Comparative aerodynamic performance of flapping flight in two bat species using time-resolved wake visualization

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Bats are unique among extant actively flying animals in having very flexible wings, controlled by multi-jointed fingers. This gives the potential for fine-tuned active control to optimize aerodynamic performance throughout the wingbeat and thus a more efficient flight. But how bat wing performance scales with size, morphology and ecology is not yet known. Here, we present time-resolved fluid wake data of two species of bats flying freely across a range of flight speeds using stereoscopic digital particle image velocimetry in a wind tunnel. From these data, we construct an average wake for each bat species and speed combination, which is used to estimate the flight forces throughout the wingbeat and resulting flight performance properties such as lift-to-drag ratio ($L/D$). The results show that the wake dynamics and flight performance of both bat species are similar, as was expected since both species operate at similar Reynolds numbers ($Re$) and Strouhal numbers ($St$). However, maximum $L/D$ is achieved at a significantly higher flight speed for the larger, highly mobile and migratory bat species than for the smaller non-migratory species. Although the flight performance of these bats may depend on a range of morphological and ecological factors, the differences in optimal flight speeds between the species could at least partly be explained by differences in their movement ecology.

Keywords: bats; flight; aerodynamics; wind tunnel; particle image velocimetry; vortex wake

1. INTRODUCTION

Bat wings are known to be extremely flexible compared with wings of members of the two other taxa of actively flying animals, birds and insects. The bat wing consists of thin and highly compliant membranes spanned between stiffeners, consisting of elongated finger bones [1,2]. This gives the potential for fine-tuned active control to optimize aerodynamic performance throughout the wingbeat. As a result of this, the bat airframe solution is often associated with high maneuverability, but has also been associated with reduced energetic flight efficiency compared with birds [3–5]. However, bat wings are thin when compared with bird wings and resemble cambered flat plates rather than standard wing profiles. In a steady state configuration, such cambered flat plates outperform standard wing profiles at the Reynolds numbers ($Re$) relevant for bats and birds ([6,7]; $2.0 \times 10^3 \leq Re \leq 7.0 \times 10^4$, $Re = Uc/\nu$, where $U$ is the speed of the wing through the air, $c$ is the mean chord length of the wing and $\nu$ is the kinematic viscosity of air). There is, however, a large variation in wing size and morphology among bat species, which is related to variation in ecology [8,9]. The available data on flapping bat wing performance are too limited to draw any general conclusions on how bat wing performance varies between different bat species as a result of physical scaling laws, morphology or due to differences in their ecology.

Here, we compare the aerodynamic performance of two bat species, Glossophaga soricina and Leptonycteris yerbabuenae. Both species are New World nectar-feeding bats of the family Glossophaginae, which have similar morphology and life-history strategy [9]. We recognize two main differences between these species, their size and their movement ecology [9].

Leptonycteris yerbabuenae is about twice the weight of G. soricina. Based on this difference in weight we expect that characteristic flight speeds (e.g. minimum
power speed and maximum range speed [10]) are higher for *L. yerbabuenae* than for *G. soricina*. According to isometric scaling laws for animal flight [9,10], this difference should be in the order of $U_{\text{char}}^2 \sim (M^*)^{1/6}$, where $U_{\text{char}}$ is the characteristic flight speed ratio and $M^*$ is the mass ratio for the two bat species.

As for movement ecology, *G. soricina* is a resident species, which has a relatively small home range in which it both roosts and feeds. Its mean recapturing area is only 200 m$^2$ [11]. On the other hand, *L. yerbabuenae* makes long commuting flights between its roosting and feeding sites, travelling around 100 km every night [12]. Also, *L. yerbabuenae* migrates annually up to 1000–1600 km between southern Mexico and southern Arizona [13], which is among the longest known migration routes in bats.

On the basis of these ecological differences, one can assume that evolutionary selection pressure for efficient fast-forward flight should be stronger for *L. yerbabuenae*, and selection pressure for efficient hovering and slow flight should be stronger for *G. soricina* [9]. Thus, our hypothesis is that, when controlling for the differences in weight, optimal flight speeds for *L. yerbabuenae* should be significantly higher than for *G. soricina* ($U_{\text{char}}^2 > (M^*)^{1/6}$). A second hypothesis is that we do not expect the general wake morphology of the two studies species to differ. This is based on the large similarities between the wake morphology of *G. soricina* and *L. yerbabuenae* at a flight speed of 4 m s$^{-1}$ [14], and the similarities in wake morphology with a much larger bat, *Cynopterus brachyotis* [15,16].

To test these hypotheses, we studied the aerodynamic performance of both bat species flying freely in a wind tunnel across a range of flight speeds using time-resolved stereoscopic particle image velocimetry (PIV). The experimental set-up is described in Hedenström *et al.* [14], which is a methods paper showing preliminary data for these bats flying at a forward flight speed of 4 m s$^{-1}$. Here, we present a complete experimental dataset for these bats, over a flight speed range from 2 to 7 m s$^{-1}$. Using the time-resolved PIV data, we construct an average vortex wake based on multiple wingbeats for each species and flight speed combination [17]. From these average vortex wakes, we determine the flight force distribution throughout the wingbeat and measures of flight performance, such as the lift-to-drag ratio $L/D$. The resulting wake dynamics, temporal force production and flight performance measures are compared between the two nectar-feeding bat species, and with flight performance data of birds.

