

# Wingbeat frequency of barn swallows and house martins: a comparison between free flight and wind tunnel experiments

Felix Liechti\* and Lukas Bruderer

Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

\*e-mail: felix.liechti@vogelwarte.ch

Accepted 14 May 2002

## Summary

The flight paths and wingbeat patterns of 39 barn swallows (*Hirundo rustica*) and 26 house martins (*Delichon urbica*) were recorded by tracking radar during the spring migration. Depending mostly on flight angle, hirundines performed anything from continuous flapping flight during climbing to single pulse-like wing beats during descent. Unlike most other passerines, hirundines rarely showed regular flapping and rest phases, allowing them to be distinguished from other bird migrants by radar echo signatures. Effective wingbeat frequency ( $F_{\text{eff}}$ ) was calculated as the mean number of wing beats per second, including non-flapping phases. Under comparable flight conditions,  $F_{\text{eff}}$  was higher in house martins than in barn swallows. Within species,  $F_{\text{eff}}$  values were higher during climbing and slow flying than during descent. Of the variance in  $F_{\text{eff}}$ , 71% could be explained by climb

rate, air speed and species; similar results were obtained in the wind tunnel. Under comparable flight conditions, barn swallows and house martins in free flight had significantly lower values of  $F_{\text{eff}}$  than individuals in wind tunnel experiments (by 40% and 32%, respectively). This difference may at least partly be due to the shorter wings of the juveniles tested in the wind tunnel during autumn. However, it seems unlikely that this can account for all of the large difference. It is suggested that wind tunnel experiments might overestimate birds' flight costs compared with free flight.

Key words: barn swallow, *Hirundo rustica*, house martin, *Delichon urbica*, wingbeat pattern, intermittent flight, effective wingbeat frequency, wind tunnel, free flight, flight costs.

## Introduction

Flapping flight has the highest metabolic rate of any form of vertebrate endurance locomotion, and it has been suggested that this provides a strong selection pressure to adopt a flight mode that minimises the rate of energy consumption (Pennycuick, 1990). In numerous studies, the flight costs of a variety of bird species have been investigated in wind tunnel studies (for reviews, see Masman and Klaassen, 1987; Rayner, 1999), but few authors have investigated this subject for birds in free flight (e.g. Hails, 1978). Direct comparisons between wind tunnel flight and free flight are scarce and questionable since the details of the flight path in free-flying birds were mostly unknown (but see Tobalske et al., 1997). However, tracking free-flying individual birds by radar allows information to be gathered not only about their movement through space but also about their wingbeat pattern (Bruderer and Joss, 1969), a variable highly correlated with mechanical power output (Dial et al., 1997; Pennycuick, 1996; Pennycuick et al., 2000; Tobalske et al., 1999). Gaining equivalent data from wind tunnel experiments would allow a comparison of this fundamental factor concerning flight costs. In the present study, we describe the flight behaviour of barn swallows and house martins during free migratory flight. The wingbeat frequency, a major aspect of power output, is analysed with

respect to horizontal and vertical flight speed to estimate differences in flight costs between hirundines on migration and individuals flying in a wind tunnel (Bruderer et al., 2001).

## Materials and methods

### *Flight paths of visually identified hirundines*

In spring 1997 (19 March to 26 May), the Swiss Ornithological Institute carried out a study on the courses of birds migrating across the western Mediterranean (Bruderer and Liechti, 1999). One of the study sites was 25 km east of Malaga (Spain), next to the coastline. A tracking radar of the type 'Superfledermaus', providing data on the position of selected targets every second, was used to record the flight paths of migrating birds (Bruderer, 1997a,b). Single birds of the size of a swallow may be tracked for up to 4.5 km by the radar. Information on variables such as flight direction (track), height above the ground, vertical speed ( $v_z$ ) and ground speed are recorded automatically at 20 s intervals. The horizontal air speeds ( $v_a$ ) and headings of birds were calculated by subtracting the wind vector at the specific height from the flight vector. Wind profiles were gathered every 4 h by tracking a pilot balloon, treated in the same way as bird tracks, up to 4 km.

For comparisons of climbing rates between birds flying at different speeds, flight angles were calculated as  $\arctan(v_z/v_a)$ . In contrast to wind tunnel experiments, variables such as air speed, vertical speed and flight angle for birds in free flight were averaged over intervals of 20 s. The flight behaviour of single tracked birds may be quite variable within such intervals. However, 20 s intervals cover flight distances of 200–300 m and give a robust estimate of the resulting flight vector.

Hirundines were tracked on spring migration approaching the coast from the Mediterranean Sea in a northerly flight direction. Birds passing closer than 900 m were identified visually during daylight hours by means of a 12.4× telescope mounted parallel to the radar beam. We recorded 39 flight paths of visually identified barn swallows and 26 flight paths of visually identified house martins; for these birds, wingbeat frequencies could be determined from echo signatures, allowing single wing beats to be analysed. Once a bird had been identified, it was tracked for as long as possible (a maximum of 5 min). To reduce the interdependence of 20 s intervals within individual flight paths, no neighbouring intervals were chosen for analysis. In addition, more than one interval per bird was accepted only if flight angles differed by more than  $\pm 2.5^\circ$ , representing different types of flight behaviour, e.g. climbing, horizontal flight or descent. As a consequence, any individual contributed at most four intervals to the analysis of wingbeat frequency.

