The wake of hovering flight in bats

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Hovering means stationary flight at zero net forward speed, which can be achieved by animals through muscle powered flapping flight. Small bats capable of hovering typically do so with a downstroke in an inclined stroke plane, and with an aerodynamically active outer wing during the upstroke. The magnitude and time history of aerodynamic forces should be reflected by vorticity shed into the wake. We thus expect hovering bats to generate a characteristic wake, but this has until now never been studied. Here we trained nectar-feeding bats, Leptonycteris yerbabuenae, to hover at a feeder and using time-resolved stereoscopic particle image velocimetry in conjunction with high-speed kinematic analysis we show that hovering nectar-feeding bats produce a series of bilateral stacked vortex loops. Vortex visualizations suggest that the downstroke produces the majority of the weight support, but that the upstroke contributes positively to the lift production. However, the relative contributions from downstroke and upstroke could not be determined on the basis of the wake, because wake elements from down- and upstroke mix and interact. We also use a modified actuator disc model to estimate lift force, power and flap efficiency. Based on our quantitative wake-induced velocities, the model accounts for weight support well (108%). Estimates of aerodynamic efficiency suggest hovering flight is less efficient than forward flapping flight, while the overall energy conversion efficiency (mechanical power output/metabolic power) was estimated at 13%.

1. Introduction

Hovering in animals is a special case of flapping flight where the forward speed is zero and where all the required aerodynamic force is generated by muscle powered wing beats. This flight mode allows an animal to remain stationary in the air while ingesting food, such as nectar from flowers, or looking out for food when lacking a suitable perch. In the absence of forward flight velocity, there is no net thrust, and neither any lift nor drag from the body, which simplifies the analysis to the lift and drag of the flapping wings. Among animals, we find two main types of hovering related to the kinematics and aerodynamic function of the downstroke and upstroke. In symmetric (‘normal’) hovering, the wings move in a horizontal stroke plane and both the kinematic downstroke and upstroke are aerodynamically active. At the end of the downstroke, the wing is rotated spanwise (pitch up) so that the morphological underside of the outer wing is facing upwards during the upstroke. Ideally, symmetric hovering, i.e. the downstroke ratio is 0.5 and each half-stroke generates an equal amount of lift. Superficially hummingbirds conform kinematically to symmetric hovering [1], but the downstroke generates about 66–75% of the total lift [2–4] due to small differences in stroke plane angle, angle of attack, camber and wing twist.

The second mode of hovering is ‘asymmetric hovering’, where the stroke plane is inclined to the horizontal and the downstroke generates the majority of the aerodynamic force, while the upstroke is more or less inactive (‘feathered’). Birds other than hummingbirds that are capable of hovering show this mode [5], sometimes with split primary feathers to allow air through and thereby minimize profile drag during the upstroke. Also bats in hovering flight show a kind of asymmetric hovering kinematics with an inclined stroke plane...
The flapping wings of a hovering animal induce a momentum flux that ideally forms a uniform jet directed downwards below the stroke plane [10], and the associated impulse represents the aerodynamic force that keeps the animal stationary in the air. In reality, the vorticity shed into the wake rolls up into structured vortices, which reflects the magnitude and time history of the aerodynamic force. The two modes of hovering are therefore associated with two main wake types, which can be illustrated as shown in figure 1. In symmetric hovering, there is one vortex loop shed as the result of each half-stroke, and due to the induced self-convection they will be seen as a series of stacked and tilted vortex loops (figure 1a), or a stack of bilateral loops originating from each wing in the case when the body is aerodynamically inactive (figure 1b; [10,13]). In asymmetric hovering, the wake has been postulated to consist of a single vortex loop shed as the result of a powerful downstroke and in the case of an inactive upstroke no vortices are shed during the upstroke (figure 1c). Flow visualization of wakes in hummingbirds suggest the model in figure 1b as most plausible [4,12], or a more complex arrangement of bi-lateral vortices [14]. An aerodynamic analysis based on wingbeat kinematics of a hovering pied flycatcher (Ficedula hypoxena) suggested an active downstroke and an inactive upstroke [5], as expected for asymmetric hovering with an inclined stroke plane. The wake of slowly flying (3 m s⁻¹) pied flycatchers showed vortex loops according to figure 1c [15], which suggests a similar wake may also count for hovering. The wakes of slowly flying bats show bilateral vortex loops and suggest an active upstroke attributed to the rotation and back-flick of the outer wing [16,17], with a lift-enhancing leading-edge vortex attached to the dorsal wing surface during downstroke [18], and a leading-edge vortex on the ventral outer wing surface during the upstroke [19]. However, the wake of asymmetric hovering in birds or bats has to our knowledge never been studied in quantitative detail, mainly due to technical difficulties. In this study, we present data on lesser long-nosed bats (Leptonycteris yerbabuenae), by using time-resolved flow visualization of the wake in a horizontal plane below hovering bats. The actuator disc model uses a helicopter analogue to generate a momentum jet that is often applied also when analysing hovering animal flight [10,20]. We use a modified actuator disc model based on our measurements of downwash distribution to derive aerodynamic force and induced power. In addition, we also estimate the energy conversion efficiency on the basis of our wake measurements and published information about the metabolic rate of hovering bats.