### 2. METHOD

#### 2.1. Study animals

The flight kinematics of *G. soricina* is described in Norberg & Winter [18] and Wolf *et al.* [19], and of *L. yerbabuenae* in R. von Busse, L. C. Johansson, Y. Winter & A. Hedenström (2011, unpublished data). The downstroke-to-upstroke ratio of both species is consistent across the studied flight speed range (2–7 m s$^{-1}$), being 0.52 ± 0.01 (mean ± s.d. $n=14$) for *G. soricina* and 0.51 ± 0.01 ($n=16$) for *L. yerbabuenae*. The Strouhal number ($St=f A/U_w$, where $U_w$ is the forward flight speed, $f$ is the flapping frequency and $A$ is the tip-to-tip vertical flapping amplitude of the wing tip) for *G. soricina* ranges from 0.67 at 2 m s$^{-1}$ to 0.25 at 7 m s$^{-1}$, while for *L. yerbabuenae*, it ranges from 0.68 at 2 m s$^{-1}$ to 0.23 at 7 m s$^{-1}$. In this study the $Re$ number range is $0.5 \times 10^4 \leq Re \leq 1.7 \times 10^4$ for *G. soricina*, and $0.6 \times 10^4 \leq Re \leq 2.1 \times 10^4$ for *L. yerbabuenae*. Of each bat species, a male and a female bat were used in our experiments, of which the morphological characteristics are shown in table 1.

Since the $Re$ range and the relation between the Strouhal number and flight speed are very similar between these two species, we assume that the wake dynamics scales similar with flight speed for both species. Therefore, we will directly compare the flight dynamics of the two species at each flight speed.

#### 2.2. Experimental set-up

The experimental set-up (electronic supplementary material, figure S1) was the same as the set-up described in Hedenström *et al.* [14], in which preliminary wake data were presented (the wake at 4 m s$^{-1}$). The bats were trained to fly at a feeder in the test section of the Lund low-turbulence wind tunnel [20], at wind tunnel speeds $U_w=2–7$ m s$^{-1}$, with 1 m s$^{-1}$ increments. An intermediate speed of 2.5 m s$^{-1}$ was included because a large change in kinematics was observed between 2 and 3 m s$^{-1}$ for *G. soricina* [19]. The PIV system image plane (approx. 20 × 20 cm) was positioned 20 cm downstream from the feeder. The PIV system consists of a transversely positioned $(y,z)$ plane (for the coordinate system see electronic supplementary material, figure S1) laser light sheet, generated by a 200 Hz pulsed 50 mJ Laser (Litron LPY732 series, Nd: YAG, 532 nm), and two synchronized, double frame, CMOS-cameras (High-SpeedStar3; 1024 × 1024 pixels) in stereo set-up. The system is controlled by the Lavision PIV software.
package DaVis (LaVision, DaVis 7.2.2.110). When a bat was flying steadily in front of the feeder, a sequence of 50 PIV measurements (1/4 s at 200 fps) of the wake was recorded. Simultaneously, a synchronized kinematics camera filmed the feeding bat from above at 250 Hz, which was used to determine the animal’s behaviour, position, attitude and wing morphology.

### 2.3. Particle image velocimetry analysis

The PIV images were analysed using DaVis (7.2.2.110), as described in Hedenström et al. [14] (multi-pass stereo cross-correlation {64 × 64 and 32 × 32, 50% overlap}, followed by a smoothing {3 × 3}). The resulting three-component transverse PIV data (\{u, v, w\} velocity matrix) are imported into a custom-made Matlab (7.7.0.471, R2008b) PIV analysis program, in which the location, vorticity and circulation of different vortices within a PIV frame can be measured. We have not determined if the patches of high vorticity that we call vortices are indeed vortices in the strict fluid-dynamics sense [21]. However, for convenience, we will refer to them as vortices in the rest of this paper.

The circulation \( \Gamma \) of a vortex is estimated by determining a vortex area of which the edge is defined by the \( |\omega|_{\text{max}} = 60 \text{ s}^{-1} \) vorticity iso-line. The threshold vorticity \( |\omega|_{\text{min}} \) is determined by the maximum vorticity caused by measurement uncertainties for the worst case with \( U_a = 7 \text{ m s}^{-1} \), estimated from background flows of an empty wind tunnel. The vortex circulation (\( \Gamma_{\text{measured}} \)) was determined by integrating the stream-wise vorticity (\( \omega_z \)) across the vortex area. Assuming that the vorticity in the vortex has a normal Gaussian distribution, the tails outside the cut-off \( (|\omega| < |\omega|_{\text{min}}) \) were added to determine the total vortex circulation as [22]

\[
\Gamma = \left( 1 + \frac{|\omega|_{\text{min}}}{|\omega|_{\text{max}}} \right) \Gamma_{\text{measured}},
\]

where \( |\omega|_{\text{max}} \) is the absolute peak vorticity of the vortex. The peak of the vortex is defined as the location of the peak vorticity \( |\omega|_{\text{max}} \).