#### Wingbeat patterns and wingbeat frequencies

If a single bird is tracked, recording the fluctuations in its echo signature offers the possibility of obtaining its wingbeat pattern (Eastwood, 1967; Bruderer, 1969; Bruderer et al., 1972). The amount of radar energy reflected depends on the size and reflective properties of the target; it changes with the distance and aspect presented to the radar (Bruderer and Joss, 1969; Bruderer et al., 1995). The fluctuations in echo signatures are related to rapid changes in the circumference and volume of the bird's body (Bruderer, 1997a), which are due to the movements of pectoral muscles during down- and upstrokes. However, peaks of echo signatures of radar-tracked birds may not be interpreted unambiguously as single wing beats. Because of phase shifts in radar waves bent around the target, a single wing beat of a bird of the size of a hirundine may produce two peaks (Mi-effect, occurring if wavelengths and target size are of the same order of magnitude; see Bruderer, 1969). The relative size of these two peaks may change within a flight path, depending on the aspect a bird is presenting to the incident radar waves. In hirundines, great attention had to be paid to this potential doubling of single wing beats caused by the Mi-effect (see Fig. 1). Within one 20 s interval, either main or secondary peaks had to be marked consistently. Before interactively marking single wing beats, the signal of the raw echo signature was passed through a band-pass filter that eliminated high-frequency oscillations ( $>18$  Hz) caused by the rotation of the radar feed and low-frequency

oscillations ( $<4$  Hz) caused mainly by tracking movements of the radar antenna.

In general, wingbeat frequencies are measured as the number of flapping cycles per second for a phase of continuous flapping. However, unless in a steady climb, hirundines rarely flap their wings continuously, nor do they show regular patterns of flapping and rest phases, as do most other small passerines (Bruderer et al., 2001). Single, pulse-like wing beats are often interspersed over time and, especially in free flight, very few successive flapping cycles are of exactly equal duration. We therefore calculated the number of wingbeat cycles per unit time, termed the effective wingbeat frequency, according to the formula:

$$F_{\text{eff}} = [\text{mean}(\Delta t_{\text{wingbeat}})]^{-1}, \quad (1)$$

where  $\Delta t_{\text{wingbeat}}$  is the duration of a complete flapping cycle, including variable-duration resting phases (Bruderer et al., 2001). In contrast to the wingbeat frequency usually used (e.g. Pennycuik, 1996), the effective wingbeat frequency is related to the mechanical power output irrespective of whether a bird is flapping continuously like a wader or intermittently like a passerine. This allows levels of mechanical power output to be compared (i) among different flight situations for an individual bird, (ii) among different individuals of one species and (iii) among species of comparable size. In this study, a birds' effective wingbeat frequency is the mean number of wing beats per second (Hz) averaged across a 20 s interval.

#### Wind tunnel experiments

Seven juveniles, four barn swallows (*Hirundo rustica*) and three house martins (*Delichon urbica*), were hand-raised and later tested in a wind tunnel at different flight angles ( $-10$ ,  $-5$ ,  $0$  and  $5^\circ$ ) and air speeds (5.1, 8.2, 10.2 and  $12.5 \text{ m s}^{-1}$ ) at the University of Saarbrücken. Flight intervals of 20 s at a constant air speed and flight angle were recorded on video ( $50 \text{ frames s}^{-1}$ ). The movement of the wingtips relative to the body axis were analysed using the same software as for the radar data (see above). Mean values of body mass and wing span for the individuals tested are given in Table 1. A detailed description of the experimental settings and the analysis are presented in Bruderer et al. (2001).

Table 1. Body mass and wing span of the juvenile birds tested in the windtunnel and values taken from the literature for adult free-living birds

	<i>Hirundo rustica</i> (N=3)		<i>Delichon urbica</i> (N=4)	
	Wind tunnel	Literature	Wind tunnel	Literature
Body mass (g)	19.0–22.0 <sup>3</sup>	11.0–28.2 <sup>1</sup>	16.5–18.0 <sup>3</sup>	10.3–19.8 <sup>1</sup>
Mean (g)	20.4 <sup>3</sup>	16.0 <sup>1</sup>	17.3 <sup>3</sup>	14.5 <sup>1</sup>
Wing span (mm)	274–284 <sup>3</sup>	320–345 <sup>2</sup>	240–258 <sup>3</sup>	260–290 <sup>2</sup>

<sup>1</sup>Ash (1969), Morocco spring migration; <sup>2</sup>Cramp (1985/88); <sup>3</sup>Bruderer et al. (2001).

