

Research



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Integrating morphology and kinematics in the scaling of hummingbird hovering metabolic rate and efficiency

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Wing kinematics and morphology are influential upon the aerodynamics of flight. However, there is a lack of studies linking these variables to metabolic costs, particularly in the context of morphological adaptation to body size. Furthermore, the conversion efficiency from chemical energy into movement by the muscles (mechanochemical efficiency) scales with mass in terrestrial quadrupeds, but this scaling relationship has not been demonstrated within flying vertebrates. Positive scaling of efficiency with body size may reduce the metabolic costs of flight for relatively larger species. Here, we assembled a dataset of morphological, kinematic, and metabolic data on hovering hummingbirds to explore the influence of wing morphology, efficiency, and mass on hovering metabolic rate (HMR). We hypothesize that HMR would decline with increasing wing size, after accounting for mass. Furthermore, we hypothesize that efficiency will increase with mass, similarly to other forms of locomotion. We do not find a relationship between relative wing size and HMR, and instead find that the cost of each wingbeat increases hyperallometrically while wingbeat frequency declines with increasing mass. This suggests that increasing wing size is metabolically favourable over cycle frequency with increasing mass. Further benefits are offered to larger hummingbirds owing to the positive scaling of efficiency.

1. Background

Wing size has a large effect upon the inertial power required to accelerate the wing during a half wingbeat, the wingbeat frequency (f) needed for flight, and the aerodynamics of the wing [1–3], which help determine the metabolic requirements for flight. However, the relationships that link the scaling of morphology and kinematics to flight metabolism have not yet been examined in flying vertebrates owing to the difficulty in measuring metabolic expenditure during flight. Thus, we presently lack general understanding of how variation in wing morphology and kinematics interacts with the energetic costs of flight, and whether there are avenues for morphological variation to reduce energetic expenditure or increase the efficiency of converting metabolic to mechanical power. In one extreme example, hummingbirds have some of the highest metabolic rates (MRs) among vertebrates during hovering flight [4]. Hummingbirds are also unusual among birds in that the wing area scales with body mass (M_b) with an exponent of 1.0 (i.e. wing area $\propto M_b^{1.0}$) [5], whereas wing area tends to scale proportionally to $M_b^{0.7}$ in other avian taxa [6]. This unusual allometry may have allowed for hummingbirds to moderate the increased energetic costs associated with hovering flight with larger body size. If true, this leads to the prediction that flight MR would scale with wing area and/or wing length, after taking into account the effect of body mass.

The scaling of mechanochemical efficiency (mechanical work output divided by metabolic energy input) may also have implications upon flight performance, as it varies as a function of body size [7], at least among cursorial vertebrates. However, the few studies that have examined mechanochemical efficiency in hovering hummingbirds concluded that efficiency does not change with increasing mechanical demand (such as variation in body mass or air density) [8], is consistently 10% both within and among species [9–11], and is thought to be constant across body sizes [12]. However, the species examined in these studies were of similar body mass, and any scaling of efficiency may not be readily apparent across such a narrow size range. Instead, if mechanical power output for hovering flight tends to scale with body size with an exponent of 1.0 [5,13], while the metabolic costs of hovering flight scale hypoallometrically with body mass [14], mechanochemical efficiency must increase in larger hummingbirds relative to smaller species. This scaling of efficiency may have implications upon currently observed elevational distribution patterns of hummingbirds [13,15], particularly how much daily energy is partitioned towards locomotor costs and the capacity to perform flight that requires high rates of metabolism.

In this study, we use hummingbirds as a model to explore the relationship between morphology, kinematics and flight metabolism, as hummingbirds are amenable to measurements of hovering metabolic rate (HMR) and wingbeat kinematics. Furthermore, recent research into the mechanical and metabolic costs of hovering flight in hummingbirds permit us to test how efficiency of hovering flight varies over a relatively broad range of body sizes and within a phylogenetic context. We also investigate the mechanochemical efficiency of flight and explore the potential implications of scaling of mechanochemical efficiency. We integrate new data collected in the field with published data to assemble a database of hummingbird HMRs, kinematics, and wing morphometrics across body masses of 2.6–17.5 g, and examine the scaling relationships of these measures across body size.