The analysed PIV frames were given a normalized time stamp, \( \tau \), defined as

\[
\tau = \frac{t}{\Pi},
\]

where \( \Pi \) is the wingbeat period and \( t \) is the time of measurement in relation to the start of the downstroke within each wingbeat. The start of the downstroke \( (t = 0) \) is defined as the PIV frame when the tip vortex is at the highest vertical position (highest value in \( z \)-direction). By assuming that the wake convects downstream with the forward flight speed \( U_a \), the PIV frame time stamps can be converted into a stream-wise spatial value (along the \( x \)-axis) as

\[
x = U_a t.
\]

Using the \( x \) values for the collection of PIV frames of a single wingbeat, and assuming that the vortex wake interactions are negligible within the time scale of one wingbeat period \( \Pi \), a \( \{x,y,z\} \) wake matrix of this wingbeat is constructed. From this wake matrix a three-dimensional vortex wake can be constructed by creating iso-surfaces of the stream-wise vorticity.

Hedenström et al. [14] identified three main wake structures for \( G. \text{soricina} \) and \( L. \text{yerabuena} \) flying at 4 m s\(^{-1}\), being the tip vortex, root vortex and the reversed vortex dipole (see also [15,23,24]). If present in the PIV frame, all these vortex types are measured using the Matlab PIV analysis program. For each measured vortex, the peak vorticity (\( \omega_{\text{max}} \)), circulation (\( \Gamma \)), location of the peak vorticity (\( \{x, y, z\} \)) and time stamp (\( \tau \)) are stored in a database. For each individual and flight speed combination, at least five flight sequences (on average 11 wingbeats) were analysed.

### 3. VORTEX WAKE MODEL OF FLYING BATS

The three main wake structures for \( G. \text{soricina} \) and \( L. \text{yerabuena} \) flying at 4 m s\(^{-1}\), being the tip vortex, root vortex and reversed vortex dipole [14,23], are found in the wake of these bats throughout the complete flight speed range (figures 1 and 2), and are
therefore the vortex structures that we will use to define the wakes for both bat species. The flight forces associated with these different vortex structures can be estimated using Kelvin’s theorem and inviscid vortex theory [25] as follows (for details see electronic supplementary material, ‘Vortex wake model of flapping flight’):

\[
\begin{align*}
F_{\text{tip}}(\tau) &= \rho U_\infty b_{\text{tip}}(\tau) \Gamma_{\text{tip}}(\tau), \\
F_{\text{root}}(\tau) &= \rho U_\infty b_{\text{root}}(\tau) \Gamma_{\text{root}}(\tau), \\
F_{\text{rev}}(\tau) &= \rho U_\infty d_{\text{rev}}(\tau) \Gamma_{\text{rev}}(\tau),
\end{align*}
\]

(3.1)

where \(\rho\) is air density, \(\Gamma_{\text{tip}}(\tau)\) is the circulation of the tip vortex and \(\Gamma_{\text{root}}(\tau)\) is the circulation of the root vortex. \(\Gamma_{\text{rev}}(\tau)\) is the circulation of the reversed vortex dipole, defined as the mean value of the inner and outer vortex of the vortex dipole (respectively, \(\Gamma_{\text{rev}}^+\) and \(\Gamma_{\text{rev}}^-\))

\[
\Gamma_{\text{rev}} = \frac{(\Gamma_{\text{rev}}^+ + \Gamma_{\text{rev}}^-)}{2}.
\]

(3.2)

The \(b_{\text{tip}}(\tau)\) is the distance between the tip vortices of the left and right wing at \(\tau\), which is equal to twice the \(y\)-directional distance between the tip vortex to the body centreline (figure 1), \(b_{\text{root}}(\tau)\) is the distance between the root vortices, \(d_{\text{rev}}(\tau)\) is the width of the reversed vortex dipole (defined as the horizontal component of the red bar in figure 1b,d). Thus, we ignored the sideline forces (in \(y\)-direction), as these forces will cancel out owing to the symmetry of the left and right wing during steady flight.

The lift and thrust components of the forces in equation (3.1) can be determined by

\[
\begin{align*}
L(\tau) &= F(\tau) \cos(\gamma(\tau)), \\
T(\tau) &= F(\tau) \sin(\gamma(\tau)).
\end{align*}
\]

(3.3)

