The aerodynamic cost of flight in the short-tailed fruit bat (Carollia perspicillata): comparing theory with measurement

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Aerodynamic theory has long been used to predict the power required for animal flight, but widely used models contain many simplifications. It has been difficult to ascertain how closely biological reality matches model predictions, largely because of the technical challenges of accurately measuring the power expended when an animal flies. We designed a study to measure flight speed-dependent aerodynamic power directly from the kinetic energy contained in the wake of bats flying in a wind tunnel. We compared these measurements with two theoretical predictions that have been used for several decades in diverse fields of vertebrate biology and to metabolic measurements from a previous study using the same individuals. A high-accuracy displaced laser sheet stereo particle image velocimetry experimental design measured the wake velocities in the Trefftz plane behind four bats flying over a range of speeds (3–7 m s\(^{-1}\)). We computed the aerodynamic power contained in the wake using a novel interpolation method and compared these results with the power predicted by Pennycuick’s and Rayner’s models. The measured aerodynamic power falls between the two theoretical predictions, demonstrating that the models effectively predict the appropriate range of flight power, but the models do not accurately predict minimum power or maximum range speeds. Mechanical efficiency—the ratio of aerodynamic power output to metabolic power input—varied from 5.9% to 9.8% for the same individuals, changing with flight speed.

1. Introduction

The evolution of vertebrates capable of flapping flight has produced tremendous diversity in ecology; specialists may hover to extract nectar from flowers, catch insects on the wing, or snatch smaller vertebrates from the ground. Some species migrate thousands of kilometres annually, whereas others never travel further than a few metres from their roost or nest. The great diversity in flight ecology and behaviour is mirrored in a wide range of wing architecture and musculoskeletal structure in bats and birds.

One way in which efforts have long been made to relate wing morphology and motion to flight performance is by understanding flight energetics, and for decades, biologists have tried to estimate the flight power curve, the relationship between aerodynamic energy required for flight and flight speed [1]. However, measuring or estimating aerodynamic power of flapping vertebrates is challenging; thus necessitating the use of simple models derived from fixed-wing aircraft and helicopter theory. In particular, two models, developed by Pennycuick [2] and Rayner [3], have dominated the animal flight literature.
Because of the difficulty in making direct measurements of the aerodynamic power required for animal flight, there has been only one attempt to validate these models [4]. Nevertheless, they have been widely used to generate diverse predictions, including not only the speed-dependent cost of flight, but also seasonal or life cycle changes in flight behaviour, habitat use, migration behaviour and morphological as well as kinematic scaling [5–8].

Both models assume that we can express the total aerodynamic power as the sum of three subcomponents: induced power, parasite power and profile power. The induced power, \( P_{\text{ind}} \), is the rate of work required to support body weight

\[
P_{\text{ind}} = \frac{2\kappa \cdot (mg)^2}{\pi \rho UL^2}, \tag{1.1}
\]

where \( m \) is the mass of the animal, \( g \) the acceleration owing to gravity, \( \rho \) the air density, \( b \) the wingspan, \( U \) the flight speed and \( \kappa \) a constant that both the Pennycuick and Rayner models assign a value of 1.2, supported by recent experiments on two nectar-feeding bat species [9].

Parasite power, \( P_{\text{par}} \), originates from the drag of the non-lifting parts (i.e. the body) and again, both models have the same functional structure

\[
P_{\text{par}} = \frac{1}{2} \rho S_b C_{\text{D,par}} U^3, \tag{1.2}
\]

where the body frontal area \( S_b = (8.13 \times 10^{-3} \text{ m}^2 \text{ kg}^{-2/3}) \cdot \text{m}^2/\text{s}^3 \), and the parasite drag coefficient \( C_{\text{D,par}} = 0.4 \) (as first introduced by Pennycuick et al. [10]).

