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Published in:
Journal of Experimental Biology

2002

The Journal of Experimental Biology 205, 905–910 (2002)
Printed in Great Britain © The Company of Biologists Limited
JEB3867

Harmonic oscillatory orientation relative to the wind in nocturnal roosting flights of the swift *Apus apus*

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Accepted 11 December 2001

Summary

Swifts regularly spend the night flying at high altitude. From previous studies based on tracking radar observations, we know that they stay airborne during the night and prefer to orient themselves into the wind direction with an increased angular concentration with increasing wind speed. In this study, we investigated the orientation relative to the wind of individual swifts by frequency (discrete Fourier transform) and autocorrelation analysis based on time series (10 s intervals) of the angle between the swifts' heading and the wind direction for radar trackings of long duration (9–60 min). The swifts often showed a significant harmonic oscillation of their heading direction relative to the wind, with a frequency mostly in the range 1–17 mHz, corresponding to cycle periods of 1–16 min. The swifts also sometimes performed circling flights at low wind speeds. Wind speed ranged from 1.3 to 14.8 $m\,s^{-1}$, and we expected to find different patterns of orientation at different wind speeds, assuming that the swifts adapt their orientation to avoid substantial displacement during their nocturnal flights. However, oscillatory orientation was found at all wind speeds with variable frequencies/periods that did not show any consistent relationship with wind speed. It remains to be shown whether cyclic heading changes are a regular feature of bird orientation.

Key words: common swift, *Apus apus*, flight, Fourier transform, harmonic oscillation, orientation, roosting, wind, tracking radar, autocorrelation.

Introduction

Common swifts (*Apus apus*) are remarkable flyers, spending most of their lives on the wing. Some swifts ascend at dusk and fly during the night at high altitude until daybreak, when they return to their home colony (Weitnauer, 1952, 1954, 1960; Lack, 1956). These nocturnal flights take place at altitudes up to 3000 m, in more-or-less complete darkness and often in windy conditions. The nocturnal flight of the swift requires considerable navigational skills to avoid drifting far away from the presumed home area. In a previous study (Bäckman and Alerstam, 2001), we analysed short-duration radar trackings of swifts. We found that, at higher wind speeds (>9 $m\,s^{-1}$), the swifts orient themselves accurately into the wind, but that they are still vulnerable to being carried away with the wind, e.g. if the wind speed is greater than the swifts' flight speed. Interestingly, the swifts did not increase their flight speed to any pronounced degree to avoid displacement. Bruderer and Weitnauer (1972) suggested that roosting swifts choose to fly at the minimum power air speed to minimise energy consumption per unit time. In weak winds, the swifts were less accurate in orienting themselves towards the wind direction, showing a rather large scatter around the mean heading direction, which was still oriented into the wind. Since the trackings we analysed lasted only 30–300 s, we could draw no conclusions about the possible presence of a consistent movement pattern in swifts flying at low wind speeds (Bäckman and Alerstam, 2001).

Here, we have chosen a selection of trackings of considerably longer duration, lasting up to 1 h, to analyse in detail the flight behaviour of individual roosting swifts. If we assume that the swifts try to remain as stationary as possible relative to the ground, there will be three different situations with respect to the wind: (i) the wind speed is higher than the flight (air) speed of the swift, (ii) the wind speed is approximately equal to the air speed of the swift and (iii) the wind speed is lower than the air speed of the swift. We predict that, in situations i and ii, the swifts should orient consistently into the wind direction, as we observed previously from the short-duration trackings. The variation in flight direction relative to the wind should be small, and flight paths relative to the air should be straight. In case i, we would expect the swifts to drift 'backwards'. In case ii, in contrast, we would expect the drift to be small and in a random direction. An especially interesting situation emerges in case iii, when the wind speed is considerably lower than the flight speed of the swift. In this case, there is a potential risk that the swifts will overshoot their desired stationary position relative to the ground.

When swifts maintain their mean flight direction into the wind in a weak wind, as demonstrated in our previous study (Bäckman and Alerstam, 2001), the risk of displacement could be dealt with in a number of ways. (i) 'Don't care' – maintain the headwind direction without variation. The swift will overshoot maximally by air speed × time (for negligible wind speed) and potentially face a return flight in the morning of the same distance. Usually, there is some wind, and the displacement distance will then be shorter and the return flight will also take place with a favourable tail wind. (ii) Circle – in the absence of wind, this will be the optimal solution. In light winds, the phase of headwind flying should, on average, be longer than the tailwind phase, with the proportion of time spent flying into opposing winds increasing with increasing wind speed. (iii) Keep the average flight direction into the wind and let the instantaneous flight direction fluctuate around the mean direction, alternately to the left and right of the headwind course in a more-or-less cyclic way.

