FLEXIBILITY IN FLIGHT BEHAVIOUR OF BARN SWALLOWS (*HIRUNDO RUSTICA*) AND HOUSE MARTINS (*DELICHON URBICA*) TESTED IN A WIND TUNNEL

LUKAS BRUDERER, FELIX LIECHTI* AND DIETRICH BILO

Swiss Ornithological Institute, CH-6204 Sempach, Switzerland and *University of the Saarland, D-66123 Saarbrücken, Germany*

*Author for correspondence (e-mail: felix.liechti@vogelwarte.ch)

Summary

The flight behaviour of barn swallows (*Hirundo rustica*) and house martins (*Delichon urbica*) was tested in a wind tunnel at 15 combinations of flight angles and speeds. In contrast to that of most other small passerines, the intermittent flight of hirundines rarely consists of regular patterns of flapping and rest phases. To vary mechanical power output, both species used intermittent flight, controlling the number of single, pulse-like wingbeats per unit time. House martins in descent tended to concentrate their wingbeats into bursts and performed true gliding flight during rest phases. Barn swallows mainly performed partial bounds during brief interruptions of upstrokes, which they progressively prolonged with decreasing flight angle. Thus, identification of distinct flapping phases to calculate wingbeat frequencies was not feasible. Instead, an effective wingbeat frequency for flight intervals of $20\,\mathrm{s}$, including partial bounds, was introduced. The effective wingbeat frequencies of house martins ($N=3$) ranged from 2 to $10.5\,\mathrm{s}^{-1}$, those of barn swallows ($N=4$) from 2.5 to $8.5\,\mathrm{s}^{-1}$. In both hirundine species, effective wingbeat frequency was found to decrease almost linearly with decreasing flight angle. With changes in air speed, wingbeat frequency varied according to a U-shaped curve, suggesting a minimum power speed of roughly $9\,\mathrm{m}\,\mathrm{s}^{-1}$. The duration of the down- and upstrokes varied systematically depending on flight angle and air speed.

Key words: barn swallow, *Hirundo rustica*, house martin, *Delichon urbica*, intermittent flight, partial bounding, wind tunnel, flight energetics, minimum power speed.

Introduction

Pennycuick (Pennycuick, 1990; Pennycuick, 1996) proposed that, like a pendulum, a bird in level flapping flight has a natural wingbeat frequency that is to a large extent determined by its body mass, wing morphology and the ultrastructure of its muscles, but can vary slightly depending on air density and gravity. On the basis of this 'concept of a natural wingbeat frequency', models were developed to predict wingbeat frequencies for a species whose mass, wingspan and wing area were known. If such a natural frequency exists, the general expectation would be for a bird to select a wingbeat frequency close to this value as often as possible (Pennycuick, 1996). In what has become known as the 'muscle efficiency hypothesis', Rayner (Rayner, 1977; Rayner, 1985) and Goldspink (Goldspink, 1977) pointed out that vertebrate muscle fibres contract most efficiently only over a narrow range of contraction speeds. Rayner argued that birds are subject to strong constraints to minimise body mass, and that they may therefore be unable to transport muscles comprising a sufficient variety of fibres for various flapping speeds. This homogeneity in the ultrastructure of flight muscles and the need to maintain efficiency were suggested to constrain small birds to flap their wings at fixed speeds (Rayner, 1985). To vary mean power output, they should use the optimal wingbeat frequency intermittently and control the relative duration of flapping phases. The different power requirements of climbing, horizontal flight and descent, etc., could then be met without major changes in wingbeat frequency (Rayner, 1985).

On long-distance flights, e.g. migration, the majority of small birds use intermittent flight styles, characterised by regularly alternating phases of flapping and resting (Bruderer and Steidinger, 1972; Emlen, 1974; Bloch et al., 1981). In contrast, flapping flight in hirundines is characterised by a high degree of flexibility, with no obvious regularity in the timing of wingbeats. These aerial insectivores spend a large part of their lives in flight, hunting or on migration. Barn swallows and house martins thus share a common need for economic flight performance and maintenance of sufficient manoeuvrability for hunting. Indirect measurements of flight costs in free-living birds using the doubly labelled water technique (Bryant and Westerterp, 1980; Bryant and Westerterp, 1983; Hails, 1979) showed that the flight costs of hirundines are 50–70 % lower than those of other birds of similar size (Hails, 1979). Thus, this wind tunnel study was designed to investigate how hirundines apply intermittent flight as a flexible means to adjust mechanical power output to different flight situations. The consequences of this flexibility

are discussed with respect to theoretical predictions on the flight of small birds. The wind tunnel experiments were designed to obtain data on the temporal distribution of wingbeats (wingbeat patterns) of known individuals under controlled flight conditions, allowing a comparison with similar data (to be presented elsewhere) on hirundines in free flight, tracked by radar.

Materials and methods

The wind tunnel used for this study at the University of Saarbrücken is a closed-circuit variable-speed wind tunnel designed to accommodate living birds in flight (for technical details, see Biesel, 1983; Biesel et al., 1985). The flight chamber (1 m×0.9 m×0.9 m), attached to a contraction section, can be tilted as a unit to simulate climbing or sinking flight for the birds. Experimental air speeds of approximately $5–14\,\mathrm{m\,s^{-1}}$ can be produced; airspeed was measured using a hot-wire anemometer (TSI, model 8460, range $0–20\,\mathrm{m\,s^{-1}}$) placed at one of the downstream corners of the flight cage, approximately 25 cm away from the corner. Air speed measurements during flight experiments had to be a trade-off between accuracy and obstruction of the flying birds. Preliminary measurements showed that air speeds at the anemometer site during experiments were between 2 % (low speeds) and 4 % (high speeds) lower than those in the central parts of the flight chamber. The actual test speeds during experiments were $5.11\,\mathrm{m\,s^{-1}}$ instead of $5\,\mathrm{m\,s^{-1}}$, $8.21\,\mathrm{m\,s^{-1}}$ instead of $8\,\mathrm{m\,s^{-1}}$, $10.23\,\mathrm{m\,s^{-1}}$ and $12.49\,\mathrm{m\,s^{-1}}$. The turbulence-level T [$=100$(standard deviation of instantaneous air speed)/(mean air speed)] was assessed using a very fast response tungsten hot-wire anemometer (DISA 55D05 and DISA 55D15, upper cut-off frequency at $-3\,\mathrm{dB}$ $>10\,\mathrm{kHz}$). Mean T was approximately 2 % for air-speed fluctuations of $0.5–1000\,\mathrm{Hz}$ and air speeds of $0–14\,\mathrm{m\,s^{-1}}$ (Möller, 1998).

Eight barn swallows and five house martins were hand-reared in summer 1998 and slowly accustomed to feed, by themselves, on minced meat, mealworms, flies and dry food for insectivores. We planned to use four barn swallows (two juveniles, two adults), trapped at a roosting site, as control group. Since they did not learn to feed by themselves and force feeding was not practicable in the long term, they had to be released. All data presented here originate from birds that had learned to fly in closed rooms and in an open-air aviary of $20\,\mathrm{m^3}$. Four barn swallows and three house martins showing spontaneous, relatively calm flight in the wind tunnel were trained to fly at several speeds and angles for roughly 1 h daily over a period of 3 weeks. Morphological data for these birds are given in Table 1. Wing areas, including the area of the body between the wings, were determined by taking photographs of the awake birds, projecting these onto paper and using an area curvimeter (x-plan 360i) to measure wing area. For photography, the birds were restrained, and the wings were kept fully spread by an assistant. Since all test birds were juveniles, their wing spans were still somewhat small compared with values in the literature of 26–29 cm for house martins and 32–34.5 cm for barn swallows (Cramp, 1985/88). Body masses were well within the given ranges of 14–20 g (mean 17 g) for house martins and 17–25 g (mean 19 g) for barn swallows (Glutz von Blotzheim and Bauer, 1985/88).

