

Upstroke wing flexion and the inertial cost of bat flight

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Flying vertebrates change the shapes of their wings during the upstroke, thereby decreasing wing surface area and bringing the wings closer to the body than during downstroke. These, and other wing deformations, might reduce the inertial cost of the upstroke compared with what it would be if the wings remained fully extended. However, wing deformations themselves entail energetic costs that could exceed any inertial energy savings. Using a model that incorporates detailed three-dimensional wing kinematics, we estimated the inertial cost of flapping flight for six bat species spanning a 40-fold range of body masses. We estimate that folding and unfolding comprises roughly 44 per cent of the inertial cost, but that the total inertial cost is only approximately 65 per cent of what it would be if the wing remained extended and rigid throughout the wingbeat cycle. Folding and unfolding occurred mostly during the upstroke; hence, our model suggests inertial cost of the upstroke is not less than that of downstroke. The cost of accelerating the metacarpals and phalanges accounted for around 44 per cent of inertial costs, although those elements constitute only 12 per cent of wing weight. This highlights the energetic benefit afforded to bats by the decreased mineralization of the distal wing bones.

Keywords: bat; Pteropodidae; flight; upstroke wing flexion; inertial power; wing inertia

1. INTRODUCTION

As a flying animal flaps its wings, it transfers energy from its muscles to the surrounding fluid, producing the aerodynamic forces necessary to fly. Because the wings themselves have mass, the total metabolic energy required to fly includes both the energy imparted to the fluid and the additional cost of accelerating and decelerating the wings during the flapping cycle [1]. The cost of accelerating the wings, the inertial work, can exceed the cost of moving the wings through the air, the aerodynamic work [2,3], so understanding the mechanics of animal flight requires an accurate understanding of its inertial cost [3].

The inertial cost of flapping flight was an important constraint in the evolution of animal wings, and its influence is clear from the shapes of wings today [4–6]. For a flapping flier, inertial cost increases linearly with the moment of inertia of the wing, \mathcal{J}_w , which itself increases linearly with wing mass, and with the square of the distance of that mass from the centre of rotation of the wing. Thus, the inertial cost is reduced by keeping the wings light, and by having the heaviest parts of the wing as close to the base of the wing as possible [5]. Insect wings are extremely light. Bird wing bones are reduced, and extend only slightly past the wrist, with lighter feathers making up a sizeable portion of the wing surface. Similarly,

the bones of a bat's wing become more tapered and less dense as their distance from the shoulder increases [7].

The influence of inertial costs on the evolution of wing anatomy is clear, but less attention has been paid to the possible role inertial costs have played in the evolution of wing kinematics. In birds and bats, for instance, the majority of thrust and lift are generated during the downstroke when the wings are fully outstretched. In the subsequent upstroke, the joints of the wings are flexed, adducted and, especially in birds, supinated, to varying degrees. These motions together have the effect of producing a folded-wing posture [2,8–11], reducing \mathcal{J}_w on the upstroke, which should in turn reduce the overall inertial cost of the wingbeat cycle compared with what the cost would be if wing posture was not changed. Inertial costs might therefore be one factor underlying upstroke wing flexion and adduction, hereafter termed folding [5,6,12,13]. However, wing folding and unfolding themselves require inertial energy expenditures, and those could very well exceed the savings afforded by the folded-wing upstroke. Indeed, the use of upstroke wing folding might not necessarily reduce the inertial cost of flight compared with simply leaving the wing outstretched. In this paper, we examine the influence of wing configuration changes on the inertial cost of flight, using a broad size range of pteropodid bats. Pteropodids are a particularly good model for this investigation because bats have the heaviest wings among flying animals, and among bats, pteropodids have especially pronounced upstroke wing folding [6,14,15].