In this study, we investigate long nocturnal flights of swifts, as recorded by tracking radar, to determine the patterns of flight paths and orientation behaviour at different wind speeds. At high wind speeds, we expect straight flights relative to the air, with the swifts consistently oriented into the wind, thus minimising displacement during the night. In contrast, at wind speeds below the swifts' air speed, we expect more sophisticated strategies of circling, or oscillating and meandering orientation, effectively neutralising any long-term resulting movement over the ground.

Materials and methods

We observed swifts *Apus apus* (L.) in roosting nocturnal flights using a tracking radar (200 kW peak power, 0.25 µs pulse duration, 504 Hz pulse repetition frequency, 1.5 ° beam width, X-band). The radar is situated on the roof of the Ecology Building in Lund (55°42′N, 13°12′E), 91.5 m above sea level. We recorded the flight paths of swifts during the summer of 1999 between 4 July and 5 August and in the summer of 2001 between 26 June and 6 July. The radar echoes of swifts are quite easy to distinguish from those of other birds on the basis of their characteristic echo signature. Swifts display a typical alternation between wing beating and longer or shorter gliding intervals. During gliding, the swifts often 'tilt' and make short turns, which appear as rapid changes in the radar echo signal. The wingbeat frequency of swifts is low enough to be clearly visible on the radar display, and this, together with the criteria mentioned above, gives the observer a good indication of whether the target is a swift. Also, in Lund at this time of the year, we do not expect any other species to use such flap-gliding flight at night and at high altitude.

For a sample of targets considered to be swifts (N=21), we recorded and analysed the wingbeat frequency. The wingbeat frequency was 7.0–8.3 Hz (mean 7.6 Hz), which is in good agreement with earlier recordings for roosting swifts (Bruderer and Weitnauer, 1972). We tracked only single birds, and our intention was to track each individual for as long as possible. The radar recorded azimuth, elevation and range every 2 s. The accuracy of radar measurements was limited to 0.06 ° in angle (azimuth, elevation) and 10 m in range. Wind data were collected every second hour by releasing and tracking helium balloons. Azimuth, elevation and range were transferred from the radar to a computer every 2 s by automated data-logging software. Horizontal and vertical positions were calculated. The position data were averaged from five successive readings, and the resulting 10 s intervals were used to calculate the speed and track direction (the ground speed vector) of the target. Air speed and heading direction (the air speed vector) were calculated for each 10 s interval by vector subtraction of the wind velocity at the altitude at which the bird was flying from its ground speed vector. We used the heading, which is the directional part of the air speed vector, for further analyses of the swifts' orientation.

Calculations of mean directions, mean vector lengths (**r**) and circular statistics were performed according to Batschelet (1981). The heading in relation to the wind (H-W) corresponds to the angular difference between heading (H) and wind (W) direction; H-W=0 ° thus means that the swift is flying straight into the headwind, H-W=90 ° that it is heading perpendicular to the wind and H-W=180 ° that it is flying in the direction of the tailwind. An index of straightness (IS) was calculated by dividing the length of the resulting flight vector by the cumulative sum of the subvectors of each 10 s interval. IS is a measure of the straightness of the flight path and ranges from 0 for a flight with the same start and end positions to 1 for a perfectly linear flight path. We calculated the index of straightness for the flight path both relative to the ground (IS_g) and relative to the surrounding air (IS_a).

To investigate the flight behaviour in relation to the wind, we focused on the variations in H-W during a single flight of a swift. To detect any periodicity in the heading fluctuations relative to the wind direction, individual H-W data were analysed (i) by autocorrelation for periods up to n/2, where n is the total number of 10 s intervals for the complete track of an individual swift, and (ii) by frequency analysis, using the discrete Fourier transform (DFT) (Chatfield, 1996; Priestley, 1981). In the DFT analysis, the H-W data were first 'normalised' (residual values from a linear regression were used) and windowed with the Hanning function. We then applied a discrete Fourier transform to the data. The resulting power spectrum was tested for significant (P<0.05) frequency components (χ^2-test of sample spectrum estimator for white noise) (Jenkins and Watts, 1968). If there was more than one significant frequency component, we selected the strongest. We used MATLAB v5.2 (The MathWorks Inc., MA, USA) for all calculations, and the built-in FFT function for the DFT analysis. As a control, we applied DFT analysis to 12 long trackings of climbing helium balloons, using the same criteria as for the analysis of bird trackings, and found no significant frequency components.

