# Wing beat kinematics of a nectar-feeding bat, *Glossophaga soricina,* flying at different flight speeds and Strouhal numbers

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## Summary

High-speed film analysis showed that the wing beat kinematics in *Glossophaga soricina* change gradually with increasing flight speed, indicating that there is no sudden gait change at any particular, critical, flight speed. The flight of two adult specimens was studied over a range of flight speeds ($1.23-7.52$ ms$^{-1}$) in a 30 m long flight tunnel. During the upstroke in hovering and slow flight there is a tip-reversal or supination of the handwings, which thus produce a backward flick. This backward motion successively disappears at speeds $V \approx 3.2$ ms$^{-1}$, above which the wingtip path becomes more vertical or directed upwards–forwards relative to the still air (the stroke plane angle increasing with flight speed as $\alpha = 44.8 V^{0.29}$). We found no correlations between either span ratio $SR$ (the ratio of the wing span on the upstroke to that on the downstroke) and $V$, or downstroke ratio (the duration of the downstroke divided by the total stroke period) and $V$. On the other hand, $SR$ decreases significantly with increasing wing beat frequency $f$, $SR \propto f^{-0.40}$. The Strouhal number ($St = f \times$amplitude$/V$), a dimensionless parameter describing oscillating flow mechanisms and being a predictor of the unsteadiness of the flow, decreases with the speed as $St \propto V^{-1.37}$. Close to the theoretical minimum power speed ($4-6$ m s$^{-1}$) *G. soricina* operates with a Strouhal number in the region $0.17 < St < 0.22$, which is associated with efficient lift and thrust production. At slower speeds, $3.4-4$ m s$^{-1}$, $St$ is $0.25-0.4$, which is still within the favourable region. But at speeds below 3 m s$^{-1}$ $St$ becomes higher ($0.5 < St < 0.68$), indicating that unsteady effects become important, with unfavourable lift and thrust production as a result. Only at these speeds do the bats perform the backward flick during the upstroke, which may produce thrust. This may serve as a compensation in some bats and birds to increase aerodynamic performance.

Key words: flight, wing beat kinematics, Strouhal number, bat, *Glossophaga soricina.*

## Introduction

The wing kinematics of bats have been described (e.g. Norberg, 1970; Norberg, 1976a; Norberg, 1976b; Aldridge, 1986; Aldridge, 1987). The downstroke starts with the wings extended dorsolaterally and they sweep forwards and downwards relative to the body, fully extended. The upstroke starts with a slight flexion of the elbow and wrist and the wings are brought upwards and backwards relative to the body. As seen from the side of a left wing the wing is moved clockwise in an ellipse, while in birds it is moved counterclockwise. At slow speeds the upstroke can produce a forward thrust and sometimes a slight upward force, while at medium speeds the upstroke is mainly a recovery stroke (Norberg, 1976a; Norberg, 1976b). At faster speeds the wings may again produce slight vertical lift during the upstroke (Rayner et al., 1986). The tail membrane, when it exists, is continuous with that of the wings at the trailing edge, and moves up and down with the legs and wings relative to the body (Norberg, 1970).

The flapping wings generate thrust and vertical lift but also a system of trailing vortices behind the wing tips, the strength of which is determined by the magnitude of the lift. Without wake vortices there could be no momentum transport and thus no lift (Weis-Fogh, 1973; Weis-Fogh, 1975; Rayner, 1979a; Rayner, 1979b; Rayner, 1979c; Rayner, 1995). Vorticity is highly dependent on the animal size, wing form, flight speed and kinematics.

Horses are known to change from walking to trotting and then to galloping as they increase speed, because at a certain speed it would cost more to walk than to trot etc. (Hoyt and Taylor, 1981). Thus, by changing gaits, horses save energy. Alexander gave the definition of gait as follows: "*A gait is a pattern of locomotion characteristic of a limited range of speeds, described by quantities of which one or more change discontinuously at transitions to other gaits*" (Alexander, 1989). Walking and running in humans are also distinct movement patterns, which do not merge into each other (Alexander, 1989).

Flight gaits have been defined by different wake structures rather than by the different footfall patterns or kinetic *vs* potential energy relationships used in terrestrial locomotion. The wake vorticity structure has been visualized with birds and bats flying through smoke, helium bubbles, or clouds of small particles (Magnan et al., 1938; Kokshaysky, 1979; Spedding, 1982; Spedding, 1986; Spedding, 1987a; Spedding, 1987b; Spedding et al., 1984; Spedding et al., 2003; Rayner et al., 1986; Rosén et al., 2004; Hedenström et al., 2005).

Rayner modelled upstroke lift as a function of speed (Rayner, 1995) and concluded that in short-winged or slow-flying birds, the upstroke should not be used in force generation, but all aerodynamic lift should be generated by the downstroke. In birds with relatively large wings, a lifting upstroke would become effective above a critical speed, which should determine a gait transition. Rayner et al. described the vortex wakes in the noctule bat (*Nyctalus noctula*), a 26–27 g bat with rather short wing span, average aspect ratio and high wing loading (Rayner et al., 1986), and in the long-eared bat (*Plecotus auritus*), a 7–9 g bat with low aspect ratio and low wing loading (Norberg and Rayner, 1987). Both the faster-flying noctule bat and the slow-flying long-eared bat showed a vortex-ring gait at very slow speeds (<minimum power speed), whereas at speeds near maximum range speeds the wake consisted of undulating vortex tubes in the noctule bat. But *Plecotus* did not show any change in vorticity with changes in speed.

Variations in wake geometry may be explained by, or reconciled with, the overall wing kinematic data (Spedding et al., 2003; Rosén et al., 2004; Hedenström et al., 2005). Spedding et al. investigated the wake structure of a thrush nightingale (*Luscinia luscinia*) in free flight in a wind tunnel over a range of flight speeds (Spedding et al., 2003). They found that the wake cannot be categorised as one of the two standard types, but has an intermediate structure with approximations to the 'closed-loop model' at the slowest speeds and to the 'constant circulation model' at the highest speeds. Rosén et al. measured the wing beat kinematics of the same species for steady flight in the wind tunnel over the same range of flight speeds, 5–10 m s$^{-1}$, which were compared with the wake analysis (Rosén et al., 2004). They found that neither the wing beat frequency nor the wing beat amplitude change significantly with flight speed; the only kinematic variations come from changes in downstroke fraction and span ratio. They noted that there is no sign of discontinuous or sudden variation with speed in any of the measured quantities in the wake studies or kinematic parameters.

Pennycuick introduced the 'span-ratio method' to estimate the effective lift:drag ratio of birds in the field, which is related to the ratio of lift to thrust (Pennycuick, 1989). It assumes that a bird in cruising flight generates a concertina wake (with active upstroke) and that the spanwise lift distribution is the same in the upstroke and the downstroke. If this is the case the ratio of the lift on the upstroke to that on the downstroke must be the same as the span ratio, which is the ratio of the wing span on the upstroke to that on the downstroke. In slow flight,

when there is no active upstroke, the wings are flexed much more than in cruising flight, and the span ratio is thus much higher.