We make two specific predictions concerning the inertial costs of flapping kinematics that can be tested by calculating the changes in the inertial energy of the wings that occur over the course of the wingbeat cycle:

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Table 1. We used 27 individuals from six species. (Five wingbeat cycles were recorded for each individual for a total of 135 trials. Wingspan and body mass are reported as the mean and s.d. of individuals. Flight speed is reported as the mean and s.d. of all trials.)

species name	abbreviation	flight conditions	wingspan (m)	body mass (g)	flight speed (m s ⁻¹)
<i>Cynopterus brachyotis</i> ($n = 5$)	Cb	wind tunnel	0.36 ± 0.02	34 ± 4	5.46 ± 1.53
<i>Rousettus aegyptiacus</i> ($n = 3$)	Ra	flight corridor	0.56 ± 0.03	134 ± 20	4.41 ± 0.54
<i>Pteropus pumilus</i> ($n = 5$)	Pp	flight corridor	0.74 ± 0.04	190 ± 15	4.70 ± 0.68
<i>Eidolon helvum</i> ($n = 5$)	Eh	flight corridor	0.82 ± 0.04	291 ± 33	4.24 ± 0.91
<i>Pteropus hypomelanus</i> ($n = 5$)	Ph	flight corridor	1.05 ± 0.03	480 ± 26	5.64 ± 0.57
<i>Pteropus vampyrus</i> ($n = 4$)	Pv	flight corridor	1.45 ± 0.05	1080 ± 50	5.24 ± 0.68

(i) the total inertial cost of flapping flight for bats using wing folding should be lower than it would be if the wing posture remained unchanged; and (ii) the inertial cost of the upstroke, when wings are folded, should be less than that of the downstroke. In this study, we also estimate the isolated inertial cost of folding and expanding the wings, and investigate how the inertial cost of flight is distributed among the segments of the wing.

2. MATERIAL AND METHODS

To estimate the inertial cost of flight, we compute inertial work—the work performed by the bat during a wingbeat cycle to accelerate the mass of its wings—and inertial power—the average power exerted by the bat during a wingbeat cycle to accelerate the mass of its wings. We approximate wing beats as periodic. Inertial power for a particular wingbeat cycle is, therefore, equal to inertial work multiplied by the flapping frequency.

We compute the inertial power of a wingbeat cycle from the kinetic energy the wings of a bat possess during a wingbeat cycle. The instantaneous power exerted by a bat to accelerate its wings' mass is the time derivative of their inertial energy. The wingbeat cycle consists of periods where the instantaneous power is positive—as masses are accelerated in the direction of their velocity—and of periods where the instantaneous power is negative—as masses are accelerated opposite to their velocity. Because the wingbeat cycle is (nearly) periodic, the integrated positive and negative power exerted during a wingbeat cycle cancel. This cancellation, however, does not affect the actual work exerted by a bat to flap its wings. The contribution of negative work to the overall inertial cost of flight should be no more than 20 per cent of the total, because muscle is roughly four times more efficient at performing negative work than positive work [16]. We therefore compute the inertial work by integrating the positive instantaneous power exerted over the course of the wingbeat cycle.

The inertial cost of flight is traditionally estimated based on models that consider the wing to be rigid and to rotate about a single axis through the shoulder joint [5,6,12–14,17]. Here, we use that method to predict the inertial power required for flight if the wing is fully outstretched throughout the wingbeat cycle, $P_{\text{rigid-wing}}$. To more accurately estimate the inertial power required to fly, P_{tot} , we develop a method that accounts for the changes in wing conformation that realistically occur during flight. Our model treats the wing as a jointed set of masses that move independently relative to each other, and thus gives a more accurate estimate of the inertial cost of flight than a rigid-wing model does. Furthermore, it permits us to identify the times in the

wingbeat cycle, and the anatomical locations on the wing in which inertial power are consumed. For these calculations, gravitational effects are negligible relative to other factors and are omitted (see the electronic supplementary material).

(a) Kinematic recordings

We used 1000 frame per second videography to record three-dimensional wing kinematics of 27 bats from six species representing 4.8-fold variation in wingspan and a 41-fold variation in body mass (table 1). Bats flew in a flight corridor or wind tunnel, and we recorded five flights for each individual. A single wingbeat cycle was isolated from each flight for analyses. Seventeen kinematic markers were tracked on the midline and one wing of each bat (figure 1). Wingbeat frequency and wing stroke amplitude were calculated from the motions of the wrist. Downstroke ratio was defined as the duration of the downstroke divided by the duration of the whole wingbeat cycle [17]. Summary statistics for all 135 wingbeat cycles have been reported previously, and we refer readers to that paper for a detailed description data collection methods [11]. All bats were provided on loan from the Lube Bat Conservancy (Gainesville, FL, USA).

