

MUSCLE PERFORMANCE IN HOVERING HUMMINGBIRDS

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Summary

The flight energetics of hovering hummingbirds was examined by simultaneous collection of metabolic and kinematic data followed by a morphometric analysis of wing characteristics. These data were then used for an aerodynamic analysis of the power output required to generate sufficient lift; this, together with the metabolic power input, allowed an estimate of the flight efficiency. The use of two closely related species demonstrated common design features despite a marked difference in wing loading. Considerations of the inertial power costs strongly suggest that hummingbirds are able to store kinetic energy elastically during deceleration of the wing stroke. This analysis predicts that hummingbirds hover with a muscle power output close to $100\text{--}120\text{ W kg}^{-1}$ at 9–11% mechanochemical efficiency.

Introduction

Hovering flight has been described as the most energetically expensive form of locomotion (Weis-Fogh, 1972). Amongst the vertebrates, hummingbirds weighing only 2–20g are the elite practitioners of this aerial art. They are also a very successful group of birds; the 342 different species forming the largest nonpasserine family (Johnsgard, 1983). Many investigators have examined the metabolic cost of hovering flight in this highly specialised and successful group (Pearson, 1950; Lasiewski, 1963; Wolf and Hainsworth, 1971; Schuchmann, 1979; Berger and Hart, 1972; Berger, 1974; Epting, 1980; Bartholomew and Lighton, 1986; Suarez *et al.* 1990). Unfortunately, in view of the considerable variation recorded between individual birds as well as the variation between studies, any estimate of metabolic costs derived from the literature potentially carries significant errors.

The mechanical power output during hovering flight in hummingbirds has also received considerable attention (Hertel, 1966; Pennycuick, 1968; Weis-Fogh, 1972, 1973; Epting and Casey, 1973; Hainsworth and Wolf, 1972, 1975; Greenewalt, 1975; Rayner, 1979; Epting, 1980; Ellington, 1984*a–f*). Perhaps not surprisingly, these studies

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have presented a very wide range of calculated mechanical power output and efficiency. Furthermore, no single study has examined both the metabolic power input and the mechanical power output in the same birds. The present report seeks to address this deficiency with analyses of the flight energetics of individual birds of two closely related species.

In several of the previous studies, oxygen consumption was determined using an open-flow mask attached to a feeder; a respirometry method originally developed by Berger and Hart (1972). The feeder-mask arrangement avoids physical restraint of the bird and, when used in a large space, it eliminates the problems with air currents inherent in closed-chamber studies. Additionally, the system is suitable for simultaneous video recordings of wing kinematics. Measurement of wingbeat amplitude and frequency, stroke plane angle and morphological variables thus allows a detailed aerodynamic analysis for determination of the muscle power output (Ellington, 1984*a-f*). Values for power input (respirometry) and power output (aerodynamic analysis) can then be combined to estimate the mechanochemical efficiency of hummingbird flight muscle. The following account presents analyses for twelve individuals from two sympatric species.

Materials and methods

Hummingbirds

Broad-tailed (*Selasphorus platycercus* Swainson) and rufous (*Selasphorus rufus* Gmelin) hummingbirds used in this study were caught in the environs of Laramie, Wyoming, USA, in the summer (June to September) of each year of the study using both mesh feeder traps and mist nets. After capture, birds were placed in a large walk-in aviary at the Red Buttes Environmental Biology Laboratory near Laramie. This facility is 2195m above sea level, and the corresponding air density is 0.924kg m^{-3} . The birds were maintained year-round on Nektar-Plus (Nekton USA, Florida), an artificial diet, with enough feeders to prevent birds from being excluded by competition with others. Fresh water was available at all times. *S. platycercus* and *S. rufus* are referred to in the tables and figures by the abbreviations Bt and R, respectively.

Respirometry

Oxygen consumption was measured using a modified version of the open-flow feeder-mask system originally developed by Berger and Hart (1972). Air was drawn through the mask at a flow rate of $1860 \pm 120 \text{ml min}^{-1}$ STP; this rate was selected to ensure the most rapid response. An 18l surge tank was installed upstream of the pump to reduce flow fluctuations. Flow rate was measured with a 5l min^{-1} mass flow probe. Water vapour was removed using a small Drierite column prior to passing through the flow probe. This column was designed as a removable 'cassette' system to allow rapid replacement, avoiding changes in the flow characteristics of the system. After flowing through the flow probe, a sample of the air was then passed through an Applied Electrochemistry S-3A oxygen analyzer at a flow rate of 325ml min^{-1} STP, with the pump and another flow probe downstream of the cell. The change in oxygen concentration was registered on a chart recorder.

Carbon dioxide was not removed since the inclusion of an absorbant, i.e. Ascarite, prolonged the response time of the system and required replacement too often. Oxygen consumption (\dot{V}_{O_2}) was calculated assuming a respiratory quotient of 1, which allowed for a simple calculation knowing the flow rate through the system (\dot{V}_E , at STP) and the change in oxygen concentration ($F_{IO_2} - F_{EO_2}$) for dry samples (equation 3a of Withers, 1977):

$$\dot{V}_{O_2} = \frac{\dot{V}_E (F_{IO_2} - F_{EO_2})}{1 - (1 - RQ) F_{IO_2}}, \quad (1)$$

where F_{IO_2} and F_{EO_2} are the inspired and expired air oxygen concentrations, respectively, and RQ is the respiratory quotient.