The profile power, \( P_{\text{pro}} \), is associated with the aerodynamic drag of the wings moving through the air. Pennycuick concluded that parasite power remains approximately constant in the mid-range of natural flight speeds [2]:

\[
P_{\text{pro}} = \frac{8.4 P_{\text{am}}}{\lambda R}, \tag{1.3}
\]

where \( \lambda R \) is the aspect ratio of the wing, and \( P_{\text{am}} \) is the sum of \( P_{\text{par}} \) and \( P_{\text{ind}} \) at the minimum power speed. By contrast, Rayner incorporates a drag-based calculation that varies with the cube of the flight speed to estimate the profile power. Rayner’s original strip analysis model [3] was later modified by Norberg [11], and is applied here

\[
P_{\text{pro}} = \frac{1}{2} \rho S C_{\text{D,pro}} U^3, \tag{1.4}
\]

where \( S \) is the wing area and \( C_{\text{D,pro}} \) is the coefficient of profile drag, with a typical value of 0.02.

### 1.1. Measurements of the energetic cost of flight

Just as the conservation of momentum dictates that the weight of a flyer is supported by imparting equal but opposite momentum to the air in the wake, the conservation of energy dictates that the work done by the flyer on the air is reflected in the kinetic energy of the wake. Measurements of animal wakes using particle image velocimetry (PIV) have become common in recent years [12–14]. However, the technical challenges are numerous. For bats and birds whose wings beat at frequencies of approximately 5–16 Hz, high-speed PIV systems capable of time-resolving the flapping cycle are required. Constraints on laser energy and camera resolution limit the size of the measured area, and compromises in the experimental design can lead to inaccurate measurements of the vorticity (or circulation) contained in the wake [15,16]. In the only study that has measured the kinetic energy in the wake of a flying vertebrate [4], the calculated self-energy was less than 60% of the expected value predicted by theory, and the estimated lift was only slightly greater than 50% of that required for weight support. Several other studies have reported that the measured vortex structures contained only 50–60% of the circulation required to support body weight [4,17–21]. In one study that demonstrated weight support [22], vortex circulation was not computed directly, but instead was estimated by thresholding the measured vorticity below a cut-off value and then extrapolated outside the vortices using an assumed Gaussian tail to the vorticity distribution. This assumption may not represent the actual circulation profile [16]. Other studies have used a variety of ad hoc assumptions and explanations to account for the missing lift [13,15,23]. Recently, a novel PIV method (dual-plane illumination) was developed and used to capture the complete circulation in the wake and to identify the sources of previous difficulties associated with this challenging measurement [16].

### 1.2. Metabolic cost of flight and efficiency

Another approach to estimating the cost of animal flight is to measure metabolic energy used and thus estimate power input rather than power output. Metabolic power can be measured directly from flying animals using a variety of techniques, including respirometry (open flow or closed system), isotope labelling techniques (doubly labelled water or the sodium bicarbonate method) and heat transfer modelling [24]. If both metabolic power input and aerodynamic power output can be measured, then it is possible to estimate flight efficiency, \( \eta \), the ratio of metabolic and aerodynamic power of flight. Efficiency is notoriously difficult to measure empirically and hence not well understood for animal flight or even for terrestrial or aquatic locomotion. Estimates for efficiency during flight obtained using diverse techniques range between 3% and 33% for birds [25] and between 5% and 30% for bats [26–28]. Flight efficiency may vary with body mass both among and within species, and some evidence has suggested it may change with flight speed [29].