The flight performance of the seven test birds was investigated at all combinations of four flight speeds (5.1, 8.2, 10.2 and $12.5\,\mathrm{m\,s^{-1}}$) and four flight angles ($+5\,°$, $0\,°$, $-5\,°$ and $-10\,°$) except for climbing flight ($+5\,°$) at $12.5\,\mathrm{m\,s^{-1}}$. Experiments started with climbing flight, continued with horizontal flight and ended with descent. Within a flight angle, flight speed was increased in a stepwise fashion. Test birds adjusted their flight behaviour to new flight conditions within seconds and did not need a settling period. To avoid unnecessary tiring of a bird, it was tested under all flight conditions in rapid succession, the entire series taking approximately 30 min. The physiology of hirundines is designed to allow non-stop flights of several hours; the test birds had enough practice to accomplish 30 min flights without problems. Lateral and ventral views of the flying birds were recorded using two digital video cameras (Sony DCR-VX1000); the ventral view was recorded *via* a mirror placed below the flight chamber at an angle of 45 °. During the experiments, each bird was filmed for 80 s at $50\,\mathrm{frames\,s^{-1}}$ at each speed/angle combination. From these 80 s, 20 s was selected that contained no unusual flight manoeuvres or mechanical obstruction of the birds by the boundaries of the flight chamber.

For a quantitative analysis, the complex patterns of wing movements in space and time needed to be reduced to the up and down movement of one wing-tip relative to a bird-fixed

Table 1. *Morphological variables for the birds used in the wind tunnel*

Species	Bird no.	Body mass (kg)	Wing span (m)	Wing area (m²)	Aspect ratio	Wing loading (N m⁻²)
Delichon urbica	2	0.0165	0.240	0.0088	6.55	18.8
	3	0.0175	0.250	0.0102	6.13	17.2
	4	0.0180	0.258	0.0100	6.66	18
Mean		0.0173	0.250	0.0097	6.45	17.8
Hirundo rustica	5	0.0205	0.284	0.0128	6.30	15.6
	6	0.0190	0.274	0.0123	6.10	15.4
	7	0.0200	0.274	0.0123	6.10	16.3
	8	0.0220	0.276	0.0125	6.09	17.6
Mean		0.0204	0.277	0.0125	6.15	16.3

frame of reference. Selected lateral-view film sequences were transmitted to a computer by means of custom-made software. For each frame, three anatomical landmarks on the bird ('beak-tip', 'tail-tip' and 'right wing-tip') were digitised in a camera-fixed, orthogonal coordinate system (X,Y,Z; X axis parallel to air flow, forward/backward bird movements; Y axis, bird movements towards/away from the lateral camera, Z axis, altitude, bird movements up/down). To correct for the bird's movements in the X,Z plane, a new, bird-fixed frame of reference (x,y) was constructed. The x axis was defined by the landmarks 'beak-tip' and 'tail-tip', with the origin positioned half-way between them; the y axis was perpendicular to the x axis. Frame by frame, a coordinate transformation was applied to the landmark 'right wing-tip', allowing the instantaneous position of the right wing-tip to be determined for each frame relative to the bird's longitudinal (x) and dorsoventral (y) axes. The wingbeat pattern was defined as the change in the y coordinate with time (y/t plot) of the right wing-tip relative to the bird's body axis. Since lateral recordings do not allow correction for the bird's movements along the Y-axis in space (depth of the flight chamber) and ventral video recordings would not allow correction for rolling, only the relative changes in amplitude between different flight conditions can be discussed. Even a three-dimensional analysis would not allow us to calculate absolute values of wingbeat amplitude, since only one wing-tip was visible continuously in lateral view. Because of the construction of the wind tunnel, it was not possible to take pictures from behind or ahead for a three-dimensional analysis.

The y/t plots obtained from approximately 5–10 known positions of the right wing-tip per wingbeat did not necessarily include the upper and lower wing reversals. Therefore, the y/t curve between consecutive frames was interpolated by means of a cubic spline function (e.g. Press et al., 1996). This allowed the original y/t plots to be adapted to approximate the actual reversal points of the wing-tip. The number of wing-tip coordinates obtained by recording at 50 frames s^{-1} could therefore be increased to 500 scan points s^{-1}. Provided that the interpolation is correct, the timing of wing-tip reversal can be determined with an accuracy of ±0.002 s. To facilitate determination of the wing-tip reversal points, y/t plots were filtered by means of a finite input response (FIR) digital bandpass (Barr and Chan, 1986), which eliminated frequencies below 4 Hz and above 18 Hz.

Wingbeat frequency is usually determined as the number of flapping cycles per second for phases of continuous flapping. Unless in steady climbing flight, hirundines rarely flap their wings continuously, nor do they show regular patterns of flapping and rest phases, as do most other small passerines (see Fig. 1). Even during climbing flight, irregular short pauses were observed. The duration of a flapping cycle ($\Delta t_{\text{wingbeat}}$) was highly variable in both species, which makes the application of a Fast Fourier analysis, designed to determine frequencies of harmonic oscillations, inadvisable. For barn swallows, it was not even possible to define flapping and pause phases clearly (see Fig. 1B). Therefore, to analyse wingbeat patterns representing non-harmonic oscillations, a method was needed that not only considers flapping phases, but also includes rest phases. To avoid confusion with wingbeat frequencies calculated for flapping phases only, frequencies determined in this manner are termed effective wingbeat frequencies (F_{eff}). A bird's effective wingbeat frequency was defined as its mean number of wingbeats per second, averaged across a 20 s interval, $F_{\text{eff}}=[\text{mean}(\Delta t_{\text{wingbeat}})]^{-1}$. In addition, the durations of the down- and upstrokes were determined. The upper and lower wing reversals were identified for consecutive wingbeats, thereby separating the downstrokes from the intervening intervals comprising the upstroke and potential rest phases. Samples of 30 wingbeats per bird of horizontal flight at all four flight speeds and of flights at 10.2 m s^{-1} at all four angles were analysed.

As noted above, we cannot measure absolute wingbeat amplitudes from our video recordings. However, reasonable estimates of the relative amplitudes can be obtained by taking the mean amplitude recorded by the side-view camera. These recorded amplitudes will be larger when the bird is flying close to the side-view camera and smaller when it is further away. However, the birds did not fly close to one wall of the flight chamber under one flight condition and close to the wall in another, but moved rather erratically from side to side during each recording. Even if these side-to-side motions occurred more frequently under one flight condition, this would mainly affect the variability of the amplitude estimates while not altering the mean values. Similarly, rolling effects would primarily affect the variability of the measurements rather than the mean values, since rolling must be balanced to avoid collisions with the walls of the wind tunnel. Mean wingbeat amplitude was calculated from 50 (descent) to 200 (climbing flight) wingbeats per bird and flight condition, so we believe the relative comparisons to be fairly reliable.

A variance components analysis for unbalanced designs (residual maximum likelihood, REML, Software package Genstat 5.0; Patterson and Thompsen, 1971; Robinson et al., 1982; Dempster et al., 1984) was used to identify variables significantly affecting the duration of the up- and downstroke, effective wingbeat frequency and estimated wingbeat amplitude. This type of linear mixed model allows the separation of fixed effects, which are of predictive interest, from random effects, which are responsible for additional variance. The effects of flight angle, speed and differences between the two species were of interest, but not the variance among individuals within species per flight condition.

