates the complexity behind the superficially simple behavioural decision of selecting an appropriate airspeed in birds. The realized airspeed is a compound function of both internal and external factors, which not only include the ecological objective and wing morphology, but also wind strength and direction and number of flock mates. Flock size has hitherto been largely a neglected factor in studies of bird flight speeds, but since many bird species migrate in flocks it is clearly an issue that warrants further study also in other species than terns [20], as well as how different types of flocks and within flock social hierarchies affect flight speed. The lack of quantitative agreement between predicted and observed airspeeds in previous comparisons has often been attributed to shortcomings in the theory [51]. Although this is partly true, disagreement between theory and field measurements may likewise arise due to failure to standardize the observations to represent a single bird flying in neutral wind conditions, and thereby controlling for the factors affecting airspeed. When analysing the intercept of statistical models accounting for significant variation in observed airspeed for terns, we found a remarkable agreement between maximum range speed calculated from an aerodynamic model [30] and observed speed on autumn migration. This suggests that aerodynamic theory as a research tool has a bright future.

Ethics. This study involved remote observations on animal subjects, which were carried out under permission M 173-09 from the Malmö-Lund animal ethics committee.

Data accessibility. Data files have been uploaded to the Dryad Digital Repository (doi:10.5061/dryad.hj13q) [52].

Author contributions. A.H. and S.Å. conceived the study and carried out the fieldwork; A.H. analysed the data and drafted the manuscript. Both authors gave final approval for publication.

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References

- Butler PJ. 2016 The physiological basis of bird flight. *Phil. Trans. R. Soc. B* **371**, 20150384. (doi:10.1098/rspb.2015.0384)
- Gill Jr RE *et al.* 2009 Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier. *Proc. R. Soc. B* **276**, 447–457. (doi:10.1098/rspb.2008.1142)
- Hedenström A. 2010 Extreme endurance migration: what is the limit to non-stop flight? *PLoS Biol.* **8**, e1000362. (doi:10.1371/journal.pbio.1000362)
- Pennycuik CJ. 1968 Power requirements for horizontal flight in the pigeon. *J. Exp. Biol.* **49**, 527–555.
- Pennycuik CJ. 1975 Mechanics of flight. In *Avian biology*, vol. 5 (eds DS Farner, JR King, KC Parkes), pp. 1–75. New York, NY: Academic Press.
- Tobalske BW, Hedrick TL, Dial KP, Biwener AA. 2003 Comparative power curves in bird flight. *Nature* **421**, 363–366. (doi:10.1038/nature01284)
- Engel S, Bowlin MS, Hedenström A. 2010 The role of wind-tunnel studies in integrative research on migration biology. *Integr. Comp. Biol.* **50**, 323–335. (doi:10.1093/icb/icq063)
- Hedenström A, Ålerstam T. 1995 Optimal flight speed of birds. *Phil. Trans. R. Soc. Lond. B* **348**, 471–487. (doi:10.1098/rspb.1995.0082)
- Hedenström A, Ålerstam T. 1996 Skylark optimal flight speeds for flying nowhere and somewhere. *Behav. Ecol.* **7**, 121–126. (doi:10.1093/beheco/7.2.121)
- Norberg RÅ. 1981 Optimal flight speed in birds when feeding young. *J. Anim. Ecol.* **50**, 473–477. (doi:10.2307/4068)
- Pennycuik CJ. 1978 Fifteen testable predictions about bird flight. *Oikos* **30**, 165–176. (doi:10.2307/3543476)
- Tucker VA. 1974 Energetics of natural avian flight. In *Avian energetics* (ed. RA Paynter Jr), pp. 298–333. Cambridge, MA: Publ. Nuttall Ornithol. Club no. 15.
- Chapman JW, Klaassen RHG, Drake VA, Fossette S, Hays GC, Metcalfe JD, Reynolds AM, Reynolds DR,

