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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.

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, Ákos, 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 & Alerstam, 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 & Alerstam, 1995; Pennycuick, 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; Alerstam, 1976, 1979; Green & Alerstam, 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 (Alerstam & 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 (Alerstam, 1979). Radar studies at different latitudes suggest that such adaptive drift/compensation behaviour may occur in migratory birds (Green, Alerstam, 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 (Haccom 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).

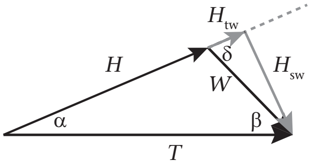

Figure 1. The triangle of velocities defining the relationship between heading (H), wind (W) and track (T) with the length of the vectors representing the airspeed (U), wind speed (U_w) and ground speed (U_g). The diagram also shows how the tail wind (H_{tw}) and side wind (H_{sw}) components are calculated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

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

$$b_{track} = \frac{T_1 - T_2}{\alpha_1 - \alpha_2}, \tag{1}$$

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 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 $\log_e$-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.