Figure 2. Different views of iso-surfaces of the stream-wise component of vorticity in the wake of a flying \(G.\) soricina and \(L.\) yerabuenae for a whole wingbeat. The red tube-like iso-surfaces show positive stream-wise vorticity and the blue iso-surfaces show negative stream-wise vorticity. The different panels are: (a) male \(G.\) soricina at 3.2 m s\(^{-1}\), isovalue: \(\omega_{\text{iso}} = 54\) s\(^{-1}\); (b) female \(G.\) soricina at 6.1 m s\(^{-1}\), isovalue: \(\omega_{\text{iso}} = 36\) s\(^{-1}\); (c) male \(L.\) yerabuenae at 3.3 m s\(^{-1}\), isovalue: \(\omega_{\text{iso}} = 53\) s\(^{-1}\); (d) female \(L.\) yerabuenae at 6.3 m s\(^{-1}\), isovalue: \(\omega_{\text{iso}} = 35\) s\(^{-1}\). Each (a)–(d) consist of four different views: perspective view (northwest); top view (northeast); front view (southwest); side view (southeast). Wind tunnel velocity vectors \(U_\infty\) are found in the perspective view, and in between the top and side view.
‘vortex wake model of flapping flight’). The mean vortex sheet angle for the tip- and root-vortex structures were estimated as

$$\gamma(\tau) = \frac{\gamma(\tau) + \gamma_{\text{body}}(\tau)}{2} = \frac{(1 - (A_{\text{body}}/A_g)) \gamma(\tau)}{2}, \quad (3.4)$$

where $\gamma(\tau)$ is the tip- or root-vortex angle, $A_{\text{body}}/A$ is the ratio between the vertical body movement amplitude and the vertical wing movement amplitude at the vortex position (see electronic supplementary material, ‘vortex wake model of flapping flight’). There is a minus sign in front of $A_{\text{body}}/A$ because the body movement is in antiphase compared with the wing movement (the body moves up when the wing moves down). Kinematics analysis showed that throughout the flight speed range $A_{\text{body}}/A_{\text{tip}} = 0.055 \pm 0.006$ for G. soricina (based on data presented by [19]), and $A_{\text{body}}/A_{\text{tip}} = 0.059 \pm 0.009$ for L. yerbabuenae (based on R. von Busse, L. C. Johansson, Y. Winter & A. Hedenström 2011, unpublished data). Since the relative body movement is consistent between species and flight speeds, $A_{\text{body}}/A_{\text{tip}} = 0.06$ is used in equation (3.4) for all flight speeds and both species. The body to root vortex movement is determined as $A_{\text{body}}/A_{\text{root}} = A_{\text{body}}/A_{\text{tip}} \times A_{\text{tip}}/A_{\text{root}}$. Since the root vortex cannot directly be linked to a certain wing section, $A_{\text{tip}}/A_{\text{root}}$ is determined using the vertical paths of the tip and root vortices. For the reversed vortex dipole, the mean vortex angle is equal to the mean $\gamma(\tau)$ of the outer and inner vortex of the dipole. The angle of each vortex structure ($\gamma(\tau)$) can be determined from the horizontal vortex path as

$$\gamma(\tau) = \tan^{-1}\left(\frac{dz(\tau)}{dx}\right) = \tan^{-1}\left(\frac{d\tau dz(\tau)}{dx}\right) = \tan^{-1}\left(\frac{1}{U_{\text{avg}}} \frac{dz(\tau)}{d\tau}\right). \quad (3.5)$$

We tested the sensitivity of the lift and thrust estimates on the wake angle assumptions in equation (3.4) by alternatively assuming no vertical body movement ($\gamma_{\text{body}} = 0$), instead of a 6 per cent antiphase body movement. This resulted in a mean reduction in lift force of 0.4 \pm 0.1\% of the total lift, and a mean thrust force increase of 5.6 \pm 0.4\% of the total thrust.

The total lift and thrust for a flying bat are determined by summing up the different components (note that each single wing generates a reversed vortex dipole)

$$L(\tau) = L_{\text{tip}}(\tau) + L_{\text{root}}(\tau) + 2 L_{\text{rev}}(\tau)$$

and

$$T(\tau) = T_{\text{tip}}(\tau) + T_{\text{root}}(\tau) + 2 T_{\text{rev}}(\tau) \quad (3.6)$$

From the $L(\tau)$ and $T(\tau)$ distribution of the flying bat, the mean effective lift and thrust for one wingbeat can be determined by integrating $L(\tau)$ and $T(\tau)$ throughout the wingbeat as

$$L = \int_{\tau=0}^{1} L(\tau) d\tau$$

and

$$T = \int_{\tau=0}^{1} T(\tau) d\tau \quad (3.7)$$

For a steady flying bat, the mean effective lift $L$ should be equal to the weight of the bat ($L = -W$), while the mean thrust should be equal to the mean drag produced by the whole animal ($T = -D$). Hence, by comparing $L$ with the body weight of the bat, the validity of the vortex wake model can be tested. The lift-to-drag ratio, which is an important value for flight efficiency, can be determined by $L/D = L/(-T)$.

To compare $F(\tau), L(\tau)$ and $T(\tau)$ for both bat species, we have normalized them using the weight of the animal

$$F^*(\tau) = \frac{F(\tau)}{W}, \quad L^*(\tau) = \frac{L(\tau)}{W}, \quad T^*(\tau) = \frac{T(\tau)}{W}, \quad (3.8)$$

where $W$ is the weight of the bat. The vertical movement of the different vortex structures, required to determine the force angle, is normalized by:

$$z^*(\tau) = \frac{z(\tau)}{b/2}, \quad (3.9)$$

where $b$ is the wingspan (table 1).