The assumption that the respiratory quotient is 1 would introduce a 6.7% underestimation of oxygen consumption if the hummingbirds were using fat instead of carbohydrate as the metabolic fuel. Berger (1974) recorded respiratory quotients of 0.9–1.0, which indicated carbohydrates as the metabolic fuel. Suarez *et al.* (1986) presented biochemical evidence that carbohydrate was the preferred fuel for hovering and that fats were the preferred fuel for migration and, in subsequent experiments (Suarez *et al.* 1990), showed a rapid switch from fats to carbohydrates with the onset of regular foraging. Carbohydrates yield 21.1J of available energy per millilitre of oxygen consumed whereas fats yield 19.7J (Brobeck and DuBois, 1980). Fortuitously, this is a difference of 7.1%; hence the underestimate of oxygen consumption arising from a mistaken RQ (assuming solely carbohydrate utilisation) would be balanced by the higher energy yield for a given oxygen consumption.

The system's full response time was determined by infusing nitrogen into the feeder mask using a syringe pump. The nitrogen flow rate was selected to mimic the change in oxygen consumption seen when a hummingbird used the feeder. Full response time of the system was 3–3.5s with a 90% response in 2–2.5s, which is approximately 20 times faster than the system used by Berger and Hart (1972). Sample oxygen consumption records are presented in Fig. 1. There is no significant change in oxygen consumption during the long feeding bout illustrated in Fig. 1B. This further confirms the accuracy of the measurements made during the shorter repeated feeding bouts illustrated in Fig. 1A.

Wing kinematics

During stationary hovering flight, the wings describe a figure-of-eight pattern with an approximately horizontal stroke plane (Stolpe and Zimmer, 1939; Greenewalt, 1960). Analysing the films of Stolpe and Zimmer, Hertel (1966) noted that the angle of attack is attained very rapidly at the beginning of either stroke and remains almost constant until the wing reaches the end of its travel. Weis-Fogh (1972) calculated the mean angle of attack to be 23° during both strokes of the wingbeat cycle. The pattern of the wing motion is very close to perfectly sinusoidal (Stolpe and Zimmer, 1939; Hertel, 1966; Weis-Fogh, 1972). Hence, it seemed reasonable to assume (1) that the wings undergo simple harmonic motion and (2) that the kinematics could be determined without the need for high-speed cinematography.

Wingbeat frequency and wingbeat amplitude were recorded simultaneously with the

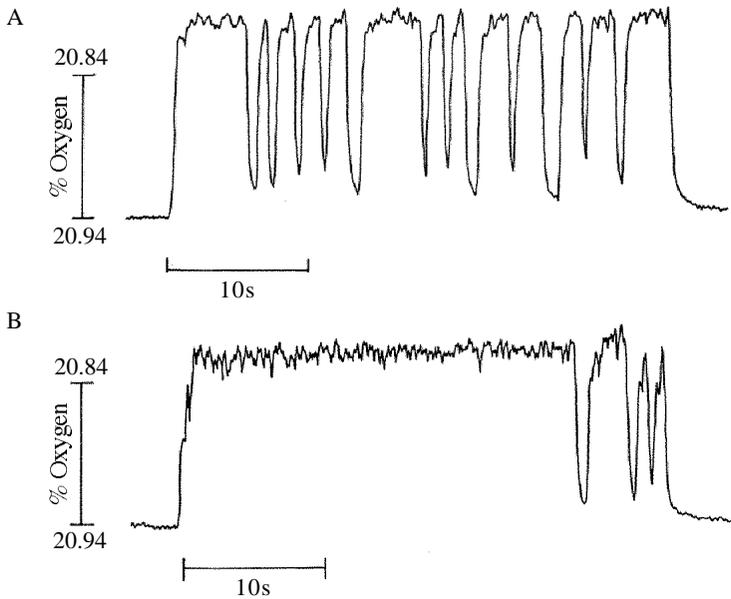


Fig. 1. Examples of oxygen consumption records obtained whilst the hummingbird hovered at the feeder equipped with an open-flow respirometry mask. (A) A typical record with intermittent feeding in the mask; (B) a less common record from a prolonged feeding bout.

measurement of oxygen consumption. Wingbeat frequency was detected using a light beam directed vertically through the stroke plane onto a photocell, the output of which was recorded on a polygraph. Wingbeat amplitude was recorded using a vertically mounted CCTV black and white video camera and a Panasonic AG 6200 video recorder. The area of the wingbeat amplitude was clearly visible as a white image on a black background due to illumination from above the hovering bird. The angle swept out was measured from the monitor screen using freeze-frame playback. The screen and camera were checked for distortion using standard grids and known angles. In some cases, stroke plane angle was also recorded using a horizontally mounted video camera and a calibrated background for reference.

Morphology

Hummingbirds were captured under Federal Permit (fish and Wildlife Service PRT-721003) and State Permit (Wyoming Game and Fish Department 1988 no. 60 and 1989 no. 45). They were killed by cervical dislocation as soon as possible following the completion of the *in vivo* recordings. Bird mass (m), wing length (R), wing mass (m_w), pectoralis mass and supracoracoideus mass (together denoted as mm) were determined as soon as possible following death.

The mechanics of flight depend not only on the gross morphological quantities but also on their distributions along the wing length, which are given as moments about the wing base (Ellington, 1984*b*). The first, second and third moments describe the mean, variation and skewness of the distribution, all of which are of biomechanical

importance. Shape variables can be derived from the non-dimensional radii of the moment of wing area (S), wing mass (m) or wing virtual mass (v). These variables were determined as follows.