Results

In contrast to larger birds used for wind tunnel studies (e.g. starlings, pigeons), the flight of hirundines is very agile. The flying position within the flight chamber varied greatly in all test birds, with a tendency to drift backwards slightly at higher air speeds. Apart from this, no general pattern was observed; every bird developed its own slightly different way of coping with a given combination of air speed and flight angle in the wind tunnel.
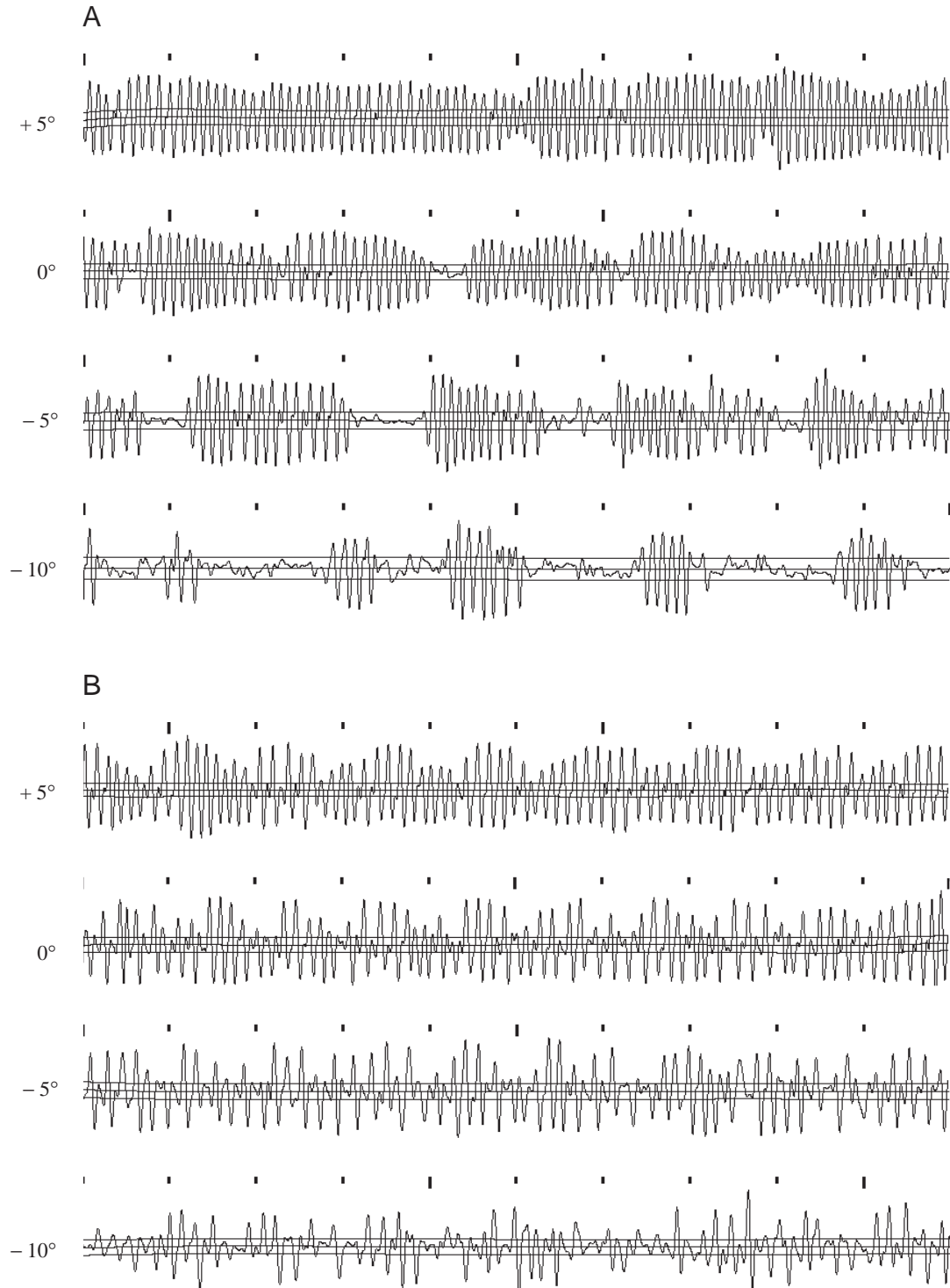
A

B

Fig. 1. Representative 10 s intervals of wingbeat patterns of a house martin (A) and a barn swallow (B) during climbing (+5 °), horizontal flight (0 °) and descent (−5 ° and −10 °). Small vertical bars above patterns indicate 1 s intervals, and longer bars indicate 5 s intervals. The traces represent the change in the y coordinate over time (y/t plot), i.e. the lateral view of the movement of the bird's right wing-tip with respect to the bird's body axis. The three horizontal lines are the baseline (approximate bird midline) and the two threshold levels necessary for the semi-automatic determination of extrema.

Flapping cycles

During climbing flight, hirundines performed continuous flapping flight; one wingbeat following the next with little or no delay (Fig. 1). With decreasing flight angle, the number of wingbeats within a 20 s period declined and the flapping cycle duration increased accordingly. During descent, house martins
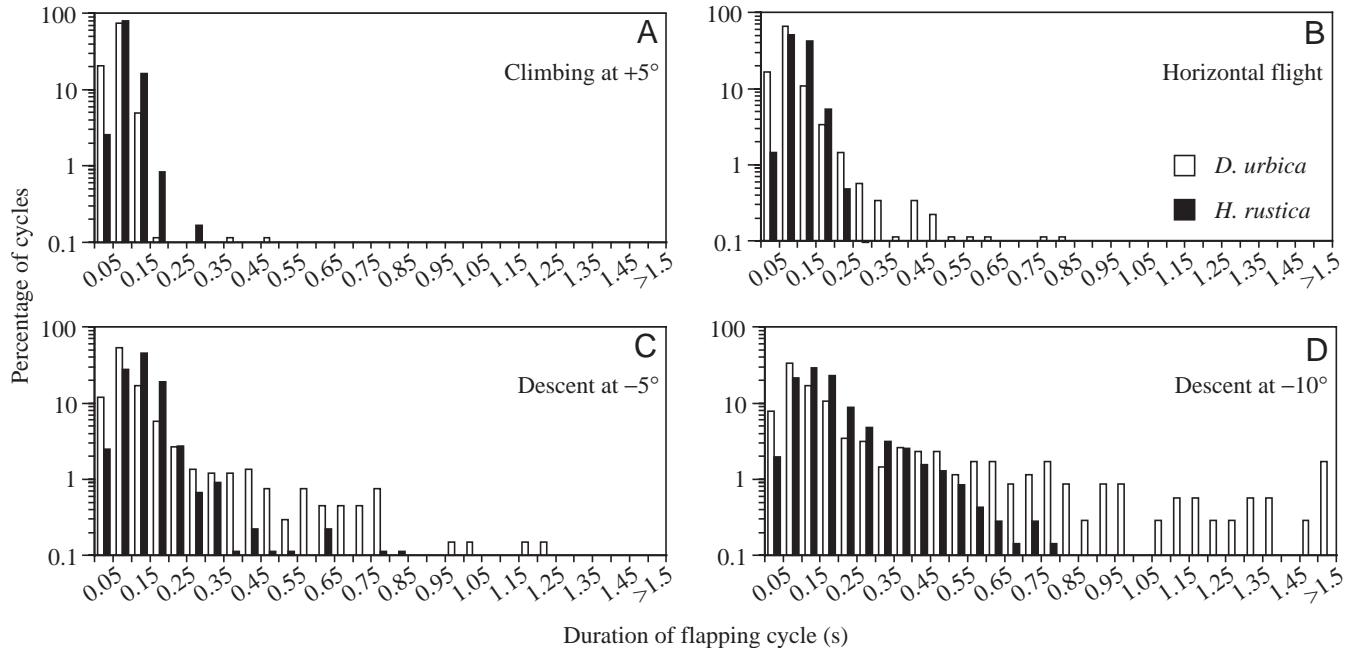
Fig. 2. Frequency distribution for the duration of flapping cycles of house martins (open columns, *N*=3) and barn swallows (filled columns, *N*=4) during climbing flight (A), horizontal flight (B), descent at −5 ° (C) and descent at −10 ° (D). Measurements at flight speeds of 8.2 and 10.2 m s^{-1} were combined for this figure. The logarithmic vertical scale was chosen to emphasise differences in the number of long-duration flapping cycles between the two species during descent.

tended to concentrate wingbeats into bursts interspersed with rest phases, whereas barn swallows evenly increased the intervals between single flaps (Fig. 1, 2). Differences in the frequency of the flapping cycle distributions were not investigated statistically, since consecutive flapping cycles of an individual bird are not independent. The mode for house martins is at a shorter flapping cycle duration than for barn swallows in climbing flight, horizontal flight and descent. During flight at negative angles, only house martins have flapping cycles longer than approximately 0.8 s.

A flapping cycle consists of a down- and an upstroke; in addition, most upstrokes include a rest phase of variable duration. The proportion of the flapping cycle made up by the upstroke (including the optional rest phase) increased from 63 % for climbing flight to 75 % for descent at −10 ° in house martins and from 68 to 79 %, respectively, in barn swallows. Upstroke duration differed significantly between the two species and changed significantly with flight speed as well as with flight angle (REML, multiple variance component analysis; all *P*<0.001); flight angle explained the greatest share of the measured variance (Fig. 3). Compared with the upstroke, the variability in the downstroke duration was very small. However, downstroke duration differed significantly between the two species and varied with flight speed and flight angle (REML; *P*$_{species}$=0.003, other *P*<0.001; Fig. 4). Downstroke duration increased by approximately 10 % between climbing at +5 ° and descent at −10 ° in house martins and by 20 % in barn swallows. It decreased between flight speeds of 5.1 and 12.5 m s^{-1} by approximately 7.5 % and 15 %, respectively. Although there is some variation in downstroke duration, we

can still conclude that the high variability in the duration of flapping cycles is mainly due to the variation in upstroke duration.