4. STATISTICS

4.1. Average wingbeat wake

The average wingbeat wake is defined, for each species and flight speed combination, by determining the average $F^*(\tau)$ and $z^*(\tau)$ distribution of the tip vortex, root vortex and the reversed vortex dipole [17]. With these characteristics the average wake for each species and speed combination can be modelled and analysed. The distributions were determined by fitting a cubic smoothing spline (Matlab, csaps, smoothing parameter = 1–10$^{-3}$) through the data points of the different PIV measurements. To ensure that the mean wingbeat splines are periodic, meaning that the slope and position of each spline is the same at $\tau = 0$ and at $\tau = 1$, the data points were multiplied twice and distributed over three wingbeat periods ($-1 \leq \tau \leq 2$). The mean wingbeat is described by the middle sub-spline (0 \leq \tau \leq 1). The relative deviation of the data points from the mean was estimated using a sliding 95\% confidence interval, determined from a sliding window of 20 local data points, where the value of 20 corresponds to the average amount of wingbeats used to construct the mean wingbeat.

4.2. Temporal force distribution

To determine any between-species differences in the temporal force distributions we used a mixed linear model, for each flight speed separately. The
normalized tip-vortex force estimates $F_{\text{tip}}^*(\tau)$ for each PIV measurement at a certain flight speed was set as dependent variable, with species as fixed factor. Individual was nested within species, sequence nested within individual and wingbeat nested within sequence, were set as random variables, $\tau$ is used as a covariate and was included as $\tau$, $\tau^2$, $\tau^3$ and $\tau^4$, which corresponds to fitting a fourth-order polynomial to the data. The two species were allowed to vary in the different coefficients in the polynomial by adding the interaction between species and $\tau$ and any higher orders of $\tau$. Since we do not have an a priori hypothesis about how $F_{\text{tip}}^*$ should vary with $\tau$, we first tested the fourth-order polynomial and successively removed the highest order non-significant combination. To allow for a better fit of the rather low-order polynomials (without affecting any differences between the species), the data were time shifted $\tau^* = \tau + \Delta \tau$ so that the minimum value of $F_{\text{tip}}^*$ coincided with $\tau^* = 0$.

4.3. Maximum lift-to-drag ratio and its corresponding flight speed

To determine any between species differences in the lift-to-drag polars ($L/D(U_{\text{in}})$), while controlling for difference in weight of the bats, the flight speeds are normalized. We normalized $U_{\text{in}}$ for $G. \text{soricina}$ with the unit speed ($U_{\text{in}}' = U_{\text{in}}/U_{\text{char}}$ with $U_{\text{char}} = 1$), so we normalized $U_{\text{in}}$ for $L. \text{yerbabuenae}$ by $U_{\text{char}} = M^*/10$.

Since the $L/D$ estimates are based on average wingbeats, error estimates are lost in the $L/D(U_{\text{in}}')$ distributions. Therefore, a jack-knife method was used to evaluate the variation in the $L/D(U_{\text{in}}')$ estimates, for each species–speed combination separately [26]. For a certain species–speed combination all the measured flight sequences are consecutively removed and replaced. At each removal $L/D$ is estimated, resulting in a distribution of $N$ $L/D$ estimates per species–speed combination, with $N$ being the amount of sequences measured at that species–speed combination. Through the resulting $L/D(U_{\text{in}}')$ distribution a third-order polynomial is fitted, for each species separately, which is used to estimate the maximum lift-to-drag ratio ($L/D_{\text{max}}$) and the corresponding flight speed ($U_{\text{in}}^*_{L/D_{\text{max}}}$). The variation in $L/D_{\text{max}}$ and $U_{\text{in}}^*_{L/D_{\text{max}}}$ was determined using the covariance matrix of the polynomial error. From the covariance matrix, we sampled 10,000 sets of polynomial coefficients resulting in 10,000 estimates of $L/D_{\text{max}}$ and $U_{\text{in}}^*_{L/D_{\text{max}}}$ per species. These distributions were used to determine the 95% confidence interval of the $L/D_{\text{max}}$ and $U_{\text{in}}^*_{L/D_{\text{max}}}$ estimates.

5. RESULTS AND DISCUSSION

5.1. Wake topology

The overall vortex wake topology for one wingbeat for both $G. \text{soricina}$ and $L. \text{yerbabuenae}$ flying at $U_{\text{in}} = 3$ and 6 m s$^{-1}$ is shown in figure 2. In the is-surface vorticity wake plots both the tip- and root vortices are distinguishable throughout almost the complete wingbeat (figure 2). Also the reversed vortex dipole is visible at the end of the upstroke and start of the downstroke, although they are more prominent at 6 m s$^{-1}$ than at 3 m s$^{-1}$ (best seen on the left side of the top views in figure 2). It is assumed that the reversed vortex dipole consists of the inner and outer vortices of a closed vortex loop, called the reversed vortex loop [23]. The spanwise parts of the vortex loop (the parts along the y-axis) are not visible because figure 2 shows only stream-wise vorticity, which is also the reason why no start or stop vortices are visible. The wake patterns for both species are qualitatively strikingly similar. The same structures are visible in both species, and only minor differences are present, such as the position of the root vortices at 3 m s$^{-1}$ and the relative strength of the reversed vortex dipole.

