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Body lift, drag and power are relatively higher in large-eared than in small-eared bat species

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Bats navigate the dark using echolocation. Echolocation is enhanced by external ears, but external ears increase the projected frontal area and reduce the streamlining of the animal. External ears are thus expected to compromise flight efficiency, but research suggests that very large ears may mitigate the cost by producing aerodynamic lift. Here we compare quantitative aerodynamic measures of flight efficiency of two bat species, one large-eared (*Plecotus auritus*) and one small-eared (*Glossophaga soricina*), flying freely in a wind tunnel. We find that the body drag of both species is higher than previously assumed and that the large-eared species has a higher body drag coefficient, but also produces relatively more ear/body lift than the small-eared species, in line with prior studies on model bats. The measured aerodynamic power of *P. auritus* was higher than predicted from the aerodynamic model, while the small-eared species aligned with predictions. The relatively higher power of the large-eared species results in lower optimal flight speeds and our findings support the notion of a trade-off between the acoustic benefits of large external ears and aerodynamic performance. The result of this trade-off would be the eco-morphological correlation in bat flight, with large-eared bats generally adopting slow-flight feeding strategies.

1. Introduction

Most bats rely on echolocation to navigate the environment in the dark, and in many cases to locate prey [1–3]. Large external ears play an important role in the bat's ability to detect and localize objects in its surroundings; large external ears amplify incoming soundwaves, improve the sensitivity of echolocation and improve detection of passive acoustic cues [4–6]. The ears also provide important directional cues for sound localization [4,7,8]. While large external ears clearly enhance echolocation, the aerodynamic efficiency of bat flight may be compromised by the ears, due to increased drag and reduced lift generated by the body [9,10]. The result is an evolutionary conflict between echolocation and aerodynamic performance. Very large ears have, however, been suggested to produce some lift on their own, which may mitigate some of their negative aerodynamic impact [11–14]. This hypothesis has gained support through wind tunnel studies on three-dimensional models of bat heads, which have suggested the body and head of a brown long-eared bat, *Plecotus auritus*, is capable of producing enough lift to keep the entire bat aloft at flight speeds exceeding 8 m s^{-1} [12]. Recently, aerodynamic wake studies of freely flying *P. auritus* have shown a clear downwash behind the body [13], indicating that the body generates lift, while small-eared bats do not generate downwash behind the body, presumably because the ears disrupt the flow over the body [15–18]. The lift generated by the ears and body may have a positive effect on the lift-to-drag ratio of bats with large ears [11]. However, it is not

Table 1. Morphological parameters of the individual bats used in this experiment: mass (m), wingspan (b), wing area (S_w), body frontal area (S_b) according to Pennycuik's standard approximation for bird bodies, mean chord (c), aspect ratio (AR) and wing loading (Q).

individual	species	m (g)	b (cm)	S_w (cm ²)	S_b (cm ²)	c (cm)	AR	Q (N m ⁻²)
tails	<i>P. auritus</i>	9.1	29.5	146	3.5	4.9	6.0	6.1
RS	<i>P. auritus</i>	8.4	30.2	155	3.4	5.1	5.9	5.3
LS	<i>P. auritus</i>	9.2	27.8	131	3.6	4.7	5.9	6.9
B	<i>G. soricina</i>	9.5	24.3	94	3.6	3.9	6.3	9.9
S	<i>G. soricina</i>	10.1	23.7	88	3.8	3.7	6.4	11.3

known how much lift and drag the bat body and ears generate during free flight.

Even if large ears generate lift and partly mitigate their negative effects, drag increase is likely to be substantial. Foraging style in bats correlates with morphology, such that bats with large ears tend to be slow flyers in cluttered habitats and bats with small ears are fast flyers in more open habitats [19–21]. This suggests that, if large ears result in drag penalties at high flight speeds, large-eared bats are less suited for a lifestyle involving fast flight than bats with smaller ears. Birds, which lack external ears, outperform bats with regard to flight speed ([22], but see [23]) and aerodynamic efficiency [9,10], and they also migrate longer distances [24]. The relationship between flight speed and power theoretically follows a U-shaped curve [25,26] as a result of adding power components proportional to $1/\text{flight speed}$ (induced power, P_i , the cost of generating lift) and to the cube of flight speed (profile power, P_{pro} , the cost related to wing drag, and parasite power, P_{par} , the cost related to body drag). An increase in parasite power shifts the right-hand side of the power curve upwards, thereby shifting the minimum power speed (speed of minimum energy usage per unit time) towards lower speeds. The higher power and steeper slope at high speeds also lowers the maximum range speed (the speed of minimum cost of transport). In addition to lowering the optimal flight speeds, increased energy requirements of flying related to higher body drag may limit the maximum flight speed as the maximum power available from the muscles is reached at a lower speed. Understanding how bat ears influence the aerodynamics and cost of flight thus has direct implications for our understanding of the ecology and life history of bats, but so far our knowledge of how power varies with speed is limited [27].