2. Material and methods

2.1. Experimental animals

Three individuals, one female and two males, of L. yerbabuenae, a nectar-feeding bat species found in southern parts of USA and Mexico, were used in this study. The species feeds by hovering in front of flowers of columnar cacti in the Sonoran Desert, and perform annual migration between Mexico and Arizona [21]. Morphological data of the specimens used in this study are presented in table 1.

2.2. Experimental set-up

2.2.1. Wind tunnel

The experiments were performed in the Lund University low-turbulence, low-speed wind tunnel [22]. The wind tunnel was set to run at 0.3 m s⁻¹ (0.32 ± 0.04 m s⁻¹ (mean ± s.d.)) to allow the smoke particles (see below) to disperse in a way that made particle image velocimetry (PIV) measurements possible. Hovering is defined as zero forward flight speed, while a more liberal definition is having an advance ratio, J, below 0.1 [23]. J is defined as the ratio between the flight speed (Uf) and the mean wingtip speed (Ut) in the animal’s coordinate system during a wingbeat as

\[ J = \frac{U_f}{U_t}. \]

The mean magnitude of wingtip velocity during the hovering was estimated from high-speed video recordings (see below), which yields an average advance ratio of 0.046 ± 0.0014 (mean ± s.e., n = 57) for our experiment, thus kinematically qualifying as hovering sensu [23]).

The bats were trained to hover in front of a feeding tube (figure 2). An infrared (IR) barrier positioned in front of the tube was connected to a microprocessor (Arduino Uno), programmed to detect when the IR barrier was broken for a user-specified period of time. When triggered, the program activated a syringe pump filled with honey water connected to the feeding tube via silicone tubing. This set-up allowed for training the bats to extend their hovering periods before getting the food reward, resulting in sequences of hovering for up to nine wingbeats. Between feeding bouts, the bats roosted on a nest 6 m upstream of the test section in the settling chamber. During the experiments, the bats would fly into the test section, perform a
Table 1. Morphological and kinematic data for the bats in this study. The data consist of mass \((m)\), wing span \((b)\), surface area \((S)\), mean chord length \((c = S/b)\), aspect ratio \((AR = b^2/S)\), wing loading \((Q = mg/S)\), where \(g = 9.81 \text{ m s}^{-2}\) is the gravitational acceleration, wingbeat frequency \((f)\), span ratio \((\text{upstroke span}/\text{downstroke span})\) downstroke ratio \((\tau = t_d/T)\), where \(t_d\) is the downstroke period and \(T\) is the total wingbeat period.

