THE RO
SOCIETY

Confronting the winds: orientation and flight behaviour of roosting swifts, *Apus apus*

Johan Bäckman* **and Thomas Alerstam**

Department of Animal Ecology, Ecology Building, Lund University, SE-22362 Lund, Sweden

Swifts, *Apus apus*, spend the night aloft and this offers an opportunity to test the degree of adaptability of bird orientation and flight to different ecological situations. We predicted the swifts' behaviour by assuming that they are adapted to minimize energy expenditure during the nocturnal flight and during a compensatory homing flight if they become displaced by wind. We tested the predictions by recording the swifts' altitudes, speeds and directions under different wind conditions with tracking radar; we found an agreement between predictions and observations for orientation behaviour, but not for altitude and speed regulation. The swifts orientated consistently into the head wind, with angular concentration increasing with increasing wind speed. However, contrary to our predictions, they did not select altitudes with slow or moderate winds, nor did they increase their airspeed distinctly when flying into strong head winds. A possible explanation is that their head-wind orientation is sufficient to keep nocturnal displacement from their home area within tolerable limits, leaving flight altitude to be determined by other factors (correlated with temperature), and airspeed to show only a marginal increase in strong winds. The swifts were often moving `backwards', heading straight into the wind but being overpowered by wind speeds exceeding their airspeed. The regular occurrence of such flights is probably uniquely associated with the swifts' remarkable habit of roosting on the wing.

Keywords: bird orientation; bird flight; wind drift; radar tracking

1. INTRODUCTION

Swifts, *Apus apus*, have a peculiar way of spending the night. They climb at dusk to high altitudes, 1000–3000 m above ground level, where they fly during the dark hours before returning to their breeding colonies early in the morning (Lack 1956). This remarkable behaviour has been established by the field, telescope, aircraft and radar evidence reported mainly by Weitnauer (1952, 1954, 1960). Flight altitudes have also been measured by altimeters pasted on the swifts' backs (Gustafson *et al.* 1977). It is mainly one-year-old immature birds that spend the night aloft but at the end of the breeding season adult birds also take part in nocturnal flights (Weitnauer 1954, 1960). However, in poor weather this regular habit of local nocturnal flying is temporarily interrupted and the swifts may set out on extensive weather movements (Koskimies 1950, Lack 1956).

We expect that swifts behave quite differently during nocturnal flights compared with foraging or migration flights because of fundamental differences in optimization criteria (Hedenström & Alerstam 1995; cf. §2). However, more advanced adaptive behaviours may be constrained by a lack of necessary cues in the darkness at high altitudes or by a reduced level of alertness if the swifts, in some sense, sleep during these flights (Lack 1956).

Swifts on nocturnal flights were recorded, using tracking radar, by Bruderer & Weitnauer (1972). They reported that the swifts were flying at distinctly slower airspeeds, on average 6.5 m s^{-1}, than during presumed migratory flights (mean of 11 m s^{-1}) and low-level diurnal flights (*ca.* 16 m s^{-1}; Oehme 1968). They suggested that during nocturnal flights the swifts fly at the minimum power speed, to minimize energy consumption per unit time, while during migration they fly at the maximum range speed, to minimize energy consumption per unit distance covered (Pennycuick 1969, 1975, 1989).

In this paper we further develop predictions about the swifts' altitudes, flight speeds and orientation during their nocturnal flights in relation to winds, and test these predictions using detailed tracking-radar observations.

2. PREDICTIONS

At their high nocturnal altitudes swifts are very exposed to the effects of the wind. We expect them to behave in such a way as to avoid extensive dislocation and to minimize total energy consumption during the night.

Flapping flight power, P, is a U-shaped function of flight velocity (airspeed), V, where V_{mp} is the characteristic speed associated with minimum power and V_{mr} is the speed associated with minimum energy per unit of distance covered (e.g. Pennycuick 1969, 1975, 1989; Tucker 1973; Rayner 1979, 1999). While V_{mp} is independent of wind, V_{mr} is a function of wind direction and speed because the distance covered relative to the ground is determined by the ground speed, which in turn is determined by the bird's flight vector and the wind vector (Pennycuick 1975; Liechti *et al.* 1994). We designate $V_{\mathrm{mr}}(0)$ as the maximum range speed in still air, and $V_{\mathrm{mr}}(w)$ and $V_{\mathrm{mr}}(W)$ as the corresponding speeds in head winds of speeds w and W, respectively, where $0 \leqslant w \leqslant W$. Since we are considering only head winds, $V_{\mathrm{mp}} < V_{\mathrm{mr}}(0) \leqslant V_{\mathrm{mr}}(w) \leqslant V_{\mathrm{mr}}(W)$. The head-wind speeds W and w refer to the wind conditions during the swifts' high-altitude nocturnal flight and low-altitude homing flight, respectively.