To quantify the aerodynamic costs associated with flying with large ears, we measured the body drag and the mass-specific aerodynamic power of two similar-sized bat species, one large-eared species and one small-eared species, using quantitative flow measurements behind the bats as they were flying in a wind tunnel. From the reasoning above, we expect the large-eared species to generate relatively higher parasite drag and relatively more body lift. We also compare the measured mass-specific power of the two species with theoretical predictions from an aerodynamic model [26], to remove the effect of morphological differences between the two bats other than the size of the ears. We expect the large-eared species to deviate more from theoretical predictions than the small-eared species since the large-eared species should generate relatively more parasite power than the small-eared species.

2. Method

2.1. Experimental animals

We trained three wild-caught brown long-eared bats, *P. auritus*, to fly in the wind tunnel at Lund University, Sweden [28]. The free stream speed, U_∞ , was set to 2, 3, 4 and 5 m s⁻¹. To motivate the animals to fly steadily in the measurement section we trained them to approach a feeder with a mealworm attached to it. We recorded the mass of the animals shortly after each flight session.

For comparison we reanalysed data captured from two Pallas's long-tongued bats, *Glossophaga soricina*, flown using a similar set-up in the Lund University wind tunnel in 2008 [29]. These bats were flown at $U_\infty = 2, 3, 4, 5, 6$ and 7 m s⁻¹.

The wing area and wingspan of *P. auritus* was measured from images of the bats in flight taken with a downward-facing camera. Morphological data for *G. soricina* are from [29]. The morphological parameters of the experimental animals are summarized in table 1. The wing planform outlines of the two species seen from above are presented in figure 1. Note the larger and somewhat broader wings of *P. auritus* as well as its larger ears and significantly larger tail membrane than *G. soricina*.

2.2. Experimental set-up

We measured the airflow behind *P. auritus*, using stereo particle image velocimetry (sPIV), with two high-speed cameras (LaVision Imager pro HS 4M, 2016 × 2016 pixels). The cameras were directed obliquely down, focused at a laser light sheet (LDY304PIV laser; Litron Lasers Ltd, Rugby, UK) perpendicular to the airflow and situated approximately 10 cm downstream of the bats [13]. The measurement area was approximately 30 × 20 cm², and the acquisition rate was 640 Hz. We derived three-component vector fields using the Davis (LaVision v. 8.3.0) software utilizing the graphics processing unit (GPU) routine with decreasing box size from 64 × 64 pixels followed by 32 × 32 pixels with 50% overlap. The vector fields were post-processed by a 2 × remove and iteratively replace filter and an interpolation to fill up empty spaces. The resulting vector fields have a resolution of approximately 4 vectors cm⁻¹.

The original data for *G. soricina* are from a previous study; for a detailed description of the experimental set-up, see [29]. Here data were captured with a measurement area of 20 × 20 cm² at an acquisition rate of 200 Hz. We re-analysed the original images using the same method and settings as for *P. auritus*, resulting in a vector field with a resolution of approximately 3.2 vectors cm⁻¹.

For both set-ups, the measurement area was too small to capture the entire wake. We therefore focused on capturing the whole body wake, and the wake of one wing. The centre of the body was determined from visual inspection of the wake symmetry in the body region. For lift and power estimates, we assumed a bilateral symmetry in the wake structures, and either doubled the measurements (i.e. for the lift measurements;

Figure 1. Scaled outline of the two species used, *G. soricina* (a) and *P. auritus* (b). Note the relatively larger ears, relatively broader wings and larger tail membrane of *P. auritus*. Scale bar is 10 cm.

see below) or mirrored the wake in the sagittal plane (i.e. for the power measurements) to arrive at the totals. We used the full body wake for body drag measurements. We used a right-handed coordinate system, with x directed in the free-stream flow direction and z vertically upwards.

2.3. Force estimates

2.3.1. Body drag

We imported velocity matrices from the particle image velocimetry (PIV) measurements into a custom Matlab (R2016b; Mathworks Inc.) graphical user interface (GUI). For each frame, we inspected the in-plane distributions of the velocity components, vorticity components and swirl, in order to manually determine the area of the body wake (figure 2). We then determined U_∞ for each sequence by calculating the mean out-of-plane velocity at an undisturbed section of the frame. With the area of the body wake and U_∞ defined for each sequence, we used a wake deficit model to obtain the body drag, D_b , according to

$$D_b = \rho \iint_{\text{body wake area}} u(y, z) \cdot (U_\infty - u(y, z)) \, dA, \quad (2.1)$$

where ρ is the density of the air, $u(y, z)$ is the measured out-of-plane airspeed at horizontal position y and vertical position z within the measurement area, and dA is the area of integration, given as the product between the grid space in the (y, z) -directions [30].