One wing was photographed on a background of metric graph paper for determination of wing area (S). From these photographs, the wing chord (c) was determined for 100 equally spaced intervals along the wing span using a custom-built digitizer (described by Ellington, 1984c). The first, second and third moments of wing area S_1 , S_2 and S_3 were calculated from:

$$S_k = 2 \int_0^R c r^k dr, \quad (2)$$

for k is equal to 1, 2 or 3, where r is the distance from the base of the wing to a strip of wing area dS . The corresponding non-dimensional radii for the moments of wing area, $\hat{r}_1(S)$, $\hat{r}_2(S)$ and $\hat{r}_3(S)$ were determined from:

$$\hat{r}_k^k(S) = S_k/SR^k. \quad (3)$$

The mass distribution along the wing was determined before calculating the moments of wing mass about the wing base. The distribution was found using a strip-weighing technique. The wing was cut into 4mm strips, starting from the wing tip; at each cut the remaining wing was weighed to determine the mass of the removed segment. The first (m_1) and second (m_2) moments of wing mass were calculated for k equal to 1 and 2 using the following formula:

$$m_k = 2 \int_0^R m' r^k dr, \quad (4)$$

where m' is the mass per unit wing length. The corresponding non-dimensional radii for the moments of wing mass, $\hat{r}_1(m)$ and $\hat{r}_2(m)$ were determined from:

$$\hat{r}_k^k(m) = m_k/m_w R^k. \quad (5)$$

To correct for evaporative weight loss during the strip-weighing procedure, calculated values of m_k were multiplied by the ratio of the initial wing mass to the sum of the strip masses (Ellington, 1984b). The absolute wing mass is proportional to the product of wing area and the mean wing thickness. The latter, expressed as a fraction of the wing length is given by:

$$\hat{h} = m_w/\rho_w SR, \quad (6)$$

where ρ_w is the wing density, determined by first weighing an isolated wing and then estimating the volume using the water displacement technique (Scherle, 1970).

The inertia of a wing is increased by the mass of air that is accelerated with the wing; this apparent increase in wing mass is the virtual mass. The virtual mass of the wing pair is given by:

$$v = 2 \int_0^R v' dr, \quad (7)$$

where v' is the virtual mass per unit wing length, equal to $\frac{1}{4}\rho\pi c^2$, and ρ is the density of air. A non-dimensional virtual mass (\hat{v}) can be calculated from:

$$\hat{v} = vAR^2/2\pi\rho R^3, \quad (8)$$

where AR is the aspect ratio of the wing. The first and second moments of wing virtual mass are calculated as in equation 4, substituting v' for m' . The non-dimensional radii of moments of virtual mass are similarly calculated using equation 5 and the moments of virtual mass.

Aerodynamic analysis

The aerodynamic analysis was performed as described by Ellington (1984a–f), who presented the mathematics fully. The rationale for the analysis is as follows.

The mean inertial power can be calculated from the work done in accelerating the wing pair up to its maximum angular velocity during the first half of a wingstroke. This work is equal to the kinetic energy gained by the wing pair, and the inertial power is this value divided by the duration of acceleration. The wing chord is nearly perpendicular to the stroke plane during the rapid accelerations and decelerations at either end of the wingbeat. Therefore, the inertia of the wing will be increased by the mass of air which it accelerates, leading to an apparent increase in the wing mass, known as the virtual mass. Hence, P_{acc}^* is calculated as the mean mass-specific inertial power required to accelerate the wing *and* virtual masses during the first half of a stroke.

The mean mass-specific induced power (P_{acc}^*) is assessed using vortex theory. The induced power is calculated from the Rankine–Froude estimate of induced power modified by a temporal correction factor for wake periodicity and a spatial correction factor for the circulation profile. The Rankine–Froude estimate is based on the wing disc loading, the wing disc being the experimentally determined area swept out by the wings. The mean mass-specific profile power (P_{pro}^*) is calculated using a blade-element analysis based on the relative velocity of the wing and a chosen mean profile drag coefficient. It was assumed that the mean profile drag coefficient ($C_{D,pro}$) was close to 0.08 and could be described by equation 27 from Ellington (1984f) as:

$$C_{D,pro} \approx 7 / Re. \quad (9)$$

The Reynolds number (Re) is calculated from the product of the mean wing chord and mean wing-tip velocity divided by the kinematic viscosity for air. Wind tunnel tests of isolated bird wings from a variety of species have produced minimum drag coefficients of 0.03–0.13 (Nachtigall and Kempf, 1971; Reddig, 1978; Nachtigall, 1979; Withers, 1981; Wells, 1990). Recently, Pennycuick *et al.* (1992) reported a $C_{D,pro}$ of 0.02 for a Harris hawk gliding in a wind tunnel. However, $C_{D,pro}$ values for hovering hummingbirds are likely to be higher because pressure drag will increase with the increased angle of attack.

The mean lift coefficient (C_L) was calculated from a simplified form of equation 12 from Ellington (1984d) as:

$$C_L = 8\rho_w/n\Phi^2R^2r_2(S)^2\rho(d\hat{\phi}/d\hat{t})^2, \quad (10)$$

where n is the wingbeat frequency, Φ is the wingbeat amplitude and $(d\hat{\phi}/d\hat{t})^2$ is the mean square of the non-dimensional angular velocity of the wing.

Results of the analysis are presented for the two extreme conditions of zero and total elastic storage of the kinetic energy of the wing and virtual masses. For perfect elastic storage, it is assumed that the kinetic energy is stored as elastic potential energy, during

deceleration of the wing, and then released to accelerate the wing on the next stroke. If no energy is lost during storage, then the net inertial power requirement over the cycle is zero. The mean mass-specific mechanical power output of the muscles is just the aerodynamic power (P_a^*), given by:

$$P_a^* = P_{\text{ind}}^* + P_{\text{pro}}^*, \quad (11)$$

where P_{ind}^* is mean mass-specific induced power.

In the absence of elastic storage, the muscles must actively decelerate the wing in the second half of the stroke. This negative work is much less metabolically expensive than positive work (Margaria, 1968) and, in common with most locomotion studies, this metabolic cost is ignored (e.g. Norberg, 1976; Ellington, 1984f; Dudley and Ellington, 1990). The total mean mass-specific mechanical power output of the muscles for zero elastic storage is therefore:

$$\frac{1}{2}(P_{\text{acc}}^* + P_{\text{ind}}^* + P_{\text{pro}}^*). \quad (12)$$

Muscle power output was calculated from the total body mass-specific power output divided by the fraction of the body mass attributable to the flight muscles. Flight efficiency was calculated from power output divided by power input. Comparisons between the two species were examined with two-tailed *t*-tests for small sample sizes (Bailey, 1981). All reported values are means \pm one standard error.