Estimated mean wingbeat amplitude declined significantly with flight angle (*P*<0.001) and also varied with flight speed (no significant trend) (Fig. 5). Values were largest during climbing flight at +5 ° and decreased with declining flight angle by approximately 40 % (range 30–50 %) in house martins and 50 % (range 30–70 %) in barn swallows. This result was consistent for both species and every individual. Barn swallows tended to vary the estimated amplitude with flight speed according to a U-shaped curve (not significant); however, there was no such trend in house martins.

Effective wingbeat frequency

Mean *F*$_{eff}$ of house martins varied between 2 and 10.5 Hz; that of barn swallows between 2.5 and 8.5 Hz. *F*$_{eff}$ averaged across all tested flight conditions was 6.2 Hz for house martins and 6.1 Hz for barn swallows. Fig. 6 illustrates three points using representative data for two birds from each species: (i) that variance among measurements for consecutive 5 s intervals for a single bird is generally small, although considerable for descent of house martins; (ii) that, within individuals, *F*$_{eff}$ generally differed more among flight conditions than among consecutive measurements within conditions; and (iii) that, even at the level of individual birds, *F*$_{eff}$ consistently followed a U-shaped curve with air speed; values were shifted towards a lower *F*$_{eff}$ at negative flight angles. *F*$_{eff}$ was therefore averaged for each species and flight condition (Fig. 7). *F*$_{eff}$ was highest during climbing at low
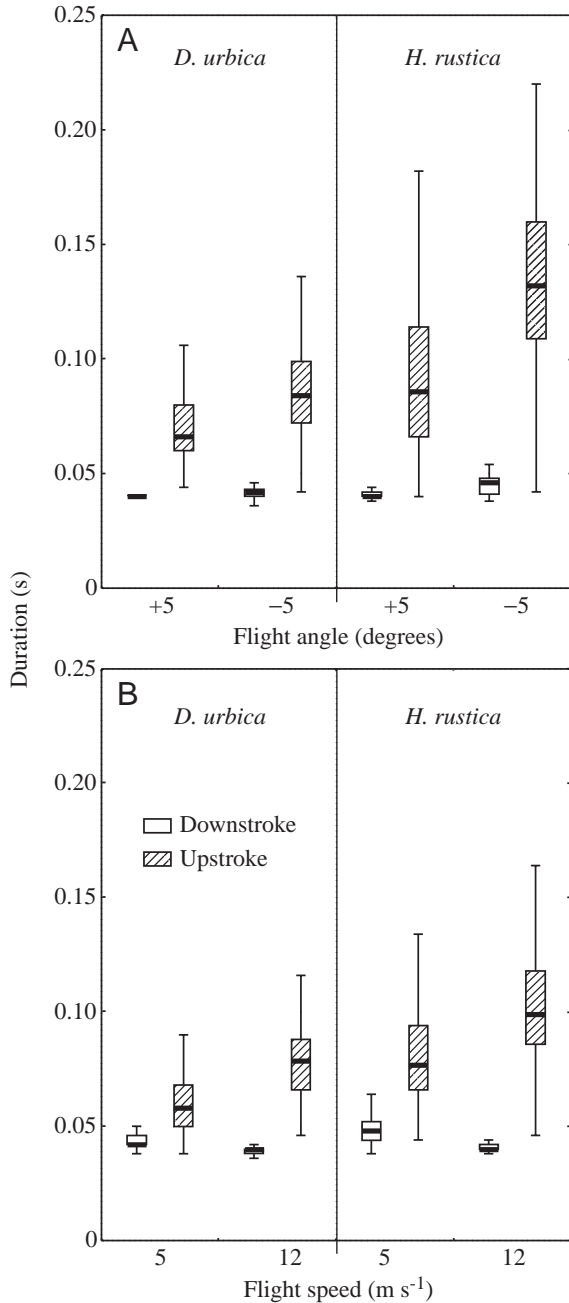
Fig. 3. Duration of down- and upstrokes in hirundines. Comparison between climbing and descent (A) and between slow and fast flight (B). Error bars show the non-outlier minimum/maximum, boxes show the second to third quartile range and the median (bar). Stroke durations were measured from 30 wingbeats per bird for each speed during horizontal flight and each angle during flight at $10.2\,\mathrm{m\,s^{-1}}$. Upstrokes with rest phases longer than $0.5\,\mathrm{s}$ were not included in the analysis.
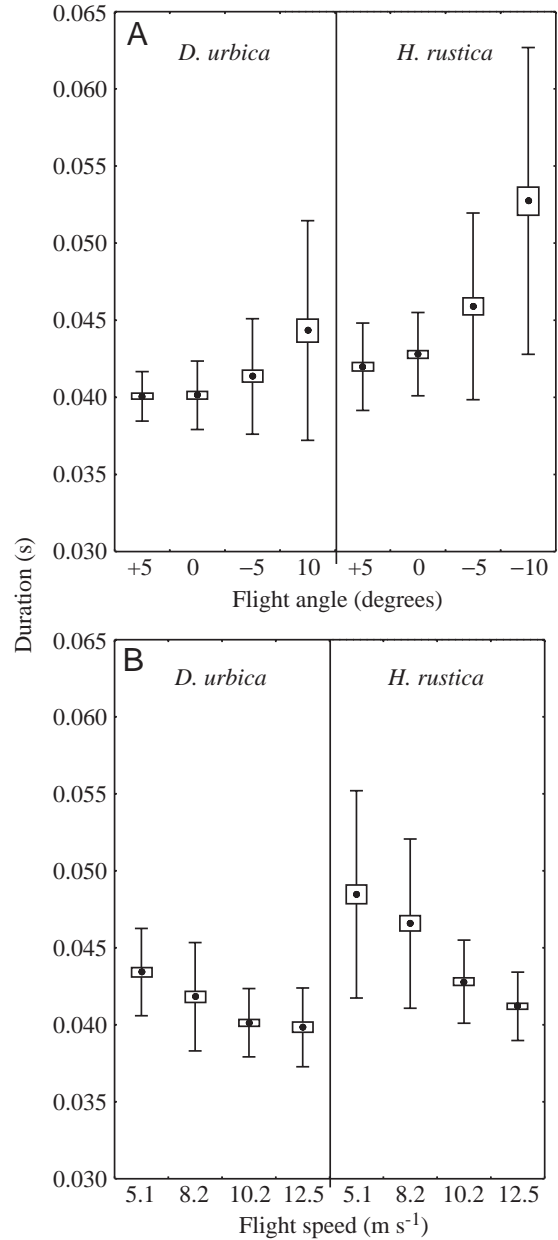

Fig. 4. Downstroke duration in hirundines, plotted against flight angle (A) and flight speed (B). The mean (filled circle), S.E.M. (box) and S.D. (bars) are plotted; for sample sizes, see Fig. 3.

speeds (house martin $9.9\,\mathrm{Hz}$, barn swallow $8.0\,\mathrm{Hz}$) and lowest during descent at $-10°$ at intermediate speeds. In response to increasing air speed at a constant flight angle, mean F_{eff} followed a U-shaped curve with a minimum at approximately $9\,\mathrm{m\,s^{-1}}$. In both species, the curves were shifted towards lower F_{eff} as flight angle decreased from climbing to descent.

The linear mixed model (REML; Genstat 5.0) for F_{eff} was developed by first assigning variance among individuals within species (per flight condition) to the random model. The fixed model was then designed by investigating the significance of the variables species, flight angle, flight speed and the squares and cubes of the latter two, as well as all interactions (see global model, Table 2). Step by step, those factors with little effect on F_{eff} were eliminated from the global model. A model including only significant terms plus the terms of the random model (the reduced model) resulted in a very high correlation between fitted and observed values ($r^2=0.97$). For the fixed model alone (see equation below), which was used to derive
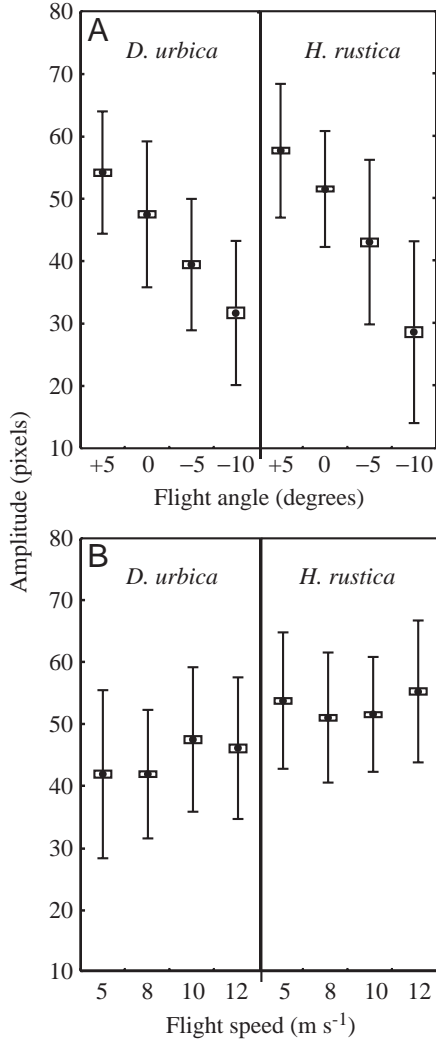
Fig. 5. Mean relative wingbeat amplitude for the downstroke, plotted against flight angle (A) and flight speed (B). The y axis scale is relative, based on differences in the numbers of pixels on the computer screen. The mean (filled circle), S.E.M. (box) and S.D. (bars) are plotted. Depending on the individual bird and the flight condition, the sample sizes varied from approximately 50 downstrokes (birds in descent) to 200 downstrokes (birds in climbing flight).