An analytical expression for the body drag is as follows [25]:

$$D_b = \frac{1}{2} \rho C_{D_b} U_\infty^2 S_b, \quad (2.2)$$

where C_{D_b} is the body drag coefficient of the animal and S_b is the projected body frontal area of the animal. To account for scaling effects related to size differences between the species, we estimated S_b according to Pennycuik's standard approximation for bird bodies [31] ($S_b = 0.00813 \cdot m^{2/3}$, where m is the mass of the animal). Although this approximation was originally devised for bird bodies, it has been used in studies of bat flight (e.g. [27,32,33]). Rearranging equation (2.2) to obtain C_{D_b} results in

$$C_{D_b} = \frac{2D_b}{\rho U_\infty^2 S_b}. \quad (2.3)$$

To obtain a measure of C_{D_b} , we fitted a second-degree polynomial to D_b , normalized by $1/2\rho S_b$, against flight speed and forced the equation through the origin. The statistical estimate of the factor to the second-degree term was taken as a measure of C_{D_b} (see statistics section).

Figure 2. An example of the cross-sectional wake structure behind *P. auritus*. (a) Colouring represents the in-plane vorticity scaled according to the colour bar below the panel. (b) Colouring represents the out-of-plane component of velocity scaled according to the colour bar below the panel. The lines show the masking procedure. The outer line encircles the wake used in the analysis, i.e. removing the wake of the feeder and edges. The inner polygon encircles the body wake with the central dot defining the centre of the body.

To verify the wake deficit model, we determined the drag from the wake of a smooth sphere (diameter = 56 mm) mounted on a cylindrical L-bracket in the wind tunnel for a speed range of 3–5 m s⁻¹. We used the same method as for the bat data to estimate the drag coefficient of the sphere. The drag coefficient of the sphere was 0.527, 95% CI [0.515, 0.539], which is less than 6% higher than the drag coefficient of a smooth sphere at the measured speed range of 3–6 m s⁻¹, i.e. 0.5 [34,35].

2.3.2. Vertical force

We determined the in-plane position of the centre of the bat's body by visual inspection and masked out the wake of the feeder together with the noisy edges of the measurement area (figure 2). We then obtained the vertical force (F_{vert}) production of the bat, at each time step, by doubling the integrated in-plane product of vorticity and horizontal distance to the

centre of the body over half of the wake area (between the centre of the body and the edges of the outer mask in figure 2) according to

$$F_{\text{vert}} = 2 \cdot \rho U_{\infty} \iint_{\substack{\text{half wake} \\ \text{area}}} \omega_x(y, z) \cdot |y - y_B| \cdot dA, \quad (2.4)$$

where $\omega_x(y, z)$ is the in-plane vorticity at position (y, z) and y_B is the horizontal in-plane position of the centre of the bat's body. We calculated the mean weight support by averaging the vertical force over the number of wingbeats in the session and dividing it by the weight of the bat.

2.3.3. Body lift

The vertical force production of the body, including the ears and tail, L_b , was calculated by integrating equation (2.4), using the distance to the edge of the body region instead of to the centre of the body, and subtracting the result from the total vertical lift production,

$$L_b = F_{\text{vert}} - 2 \cdot \rho U_{\infty} \iint_{\substack{\text{half wake} \\ \text{area} \\ - \text{body wake} \\ \text{area}}} \omega_x(y, z) \cdot |y - y_{bw}| \cdot dA, \quad (2.5)$$

where y_{bw} is the edge of the body wake region.

Subsequently, we obtained the mean body lift contribution to the weight support by averaging the body lift over the number of wingbeats in the sequence and dividing it by the average total lift production over the same number of wingbeats.

2.4. Energy and power

We calculated the mechanical power of flight as the rate of added kinetic energy to the wake by the bat. We used a version of the method proposed by von Busse *et al.* [27], in which the Helmholtz–Hodge decomposition is used to infer the velocity fields beyond the measurement plane, based on the vorticity in the measurement area (see the electronic supplementary material). We estimated the flow to a rectangular approximation of the whole cross-sectional area of the test section of the wind tunnel [36]. The method requires a full three-dimensional (3D) matrix of the flow to resolve the 3D vorticity. Since our data contain 3D velocity vectors sampled in a plane as the wake moves across the plane by the free stream flow, we first constructed a 3D matrix assuming a distance between frames in the free stream direction of $U_{\infty} dt$, where dt is the time between frames. We then interpolated a homogeneously spaced matrix with the same resolution as the in-plane vector resolution, using the 'interp3' function in Matlab, and calculated the vorticity in all three dimensions using the curl function. The kinetic energy added to the wake (E_{wb}) was then calculated using the Newtonian formula for kinetic energy (mass $\times$ speed²/2) [35], summed over a fixed number of wingbeats, and divided by the number of wingbeats as

$$E_{wb} = \frac{1}{2} \rho \frac{1}{n_{wb}} \sum_{n_f=1}^{N_f} \iint_{\substack{\text{extended} \\ \text{wake}}} (u(y, z, n_f) - U_{\infty})^2 u / U_{\infty} dV, \quad (2.6)$$

where $u(y, z, n_f)$ is the velocity vector at position y, z and frame number n_f , n_{wb} is the number of wingbeats and N_f is the total number of frames.