Results

In vivo recordings

In most cases trials for each bird were run on three different days. Birds were left in the recording area the previous day to become accustomed to the modified feeder. Early morning flights and any flights after a prolonged absence from the feeder were discarded to avoid changes in RQ associated with a period of fasting (Suarez *et al.* 1990). In general, the hummingbirds showed no difference in behaviour when foraging from the feeder fitted for respirometry compared with a standard feeder. Flights were only analysed if they fulfilled *all* of the following criteria: the duration of flight exceeded 3.5s, the bird's head was fully in the mask, there were no fluctuations in system flow rate and there were simultaneous recordings of wingbeat frequency and amplitude.

Temperature during the runs averaged $21.8 \pm 0.2^\circ\text{C}$ (range $20\text{--}26^\circ\text{C}$). Barometric pressure during the runs averaged $77.7 \pm 0.1\text{kPa}$ (range $76.0\text{--}78.8\text{kPa}$). Wingbeat frequency remained very constant during a flight but wingbeat amplitude varied as the birds made very small adjustments in position. As 20–30 flights were analysed for each bird, a satisfactory mean amplitude could be calculated by randomly sampling three frames during each flight and taking the mean value as representative for that flight. The video record from both the vertically and horizontally mounted cameras confirmed that the birds were not gaining any support from the mask.

Initially, a perch suspended from a calibrated strain gauge in the aviary was used for frequent but voluntary weighing of cooperative experimental subjects. However, it proved less time-consuming to catch the birds with a hand net and weigh them several

Table 1. In vivo recordings of oxygen consumption (\dot{V}_{O_2}), wingbeat frequency (n), wingbeat amplitude (Φ) and stroke plane angle (β)

Bird	Number of flights	Mass (g)	\dot{V}_{O_2} (ml g ⁻¹ h ⁻¹)	n (Hz)	Φ (degrees)	β (degrees)
Bt3-J	19	4.22	50.46 (±0.50)	41.32 (±0.25)	135.94 (±1.40)	–
Bt4-F	32	3.46	57.70 (±0.45)	36.38 (±0.15)	143.17 (±0.54)	7.00 (±0.26)
Bt5-M	34	3.66	59.90 (±0.40)	38.71 (±0.15)	149.81 (±0.66)	5.85 (±0.28)
Bt6-M	18	5.16	50.09 (±0.35)	39.25 (±0.17)	165.92 (±0.68)	–
Bt7-J	18	3.60	44.16 (±0.29)	39.53 (±0.26)	141.26 (±1.93)	–
Bt9-J	18	3.61	46.48 (±0.44)	37.17 (±0.43)	141.97 (±1.68)	–
Bt10-J	30	3.93	50.76 (±0.40)	38.10 (±0.13)	127.80 (±0.52)	10.24 (±0.74)
Bt12-J	32	4.10	44.24 (±0.22)	37.94 (±0.10)	138.34 (±0.48)	7.20 (±0.39)
R4-J	20	4.24	53.93 (±0.56)	53.25 (±0.20)	151.36 (±1.21)	11.67 (±1.32)
R5-J	31	4.24	49.74 (±0.17)	49.10 (±0.10)	162.90 (±0.59)	5.72 (±0.27)
R13-J	30	4.10	49.35 (±0.19)	47.30 (±0.08)	143.66 (±0.64)	7.70 (±0.89)
R14-J	27	4.54	46.44 (±0.31)	42.57 (±0.18)	158.24 (±0.68)	–

Birds are identified as male (M), female (F) or juvenile (J).
 Figures are mean values ± standard error.
 β is from 13 (Bt4), 10 (Bt5), 5 (Bt10), 5 (Bt12), 10 (R4), 11 (R5), 4 (R13) records.

times during each daily series. The latter method was as satisfactory as the more frequent weighing system as neither could account accurately for changes in weight due to food intake and defecation during flight.

The wing kinematics presented in Table 1 show considerable variation between individual birds, underlining the need to analyse flight energetics for a number of individuals. The few values of the stroke plane angle confirm the observation of Weis-Fogh (1972) that the stroke plane angle is tilted slightly forwards, approximately 11° in the tracings from Stolpe and Zimmer (1939) compared with a mean of 7.9° in the present study, and is not precisely horizontal.

Post mortem analysis

The gross morphological data from the basic *post mortem* measurements are presented