There are significant uncertainties affecting the aerodynamic theory of bird flight, making quantitative predictions of flight speeds provisional. For the swift (body mass of 0.041 kg; wing span of 0.45 m; aspect ratio

Received 25 July 2000 *Accepted* 15 February 2001

of 13.2), predicted V_{mp} is 7.3 m s^{-1} and $V_{\mathrm{mr}}(0)$ is 12.4 m s^{-1} at sea-level standard air density (1.23 kg m^{-3}), according to the revised flight mechanical program described by Pennycuick (1999). Our derivations and tests are not dependent on the precise values of these speeds (Alerstam 2000). For an ideal bird *sensu* Pennycuick (1975), $V_{\mathrm{mr}}(0)$ is expected to exceed V_{mp} by a factor of 1.32.

If swifts are displaced by the wind during nocturnal high-altitude flights, we expect them to make compensatory homing flights in the early morning. We assume that they then encounter a reduced wind speed by travelling at a lower altitude, where wind speeds are usually lower than the high-altitude geostrophic wind speeds. Given W as the wind speed during the nocturnal high-altitude flight and w as the head-wind speed during a possible homing flight, we distinguish three possible situations.

(a) *Case A: $W \leqslant V_{mp}$*

If $W \leqslant V_{\mathrm{mp}}$ then the swifts are expected to fly at V_{mp} and remain stationary by varying their orientation around the head-wind direction. This variation in orientation may be performed in different ways (shifting between two or more courses or gradually changing orientation within a sector centred on the head-wind direction). The swifts' heading directions should be very variable around a mean direction that coincides with the head-wind direction (the slower the wind speed, the higher scatter in heading directions). Resulting track directions are expected to show an even higher scatter than the heading directions, relative to the wind direction.

(b) *Case B: $V_{mp} \leqslant W \leqslant V_{mr}(w)$*

If $V_{\mathrm{mp}} \leqslant W \leqslant V_{\mathrm{mr}}(w)$ then the swifts are expected to fly at an airspeed equal to the wind speed and maintain position by heading straight into the wind. Ground speeds will be low, approaching zero in the ideal situation, and track directions are expected to show random variation relative to the wind direction. In this case, the swifts increase their airspeed above V_{mp} to match the wind speed. It is the expected head-wind speed, w, during the eventual homing flight that determines the maximum wind speed that the swifts should be prepared to match to remain stationary during the nocturnal flight rather than allowing themselves to be displaced by wind (as in Case C, §2(c)). If the swifts would not expect any wind reduction during the homing flight compared with the nocturnal flight ($w = W$), they are expected to match the wind speed up to the maximum speed that their power capacity allows (because $V_{\mathrm{mr}}(W) > W$). If, on the other hand, they can make the homing flight completely sheltered from the wind, they will not increase their airspeed during the nocturnal flight beyond $V_{\mathrm{mr}}(0)$.

(c) *Case C: $W > V_{mr}(w)$*

If $W > V_{\mathrm{mr}}(w)$ then the swifts are expected to fly at an airspeed of $V_{\mathrm{mr}}(w)$, heading straight into the wind. By doing so, they will be overpowered by the wind (with speed W) and carried backwards along track directions in the downwind direction. The displacement during the night will be compensated by a homing flight at airspeed $V_{\mathrm{mr}}(w)$ into a wind of speed w. This behaviour is associated with minimum energy costs according to the following derivation.