The Strouhal number (*St*; wing beat frequency× amplitude/forward speed) is a dimensionless parameter that describes oscillating flow mechanisms and can be a predictor of the unsteadiness of the flow. It is known to govern a well-defined series of vortex growth and shedding regimes for airfoils undergoing pitching and heaving motions (Andersson et al., 1998; Wang, 2000). The region for favourable force production peaks within the interval 0.2<*St*<0.4, and outside this region unsteadiness of the flow may become crucial.

Cruising flying animals converge at a narrow range of *St* corresponding to a regime of vortex growth and shedding in which the propulsive efficiency of flapping wings peaks (Taylor et al., 2003). Alexander [(Alexander, 2003), p. 60] wrote "*The natural frequencies of vibration of spring-mass systems are proportional to (S/m)$^{1/2}$ [where S is stiffness of the spring and m its mass] implying that the motions must have equal values of v$^2$/f$^2$l$^2$, where f is the natural frequency of a system [and v is velocity and l is length]; hence they must have equal values of fl/v, which is called the Strouhal number. Any two dynamically similar cyclic motions must have equal Strouhal numbers. Hovering hummingbirds of different sizes beat their wings at frequencies that make their Strouhal numbers about equal*".

The purpose of this investigation was to find out if *Glossophaga soricina* makes an abrupt change in wing beat kinematics at particular flight speeds, or if its flight pattern gradually changes with increasing speed. Does a lifting upstroke become effective above a critical flight speed, which should determine a gait transition? Sudden changes in wing morphometry, wing stroke amplitude and frequency, Strouhal number, and decrease in span ratio would indicate this. However, such a change in wing kinematics would only highlight a speed at which the bats might change gait, and this has to be confirmed from a flow visualization study.

## Materials and methods
### Animals and morphological measurements

We studied the wing beat kinematics of two adult specimens of the nectar-feeding, phyllostomid bat *Glossophaga soricina antillarum* (Rehn), one pregnant and one non-pregnant bat, over a range of flight speeds (1.23–7.52 m s$^{-1}$). Animals were born in captivity in a breeding colony at Erlangen University. The colony of about 60 individuals was maintained in a tropical greenhouse where animals could fly freely. For the experiments, single animals were caught in the colony with a butterfly net and released into a 35 m flight tunnel used for this kinematic study (see also Winter, 1999). Bats adapted immediately to the new surroundings and did not require any special flight training. The only resting place in the flight tunnel was connected to an electronic balance connected to a computer (Winter and von Helversen, 1998). This allowed the monitoring of body mass during experiments without the need

to handle the animal. Computer controlled feeders at the opposite ends of the flight tunnel provided sugar water food to an experimental animal. This was collected during a bat's brief hovering visit to a feeder. Feeders were programmed so that food at the opposite ends of the flight tunnel was provided in an alternating fashion. This motivated a bat to fly between the ends of the tunnel in order to collect its daily food, thus passing the measurement section (see below). For a 1–2 day period before measuremens, bats were accustomed to the flight tunnel and the feeders to which they adopted quickly. During that time period they also had food available to them from small cups. The bats used did not carry any individual markers. Animal maintenance and care procedures followed legal requirements.

The following morphological characters were measured or calculated: body mass $M_b$ (kg) was measured using a digital balance (Mettler PM300) before or after each flight. Wing span $b$ (m) and wing area $S$ (m$^2$) were measured on the live bats with the wings outstretched as in the middle of the downstroke (Norberg and Rayner, 1987). Wing loading ($m\boldsymbol{g}$ $S^{-1}$ in Nm$^{-2}$, where $\boldsymbol{g}$ is acceleration of gravity) and the non-dimensional aspect ratio $b^2/S$ were then calculated.

### Flight tunnel and filming

The flights of the bats were filmed from the side and from below using a Photosonics high-speed film camera (100–200 frames s$^{-1}$; with time marking) in a 35 m long flight tunnel. Feeders were positioned at opposite ends of the tunnel. A string grid, forming 2 cm×2 cm squares, was used as a background scale at the filming section, allowance being made for the distance between the grid and the bat. The bats were also used as scale.

Infrared photosensors installed along the length of the tunnel recorded the passage of a passing bat, which was timed and stored by a computer and used to calculate the instantaneous speed within the section between the sensors (Winter, 1999). Based on this information the computer triggered the film camera shortly before a bat entered the filming section, but only at those flight speeds $V$ (m s$^{-1}$) for which film clips were still needed. We tried to obtain ten film records for each flight speed range and individual. Light sensors triggered the film camera when the bat was flying at a particular, chosen, flight speed. Different speeds were obtained by introducing obstacles and varying the length of the flight tunnel from both ends.

The actual flight speeds for the flights at which the kinematics were recorded were then carefully estimated from the films at the particular filming section. All flights included in the regressions were drawn picture by picture from the films and used for measurements of the various flight parameters. The final, instantaneous, speeds used for the various regressions were the speed recorded over two or three wing strokes, and which were close to the average speeds obtained between the light sensors. Only those flights that showed no or only very slight acceleration or deceleration were used in the analysis.

### Optimal flight speeds

Aerodynamic theory predicts that the power required to fly depends on flight speed, that the power *versus* speed curve is ∪-shaped (Pennycuick, 1968), and that the flying animal can fly at a speed optimal for a particular situation (Pennycuick, 1968; Norberg, 1981; Norberg, 1983; Norberg, 1990). Several comparisons have been made between observed flight speeds in the field or laboratory and theoretical values of optimal speeds derived from fixed wing aerodynamics. But it is difficult to verify if the theoretical values coincide with those used by flying birds and bats. Physiological measurements (see Norberg, 1990) indicate, however, that the power curve in some birds and bats is typically ∪-shaped, as predicted (Pennycuick, 1968), and that theoretical values may give a rough indication of the optimal speeds used. The speeds recorded in our bats were compared with the theoretical optimal flight speeds (minimum power speed $V_{mp}$ and maximum range speed $V_{mr}$), calculated according to the theoretical expressions (Rayner, 1986; Pennycuick, 2001a).

### Flight kinematics

Kinematic parameters obtained from the films were: wing beat frequency $f$ (s$^{-1}$), stroke plane angle $\alpha$ (degrees), wingtip excursion $a$ (m) and wing stroke amplitude $\theta$ (degrees). The vertical projection of the wingtip excursion was measured directly from the films, and the wingtip positions at the top and bottom of the stroke relative to the body axis determined the amplitude parts above and below the transverse line through the body. Compensation was made for deviations in the horizontal plane. The wing stroke amplitude $\theta$ (degrees) was then calculated with the cosine theorem using wing length and true wingtip excursion.