The vortex wake topology described here is similar to the wakes earlier described for bats [14–16,23,24]. When comparing the bat wake data with bird wake data at similar time resolution [17,27], it can be concluded that the bat wake topology is more complex than for birds that have weaker root vortices and no reversed vortex dipoles (cf. [27]).

5.2. Lift and drag estimates

To investigate if the similarities and differences in the vortex wakes of the different bat species have also quantitative merit, the average force distribution over the wingbeats were constructed for each species and speed combination (figure 3 and electronic supplementary material, figures S4 and S5). From these two distributions, the lift and thrust components for each wake structure were determined using equations (3.3)–(3.5) (electronic supplementary material, figures S6 and S7), and by adding these (equation (3.6)) the total lift ($L^*(\tau)$) and thrust ($T^*(\tau)$) distributions were determined (figure 4 and electronic supplementary material, figure S8). By integrating $L^*(\tau)$ and $T^*(\tau)$ throughout the wingbeat (equation (3.7)), the mean effective lift-to-weight ratio ($L/W$) and thrust-to-weight ratio ($T/W$) were determined.

To test the accuracy of our vortex wake model, we focus on the $L/W$ (figure 5a). Across the flight speed range $L/W = 0.97 \pm 0.03$ for $G. \text{soricina}$ and $L/W = 0.93 \pm 0.05$ for $L. \text{yerbabuenae}$, which are sufficiently close to 1, suggesting that the flight force estimate based on the model and measurements are reasonable (cf. [15]).

If assuming that the estimated mean thrust generated throughout the average wingbeat equals drag of the flying bat, we can determine the effective lift-to-drag ratio $L/D = -L/T$ for the bats (figure 5b). From the statistical analysis of the $L/D(U_{\text{in}})$ distribution, we find that both the maximum lift-to-drag ratio ($L/D_{\text{max}}$) and the corresponding normalized flight speed ($U_{\text{in}}^*_{L/D_{\text{max}}}$) are significantly different between the species (electronic supplementary material, figure S9). For $L. \text{yerbabuenae}$ the maximum lift-to-drag ratio ($L/D_{\text{max}} = 6.93$ (6.77–7.11, 95% confidence interval)) is
lower and occurs at a higher flight speed ($U_{L/D_{max}} = 4.39$ (4.18–4.57)) than for G. soricina ($L/D_{max} = 7.54$ (7.44–7.65) and $L/D_{max} = 3.45$ (3.42–3.49)). The differences in $U_{L/D_{max}}$ between the species are in line with our prediction that the highly mobile L. yerbabuenae should fly more efficiently at fast-forward flight speeds, while the more stationary G. soricina should fly more efficiently at hovering and slow flight speeds. Since both species operate at similar $Re$, the difference in $L/D_{max}$ is not expected, but can partly be explained by the fact that $L/D_{max}$ for L. yerbabuenae is underestimated using the third-order polynomial fit (figure 5b and electronic supplementary material, figure S9).

To the best of our knowledge, this is the first direct estimate of $L/D$ for flapping flight of bats, but the values are similar to $L/D$ for a gliding dog-faced bat.

Figure 3. $F^*(\tau)$ and $z^*(\tau)$ distributions for the different wake structures throughout the wingbeat of G. soricina and L. yerbabuenae, consisting of the average spline and the 95% confidence interval. (a) $F^*(\tau)$ at 2 m s$^{-1}$, (b) $F^*(\tau)$ at 6 m s$^{-1}$, (c) $z^*(\tau)$ at 2 m s$^{-1}$, and (d) $z^*(\tau)$ at 6 m s$^{-1}$. The results for the different species and wake structures are colour-coded as follows: red dashed lines, G. soricina tip vortex; orange dashed lines, G. soricina root vortex; brown dashed lines, G. soricina reversed vortex loop; dark blue dashed-dotted lines, L. yerbabuenae tip vortex; light blue dashed-dotted lines, L. yerbabuenae root vortex; turquoise dashed-dotted lines, L. yerbabuenae reversed vortex loop. The white-grey colour bars at the bottom of each panel show the downstroke (white) and upstroke (grey) section of the wingstroke. The gradient indicates the difference in the downstroke/upstroke transition between the two species, where G. soricina has a consistently earlier transition.