Let V_1 and V_2 be the airspeeds of the swifts during the high-altitude nocturnal flight into a wind speed of W ($W \geqslant V_1$) and during the homing flight into a wind speed of w ($w < V_2$), respectively. The displacement distance, D, during nocturnal-flight time, t_1, requiring homing-flight time, t_2, will be

$$D = (W - V_1)t_1 = (V_2 - w)t_2. \tag{1}$$

The total energy consumption, E, for the nocturnal and homing flights will be

$$E = P(V_1)t_1 + P(V_2)t_2, \tag{2}$$

where P is a function of V according to the flapping flight power curve. Inserting equation (1) into equation (2) gives

$$E = t_1\left[P(V_1) + P(V_2)\frac{(W - V_1)}{(V_2 - w)}\right]. \tag{3}$$

Taking the partial derivative of E with respect to V_2 and solving for minimum E shows that the optimal V_2 is independent of V_1 and equal to $V_{\mathrm{mr}}(w)$. Solving for the optimal V_1 in the same way shows that V_1 depends on V_2. Given that the optimal V_2 is equal to $V_{\mathrm{mr}}(w)$, the optimal V_1 also equals $V_{\mathrm{mr}}(w)$. With $V_1 = V_2 = V_{\mathrm{mr}}(w)$ the energy consumption becomes

$$E_{\mathrm{min}} = t_1 P(V_{\mathrm{mr}}(w))\frac{(W - w)}{(V_{\mathrm{mr}}(w) - w)}. \tag{4}$$

It can be easily shown that E_{min} falls below the total energy consumption for a stationary flight into the wind at speed W, under the conditions of a convex power function $P(V)$ with $W > V_{\mathrm{mr}}(w)$.

We thus predict that swifts will behave in the following ways with respect to flight altitude, speeds and orientation if they are adapted to minimize total energy consumption under different wind conditions during their nocturnal flights.

- (i) Altitude. The swifts are expected to prefer nocturnal-flight altitudes with wind speeds slower than or equal to V_{mp}. If there is no wind, we expect the swifts to fly at low altitudes because flight power increases with altitude. Flight power is proportional to (air density)$^{-1/2}$ for an ideal bird, *sensu* Pennycuick (1975). This corresponds to a 5% increase in flight power per 1000 m increase in altitude in the standard atmosphere. However, this effect of air density on flight economy is small in comparison to the potential costs of strong winds causing long-distance displacement. Hence, we expect the swifts to primarily avoid altitudes with wind speeds exceeding V_{mp} (V_{mp} also increases with altitude at about the same proportional rate as flight power; Pennycuick 1975).
- (ii) Flight speed. The swifts are expected to fly at a constant airspeed of V_{mp} up to wind speeds of $W = V_{\mathrm{mp}}$. At higher wind speeds they are expected to increase their airspeed to exactly match the wind speed, up to a threshold wind speed of $W = V_{\mathrm{mr}}(w)$, above which they will not increase their airspeed any further. Ground speeds are expected to be lowest, close to zero, in the wind-speed interval

Table 1. *Means and standard deviations of speeds* ($\mathrm{m\,s^{-1}}$) *and altitudes* (m above sea level) *for swifts tracked by radar during nocturnal flights*

(Results are given for all data combined as well as for flights in low, intermediate and high wind speeds. Statistical tests refer to the existence of differences between wind-speed classes. V_a, true airspeed; V_g, ground speed; V_z, vertical speed; V_e, equivalent airspeed.)

	all winds	wind $< 6\ \mathrm{m\,s^{-1}}$	wind 6–9 $\mathrm{m\,s^{-1}}$	wind $> 9\ \mathrm{m\,s^{-1}}$	ANOVA	
	mean ± s.d.	mean ± s.d.	mean ± s.d.	mean ± s.d.	$F_{2,221}$	p
V_a	9.3 ± 2.3	8.8 ± 1.7	9.2 ± 2.3	9.8 ± 2.8	3.63	0.030
V_g	7.1 ± 4.0	8.0 ± 2.9	6.4 ± 4.5	6.9 ± 4.3	3.07	0.048
altitude	1683 ± 489	1673 ± 405	1824 ± 504	1585 ± 531	4.35	0.014
V_z	−0.03 ± 0.48	0.04 ± 0.43	−0.06 ± 0.35	−0.08 ± 0.59	1.40	> 0.05
V_e	8.5 ± 2.2	8.1 ± 1.5	8.4 ± 2.1	9.0 ± 2.7	3.93	0.02
n	224	80	62	82	—	—

$V_{mp} \leqslant W \leqslant V_{mr}(w)$, when the swifts are expected to remain stationary by flying straight into the wind with an airspeed equal to the wind speed.