2. Material and methods

(a) Brazilian field experimental study

Data collection occurred in August–September 2012, May–July 2013 and February–March 2015. Three locations were used, Ubatuba, São Paulo; Guainumbi Reserve, Santa Virginia District, São Luiz do Paraitinga, SP; and Campos do Jordao, SP, Brazil. These sites correspond to 0, 1000 and 1800 m above sea level, respectively. All eight species of hummingbird were found within 80 m of elevation from the experimental site.

Hummingbirds were captured using a mist net or a modified box trap, quickly transported to the nearest field station and acclimated to feed from syringe feeders. Hummingbirds were maintained in 61 × 61 × 61 cm mesh cages (Bioquip, Rancho Dominguez, CA, USA) and fed 25% sucrose solution. Following data collection, hummingbirds were either released at site of capture, or euthanized for use in another study.

MR was recorded using open-flow mask respirometry, as previously described [8,16,17]. Briefly, hummingbirds were trained to receive sugar solution from the mask made from a 25 ml Luer-Lok syringe (BD, Franklin Lakes, NJ, USA). Multiple masks of different lengths were made to accommodate the length of the head and bill of different species. Air was withdrawn from the mask at 2000–2500 ml min⁻¹, and pumped to the respirometer for gas analysis (Turbofox, Sable Systems International, North Las Vegas, NV,

USA). Air was subsampled from the mainline at 500 ml min⁻¹, and humidity was immediately measured using a water vapour meter before being dried with Drierite (W.A. Hammond Drierite, Xenia, OH, USA). Sampled air was then drawn into oxygen and CO₂ analysers. An infrared (IR) emitter and detector was placed at the opening of the mask, and was used to record the length of a feeding event by measuring the length of time the head of the hummingbird occluded the IR beam. Outputs from the IR detector, inline barometer, flow meters, water vapour meter and gas analysers were recorded every 0.1 s using EXPEDATA (v. 1.72, Sable Systems International, North Las Vegas, NV, USA) on a laptop computer. Oxygen consumption and CO₂ production rates were calculated as previously described [17].

Wingbeat kinematics were recorded as previously described [18]. Briefly, hummingbirds were trained to feed from a 2 ml syringe containing 25% sucrose solution within a 61 × 61 × 61 cm mesh cage with a clear acrylic top panel. A high-speed camera (S-PRI, AOS Technologies AG, Baden Daettwil, Switzerland) was positioned directly above the syringe and recorded feed bouts at 1000 frames s⁻¹ and shutter speed of 200 μs. Wingbeat frequency (Hz) was determined by dividing the frame rate by the number of frames required to complete a wingbeat. Stroke amplitude (deg) was the angle defined by the wing's trajectory between the start and end of spanwise supination and pronation denoting the start and end of upstroke, respectively. All kinematic recordings were analysed using IMAGEJ 64 (v. 1.47, US National Institutes of Health, Bethesda, MD, USA).

Body mass (g) was measured using an electronic balance (± 0.01 g) before and after respirometric and kinematic trials. The mean value was used to estimate body mass. Wings from each hummingbird were outstretched into a position approximating that of flight, and photographed against graph paper. Images were analysed using a custom MATLAB script (from Dr Douglas Altshuler, MATLAB v. 7.12, Mathworks, Natick, MA, USA) to measure wing area (mm²), wing length (m), non-dimensional variables associated with hovering flight including aspect ratio [19].

Mechanical power output was calculated as the sum of the profile (P_{pro}) and induced (P_{ind}) power requirements to sustain hovering flight, calculated using the Ellington quasi-steady state model of flight, where the stroke amplitude was used to determine the disk area for a momentum-jet model of induced power [20,21]. P_{pro} and P_{ind} were each calculated using kinematic and morphological parameters measured for each individual, and the measured air density at each site [21]. For all calculations, the stroke plane angle was assumed to be 0°, as the stroke plane angle has previously been found to be low during hovering flight [22], and simple harmonic motion was assumed to estimate angular velocities and accelerations of the wing over the wingbeat cycle [9]. A constant coefficient of profile drag ($C_{d,\text{pro}}$) of 0.139 was used, based on empirical measurements of a hummingbird wing on a spinner [23]. However, a constant $C_{d,\text{pro}}$ should be used cautiously, as $C_{d,\text{pro}}$ probably varies as the angle of attack changes over the wingbeat cycle.