For geometrically similar flying animals, the minimum wing beat frequency $f_{min}$ should scale with body mass as $f_{min} \propto M_b^{-1/6}$ (Pennycuick, 1975) and the maximum frequency $f_{max}$ as $f_{max} \propto M_b^{-1/3}$ (Hill, 1950). Because any optimal flight speed should vary as $V \propto M_b^{0.17}$ (Pennycuick, 1975), the minimum and maximum wing beat frequencies should scale with flight speed as:

$$f_{min} \propto V^{-1/36(=-0.028)} \text{ and } f_{max} \propto V^{-1/18(=-0.056)} . \qquad (1)$$

Given the small exponents, the frequency should be almost independent of the flight speed for both cases. However, morphological characters besides body mass influence frequency. Pennycuick used a combination of multiple regression and dimensional analysis on empirical data for morphologically diverse bird species (Pennycuick, 1996; Pennycuick, 2001b), and showed that the natural wing beat frequency may be estimated by:

$$F = M_b^{3/8}(\boldsymbol{g}/q)^{1/2}b^{-23/24}S^{-1/3}\rho^{-3/8} , \qquad (2)$$

where $\boldsymbol{g}$ is acceleration of gravity, $q$ is a 'power fraction' accounting for the increased acceleration in bounding birds (equal to 1 for birds in level flight), and $\rho$ is air density. This equation predicts that if, for example, the body mass were to change in the course of a flight in one individual (at the same

air density), this should cause the wing beat frequency to change in proportion to the mass raised to 3/8. Pennycuick's computer model permits easy calculation of $f$ (Pennycuick, 2001a).

Bullen and McKenzie (Bullen and McKenzie, 2002) showed that, for 23 species of Australian bats of six families, the wing beat frequency varied with body mass and flight speed as:

$$f = 5.54 - 3.068\log_{10}(M_b - 2.875V) , \qquad (3)$$

and the amplitude varied as

$$\theta = 56.92 + 5.18V + 16.06\log_{10}(S) , \qquad (4)$$

The wing beat frequency for each species was found to vary slightly with flight speed over the lower half of the speed range, whereas it is almost independent of velocity at higher speeds.

Measurements from high-speed ciné films (200 frames s$^{-1}$) showed that the wing beat frequency in insectivorous bats in slow flight was:

$$F = 2.92M_b^{-0.274} , \qquad (5)$$

($R^2$=0.56, $N$=23; U.M.L.N. and R. Å. Norberg, unpublished observations).

The dimensionless Strouhal number $St$ is useful for describing oscillating flow mechanisms and unsteady flow (e.g. Hertel, 1966). It represents a measure of the ratio of inertial forces due to the unsteadiness of the flow or local acceleration to the inertial forces due to changes in velocity from one point to another in the flow field. The reduced frequency $k$ (the ratio between flapping velocity and forward speed at the half chord, and the inverse of the advance ratio) has long been used as a measure of the importance of unsteady effects, and because the biologically defined Strouhal number is linearly related to the reduced frequency, it can thus be used as an indicator of unsteady flow. The reduced frequency is simply $2\pi$ times the corresponding $St$ number. When $k \approx 0.1$ unsteady effects can usually be ignored, while at $k \approx 1$ there is probably a strong influence of unsteady phenomena.

The frequency $f_e$ of a series of eddies in a Kármán street behind a circular cylinder is proportional to the velocity of the incident flow $V$ and inversely proportional to the diameter $d$ of the circular cylinder (Hertel, 1966), which describe the Strouhal number as:

$$St = f_e d / V . \qquad (6)$$

At medium Reynolds numbers, in the region 200<Re<200 000, the Strouhal number is assumed to be constant $\approx$0.2. This means that, if an air current moving at 5 m s$^{-1}$ impinges upon a wire 5 mm in diameter, eddies separate at a frequency $f_e$=0.2×5/0.005=200 s$^{-1}$.

For flying animals $f_e$ is taken to be the wing beat frequency, and the cylinder diameter $d$ (referred to above) is represented by the amplitude $a$, such as the wingtip excursion. Flight speed affects $St$ strongly because wing beat frequency and amplitude are tightly constrained. If $St$ is too low (too low wing beat frequency) then the resulting vorticity will be insufficient to provide a thrust component of the lift to overcome the drag on the wing. Also at too high $St$ (too low speed) the efficiency is decreased. $St$ is significantly higher in bats ($St \approx$0.2–0.5) than in birds ($St \approx$0.2–0.4) in cruising flight (Taylor et al., 2003). In their investigation they used the equation $a=b\sin(\theta/2)$ to calculate the amplitude $a$ from predicted $\theta$ (Bullen and McKenzie, 2002).

Flying animals fly at a $St$ number tuned for high power efficiency, and $St$ is a simple and accurate predictor of wing beat frequency in birds (Nudds et al., 2004). In birds of various sizes and morphology the wing stroke angle $\theta$ scales with wing span as $\theta$=67$b^{-0.24}$ (Taylor et al., 2003). This equation was used by Nudds et al. to predict $\theta$ for 60 new species for which they could find measurements of $f$ and $V$ in cruising flight (Nudds et al., 2004). The following relationship was then obtained:

$$f \approx StV / b\sin(33.5b^{-0.24}) , \qquad (7)$$

where $St$ is shown to fall in the range 0.2<$St$<0.4. This equation thus requires knowledge of only cruising speed and wing span, the two of which must covary. The authors noted that the coincidal scaling of stroke angle with span is peculiar to birds. Within a narrow range of $St$ the product of frequency and amplitude should scale as $fa \propto M_b^{0.17}$ (Nudds et al., 2004).

We estimated the Strouhal number for various flight speeds to receive an indicator of the steadiness of the flow and to compare our data for $G. soricina$ with Eqn 6 and Eqn 7 for bats and birds. $St$ is essentially proportional to $k\theta$ (Lewin and Haj-Hariri, 2003), but although neither $St$ nor $k$ by themselves are sufficient to characterize the flow, the reduced frequency $k$ will not be treated further in this investigation.

### Span ratio

The ratio of lift $L$ to thrust $T$ is related to the span ratio $SR$ (the ratio of the wing span on the upstroke to that on the downstroke) as

$$L / T = [(1+SR) / (1-SR)] / \tan\beta , \qquad (9)$$

(Pennycuick, 1989), where $\beta$ is the lift angle. While the bat moves forward a distance equal to half the flapping wavelength $\lambda$ (Fig. 1B), the wingtip descends linearly through its vertical excursion $h$ during the downstroke. The angle between this line and the horizontal line is assumed to be a maximum estimate for the lift angle $\beta$ (Pennycuick, 1989), here termed $\beta_{max}$. The flapping wavelength is defined as $\lambda$=$V/f$ (Pennycuick, 1989), giving $\tan\beta_{max}$=$2h/\lambda$. Span ratios in our bats were measured from films taken from below the bats in horizontal flight.

### Downstroke ratio

The downstroke ratio $\tau$ is the duration of the downstroke, determined by the top and bottom points of the wingtip, divided by the total stroke period. It was measured in a number of wing strokes at different flight speeds.

### Regressions

The regressions were performed with Microsoft Excel for Macintosh, including least-squares regression and Student's $t$-test.

Table 1. *Body mass, wing measurements and optimal flight speeds in Glossophaga soricina antillarum*

| Bat | Body mass (g) | Wing span (m) | Wing loading (Nm$^{-2}$) | Aspect ratio | $V_{mp}$ (m s$^{-1}$) | $V_{mr}$ (m s$^{-1}$) |
|---|---|---|---|---|---|---|
| Non-pregnant | 10.2–11.4 | 0.273 | 8.8–8.9 | 6.6 | P: 5.9–6.1 | 11.4–11.7 |
| | | | | | R: 3.4 | 4.6–4.7 |
| Pregnant | 13.4 | 0.274 | 13.0 | 7.4 | P: 6.4 | 12.0 |
| | | | | | R: 3.9 | 5.2 |

The minimum power speed $V_{mp}$ and maximum range speed $V_{mr}$ were estimated with theoretical expressions by P (Pennycuick, 2001a) and R (Rayner, 1986).