Results

For our analysis, we selected all trackings (N=30) from 1999 with durations of at least 20 min and up to 60 min. In addition,

Table 1. *Characteristics of 49 common swift trackings*

	Mean	Minimum	Maximum	S.D.
Duration of tracking (s)	1366	560	3580	696
Distance relative to the ground (m)	5012	1513	11 252	2118
Distance relative to the air (m)	11 793	4728	42 800	7224
IS relative to the ground IS_g	0.771	0.165	0.991	0.205
IS relative to the air IS_a	0.938	0.314	0.997	0.127
Mean flight altitude (m)	1696	918	2838	429
Ground speed, V_g (m s^{-1})	4.3	1.2	9.6	2.1
Air speed, V_a (m s^{-1})	8.7	5.6	13.3	1.5
Wind speed, V_w (m s^{-1})	7.1	1.3	14.8	2.9
Climbing speed, V_z (m s^{-1})	–0.02	–0.64	1.08	0.32
Mean vector direction, *H-W* (degrees)	–0.5 **r**=0.88			
Mean vector direction, *T-W* (degrees)	–44.5 **r**=0.14			

The duration of trackings is from the moment when we locked the radar onto the target until we stopped tracking or lost the target.

The cumulative distances are the sum of the distances travelled in each 10 s interval.

The index of straightness *IS* was calculated as the resultant distance (the straight line travelled from the start to the end of tracking) divided by the cumulative distance.

r, mean vector length (Batschelet, 1981) for the mean heading direction relative to the wind (*H-W*) and mean track direction relative to the wind (*T-W*) for the 49 trackings analysed.

we selectively included 19 shorter trackings from 1999 and 2001 of swifts that were flying in low wind speeds; the duration of these ranged from 9 to 18 min. Table 1 presents the characteristics of the swift trackings. The mean flight altitude of our present sample of 49 swift trackings is very similar to our earlier mean (altitude 1683±489 m; mean ± S.D.) of a large sample (*N*=224) of swift trackings (Bäckman and Alerstam, 2001). The ground speed varied greatly because of the varying wind conditions to which the swifts were exposed. The small mean difference between heading and wind direction shows that the swifts were, on average, well oriented into the wind direction (Table 1).

Fig. 1 illustrates three sample tracks. Tracks A and B are from swifts flying in moderate winds (7–8 m s^{-1}), and track C is from a swift flying in weak winds. In moderate winds, the swifts often move rather slowly over the ground.