(iii) Orientation. The mean heading direction is expected to coincide with the head-wind direction at all wind speeds. The scatter of headings will be substantial at low wind speeds but will decrease with increasing wind speed. At wind speeds of $W \geqslant V_{mp}$ the swifts are expected to orientate within a very narrow sector straight into the wind. Track directions will show a very wide scatter at wind speeds below $V_{mr}(w)$, when the swifts will remain in their local area during the night. However, at higher wind speeds track directions are expected to be concentrated in the downwind direction, as the swifts are carried away by the wind.

3. METHODS

We used tracking radar (X-band, 200 kW peak power, 0.25 µs pulse duration, 504 Hz pulse repeat frequency, 1.5° pencil beam width, antenna 91.5 m above sea level), permanently situated on the roof of the Ecology Building in Lund (55°42′ N, 13°12′ E), to record nocturnally flying swifts between 4 July 1999 and 5 August 1999. Radar echoes of swifts are easily distinguished from other birds due to their characteristic signature. We used the following cues to classify a target as a swift: first, the wing beats are slower than for all other small birds we expected to encounter; second, the sequence of wing-beat phases and resting phases is quite specific; and, third, the signal amplitude often changes rapidly when a gliding swift tilts (Bruderer & Weitnauer 1972). In addition, we recorded the echo signals for a sample of targets considered to be swifts, and analysed the wing-beat frequency. The average wing-beat frequency for these 21 sample individuals ranged from 7.0 to 8.3 Hz with a mean of 7.6 Hz, which is in agreement with earlier records of wing-beat frequencies for swifts during nocturnal flights (6–8 Hz recorded by Bruderer & Weitnauer (1972)).

During radar operation, which took place between 22.00 and 04.00 Universal Time Coordinated (UTC) (21.00–03.00 local normal time), we searched elevations between 5 and 40° to find targets at different altitudes. We concentrated our radar search in azimuth sectors with minimal disturbance from ground echoes and, normally, at ranges of 2–8 km from the radar.

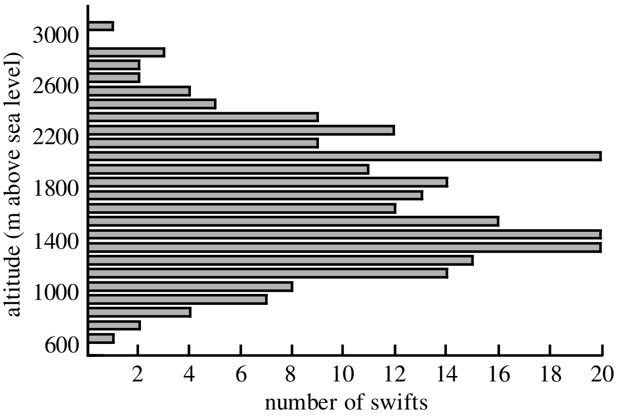

Figure 1. Distribution of altitudes (m above sea level) for swifts tracked by radar during nocturnal flights.

Only targets considered to be single birds were tracked. The durations of trackings used for further analysis were at least 30 s but no longer than 300 s. Azimuth, elevation and range, as registered by the radar in automatic-tracking mode, were transferred to a computer every 2 s. Horizontal and vertical coordinates were then calculated. The position data were averaged from five successive readings and the resulting 10 s intervals were used for calculations of speed and direction. To collect information about the wind direction and speed at the altitudes at which the birds were flying, we released and tracked helium-filled balloons at *ca.* 2 h intervals.

Airspeed and heading for each swift were calculated by vector subtraction of the wind velocity (at the proper altitude) from the bird's flight track. Altitudes refer to the height above sea level. Values for altitude, speed and direction were averaged over all 10 s intervals for each tracking and used in further analysis. Calculations of mean directions, mean vector lengths (r) and circular statistics were performed according to Batschelet (1981). Other statistical calculations were performed using SPSS v. 8.0 (SPSS, Inc., Chicago, IL, USA). We have mainly used the true airspeed in our analyses, but we also calculated the equivalent airspeed, V_e, (airspeed corrected to standard sea-level air density, $1.23\ \mathrm{kg\,m^{-3}}$) by taking the altitude and barometric pressure into account according to Pennycuick (1999). Barometric pressures and temperatures were obtained from Falsterbo weather station (sea-level data) and