Table 2. Results of the post mortem morphological analysis

	Bt3	Bt4	Bt5	Bt6	Bt7	Bt9	Bt10	Bt12	R4	R5	R13	R14
m (mg)	4220	3460	3660	5160	3600	3610	3930	4100	4240	4240	4100	4540
R (mm)	55	54	55	57	52	56	55	57	45	48	51	52
S (cm ²)	15.61	14.73	14.96	15.99	13.61	16.35	17.21	16.75	9.88	11.68	13.37	13.25
p_w (N m ⁻²)	26.52	23.05	24.01	31.67	25.96	21.66	22.40	24.02	42.11	35.61	30.08	33.60
\bar{A}	7.75	7.92	8.09	8.13	7.95	7.67	7.03	7.76	8.20	7.89	7.78	8.16
mm (%)	22.73	24.48	32.25	20.84	24.68	23.58	26.27	22.21	25.44	21.79	23.74	22.61
$p:s$	1:0.50	1:0.48	1:0.56	1:0.73	1:0.46	1:0.51	1:0.60	1:0.48	1:0.57	1:0.62	1:0.54	1:0.47
m_w (%)	5.07	5.73	5.34	5.31	4.36	6.19	5.69	5.53	2.56	3.40	4.63	3.97
\hat{v}	1.10	1.08	1.12	1.13	1.08	1.07	1.07	1.08	1.11	1.08	1.07	1.10
\hat{h} (%)	0.322	0.323	0.307	0.389	0.287	0.316	0.306	0.307	0.316	0.332	0.360	0.339
I ($\times 10^{-8}$)	2.180*	1.780	1.825	2.780*	1.470*	2.460*	2.500	2.955	0.696	1.050	1.510	1.380
$\hat{r}_1(m)$	0.184*	0.179	0.180	0.184*	0.184*	0.184*	0.187	0.190	0.178	0.177	0.168	0.176
$\hat{r}_2(m)$	0.259*	0.248	0.249	0.250*	0.264*	0.265*	0.272	0.283	0.252	0.252	0.248	0.238
$\hat{r}_1(S)$	0.453	0.468	0.442	0.441	0.461	0.460	0.453	0.457	0.440	0.454	0.458	0.453
$\hat{r}_2(S)$	0.520	0.534	0.507	0.506	0.530	0.530	0.522	0.524	0.508	0.523	0.528	0.519
$\hat{r}_3(S)$	0.569	0.582	0.555	0.555	0.580	0.580	0.572	0.573	0.559	0.574	0.578	0.568
$\hat{r}_1(v)$	0.418	0.442	0.406	0.402	0.428	0.430	0.423	0.428	0.399	0.418	0.427	0.419
$\hat{r}_2(v)$	0.479	0.502	0.464	0.461	0.493	0.496	0.486	0.490	0.461	0.483	0.493	0.478
$\int \hat{v}^3 \hat{r} df$	0.489	0.508	0.503	0.500	0.483	0.478	0.479	0.489	0.473	0.470	0.474	0.497
$\int \hat{v}^3 \hat{r}^5 \hat{r} df$	0.207	0.223	0.193	0.192	0.219	0.219	0.209	0.212	0.193	0.210	0.216	0.206

Abbreviations are defined in the Appendix.

I was calculated for these birds because no direct measurements were available (see text).

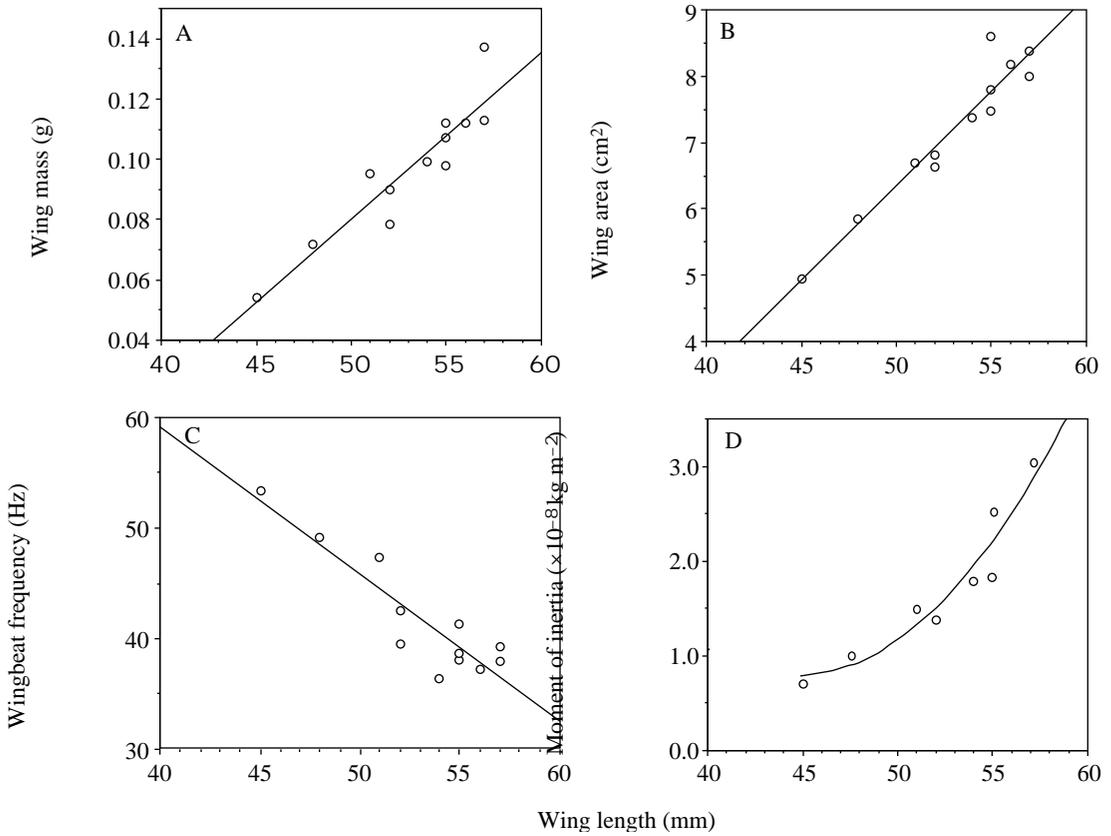


Fig. 2. The relationship of wing length (mm) to (A) wing mass (g), $y=0.0055x - 0.195$, ($45 \leq x \leq 57$), $r^2=0.86$, $P<0.001$; (B) wing area (cm^2), $y=0.285x - 7.89$ ($45 \leq x \leq 57$), $r^2=0.92$, $P<0.001$; (C) wingbeat frequency (Hz), $y=112.2 - 1.33x$ ($45 \leq x \leq 57$), $r^2=0.83$, $P<0.001$; (D) the moment of inertia ($\times 10^{-8} \text{kg m}^2$), $y=27.64 - 1.2x + 0.0134x^2$ ($45 \leq x \leq 57$), $r^2=0.91$, $P<0.001$. Regression lines were calculated as least-square first-order (A,B,C) or second-order (D) regressions.

in Table 2. Flight muscle weight was corrected by adding 5% to allow for losses in failing to remove all of the flight muscle from the sternum together with losses of muscle when the wing was removed at the shoulder joint. Wing density was approximately 775kg m^{-3} . Wing length was significantly correlated with wing area, mass, moment of inertia and wingbeat frequency ($P<0.001$ in all cases; Fig. 2). These correlations suggest that *in vivo* measurements alone might be adequate for many future studies.