(b) Measurement of wing mass distribution

To measure the mass distribution of a wing, it must be dissected into constituent pieces to be weighed individually [5,8,14]. Owing to the conservation directive of the organization that loaned us animals for this study, it was not feasible to euthanize the bats from which kinematic recordings were taken. Thus, wing mass measurements were made using a specimen of *Cynopterus brachyotis* that had died unexpectedly, but that had not been used for kinematic recordings. That bat was kept frozen in an air-sealed bag from shortly after its death to the time of dissection. Its right wing was cut into 32 segments (figure 1), and the mass of each weighed with a precision balance to 0.001 g. The distribution of mass across those segments is provided in the electronic supplementary material.

(c) Model descriptions

(i) The estimated cost of moving a rigid-wing: $P_{\text{rigid-wing}}$

In the rigid-wing model, the wing moves with some frequency f , through an arc of amplitude ϕ , about an average angle of $\bar{\gamma}$. Then, the wing angle γ at any point in time t can be described by the following equation:

$$\gamma(t) = \frac{1}{2} \phi \times \cos(2\pi ft) + \bar{\gamma}. \quad (2.1)$$

The angular velocity of the wing is then given by

$$\frac{d\gamma}{dt} = -\pi f \phi \times \sin(2\pi ft), \quad (2.2)$$

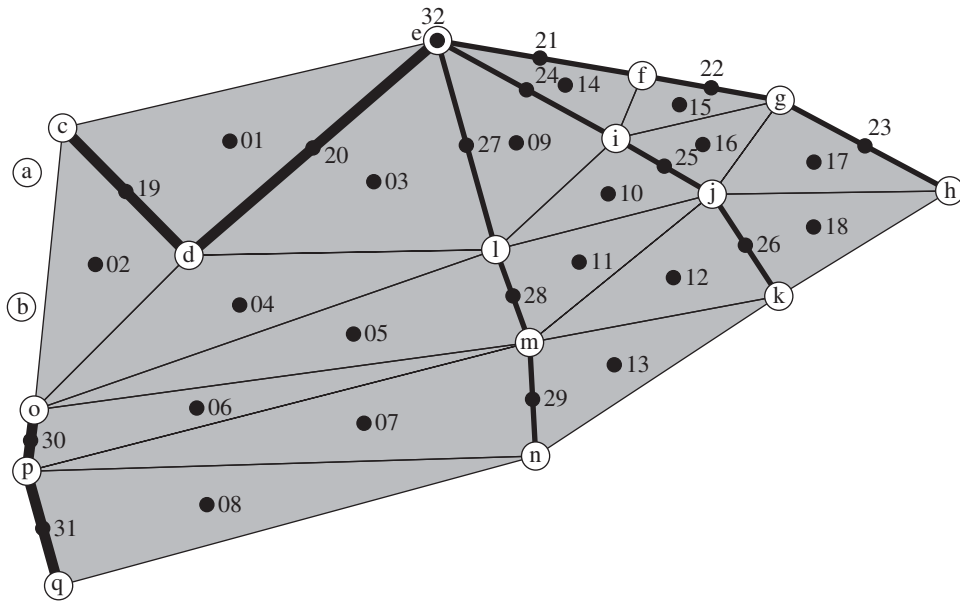


Figure 1. The mass distribution among 32 fragments of the wing of a dissected *Cynopterus brachyotis* was used to estimate the inertial cost of flight. Fragments are defined in the electronic supplementary material, and the locations of the fragment centroids are shown as a black circles, labelled from 01 to 32. For kinematic recordings, we tracked the three-dimensional trajectories of seventeen markers on the body and one wing, labelled a–q. The motions of the 32 masses were interpolated based on those movements.