## Results

### *Morphology and optimal flight speeds*

Body mass, wing measurements and the theoretical values of the optimal flight speeds are shown in Table 1. All calculated regression equations in this analysis are numbered from 10 to 22 and presented in Table 2. These are referred to when the results are discussed below.

With Pennycuick's program (Pennycuick, 2001a) the minimum power speed is estimated to $V_{mp} \approx 6$ m s$^{-1}$ for the non-pregant bat and $V_{mp} = 6.4$ m s$^{-1}$ for the pregnant bat, whereas Rayner's equations (Rayner, 1986) give about 3.5 m s$^{-1}$ and 3.9 m s$^{-1}$, respectively, amounting to only about 60% of the values obtained with Pennycuick's model. Maximum range speed would be $V_{mr} \approx 11.5$ m s$^{-1}$ in the non-pregant bat and $V_{mr} \approx 12$ m s$^{-1}$ in the pregnant bat with Pennycuick's model, and 4.6–4.7 m s$^{-1}$ in the non-pregnant bat and 5.2 m s$^{-1}$ in the pregnant bat with Rayner's equations.

When the flight tunnel was at its full length, *G. soricina* usually flew at speeds of 5–8 m s$^{-1}$. The average flight speed for 115 flights for the non-pregnant bat (here 10.7–11 g) was 6.6 m s$^{-1}$ (1.2–7.5 m s$^{-1}$) during straight flights when the bat was foraging in alternating fashion between the two ends of the flight tunnel. The average speed (for 21 flights) during more irregular flights for the same bat was 5.0 m s$^{-1}$. The speed of the pregnant bat was recorded only in the restricted flight tunnel, and was thus slow (1.75–4.8 m s$^{-1}$ during 17 flights).

### *Wing pattern*

We reconstructed the paths of the wingtip, thumb, nose and tail tip of the flying bat relative to the ground (Figs 1–5), and the paths of the wingtip, thumb and tail tip relative to the body of the bat (Fig. 6). Figs 1 and 2 show side views of the paths of the wingtip and thumb of the bat relative to the ground and at various flight speeds, and Figs 3–5 show views from below.

During the upstroke in hovering flight and at slow flight speeds the wingtip moves upwards–backwards relative to the still air, the bat thus producing a backward flick (Fig. 1A, Fig. 3). The handwings are strongly twisted and form inverted profiles with their ventral sides upwards. A positive thrust is then produced (Norberg, 1970; Norberg, 1976b). The upstroke thus seems to be aerodynamically active. This backward motion of the wings during the upstroke successively disappears at speeds $\approx 3.2$ m s$^{-1}$, above which the wingtip path becomes more vertical or directed upwards-forwards relative to the still air (Fig. 1C, Fig. 2, Fig. 5). However, we did not find any sudden change in wing kinematics with increasing flight speed.

The tail tip moves up and down with the wings and with the help of the leg movements, relative to the body, and its amplitude is most pronounced at slow speeds (Fig. 6). The legs also move outwards and inwards during the wing beat, attaining their outermost positions in the middle of the downstroke (Fig. 4).

Table 2. *Power functions of kinematic parameters against body mass, flight speed or wing beat frequency*

| Parameter | Equation | Number of observations | Power function | $R^2$ | $P$ |
|---|---|---|---|---|---|
| Wing beat frequency $f$ | (10) | 115 | $14.8V^{-0.277}$ | 0.288 | $<0.001 \times 10^{-6}$ |
|   Pregnant bat, slow speed | (11) | 16 | $18.5V^{-0.393}$ | 0.340 | $<0.01$ |
|   Pregnant bat, slower speeds | (12) | 14 | $12.7V^{0.007}$ | 0.0002 | $=0.84$ |
| Stroke plane angle $\alpha$ | (13) | 29 | $44.8V^{0.297}$ | 0.631 | $<0.001 \times 10^{-3}$ |
| | (14) | 29 | $184f^{-0.438}$ | 0.685 | $<0.001 \times 10^{-3}$ |
| Wing stroke amplitude $\theta$ | (15) | 24 | $67.1V^{0.174}$ | 0.146 | $=0.035$ |
| | (16) | 24 | $135f^{-0.204}$ | 0.081 | $=0.16$ |
| Wingtip excursion $a$ | (17) | 24 | $0.095V^{0.137}$ | 0.132 | $=0.048$ |
| | (18) | 24 | $0.164f^{-0.158}$ | 0.071 | $=0.20$ |
| Strouhal number $St$ | (19) | 24 | $1.93V^{-1.37}$ | 0.869 | $<0.001 \times 10^{-4}$ |
| Span ratio $SR$ | (20) | 17 | $0.588V^{-0.0216}$ | 0.002 | $=0.86$ |
| | (21) | 17 | $1.55f^{-0.397}$ | 0.247 | $=0.037$ |
| Downstroke ratio $\tau$ | (22) | 22 | $0.634V^{-0.179}$ | 0.099 | $=0.18$ |

$M_b$, body mass (kg); $V$, flight speed (m s$^{-1}$), $f$, wingbeat frequency.

2.4 m s$^{-1}$
14.7 wb s$^{-1}$
0.0064 s

3.1 m s$^{-1}$
11.6 wb s$^{-1}$
0.0055 s

3.5 m s$^{-1}$
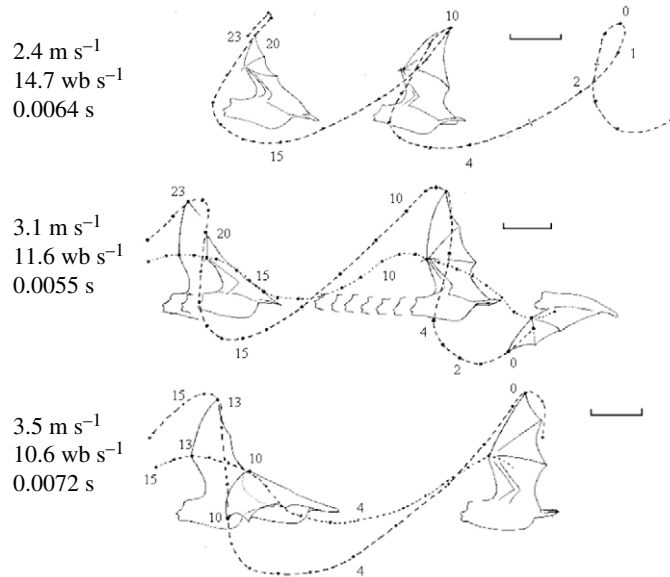10.6 wb s$^{-1}$
0.0072 s

Fig. 1. Lateral projection of the wing movements relative to the ground of *Glossophaga soricina* flying from right to left at slow flight speeds, 2.4–3.5 m s$^{-1}$. The top flight shows the tracks of the wingtip of the bat and the other two flights also include the tracks of the thumb. In slow flight (top flight) the wings are moved backwards relative to the ground during the upstroke. As speed increases the wingtip path becomes more vertical. Wing beat frequency (wb s$^{-1}$) decreases with increasing flight speed. The times indicated to the left, 0.0055–0.0072 s, are the times between each dot (numbered on the traces). Scale bars, 5 cm.