- Alerstam T. 2011 Animal orientation strategies for movement in flows. *Curr. Biol.* **21**, R861–R870. (doi:10.1016/j.cub.2011.08.014)
14. Liechti F, Hedenström A, Alerstam T. 1994 Effects of sidewinds on optimal flight speed of birds. *J. Theor. Biol.* **170**, 219–225. (doi:10.1006/jtbi.1994.1181)
15. Karlsson H, Henningsson P, Bäckman J, Hedenström A, Alerstam T. 2010 Compensation for wind drift by migrating swifts. *Anim. Behav.* **80**, 399–404. (doi:10.1016/j.anbehav.2010.05.023)
16. Hedenström A, Alerstam T. 1992 Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *J. Exp. Biol.* **164**, 19–38.
17. Lissaman PBS, Shollenberger C. 1970 Formation flight in birds. *Science* **168**, 1003–1005. (doi:10.1126/science.168.3934.1003)
18. Portugal SJ, Hubel TY, Fritz J, Heese S, Trobe D, Voelkl B, Hails S, Wilson AM, Usherwood JR. 2014 Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* **505**, 399–402. (doi:10.1038/nature12939)
19. Hummel D. 1983 Aerodynamic aspects of formation flight in birds. *J. Theor. Biol.* **104**, 321–347. (doi:10.1016/0022-5193(83)90110-8)
20. Noer H. 1979 Speeds of migrating waders Charadriidae. *Dansk Orn. Foren. Tids.* **73**, 215–224.
21. Egevang C, Stenhouse U, Phillips RA, Petersen A, Fox JW, Silk JRD. 2010 Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc. Natl Acad. Sci. USA* **107**, 2078–2081. (doi:10.1073/pnas.0909493107)
22. Fijn RC, Hiemstra D, Phillips RA, Winden J. 2013 Arctic terns *Sterna paradisaea* from the Netherlands migrate record distances across three oceans to Wilkes Land, East Antarctic. *Ardea* **101**, 3–12. (doi:10.5253/078.101.0102)
23. Fransson T, Österblom H, Hall-Karlsson S. 2008 *Swedish bird ringing atlas*, vol. 2. Stockholm, Sweden: Museum of Natural History.
24. Shiomi K, Lötberg U, Åkesson S. 2015 Seasonal distributions of Caspian terns *Hydroprogne caspia* from Swedish populations, revealed by recoveries and resightings of ringed birds. *Ring. Migr.* **30**, 22–36. (doi:10.1080/03078698.2015.1059637)
25. Alerstam T. 1985 Strategies of migratory flight, illustrated by Arctic and common terns *Sterna paradisaea* and *Sterna hirundo*. In *Migration: mechanisms and adaptive significance* (ed. MA Rankin), pp. 580–603. Contributions in Marine Science, vol. 27(suppl.). Austin, TX: University of Texas.
26. Pennycuik CJ. 1982 The ornithodolite: an instrument for collecting large samples of bird speed measurements. *Phil. Trans. R. Soc. Lond. B* **300**, 61–73. (doi:10.1098/rstb.1982.0157)
27. Pennycuik CJ, Åkesson S, Hedenström A. 2013 Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. *J. R. Soc. Interface* **10**, 20130419. (doi:10.1098/rsif.2013.0419)
28. Pennycuik CJ. 2008 *Modelling the flying bird*. Amsterdam, The Netherlands: Elsevier.
29. Green M, Alerstam T. 2002 The problem of estimating wind drift in migrating birds. *J. Theor. Biol.* **218**, 485–496. (doi:10.1016/S0022-5193(02)93094-8)
30. Klein Heerenbrink M, Johansson LC, Hedenström A. 2015 Power of the wingbeat: modelling the effects of flapping wings in vertebrate flight. *Proc. R. Soc. A* **471**, 20140952. (doi:10.1098/rspa.2014.0952)
31. Grönroos J, Green M, Alerstam T. 2012 Fine-scaled orientation changes in migrating shorebirds. *Ardea* **100**, 45–53. (doi:10.5253/078.100.0108)
32. Gudmundsson GA, Alerstam T, Larsson B. 1992 Radar observations of northbound migration of the Arctic tern *Sterna paradisaea*, at the Antarctic Peninsula. *Antarct. Sci.* **4**, 163–170. (doi:10.1017/S0954102092000257)