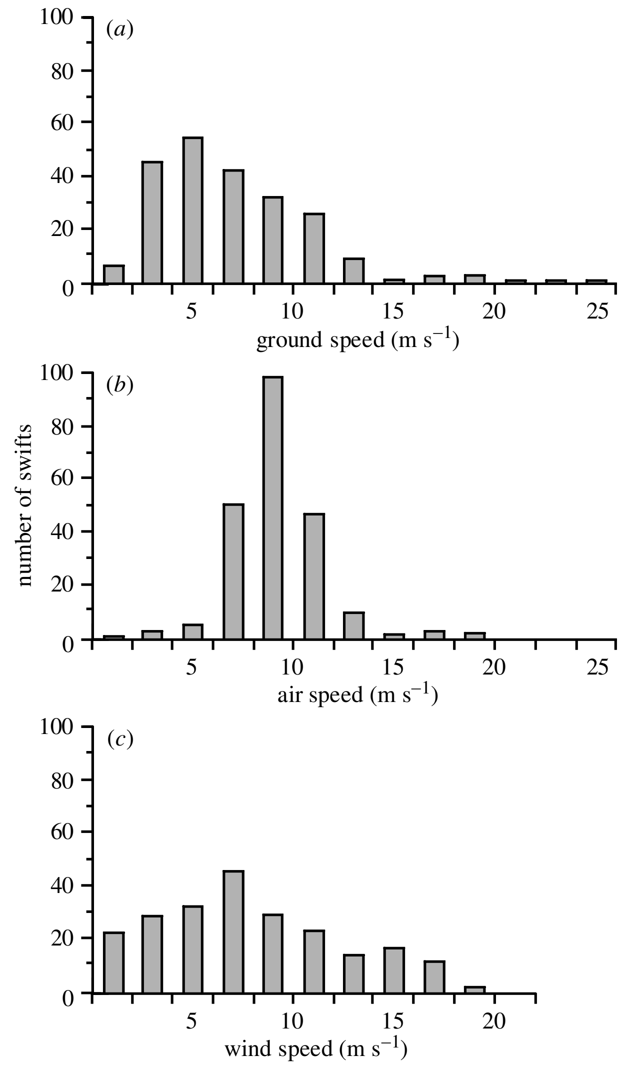

Figure 2. Distribution of (*a*) ground speeds, (*b*) air speeds and (*c*) wind speeds for swifts tracked by radar during nocturnal flights.

from Copenhagen (radiosonde measurements) at 22.00 and 23.00 UTC, respectively; both places are within 50 km of our study site.

4. RESULTS

Tracking-radar data were collected on 18 nights and a total of 224 tracks of targets classified as single swifts were recorded. On 14 nights the sky was clear, three nights were overcast (high clouds) and on one night there were thunderclouds. The means and standard deviations of the altitudes and speeds for the total data set, and for swifts flying in weak, intermediate and strong winds, are given in table 1.

(a) *Altitude*

More than 80% of all tracked swifts were flying at altitudes between 1000 and 2200 m (figure 1), the mean altitude being 1683 m. Swifts differed in their choice of altitudes between nights, and the between-night variation in altitude was highly significant (one-way ANOVA, $F_{16,206} = 3.37$, $p < 0.001$). To test the prediction that the swifts prefer altitudes with wind speeds slower than or equal to V_{mp}, we performed the following calculations. For each wind profile (wind speeds at different altitudes) associated with tracks of swifts, we extracted the minimum and maximum wind speeds in the height interval 900–2400 m, and calculated the average of these two speeds. We then calculated the mean deviation of the wind speeds experienced by the swifts from this average wind speed for each wind profile with two or more trackings of swifts ($n = 29$ wind profiles). The average wind speed ranged from 3 to 15 m s^{-1} on these different nights, and we expected the swifts to select altitudes with below-average wind speeds to an increasing degree with increasing mean wind speed. However, contrary to our prediction, the nightly mean deviations of the wind speeds experienced by the swifts from the average wind speed in the 900–2400 m altitude interval showed a similar pattern on nights with weak winds (for 15 wind profiles with mean wind speed 3–7.5 m s^{-1} the mean deviation was positive in six cases and negative in nine cases) to the pattern on nights with strong winds (corresponding data for 14 wind profiles with mean wind speed 7.5–15 m s^{-1} showed positive deviations in five cases and negative deviations in nine cases). There was no statistically significant correlation between mean deviation and average wind speed (Kendall rank correlation, $\tau = 0.042$, $n = 29$, $p \gg 0.05$).