We calculated the mean mass-specific mechanical power, P_{tot}/m , during a wingbeat as the product between the kinetic energy and the wingbeat frequency, f , divided by the mass of

the animal, m , as

$$\frac{P_{\text{tot}}}{m} = \frac{E_{wb} \cdot f}{m}. \quad (2.7)$$

From the extended velocity field, we then calculated the mass-specific induced power, P_i , as [37]

$$\frac{P_i}{m} = \frac{\rho U_{\infty}}{2m} \iint_{\substack{\text{extended} \\ \text{wake}}} (v(y, z)^2 + w(y, z)^2) dA, \quad (2.8)$$

where $v(y, z)$ is the in-plane horizontal velocity component at position (y, z) and $w(y, z)$ is the vertical velocity component at position (y, z) . To obtain the mean induced power we then averaged the induced power over a fixed number of wingbeats.

The mass-specific induced power is given analytically as follows [25]:

$$\frac{P_i}{m} = \frac{2L^2 k}{\rho U_{\infty} m S_d}, \quad (2.9)$$

where S_d is the area of a disc with a diameter equal to the wing span, b .

The mass-specific profile power is given as [25]

$$\frac{P_{\text{pro}}}{m} = \frac{\rho U_{\infty}^3 C_{D,\text{pro}} S_w}{2m}, \quad (2.10)$$

where $C_{D,\text{pro}}$ is the profile power coefficient and S_w is the wing area.

The parasite power is given as [25]

$$\frac{P_{\text{par}}}{m} = \frac{U_{\infty} \cdot D_b}{m} = \frac{\rho U_{\infty}^3 C_{D,b} S_b}{2m}. \quad (2.11)$$

The total mechanical power is the sum of the induced power, the profile power and the parasite power; therefore, by summing equations (2.9) to (2.11) we get that the mass-specific mechanical power varies with speed according to

$$\begin{aligned} \frac{P_{\text{tot}}(U_{\infty})}{m} &= \frac{(P_i + P_{\text{pro}} + P_{\text{par}})}{m} \\ &= \left(\frac{2L^2 k}{\rho U_{\infty} S_w} + \frac{1}{2} \rho U_{\infty}^3 (C_{D,\text{pro}} S_w + C_{D,b} S_b) \right) \frac{1}{m}. \end{aligned} \quad (2.12)$$

From equation (2.12) it can be seen that P_{tot}/m is expected to be proportional to $1/U_{\infty}$ and U_{∞}^3 . To account for the expected variation in power with speed we therefore fitted the data with the following function:

$$\frac{P_{\text{tot}}(U_{\infty})_{\text{mech fit}}}{m} = \frac{a}{U_{\infty}} + b \cdot U_{\infty}^3. \quad (2.13)$$

2.5. Theoretical predictions of mechanical power

The expected power requirement of a flying animal depends on size, wing morphology and body drag [26]. To normalize for differences in morphology, and thereby for differences in expected power between the two species, we compared our measurements with theoretical predictions derived from Klein Heerenbrink *et al.*'s [26] model of flapping flight. We entered the known morphological parameters for each species (table 1) into the model. To account for expected scaling differences in the cross-sectional areas of the bat bodies, we calculated the projected body frontal areas according to Pennycuik's standard approximation for bird bodies [31] ($S_b = 0.00813 \cdot m^{2/3}$, where m is the mass of the animal). We set the body drag coefficients, $C_{D,b}$, for both species to 0.4, based on previous assumptions in the literature [38,39].

The induced power factor, k , a measure of the degree by which the physical velocity distribution deviates from the theoretical optimal, is derived from dividing the measured induced power by the ideal induced power. The ideal induced power is, however,

normally calculated assuming non-flapping flight. We therefore report the flapping flight-induced power factor, k_{flap} , i.e. the ratio between our measured induced power and the theoretical induced power derived using Klein Heerenbrink *et al.*'s model for flapping flight ($P_{\text{ind, Model}}$) [26] defined as

$$k_{\text{flap}} = \frac{P_i}{P_{\text{ind, Model}}}. \quad (2.14)$$

2.6. Statistics

We performed the statistical calculations using the GLM (general linear model) function in JMP (JMP v. 13.0.0; SAS Institute Inc.). For body lift-to-drag (L_b/D_b), induced power factor (k), flapping flight-induced power factor (k_{flap}) and relative contribution of body lift to weight support (L_b/F_{vert}), we had individual nested within species as a random factor and flight speed (U_∞) and the flight speed–species interaction as covariates. We used the number of wingbeats in each sequence as weights, and centred the polynomials around the mean flight speed. We also determined the mean value of the dependent variable using the same settings, but removed the covariates from the analysis.