4.0 m s$^{-1}$
10.6 wb s$^{-1}$
0.0072 s

4.7 m s$^{-1}$
7.5 wb s$^{-1}$
0.0088 s

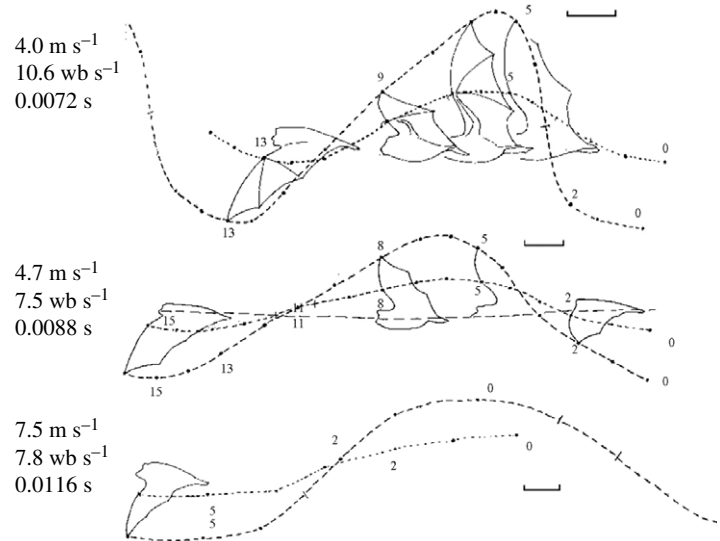7.5 m s$^{-1}$
7.8 wb s$^{-1}$
0.0116 s

Fig. 2. Lateral projection of the wing movements relative to the ground of *Glossophaga soricina* flying from right to left at flight speeds of 4.6–7.5 m s$^{-1}$. The wingtip paths become more sinusoidal relative to the ground as speed increases. Scale bars, 5 cm. For further explanation, see Fig. 1.

### Wing beat frequency

The wing beat frequency $f$ in the two bats varies with flight speed as $V^{-0.277}$ (Eqn 10, Table 2). It thus decreases with increasing flight speed, and the slope is significantly different from zero, which would be expected from geometric similarity (cf. Eqn 1). Our 10.2–13.4 g bats would thus have a frequency of 9 s$^{-1}$ at the theoretical minimum power speed ($\approx$6 m s$^{-1}$). With Eqn 5 (U.M.L.N. and R. Å. Norberg, unpublished); the frequency would become 10.3 and 9.52, respectively. According to Pennycuick's program (Pennycuick, 2001a) a 10.2 g bat is predicted to have a frequency of 8.0 s$^{-1}$ and a 13.4 g bat 9.0 s$^{-1}$, when flying at $V_{mp}$ (5.9 and 6.4 m s$^{-1}$, respectively).

The wing beat frequency in the pregnant bat alone, flying at slow speeds (1.75–4.78 m s$^{-1}$, 17 flights), varies with flight speed as $V^{-0.393}$ (Eqn 11, Fig. 7), where the slope is significantly different from zero. But at the lower speed interval 1.75–3.88 ms$^{-1}$ ($N$=15) the frequency does not change with speed, $f \propto V^{0.007}$ (Eqn 12, Fig. 7), which is contrary to the results found within a species among the Australian bats investigated (Bullen and McKenzie, 2002).

### Stroke plane angle

The stroke plane angle $\alpha$ becomes more vertical the higher the flight speed (Fig. 6). It changes with flight speed as $\alpha \propto V^{0.297}$ and with wing beat frequency as $\alpha \propto f^{-0.438}$ (Eqn 13 and Eqn 14).

Both slopes are significantly different from zero. The stroke plane angle varied from 45° at slow flight to 78° at faster flights.

### Wing stroke amplitude

The wing stroke amplitude $\theta$ is proportional to flight speed $V$ raised to 0.174, where the slope is significantly different from zero (Eqn 15). But there is no correlation between amplitude and frequency, where $\theta \propto f^{-0.204}$ (Eqn 16). The scatter around the regression line is large.

### Wingtip excursion

The wingtip excursion $a$ during a half-wing stroke (downstroke) changes with flight speed as $a \propto V^{0.137}$ (Eqn 17), where the coefficient is different from zero at the 5% level. When plotted against wing beat frequency it is $a \propto f^{-0.158.}$ (Eqn 18), but here the slope is not significantly different from zero. There is thus no correlation between wingtip excursion and wing beat frequency.

### Strouhal number

The propulsive efficiency in an oscillating system is high over a narrow range of the Strouhal number and usually peaks within the interval $0.2 < St < 0.4$ (e.g. Anderson et al., 1998; Wang, 2000). At lower and higher values the aerodynamic force production will be less efficient.

When cruising at speeds close to the theoretical minimum power speed (4–6 m s$^{-1}$), *G. soricina* operates with a Strouhal number associated with efficient lift and thrust production, $0.17 < St < 0.22$ (Fig. 8). At speeds >3.8–4 m s$^{-1}$ the wingtips describe a sinusoidal curve relative to the still air during the wing stroke (Figs 2 and 5). At speeds in the range 3.4–4 m s$^{-1}$ the Strouhal number is 0.25–0.4, which still is in a favourable

1.7 m s⁻¹
11.6 wb s⁻¹
0.0082 s
$M_b$=13.4 g
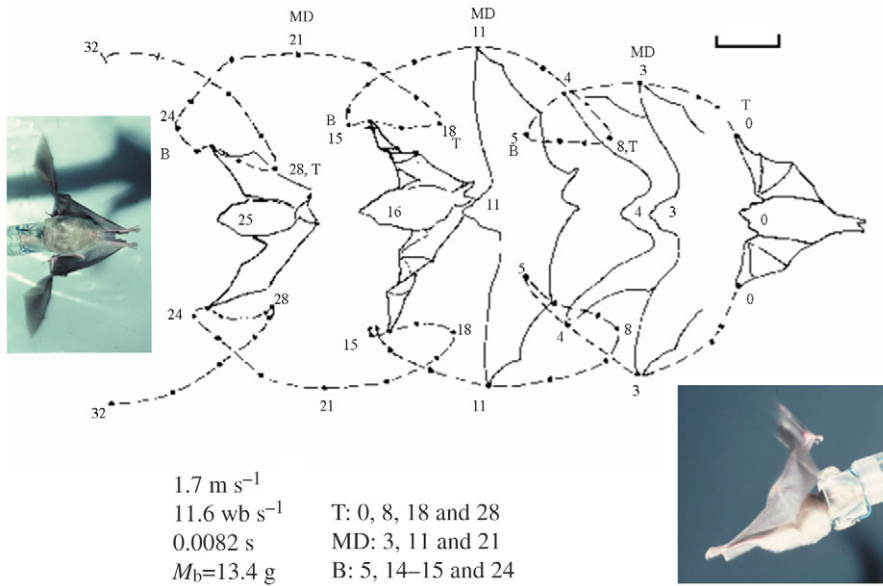
T: 0, 8, 18 and 28
MD: 3, 11 and 21
B: 5, 14–15 and 24

Fig. 3. Ventral projection of the wing-tip movements of *Glossophaga soricina* flying at 1.7 m s⁻¹. It can be seen that the backward flick of the wingtips is pronounced. The photographs show a hovering bat from below (left) and from the side (right) twisting the wings in the upstroke as in slow flight. T, top position; MD, middle position; B, bottom position of the wings, where the numbers refer to the numbers on the track. The time between each dot (numbered) is 0.0082 s for the two last (left) strokes. Scale bar, 5 cm.

region. When $V$ is less than about 3 m s⁻¹ the Strouhal number becomes higher (0.5<$St$<0.68), indicating that unsteady effects are important and that the production of lift and thrust is unfavourable.