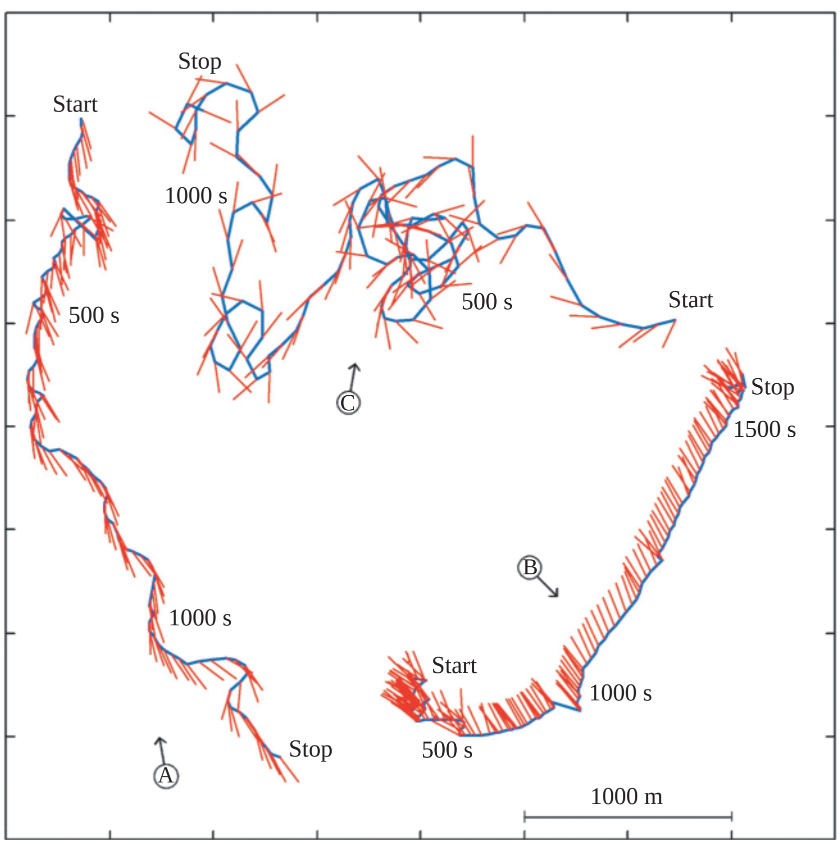

Fig. 1. Three selected tracks of swifts in nocturnal roosting flight. The blue line shows the ground track, and the red lines represent the heading direction every 10 s. Numbers denote the time (in s) after the start of tracking. The arrows beside the letters indicate the wind direction. Geographic north is upwards. Track A is a swift flying into a wind with a mean direction of 161 ° and a speed of 6.9 m s^{-1}. The index of straightness relative to the ground, IS_g, is 0.67. In track B, the swift is facing a wind of 8.1 m s^{-1} at 314 °, and IS_g is 0.59. The corresponding values for track C are 2.9 m s^{-1}, 190 ° and 0.22.

The swift in track A has a net movement towards the wind direction because the air speed of the swift (9.9 m s^{-1}) is higher than the wind speed (6.9 m s^{-1}). The resulting ground speed is much lower (3.9 m s^{-1}). The heading direction of the swift in track A fluctuates around the headwind direction and causes an

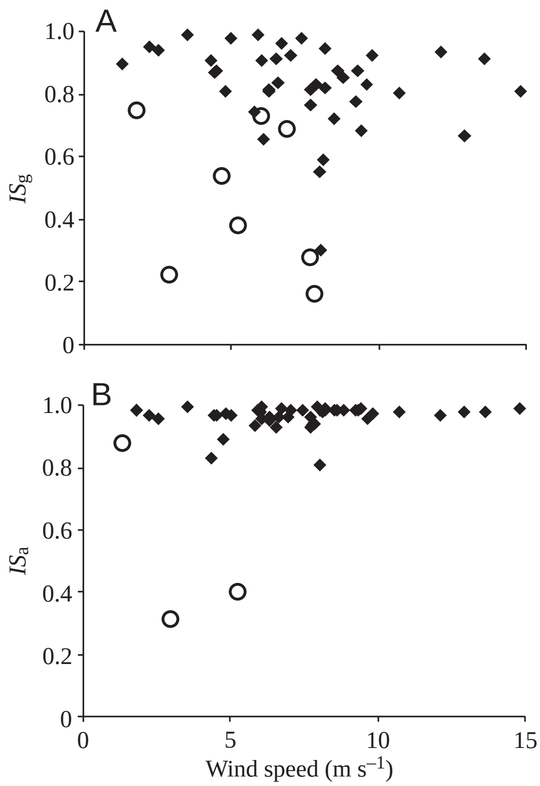

Fig. 2. Straightness indices in different wind speeds. (A) The straightness index relative to the ground, IS_g. A low value means that the resulting flight path is greatly convoluted (see Fig. 1 track C), while a value close to 1 means that the swift has been flying on a straight course. (B) The straightness index relative to the surrounding air, IS_a. Circles indicate that the swift has been circling, i.e. that the bird has crossed its own flight path relative to the ground (IS_g) and the air (IS_a).

undulating movement sideways but, on average, the difference between the heading and wind direction (*H-W*) is only 0.6° and IS_a=0.97. The swift in track B also flies with a mean heading direction almost straight towards the wind (*H-W* is on average 9°). In track B, the air speed of the swift (8.9 m s^{-1}) and the average wind speed (8.1 m s^{-1}) are very similar. Early in the observed track, the swift shows the same behaviour as in track A, with *H-W* fluctuating around zero, but after approximately 500 s the heading direction is on average slightly to the right of the wind direction; *H-W*>0. This causes a resulting slow movement relative to the ground, perpendicularly and to the right of the wind direction (track B). The IS_a is 0.98, revealing a very consistent orientation into the wind.