For normalized body drag ($D_b/(1/2)\rho S_b$), we included individual nested within species as a random factor and speed squared (U_∞^2) and the interaction between speed squared and species as covariates. The curve was forced through the origin. The data were weighted by the number of wingbeats in each sequence.

For the estimate of the drag coefficient of the sphere, we normalized the drag in the same way as for the bats and included speed squared as a covariate and forced the curve through the origin.

For the curve fitting of the mass-specific mechanical power (P_{tot}/m), we set individual as a random factor with flight speed cubed (U_∞^3) and inverse flight speed ($1/U_\infty$) as covariates. No intercept was included in the model. The data were weighted by the number of wingbeats in each sequence.

For mass-specific induced power, we included individual nested within species as a random factor with the inverse of the flight speed ($1/U_\infty$) and the interaction between the inverse flight speed and species as covariates. We used the number of wingbeats in each sequence as weights, and centred the polynomials around the mean flight speed. The calculations were repeated without the covariates to calculate the mean value of the mass-specific induced power.

3. Results

3.1. Body drag

The normalized body drag increased with flight speed, following the expected quadratic function (figure 3). The body drag coefficient was estimated to 1.66, 95% CI [1.51, 1.81], for *P. auritus* and 1.20, 95% CI [1.05, 1.35], for *G. soricina*. There was a significant effect of the interaction between species and speed squared ($\text{species} \times U^2$, $p < 0.0001$), showing that C_{D_b} for *P. auritus* was significantly higher than for *G. soricina*. Additionally, we found that the *P. auritus* individuals were unable to fly faster than around 5 m s⁻¹ in our set-up, while the *G. soricina* individuals were capable of flying at 7 m s⁻¹ in a similar set-up. At wind tunnel speeds of 6 m s⁻¹ and above the *P. auritus* individuals did not take off or landed shortly after take-off.

3.2. Body lift

The vector fields show a clear difference in the flow behind the body during the middle of the downstroke in the two species (figure 4). In *P. auritus* we found a downwash

Figure 3. Body drag normalized by $1/2\rho S_b$ against flight speed for *P. auritus* (red) and *G. soricina* (blue), calculated from PIV measurements. The lines show the fitted second degree polynomial forced through zero with 95% CIs indicated by dashed lines.

behind the body (figure 4a), while in *G. soricina* the average flow indicated an upwash (figure 4b). This is indicative of a larger body lift production for *P. auritus*, which is also what we found when measuring the body lift quantitatively. The body wake of *P. auritus* generated on average 33.7%, 95% CI [26.7%, 40.7%], of the weight support, whereas the body wake of *G. soricina* generated 22.6%, 95% CI [15.6%, 29.6%], of the weight support. The contribution to weight support from body lift was significantly higher for *P. auritus* than for *G. soricina* (species , $p = 0.028$). The body lift contribution to weight support showed no dependency on flight speed (U_∞ , $p = 0.1026$) and did not differ in slope between species ($U_\infty \times \text{species}$, $p = 0.4491$).

The lift and drag contributions of the body can be used to estimate lift-to-drag ratios of the respective bat bodies, i.e. L_b/D_b . L_b/D_b of *P. auritus* was on average 4.64, 95% CI [1.92, 7.36], and 5.28, 95% CI [2.56, 8.00], for *G. soricina*. The average L_b/D_b did not differ significantly between the two species (species , $p = 0.640$). However, there was a significant difference in intercept of the linear model showing that *P. auritus* had lower values than *G. soricina* (species , $p = 0.0454$). L_b/D_b decreased significantly with flight speed ($L_b/D_b \propto -1.84$, 95% CI [-2.47, -1.20], U_∞ , $p < 0.0001$), which did not differ between the two species ($U_\infty \times \text{species}$, $p = 0.53$).

3.3. Power

The mass-specific mechanical power curve for *P. auritus* followed a U-shaped function (figure 5a), with a minimum value of 6.10 W kg⁻¹, 95% CI [4.71, 7.49], at 4.0 m s⁻¹ (the theoretical curve based on Klein Heerenbrink *et al.*'s [26] model for flapping flight had a minimum value of 5.02 W kg⁻¹ at 3.5 m s⁻¹). The estimated maximum range speed is 5.6 m s⁻¹, which is higher than the fastest speed we recorded for *P. auritus*. For *P. auritus* the measured mechanical mass-specific power was consistently higher during experiments than the theoretical curve predicted by Klein Heerenbrink *et al.*'s [26] model for flapping flight. Between 2 m s⁻¹ and 3.5 m s⁻¹ the theoretical curve was lower than the lower limit of the 95% CI of the measurements.