Given that hovering flight has a forward velocity of zero, parasite power was ignored. The inertial power (or the cost of accelerating and decelerating the wing over the wingbeat cycle) was assumed to be zero, meaning we assumed all inertial work in the first half of a stroke to accelerate the wing was recovered as aerodynamic work in the latter half of the stroke [21]. As we were unable to quantify some details of wingbeat kinematics (e.g. variation in stroke angle, attack angle, etc.) and how these varied over a wingbeat cycle during our fieldwork, and because published kinematics data did not include such kinematic details, we are unable to estimate unsteady aerodynamic effects (e.g. rotational circulation at the ends of the half strokes, [24,25]). Instead, we assume that the scale of variation in mechanical power production among species and trials is reasonably approximated despite the absence of such data.

(b) Arizona field experimental study

Metabolic data were collected in July 2006 and 2008 along Harshaw Creek, Patagonia, AZ and in July 2007 at the Southwestern Research Station in the Chiricahua Mountains in southeastern Arizona from seven species of free-living hummingbirds. These two sites correspond to 1250 m and 1675 m above sea level, respectively.

Hummingbirds fed from a mask constructed from a 25 ml syringe barrel. Masks of different lengths were constructed to accommodate the different head and bill lengths of our study species. Oxygen consumption rates were measured similarly to the Brazilian hummingbirds using oxygen and carbon dioxide gas analysers (FoxBox, Sable Systems International, North Las Vegas, NV, USA), and recorded using Warthog LABANALYST on an Apple laptop computer. Air was withdrawn from the mask at between 2000 and 3000 ml min⁻¹. The length of feeding events was determined by simultaneous video recording. Body masses are based on bird banding data that was taken within one week of respirometry measurements. Measurements of wing area and wing length were performed on calibrated infrared images (FLIR SC6700) and analysed using IMAGEJ 64 (v. 1.47, US National Institutes of Health, Bethesda, MD, USA).

(c) Analyses and statistics

Supplemental to the oxygen consumption rate measurements presented here (electronic supplementary material, table S1), literature values were also integrated in the analyses (electronic supplementary material, table S2). Any oxygen consumption rates determined using closed-system respirometry were discarded. All oxygen consumption rates were converted to Watts using the oxyJoule equivalent of 21.1 W ml O₂⁻¹ [26]. A variety of morphological and kinematic sources were compiled if the data were not provided with the measures of oxygen consumption rate (electronic supplementary material, table S3). Currently, the patterns of intraspecific variation in wing morphology across elevations are not well understood, with previous studies finding only some species showing variation while others do not [8,27,28]. Furthermore, work by Graham *et al.* [15] has found that the standard deviation of morphological traits across species is much greater than intraspecific standard deviation. Wingbeat frequency does not vary with elevation or air density [9,18] and instead scales with body mass [8,29]. Thus, we assumed that morphology and kinematics do not vary across elevations within a species for the purposes of this study. If multiple sources of morphological or kinematic data were reported for a single species, a weighted average was used. Wing loading was calculated based upon the species-specific wing areas and the body mass measurements that accompanied the MR data. Aspect ratio was calculated as b^2/A , where b is the twice the wing length and A is the wing area. Cost per wingbeat was calculated by dividing HMR (in Watts) by wingbeat frequency (Hz).

All statistical analyses were performed in R (v. 3.0.2). Data was log₁₀-transformed before analysis. Phylogenetic generalized least squares (PGLS) were used to examine the scaling of MR across morphological and kinematic variables [30–32] using the R package *caper* [33]. The phylogenetic tree was based on the comprehensive hummingbird phylogeny of McGuire *et al.* [34] and pruned down to the species represented in the dataset using the R package *ape* [35]. Any hummingbird species that were not included in the phylogeny were omitted from the final analysis. Since many morphological traits (e.g. wing area and wing length) correlate with body mass, residual analysis was performed to size correct the morphological and physiological traits against body mass. The residuals of morphological and kinematic traits were regressed against the residuals of HMR, while incorporating phylogenetic information, as described in Revell [36].

Efficiencies were calculated using mechanical power output and oxygen consumption data as described previously [8].