### Statistical analyses

Statistical analyses were performed with the software package Genstat 5.0 (1993). To analyse minimum wingbeat duration, the 5% range per individual was taken instead of the absolute minimum. Differences were tested using a *t*-test for independent samples. The influence of flight variables and species on effective wingbeat frequency was modelled by multiple linear regression analysis. To compare wind tunnel results with data for free-flying birds, an analysis of variance (ANOVA) with the factors flight angle and treatment (free or wind tunnel) was performed. Differences were tested using Tukey's honest significant difference (HSD) test for unequal sample sizes.

## Results

### Radar tracking

The raw echo signatures revealed the detailed flight behaviour of hirundines (Fig. 1). During the rather steep climbs of barn swallows (BS), flapping may be nearly continuous (BS1), whereas intervals between single wing beats become increasingly longer during horizontal flight and descent (BS2, BS3). Similarly, in house martins (HM), intervals between wing beats were greater during descent than during climbing. In addition, flaps tended to occur consecutively, which resulted in a more intermittent flight style than that of barn swallows (HM3).

The frequency distribution of the duration of flapping cycles was skewed in both species, whether in climbing or horizontal flight (Fig. 2). As flight angle decreased, the proportion of longer flapping cycles increased gradually, while the mode remained constant. Some flapping cycles of the barn swallows during climbing were rather long, caused by temporary interruptions to climbing flight by short rest phases. In general, the flapping cycles of barn swallows were slightly longer than those of house martins. Minimum values (see Materials and methods) per individual for the duration of flapping cycles differed significantly between the two species (all angles, one

Fig. 2. Relative frequency distribution of the duration of flapping cycles for barn swallows (A) (BS) and house martins (B) (HM) in free flight. Only one 20 s interval per bird was included per flight situation. Climbing (flight angles  $3.5 \pm 1.5^\circ$ ),  $N_{BS}$  individuals=4,  $N_{BS}$  flapping cycles=372,  $N_{HM}$  individuals=6,  $N_{HM}$  flapping cycles=779; horizontal flight (flight angles  $0 \pm 1.5^\circ$ ),  $N_{BS}$  individuals=13,  $N_{BS}$  flapping cycles=1387,  $N_{HM}$  individuals=8,  $N_{HM}$  flapping cycles=890; descent (flight angles  $-3.5 \pm 1.5^\circ$ ),  $N_{BS}$  individuals=18,  $N_{BS}$  flapping cycles=1691,  $N_{HM}$  individuals=9,  $N_{HM}$  flapping cycles=952. True air speed was restricted to 10–16 m s<sup>-1</sup>.

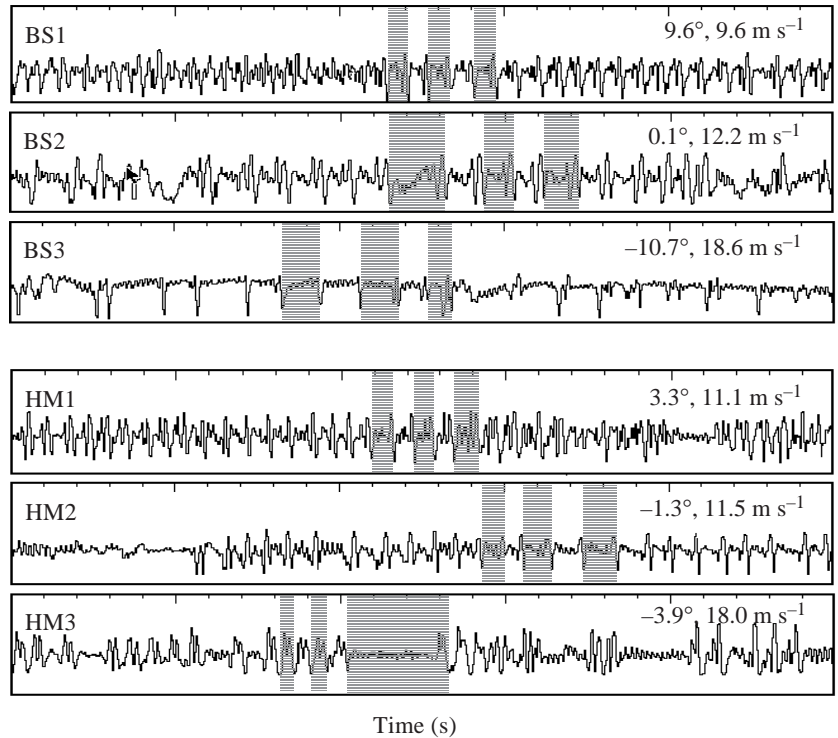
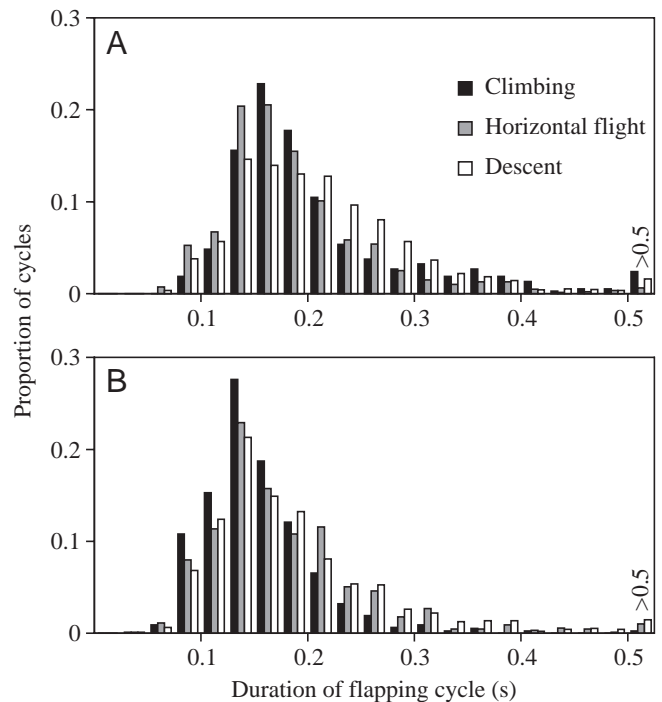