### 1.3. Current work

Here, we report on a series of experiments designed to measure the aerodynamic power of Seba’s short-tailed bats, *Carollia perspicillata*, flying in a wind tunnel. We compare these measurements with values predicted using the prevailing theories and estimate the energetic efficiency of bat flight over a range of flight speeds. We estimate the cost of flight from wake velocity measurements using an approach that is novel in several ways. First, we use dual-plane, three velocity-component PIV, which enables high-accuracy velocity measurements in the Trefftz plane and which captures all of the wake vorticity, without the need for corrections [16]. Second, we describe and apply an analytical method, the Helmholtz–Hodge decomposition, with which we can accurately calculate the energetically significant wake velocity outside the measurement zone, and therefore calculate the total aerodynamic power contained in the wake. Finally, we combine the measurements of flight power with measurements of metabolic power from a separate study, obtained in the same facility, from the same individuals [30], to test the hypothesis that flight efficiency is flight-speed-dependent.
2. Material and methods

2.1. Wind tunnel

Four non-reproductive Seba’s short-tailed bats (C. perspicillata) were flown in the closed-loop, low-turbulence wind tunnel at the School of Engineering at Brown University. The test section is 3.8 m long and has a cross section of 0.60 × 0.82 m, relative to a mean wing-span of 0.28 m of the experimental animals. The turbulence level in the wind tunnel for this experimental configuration is approximately 0.5% of the freestream velocity [20]. Experiments were conducted at free stream velocities from 1 to 6 m s⁻¹, measured with a Pitot tube and differential pressure transducer (Setra model no. 239). True forward flight speed, determined from the sum of the freestream velocity and the animal’s velocity relative to the laboratory frame, ranged from 3 to 7 m s⁻¹. Wind tunnel temperature was monitored with a thermistor probe and digital controller (Omega DP25-TH) and was 21.3 ± 0.6°C (mean ± 1 s.d.) during experiments. The atmospheric pressure was monitored by an absolute pressure transducer (Setra model no. 270) and averaged 101.0 ± 0.9 kPa (mean ± 1 s.d.). The animals were released into the wind tunnel and trained to fly through a hole in a net, emerging in the correct position within the test section such that forward flight would take the bats through the PIV and kinematic interrogation areas. The laser was triggered after the bats passed through the plane of the laser sheet so as to prevent direct exposure of the animals to any laser light. A right-handed coordinate system was defined with the x-axis aligned with the direction of the flow, the y-axis transverse to the flow and the z-axis vertical.

2.2. Particle image velocimetry measurement

The PIV experiment was controlled using commercial PIV software (DAVs v. 8). The image pairs were captured with four high-speed cameras (three Photon FASTCAM SA3 and one Photon FASTCAM SA5) using a 105 mm f/2.8D, a 60 mm f/2.8D and two 85 mm f/1.4D Nikkor lenses on Scheimpflug mounts. Optical bandpass filters of 531 ± 22 nm were used to minimize stray light. The four cameras were arranged into two stereo pairs with fields of view stacked vertically to give an increased measurement region. The resulting combined field of view was approximately 22.7 × 31.1 cm² with a resolution of R = 4.5 pixel mm⁻¹. The cameras were calibrated using a LaVision type 31 calibration target and the software’s stereo camera calibration routine. Laser sheet illumination (532 nm) was provided by a double-pulsed 200 Hz, 50 mJ laser (Litron LPY-732). The wind tunnel was filled with 1 μm droplets of di(2-ethylhexyl) sebacate generated using a Laskin nozzle. Image pairs were captured in the Trefftz plane (y,z) behind the flying animal. At lower wind speeds (1–3 m s⁻¹), where wake structures are of comparable strength to the freestream, we used single-plane stereo PIV. At higher wind speeds (4–6 m s⁻¹), we used a dual-plane PIV measurement system [16] (electronic supplementary material, table S1 and figure S1). PIV images were processed in DAVs, and cross-correlation was performed on a GPU using a multi-pass algorithm. Analysis used two initial passes with 4.5 pixel mm⁻¹, with an equivalent independent vector spacing of 7.4 mm [31]. The resulting three component velocity fields, \( \mathbf{u} \), were imported from a custom Matlab analysis program (Matlab R2011b, The MathWorks Inc., Natick, MA), where images from the upper and lower regions were stitched together into a composite vector field. The wake vorticity was computed from the measured velocity field, using finite differences. Only PIV trials that captured the entire vorticity within our measurement region during a complete wingbeat cycle were included in the analysis.