Assuming that 90% of oxygen consumed is used by the flight muscles during hovering flight in hummingbirds [4,37], efficiency was calculated as: $\text{efficiency} = P_{\text{mechanical}} / (P_{\text{metabolic}} \times 0.9)$, similar to Chai & Dudley [9]. Our efficiency data were combined with other estimates of efficiency provided in the literature for analysis (electronic supplementary material, table S2). The original estimates of mechanical power output provided by Wells [11] estimated the coefficient of profile drag as $7/\sqrt{Re}$, where Re is the mean Reynolds number of the wing over the wingbeat [21]. The estimates of mechanical power output by Wells [11] were recalculated with an assumption of $C_{D,\text{pro}}$ of 0.139 [23]. Efficiency data were then analysed using PGLS, as described above.

3. Results

(a) Morphological and kinematic scaling

Wing morphological variables and wingbeat frequency scaled with body size with the exception of wing loading, which did not vary across body sizes (electronic supplementary material, table S4).

(b) Metabolic rate across body mass, size and wingbeat kinematics

Including all available data from 25 hummingbird species, reported mean hummingbird masses ranged from 2.56 g for *Archilochus colubris* to 17.5 g for *Patagona gigas*. HMR scaled proportional to $M_b^{0.764}$ (95% confidence interval (CI): 0.619, 0.911; table 1; figure 1). With the exclusion of *P. gigas* from analysis, $\text{HMR} \propto M_b^{0.725}$ (95% CI: 0.548, 0.901; table 1). The scaling coefficients for HMR versus wing loading were not significantly different from zero regardless of whether *P. gigas* was included (table 1; figure 2). MR declined with increasing wingbeat frequency, with MR proportional to $f^{-1.05}$ (table 1), both including and excluding *P. gigas*. The energetic cost per wingbeat was found to scale $\propto M_b^{1.40}$ for all species, and $\propto M_b^{1.36}$ when excluding *P. gigas* (table 1). Residual analysis did not reveal any significant relationships between morphology or wingbeat frequency, and MR with both the inclusion and exclusion of *P. gigas* ($p > 0.1$).

(c) Hovering flight efficiency across body sizes

PGLS regression of hovering flight efficiencies against hummingbird body mass revealed a positive relationship between these parameters ($F_{1,10} = 8.703$; $p = 0.0145$; $n = 12$; figure 3). The efficiency of hovering flight scales as $M_b^{0.379}$ (95% CI: 0.093, 0.665).

4. Discussion

(a) Scaling of hummingbird hovering metabolic rate

Hummingbird hovering oxygen consumption rates scale proportional to $M_b^{0.764}$, which is in agreement with the other metabolic scaling relationships, such as basal MR and field MR [38–40]. This estimate of the power coefficient is in close agreement with previous studies of hummingbirds [14], and is much lower than the near isometric estimation of the scaling coefficient in hummingbirds and bats reported by Voigt & Winter [41]. Furthermore, the lack of relationship observed during residual analysis suggests that there are no

Table 1. PGLS regression coefficient estimates of the scaling of wingbeat frequency, wing area, wing loading, and wing disc loading against hovering oxygen consumption rates, and the scaling of cost per wingbeat with body mass. (All variables were \log_{10} -transformed before analysis. 95% confidence intervals are provided with the slopes within the brackets.)

	<i>N</i>	intercept	slope	<i>R</i> ²	<i>p</i> -value
body mass					
all	25	−0.526	0.764 (0.619, 0.911)	0.836	<0.001
excluding <i>P. gigas</i>	24	−0.497	0.725 (0.548, 0.901)	0.766	<0.001
wing area					
all	20	−0.723	0.597 (0.444, 0.750)	0.789	<0.001
excluding <i>P. gigas</i>	19	−0.738	0.609 (0.398, 0.821)	0.684	<0.001
wingbeat frequency					
all	20	1.63	−1.05 (−1.34, −0.763)	0.764	<0.001
excluding <i>P. gigas</i>	19	1.48	−0.958 (−1.29, −0.625)	0.684	<0.001
wing length					
all	20	−2.12	1.22 (0.898, 1.54)	0.778	<0.001
excluding <i>P. gigas</i>	19	−2.66	1.52 (0.986, 2.05)	0.682	<0.001
wing loading					
all	20	−0.793	0.520	0.063	0.285
excluding <i>P. gigas</i>	19	−0.502	0.404	0.039	0.415
cost per wingbeat (against mass)					
all	20	−2.49	1.40 (1.23, 1.56)	0.940	<0.001
excluding <i>P. gigas</i>	19	−2.47	1.36 (1.16, 1.57)	0.915	<0.001