Figure 4. The overall $L^*(\tau)$ and $T^*(\tau)$ distribution throughout the average wingbeat for G. soricina and L. yerbabuenae at (a) 2 m s$^{-1}$ and (b) 6 m s$^{-1}$. The results of $L^*(\tau)$ and $T^*(\tau)$ for the different species are colour-coded as follows: red dashed lines, G. soricina $L^*$; orange dashed lines, G. soricina $T^*$; dark blue dashed-dotted lines, L. yerbabuenae $L^*$; light blue dashed-dotted lines, L. yerbabuenae $T^*$. The white-grey colour bars at the bottom of each panel show the downstroke (white) and upstroke (grey) section of the wingstroke. The gradient indicates the difference in the downstroke/upstroke transition between the two species, where G. soricina has a consistently earlier transition.
Rousettus aegyptiacus ([28]; figure 6). L/D at the largest measured flight speed ($U_w = 7 \text{ m s}^{-1}$) for G. soricina (L/D = 6.0) and L. yerbabuenae (L/D = 6.8) are compared with L/D of flapping birds (figure 6), for details on the L/D calculations [30]. For the flapping birds a positive correlation can be distinguished between L/D and Re. Our bats operate at the low end of this Re range, and when taking the L/D–Re correlation into account, the bats perform similar to birds, which seem to confirm that thin flexible bat wings perform relatively well at low Re [6,35]. If bat wings, in general, are more optimized for lower Re than birds, this would suggest that migrating bats should fly at lower flight speeds than birds, which could be one explanation for why bats migrate less and in general shorter distances than birds [30].

5.3. Force dynamics throughout the average wingbeat

The results of the analysis of how $F_{\text{tip}}(\tau)$ varies over the wingbeat in the two species (table 2 and electronic supplementary material, figure S10) show that for all speeds except 3 m s$^{-1}$, we find significant differences between the two bat species. This corresponds well with the fact that the 95% confidence intervals of $F_{\text{tip}}(\tau)$ for the two species do not overlap for at least part of the wingbeat (figure 3a,b,c and electronic supplementary material, figure S4), except for the force distribution at 3 m s$^{-1}$ (electronic supplementary material, figure S4c).

The main difference in $F_{\text{tip}}(\tau)$ between the species is that the force production is more equally distributed throughout the wingbeat for L. yerbabuenae than for G. soricina, resulting in a consistently lower maximum $F_{\text{tip}}(\tau)$ value for L. yerbabuenae. The tip vortex vertical movement throughout the wingbeat varies a lot between the different flight speeds (figure 3c,d and electronic supplementary material, figure S5). The root vortex follows the tip vortex movement closely at the lowest flight speeds (figure 3c), while it moves very little up and down at the highest speed (figure 3d). This is because, at higher speeds, the root vortex is shed from the inner wing or from the tail membrane (figure 2b), while at low flight speeds, the root vortex is shed further out on the wing (figure 2a). This means that, at low flight speeds, the outer wing generates most of the aerodynamic forces, probably because the effective airflow over the outer wing is higher than at the inner wing and body.

The force contribution of the reversed vortex dipole ($F_{\text{rev}}(\tau)$) is small compared with that of the tip and root vortex. At the lowest flight speed it is negligibly small (figure 3a), while for the higher speeds it is only present at the upstroke, where $F_{\text{rev}}(\tau)$ is of similar size as that of the other vortex forces. $F_{\text{rev}}(\tau)$ is consistently larger for G. soricina than for L. yerbabuenae. The vertical movement of the reversed vortex dipole throughout the wingbeat is similar for the two bat species (figure 3c,d and electronic supplementary material, figure S5).

Figure 5. Aerodynamic measures in relation to forward flight speed in G. soricina and L. yerbabuenae. (a) The lift-to-weight ratio $L/W$; (b) the lift-to-drag ratio $L/D$; (c) the maximum effective force coefficient $C_{\text{eff max}}$. The filled circles represent data for G. soricina and the open circles for L. yerbabuenae. (d) The relative contribution of the reversed vortex dipole on $L$ (filled and open circles) and $T$ (filled and open squares), defined as $U_r = L_{\text{rev}} / L \times 100$ and $T_r = T_{\text{rev}} / T \times 100$.

J. R. Soc. Interface (2011)
where

At flight speeds below 4–5 m s\(^{-1}\), thrust production varies significantly with flight speed. However, during the upstroke, the lift and thrust are generated during the downstroke at all flight speeds (figure S8). For both bat species, the majority of lift and thrust is generated during part of the upstroke (figure 4 and electronic supplementary material, figure S8), and this thrust production is negative (drag production) during the upstroke, while for higher speeds a small amount of negative lift in combination with positive thrust (figure 5d; see also [24]). The relative contribution of the reversed vortex dipole to the total lift and thrust production (respectively, \(L'_{\text{rev}}\) and \(T'_{\text{rev}}\)) varies almost linear with flight speed (figure 5d) resulting in a negligibly small contribution at the lowest speeds, but a significant contribution at the highest speeds.

To determine the influence of the reversed vortex dipole on the flight forces, we consider how the different wake structures contribute to lift and thrust production throughout the wingbeat (electronic supplementary material, figures S6 and S7). The reversed vortex dipole is present at the end of the upstroke [3,14,15,23], and generates negative lift in combination with positive thrust (figure 5d; see also [24]). The relative contribution of the reversed vortex dipole to the total lift and thrust production (respectively, \(L'_{\text{rev}}\) and \(T'_{\text{rev}}\)) varies almost linear with flight speed (figure 5d) resulting in a negligibly small contribution at the lowest speeds, but a significant contribution at the highest speeds.

