

## TRANSIENT HOVERING PERFORMANCE OF HUMMINGBIRDS UNDER CONDITIONS OF MAXIMAL LOADING

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### Summary

Maximal load-lifting capacities of six ruby-throated hummingbirds (*Archilochus colubris*) were determined under conditions of burst performance. Mechanical power output under maximal loading was then compared with maximal hovering performance in hypodense gas mixtures of normodense air and heliox. The maximal load lifted was similar at air temperatures of 5 and 25 °C, and averaged 80 % of body mass. The duration of load-lifting was brief, of the order of 1 s, and was probably sustained *via* phosphagen substrates. Under maximal loading, estimates of muscle mass-specific mechanical power output assuming perfect elastic energy storage averaged 206 W kg<sup>-1</sup>, compared with 94 W kg<sup>-1</sup> during free hovering without loading. Under conditions of limiting performance in hypodense mixtures, maximal mechanical power output was much lower (131 W kg<sup>-1</sup>, five birds) but was sustained for longer (4 s), demonstrating an inverse relationship between the magnitude and duration of maximum power output. In free hovering flight, stroke amplitude and wingbeat frequency varied in inverse proportion between 5 and 25 °C, suggesting thermoregulatory contributions by the flight muscles. Stroke

amplitude under conditions of maximal loading reached a geometrical limit at slightly greater than 180°. Previous studies of maximum performance in flying animals have estimated mechanical power output using a simplified actuator disk model without a detailed knowledge of wingbeat frequency and stroke amplitude. The present load-lifting results, together with actuator disc estimates of induced power derived from hypodense heliox experiments, are congruent with previous load-lifting studies of maximum flight performance. For ruby-throated hummingbirds, the inclusion of wingbeat frequency and stroke amplitude in a more detailed aerodynamic model of hovering yields values of mechanical power output 34 % higher than previous estimates. More generally, the study of performance limits in flying animals necessitates careful specification of behavioral context as well as quantitative determination of wing and body kinematics.

Key words: aerodynamics, *Archilochus colubris*, hovering, hummingbird, load-lifting, maximal locomotor performance, muscle power output, temperature.

### Introduction

Animal flight performance varies systematically with body size (Pennycuik, 1968; Ellington, 1991), and small hummingbirds are among the most versatile of vertebrate fliers (Greenewalt, 1960). Their remarkable maneuverability and sophisticated flight control require the capacity to vary force and power output substantially over brief intervals (Norberg, 1990). The power reserves of hummingbirds are considerable relative to normal hovering performance. Chai and Dudley (1995) determined maximal aerobic capacity and limits to flight performance on ruby-throated hummingbirds hovering in normoxic but hypodense gas mixtures of sea-level air and heliox. Maximal hovering performance was unequivocally indicated by aerodynamic failure at low air densities. Immediately prior to such failure, muscle mass-

specific power assuming perfect elastic energy storage increased to 130–135 W kg<sup>-1</sup>, approximately 36 % greater than that in normal hovering. Another manipulation that requires hummingbirds to increase their mechanical power output is load-lifting. When loaded by the addition of backpacks containing small weights, four *Selasphorus platycercus* individuals could hover with an attached mass averaging 24 % of body mass. Power output increased by 32 % and ranged from 89 to 141 W kg<sup>-1</sup> (Wells, 1993a). The experimental procedures of both the heliox and load-lifting studies required hover-feeding in excess of 3 s (i.e. the birds flew to a feeder and fed), although the physical characteristics of the gaseous flight medium were considerably different between the two studies.

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The generally similar results of these two aforementioned studies and their associated mechanical power estimates do not match the reported transient capacity of hummingbirds to lift loads vertically. For example, a 6 g hummingbird was able to take off and lift a maximal load of nearly 80% of its body mass in a loading study that tested transient load-lifting performance of a large number of insects, bats and birds (Marden, 1987). Another male hummingbird was observed in the field to ascend approximately 1 m while carrying a passive female conspecific by the bill (Weydemeyer, 1971). This apparent burst performance suggests an even greater capacity to generate additional power and is consistent with recent evidence that hummingbird flight muscles contain high levels of creatine phosphokinase and thus of creatine phosphate for short-term but high power output (Suarez *et al.* 1986; Hochachka, 1994).