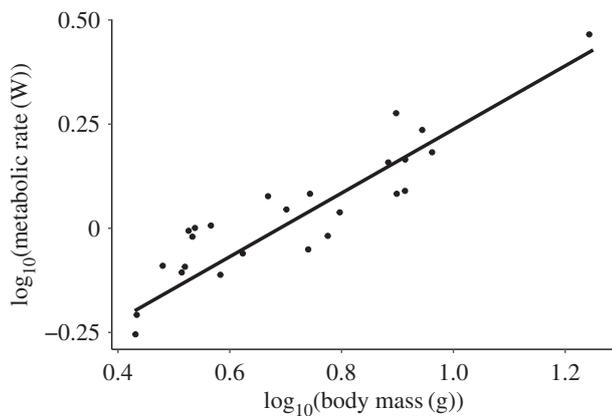


Figure 1. The relationship between body mass and hovering metabolic rates. Phylogenetic generalized least-squares regression equations and statistics can be found in table 1.

compensatory effects of wing size (area and length) or kinematics upon oxygen consumption rates during hovering.

Body mass and wing size (area and length) have profound effects upon wingbeat frequency. Wingbeat frequency scales with wing size through changes in the inertial cost of accelerating the wing pair, affecting the oscillation of the wings over the wingbeat cycle [1], and this is reflected in the hyperallometric scaling of the energy cost per wingbeat with body mass. While wing area itself does not directly influence the moment of inertia, it may be a good proxy for the mass and mass distribution of the wing. For example, Altshuler & Dudley [29] found that, despite the close body masses of three different sex/species classes of *Selasphorus rufus* and *S. platycercus* hummingbirds, wingbeat frequency variation

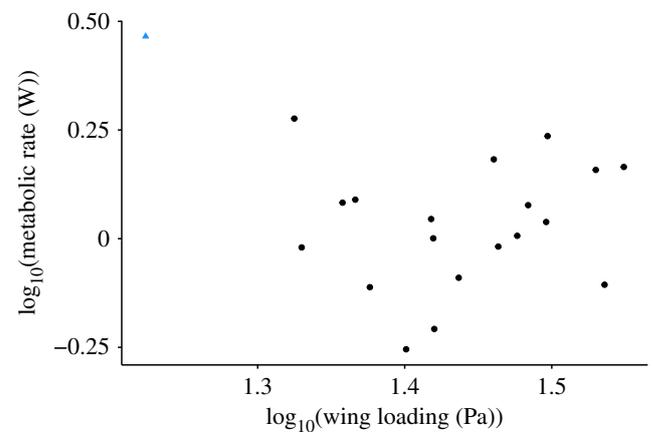


Figure 2. The relationship between wing loading and hovering metabolic rates. The blue triangle represents *Patagona gigas*, the largest hummingbird species represented. Phylogenetic generalized least-squares regression equations and statistics can be found in table 1. (Online version in colour.)

was related to the length of the wing. While wing areas were not reported in Altshuler & Dudley [29] across the sex/species classes, wing areas probably show similar patterns. This higher wingbeat frequency associated with the smaller wings of small hummingbird species may in part explain the higher mass-specific MRs during flight compared to larger species, despite the higher cost per wingbeat of larger hummingbirds. Similar to hummingbirds, there is a relationship in operating frequency of the wings and metabolic expenditure seen in orchid bees [42], with larger bees maintaining lower mass-specific HMRs, potentially related to the lower cycling frequencies afforded to them by their relatively larger wings [42]. Thus, much of the variation