Fig. 1. Characteristic unfiltered echo signatures of barn swallows (BS) and house martins (HM) during climbing (BS1, HM1), horizontal (BS2, HM2) and descending (BS3, HM3) flight recorded by tracking radar. The examples show wingbeat patterns for 5 s intervals. Flight angle and mean air speed are given in the upper right corner. Large ticks above each signature indicate time in seconds. For each example, five consecutive flapping cycles are marked (three shaded + two in between).



value per individual, BS,  $N=39$ , mean 0.1054 s,  $F_{\text{eff}}=9.5$  Hz; HM  $N=27$ , mean 0.0891 s,  $F_{\text{eff}}=11.2$  Hz;  $t$ -test for independent samples,  $t=5.4$ ,  $P<0.001$ ).

The effective wingbeat frequencies ( $F_{\text{eff}}$ ) of barn swallows, including all flight angles and speeds, ranged from 2.5 to 8.4 Hz; those of house martins ranged from 3.0 to 8.1 Hz (Fig. 3). Mean  $F_{\text{eff}}$  was 4.4 Hz for barn swallows and 5.3 Hz for house martins. A large proportion of the tracked hirundines descended during their approach to the coast. Including only horizontal flight paths in the analysis (flight angle  $\pm 1.5^\circ$ ) gave somewhat higher mean  $F_{\text{eff}}$  values of 5.4 Hz for barn swallows and 6.0 Hz for house martins. Overall,  $F_{\text{eff}}$  of barn swallows was significantly lower than that of house martins ( $t$ -test for independent samples,  $N_{\text{BS}}=65$ ,  $N_{\text{HM}}=51$ ,  $t=3.8$ ,  $P<0.001$ ), but  $F_{\text{eff}}$  values did not differ significantly between species for individuals during horizontal flight (flight angle  $0 \pm 1.5^\circ$ ,  $N_{\text{BS}}=13$ ,  $N_{\text{HM}}=9$ ,  $t=1.9$ ,  $P=0.07$ ).

A multiple linear regression was performed to examine the variability of  $F_{\text{eff}}$  for barn swallows and house martins in free flight with respect to flight angle, true air speed and flight altitude (Table 2). Flight angle was by far the most important factor, explaining approximately two-thirds (71.3%) of the variance. In addition,  $F_{\text{eff}}$  increased with true air speed in house martins but not in barn swallows. Remarkably, true air speed was strongly correlated with flight angle in barn swallows ( $r=-0.71$ ), but only moderately in house martins ( $r=-0.44$ ) (Fig. 4). For barn swallows  $F_{\text{eff}}$  decreased ( $r=-0.61$ ,  $P<0.001$ ) with increasing true air speed (Fig. 3A). However, as demonstrated by the multiple regression, this was caused by the general increase in true air speed during descent (Fig. 4). The effective wingbeat frequency of both species increased significantly (BS:  $r=0.87$ ,  $P<0.001$ ; HM:  $r=0.75$ ,  $P<0.001$ ) with increasing flight angle (Fig. 3B). Flight altitude varied between 50 and 900 m above sea level, but had no significant influence on  $F_{\text{eff}}$ . The second and third powers of the three

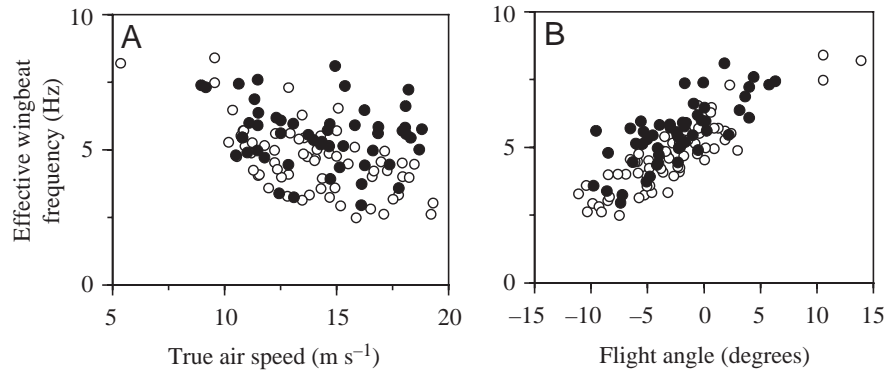


Fig. 3. Effective wingbeat frequency averaged over 20 s with respect to true air speed (A) and flight angle (B). Barn swallows, open circles,  $N=65$ ; house martins, filled circles,  $N=51$ .

variables did not explain any significant proportion of the variance.