In track C, the wind speed is only 2.9 m s^{-1}, which is far below the air speed of the swift (10.2 m s^{-1}). Ground speed is on average 9.6 m s^{-1}. The swift changes its heading continuously and apparently without consideration of the wind direction. There are several circling flights, and the IS_a is only 0.31. The slightly higher air speed of this swift may be associated with the fact that it is descending gently (vertical speed –0.4 m s^{-1}) in contrast to cases A and B where the swifts fly at almost constant altitude (vertical speeds +0.15 m s^{-1} and –0.1 m s^{-1} respectively).

The index of straightness relative to the ground IS_g does not vary significantly with wind speed (Fig. 2A). However, we observed only a small number of swifts flying at wind speeds lower than 5 m s^{-1}. For the index of straightness relative to the air, IS_a (Fig. 2B), the result is slightly clearer. For wind speeds over 8 m s^{-1}, the flight paths in relation to the surrounding air are very straight, but there are a few cases with low IS_a values at lower wind speeds.

We were particularly interested in analysing the flight behaviour of the swifts in relation to the wind direction. In

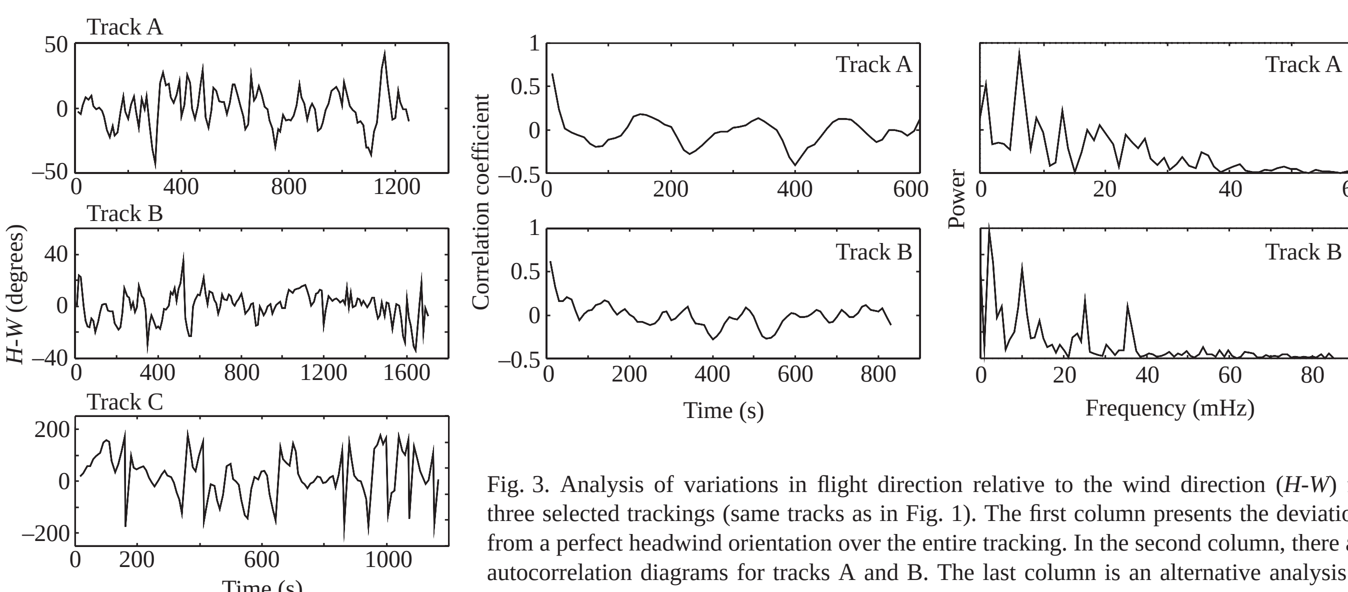

Fig. 3. Analysis of variations in flight direction relative to the wind direction (*H-W*) for three selected trackings (same tracks as in Fig. 1). The first column presents the deviations from a perfect headwind orientation over the entire tracking. In the second column, there are autocorrelation diagrams for tracks A and B. The last column is an alternative analysis of periodicity, in the form of a DFT power spectrum, showing the relative frequency content of the *H-W* data series. Track A has an autocorrelation period of approximately 160 s and a significant frequency component of 6.74 mHz. Track B shows no distinct period, and the frequency peaks fail to pass the significance level.