We analysed a total of 75 trials: 2, 3, 13, 18 and 38 wingbeats at forward flight speeds of 3, 4, 5, 6 and 7 m s⁻¹, respectively. Because we analysed only level flights with zero roll, we assumed sagittal plane symmetry and mirrored the measurements about the median plane of the animal.

2.3. Kinematics measurement

Bat kinematics were recorded synchronously with the PIV to enable spatial registration of the bat position and wake structures. Bats were filmed in ventral (x,y) and lateral (x,z) views at 400 Hz with a pair of high-speed cameras (Photron FASTCAM1024; electronic supplementary material, figure S1). Positions of the body, defined as the midpoint between the legs (the tip of the caudal vertebrae) and wrist, were digitized in both views and transformed into three-dimensional coordinates by direct linear transformation (DLT) using a custom tracking routine [32]. The three-dimensional marker locations were exported to Matlab and transformed to the PIV coordinate system for analysis. The bat’s velocity relative to the PIV coordinate system was measured using a linear least-squares fit of body position versus time. Wingbeat frequency was calculated by fitting a sinusoid to vertical wrist position. Each PIV frame was assigned a wingbeat phase by adjusting the phase of the concurrent kinematic frame by the upstream position of the bat and the freestream.

3. Results

3.1. Wake structure

We quantified the wake structure in the Trefftz plane behind the four Seba’s short-tailed bats (C. perspicillata) flying freely in a wind tunnel at forward flight speeds of \( U = 3–7 \text{ m s}^{-1} \). The vortex structure of the wake (figure 1 and the electronic supplementary material, figure S2) is consistent with previous studies [13,15,20,22,23,33–35]. We find a strong tip vortex at the beginning of the downstroke that persists until mid-upstroke (figure 1a,b), a wing root vortex that is observed at the beginning of downstroke (figure 1a), and a reversed vortex loop at the end of upstroke (figure 1c). The velocity fields (figure 1d–f) show a velocity deficit associated with the vortex core during the beginning of the downstroke. However, this changes to a wake velocity surplus by the end of downstroke. The velocity field extends over a far greater area than the vorticity field and well beyond the measurement area (figure 1g–i).

3.2. Lift

The wingbeat-averaged lift, \( L \), can be calculated from the wake vorticity, \( \omega \):

\[
L = \frac{\rho \omega L_w}{T} \int_{wb} \int_{\text{Trefitz}} y \cdot \omega \, dA \, dt,
\]

where \( wb \) denotes integration over a wingbeat cycle, \( T \) is the wingbeat period. We calculated lift-to-weight ratio as a function of flight speed for each of 75 wingbeats using the appropriate average weight for each individual (figure 2). At higher speeds, the average of the measured lift equals weight with no additional assumptions (mean \( L/W = 1.02 \pm 0.15 \text{ s.d.} \)). At lower speeds, where we did not use the dual-plane PIV method, the measured lift was less than weight (mean \( L/W = 0.83 \pm 0.05 \text{ s.d.} \)).

3.3. Aerodynamic power

Aerodynamic power was computed by measuring the total kinetic energy in the wake. In the absence of flight, we
observe only wind tunnel freestream flow, and any difference between the wake velocity field and the undisturbed freestream derives from energy put into the wake by the bat. By measuring the wake velocities using PIV, we can simply integrate the wake energy to find the aerodynamic power. As noted above, velocity magnitude contours (figure 1g–i) indicate that non-zero wake velocities lie beyond the measured region, and thus a simple wake integration of the measured velocities will underestimate the power. However, because we have measured all of the wake vorticity (figure 1a–c), the velocity outside the measurement area can be uniquely calculated using an exact extrapolation technique based on the Helmholtz–Hodge decomposition [36]—a vector calculus theorem from nineteenth-century mathematical physics. Given a vorticity field and assuming incompressible flow, we can use the Helmholtz–Hodge decomposition [36]—a vector calculus theorem from nineteenth-century mathematical physics. Given a vorticity field and assuming incompressible flow, we can use the Helmholtz–Hodge...
and subsequently, the average aerodynamic power was calculated to extend the wake velocity field (without approximation) to include the entire wind tunnel test section, and with this, we obtain a much more complete measurement of the aerodynamic power (see the electronic supplementary material and figure 3).