Figure 4. Velocity vector field at approximately mid-downstroke behind *P. auritus* (a) and *G. soricina* (b). Background shows vorticity (s^{-1}), scaled according to the colour bar below the panels. Both bats are flying at 4 m s^{-1} . Stars indicate the location of the centre of the body. Note the difference in downwash behind the body (approx. 20–25 mm on each side of the star for *P. auritus* and approx. 15–20 mm on each side of the star for *G. soricina*) and the more complex wake behind *P. auritus*.

The mass-specific power curve for *G. soricina* also followed a U-shaped function (figure 5b), with a minimum value of 6.57 W kg^{-1} , 95% CI [5.52, 7.62], at 4.3 m s^{-1} (the theoretical curve had a minimum value of 6.80 W kg^{-1} at 4.3 m s^{-1}). The theoretical curve was above the upper limit of the 95% CI of the measurement until 2.8 m s^{-1} and then stayed within the 95% CI until the highest measured speed (7 m s^{-1}). The estimated maximum range speed was 6 m s^{-1} , which is below the maximum recorded speed in our study.

The mass-specific induced power across the speed range (figure 6) was on average $5.30 \text{ W kg}^{-1} \pm 0.80$ for *P. auritus* and 6.02 W kg^{-1} , 95% CI [5.22, 6.82], for *G. soricina*, and did not differ significantly between the species (species, $p = 0.075$). The mass-specific induced power did not depend significantly on the inverse of flight speed (equation (2.9)) ($1/U_\infty$, $p = 0.57$), but the interaction between the inverse of flight speed and species was significant ($1/U_\infty \times \text{species}$, $p = 0.0016$).

The flap-induced power factor, k_{flap} , was on average 2.50, 95% CI [1.81, 3.19], for *P. auritus*, and 2.14, 95% CI [1.45, 2.83], for *G. soricina*, and did not differ significantly between the species (species, $p = 0.30$). Nor was there a difference between species in the model including the flight speed

Figure 5. Mechanical mass-specific power of *P. auritus* (a) and *G. soricina* (b) calculated from PIV measurements (o) and fitted to equation (2.13) (black line) with 95% CIs indicated by dashed lines. The theoretical prediction from Klein Heerenbrink *et al.*'s [26] model of flapping flight using the morphological data in table 1 is added for comparison (blue).

Figure 6. Mass-specific induced power of *G. soricina* (blue) and *P. auritus* (red) calculated from PIV measurements according to equation (2.8) (fitted line) with 95% CIs indicated by dashed lines. Note that the induced power increases with increased air speed contrary to most models.

(species, $p = 0.0638$). k_{flap} varied significantly with flight speed ($k_{\text{flap}} \propto 0.55$, 95% CI [0.49, 0.62], U_∞ , $p < 0.0001$), but this dependency did not differ significantly between the two species ($U_\infty \times \text{species}$, $p = 0.37$).

4. Discussion

Our results show that mass-specific power production of a large-eared bat species, *P. auritus*, is higher than expected from a model of flapping flight (figure 5), while this is not the case for the small-eared *G. soricina* (figure 5b). We also

found a higher body drag coefficient in *P. auritus* as well as higher relative body lift production than in *G. soricina*. Our findings support the hypothesis of lift generation by large ears, but also that the cost of flying with large ears is higher than flying with small ears. At this stage, we cannot determine the degree to which the difference in power, body drag and body lift should be attributed to the larger ears alone, since the bats' morphologies also differ in other aspects than the ears. We specifically note that *P. auritus* has a more pronounced tail membrane than *G. soricina*, which basically has no tail membrane. However, a previous study on a model of *P. auritus* showed that the tail membrane of the bat lowers the drag coefficient, while it has no significant effect on the lift coefficient [40]. In addition, a study on *Tadarida brasiliensis* and *Myotis velifer*, which both have pronounced tail membranes but small ears, did not find that the tail membranes produce any vortices indicative of additional lift production [18]. We therefore consider the tail membrane of *P. auritus* to be unlikely to contribute significantly to the difference in body drag coefficient and relative body lift production between our two study species. We rather attribute the difference to the larger ears of *P. auritus*. Future studies of other bats with varying relative ear and tail size should be able to conclusively separate the contribution from the ears from that from the tail membrane.