33. Gudmundsson GA. 1993 The spring migration pattern of arctic birds in southwest Iceland, as recorded by radar. *Ibis* **135**, 166–176. (doi:10.1111/j.1474-919X.1993.tb02828.x)
34. Åkesson S. 1993 Coastal migration and wind drift compensation in nocturnal passerine migrants. *Ornis Scand.* **24**, 87–94. (doi:10.2307/3676357)
35. Gudmundsson GA. 1994 Spring migration of the Knot *Calidris c. canutus* over southern Scandinavia, as recorded by radar. *J. Avian Biol.* **25**, 15–26. (doi:10.2307/3677290)
36. Chapman JW, Nilsson C, Lim KS, Bäckman J, Reynolds DR, Reynolds AM. 2015 Detection of flow direction in high-flying insect and songbird migrants. *Curr. Biol.* **25**, R733–R752. (doi:10.1016/j.cub.2015.07.074)
37. Alerstam T. 1976 Bird migration in relation to wind and topography. Thesis, Lund University, Sweden.
38. Alerstam T. 1979 Optimal use of wind by migrating birds: combined drift and overcompensation. *J. Theor. Biol.* **79**, 341–353. (doi:10.1016/0022-5193(79)90351-5)
39. Alerstam T, Pettersson SG. 1976 Do birds use waves for orientation when migrating across the sea? *Nature* **259**, 205–207. (doi:10.1038/259205a0)
40. Alerstam T. 1979 Wind as selective agent in bird migration. *Ornis Scand.* **10**, 76–93. (doi:10.2307/3676347)
41. Green M, Alerstam T, Gudmundsson GA, Hedenström A, Piersma T. 2004 Do arctic waders use adaptive wind drift? *J. Avian Biol.* **35**, 305–315. (doi:10.1111/j.0908-8857.2004.03181.x)
42. Grönroos J, Green M, Alerstam T. 2013 Orientation of shorebirds in relation to wind: both drift and compensation in the same region. *J. Ornithol.* **154**, 385–392. (doi:10.1007/s10336-012-0902-7)
43. Schifferer I, Srinivasan MV. 2015 Direct evidence for vision-based control of flight speed in budgerigars. *Sci. Rep.* **5**, 10992. (doi:10.1038/srep10992)
44. Hedenström A, Alerstam T, Green M, Gudmundsson GA. 2002 Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. *Behav. Ecol. Sociobiol.* **52**, 308–317. (doi:10.1007/s00265-002-0504-0)
45. Kogure Y, Sato K, Watanuki Y, Wanless S, Daunt F. 2016 European shags optimize their flight behavior according to wind conditions. *J. Exp. Biol.* **219**, 311–318. (doi:10.1242/jeb.131441)
46. Weimerskirch H, Martin J, Clerquin Y, Alexandre P, Jiraskova S. 2001 Energy saving in flight formation. *Nature* **413**, 697–698. (doi:10.1038/35099670)
47. Hedenström A. 2003 Twenty-three testable predictions about bird flight. In *Avian migration* (ed. E Gwinner), pp. 563–582. Berlin, Germany: Springer.
48. Pettit B, Ákos Z, Vicsek T, Biro D. 2015 Speed determines leadership and leadership determines learning during pigeon flocking. *Curr. Biol.* **25**, 3132–3137. (doi:10.1016/j.cub.2015.10.044)
49. Alerstam T, Rosén M, Bäckman J, Ericson PGP, Hellgren O. 2007 Flight speeds among bird species: allometric and phylogenetic effects. *PLoS Biol.* **5**, e197. (doi:10.1371/journal.pbio.0050197)
50. Hedenström A, Alerstam T. 1997 Optimum fuel load in birds: distinguishing between time and energy minimization. *J. Theor. Biol.* **189**, 227–234. (doi:10.1006/jtbi.1997.0505)
51. Welham CVJ. 1992 Flight speeds of migrating birds: a test of maximum range speed predictions from three aerodynamic equations. *Behav. Ecol.* **5**, 1–8.
52. Hedenström A, Åkesson S. 2016 Data from: Ecology of tern flight in relation to wind, topography and aerodynamic theory. Dryad Digital Repository. (doi:10.5061/dryad.hj13q)