In addition, we analysed five individual flight paths with a relatively long tracking time ( $\geq 100$  s) and considerable variability in flight angles (Fig. 5). Within each individual track, flight angle accounted for a significant 65.1–93.5% of the variance (simple linear regression). Including true air speed in a multiple regression did not add significantly to the amount of variance explained. However, for one house martin (see Fig. 5, filled circles;  $F_{\text{eff,minimum}}=3.2$  Hz, six flight intervals), true air speed explained slightly more of the variance ( $t=3.6$ ) than flight angle ( $t=3.4$ ; simple linear regression). In this case, the

Table 2. Results of multiple linear regression analysis for the effective wingbeat frequencies of hirundines

	Estimates of regression coefficients			
	Estimate	S.E.M.	$t_{112}$	$P$
Constant	5.164	0.393	13.16	<0.001
Flight angle	0.2382	0.0185	12.91	<0.001
True air speed $\times$ species (HM)	0.0653	0.0291	2.24	0.027
True air speed $\times$ species (BS)	0.0137	0.0304	0.45	0.652

Species was introduced as a factor (0,1).

Number of intervals  $N=116$ ,  $r^2_{\text{adj}}=71.3\%$ .

BS, barn swallows; HM, house martins.

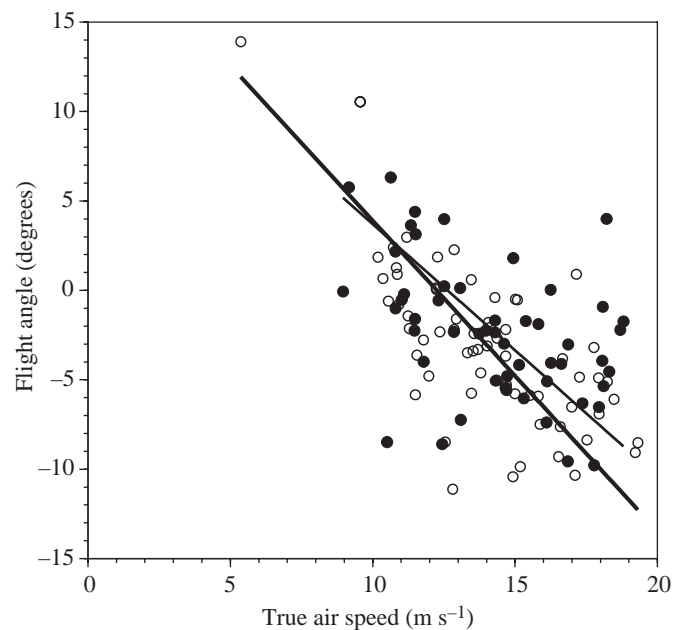


Fig. 4. Flight angle with respect to true air speed for barn swallows (open symbols,  $N=65$ ) and house martins (filled symbols,  $N=51$ ). The geometric mean regressions for barn swallows (thin line) and house martins (bold line) are shown. The correlation between air speed and flight angle is much higher for barn swallows ( $r=-0.71$ ) than for house martins ( $r=-0.44$ ) even when the two highest values of flight angle for barn swallows are excluded.

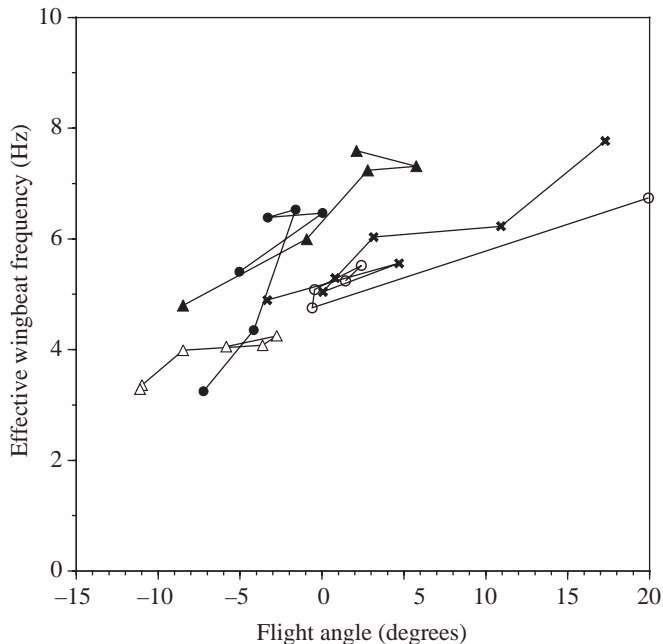


Fig. 5. Effective wingbeat frequency with respect to flight angle for two barn swallows (open symbols), two house martins (filled symbols) and one unidentified hirundine (black crosses) for continuous flight intervals of 20 s. Lines connect consecutive 20 s intervals of an individual flight path.

correlation between the two variables was strongly positive ( $r=0.91$ , see above). In contrast to most other tracks, this bird decreased its true air speed from  $16.2 \text{ m s}^{-1}$  during horizontal flight to  $13.0 \text{ m s}^{-1}$  during descent.