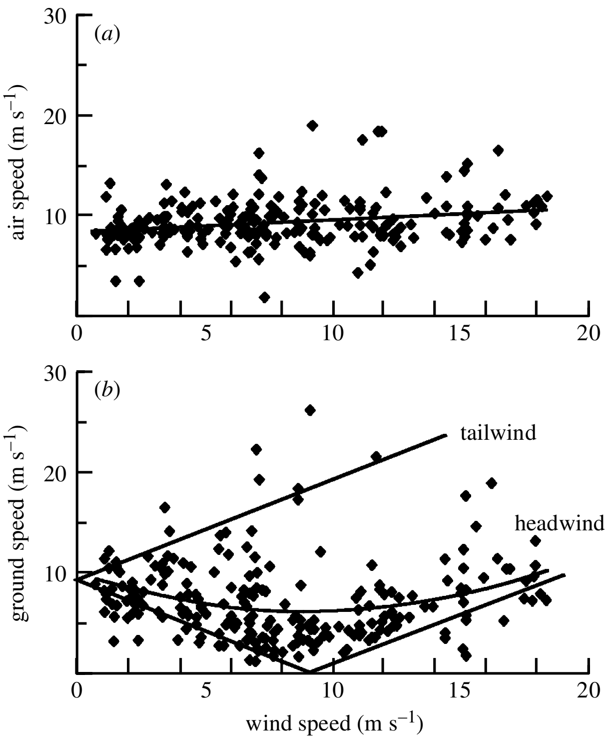

Figure 3. (*a*) Airspeed of swifts in relation to wind speed. The regression line has intercept 8.4 m s^{-1} and slope 0.11 (correlation coefficient = 0.21, $p < 0.01$). (*b*) Ground speed of swifts in relation to wind speed. Swifts flying with a constant airspeed of 9 m s^{-1} would have the ground speeds shown by the upper line with due tailwinds and those shown by the V-shaped lower line with due head winds (travel in the forward direction at wind speeds under 9 m s^{-1} and in the backward direction at wind speeds over 9 m s^{-1}). The curve shows a least-square fit of a quadratic function to the observed data (no significant improvements in fit with higher-order polynomials).

Figure 4. Orientations of swifts in relation to wind direction for all data combined and for flights in weak, medium and strong winds: (

with respect to flight altitude and speed, possibly because of a lack of the necessary sensory cues in darkness at high altitudes or because of a reduced responsiveness when in a nocturnal resting mode. Why then do the swifts not adjust their altitude and speed in relation to the wind conditions as predicted?

(a) *Altitude*

Weitnauer (1960) suggested that thermals and ambient temperature may influence the altitude of swifts during their nocturnal flights. We analysed temperatures (at altitudes where the swifts were flying) for the swifts in our data set, and found that the average temperature experienced by the swifts ranged from 5.5 to 14.4 °C on different nights and the between-night variation was highly significant ($F_{16,206} = 12.0$, $p < 0.001$). There was a significant correlation between mean altitude and mean temperature (correlation coefficient = 0.54, $n = 18$ nights, $p < 0.05$), showing that the swifts were flying at higher altitudes on warmer nights. We have no plausible explanation for this, but since the flights lasted for several hours it could be connected with maintenance of the water balance (Kvist *et al*. 1998). The occurrence of insects at the high altitudes used by swifts for their nocturnal flights is normally (at least at night when there are no thermals) negligible (C. Solbreck, personal communication) making it quite improbable that aspects of foraging influence the swifts' altitudes.

(b) *Speed*

The equivalent airspeed was, on average, $8.5\,\mathrm{m\,s^{-1}}$, being somewhat slower in weak winds (mean of $8.1\,\mathrm{m\,s^{-1}}$) than in strong winds ($9.0\,\mathrm{m\,s^{-1}}$) (table 1). These speeds are only slightly higher than the V_{mp} of $7.3\,\mathrm{m\,s^{-1}}$ predicted by flight mechanical theory (Pennycuick 1999). Hence, it seems likely that the swifts were flying at or near V_{mp}, as expected if the energy per unit time is minimized. The true airspeed was, on average, $9.3\,\mathrm{m\,s^{-1}}$ (table 1), which is faster than the value of $6.5\,\mathrm{m\,s^{-1}}$ reported by Bruderer & Weitnauer (1972). The reason for this discrepancy is not entirely clear, but could, at least partly, be due to differences in the methods used to calculate the flight track. In our study we used 10-s intervals for speed calculations (based on five 2-s readings), while Bruderer & Weitnauer (1972) measured flight distances from a paper printout.