the F_{eff} curves in Fig. 7, the correlation was $r^2=0.87$. The most important variables explaining the variability in F_{eff} were flight angle and the square of air speed (see Table 2 Wald statistic). Thus, the approximately linear decrease in F_{eff} with decreasing flight angle and the U-shaped curve with respect to air speed discussed above were confirmed statistically. The reduction in F_{eff} with decreasing flight angle was greater in house martins than in barn swallows, hence the significance of the interaction term species × angle (Table 2). In contrast to the global model, the interaction term species × (speed)^2 was no longer significant in the reduced model; nevertheless, it was maintained in the final model because this allows differently shaped parabolas for the two species, which makes sense biologically. The effect of this variable on the explanatory

Table 2. *Results of residual maximum likelihood variance components (REML) analysis modelling effective wingbeat frequency with respect to species, flight angle and air speed*

Variables	Wald statistic			P		
	Global model	Reduced model	d.f.	Global model	Reduced model	
Species	1.5	1.4	1	0.2207	0.2367	
Angle	**540.0**	**575.2**	**1**	**<0.0001**	**<0.0001**	
Speed	**7.6**	**6.0**	**1**	**0.0058**	**0.0143**	
Angle × speed	2.7	–	1	0.4028	–	
Species × angle	**44.6**	**46.7**	**1**	**0.0001**	**<0.0001**	
Species × speed	0.7	–	1	0.1003	–	
(Angle)^2	**4.6**	**5.9**	**1**	**0.0320**	**0.0151**	
(Speed)^2	**30.5**	**22.6**	**1**	**<0.0001**	**<0.0001**	
(Angle)^2 × (speed)^2	1.7	–	1	0.1923	–	
Species × (angle)^2	1.8	–	1	0.1797	–	
Species × (speed)^2	**5.5**	**0.2**	**1**	**0.0190**	**0.6547**	
(Angle)^3	0	–	1	>0.9999	–	
(Speed)^3	0.4	–	1	0.5271	–	
(Angle)^3 × (speed)^3	0.2	–	1	0.6547	–	
Species × (speed)^3	0	–	1	>0.9999	–	
Species × (angle)^3	0	–	1	>0.9999	–	

Significant factors of the global and reduced models are given in bold type.

value of the model was small. The equation for the final model derived from the REML analysis was:

$$F_{eff} = \begin{pmatrix} H & 0 \\ \frac{}{B} & -1.05 \end{pmatrix} A \times 0.32 + A \times \begin{pmatrix} H & 0 \\ \frac{}{B} & -0.15 \end{pmatrix}$$
$$+ S \times (-1.23) + S^2 \times 0.065 + S^2 \begin{pmatrix} H & 0 \\ \frac{}{B} & 0.0016 \end{pmatrix}, \quad (1)$$

where A is angle, S is speed, H is house martin and B is barn swallow.

Discussion

Hirundines are coursing aerial insectivores (Blake, 1948) for which economic flight performance and the maintenance of manoeuvrability are essential (Warrick, 1998). They are among the few small birds that manage to migrate for long distances during the day in spite of turbulent air. Hirundines achieve their outstanding agility in flight by demonstrating a high degree of flexibility in such variables as the mean number of wingbeats per second (F_{eff}) and the duration of the down- and upstrokes. This flexibility appears to be used to control the mechanical power output during flight at different angles and speeds.

Pennycuick (Pennycuick, 1990; Pennycuick, 1996) presented a model for the prediction of wingbeat frequencies of birds during level cruising flight. Wingbeat frequencies f for the hirundines tested in this study were predicted by inserting the morphological data given in Table 1 into the equation:

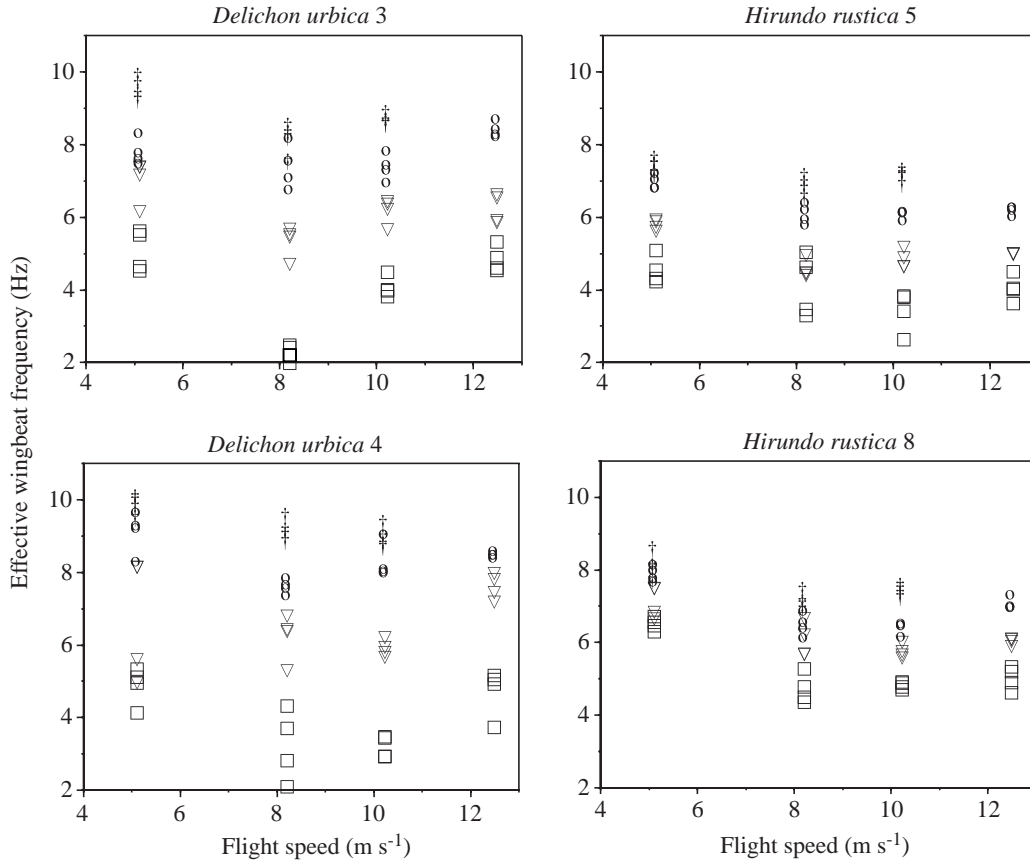$$f = m^{3/8} g^{1/2} b^{-23/24} S^{-1/3} \rho^{-3/8} \quad (2)$$