<table>
<thead>
<tr>
<th>bat</th>
<th>(m) (g)</th>
<th>(b) (cm)</th>
<th>(S) (cm²)</th>
<th>(c) (cm)</th>
<th>(AR)</th>
<th>(Q) (N m⁻²)</th>
<th>(f) (Hz)</th>
<th>span ratio</th>
<th>(\tau)</th>
</tr>
</thead>
<tbody>
<tr>
<td>female</td>
<td>24.5</td>
<td>33.2</td>
<td>151.1</td>
<td>4.5</td>
<td>7.3</td>
<td>15.9</td>
<td>11.4</td>
<td>0.56</td>
<td>0.44</td>
</tr>
<tr>
<td>male 1</td>
<td>30.1</td>
<td>34.9</td>
<td>176.4</td>
<td>5.0</td>
<td>6.9</td>
<td>16.8</td>
<td>12.4</td>
<td>0.53</td>
<td>0.46</td>
</tr>
<tr>
<td>male 2</td>
<td>25.2</td>
<td>33.4</td>
<td>156.9</td>
<td>4.7</td>
<td>7.1</td>
<td>15.8</td>
<td>12.4</td>
<td>0.53</td>
<td>0.45</td>
</tr>
<tr>
<td>mean</td>
<td>26.6</td>
<td>33.8</td>
<td>161.5</td>
<td>4.7</td>
<td>7.1</td>
<td>16.2</td>
<td>12.1</td>
<td>0.54</td>
<td>0.45</td>
</tr>
</tbody>
</table>

For illustration purposes, we generated three-dimensional velocity matrices using the self-induced vortex migration speed, calculated as the mean downwash speed of each frame [24], multiplied by the time difference between frames \((1/200 \text{ s})\) to estimate the distance between frames in the \(z\)-direction. This is an approximation, but affecting only the visualization of the wake and not the force estimates. The resulting matrix of three-dimensional vorticity was used to construct iso-surface plots. Iso-surfaces were coloured coded according to the downwash speed and the isovalue threshold was varied until the major vortex structures were clearly visible.

2.2.3. Kinematics

An additional pair of cameras (Redlake MotionScope PCI 500), running at 250 Hz, was pointed at the bats during the experiments and was triggered by the same manual trigger that started PIV recording IR light (VDI-IR607, Video Security Inc. Taiwan, Specify) was used to illuminate the bat without interfering with the PIV cameras and to minimize disturbance of the bats. The two cameras were calibrated and the videos were analysed using a customized Matlab (5.0.0.783, 64-bit, R2012b) program, to generate three-dimensional coordinates of morphological markers of the hovering bats over time.

The position of the wingtip in the \((x, z)\)-plane was used for defining the transition between upstroke and downstroke, and vice versa. The mean between the time point for the maximum of the \(z\)-wise position of the wingtip and the maximum for the \(x\)-wise position of the wingtip was used to define the beginning of the downstroke (end of the upstroke). In the same manner, the mean of the time point for the minimum of the \(z\)-wise position of the wingtip and the time point for the minimum of the \(x\)-wise
position of the wingtip was defined as the end of the downstroke/the beginning of the upstroke.

The wingbeat frequency, \( f \), was calculated by taking the inverse of the period of the whole wingbeat, \( T \), as such:

\[
f = \frac{1}{T}.
\]  
(2.1)

The downstroke ratio, \( \tau \), the ratio between the time it took for the bat to perform the downstroke, \( T_d \), and the total period of the wingbeat, \( T \), is,

\[
\tau = \frac{T_d}{T}.
\]  
(2.2)

2.3. Force, power and efficiency estimates

2.3.1. Modified actuator disc model

In an actuator disc model of hovering, the animal is assumed to produce lift by accelerating air through an imaginary disc positioned horizontally at the level of the stroke plane. The disc imparts a downwards-directed momentum flux and the force associated with the impulse is the lift. As air is accelerated downwards the wake contracts until the induced velocity reaches its final value of \( 2w \) [25]. Expressing the lift, \( L \), produced and the power, \( P_t \), imparted to the air in terms of the velocity in the far wake, results in the following equations [10]:

\[
L = \rho S w^2
\]  
(2.3a)

\[
P_t = \frac{\rho}{2} S w^3,
\]  
(2.3b)

where \( \rho \) is the air density, \( S \) the cross-sectional area of the mature wake and \( w \) the induced downwash speed in the mature wake, where the induced power increases with the cube of the downwash speed. The mature wake refers to when the induced velocity has reached its final speed.

In the classical actuator disc model, the area of the disc is taken as a circle with diameter equal to that of the wingspan of the animal. In the model used here, the area of the (mature) wake is calculated as the area of measurement in which the downwash speed lies outside the 95% CI of the mean of the background speed calculated from measurements (\( n = 7 \)) done without bats. The area therefore varies with time, \( S(t) \).