The fact that the swifts did not show any distinct increase in airspeed when flying into head winds with speeds exceeding their own airspeed indicates that they are more tolerant of nocturnal displacement than we have assumed. Swifts taking part in nocturnal flights are, to a large extent, non-breeding birds (Weitnauer 1954, 1960) and are therefore not forced to be back in the colony the next day. Perhaps the swifts can combine compensatory homing flights in the morning with foraging, with similar benefits and costs as local foraging flights close to their home colonies. If so, we have overestimated the costs of displacement by assuming that displaced swifts have to pay extra costs corresponding to the full transport costs of the homing flights, compared to swifts that are already at their home areas at daybreak. Even if displacement costs are smaller than assumed, they are probably not negligible. If they were, it would not matter in which directions the swifts were flying relative to wind and we would not have observed an orientation into the head-wind direction.

Assuming that there is a small but significant extra energy cost, k, proportional to the distance displaced (this cost may be related to the probability of displacement over less-suitable foraging areas, such as the sea or unproductive habitat), the energy consumption, E, for the nocturnal flight, including the extra cost associated with displacement, becomes (for the case where wind speed exceeds the bird's airspeed)

$$E = P(V_1)t_1 + k(W - V_1)t_1, \tag{5}$$

where $P(V_1)$ is power at the swift's nocturnal airspeed (V_1), t_1 is nocturnal-flight time and $(W - V_1)t_1$ is displacement distance, with wind speed, W, greater than V_1. This equation is analogous to equation (2) with modified assumptions about the costs associated with the homing flight. Solving for the optimal V_1 associated with the minimum E gives the condition

$$\frac{\mathrm{d}P(V_1)}{\mathrm{d}V_1} = k. \tag{6}$$

This means that the optimal airspeed exceeds V_{mp} to an increasing degree with increasing k (with $k = 0$, that is with no displacement costs, the optimal airspeed is V_{mp}). We speculate that the slight but significant increase in observed airspeed with increasing wind speed (figure 3*a* and table 1) is due to the existence of a small but significant distance-related cost factor for displacement as defined above.

The swifts' orientation into the wind seems to be effective at keeping the displacement within tolerable limits. For example, by heading straight into a wind of $15\,\mathrm{m\,s^{-1}}$ with an airspeed of $9\,\mathrm{m\,s^{-1}}$, the resulting ground speed for the backward displacement is $6\,\mathrm{m\,s^{-1}}$. This corresponds to a displacement distance of 108 km during a 5 h nocturnal flight. If the swifts failed to orientate relative to the wind, their average ground speeds would be at least $15\,\mathrm{m\,s^{-1}}$, up to $24\,\mathrm{m\,s^{-1}}$ for individuals flying with a tailwind. The latter would bring about a fourfold increase in the displacement distance (432 km over 5 h), compared to the head-wind orientation.

6. CONCLUSION

We conclude that swifts spending the night aloft show a consistent orientation into the wind, with angular concentration increasing with increasing wind speed. This is the behaviour predicted if they are assumed to minimize the wind displacement and energy expenditure associated with their nocturnal flights. However, they do not select altitudes with slow or moderate winds, nor do they increase flight speed in a distinct way when flying into stronger head winds, as predicted by the same assumptions. This paradox may be explained by the fact that wind displacement involves only a small (but significant) cost, much less than the transport cost of the compensatory homing flight. This means that the swifts' orientation behaviour keeps the displacement within tolerable limits, while the flight altitude may be determined by other factors (such as temperature) and the airspeed shows only a marginal increase in strong winds.