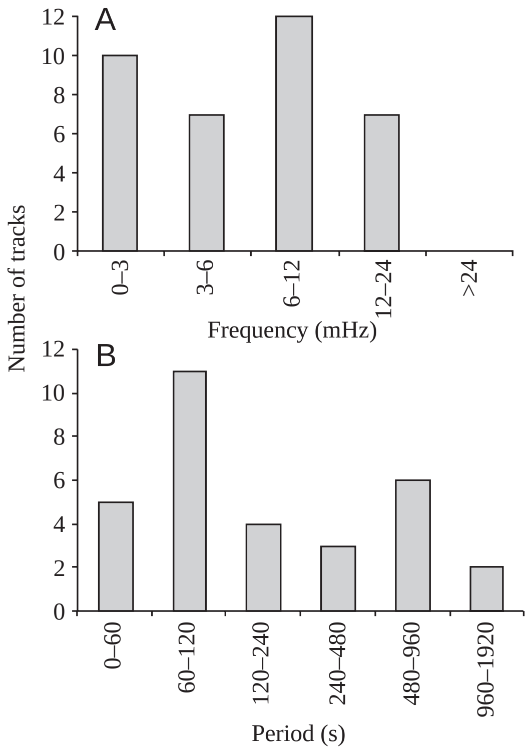

Fig. 4. Frequency histogram of the cyclic components of the heading direction relative to the wind direction (*H-W*) in our 49 trackings of swifts. We found a statistically significant frequency component in 36 out of 49 trackings and in 31 trackings with distinct autocorrelation periods.

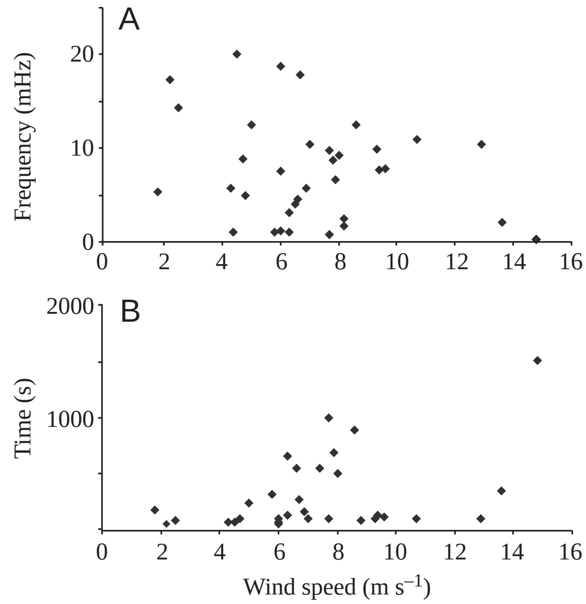

Fig. 5. The periodicity of deviations in the heading direction relative to the wind direction in relation to wind speed. (A) Significant frequency components *versus* wind speed; (B) distinct autocorrelation period *versus* wind speed. There was no significant correlation in either case.

Fig. 3, we illustrate the time series (10 s intervals) of *H-W* over the entire tracking for the same three trackings as in Fig. 1. In tracks A and B, the deviations in flight direction from the wind direction are rather small (within ±50 °). In contrast, *H-W* in track C fluctuates widely. The largest amplitudes are actually an artefact, since we are displaying data with a circular distribution on a linear scale (*H-W*=+180 ° is the same as *H-W*=-180 °). In the case of tracks A and B, this does not matter because the deviations from *H-W*=0 ° are small (*H-W* is far less than ±180 °, see below), but in case C, where the bird sometimes flies in circles, this way of analysing course fluctuations becomes inappropriate. Rapid shifts from *H-W*=+180 ° to *H-W*=-180 ° should be interpreted as circling flights.

In the second column in Fig. 3, we have analysed the autocorrelation of the *H-W* values shown in the first column for tracks A and B. There is an indication of a cyclic component in the undulating flight path of track A with a period of approximately 160 s. The corresponding DFT analysis also shows that the dominant and only statistically significant frequency component is approximately 7 mHz (seven cycles in 1000 s). In track B, there are no such clear-cut oscillations of the flight path in the autocorrelation analysis. The DFT power spectrum shows a number of components, the strongest, but not significant, component being approximately 2.5 mHz. It is not appropriate to analyse track C with this method since this swift was flying in circles.