Through the use of load-lifting manipulations, the present study investigates the maximal transient power output of ruby-throated hummingbirds (*Archilochus colubris*). Peak performance in hovering is analyzed using detailed morphological and kinematic data and a contemporary aerodynamic model of hovering flight (Ellington, 1984*a-f*). For individual birds, performance under conditions of maximal load is compared directly with limits to power production in the hypodense heliox mixture. Because of the high thermal conductivity of helium relative to air (Reid *et al.* 1987), the heat flux of hummingbirds hovering in heliox at 25 °C is comparable to that for hovering in air temperatures of only a few degrees Celsius (López-Calleja and Bozinovic, 1995). Two different air temperatures (5 and 25 °C) were therefore used in load-lifting studies to evaluate thermal effects on flight performance. Mechanical power estimates were then compared with parallel estimates based only on knowledge of wing span and the use of simplified actuator disc momentum theory. Because this latter approach has been widely used in allometric studies of flight performance, both among hummingbirds (Hainsworth and Wolf, 1972; Epting and Casey, 1973; Feinsinger and Chaplin, 1975; Feinsinger *et al.* 1979) and among diverse taxa of volant animals (Ellington, 1991; Marden, 1994), direct comparison with the more detailed

hovering model of Ellington (1984*a-f*) is methodologically germane for assessment of existing allometric conclusions.

### Materials and methods

Ruby-throated hummingbirds (*Archilochus colubris* L.) were mist-netted in the vicinity of Austin, Texas, USA, during the autumn migratory season of 1995 and were housed in screen cages with dimensions of 90 cm×90 cm×90 cm. Hummingbird care was in accordance with federal and state guidelines. Either two or three birds were housed within a single cage. Six individual hummingbirds with intact flight feathers (one adult male, bird 1; one juvenile male, bird 2; four females, birds 3–6) were used in experiments (for body masses and wing lengths, see Fig. 1). Each bird was subjected to two loading trials per day over four consecutive days. The two loading trials were conducted within a large environmental chamber using the same experimental procedure but different air temperatures. On days 1 and 3 of each 4-day study period, the birds started at a low air temperature (5 °C, range 5–6 °C); days 2 and 4 began at room temperature (25 °C, range 25–27 °C). Birds were acclimated for more than 30 min at either air temperature before each loading trial. Thus, two loading and two free flights without load at 5 °C and 25 °C were conducted for a total of four flights per bird per day.

A cylindrical enclosure constructed from nylon screen was used in loading trials. Enclosure diameter was 47 cm (more than four times of the wingspan of the bird) and enclosure length was 91 cm. The enclosure was hung 15 cm above a table, and the bottom of the enclosure was open. Enclosure dimensions confined the bird's movement so as to permit hovering flight within the enclosure to be recorded using video cameras. Uniform perforations of the mesh enclosure (perforation diameter 1.3 mm) permitted passage of air and alleviated boundary effects associated with flight in small enclosures. These effects were, in any event, small given the large enclosure dimensions relative to hummingbird wing span (see Rayner and Thomas, 1991). Two video cameras synchronized to within 1 s were used to obtain wing kinematics