and angular acceleration is given by

$$\frac{d^2\gamma}{dt^2} = -2\pi^2 f^2 \phi \times \cos(2\pi ft). \quad (2.3)$$

With the goal of calculating inertial work, the inertial energy of one wing through time can be modelled by integrating the differential equation:

$$E(t) = \int \left(\mathcal{J}_w \times \frac{d^2\gamma}{dt^2} \times \frac{d\gamma}{dt} \right) dt = \int \mathcal{J}_w \pi^3 f^3 \phi^2 \times \sin(4\pi ft) dt, \quad (2.4)$$

where \mathcal{J}_w is the rotational moment of inertia of the wing. Evaluation of this equation gives

$$E(t) = -\frac{1}{4} \mathcal{J}_w \pi^2 f^2 \phi^2 \times \cos(4\pi ft) + C, \quad (2.5)$$

where C is the integration constant. To calculate $P_{\text{rigid-wing}}$ for both wings, we sum the positive increases in $E(t)$ over the course of one wingbeat cycle from $t = 0$ to $t = 1/f$, and then multiply that sum by the wingbeat frequency. This gives the inertial cost of flapping one wing per unit time, and we multiply that by two for the total inertial cost of flapping two wings:

$$P_{\text{fixed-wing}} = 2\mathcal{J}_w \pi^2 f^3 \phi^2. \quad (2.6)$$

We calculated f and ϕ separately for each trial, but fixed \mathcal{J}_w for each individual bat across all five of its trials to allow comparison with other studies [6,12]. The rotational moment of inertia of the wing, \mathcal{J}_w , is typically estimated by cutting the outstretched wing of a rigid specimen into $k = 10$ –16 strips between shoulder and wingtip. Using this method, \mathcal{J}_w is given by

$$\mathcal{J}_w = \sum_{n=1}^k m_n r_n^2, \quad (2.7)$$

with m_n as the mass of the n th strip, and r_n as the distance from the shoulder to the midline of the n th strip [5,6,12,14]. To

make our \mathcal{J}_w estimation comparable with other studies that assume an outstretched wing, we used the frame of video for each individual where wingspan was maximal. We allocated total body mass to the segments of the wing in the same proportions as those of our dissected *C. brachyotis* wing, then distributed those masses among 16 chordwise strips, based on the proportion of each wing segment that occupied each strip in that video frame. The moment of inertia of the wing was then estimated using equation (2.7).

(ii) The cost of moving a deforming wing: P_{tot}

We created a deforming wing model to estimate the inertial cost of the full complexity of joint motion of the bats' wings by considering the independent motions of k discrete components of the wing relative to the shoulder joint. The three-dimensional velocity vector of the n th component relative to the shoulder joint, v_n , was measured from three-dimensional kinematic recordings, and the mass of that component, m_n , was inferred from measurements of a dissected specimen [8]. Then, the inertial energy of the n th segment, E_n , was calculated using the following equation:

$$E_n = \frac{1}{2} m_n v_n^2. \quad (2.8)$$

The inertial power for the n th segment is the sum of all positive changes in inertial E_n over the course of the wingbeat cycle multiplied by wingbeat frequency. The total inertial power estimate, P_{tot} , is the sum of those inertial costs across the k elements, multiplied by two to account for both wings:

$$P_{\text{tot}} = 2f \times \sum_{n=1}^k E_n^+. \quad (2.9)$$

The deforming wing model permitted deconstruction of the inertial cost in different ways. We were able to estimate the inertial power required for the upstroke alone or downstroke alone by adding only the positive increases in work