Although our results support the notion that large ears may increase weight support generated by the body, we also found that they may increase parasite drag and thereby limit flight behaviour in bats (i.e. maximum flight speed). This is in agreement with previous studies that found bats with a foraging behaviour incorporating faster flight over longer distances to have smaller ears than those whose foraging behaviour involves slower flight in cluttered habitats [19,39]. Unlike Vanderelst *et al.* [11], we did not find the large-eared bat to have a higher body lift-to-drag ratio than the small-eared species. However, the fact that the body lift-to-drag ratio was similar in our two species when drag varied suggests the large-eared bats are almost keeping up with the small-eared bats regarding efficiency of body lift production. However, the higher drag of the large-eared species influences the behaviour of the bat, favouring lower flight speeds and limiting maximum speed, as manifested in the inability of *P. auritus* to fly as fast as the small-eared *G. soricina*.

4.1. Body drag

One of the differences between our bat species is that *P. auritus* has a higher body drag coefficient than *G. soricina*, which is in accordance with our hypothesis that large ears increase the parasitic drag of the bat. However, our estimated body drag coefficients for *P. auritus* (1.66) and *G. soricina* (1.20) are higher than what is usually assumed in the literature (e.g. [38]). The values of our resulting body drag coefficients depend on our use of Pennycuick's body frontal area estimation (based on birds) to determine projected body frontal area in bats. Our reason for using Pennycuick's model was, however, not to get an accurate estimate of the drag coefficient, but to control for size effects on frontal area between the two species, and thereby allow for a comparison of differences relating to body shape and size of the ears. This means that the high coefficients we find can be the result of a larger projected frontal area in our bats than predicted by Pennycuick's model. The frontal area of *P. auritus* was measured

by Gardiner *et al.* [12] from photographs of a dried museum specimen and Pennycuick's equation accounts for about 21% of the measured body frontal area, when including the ears. Using the frontal area ($1.77 \times 10^{-3} \text{ m}^2$ at 30° body inclination angle) from Gardiner *et al.* [12] resulted in a body drag coefficient for *P. auritus* of 0.35, which is closer to what would be expected, given the drag coefficient of a sphere is 0.5. In addition, in animal flight studies, it is commonly found that the body angle relative to the flight direction varies across flight speeds (e.g. [41]), which influences the projected body frontal area and potentially the drag coefficient, a factor generally ignored in animal flight studies. To avoid comparing data from studies with different ways of estimating projected body frontal area, an alternative approach to calculating the body drag coefficient in animals would be to report the actual drag force, normalized by weight, in PIV studies (electronic supplementary material, table S1). This has the benefit of not having to measure how the animal may control body frontal area and body drag coefficient across speeds, but still give a measure of the relative drag.

The relatively higher drag found in the large-eared species than in the small-eared species in this study is in line with the interpretation of the eco-morphological correlations in bat flight, with a tendency of large-eared bats to use feeding strategies involving slow flight [14,19–21, 42,43]. A low flight speed maintains the relative contribution of the parasite drag low (equation (2.12)), and is thus expected when large ears increase drag, or alternatively a low flight speed allows for large ears that may be used for passive listening to detect prey.

4.2. Body lift

The question to what degree the lift-generating capabilities of bat ears and bodies might be able to mitigate some of the parasite drag that external ears generate has previously been examined by constructing simple models of bat heads and bodies and measuring the lift generated in headwind [11,12]. One of the major drawbacks of such studies is that they ignore the aerodynamic interference between the wings and the body and the dynamics associated with flapping wings [13]. Our lift estimates from the wake of the bats point towards a higher body lift production than previously suggested, for both small-eared and large-eared species [11]. The relative body lift was, however, higher for the large-eared species, *P. auritus*, than for the small-eared species, *G. soricina*, which supports our hypothesis that large ears can mitigate some of the increased drag by contributing some weight support. The extra body lift allows the large-eared species to maintain a relatively high body L_b/D_b . Conversely, the larger body lift of *P. auritus* could also be caused by its larger tail membrane. In support of the hypothesis of lift from ears, prior studies have found that the tail membrane has little effect on the drag and lift production in bat flight [19], but further studies are needed to separate the effects of tail and ears.

4.3. Power required to fly

To evaluate the effect of the differences in ear and body morphology between the two species, we compared our measured mass-specific power outputs with theoretical predictions from a model of flapping flight [26]. The model

generated expected power outputs for the two species using a standard body drag coefficient from the literature (0.4) and body area from Pennycuik's model [26,31]. As a result, the model generates a baseline for comparison, representing a generic bat with the weight and wing morphology of our two study species. The power curve fitted to the measurements for *P. auritus* is slightly above the model predictions (figure 5a), while that of *G. soricina* is close to, or slightly below, the model predictions (figure 5b). Higher body drag coefficient, as well as larger projected frontal area, leads to higher parasite power, suggesting that the relatively higher power curve of *P. auritus* could be a consequence of the larger ears. As mentioned above, a higher power curve has consequences for maximum and characteristic flight speeds (e.g. minimum power speed and maximum range speed), resulting in lower characteristic speeds.