#### Wind tunnel versus field data

It is not possible to compare wingbeat frequencies for identical flight conditions, since flight angle and air speed are more variable during free flight and, thus, their measurement is less exact. The air speeds of hirundines during free flight were generally somewhat higher than the speeds testable in the wind tunnel used in the complementary study. Measurements of  $F_{\text{eff}}$  recorded at the highest test speeds ( $12.5 \text{ m s}^{-1}$ , except during climbing,  $10.2 \text{ m s}^{-1}$ ) at a given angle were compared with field measurements, for which air speeds were restricted to  $10\text{--}16 \text{ m s}^{-1}$ . The mean air speeds per flight angle for free-flying barn swallows were between  $14.1 \text{ m s}^{-1}$  ( $-10^\circ$ ) and  $11.6 \text{ m s}^{-1}$  ( $+5^\circ$ ), and those of house martins were between  $14.3 \text{ m s}^{-1}$  ( $-5^\circ$ ) and  $11.4 \text{ m s}^{-1}$  ( $+5^\circ$ ). The flight angles of radar-tracked hirundines were roughly equivalent to those in the wind tunnel experiments (Fig. 6). In both species,  $F_{\text{eff}}$  was significantly higher in wind tunnel experiments than during free flight (ANOVA, Tukey's test for unequal sample sizes,  $P<0.001$ ; see Materials and methods). In barn swallows, mean  $F_{\text{eff}}$  differed by 1.8 Hz (from 1.5 to 2.6 Hz within flight angles), corresponding to an increase of 40%; in house martins, mean  $F_{\text{eff}}$  differed by 1.7 Hz (from 0.5 to 2.7 Hz within flight angles), corresponding to an increase of 32%.

## Discussion

### Wingbeat patterns

Hirundine tracked by radar during free flight produced wingbeat patterns similar to those used in a wind tunnel. The variability of the flight parameters of the birds observed during free flight tended to be larger. This is due to more variable flight conditions, but also to the limited accuracy of flight path measurements. Except during climbing, both species used intermittent flight styles during free flight and in the wind tunnel. Depending mostly on flight angle, they performed anything from continuous flapping flight without rest phases to single, pulse-like wing beats, typically separated by intervals of variable duration. In hirundines, there was no constant rhythm of wing beats comparable with that of other passerines (Bruderer, 1969; Bruderer and Steidinger, 1972; Oehme, 1991): instead, wingbeat patterns resembled non-harmonic oscillations.

Wind tunnel observations have shown that this variability is due mainly to interruptions of upstrokes during which hirundines commonly perform partial bounds (Pennycuick et al., 2000; Bruderer et al., 2001). These are characterised by completely flexed primaries and partially spread arm wings, which most probably act as small aerofoils, generating residual lift during

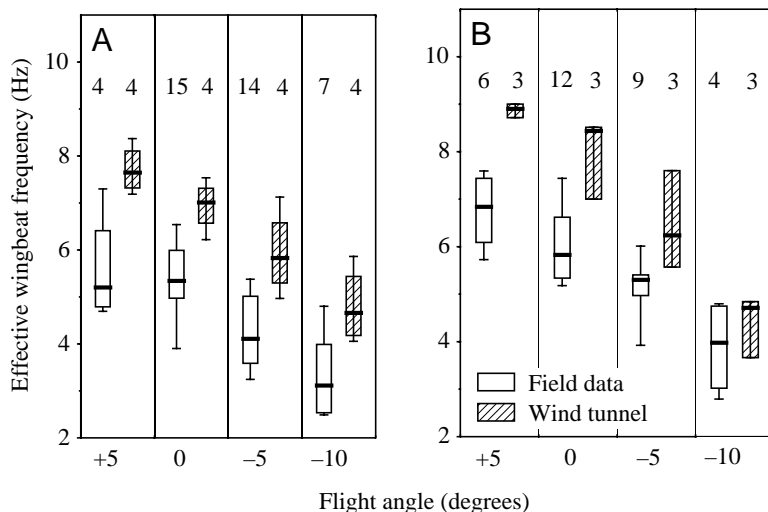


Fig. 6. Comparison of the effective wingbeat frequency for radar-tracked hirundines with wind tunnel observations. (A) Barn swallows; (B) house martins. Medians (horizontal bars), 25–75% ranges (boxes) and range (whiskers) are given. Shaded boxes represent wind tunnel data, open boxes represent field data. Flight angles of radar-tracked hirundines were restricted to climbing ( $5\pm 3^\circ$ ), horizontal flight ( $0\pm 1.5^\circ$ ), descent at  $-5\pm 1.5^\circ$  and descent at  $-10\pm 3^\circ$  (means  $\pm$  S.D.). Only one measurement per bird was included per flight angle. Numbers of individuals are given on the graph.

rest phases. During descending flight, house martins tend to aggregate their wing beats into an almost 'passerine-like' pattern, with bursts of wing beats and intermittent rest phases (Fig. 1; HM3). However, the durations of flapping and rest phases were highly variable and clearly different from the regular bursts of flappings of other small passerines (Stark, 1996).