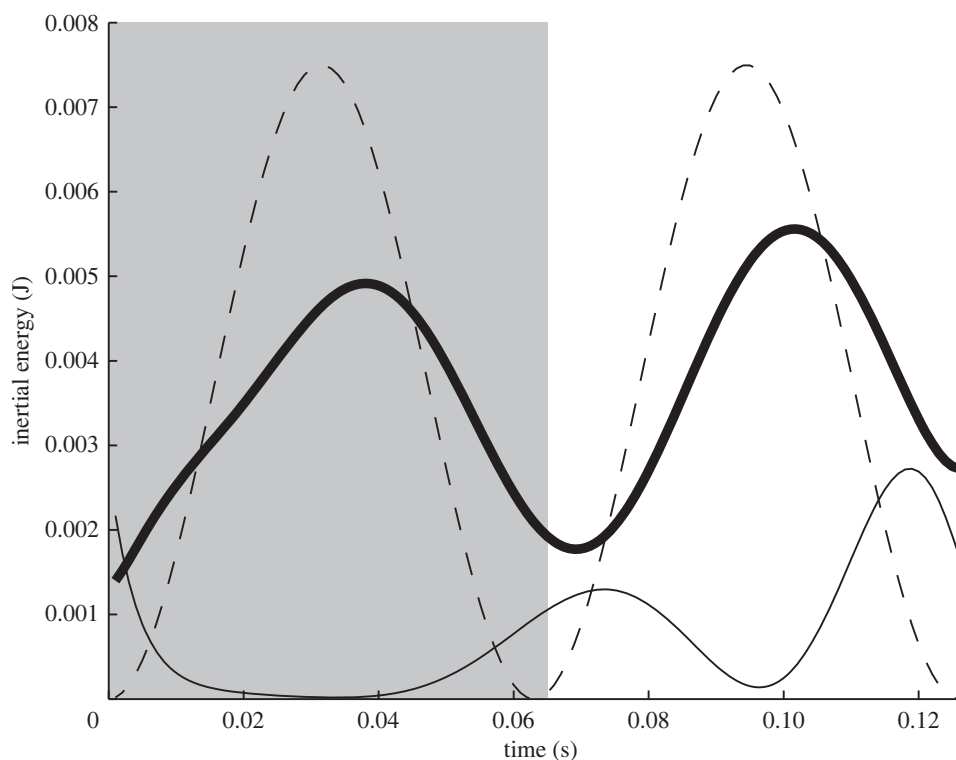


Figure 2. Inertial energy for both wings over the course of a wingbeat cycle for a 27.8 g *Cynopterus brachyotis* flying at 6.5 m s^{-1} . The downstroke is shown in grey. The dashed line is the predicted inertial energy over time according to the rigid-wing model, and the thick solid line is our estimate of inertial energy that takes three-dimensional wing kinematics into account. The thin black line is the inertial energy performed to move the masses directly towards or away from the shoulder. Note that the actual inertial work peaks once in the downstroke and once in the upstroke, as predicted by the rigid-wing model, but that the work performed to flex and extend the wing occurs mostly during the upstroke. These patterns were visible in trials from all species studied.

that occur during that phase of the wingbeat cycle. Similarly, we could isolate the inertial costs of moving different parts of the wing by summing equation (2.9) across only the body segments of interest.

(iii) *The isolated cost of wing flexion–extension: $P_{\text{in-out}}$*

Our method of estimating inertial costs also permitted us to approximate the inertial cost of wing folding and unfolding, $P_{\text{in-out}}$, by using equations (2.8) and (2.9) with v_n defined as the velocity of the n th segment only in the linear dimension pointed directly towards or away from the shoulder from its current position. If the wing rotated about the shoulder with no folding or unfolding, then $P_{\text{in-out}}$ would be zero.

(d) *Statistical methods*

Calculations were made on 135 separate wingbeat cycles in this study, each recorded during a separate flight. To avoid pseudoreplication owing to multiple recordings from the same individual, we used the means from each individual's five trials, for a total $n = 27$. We report results for each species separately, with N of three to five, depending on the species.

We used paired t -tests to determine whether the cost of the upstroke was significantly higher than that of the downstroke. We used the difference between an individual's average upstroke inertial cost across five trials compared with that individual's average downstroke inertial cost across five trials to make a pair. The number of pairs in each species was equivalent to the number of individuals of

that species in the study. The degrees of freedom for each test was the number of individuals in that species minus 1.

3. RESULTS

According to the rigid-wing model of flapping flight, there are two peaks in the inertial energy of the wing: one during the downstroke, and one during the upstroke. We found this pattern to also be true of inertial energy estimates that took changes in wing conformation into account (figure 2). However, the minima and maxima of inertial energy calculated based on the actual three-dimensional wing kinematics were not as extreme as those predicted by the rigid-wing model (figure 2). As a consequence, our estimate of the inertial power required for flapping flight, P_{tot} , was just 59–71% of what was predicted based on the rigid-wing model (table 2).

We had predicted that the inertial cost of the upstroke would be less than that of the downstroke, but our results did not support that prediction. In all six species, the average inertial cost of the upstroke was roughly equivalent to that of the downstroke. In fact, the inertial cost of the upstroke exceeded that of the downstroke in all species, but not significantly so (paired t -test: $p > 0.05$).

The power used to move the wings towards and away from the shoulder, $P_{\text{in-out}}$, was large relative to P_{tot} , with $P_{\text{in-out}}$ making up 37–59% of total inertial cost of the wingbeat cycle as a whole (table 2). There were two peaks in the in–out component of inertial energy: one during wing folding at the beginning of the upstroke,

Table 2. Inertial cost estimates for the six species in this study.