The lift and power expressed as time-dependent integrals yield

\[
L(t) = \rho \int_{S(t)} w(x, y, t)^2 \, dx \cdot dy
\]  
(2.4)

and

\[
P_t(t) = \frac{\rho}{2} \int_{S(t)} w(x, y, t)^3 \, dx \cdot dy,
\]  
(2.5)

where the downwash speed \( w(x, y, t) \) varies with position in the horizontal plane, as well as with time throughout the wingbeat.

The lift during a wingbeat was normalized by the weight of the animal. To remove unsteady events, such as decelerations when arriving at feeder and accelerating when leaving the feeder, only wingbeats showing an average deviation less than \( \pm 20\% \) of weight support were included in the further analysis. The vertical force production over a normalized wing beat was estimated using a smoothing spline of the data from the individual wingbeats (Matlab, settings for smoothing: Matlab function ‘fit’ using the smoothing spline method ‘smootherspline’ and a smoothing parameter ‘SmoothingParam’ of 0.99981). The standard error of the spline was determined using a sliding box, with a normalized time equal to the average time between measurements, with the s.e. centred around each measurement then subject to the same smoothing spline settings as the raw data. The overall means reported are estimated as the intercept \( \pm \) s.e. estimated using a repeated measures set-up with wingbeat nested within sequence and sequence nested within individual.

We define a normalized time

\[
\tau_n = \frac{t}{T},
\]  
(2.6)

where \( t \) is the time, and \( T \) is the wingbeat period.

The mean induced power generated over the whole wingbeat is given by

\[
P_{\text{wb}} = \frac{\rho}{2} \int_{S(t)} w(x, y, \tau_n)^3 \, dx \cdot dy \cdot d\tau_n.
\]  
(2.7)

To minimize induced power over the whole wingbeat requires a uniform induced downwash over the wingbeat period [10]. This optimal time-invariant downwash speed can be calculated as

\[
w_{\text{filp, ideal}} = \frac{\int_{n=0}^{1} \int_{S(t)} w(x, y, \tau_n)^3 \, dx \cdot dy \cdot d\tau_n}{\int_{n=0}^{1} \int_{S(t)} dx \cdot dy \cdot d\tau_n}
\]  
(2.8)

The mean induced power generated over this ideal wingbeat is given by

\[
P_{\text{ideal, wb}} = \frac{\rho}{2} \int_{n=0}^{1} \int_{S(t)} w_{\text{filp, ideal}}^3 \, dx \cdot dy \cdot d\tau_n,
\]  
(2.9)

and the ratio between this ideal induced flap power and the induced power generated by the actual wingbeat is the flap efficiency defined as

\[
eff_{\text{filp}} = \frac{P_{\text{ideal, wb}}}{P_{\text{wb}}}.
\]  
(2.10)

3. Results

3.1. Kinematics

During the downstroke, the wings flap forwards and downwards, fully outstretched, in a stroke plane tilted \( 30^\circ \pm 0.9^\circ \) (\( n = 57 \) wing beats) relative to the horizontal (figure 3a,b). During the upstroke, the motion is reversed and the span is reduced to \( 54\% \pm 1\% \) (\( n = 57 \)) of full span by folding the inner part of the wing, resulting in the wingtip moving backwards closer to the body than during the downstroke (figure 3b). At the end of the downstroke/beginning of upstroke, the wing goes through a fast pitch-up motion. The pitch-up is faster towards the tip, resulting in twist along the span during the upstroke, which results in the outer wing (dactylopatagium) moving backwards and upwards inverted, i.e. the air meets the morphological dorsal side of the hand wing, which is facing downwards. The average flapping frequency was \( 12.1 \pm 0.34 \) Hz (\( n = 57 \)) and the downstroke ratio was \( \tau = 0.45 \pm 0.01 \) (\( n = 57 \), table 1).