Hirundines hunt in free flight and are among the small number of diurnal long-distance passerine migrants. We speculate that this highly variable wingbeat pattern might be an adaptation to flying long distances through air that is much more turbulent during the day than at night. Migrating swifts mostly combine several wing beats into bursts of variable length, followed by relatively long gliding phases (Bruderer and Weitnauer, 1992). Provided that the radar echo signatures are of good quality, hirundines as a group can be identified by their characteristic wingbeat pattern alone.

#### *Effective wingbeat frequency*

During powered flight, wingbeat frequency is closely related to mechanical power output, although other factors (amplitude, angle of attack, etc.) may be of considerable importance (e.g. Tobalske et al., 1999). To account for the restricted spatial accuracy of radar tracks, rather long flight intervals of 20 s were selected, corresponding to flight paths of a few hundred metres (mean flight speed approximately  $14 \text{ m s}^{-1}$ ). It is obvious that, in this case, effective wingbeat frequency, rather than wingbeat frequency during short bursts of flaps, will be related to mechanical power output. A strong positive correlation between flight angle and  $F_{\text{eff}}$  was found in both species, both in the field data and in wind tunnel experiments. The difference in  $F_{\text{eff}}$  between the two species is in accordance with the differences in their wingspan and mass of 10–15%. Although hirundines on migration flew mostly at higher air speeds ( $10\text{--}20 \text{ m s}^{-1}$ ) than in the wind tunnel experiments ( $5\text{--}12.5 \text{ m s}^{-1}$ ), only house martins showed the expected increase in  $F_{\text{eff}}$  with air speed. The tail of the expected U-shaped curve for  $F_{\text{eff}}$  against air speed at low speeds was not covered by our field data. It is not surprising that in barn swallows, with their high interdependence between air speed and flight angle, no independent effect of air speed was found in the field data. The large scatter due to the heterogeneity of these data may have masked some of the expected correspondence.

All birds tested in the wind tunnel were juveniles before their first migration. They had thus not yet reached adult wingspan, whereas their body masses were within the upper half of the ranges found in the literature (Table 1). According to Pennycuick (1996), wingbeat frequency ( $f$ ) is related to body mass ( $m$ ), wing span ( $b$ ) and wing area ( $S$ ):

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

where  $g$  is the acceleration due to gravity and  $\rho$  is air density. A decrease in wing span of 20% for barn swallows and of 10% for house martins and an increase in mass of approximately 20% for both species may thus explain most of the difference observed between free-flying birds and wind tunnel

experiments. Air density was very similar for the two studies (wind tunnel  $1.205 \text{ kg m}^{-3}$ , radar  $1.230\text{--}1.155 \text{ kg m}^{-3}$ ) and did not account for the difference observed. However, in absolute terms, the theoretical values for wingbeat frequency (barn swallows, juveniles  $10.0 \text{ Hz}$ , adults  $7.2 \text{ Hz}$ ; house martins, juveniles  $11.3 \text{ Hz}$ , adults  $9.3 \text{ Hz}$ ) are well above the values we measured.

Pennycuick et al. (2000) estimated the mechanical flight power of barn swallows flying in a wind tunnel. Their estimates, based on recordings of the movements of the humerus, were higher than expected from recent theory. This result is in agreement with our observations and indicates either that hirundines (at least juveniles) may perform additional flight manoeuvres in the wind tunnel, causing flight costs to increase, or that their flight muscles might still be smaller than those of adults and thus produce less thrust and lift during a downstroke. Data presented by Tobalske et al. (1997) on magpies (*Pica pica*) also suggested that wingbeat frequency was lower outdoors than in the wind tunnel. If free-living juveniles also differ from adults in wingspan but not in body mass, we must assume higher flight costs for juveniles than for adults, which might be of some importance for the high mortality of barn swallows after fledging due to aerial predators (L. Schifferli, personal communication).

It is of great interest whether these differences in mechanical flight power observed between free-flying hirundines and wind tunnel experiments are restricted to these two species or whether there are some flight costs caused by a wind tunnel effect. However, there is theoretical evidence that flight costs in closed wind tunnels are lower than during free flight, primarily for low speeds (Rayner, 1994). We compared speeds clearly above the minimum power speed ( $>10 \text{ m s}^{-1}$ ), so this effect does not have a strong influence on our results. At present, we cannot exclude the possibility that flight cost calculations based on wind tunnel experiments overestimate mechanical power output compared with free flight.