The total kinetic energy of a wingbeat was calculated from the extended velocity field

\[ E_{wb} = \int_{wb} \frac{1}{2} \rho |u|^2 \, dV, \]

(3.2)

and subsequently, the average aerodynamic power was calculated by multiplication with the wingbeat frequency, \( f_{wb} \), as \( P_{wb} = E_{wb} \cdot f_{wb} \). The measured aerodynamic power falls between the two theoretical predictions (figure 4); Pennycuick’s model shows higher values, whereas Rayner’s model shows lower values compared with our measurements (figure 4). Aerodynamic power increases with speed. The values of the aerodynamic power do not differ significantly between the intermediate flight speeds 5 and 6 m s\(^{-1}\) (two sample t-test), but the values at 6 m s\(^{-1}\) and at 5 and 6 m s\(^{-1}\) taken together differ significantly from the power values at 7 m s\(^{-1}\) (two sample t-test, \( p = 0.0208 \) and \( p = 0.0067 \), respectively).

3.4. Mechanical efficiency of flight

In a prior study, using the \(^{13}\)C-labelled sodium bicarbonate method [37], the same individuals, flying in the same wind tunnel, were found to exhibit a U-shaped dependence of metabolic power over speeds ranging from 1 to 7 m s\(^{-1}\) [30]. Understanding that these data are also subject to experimental uncertainty, we can take the ratio of aerodynamic power to metabolic power to obtain the mechanical efficiency of locomotion, \( \eta \) (figure 5). Our measurements of both parameters from multiple individuals allow estimates of efficiency at flight speeds between 3 and 7 m s\(^{-1}\), and over this range, \( \eta \) varies from 5.9% at 6 m s\(^{-1}\) to 9.8% at 4 m s\(^{-1}\). The mechanical efficiency was calculated from the average aerodynamic power, binned to the nearest integer flight speed (m s\(^{-1}\)), divided by the median metabolic power.

4. Discussion

Dual-plane PIV measurements and the Helmholtz–Hodge decomposition analysis have allowed us to calculate the aerodynamic power expended by bats in free flight and make comparisons with the leading aerodynamic theories. There are inherent challenges associated with both measurement and theory. Theoretical predictions are sensitive to model uncertainties [38], whereas experimental estimates are sensitive to measurement accuracy.

At flight speeds above 4.5 m s\(^{-1}\), we recover full weight support without any data corrections. There is, of course, scatter about the mean, but this scatter is expected given the fact that each point represents an individual wing beat. Using single-plane PIV at lower speeds, however, we recover only 80% of the lift. The low-speed data should be viewed with caution.
First, it is difficult to obtain PIV measurements of complete wingbeats at low wind tunnel speeds; animals often prefer to fly through the measurement volume at a higher net airspeed, or fly in an unsteady manner. Consequently, the low-speed results are based on only five wingbeats. Second, PIV measurement uncertainty is inversely proportional to the time between laser pulses [16]; thus, our highest uncertainty occurs at low free-stream velocities (electronic supplementary material, table S1). Third, for our calculations to be valid, we assume that the free-stream dominates the streamwise velocity fluctuations in the wake. However, this assumption breaks down at low flight speeds, where streamwise wake structures increase in strength relative to the freestream, and the relative importance of wind tunnel flow inhomogeneities and free stream turbulence rises. Nevertheless, there is no reason to exclude the data from low-speed flights, and we present them for completeness.