The nocturnal flights of swifts show a new and conspicuous feature not seen in migrating birds (when flight with tailwinds is preferred; Alerstam 1990) or in song flight (Hedenström & Alerstam 1996): the swifts are often flying 'backwards', heading straight into the wind but being overpowered by wind speeds exceeding their airspeed. The fact that they regularly spend nights aloft under such conditions, rather than using roosting sites on the ground (which is known to occur in the foliage of trees and on masts, especially among juvenile birds; Holmgren 1993), bears witness to their extraordinary qualifications for life in the wind.

We are grateful to C.-G. Carlsson and Ulf Olsson at Aerotech Telub for skilfully installing and adapting the radar, and to meteorologist Bertil Larsson for developing efficient software for the treatment of the radar data. Weather data were obtained from the Danish Meteorological Institute (radiosonde data from Copenhagen) and the Swedish Meteorological and Hydrological Institute. We are grateful for the valuable comments of two anonymous referees. This work was supported by grants from the Swedish Natural Science Research Council.

REFERENCES

Alerstam, T. 1990 *Bird migration*. Cambridge University Press.

Alerstam, T. 2000 Bird migration performance on the basis of flight mechanics and trigonometry. In *Biomechanics in animal behaviour* (ed. P. Domenici & R. W. Blake), pp. 105–124. Oxford, UK: Bios Scientific Publishers.

Batschelet, E. 1981 *Circular statistics in biology*. London: Academic Press.

Bruderer, B. & Weitnauer, E. 1972 Radarbeobachtungen über Zug und Nachtflüge des Mauerseglers (*Apus apus*). *Rev. Suisse Zool.* **79**, 1190–1200.

Gustafson, T., Lindkvist, B., Gotborn, L. & Gyllin, R. 1977 Altitudes and flight times for swifts *Apus apus*. *Ornis Scand.* **8**, 87–95.

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.

Hedenström, A. & Alerstam, T. 1995 Optimal flight speed of birds. *Phil. Trans. R. Soc. Lond.* B **348**, 471–487.

Hedenström, A. & Alerstam, T. 1996 Skylark optimal flight speeds for flying nowhere and somewhere. *Behav. Ecol.* **7**, 121–126.

Holmgren, J. 1993 Young common swifts roosting in foliage of trees. *Br. Birds* **86**, 358–369.

Koskimies, J. 1950 The life of the swift, *Micropus apus*, in relation to the weather. *Annls Acad. Sci. Fenn.* A **IV**(**15**), 1–152.

Kvist, A., Klaassen, M. & Lindström, Å. 1998 Energy expenditure in relation to flight speed: what is the power of mass loss estimates? *J. Avian Biol.* **29**, 485–498.

Lack, D. 1956 *Swifts in a tower*. London: Methuen.

Liechti, F., Hedenström, A. & Alerstam, T. 1994 Effects of sidewinds on optimal flight speed of birds. *J. Theor. Biol.* **170**, 219–225.

Oehme, H. 1968 Der Flug des Mauerseglers (*Apus apus*). *Biol. Zentralblatt* **87**, 287–311.

Pennycuick, C. J. 1969 The mechanics of bird migration. *Ibis* **111**, 525–556.

Pennycuick, C. J. 1975 Mechanics of flight. In *Avian biology*, vol. 5 (ed. D. S. Farner & J. R. King), pp. 1–75. New York: Academic Press.

Pennycuick, C. J. 1989 *Bird flight performance: a practical calculation manual*. Oxford University Press.

Pennycuick, C. J. 1999 *Measuring birds' wings for flight performance calculations*, 2nd edn. Bristol, UK: Boundary Layer Publications.

Rayner, J. M. V. 1979 A new approach to animal flight mechanics. *J. Exp. Biol.* **80**, 17–54.

Rayner, J. M. V. 1999 Estimating power curves of flying vertebrates. *J. Exp. Biol.* **202**, 3449–3461.

Tucker, V. A. 1973 Bird metabolism during flight: evaluation of a theory. *J. Exp. Biol.* **58**, 689–709.

Weitnauer, E. 1952 Übernachtet der Mauersegler, *Apus apus*, in der Luft? *Der Ornithologische Beobachter* **49**, 37–44.

Weitnauer, E. 1954 Weiterer Beitrag zur Frage des Nächtigens beim Mauersegler, *Apus apus*. *Der Ornithologische Beobachter* **51**, 66–71.

Weitnauer, E. 1960 Über die Nachtflüge des Mauerseglers, *Apus apus*. *Der Ornithologische Beobachter* **57**, 133–141.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.