We are most grateful to all members of the field team who helped collect the data on migrating hirundines in Spain, especially Susanna Meyer and Herbert Stark. Thomas Steuri developed the hardware and software for the data processing. The software for analysis of effective wingbeat frequencies was developed by Martin Mörz. We thank Professor W. Nachtigall for permission to use the wind tunnel at the University of Saarbrücken and Professor D. Bilo for his assistance and valuable advice. We are grateful to Professor B. Bruderer for his permanent support and encouragement. Lukas Jenni, Beat Naef-Daenzer, Luc Schifferli, Reto Spaar and B. Tobalske made valuable comments on the manuscript. This study was part of a project on bird migration across the western Mediterranean that was supported financially by the Swiss National Science Foundation (Grant 31-432 42.95) and the Silva-Casa Foundation.

## References

- Ash, J. S. (1969). Spring weights of trans-Saharan migrants in Morocco. *Ibis* **111**, 1–10.
- Bruderer, B. (1969). Zur Registrierung und Interpretation von Echosignaturen an einem 3-cm-Zielverfolgeradar. *Ornithol. Beob.* **66**, 70–88.
- Bruderer, B. (1997a). The study of bird migration by radar. I. The technical basis. *Naturwissenschaften* **84**, 1–8.
- Bruderer, B. (1997b). The study of bird migration by radar. II. Major achievements. *Naturwissenschaften* **84**, 45–54.
- Bruderer, B., Jacquat, B. and Brückner, U. (1972). Zur Bestimmung von Flügelschlagfrequenzen tag- und nachziehender Vogelarten mit Radar. *Ornithol. Beob.* **69**, 189–206.
- Bruderer, B. and Joss, J. (1969). Methoden und Probleme der Bestimmung von Radarquerschnitten freifliegender Vögel. *Rev. Suisse Zool.* **76**, 1106–1118.
- Bruderer, B. and Liechti, F. (1999). Bird migration across the Mediterranean. In *Proceedings of the International Ornithological Congress, Durban* (ed. N. Adams and R. Slotow), pp. 1983–1999. Johannesburg: Bird Life South Africa.
- 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.
- Bruderer, B., Steuri, T. and Baumgartner, M. (1995). Short-range high-precision surveillance of nocturnal migration and tracking of single targets. *Isr. J. Zool.* **41**, 207–220.
- Bruderer, B. and Weitnauer, E. (1972). Radarbeobachtungen über den Zug und Nachtflüge des Mauerseglers *Apus apus*. *Rev. Suisse Zool.* **79**, 1190–1200.
- Bruderer, L., Liechti, F. and Bilo, D. (2001). Flexibility in flight behaviour of barn swallows (*Hirundo rustica*) and house martins (*Delichon urbica*) tested in a wind tunnel. *J. Exp. Biol.* **204**, 1473–1484.
- Cramp, S. (1985/88). *Handbook of the Birds of Europe, the Middle East and North Africa*, vol. 4/5. London: Oxford University Press.
- Dial, K. P., Biewener, A. A., Tobalske, B. E. and Warrick, D. R. (1997). Mechanical power output of bird flight. *Nature* **390**, 67–70.
- Eastwood, E. (1967). *Radar Ornithology*. London: Methuen.
- Genstat 5 (1993). Release 3. *Reference Manual, Genstat 5 Committee*. Oxford: Clarendon Press. 796pp.
- Hails, L. J. (1978). A comparison of flight energetics in Hirundines and other birds. *Comp. Biochem. Physiol.* **63A**, 581–585.
- Masman, D. and Klaassen, M. (1987). Energy expenditure during free flight in trained and free-living Eurasian kestrel. *Auk* **104**, 603–616.
- Oehme, H. (1991). Time pattern of wing motion during cruising flight and its importance on flight energetics. *Acta XX Congr. Int. Orn.* **3**, 737–747.
- Pennycuik, C. J. (1990). Predicting wingbeat frequency and wavelength of birds. *J. Exp. Biol.* **150**, 171–185.
- Pennycuik, C. J. (1996). Wingbeat frequency of birds in steady cruising flight: new data and improved predictions. *J. Exp. Biol.* **199**, 1613–1618.
- Pennycuik, C. J., Hedenström, A. and Rosén, M. (2000). Horizontal flight of a swallow (*Hirundo rustica*) observed in a wind tunnel, with a new method for directly measuring mechanical power. *J. Exp. Biol.* **203**, 1755–1765.
- Rayner, J. M. V. (1994). Aerodynamic corrections for the flight of birds and bats in wind tunnels. *J. Zool., Lond.* **234**, 537–563.
- Rayner, J. M. V. (1999). Estimating power curve of flying vertebrates. *J. Exp. Biol.* **202**, 3449–3461.
- Stark, M. (1996). Flugmechanik nachts ziehender Kleinvögel. Dissertation, Universität Basel, Schweizerische Vogelwarte Sempach.
- Tobalske, B. W., Olson, N. E. and Dial, K. P. (1997). Flight style of the black-billed magpie: variation in wing kinematics, neuromuscular control and muscle composition. *J. Exp. Zool.* **279**, 313–329.
- Tobalske, B. W., Peacock, W. L. and Dial, K. P. (1999). Kinematics of flap-bounding flight in the zebra finch over a wide range of speeds. *J. Exp. Biol.* **202**, 1725–1739.