4.1. Measurement accuracy

The methodology described here makes two important contributions towards minimizing error. First, we measure all three components of velocity. The streamwise velocity component, $u$, has regions of both surplus and deficit (figure 1d–f), and if it were ignored, the energy would be underestimated by over 20% (table 1). Second, the Helmholtz–Hodge decomposition, and the subsequent interpolation of the velocity field throughout the full wind tunnel test section, ensures that all of the energy in the wake, including that falling outside the measurement field of view, is included in the energy budget. This ‘exterior’ flow contains roughly 8% of the total energy budget (table 1), thus a power estimate from only the directly measured region (e.g. figure 1) systematically underestimates the total aerodynamic power.

Analysis of tomographic PIV-based volumetric reconstructions of locust wakes has highlighted several issues that may arise when representing the wake as a pseudo-volume reconstructed from a time series of planar measurements [14]. In particular, the assumption that the wake is uniformly advected by the freestream can lead to two sources of error: (i) flow structures smaller than the spacing between successive measurements may not be detected, and (ii) wakes may undergo substantial deformation [14]. We evaluated the possibility that these phenomena could play a significant role in our results. In the present case, we seek to quantify the linear momentum and energy content of wakes. Conservation of energy ensures that the properties we measure at the interrogation plane are conserved as they advect, despite any possible distortion. The energy in the wake is contained in its large-scale structure (electronic supplementary material, figure S3), thus the smallest scale details that may be undetected between successive measurements are also the least energetically significant. We also note that viscosity dissipates kinetic energy from the viscous length scales, $\sqrt{\nu t}$. Here, $\nu$ is the viscosity of air, $t$ is the period of a wingbeat and viscous length is approximately 1.4 mm, which is smaller than the vector spacing of our PIV measurement. Viscosity critically affects the energy content of a pigeon wake only after approximately $2.7 \times 10^4$ s [4], and given that the wingbeat period for C. perspicillata is even shorter than that of a pigeon we can safely neglect the effects of viscosity. Furthermore, the far-field influence of these structures depends only on the total strength of these conserved quantities and not on the fine detail of their localized configuration. A discussion on wake deformation can be found in the electronic supplementary material.

4.2. Uncertainty in theoretical models

The magnitude of measured aerodynamic power falls between the predictions of two most commonly used models for vertebrate flight energetics, those of Pennycuick [2] and Rayner [3] (figure 4). The models differ only in their calculation of profile power, but Pennycuick’s assumption for the estimation of profile power is valid only between the minimum power and maximum range speed, in our case, from around 5.0 to 8.5 m s$^{-1}$. Given the complex flow generated by flapping flight of compliant, highly articulated wings and the relative simplicity of the models, it is not surprising that the exact form of the predicted and observed power curves differ, but these fairly simple predictions still capture the approximate magnitude of the aerodynamic power reasonably well. However, values for minimum power and maximum range speeds estimated by these models are very sensitive to the values of the input parameters [38]. For example, the variation in wingspan, wing area and body mass among the individuals in this study produces a range of predicted values for minimum power speed from 4.9 to 5.1 m s$^{-1}$ using Pennycuick’s model (figure 4). Owing to the uncertainty in the predicted power curve, however, the power cost at these minimum

**Table 1.** Percentage of total aerodynamic power obtained using (i) two-component PIV with a single camera (only $v$, $w$ components), or (ii) stereo PIV without using the Helmholtz–Hodge decomposition to interpolate the wake velocities beyond the experimental field of view.