Fig. 9 shows the Strouhal number plotted against flight speed. It decreases with increasing flight speed according to $St \propto V^{-1.37}$ (Eqn 19), with the negative slope highly significant from zero.

### Span ratio

The number of observations of span ratio $SR$ were restricted to views from below, which all were taken of the pregnant bat. The span ratio varies with flight speed as $SR \propto V^{-0.0216}$ (Eqn 20) and with wing beat frequency as $SR \propto f^{0.397}$ (Eqn 21). The span ratio does not change significantly with flight speed but it does with wing beat frequency.

Using the values from the polynomial curve, Eqn 9 (Pennycuick, 1989), the lift/thrust ratio would be about 2 for a

bat flying at 2 m s⁻¹, about 4.5 at 3 m s⁻¹ and 6.7 at 4 m s⁻¹. The ratio increases with increasing speed because the resultant force becomes more vertical at higher speeds.

### Downstroke ratio

There is no significant correlation between the downstroke ratio τ and flight speed $V$. In the speed interval 2.33–7.46 m s⁻¹ (22 flights) the downstroke ratio varied between 0.42 (at the higher speeds) and 0.67 (at the lower speeds). The ratio varies with flight speed as $\tau \propto V^{-0.179}$ (Eqn 22), and the slope is not significantly different from zero. For speeds <2.2 m s⁻¹ the downstroke ratio varies much more between those low flights where it was possible to estimate the ratio, which may depend on the estimation difficulties. Both at speeds 1.23 and 2.19 m s⁻¹ the ratio was estimated to 0.21 and 0.29, respectively, and in two flights at 1.7 m s⁻¹ the ratio was 0.63. This may depend on that the flights were somewhat irregular. No appreciable acceleration or deceleration could be observed.
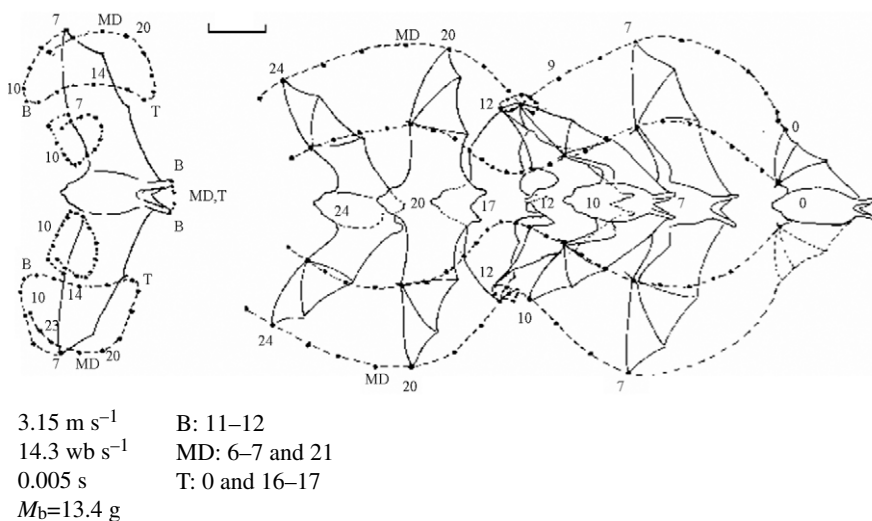


3.15 m s⁻¹
14.3 wb s⁻¹
0.005 s
$M_b$=13.4 g

B: 11–12
MD: 6–7 and 21
T: 0 and 16–17

Fig. 4. Ventral projection of the wing movements of *Glossophaga soricina* flying at 3.15 m s⁻¹. The backward flick of the wingtips is still visible. T, top position; MD, middle position; B, bottom position of the wings. The time between each dot (numbered) is 0.005 s. Scale bar, 5 cm.
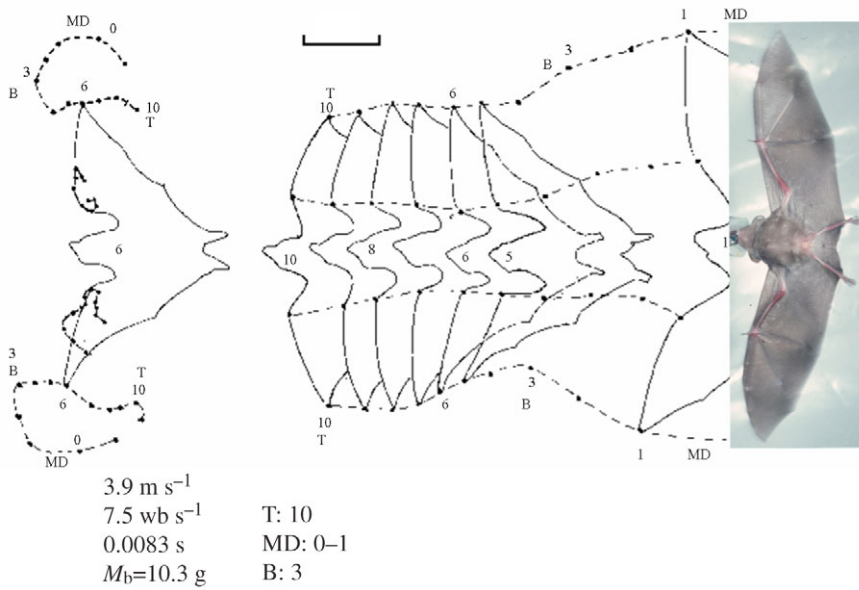
3.9 m s$^{-1}$
7.5 wb s$^{-1}$          T: 10
0.0083 s                 MD: 0–1
$M_b$=10.3 g            B: 3

Fig. 5. Ventral projection of the wing movements of *Glossophaga soricina* flying at 3.9 m s$^{-1}$. There is no backward motion of the wingtips relative to the ground. T, top position; MD, middle position; B, bottom position of the wings. The time between each dot (numbered) is 0.0083 s. Scale bar, 5 cm.

At speeds >2.2 m s$^{-1}$ there was thus a tendency towards an more rapid downstroke speed (decrease in downstroke fraction) when speed increased. A decrease in $\tau$ with increasing $V$ has been observed in birds flying in wind tunnels (Tobalske and Dial, 1996; Park et al., 2001; Rosén et al., 2004), where the values of $\tau$ commonly start at about 0.5 at the slowest speeds.