Fig. 6. Effective wingbeat frequencies (F_{eff}) of two individuals of each species plotted against flight speed. F_{eff} was calculated for four successive 5 s intervals per bird and flight condition. Plus signs indicate climbing flight, open circles horizontal flight, open triangles descent at −5° and open squares descent at −10°.
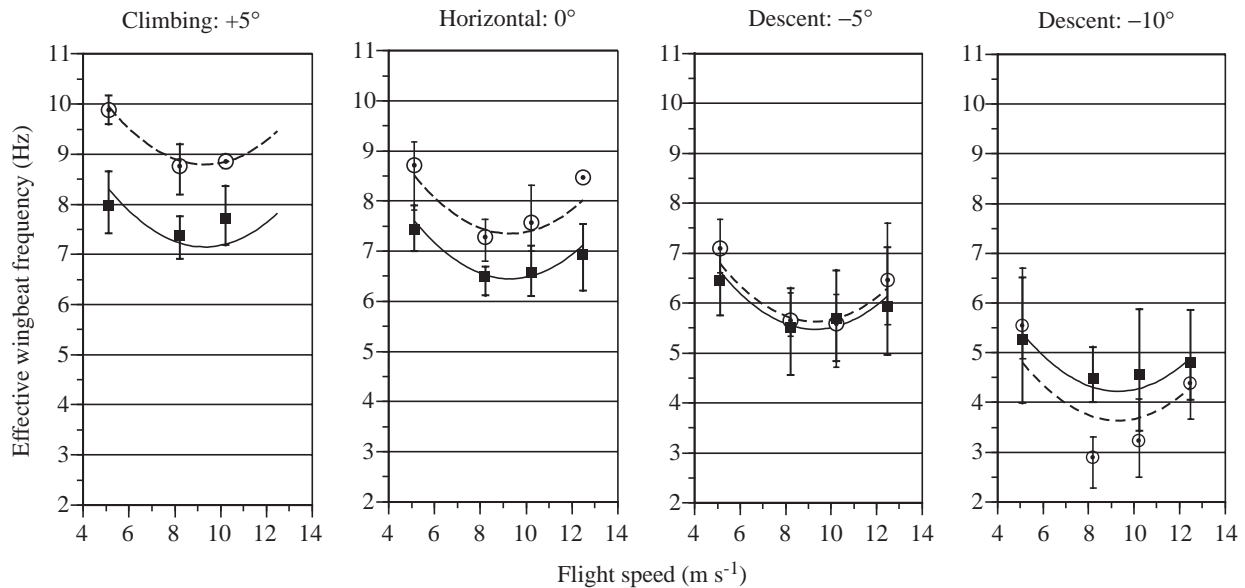

Fig. 7. Mean effective wingbeat frequency (F_{eff}) of house martins ($N=3$) and barn swallows ($N=4$) *versus* flight speed plotted separately for each flight angle. Open symbols indicate house martins, filled symbols barn swallows; error bars show the range of mean F_{eff} for all individuals. The fitted curves were calculated according to equation 1; broken lines are for house martins and solid lines are for barn swallows.

(Pennycuick, 1996), where m is body mass, $\mathbf{g}$ is the acceleration due to gravity (9.81 m s^{-2}), b is wing span, S is wing area and ρ is air density. For our experiments at Saarbrücken, air density was taken as 1.205 kg m^{-3} (at sea level, $\rho=1.23$ kg m^{-3}). In level flight, hirundines used an intermittent wingbeat pattern and had mean effective wingbeat frequencies of 7.9 Hz (house martins) and 6.9 Hz (barn swallows), approximately 30–35 % below the predicted frequencies of 11.3 Hz for house martins and 10.0 Hz for barn swallows. Since the model of Pennycuick (Pennycuick, 1996) predicts wingbeat frequencies for flapping phases only, it is more appropriate to compare predictions with frequencies observed during continuous flapping flight of hirundines, such as during climbing flight. However, the effective frequencies measured during climbing flight (9.2 Hz for house martin; 7.7 Hz for barn swallow) were still approximately 20 % lower than predicted values for level flight. However, the minimum durations recorded for single downstrokes gave frequencies of approximately 13 Hz for both species (13.6 Hz for house martins; 13.2 Hz for barn swallows).

The house martins and barn swallows tested in our experiments were juveniles with wingspans 10–15 % smaller than those of adults (Glutz von Blotzheim and Bauer, 1980/85; Cramp, 1985/88). The resulting somewhat higher wing loading of the hirundines tested here should have caused an increase in wingbeat frequency rather than a reduction. Warrick (Warrick, 1998) measured wingbeat frequencies of 14.0 Hz for barn swallows ($N=12$) during acceleration (5.5 m s^2), 9.9 Hz during prey capture and 8.2 Hz during coursing flight. During a tracking radar study on migrating hirundines, a mean effective wingbeat frequency of 5.1 Hz was measured for barn swallows in horizontal flight (L. Bruderer, unpublished data).

Although effective frequencies averaged across all tested flight conditions differ little between the two species, they are the result of differing flight behaviour. This is evident in the wingbeat patterns (Fig. 1) and in the frequency distributions for flapping cycle duration (Fig. 2). F_{eff} of hirundines was highest during slow flight; during climbing and horizontal flight, F_{eff} of house martins was at least 1 Hz greater than that of barn swallows. At low speeds, the lift required to support a bird's weight has to be produced by accelerating air downwards, implying considerable additional expense in induced drag (Pennycuick, 1968). The house martins tested here had a somewhat higher wing loading (17–19 N m^{-2}) than the barn swallows (16–18 N m^{-2}), which may explain the slightly higher F_{eff} during slow flight. Although more lift is produced by passive air currents around the wing profile with increasing air speed, compensation for increased parasite and profile drag (Rayner, 1999) requires birds to expend more power to generate thrust (Pennycuick, 1968; Rayner, 1985). This possibly explains why F_{eff} increased at high speeds in hirundines. According to Rayner (Rayner, 1985), mechanical power output is strongly correlated with the relative durations of the flapping and rest phases. Pennycuick et al. (Pennycuick et al., 1996) interpreted the minimum frequency speed found in wind tunnel experiments for a thrush nightingale (*Luscinia*

lusinia) and a teal (*Anas crecca*) as an experimental estimate of the minimum power speed. They reported continuous flapping flight in the teal and occasional, short wingbeat interruptions in the thrush nightingale. In a recent analysis of short continuous flapping phases in barn swallows flying in a wind tunnel, Pennycuick et al. (Pennycuick et al., 2000) also found short rest phases within the upstroke. For bird species regularly performing intermittent flight, especially if wingbeat patterns are non-harmonic, it is most appropriate to use effective wingbeat frequency to estimate mechanical power. We therefore interpret the curves obtained by plotting F_{eff} against air speed (Fig. 7) as representing the mechanical component of the U-shaped power curves (Pennycuick, 1969; Pennycuick, 1975; Pennycuick, 1989; Rayner, 1985; Rayner, 1990; Rayner, 1995). Our data therefore suggest a minimum power speed (v_{mp}) of 9 m s^{-1} for house martins and approximately 9.5 m s^{-1} for barn swallows. Estimates of minimum power speeds calculated according to Pennycuick (Pennycuick, 1996) and using the morphological variables presented in Table 1 vary between 7.3 and 7.6 m s^{-1} (mean 7.4 m s^{-1}). Even using the revised body drag coefficient C_{Db} of 0.1 (Pennycuick et al., 1996) rather than 0.4 (Pennycuick, 1990), which gives higher values of v_{mp} and the maximum range speed (v_{mr}), our empirical estimates are still high. For Pennycuick's (Pennycuick, 1996) predictions to match our empirical values, the body drag coefficient C_{Db} would need to be reduced to 0.04, a value 10 times smaller than the original value proposed. The mechanical power curve explicitly proposed by Rayner (Rayner, 1990) for a barn swallow shows even less correspondence with our data, since it predicts a v_{mp} of approximately 4.5 m s^{-1} and a v_{mr} of 6 m s^{-1} for an adult barn swallow.

Pennycuick (Pennycuick, 1996) states that a bird may vary its wingbeat frequency to some extent depending on whether it is climbing, descending or in level cruising flight. However, only a limited range of wingbeat frequencies are said to be available to a particular bird or species. Because of the homogeneity of fibres in the flight muscles of small birds and the need to maintain efficiency, Rayner (Rayner, 1985) predicted that the contraction speeds of flight muscles should be constant (muscle efficiency hypothesis). The hirundines tested in the present study reacted to changes in air speed and flight angle by adjusting the number of wingbeats per unit time, the duration of the up- and downstrokes and even estimated wingbeat amplitude. Downstroke duration was shortest during climbing and fast flight and longer at slow speeds and during descent. Contrary to expectations based on the concept of constant contraction speeds, estimated relative amplitude was large during climbing and decreased with declining flight angle. As expected as a result of the differences in wing spans, estimated mean wingbeat amplitude during horizontal flight was 10–20 % larger in barn swallows than in house martins. If amplitude were to remain constant, muscular contraction speed would need to vary by 10–20 % to account for the differences in downstroke duration; in fact, since amplitudes were largest when downstrokes were shortest, the variance will be even

larger. This provides strong evidence that contraction speeds are unlikely to be constant in hirundines. Similarly, Pennycuick et al. (Pennycuick et al., 2000) found an increase in the angular velocity of the humerus with increasing air speed of approximately 25 % (from 6 to 11 m s^{-1}) in barn swallows, while for starlings (*Sturnus vulgaris*), Tobalske (Tobalske, 1995) found a non-significant, slightly U-shaped variation in wingbeat amplitude with speed.