Plots of mass distribution relative to the distance from the shoulder joint for each species demonstrated a highly predictable pattern, with 50% of the wing mass being less than 10% of the distance from the shoulder joint. The moment of inertia (I) of the wing around its base is given for each animal to allow comparison with other studies (Table 2). I is related to $\hat{r}_2(m)$ as:

$$\hat{r}_2(m) = (2I/m_w R^2)^{1/2}. \quad (13)$$

Direct measurements of the mass distribution along the wing and, consequently, direct determination of the moment of inertia (I), were not available for four of the broad-tailed hummingbirds (Bt3, Bt6, Bt7, Bt9). For these individuals values for I were calculated from a second-order regression equation obtained from the measurements of the other birds, as I is proportional to the square of the wing length (Fig. 2D; $r^2=0.91$, $P<0.001$).

The non-dimensional radii of the moment of wing shape (S), wing mass (m) and wing virtual mass (v) are given in Table 2. This table includes the values for two more integrals that are required for the aerodynamic analysis. These are also moment variables of wing shape, but a direct physical interpretation cannot be assigned to them (Ellington, 1984b).

The results of the aerodynamic analysis for both perfect and zero elastic storage of inertial energy are presented in Table 3 and show marked individual variation in absolute magnitude, although the relative proportions of the total power requirement for P_{acc}^* , P_{ind}^* and P_{pro}^* are very similar between individuals.

Discussion

Respirometry and morphology

In the present study the pectoralis and supracoracoideus accounted for 23.4% of the body mass; the supracoracoideus to pectoralis ratio for both species was 0.54. The slightly lower muscle mass percentages in the present study compared with previous studies (Dubach, 1981; Hartman, 1954, 1961) may be the result of captivity and consequent fat storage. If the supracoracoideus generates the same amount of lift as the pectoralis during hovering flight, why is it only half the size of the pectoralis? The answer must be that the pectoralis is overbuilt for stationary hovering flight. The larger mass of the pectoralis is likely to be a consequence of its dominant role in forward flight, when the stroke plane angle is tilted forward, increasing in angle with increasing flight speed, to produce a combination of lift and thrust (Greenewalt, 1960). The downstroke, generated by the pectoralis, dominates in forward flight and its role increases with increasing stroke plane angle (Ellington, 1984c).

There was no significant difference in mass-specific oxygen consumption (\dot{V}_{O_2}) between the two species in the present study (rufous $49.87 \pm 1.54 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, broad-tailed $50.47 \pm 2.05 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, $P=0.425$). These values for the hovering hummingbirds are in most cases higher (on average 21%) than those found by other investigators (Lasiewski, 1963; Wolf and Hainsworth, 1971; Berger and Hart, 1972; Berger, 1974; Bartholemew and Lighton, 1986; Suarez *et al.* 1990). A possible explanation for the high values in the present study may be the altitude (2195m above sea level) compared with previous experiments (e.g. estimated altitude for Lasiewski, 1963, was 255m and for Bartholemew and Lighton, 1986, it was 30m). In order to lift the same body mass, the birds in the present study will have increased the motion of the wings to compensate for the lower air density. Berger (1974) examined the effect of altitude, demonstrating an increase in wingbeat amplitude but not the expected increase in \dot{V}_{O_2} with altitude. Loading studies (Wells, 1993) show that an increase in wingbeat amplitude with a nearly constant wingbeat frequency is coupled to an increase in \dot{V}_{O_2} . If the mean coefficient of lift and the flight efficiency are held constant, calculations predict that the power input

Table 3. Results of the aerodynamic analysis

	BE3	BE4	BE5	BE6	BE7	BE9	BE10	BE12	R4	R5	RI3	RI4
P^*_{IN}	295.8	338.2	351.1	293.6	258.8	272.4	297.5	259.3	316.1	291.5	289.2	272.2
C_L	1.48	1.47	1.32	1.29	1.58	1.27	1.65	1.41	1.78	1.27	1.30	1.47
$C_{D,pro}$	0.079	0.085	0.080	0.073	0.085	0.080	0.081	0.079	0.083	0.077	0.078	0.079
P^*_{pro}	5.15	5.11	5.84	6.37	4.97	5.89	4.12	5.26	5.24	7.31	6.59	5.83
P^*_{ind}	20.05	17.85	18.05	19.59	19.11	17.52	20.17	18.81	23.65	20.72	20.38	20.45
P^*_{acc}	103.51	80.82	100.98	132.22	79.48	109.45	89.66	113.53	87.11	120.45	124.43	91.78
Perfect elastic storage												
P^*_{O}	25.2	23.0	23.9	26.0	24.1	23.4	24.3	24.1	28.9	28.0	27.0	26.3
P^*_{m}	110.8	93.8	74.1	124.5	97.5	99.3	92.5	108.4	113.6	128.6	113.6	116.2
W^*_{o}	0.610	0.631	0.617	0.661	0.609	0.630	0.638	0.634	0.542	0.571	0.570	0.618
W^*_{m}	2.68	2.58	1.91	3.17	2.47	2.67	2.43	2.86	2.13	2.62	2.40	2.73
nm (%)	8.5	6.8	6.8	8.8	9.3	8.6	8.2	9.3	9.1	9.6	9.3	9.7
Zero elastic storage												
P^*_{O}	64.4	51.9	62.4	79.1	51.8	66.4	57.0	68.8	58.0	74.2	75.7	59.0
P^*_{m}	283.1	211.9	193.6	379.5	209.8	281.8	216.9	309.8	228.0	340.7	318.8	261.1
W^*_{o}	1.557	1.426	1.613	2.015	1.310	1.787	1.495	1.813	1.087	1.512	1.600	1.387
W^*_{m}	6.85	5.83	5.00	9.67	5.31	7.58	5.69	8.16	4.27	6.94	6.74	6.13
nm (%)	21.8	15.3	17.8	26.9	20.0	24.4	19.2	26.5	18.3	25.5	26.2	21.7

The abbreviations are defined in the Appendix.

values would be 7–18% lower at sea level, depending on the degree of elastic storage of inertial energy.