	<i>Cynopterus brachyotis</i> (<i>n</i> = 5)	<i>Rousettus aegyptiacus</i> (<i>n</i> = 3)	<i>Pteropus pumilus</i> (<i>n</i> = 5)	<i>Eidolon helvum</i> (<i>n</i> = 5)	<i>Pteropus hypomelanus</i> (<i>n</i> = 5)	<i>Pteropus vampyrus</i> (<i>n</i> = 4)	mean
body mass (g)	33.6 ± 4.4	134.3 ± 23.6	190.4 ± 16.3	291.2 ± 35.6	480.4 ± 28.7	1078.5 ± 56.7	
$P_{\text{rigid-wing}}$ (W)	0.23 ± 0.11	1.15 ± 0.31	1.59 ± 0.54	2.81 ± 0.83	3.30 ± 0.39	9.45 ± 2.97	
P_{tot} (W)	0.15 ± 0.06	0.65 ± 0.07	0.94 ± 0.31	1.73 ± 0.52	2.12 ± 0.30	6.65 ± 2.27	
$P_{\text{tot}}/P_{\text{rigid-wing}}$ (%)	69.48 ± 6.79	58.98 ± 9.45	63.05 ± 9.12	62.83 ± 7.12	64.83 ± 2.96	70.78 ± 3.93	64.99
downstroke ratio	0.48 ± 0.01	0.50 ± 0.01	0.52 ± 0.02	0.51 ± 0.01	0.56 ± 0.01	0.56 ± 0.03	0.52
P_{tot} : % downstroke	45.11 ± 4.88	36.75 ± 7.35	44.87 ± 7.80	49.80 ± 2.89	44.73 ± 6.33	40.71 ± 4.78	43.66
P_{tot} : % upstroke	54.89 ± 4.88	63.25 ± 7.35	55.13 ± 7.80	50.20 ± 2.89	55.27 ± 6.33	59.29 ± 4.78	56.34
$P_{\text{in-out}}/P_{\text{tot}}$ (%)							
wingbeat cycle	41.35 ± 9.70	58.96 ± 6.19	39.24 ± 13.65	48.94 ± 6.80	37.11 ± 2.18	39.77 ± 9.01	44.23
downstroke only	22.15 ± 5.22	53.85 ± 16.70	22.51 ± 7.26	24.53 ± 3.55	27.40 ± 4.92	30.24 ± 9.68	30.11
upstroke only	58.41 ± 15.15	67.11 ± 3.97	57.54 ± 25.30	74.92 ± 15.11	45.31 ± 3.68	47.09 ± 9.82	58.40
$P_{\text{segment}}/P_{\text{tot}}$ (%)							
arms	37.49 ± 3.24	38.36 ± 1.60	38.45 ± 3.64	38.22 ± 3.03	37.44 ± 1.90	38.88 ± 4.05	38.14
digits	45.14 ± 2.24	44.59 ± 1.55	43.05 ± 2.31	44.66 ± 2.87	43.44 ± 1.74	42.85 ± 3.63	43.96
membranes	15.82 ± 0.90	14.85 ± 0.52	16.32 ± 0.68	15.80 ± 0.81	16.72 ± 0.53	16.59 ± 0.98	16.02
hindlimbs	1.55 ± 0.34	2.20 ± 0.75	2.17 ± 1.28	1.32 ± 0.72	2.40 ± 1.67	1.68 ± 0.80	1.89

and one during wing unfolding near the end of the upstroke (figure 2). Because both of these peaks typically occurred during the upstroke, the majority of $P_{\text{in-out}}$ expenditures occurred during the upstroke. On the upstroke, $P_{\text{in-out}}$ was equivalent to 45–75% of the total inertial cost, whereas on the downstroke it made up just 22–54% (table 2).

We estimate that 37–39% of the inertial cost of flight was owing to the combined cost of accelerating the humerus, forearm and wrist. The cost of accelerating the digits accounted for another 43–45%, the membranes 15–17% and the bones of the hindlimb just 1–2% (table 2). Segments are defined in the electronic supplementary material.