The following descriptions of the flight behaviour of barn swallows and house martins are based on direct observations during experiments and on the video recordings. They are presented as an interpretation of the present results since behaviour was not documented quantitatively.

Climbing hirundines showed continuous flapping flight; the durations of the down- and upstrokes were smaller and the resulting effective wingbeat frequencies were greater than during level and descending flight. The duration of a flapping cycle is probably minimised during climbing to allow

maximum lift production. The longest flapping cycles occurred during descent at 8.2–10.2 m s^{-1}; maximal values were 2.85 s for a house martin and 0.85 s for a barn swallow. Given a downstroke duration of 0.05 s (Fig. 4), these values give interrruptions of 2.8 and 0.8 s, respectively. Except during climbing, both species regularly interrupted their wingbeats during upstrokes (see Fig. 1), either with partial bounds (short interruptions) or with real glides (longer rest phases). In Fig. 8, frames taken from video recordings show how the wings were positioned during partial bounds, real glides and, for comparison, downstrokes. For barn swallows in horizontal flight, Warrick (Warrick, 1998) measured a mean duration of 0.015 s for such short wingbeat interruptions. Although our method did not allow direct measurement of wingbeat interruptions, the mean upstroke duration for barn swallows was 0.110 s during horizontal flight and 0.088 s during climbing at 10 m s^{-1}. The difference between these two values (0.022 s) gives an estimate of the duration of wingbeat
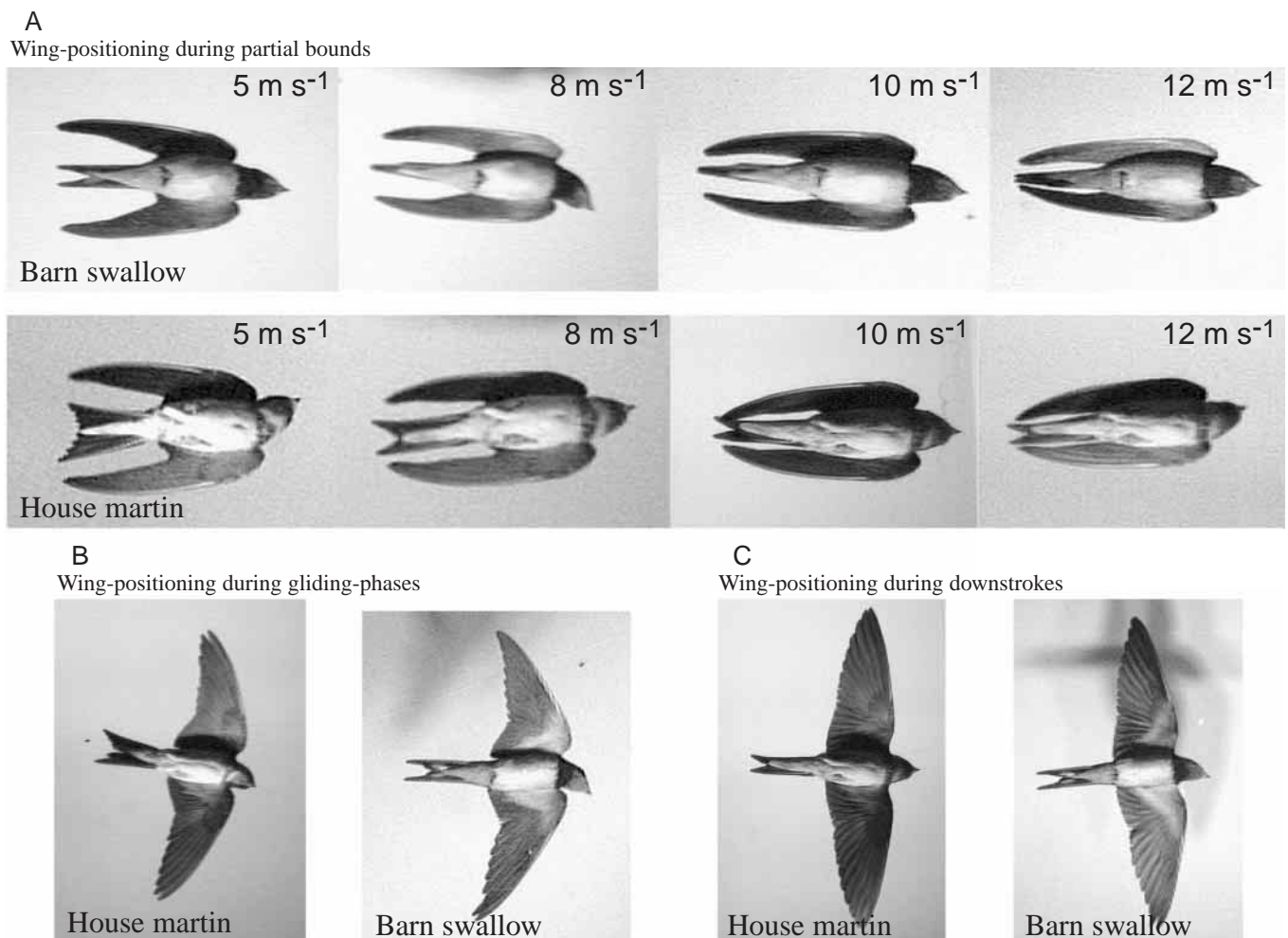

Fig. 8. Ventral views of house martins and barn swallows during horizontal flight in the wind tunnel. (A) Wing posture during brief wingbeat interruptions at mid-upstroke. These partial bounds are characterised by entirely flexed primaries and partially spread 'arm-wings' (humerus plus radius/ulna with secondaries attached to them). In both species, the wings became increasingly flexed with increasing air speed. (B) Gliding flight during actual rest phases (no wingbeats) with slightly flexed wings at 10.2 m s^{-1}. (C) Fully spread wings at mid-downstroke during horizontal flight at 10.2 m s^{-1}.

interruptions and is quite close to Warrick's (Warrick, 1998) measurements, for which the bird's air speed is not known.

Wing positioning during short wingbeat interruptions may be one of the most important aspects of the flight performance of hirundines. At mid-upstroke with the wings just passing the longitudinal body axis, they are halted for a fraction of a second in a position that makes the whole bird look arrow-shaped. This wing posture is attained by completely flexing the primaries, while keeping the 'arm-wings' (humerus plus radius/ulna with the secondaries attached to them) at least partially spread (Fig. 8A). The wings were never folded against the body during rest phases, as in true bounding, nor were they spread, as in gliding flight. In both species, the degree of wing-flexing appeared to increase with increasing air speed (see Fig. 8A). Real flap-gliding flight was restricted to descent at intermediate speeds. Compared with gliding flight, for which the profile drag is expected to increase as the square of forward speed (Pennycuick, 1968), partial wing-flexing will reduce the profile power requirement. However, partially spread arm-wings will still act as small aerofoils generating lift, helping to maintain flight altitude. Partial wing-spreading during the upstroke has been observed previously in relatively fast-flying budgerigars (*Melopsittacus undulatus*) (Tobalske and Dial, 1994), European starlings (*Sturnus vulgaris*) (Tobalske, 1995) and in the family Turdinae (Stark, 1996). It has been named partial bounding (*Tragflächenflug* in German). Partial bounding during rest phases can be regarded as a compromise between real bounding and gliding, acting as a trade-off between a reduction in profile drag and increased lift production. Apart from the energetic advantages of this trade-off, hirundines may also take advantage of the improved flight stability and avoidance of wavelike flight paths. Blake et al. (Blake et al., 1990) and Warrick (Warrick, 1998) described the behaviour of barn swallows hunting in straight, relatively fast flight, just above ground level (below 0.5 m), for which flight stability will be indispensable.