<table>
<thead>
<tr>
<th>flight speed (m s$^{-1}$)</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>single-camera PIV (%)</td>
<td>75</td>
<td>83</td>
<td>81</td>
<td>77</td>
<td>73</td>
</tr>
<tr>
<td>experimental field of view (%)</td>
<td>92</td>
<td>92</td>
<td>91</td>
<td>92</td>
<td>93</td>
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Figure 5. Aerodynamic power output (black, right y-axis) and metabolic power input (red, right y-axis) versus flight speed (metabolic data measured with sodium bicarbonate method from von Busse et al. [30]). Metabolic power measured over 1–7 m s$^{-1}$ (median ± absolute deviation); aerodynamic power from 3 to 7 m s$^{-1}$ (average ± standard deviation, at flight speeds of 5 to 7 m s$^{-1}$; at lower flight speeds, individual data points are shown). Percentages below symbols state mechanical efficiency, calculated as average aerodynamic power (data binned to the nearest integer flight speed (m s$^{-1}$) divided by median metabolic power.
power speeds does not differ from the possible values of power cost between 3 and 7 m s$^{-1}$. Therefore, energetically, those speeds are not distinguishable from the predicted minimum power speed. This broad range of speeds encompasses nearly the entire range of velocities tested in our study and suggests that defining a mathematically derived exact value of minimum power speed may be of little practical relevance. This uncertainty is often not recognized but may have significant implications where computations of minimum power speeds are used, for example, in modelling migration, predicting foraging behaviour, etc. [6,7,39–41].

### 4.3. Flight efficiency

In previous studies of mechanical efficiency, estimates have been obtained by comparing metabolic power, usually measured by respirometry, to aerodynamic power, often calculated from Pennycuick’s model [26,29,42–44]. These studies have yielded efficiency estimates that range between 12% and 40%. The estimates of mechanical efficiency we report here, using, for the first time, experimental measurements for both metabolic and aerodynamic power, ranged from 5.6% to 11.3%. Those values are at the low end of the recorded range for flying vertebrates and overlap with values reported for hovering in glossophagine bats and hummingbirds [28]. However, we note that previously reported values estimated aerodynamic power from Pennycuick’s model and did not quantify power directly. Our empirical measurement of flight power demonstrates that Pennycuick’s power curve, which makes a number of simplifying assumptions, overestimates aerodynamic power, particularly at intermediate flight speeds (figure 4), which leads to artificially inflated estimates of mechanical efficiency. Additionally, our data suggest an increase in aerodynamic power with observed lift, indicating a potential underestimation of our power estimates at low flight speeds (figure 2), which would lead to an increased mechanical efficiency at low speeds.

Although flight energetics models typically assume constant efficiency, it has been suggested previously that mechanical efficiency may vary as a function of flight speed in flying vertebrates and that this variation could depend on the ecology and flight specialization of a particular species [45]. Our results for C. perspicillata support the idea that efficiency can be flight-speed-dependent. At present, it is impossible to know whether this is a general feature of bats or a trait that characterizes this species; mainly feeding on nectar and fruit, these bats are not specialized to hunt insects on the wing, nor are they known as particularly fast fliers. High efficiency at low-to-intermediate flight speeds could be particularly beneficial for animals with this kind of feeding ecology, but only comparisons with other, divergently specialized species can test this hypothesis.

### 5. Concluding remarks

We present here a sophisticated yet tractable method to calculate aerodynamic power from the wake behind a flying animal. It is critically important that the measurement recovers lift, contains all three velocity components, and accounts for the extended spatial area that the wake energy occupies. The measured flight power does not show a clear U-shaped relationship with speed, although the difficulties associated with acquiring data at low speeds could affect this conclusion. Our aerodynamic power measurements are bracketed by the two most widely used theories for estimating aerodynamic power, which confirms the utility and power of those relatively simple models. Nevertheless, the models’ weak dependency on speed and the uncertainties associated with determining basic parameters such as wing-span and weight, reinforce the caution that must be taken when applying such theories. We document a decline in mechanical efficiency at higher flight speeds, which appears to arise primarily from the increased metabolic power requirements of flight at these speeds.

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