3.2. Wake topology

The wake of the downstroke is characterized by a pair of vortex loops, one generated by each wing and tilted relative between the wing root and wing tip (figure 4). These two vortices circulate around the area of induced downwash (figure 4c). The wakes of the left and right wings come close together at the end of the downstroke, resulting in a complex wake structure representing the interaction of the stop vortices of the two wings (figure 4a,b,d). The horizontal extension of the wake has a lunar shape (figure 4c), which can be
viewed as the realized actuator disc shape. This is because the wing is flexed during the upstroke so the tip vortex trails the wing tip path closer to the body during the upstroke than during the downstroke. In addition to the main vortex structures, in many cases we also find minor vortices apparently rotating around the main tip vortex of the downstroke (figure 4b). The wake illustrated by iso-surfaces according to downwash shows the asymmetry of generated induced downwash between upstroke and downstroke (figure 5a–d). It is also apparent that the upstroke generates a downwash pulse (figure 5a,b,d), and that the downwash is mainly generated by the outer wing (figure 5c).

The wake of the upstroke is weaker than that of the downstroke, not even visible in all wing beats due to vorticity being below the threshold value in the iso-surface plots. When visible it is represented by vortical structures connecting the central forward section of the downstroke wake and the distal lateral section of the next downstroke wake above it (figure 4a,b). Overall, the wake topology shows a pulsatile pattern associated with the downstroke and upstroke, with associated variation in vertical force generated (figure 5c).

3.3. Lift and power
Lift is associated with the rate of vertical momentum shed into the wake. The average weight support during a wingbeat was $1.08 \pm 0.034$ ($n = 37$), which suggests our measurements accounted for the vertical force required. The momentary vertical force calculated by using the modified actuator disc model, showed a clear periodicity coinciding with the wing beat period and nowhere during the wingbeat is the estimated weight support zero (figure 6).

Using equation (2.7), we estimated the induced power to $0.39 \pm 0.025 \text{W}$ ($n = 37$). Comparing the induced power with that of an ideal downwash distribution over the same disc area (equation (2.9)) yielded a flap efficiency (equation (2.10)) of $0.59 \pm 0.009$ ($n = 37$). In classical actuator disc theory, the disc area is defined as a circle with the semi-span as radius (i.e. $S = \pi r^2/4$ in equation (2.3b), and $\rho = 1.2 \text{kg m}^{-3}$ as average during the experiments), which yields an ideal induced power $P_{\text{ideal}} = 0.29 \text{W}$. The ratio between realized induced power and $P_{\text{ideal}}$ is the induced power factor, $k$, which is used as a correction factor in models of animal flight. For our bats $k = 1.33 \pm 0.02$ ($n = 37$).

4. Discussion
4.1. Wake
The wake of hovering *L. yerbabuenae* is characterized by strong bilateral vortices shed from the downstroke, but also vortices shed during the upstroke that links together successive downstroke wake structures. With the low speed of the air past the inner part of the wing and the strong speed gradient along the span when flapping wings at zero forward speed, we expect a root vortex to roll up at a position relatively distally on the wing, which appears to occur about halfway between the wing root and the wing tip. Since the wake is heavily influenced by self-induced convection, it is hard to disentangle the complicated wake originating during the downstroke.
and upstroke. At the end of the downstroke and beginning of
the next upstroke, interaction of the wake from the two wings
and the almost 180° supination of the outer wing further com-
plicate the interpretation. Also, because the start vortex
generated at the beginning of the downstroke has travelled
downwards due to self-convection, the completed downstroke
wake appears more horizontal (6°) than the kinematic stroke
plane angle (30°). In addition, during the upstroke the wing-
span is reduced (span ratio = 54%), which results in an
upstroke vortex structure that is shifted medially compared
to the downstroke vortex and where the tip vortex of the
upstroke is shed in downwash generated during the previous
and subsequent downstroke. Further to that, the self-induced
motion of the upstroke wake is directed more rearwards and
will have a slower downward motion than that of the down-
stroke. This will result in a differential motion between
upstroke and downstroke wake structures, where the down-
stroke wake will catch up and potentially overtake the
upstroke wake. However, despite the complexity of the wake
we can conclude that the downstroke wake dominates the
force contribution of the whole wingbeat, but the upstroke is
not entirely inactive. Previous studies of wingbeat kinematics
in small hovering bats, Glossophaga soricina, suggested an
active upstroke [7], which was also confirmed by flow visual-
ization of wakes in slow (1.5 m s⁻¹) forward flight [16].