## Discussion and conclusion

### *Optimum flight speeds*

Winter demonstrated a clear ability of *G. soricina* to regulate their flight speed in response to small natural changes in body

mass (Winter, 1999). Flight speed also increased with length and width of the flight tunnel. Mean and maximum flight speeds over a 50 m flight tunnel path were 7.3 and 10.5 m s$^{-1}$, respectively, for a 11–12 g bat. The mean speed is slightly larger than the minimum power speed and the maximum speed slightly lower than the maximum range speed predicted by Pennycuick's program (Pennycuick, 2001a). The average flight speed observed in this investigation is slightly less (6.6 m s$^{-1}$) than in Winter's study (Winter, 1999), reflecting the shorter tunnel.

For best flight economy during flights in the long tunnel the bats should fly at $V_{mr}$ if time minimization is important, but
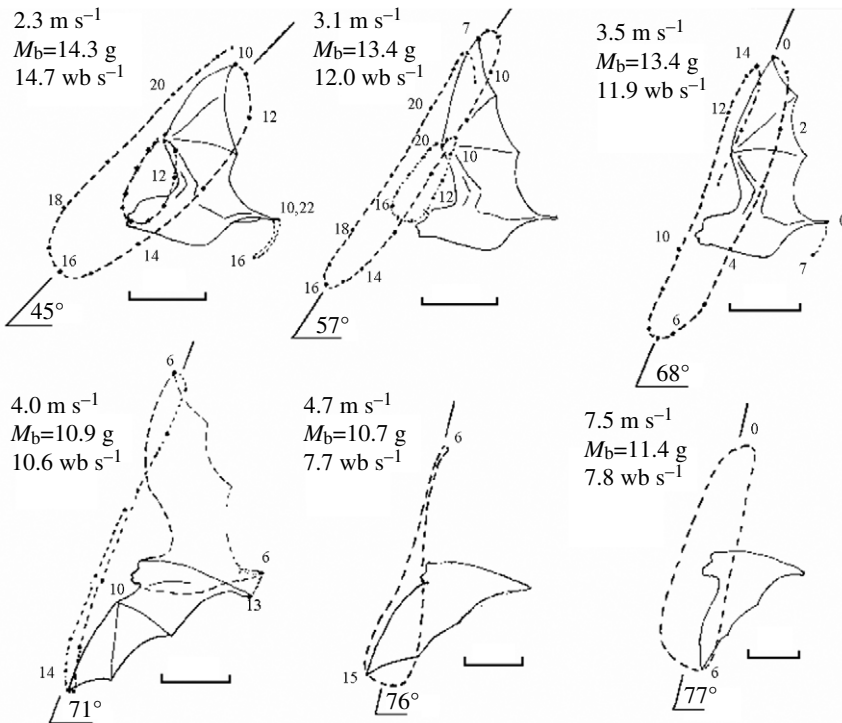


2.3 m s$^{-1}$
$M_b$=14.3 g
14.7 wb s$^{-1}$

3.1 m s$^{-1}$
$M_b$=13.4 g
12.0 wb s$^{-1}$

3.5 m s$^{-1}$
$M_b$=13.4 g
11.9 wb s$^{-1}$

4.0 m s$^{-1}$
$M_b$=10.9 g
10.6 wb s$^{-1}$

4.7 m s$^{-1}$
$M_b$=10.7 g
7.7 wb s$^{-1}$

7.5 m s$^{-1}$
$M_b$=11.4 g
7.8 wb s$^{-1}$

Fig. 6. Lateral projection of the tracks of the wingtip, thumb (at 2.3 and 3.1 m s$^{-1}$), and tail tip (at 2.3, 3.5 and 4.0 m s$^{-1}$) relative to the shoulder joint of *Glossophaga soricina* flying at different flight speeds. The stroke plane angle increases and wing beat frequency decreases with increasing flight speed. The up and down movements of the tail (uropatagium) are most pronounced at the slowest speeds.
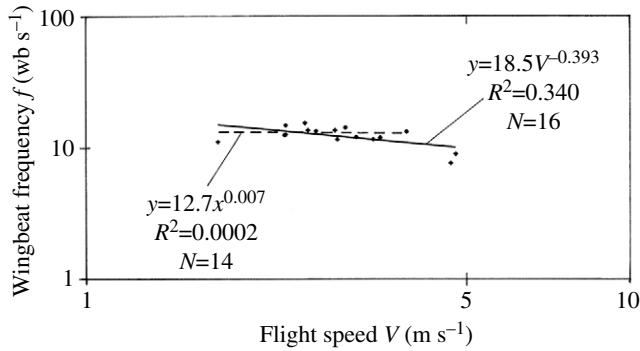
Fig. 7. Wing beat frequency plotted on logarithmic coordinates against flight speed in the pregnant specimen of *Glossophaga soricina,* flying at speeds 1.75–4.78 m s$^{-1}$ (continuous line) and at speeds 1.75–3.99 m s$^{-1}$ (broken line).
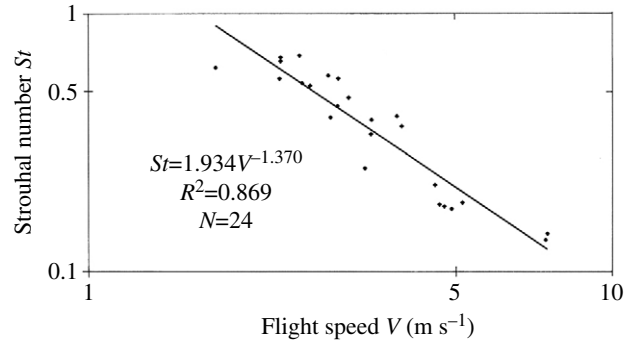


Fig. 9. Strouhal number plotted on logarithmic coordinates against flight speed in *Glossophaga soricina*.

otherwise at $V_{mp}$. The speeds used were close to Pennycuick's values for minimum power and Rayner's values for maximum range for our bats. The very slow speeds used in restricted spaces were on average lower than $V_{mp}$ with any of the two models, but closer to the value with Rayner's equation. Since the bats did not have to compete for food and could take the time they needed, we would assume that the speeds used in the unrestricted tunnel were close to minimum power speed, which thus were similar to the speed obtained with Pennycuick's model.

### Wing beat frequency, amplitude and stroke plane angle

Rosén et al. found no change in wing beat frequency or amplitude with increasing flight speed in the thrush nightingale (Rosén et al., 2004). But in *G. soricina* the wing stroke amplitude decreases slightly with increasing flight speed (with
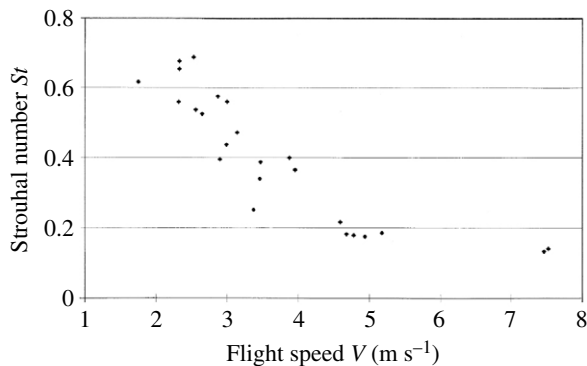


Fig. 8. Strouhal number as a function of flight speed in *Glossophaga soricina*. At speeds close to the theoretical minimum power speed (4–6 ms$^{-1}$) *G. soricina* operates with a Strouhal number associated with efficient lift and thrust production, 0.17<*St*<0.22. In the range 3.4–4 ms$^{-1}$ the Strouhal number is 0.25–0.4, which still is in a favourable region, but when *V*<3 ms$^{-1}$ the Strouhal number becomes higher (0.5<*St*<0.68), indicating that unsteady effects are important and that the production of lift and thrust is unfavourable.

the –0.17 power of speed) and wing beat frequency decreases with flight speed raised to –0.34. According to Eqn 10 our 10.2–13.4 g bats would have a frequency of 9 s$^{-1}$ at minimum power speed (6 m s$^{-1}$). With Eqn 5 (U.M.L.N. and R. Å. Norberg, unpublished) the frequency would become 10.1 and 9.4 s$^{-1}$, respectively. According to Pennycuick's program (Pennycuick, 2001a) a 10.2 g bat is predicted to have a frequency of 8.0 s$^{-1}$ and a 13.4 g bat 9.0 s$^{-1}$, when flying at $V_{mp}$ (5.9 and 6.4 m s$^{-1}$, respectively).