These data were also examined for any differences attributable to sex. Birds were classified as male (with full adult plumage), female (no oblique corrugations on the culmen, Ortiz-Crespo, 1972) or juvenile (Table 1). Details of age and sex determination for rufous hummingbirds are also provided in Stiles (1972). Mature male broad-tailed hummingbirds have modified tips to the ninth and tenth primaries that form a slot. During flight, this slot produces a metallic whistle that is important in maintenance of courting territories (Miller and Inouye, 1983). Male rufous hummingbirds show similar wing tip structures. These modifications might be expected to carry some aerodynamic cost. A *t*-test demonstrated a significant difference in oxygen consumption ($P=0.049$) when the male hummingbirds in the present study were compared with the other birds, but no significant differences in power output or efficiency. For an examination of power output differences, the wing area and shape would require a more complex analysis than is currently available.

Aerodynamic analysis

The results of the aerodynamic analyses for individual birds are presented in Table 3. Significant differences between the two species were only seen in the perfect elastic storage analysis with muscle power outputs of $118\pm 3.6 \text{ W kg}^{-1}$ and $100\pm 5.3 \text{ W kg}^{-1}$ ($P=0.025$) for rufous and broad-tailed hummingbirds, respectively. The power output and efficiency show considerable individual variation, as one would expect given the *in vivo* variation in oxygen consumption and wing kinematics (Table 1). In all cases, however, the general trend is clear. Inertial power requirements far outweigh the aerodynamic power requirements (approximately by a factor of 4, see Table 3). This result is very different from the conclusions of Weis-Fogh (1972) and Casey (1981), who calculated inertial and aerodynamic power requirements to be nearly equal in hummingbirds. However, they did not include the virtual mass of the wing in the inertial power calculations. If my values are recalculated ignoring the virtual mass, the inertial power requirement falls by an average of 22% but still substantially exceeds the aerodynamic power requirement (approximately by a factor of 3). Power requirements to overcome induced drag are, in turn, much greater than the power required to overcome profile drag (by a factor of 3.5, see Table 3). Hence, an error in the assumed value of the mean profile drag coefficient is of little consequence. The slight departure of the stroke plane from horizontal has very little effect on the calculations of power requirements.

The mean coefficient of lift in the present study was 1.44 ± 0.05 and, whilst not as high as that calculated in previous theoretical studies of hummingbirds (1.86 in Pennycuik, 1968; 1.82 in Weis-Fogh, 1972; 1.8–2.0 in Weis-Fogh, 1973), it exceeds the maximal values recorded from a number of studies of a wide range of bird wings (0.8–1.2, Nachtigall and Kempf, 1971; Reddig, 1978; Nachtigall, 1979; Withers, 1981). This emphasises the need to examine steady-state aerodynamic mechanisms, as concluded by Ellington (1984a).

During flight, energy will be required for the flight muscles, cardiovascular system, respiratory system and basic body maintenance. Energy requirements for thermogenesis

are likely to be suspended during flight because sufficient heat will be produced by flight muscle activity. It is assumed that these support systems will account for 10% of the total energy consumed in flight. This is the basal metabolic rate plus an estimate of the energy cost of increased respiration and heart rate. Figures for basal metabolic rate have been collected by Lasiewski (1963). In order to convert the flight efficiency figure into an estimate of muscle efficiency, it was assumed that the remaining 90% of the power input (oxygen consumption) was consumed by the two pairs of major flight muscles. Power outputs from the muscles remain the same as those presented in Table 3. Muscle efficiencies assuming zero elastic storage are not significantly different at $25.5 \pm 2.0\%$ and $23.8 \pm 1.6\%$ for rufous and broad-tailed hummingbirds, respectively. Assuming total elastic storage of inertial energy, rufous hummingbirds have significantly higher ($P=0.002$) muscle efficiencies, averaging $10.5 \pm 0.15\%$ compared with $9.2 \pm 0.4\%$ for broad-tailed hummingbirds.

If one assumes that there is no possibility for elastic storage of inertial energy in birds (Weis-Fogh, 1972; Alexander, 1988), then the hummingbird muscle appears to be acting as an extremely high-quality 'classic' vertebrate muscle with efficiencies near 25% and power outputs in the range of $250\text{--}300\text{ W kg}^{-1}$. This is at the upper end of the theoretical range of power outputs ($230\text{--}250\text{ W kg}^{-1}$ in Weis-Fogh and Alexander, 1977; 430 W kg^{-1} in Pennycuick and Rezende, 1984). Both of these theoretical estimates assumed shortening at a constant optimum velocity and so require a downward correction of 10–20% because the shortening velocity of the wing muscle will vary approximately sinusoidally (Josephson, 1989). The estimate of Pennycuick and Rezende (1984) will also require a correction for mitochondrial densities. For the hummingbirds in the present study, with 37.5% mitochondria in the muscle fibres (Wells, 1990), their theory predicts 360 W kg^{-1} before adjustment for non-linear shortening.