The larger L. yerbaeae shows very similar wingbeat kin-
ematics to G. soricina in hovering and slow flight ([9]; this
study), including an inverted outer wing during the upstroke.
In slow flight (1 m s⁻¹), the upwards-facing ventral wing sur-
face even generate a leading-edge vortex during the upstroke
[19], which demonstrates an aerodynamically active upstroke.

A cartoon representation of the bat hovering wake based on
figure 4 is shown in figure 1d, which differs from all suggested
principal wake topologies for vertebrate hovering (figure 1a–c).
Because the body does not generate any lift in hovering flight,
the wake is bilateral with separate vortices from the two wings.
This is also the case in hummingbirds [4,12,14], but in humming-
birds each half-stroke result in isolated vortex loops. In the
pied flycatcher Ficedula hypoleuca [14], which had an inac-
tive upstroke, the slow flight (3 m s⁻¹) wake consisted of
unilateral vortex loops according to figure 1c. Hence, the
wake of asymmetric hovering by bats may be viewed as
asymmetric hovering with an active upstroke.

4.2. Lift
Overall, the wake contained sufficient momentum to account
for the weight. The induced downwash in the wake was not
zero at any point during the wingbeat period, which is
expected both in symmetric and asymmetric hovering. How-
ever, our current method does not allow us to derive the
relative force contribution between downstroke and upstroke.
Based on vortex circulation measurements that are directly
related to lift, from transverse or parasagittal imaging
planes, the downstroke of hummingbirds was estimated to
account for between 66 and 75% [2,4] of the required
weight support. Wake measurements in pied flycatchers
suggested an inactive upstroke in slow flight [15]. In our
hovering bats, the relative downstroke contribution to lift is
likely larger than in hummingbirds (considering the relative
strength of downstroke and upstroke vortices) but less than
in the pied flycatcher.
4.3. Power and efficiency

The main aerodynamic power components in hovering flight are induced ($P_{\text{ind}}$) and profile power ($P_{\text{pro}}$), respectively. If the flight muscles and associated tendon structures provide perfect elastic storage of the energy required to accelerate the wings at the reversal points of the half-strokes, $P_{\text{ind}}$ and $P_{\text{pro}}$ represent the mechanical power output. In cases of less than perfect elastic storage, there will be an additional inertial power component to add to the aerodynamic power. There is a great deal of controversy regarding the need to account for additional inertial power or not [26,27], while the assumption of perfect elastic storage is often made in studies of hovering hummingbirds and many insects [20,28–30]. To generate the required mechanical power output, the flight muscles contract cyclically to flap the wings. A fraction of this muscle work is converted into aerodynamic work on the surrounding air and the rest is dissipated as heat. The ratio of mechanical power output and metabolic power input is the energy conversion efficiency. We may also consider the efficiency of the reciprocating system, i.e., the flapping wings, with respect to how good they are at generating lift by a uniform downwash. In the following, we use our measurements to estimate how these different efficiencies pertain to hovering flight in bats.

We measured the induced power during hovering in $L$. yerbabuenae, which is the dominating aerodynamic power component [31]. The efficiency by which the reciprocating wings can generate a uniform downwash is measured by the induced power factor, $k$, where $k = 1$ in the ideal case of constant induced downwash across the entire actuator disc. In models of animal flight, the actuator disc model is often used to calculate the induced power by selecting a value of $k$ that corrects for assumed departures from the ideal situation of uniform downwash. The value of $k$ for helicopter rotors is usually 1.1–1.2 [32], but it should be larger for reciprocating wings due to losses at the turning points. For forward flapping flight in birds $k$ is typically assumed to be...
1.1–1.2 [26], but the arrangement of slotted wing-tips such as the separated primaries in certain species may lead to values of $k < 1$ [33,34]. The periodic nature of lift generation of asymmetric hovering by necessity leads to increased $k$, and here we estimated $k$ to 1.33. This is comparable to the value (1.56) estimated for the smaller G. soricina [30], using hot-wire anemometry to measure the induced velocity. A value of $k$ of 1.3–1.5 is therefore probably a realistic range of values for hovering bats. It is interesting to note that also fixed wings at low Reynolds numbers (less than 10$^5$) may have $k \approx 1.3$ due mainly to flow separation forward of the trailing edge [35]. For many other hovering animals, including hummingbirds and insects, the induced power factor estimates range from 1.9 to 2.5 [20], suggesting asymmetric hovering in bats is at least equally efficient.