4. DISCUSSION

Pteropodid bats fold their wings in complex ways during flight [15], and our results show that the inertial cost that results from those kinematics is roughly 65 per cent of what the cost would be if the extended wing were moved sinusoidally throughout the wingbeat cycle, assuming f and ϕ were not changed. This was true for multiple pteropodid species, spanning a more than 40-fold range of body weight. By drawing the wings towards the body for part of the wingbeat cycle, bats lowered the rotational moments of inertia of their wings, and therefore paid a reduced inertial cost for rotating them about the shoulder. Folding and unfolding the wings was costly, making up roughly 44 per cent of the overall inertial cost of flapping the wings, but the overall cost of the kinematic pattern bats employed was lower than it would have been had the wings remained outstretched and rigid. We thus infer that the inertial energy savings of wing folding over the course of the wingbeat cycle might be an important benefit underlying its widespread use among flying vertebrates.

The degree to which upstroke wing folding occurs in a flying vertebrate is usually expressed as the span ratio, the

ratio of upstroke wingspan to downstroke wingspan. Hummingbirds have span ratios greater than 0.9, reflecting small changes in wingspan, but non-passerine birds and the nectar-feeding bat *Glossophaga* have span ratios around 0.6–0.8, and the span ratios of some birds can be as low as 0.2–0.4 [18–20]. The span ratio of the pteropodid bats in this study averages approximately 0.3–0.4, dropping as low as 0.16 for some wingbeat cycles [11]. Thus, the bats in this study are a good model for the inertial consequences of wing flexion, and our findings are applicable to other taxa, in future studies that use similar methods.

Inertial costs are known to be smaller than aerodynamic costs for fliers, and our results demonstrate that the inertial costs of flight can be even lower than previously assumed [1,5,17]. However, even our estimate of inertial cost might be an overestimate because it does not account for the possible transfer of kinetic energy from one wing element to another. For example, as the forearm and wrist slow down at the end of the downstroke or upstroke, they could transfer their momentum to the more distal digits, in a manner similar to the cracking of a whip, thereby accelerating the digits without metabolic work above the cost of accelerating the proximal segments of the wing. It is plausible that a linkage model which could account for such energy savings might indicate that the apparently high cost of moving the digits is overestimated in this study.

We have argued that the wing kinematics of modern birds and bats reflect the influence of inertial costs, but that is just one of several expenses for a flying organism. For birds and bats, the upstroke results in a net loss of forward and upward momentum, and those losses must be replaced by muscular work [2,8]; animals might perform upstroke wing flexion to reduce those losses. Folding the wings should reduce the horizontally oriented profile drag on the wings that slows an animal's forward velocity and should also reduce the vertical drag on the upward-moving wings that would otherwise push the body downwards [21]. Furthermore, upstroke wing folding might produce vortices on the wing that improve lift compared

with what would occur for outstretched wings [22–24]. Thus, the true value of upstroke wing folding to the metabolic cost of flight can only be understood through a detailed aeromechanical study that quantifies the influence of upstroke wing folding on lift, drag and thrust.

The distribution of inertial cost among the parts of the wing of bats is dictated mostly by the distance of those wing elements from the shoulder joint. For example, the humerus, forearm and wrist make up 60 per cent of wing weight, but accelerating their masses contributes only 38 per cent of the overall inertial cost. Conversely, the accelerations of the digits account for 44 per cent of the inertial cost of flight, despite the fact that the digits make up only 12.1 per cent of wing mass (table 2 and the electronic supplementary material). This result underlines the inertial benefit that results from the reduced mineralization of bat digits. Were the metacarpals and phalanges as mineralized as those of non-volant mammals, the inertial costs associated with wing acceleration would be notably higher. Thus, although inertial costs may comprise a relatively low proportion of the total energy cost of flight, there could well have been strong selection for reduced mineralization early in bat evolution. Of course, the increased flexibility of those elements that results from decreased mineralization might have aerodynamic benefits as well [25].

Because nearly half of the inertial cost of flight is that of moving the wing parts towards and away from the shoulder, models of wing inertia that do not take wing three-dimensional kinematics into account neglect information that is crucial for energetic cost estimates. Our results highlight the importance of wing folding and unfolding to the elevated cost of the upstroke compared to the downstroke, and to the decreased overall inertial cost of flight compared with what would occur if wing conformation was not modulated over the wingbeat cycle.

All components of this study were approved by the Institutional Animal Care and Use Committee at Brown University.

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