Not only do the power outputs recorded in this study equal or exceed the predicted maxima but there are further problems. First, the power output in the present study is an underestimate as the result of the assumption of a zero parasite power requirement. In the hovering bird, there will be air movement past the body to form the momentum jet below the wings. So the body will indeed generate some drag and, hence, a greater power output will be required to compensate for this additional drag. Second, the birds were carrying little body fat and, in premigratory fattening, hummingbirds can increase body mass by 60%, requiring an increased muscle power output (Odum and Connell, 1956; Norris *et al.* 1957; Wells, 1993). Hence, the birds in the present study were clearly operating below maximum muscle power output. Third, the muscle efficiency of 25% appears to be rather too high as there is increasing evidence that small animals operate muscles less efficiently than do large animals (e.g. Heglund *et al.* 1982; Heglund and Cavagna, 1985; Casey and Ellington, 1989). This may be due to a faster rate of muscle shortening in small compared with large animals (Heglund *et al.* 1982; Lindstedt *et al.* 1985). Also, no allowance has been made for the cost of negative work in decelerating the wings, which is a process that requires ATP. Alexander (1982) estimated that negative work would add an additional 20% to metabolic power requirements in a kangaroo if the animal were unable to take advantage of elastic storage of kinetic energy. This would require an actual muscle

efficiency for power generation in hummingbirds in excess of 30% in the absence of elastic storage.

The alternative condition analysed assumes that there is near-perfect elastic storage of inertial energy. Greenewalt (1960) argued that the constancy of wingbeat frequency in hummingbirds suggests that the beating wings of hummingbirds have the characteristics of a damped, driven oscillator. Furthermore, he argued that the close relationship between wing length and wingbeat frequency would be a characteristic only of a tuned oscillator with a truly elastic restoring force. In the case of perfect elastic storage, the muscles in the present study were calculated to be operating at an efficiency of 9–11% and 100–120 W kg⁻¹. This is only slightly above the values determined *in vitro* at flight temperature and frequency for the tobacco hawkmoth *Manduca sexta* (90–130 W kg⁻¹ at 8–11% efficiency, Stevenson and Josephson, 1990), which flies with synchronous (striated) muscles. Other studies have produced similar values; for example *in vitro* studies of *Schistocerca americana* (75 W kg⁻¹, Mizisin and Josephson, 1987; 6.4% efficiency, Josephson and Stevenson, 1989), *in vitro* studies of insects with asynchronous (fibrillar) flight muscles (30–60 W kg⁻¹, Machin and Pringle, 1959; 76 W kg⁻¹, Josephson, 1985a; 33 W kg⁻¹, Josephson, 1985b) and *in vivo* studies of insects flying with asynchronous muscles (69–186 W kg⁻¹, Ellington, 1984f; 56 W kg⁻¹, Dudley and Ellington, 1990). In the case of vertebrates, Stevens (1988) examined frog sartorius muscle and obtained a maximum power output of 35 W kg⁻¹ at 20°C. Altringham and Johnston (1990) found a maximum power output of 25–35 W kg⁻¹ in fish fast fibres at 3°C; subsequent studies have produced similar results (e.g. Johnson and Johnston, 1991; Langfeld *et al.* 1991). Examination of muscle bundles from mouse and rat diaphragm by Altringham and Young (1991) revealed maximum power outputs of 49.5 W kg⁻¹ and 43.7 W kg⁻¹, respectively. Biewener *et al.* (1992) have reported a mean muscle power output of 104 W kg⁻¹ based on *in vivo* strain gauge recordings from the pectoralis of European starlings. Compared with all of the above studies, a power output of 100–120 W kg⁻¹ from hummingbirds appears very impressive.

Are hummingbirds ‘vertebrate insects’ or unusually elite vertebrates? Consideration of the theoretical maximum power output and efficiency coupled with the results of *in vivo* and *in vitro* studies of other animals strongly suggest that hummingbirds are operating with considerable elastic storage of inertial energy. Calculations based on the data of Alexander and Bennet-Clark (1977) support the possibility of near-perfect elastic storage of kinetic energy in the series elastic components of muscle formed by the tendons and sarcomeric proteins. Further investigation of the potential for elastic storage of inertial energy in birds is clearly required.

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Appendix

Symbols and abbreviations used in the text and tables.

AR Aspect ratio of the wing pair

c	Wing chord
$C_{D,pro}$	Mean profile drag coefficient
C_L	Mean coefficient of lift
F_{IO_2}	Inspired fractional oxygen concentration
F_{EO_2}	Expired fractional oxygen concentration
h	Mean wing thickness
\hat{h}	Non-dimensional wing thickness
I	Moment of inertia of a wing about its base
m	Body mass
m'	Mass per unit wing length
mm	Muscle mass
m_w	Mass of the wing pair
n	Wingbeat frequency
nm	Mechanochemical efficiency
P_a^*	Mean mass-specific aerodynamic power
P_{acc}^*	Mean mass-specific inertial power
P_{IN}^*	Mean mass-specific whole-bird power input
P_{ind}^*	Mean mass-specific induced power
P_m^*	Mean mass-specific muscle power output
P_o^*	Mean mass-specific whole-bird power output
P_{pro}^*	Mean mass-specific profile power
$p:s$	Pectoralis to supracoracoideus ratio
p_w	Wing loading
R	Wing length from the shoulder joint
Re	Reynolds number
r	Distance from the wing base to a strip of wing
$\hat{r}_k(m)$	Non-dimensional radius of kth moment of wing mass
$\hat{r}_k(S)$	Non-dimensional radius of kth moment of wing area
$\hat{r}_k(v)$	Non-dimensional radius of kth moment of wing virtual mass
RQ	Respiratory quotient
S	Wing area
v	Virtual mass of the wing pair
v'	Virtual mass per unit wing length
\hat{v}	Non-dimensional virtual mass of the wing pair
\dot{V}_E	Flow rate
\dot{V}_{O_2}	Rate of oxygen consumption
W_m^*	Mean mass-specific muscle work output
W_o^*	Mean mass-specific whole-bird work output
β	Stroke plane angle
ρ	Air density
ρ_w	Wing density
Φ	Wingbeat amplitude
ϕ	Positional angle of wing in the stroke plane

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