Among small birds, flap-gliding is said to be restricted to species with an unusually large aspect ratio and wing area (Rayner, 1979). Hirundines are among the smallest birds known to engage regularly in flap-gliding flight (Bryant and Westerterp, 1983). In our wind tunnel experiments, house martins commonly engaged in flap-gliding flight at intermediate speeds, alternating very flexibly between partial bounds and glides. Barn swallows performed gliding flight less often than did house martins and only when descending rather steeply. This might be due to the somewhat higher aspect ratios of the wings of house martins, which, according to Pennycuick (Pennycuick, 1972), will favour gliding flight. In agreement with our observations, Hails (Hails, 1979) pointed out the existence of a gradient in the utilisation of gliding flight: common swifts (*Apus apus*) and house martins were said to glide the most, sand martins (*Riparia riparia*) less often and barn swallows the least. As illustrated by the example of barn swallows, wingbeats need not be concentrated into bursts of flaps in intermittent flight. The hypothesis of Tobalske and Dial (Tobalske and Dial, 1994) that most birds using intermittent flight should tend to flap-glide when flying at slower speeds and shift to flap-bounding at faster speeds is basically supported by our observations, except that hirundines perform partial bounding instead of true bounding. Most passerines performing flap-bounding have relatively shorter and rounder wings with lower aspect ratios than those of hirundines (Rayner, 1985). They may therefore be unable to perform partial bounds efficiently since partly stretched wings would cause more losses due to profile drag than they would gain from lift production. Hirundines, with their narrow wings, reduce height loss by partial bounding, which enables them to fly more economically at high speeds than a broad-winged passerine. The main difference between hirundines and other small birds is their combination of relatively low body mass and high-aspect-ratio wings, causing little profile drag. This, we suggest, enables hirundines to use a high degree of flexibility in wing movements without causing major changes in flight costs. We believe that further studies will increase evidence that the trade-off between profile power and the cost of lift production is the main factor governing the use of intermittent flight by small birds and that the solution to this trade-off necessarily differs among species with differently shaped wings.

References

Barr, R. E. and Chan, E. K. Y. (1986). Design and implementation of digital filters for biometrical signal processing. *J. Electrophysiol. Tech.* **13**, 73–93.

Biesel, W. (1983). Untersuchungen der Flügelgeometrie frei gleitfliegender Tauben (*Columba livia var. domestica*) mit Hilfe der Windkanaltechnik. Diplomarbeit, MNF Universität des Saarlandes, Saarbrücken.

Biesel, W., Butz, H. and Nachtigall, W. (1985). Einsatz spezieller Verfahren der Windkanaltechnik zur Untersuchung des freien Gleitflugs von Vögeln. In *Biona Report* **3** (ed. W. Nachtigall), pp. 139–160. Mainz, Stuttgart, New York: Akademie der Wissenschaften und der Literatur, G. Fischer.

Blake, C. H. (1948). The flight of swallows. *Auk* **65**, 54–62.

Blake, R. W., Kolotylo, R. and De la Cueva, H. (1990). Flight speeds of the barn swallow, *Hirundo rustica. Can. J. Zool.* **68**, 1–5.

Bloch, R., Bruderer, B. and Steiner, P. (1981). Flugverhalten nächtlich ziehender Vögel – Radardaten über den Zug

verschiedener Vogeltypen auf einem Alpenpass. *Vogelwarte* **31**, 119–149.

Bruderer, B. and Steidinger, P. (1972). Methods of quantitative and qualitative analysis of bird migration with a tracking radar. In *Animal Orientation and Navigation* (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville), pp. 151–167. Washington: NASA SP-162.

Bryant, D. M. and Westerterp, K. R. (1980). The energy budget of the house martin (*Delichon urbica*). *Ardea* **68**, 91–102.

Bryant, D. M. and Westerterp, K. R. (1983). Short-term variability in energy turnover by breeding house martins *Delichon urbica*: a study using doubly labelled water. *J. Anim. Ecol.* **52**, 525–543.

Cramp, S. (1985/88). *Handbook of the Birds of Europe, the Middle East and North Africa*, vols 4/5. London: Oxford University Press.

Dempster, A. P., Selwyn, M. R., Patel, C. M. and Roth, A. J. (1984). Statistical and computational aspects of mixed model analysis. *Appl. Statistics* **33**, 203–214.

Emlen, S. T. (1974). Problems in identifying species by radar signature analysis: ultra-specific variability. In *Proceedings of the Conference on the Biological Aspects of the Bird/Aircraft Collision Problem* (ed. S. Gauthreaux), pp. 509–524. Clemson, SC: Air Force Office of Scientific Research.

Glutz von Boltzheim, U. N. and Bauer, K. M. (1980/85). *Handbuch der Vögel Mitteleuropas*, vols 9/10. Wiesbaden: Aula-Verlag.

Goldspink, G. (1977). Mechanics and energetics of muscle in animals of different sizes, with particular reference to the muscle fibre composition of vertebrate muscle. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 37–55. New York: Academic Press.

Hails, C. J. (1979). A comparison of flight energetics in Hirundines and other birds. *Comp. Biochem. Physiol.* **63**A, 581–585.

Möller, U. (1998). Aspekte der Flugkinematik des (Gemeinen) Stars (*Sturnus vulagaris*) beim Windkanalflug mit und ohne respiratorische Maske. Diplomarbeit, MNF Universität des Saarlandes, Saarbrücken.

Patterson, H. D. and Thompson, R. (1971). Recovery of inter-block information when block sizes are unequal. *Biometrika* **58**, 545–554.

Pennycuick, C. J. (1968). Power requirements for horizontal flight in the pigeon (*Columbia livia*). *J. Exp. Biol.* **49**, 527–555.

Pennycuick, C. J. (1969). Mechanics of bird migration. *Ibis* **111**, 525–556.

Pennycuick, C. J. (1972). *Animal Flight*. London: Edward Arnold.

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

Pennycuick, C. J. (1989). *Bird Flight Performance: A Practical Calculation Manual*. Oxford: Oxford University Press.

Pennycuick, C. J. (1990). Predicting wingbeat frequency and wavelength of birds. *J. Exp. Biol.* **150**, 171–185.

Pennycuick, C. J. (1996). Wingbeat frequency of birds in steady cruising flight: new data and improved predictions. *J. Exp. Biol.* **199**, 1613–1618.

Pennycuick, C. J., Hedenström, A. and Rosén, M. (2000). Horizontal flight of a swallow (*Hirundo rustica*) observed in a wind tunnel, with a new method directly measuring mechanical power. *J. Exp. Biol.* **203**, 1755–1765.

Pennycuick, C. J., Klaassen, M., Kvist, A., Lindström, A. (1996). Wingbeat frequency and the body drag anomaly: wind tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). *J. Exp. Biol.* **199**, 2757–2765.

Press, W. H., Teukolsky, S. A., Vetterling, W. T. and Flannery, B. P. (1996). *Numerical Recipes in C – The Art of Scientific Computing*. Second edition. Cambridge, New York, Melbourne: Cambridge University Press.

Rayner, J. M. V. (1977). The intermittent flight of birds. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 437–443. New York: Academic Press.

Rayner, J. M. V. (1979). A new approach to animal flight mechanics. *J. Exp. Biol.* **8**, 17–54.

Rayner, J. M. V. (1985). Bounding and undulating flight in birds. *J. Theor. Biol.* **117**, 47–77.

Rayner, J. M. V. (1990). The mechanics of flight and bird migration performance. In *Bird Migration* (ed. E. Gwinner), pp. 284–299. Berlin, Heidelberg: Springer-Verlag.

Rayner, J. M. V. (1995). Flight mechanics and constraints on flight performance. *Israel J. Zool.* **41**, 321–342.

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

Robinson, D. L., Thompson, R. and Digby, P. G. N. (1982). REML – a program for the analysis of non-orthogonal data by restricted maximum likelihood. *Compstat 1982 Proceedings in Computational Statistics, Part II* (Suppl.), pp. 231–232. Vienna: Physica-Verlag.

Stark, H. (1996). Flugmechanik nachts ziehender Kleinvögel. Dissertation, Universität Basel.

Tobalske, B. W. (1995). Neuromuscular control and kinematics of intermittent flight in the European starling (*Sturnus vulgaris*). *J. Exp. Biol.* **198**, 1259–1273.

Tobalske, B. W. and Dial, K. P. (1994). Neuromuscular control and kinematics of intermittent flight in budgerigars (*Melopsittacus undulatus*). *J. Exp. Biol.* **187**, 1–18.

Warrick, D. R. (1998). The turning- and linear-maneuvering performance of birds: the cost of efficiency for coursing insectivores. *Can. J. Zool.* **76**, 1063–1079.