Another measure of aerodynamic efficiency is how good the wings are at generating a uniform downwash along the wingspan, which is associated with an elliptic lift distribution along the span. Our measured flap efficiency of 0.59 could be compared with the span efficiency of forward flight, which was estimated at 0.79 for the same species of bat [36]. This comparison suggests that hovering flight is aerodynamically somewhat less efficient than forward flight, probably because in hovering the body does not contribute any lift and the strong velocity gradient along the span due to the flapping without forward speed.

In order to estimate the mechnochemical efficiency, we need an estimate of the profile power $P_{\text{pro}}$. This is notoriously difficult to estimate, and therefore we adopted a value estimated for L. curasoae (synonymous to L. yerbabuenae) based on wingbeat kinematics [37], which yields 0.08 W for our bats. The total aerodynamic power, $P_{\text{ind}} + P_{\text{pro}}$ is thus 0.51 W. There are no measurements of metabolic rate during hovering available for L. yerbabuenae, but using values from a smaller species, Choeronycteris mexicana, will allow a rough (over) estimate of flight metabolic rate [38]. We used the mid-range value for C. mexicana (145 W kg$^{-1}$), which yields 3.85 W for our bats. Because of scaling effects this value should be considered as an upper bound. The ratio between aerodynamic and metabolic power is thus 13% for our hovering L. yerbabuenae. Using PIV-data to estimate aerodynamic power output and the $^{13}$C-labelled sodium bicarbonate method to estimate metabolic power, Busse et al. [39] arrived at an average conversion efficiency of 7% in forward flight, i.e. only about 50% of our estimate. This difference could be due to the comparison of different species, but it should be noted that our value of 13% is probably a low estimate because our flight metabolic rate may be an overestimation as it was based on measurements of a somewhat smaller species (cf. [38]). The discrepancy may instead be sought in the methodological procedure.

Measurements of two larger bat species, Phyllostomus hastatus and Pteropus gouldii, yielded an average mechnochemical efficiency of 25% (range 13–34%) for forward flight [40]. In birds, the mechnochemical efficiency of forward flight has been estimated at 20–30% [41–43], while in hovering hummingbirds and insects estimates at about 10% are more common [30,44]. Taken together, our estimate for hovering bats and previous studies of birds suggest that the energy conversion efficiency may be lower during hovering than in forward flight, but that bats are equally efficient as birds and insects during hovering.

5. Concluding remarks

This study revealed the complexity of the real wake of hovering bats compared to idealized models of hypothetical wake topologies (cf. figures 1 and 4). This complexity and interactions between successive half-strokes prevented the determination of the relative contribution to force production between downstroke and upstroke, while wake and downwash distribution show that both half-strokes contribute to lift in this type of asymmetric hovering with inclined stroke plane. Aerodynamic efficiency was lower for hovering than forward flight, for both measures of flap/span efficiency and as the induced drag factor $k$. This is most probably because the body does not contribute any lift when hovering (span efficiency), and that reciprocating wings operating at low advance ratio and high angle of attack during hovering cannot generate an equally uniform downwash as during forward flight. The described wake topology of tilted bilateral vortices from downstrokes and active upstrokes should be considered a ‘new’ wake type in the family of animal generated wakes during hovering, although whether it is unique to bats or not must await further studies of small hovering birds.

Ethics. This study involved experiments on animal subjects, which were carried out under permission M 173–09 from the Malmö-Lund animal ethics committee.

Data accessibility. Data are deposited in the Dryad repository (http://dx.doi.org/10.5061/dryad.nrr31).

Authors’ contributions. A.H. and J.H. conceived the study; J.H. carried out the experiments; J.H., A.H. and L.C.J. analysed the data and drafted the manuscript. All authors gave final approval for publication.

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