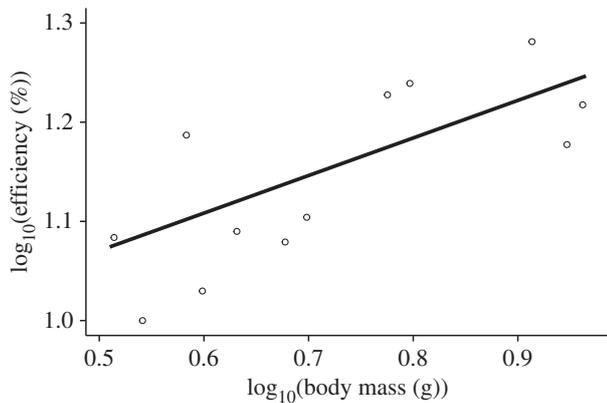


Figure 3. The scaling of efficiency across body masses of hummingbirds. The equation of the PGLS regression is $\log_{10}(\text{efficiency}) = 0.881 + 0.379 \log_{10}(\text{body mass})$. $n = 12$.

in hovering flight MRs may be mediated through changes in wingbeat frequency, which in turn are associated with wing size.

Wing area in hummingbirds scale $\propto M_b^{1.0}$ to help maintain constant wing velocity during hovering across all body sizes [5]. Instead of modulating other aspects of hovering flight with rising mass such as changes in kinematics (e.g. angle of attack) or increasing wing velocity, wing area is the primary variable that varies with size as it reduces energetic expenditure during hovering flight without compromising flight capabilities [5]. This argument is bolstered by this study, as increasing wing velocity through changes in wingbeat frequency may be more metabolically expensive. Thus, if hummingbirds were to follow the wing area scaling relationship of other bird groups (area $\propto M_b^{0.7}$), they would probably need to increase wing velocity in order to sustain hovering flight. Doing so may incur higher energetic costs than through modulation of wing size and the corresponding reduction in wingbeat frequency. Conversely, disproportionately larger increases in wing area relative to body size are accompanied by functional costs such as reducing aerial capabilities [5,43]. Thus, hummingbirds probably display wing area scaling $\propto M_b^{1.0}$ as it may balance metabolic and competitive requirements for flight.

(b) Efficiency during hovering flight

Previous studies on hovering flight efficiency within hummingbirds reported that efficiency is relatively low (approx. 10%) and is independent of body mass [44]. However, our understanding of the aerodynamic costs and requirements for flight have changed considerably in the past four decades, and more recent analyses suggest that efficiency scales across body masses for a variety of taxa and modes of locomotion [7]. Animals that possess asynchronous muscles, like Euglossine bees and bumblebees, exhibit scaling of efficiency proportional to $M_b^{0.33}$ and $M_b^{0.52}$, respectively [45]. MR in sphinx moths during hovering flight is predicted to scale to $M_b^{0.75}$, while the mechanical power requirements for hovering flight are thought to scale isometrically with mass [7,46,47]. Both scaling relationships in sphinx moths are similar to those observed in hovering hummingbirds [13] and lead to a predicted scaling of efficiency proportional to $M_b^{0.25}$. In this study, efficiency appears to scale with $M_b^{0.379}$ (and include 0.25 within the 95% CIs) which is remarkably similar to these previous studies of other

hovering animals, despite large divergence in evolutionary history and flight morphology.

Studies examining the interspecific scaling of hovering flight mechanical power requirements find that it scales with to $M_b^{1.0}$, because of the interspecific scaling of wing area with body size, and is independent of elevation [5]. Further, we, and others [14], show that hummingbird HMRs scale according to $\frac{3}{4}$ power scaling [40,48,49]. Taken together, this suggests that efficiency likewise does not scale across elevations, instead being a function of body size alone. While patterns of species mass in relation to elevational distribution may be random when viewed globally [5], locality-specific species assemblage has previously been shown to be structured in relation to bird size with larger species tending to be at higher elevations [13,50]. With their more efficient flight muscles large birds may have a higher aerobic scope or greater hypoxia tolerances during exercise because of the nearly two-fold difference in hovering flight mechanochemical efficiency among the species examined here. This conclusion relies on the assumption that differences in maximum sustainable HMRs are either similar among hummingbirds regardless of body mass, or that maximum sustainable rates decline with body mass less strongly (i.e. with an exponent greater than -0.379). The limited availability of maximum sustainable hovering metabolic data precludes exhaustive calculations of scope among hummingbird species or across elevational guilds. Thus, it is currently impossible to rigorously examine this hypothesis. So far, available evidence from Groom *et al.* [8] indicates scopes of performance are largely similar across elevations in the few species examined. Expanding the sample of species and testing across a broad elevational range is required to examine additional influences upon the efficiency of hovering flight and whether there are morphological traits that may be able to influence efficiency and corresponding elevational ranges. However, among a range of mammalian and avian species, basal MR scales proportionally to $M_b^{0.75}$ and maximum MR scales proportionally to $M_b^{0.88}$, implying aerobic scope scales positively with body size [51]. This indicates that larger hummingbird species may likely have a wider scope that may allow them to survive in energetically extreme environments, potentially facilitated by greater efficiency.