We performed these analyses on all swift tracks where there were no circling flight paths. The results of the DFT and autocorrelation analyses are presented in Fig. 4, where we have divided the values into discrete categories. We found significant frequency components in 36 trackings and distinct autocorrelation periods in 31 cases, out of 49 trackings. There was no correlation between the wind speed and the observed distinct autocorrelation periods or between wind speed and significant frequency components (Fig. 5A,B).

Discussion

The present analysis of long-duration trackings of swifts reveals that the birds often (but not always) show a pattern of regular variation in their orientation relative to the wind direction, with a cycle period usually in the range 1–16 min (corresponding to the frequency range 1–17 mHz; cf. Fig. 4). The Fourier analysis also indicated some cases of higher-frequency changes in orientation, at 17–24 mHz (corresponding to a cycle period of 40–60 s). However, contrary to our expectation, these course variations occurred during flights in both strong and weak winds (Fig. 5) and thus in both relatively straight and more meandering flights (Fig. 2). It is striking that we often find a regular rhythm in the orientation direction, but there is no obviously preferred frequency or period. It seems highly unlikely that the observed patterns are an artefact due to the tracking characteristics of the radar because the flight paths relative to the ground recorded by radar were generally very different in degree of convolution as well as in distance (Table 1) from the flight paths/heading directions relative to the air on which the frequency analysis was based.

Because of the time resolution of 10 s for the time series, we cannot detect frequencies higher than 50 mHz, corresponding to a period of 20 s. In our set of data, the shortest period was 40 s and the highest frequency was 20 mHz, which are well within our resolution. Furthermore, it is not possible to detect frequencies lower than two periods during a flight path. Since the average tracking duration is 1366 s (Table 1), there are few opportunities of finding periods longer than 683 s (approximately 11 min), corresponding to a frequency of approximately 1.5 mHz. Still, some very low significant frequencies and long periods emerged from the analyses of the longest radar trackings in our data set, with the lowest frequency at 0.3 mHz and the longest period at 25 min. Thus, it is possible that there exist even slower cyclic patterns than we have described here.

There seemed to be no consistent relationship between cycle period/frequency of orientation changes and wind speed (Fig. 5). This provides no support for our expectation that swifts might show a regular variation of their orientation primarily to remain stationary relative to the gound when flying in rather slow winds. Thus, the possible function of the cyclic orientation changes during the swifts' flights is unclear. However, we found that the swifts' flights were sometimes less straight, and occasional circling occurred, at low wind speeds (Fig. 2), which will contribute to reducing the displacement with respect to the ground during the night. The cyclic variation in the swifts' orientation may reflect a behaviour in which the birds do not adjust their orientation continuously, but rather correct or over-correct it at regular intervals. However, we found no evidence for any well-defined characteristic frequency/period for these course corrections. Such behaviour might be associated with a reduced level of alertness if the swifts are, in some sense, 'sleeping' during their nocturnal flights (Lack, 1956), or it may be a phenomenon associated with bird orientation in general.

This is, to our knowledge, the first study in which the existence of harmonic oscillations in birds' orientation has been investigated and demonstrated. We have shown that Fourier and autocorrelation analyses provide useful tools for such investigations of orientation time series. The finding that swifts flying at night orient into the wind and weave slowly from side to side by varying their heading into the wind direction with a cycle period of 1–16 min is intriguing. Perhaps this remarkable behaviour is associated with the swifts' special ability to orient into the wind during the night and at high altitudes. What is the sensory basis for such behaviour? Is such a behaviour also involved in the orientation of other birds, for example on their migratory flights? Unfortunately, these questions cannot be answered from our existing data, and we have to limit ourselves to proving that oscillatory orientation occurs in the roosting flights of swifts.

This finding may be of potential importance for understanding the process of bird orientation. Further analyses of the pattern of variation in orientation of free-flying birds and of birds in orientation cages are needed to determine whether such cyclic heading changes should be regarded as a normal feature of bird orientation or whether they are confined to the special case of nocturnal roosting flights of swifts orienting into a headwind.

We are grateful to Björn Holmquist (Department of Statistics, Lund) and Niklas Jonzén (Department of Theoretical Ecology, Lund) for helpful suggestions about the analysis of the time series we carried out with the *H-W* data. We also thank C.-G. Carlsson and Ulf Olsson at Aerotech Telub for skilfully installing and adapting the radar, meteorologist Bertil Larsson for developing efficient software for the treatment of the radar data and Bertil Ohlsson for improving the English. This study was supported by grants from the Swedish Natural Science Research Council.

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