Taken together, as a result of the vortex dipole, there is a positive total thrust during part of the upstroke for the highest flight speeds (figure 4 and electronic supplementary material, figure S8), and this thrust production is higher for \(G.\ soricina\) than for \(L.\ yerbabuenae\) (figure 5d). The \(L/D\) results show that the thrust requirements at these high flight speeds are higher than at medium flight speeds, as well as higher for \(G.\ soricina\) than for \(L.\ yerbabuenae\) (figure 5d). This suggests that the reversed vortex dipole is generated by the bat wing mainly to generate extra thrust, which is accompanied with some negative lift. A similar mechanism has been described as optimal for a flapping wing with a relatively large thrust requirement [39,40], where also both thrust and negative lift are generated by the outer part of the wing during the upstroke.

The reversed vortex dipole, resulting in negative lift and positive thrust, is generated by the bats by moving the outer wing upwards during the end of the upstroke resulting in \(U_{\text{eff}}\) with a downward component, and by positioning the outer wing at a negative effective angle of attack, \(\alpha_{\text{eff}}\) ([19], R. von Busse, L. C. Johansson, Y. Winter & A. Hedenström 2011, unpublished data).

5.4. Reversed vortex dipole

We determined the vortex wake dynamics for the average wingbeat of two microchiropteran bat species, from which we estimated the temporal flight force distributions and average flight performance, across a range of flight speeds from near hover to cruising flight speed. The results for \(G.\ soricina\) are similar to the results described by Hedenström et al. [23] and
Comparative aerodynamics in bats F. T. Muijres et al. 1427

Table 2. p-values for the $F_{2,0}(r)$ polynomial analysis at the measured flight speeds ($U_{\infty}$). The p-values in bold are significant.

<table>
<thead>
<tr>
<th>$U_{\infty}$</th>
<th>2 m s$^{-1}$</th>
<th>2.5 m s$^{-1}$</th>
<th>3 m s$^{-1}$</th>
<th>4 m s$^{-1}$</th>
<th>5 m s$^{-1}$</th>
<th>6 m s$^{-1}$</th>
<th>7 m s$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>0.0257</td>
<td>0.1532</td>
<td>0.4157</td>
<td>0.0064</td>
<td>&lt;0.0001</td>
<td>0.0002</td>
<td>0.0014</td>
</tr>
<tr>
<td>species</td>
<td>0.5719</td>
<td>0.1607</td>
<td>0.2037</td>
<td>0.2042</td>
<td>&lt;0.0001</td>
<td>0.0112</td>
<td>0.1362</td>
</tr>
<tr>
<td>time ($\tau$)</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$\tau^2$</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.1386</td>
<td>0.0096</td>
</tr>
<tr>
<td>$\tau^3$</td>
<td>0.0063</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.3051</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$\tau^4$</td>
<td>0.0648</td>
<td>&lt;0.0001</td>
<td>0.0130</td>
<td>&lt;0.0001</td>
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<td>$\tau \times$ species</td>
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<td>&lt;0.0001</td>
<td>0.7344</td>
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<tr>
<td>$\tau^2 \times$ species</td>
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<td>0.8531</td>
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<tr>
<td>$\tau^4 \times$ species</td>
<td>0.0464</td>
<td>—</td>
<td>0.9916</td>
<td>—</td>
<td>0.0147</td>
<td>0.3339</td>
<td>0.0306</td>
</tr>
</tbody>
</table>

Johansson et al. [24], but the present high-speed stereo PIV analysis allowed us to present more detailed wakes.

The wake pattern and associated measures are strikingly similar between the two species, which is in line with the fact that the bats operate at similar $St$ and $Re$ and our prediction based on the similar wake patterns of $G. soricina$ and $L. yerbabuenae$ in a previous study [3,14], and similarities with a larger megachiropteran bat flying at higher $Re$ [15]. Still, a few differences in the wake dynamics of the two bat species could be unravelled. The main difference was in the timing of the force production. $G. soricina$, generated the highest flight force during the first half of the downstroke, while $L. yerbabuenae$ generated lower forces more evenly throughout the downstroke and into the beginning of the upstroke. A typical wing has an optimal force coefficient ($C_{F_{\text{opt}}}$) at which the relative drag is lowest. This $C_{F_{\text{opt}}}$ occurs generally at moderate values of $C_F$, indicating that a wing at $C_{F_{\text{opt}}}$ should operate at relatively high speeds to generate significant/enough forces (figure 5c, [25]). If this is also the case for bat wings, a fast flying $L. yerbabuenae$ could operate at this $C_{F_{\text{opt}}}$ for a larger fraction of the wingstroke, resulting in more efficient flight at high speeds than $G. soricina$.

A direct estimate of the flight efficiency for these bat species are the determined $L/D$ values. When controlling for differences in weight between the species, the speed at which $L/D$ is maximum ($U_{L/D_{\text{max}}}$) was significantly higher for $L. yerbabuenae$ than for $G. soricina$. This is in line with our prediction that the more mobile and migratory species $L. yerbabuenae$ should fly more efficiently at higher flight speeds, and that the residential species $G. soricina$ should fly more efficiently at low flight speeds. Although the difference in flight performance between the two species may depend on a range of morphological and ecological factors, the agreement with the predictions from the species relative mobility suggests a hypothesis to be further tested in future comparative studies.

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