The efficiency of skeletal muscles during cyclical activities, such as in limbs during locomotion, is believed to be related to the velocity of muscle contraction, which is also closely associated with the necessary cycling frequency of contraction (i.e. the wingbeat frequency, in the case of hummingbirds and other flying animals) [45,52]. Small animals tend to undergo more rapid contraction cycles when compared to larger species during cyclical activities, such as locomotion [29,42,53,54], and the contraction velocity may set overall efficiencies [45]. The high rate of contraction may reduce efficiency by interfering with crossbridge kinetics of the sarcomere, strongly reducing the amount of work that can be produced per myosin head. Some such mechanisms that have been proposed to underlie this phenomenon include: early detachment of the myosin head during the cycle; poorly timed detachment of the myosin head, which causes absorption of work by the attached head; or using a smaller extension than maximally possible by the myosin [55]. Given that small hummingbirds have higher wingbeat frequencies than larger species, this probably holds true for hovering hummingbirds. Analysis of the efficiency of Euglossine and

bumblebee flight muscle reveals a close association between myofibrillar efficiency (the efficiency of converting ATP to mechanical work at the myofibril) and both body size and wingbeat frequency [45]. Since smaller bees tend to operate at higher wingbeat frequencies, smaller bees tend to possess overall lower myofibrillar efficiency at their optimum power output. It appears that differences in wing morphology may influence wingbeat frequency, which can have a large influence upon the overall efficiency of the flight muscles. However, myofibrillar efficiency is one part of the overall efficiency of an animal during locomotion, and efficiency losses during oxidative phosphorylation, calcium cycling, and the scaling of the energetic costs associated with muscle activation must also play a substantial role in setting whole-animal efficiency [45,52]. It is currently unknown what relative contributions these losses have to overall efficiency.

One factor that has not been adequately explored in birds is the effect of the elastic components upon locomotor efficiency. This study employed an assumption of perfect elasticity, whereby all the inertial work associated with accelerating and decelerating the wing over the wingbeat cycle is absorbed and returned by the antagonistic pectoralis and supracoracoideus or is dissipated as aerodynamic work in the latter half of each half stroke. Tendons, which are highly elastic structures, probably play a large role in reducing the metabolic costs and increasing efficiency of cyclical contractions during locomotor activities [56]. Direct measures of force production by the supracoracoideus in pigeons is estimated to permit up to 60% energy recovery for this muscle and up to 10% of the total work necessary for slow flight [57]. The supracoracoideus in hummingbirds also possesses a long tendon [58]. Electromyography during hovering flight suggests that activation of the supracoracoideus occurs much earlier before the onset of the upstroke, compared to the pectoralis and its corresponding downstroke, likely to account for the highly compliant (and, probably elastic) nature of the supracoracoid tendon [18].

Thus, elastic energy storage may have an important role in reducing energetic expenditure by increasing efficiency. However, the tendons are unable to return all elastically stored energy [59], and the proportion of elastic energy recovered and used to reaccelerate the wing may vary across body sizes.

Ethics. Procedures conducted in Brazil were approved by the University of Toronto Animal Care Committee and the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (SISBIO permit no. 33158-5). Procedures conducted in Arizona were approved by George Fox University IACUC (P002) and the Arizona Department of Game and Fish (SP622308 and SP565912).

Data accessibility. All data used in this manuscript are present in the manuscript and its supporting information. Raw data collected for this study can be found on Dryad (<http://dx.doi.org/10.5061/dryad.7n94f>) [60].

Authors' contributions. D.J.E.G. and K.C.W. conceived the ideas and designed methodology; D.J.E.G., M.C.B.T., D.R.P., B.W.T. and K.C.W. collected the data; D.J.E.G. analysed the data; D.J.E.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests. We have no competing interests.

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