In this study we estimate three out of the four power components (equation (2.12)), which means we should be able to estimate the fourth, profile power, by subtracting parasite and induced power from the total power. However, although the measured total power is relatively close to the model predictions (figure 5), as was the case in von Busse *et al.* [27] using a similar method to that used here, our measurements of parasite power are more than twice that used in the model. Together with a relatively high induced power, the resulting profile power is unrealistically low. Assuming our body drag estimates are robust (since we determined the validity of the method), it is likely that either our total power measurements may not capture all of the kinetic energy added to the wake or that our induced power is overestimated. The reasons for an underestimation of the total mechanical power may be related to PIV or wake evolution. Klein Heerenbrink [44] found a thrust deficit in the wake of a jackdaw and attributed it to an uncertainty in the measurement of the streamwise component of the velocity (out of plane). The thrust deficit corresponds to an underestimation of power by 25–30%. However, because we did not find a consistent thrust deficit in all our measurements, we do not consider this to be a likely explanation for our data. Alternatively, the kinetic energy could be lost as heat, making it impossible to use PIV to capture the total mechanical energy added to the wake. However, comparing the near and far wake of *G. soricina* shows that the total circulation is conserved in the far wake compared with the near wake [45], which argues against such an explanation. Another possibility is that the resolution of the velocity vector fields is insufficient to accurately capture the peak vorticity, resulting in low-quality input for the Helmholtz–Hodge decomposition used to infer the velocity outside the measurement plane. We tested the effect of the resolution of vectors on the mechanical power results by subsampling the velocity matrices for one of the sequences (only using every second, fourth or eighth vector in all three dimensions), repeating the velocity interpolation and performing the power calculations on the resulting vector matrices. This test shows little effect of a reduced resolution; in fact, lowering the resolution eightfold in each dimension results in only a 7% increase in total mechanical power and a 0.7% reduction in induced power.

Alternatively, a lower than expected profile power may stem from the complicated nature of flapping flight, which then leads to misallocation of the contributions of the different power components. The induced power factor, k_{flap} , which is the ratio between the measured induced power and the induced power

obtained from the model of flapping flight [26], suggests a relatively high induced power. Our k_{flap} [2.14] does not differ significantly between the two species, but is noticeably higher than k_{flap} estimated for *G. soricina* using a different method based on downwash only ($k_{\text{flap}} = 1/\text{span efficiency} = 1.23$) [15]. One reason why induced power is higher than expected is that the flapping motion generates thrust, and high thrust requirements require high induced velocities and hence induced power [46]. This could explain why we do not see the expected decrease in induced power with increased flight speed (figure 6), and that this discrepancy represents a real phenomenon. However, the flapping motion of the wings will inflate measured induced power by the profile drag component acting vertically, adding to the vertical velocity component of equation (2.8). There is thus reason to think that estimating induced power in flapping flight from equation (2.8) could be problematic. Resolving these matters requires studying a set-up with known output, preferably a robotic flapper to include the effects of vertically moving wings. However, the rate of kinetic energy added to the wake is a simple, physically valid, way of viewing the mechanical power generated by a flying animal, and despite difficulties to assign values to the different power components we still find the potential of the current method promising.

5. Conclusion

We find that our large-eared bats have a higher body drag coefficient than our small-eared bats. The higher drag is also associated with a higher body lift production in the large-eared bats than in the small-eared bats, suggesting a mitigation of the negative effects of large ears on drag by maintaining a high body lift-to-drag ratio. At the same time, we find a relatively higher power requirement in the large-eared species, compared with model expectations, with implications for the ecology of these bats. The relatively higher power requirements suggest that large-eared species may be adapted to fly relatively slowly, as is also found in eco-morphological studies. As a consequence, our study underscores the trade-off between aerodynamic performance and echolocation, manifested in the size of ears in bats. Although our results support current hypotheses regarding the aerodynamic effects of ears, future studies need to incorporate more species with variation in both ear size, tail size and other morphological features to conclusively determine the relative effects of these features on bat flight performance.

Ethics. The study was performed in accordance with approved experimental guidelines. Procedures were approved by the Malmö-Lund animal ethics committee (M 33-13).

Data accessibility. Raw data in the form of .dat files containing the 3D velocity vectors on an xy grid are deposited in the Dryad Digital Repository [47].

Authors' contributions. All authors contributed to the planning of the study and participated in the experiments on *P. auritus*. L.C.J. conducted the PIV analysis on both datasets. J.H. analysed body drag and body lift. L.C.J. calculated mechanical power in the wakes. J.H. drafted the manuscript. All authors contributed critical revision of the manuscript.

Competing interests. We have no competing interests.

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