In the Australian bats observed by Bullen and McKenzie the wing beat frequency varied slightly with flight speed at low speeds (Bullen and McKenzie, 2002). This was also found in the pregnant *G. soricina* flying at very slow speeds (1.7–3.9 m s$^{-1}$) (Eqn 12). Tobalske et al. found that, in the black-billed magpie flying in a wind tunnel over a wide range of flight speeds (0–13.4 m s$^{-1}$), wing beat frequency, wingtip elevation and relative intensity of electromyographic signals s$^{-1}$ from the flight muscles were least at intermediate speeds and increased at both slower and faster speeds, in agreement with the theoretical U-shaped power curve (Tobalske et al., 1997). Similar changes in wing beat frequency and wingtip elevation did not occur in *G. soricina* at the flight speeds observed.

Nudds et al. suggested that wing beat frequency in birds can be predicted from $f \approx St\ V/b\sin(33.5b^{-0.24})$ (Eqn 7) (Nudds et al., 2004). Using this equation for our bats, the wing beat frequency would become 5.4 at *St*=0.21 and *V*=5 m s$^{-1}$, but we obtained *f*=9.5 in the non-pregnant specimen. Their equation is thus not applicable for our bat species.

### Strouhal number

Eqn 19 shows that the Strouhal number decreases with the –1.37 power of the flight speed. But the region for favourable force production peaks within the interval 0.2<*St*<0.4 (Anderson et al., 1998; Wang, 2000), and outside this region unsteadiness of the flow may become crucial. Close to the theoretical minimum power speed (4–6 ms$^{-1}$) *G. soricina* operates with a Strouhal number in the region 0.17<*St*<0.22 (Fig. 8), which is associated with efficient lift and thrust production. At slower speeds (3.4–4 m s$^{-1}$) the Strouhal number

is 0.25–0.4, which still is in a favourable region. But when *V* is less than about 3 m s$^{-1}$ the Strouhal number becomes higher (0.5<*St*<0.68), indicating that unsteady effects are important and that the production of lift and thrust is unfavourable. Only at these speeds do the bats perform the backward flick during the upstroke (Figs 1top, 3 and 4), which can produce thrust (Norberg, 1970; Norberg, 1976b). This may be a way in bats (and some birds) to increase the aerodynamic performance as compensation. To modulate wing beat frequency and amplitude may be morphologically more difficult.

### Span ratio and downstroke ratio

Among all kinematic data for the thrush nightingale in wind tunnel studies, only span ratio *SR* and downstroke ratio τ varied significantly with flight speed (Rosén et al., 2004). We found no such correlations between either *SR* and *V* (17 flights) or τ and *V* (22 flights) in *Glossophaga*. On the other hand *SR* decreases significantly with increasing wing beat frequency *f* (*SR*∝*f*$^{0.40}$; Eqn 21).

### Kinematics and vorticity

Wake patterns depend on both morphology and speed and has been predicted for various flight gaits. But it is difficult from the kinematics alone to predict the shape of the vorticity at each speed. Slow flight with inactive upstroke is usually associated with a vortex-ring gait, in very slow flight with a tip-reversal or supination during the upstroke, whereas faster flights can involve an active upstroke associated with a ladder wake. Using data on the vortex wake in the thrush nightingale (*L. luscinia*) from Spedding et al. (Spedding et al., 2003), Rosén et al. (Rosén et al., 2004) discussed the relationship between wing beat kinematics and vortex wake in the same species. These studies are the only sources for quantitative experimental analysis of the vortex wake in flight at different speeds, and they found no evidence that the bird transitioned between different discrete gaits. Spedding et al. did find different wake patterns at different speeds (Spedding et al., 2003), just no gait-transition-like switch between wake patterns at a particular speed. This is consistent with prior findings (e.g. Rayner et al., 1986) but does not meet Alexander's definition of gait (Alexander, 1989) given in the Introduction. Rayner et al. (Rayner et al., 1986) showed that the large noctule bat (*N. noctula*, 26–27 g) used a vortex-ring gait at very slow speeds (< minimum power speed) but a wake consisting of undulating vortex tubes at higher speeds (near maximum range speed), whereas the long-eared bat (*P. auritus,* 7–9 g), which is slightly lighter than *G. soricina*, showed no change in vorticity with changes in speed.

*G. soricina* does not seem to make sudden gait changes at any particular flight speed, because its flight kinematics change gradually. In hovering and very slow flight the bat twists its wings during the last part of the upstroke, inverting the camber of the tips by supination, thereby producing thrust and possibly slight vertical lift, because the resultant force and its lift component are then directed upwards and more forwards [cf. *Plecotus* (Norberg, 1976a; Norberg, 1976b)]. At faster, but still slow, speeds the resultant force seems to become directed downwards and backwards during the upstroke and no lift is produced. The stroke plane angle increases with flight speed raised to 0.29, and becomes more vertical as speed increases (Fig. 6). Estimates from the films of the resultant velocity in the upstroke indicate that vertical lift (and drag) are produced in the middle of the upstroke when forward flight speed is around 5 m s$^{-1}$ and higher. Spedding et al. showed that the wake in the thrush nightingale cannot be categorized as one of the two standard types, but that it has some similarity with the closed-loop model at the slowest speeds and with the constant-circulation model at highest speeds observed (Spedding et al., 2003). We suggest that similar patterns may occur also in *Glossophaga*. But this needs to be tested in wind-tunnel studies of the wake.

### List of symbols

| | |
|---|---|
| *a* | wingtip excursion |
| *b* | wing span |
| *d* | diameter |
| *f* | wing beat frequency |
| ***g*** | acceleration due to gravity |
| *h* | vertical excursion |
| *k* | reduced frequency |
| *L* | lift |
| $M_b$ | body mass |
| *q* | power fraction |
| Re | Reynolds number |
| *SR* | span ratio |
| *S* | wing area |
| *St* | Strouhal number |
| *T* | thrust |
| *V* | speed |
| $V_{mp}$ | minimum power speed |
| $V_{mr}$ | maximum range speed |
| α | stroke plane angle |
| β | lift angle |
| λ | wavelength |
| θ | wing stroke amplitude |
| ρ | air density |
| τ | downstroke ratio |

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