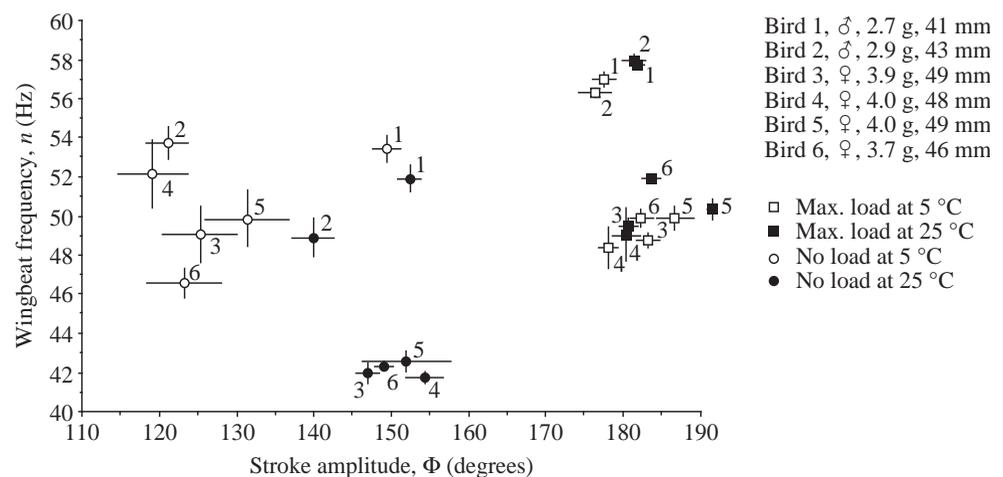


Fig. 1. Wingbeat frequency versus stroke amplitude (mean  $\pm$  1 S.E.M.,  $N=4$ ) for six individual *Archilochus colubris* in unloaded free hovering flight and under maximal loading at 5 and 25 °C. Bird identification number, sex, body mass and wing length are also given.

and loading values (see below). One camera (Panasonic AG-160), placed laterally, filmed the table immediately beneath the hanging enclosure, whereas the other camera (Sony CCD-FX420) captured horizontal projections of wingbeat kinematics *via* a mirror oriented at  $45^\circ$  above the hovering birds within the enclosure (filming and subsequent analysis were at  $60 \text{ fields s}^{-1}$  with a high-speed shutter of  $1/4000 \text{ s}$ ).

A thread with added weights was used to evaluate the maximal load-lifting capacity of each bird. The thread (with negligible weight) was 76 cm long and had 20 individual weight units evenly distributed along its length. Each unit weighed 0.2 g and was made of several beads of the same color. The color-coded thread of weights weighed 4 g in total, and the location of each unit could be uniquely identified by its own and adjacent colors. A flexible loop of rubber band (0.2 g) was tied to one end of the thread so that the bird could wear it like a necklace. The bird then had to lift up the thread of weights from the table in order to hover within the screened enclosure. The maximal load during hovering was calculated from the number of weight units lifted, as distinct from those remaining on the surface of the table. The body angle of the hovering bird became more vertical as more of the thread of weights was lifted, presumably to compensate for the change in center of gravity. Typically, the thread of weights hung, in part, against the chest of the bird at maximal load. Judging from the bird's capability to lift large loads, we concluded that the hanging thread of weights only marginally interfered with hovering performance. A 4 g thread of weights was chosen because the vertical height attained during maximal lifting (0.5–0.6 m) was sufficient to minimize ground effects (see Rayner and Thomas, 1991). Of all birds, the adult male (bird 1) was the lightest (see Fig. 1) and lifted the smallest mass. A 3 g chain with each mass unit weighing 0.15 g was used for this bird.

Birds were released from the table area directly beneath the enclosure. The usual escape response of ruby-throated hummingbirds is to fly directly upwards. In the cylindrical enclosure, birds ascended almost vertically while lifting the weighted thread, and then maintained hovering flight. When maximal load was reached and the bird could no longer hover, the usual response was to land and cling to the enclosure screen without losing height. The bird was then allowed to rest for 20 s or more, and was then encouraged to fly again by tapping the wall. Birds were then reluctant to lose height and carried the load in flight across the enclosure. This flight was treated as hovering because the forward speed was very low [the estimated advance ratio was less than half the maximal numerical criterion for hovering flight (0.1) proposed by Ellington, 1984c]. This type of flight across the enclosure occurred under maximal loading at the greatest height and was the condition used for most of the kinematic measurements. However, one female bird (bird 4) in particular, and other birds occasionally, did not cling to the enclosure screen but rather was pulled downwards by the weights. After hovering close to the bottom for a while, the bird attempted to ascend again; this behavior was often repeated several times. Brief hovering at the maximal attained height was chosen for analysis in these

cases. Each experimental sequence began with the load-lifting test. Video recordings of the bird making numerous (up to 10) flights while lifting the load were made. The thread of weights was then removed. The bird was allowed to hover freely in the enclosure for several minutes, and this free hovering was recorded. Finally, the bird was weighed.

For each recorded loading experiment, those flight sequences in which the bird made an effort to hover upwards and to reach a maximal height were identified. The maximal number of weight units lifted was then determined from the video recording of weights remaining on the table. Sequences were chosen from those in which the bird hovered or flew slowly across the enclosure while maintaining the maximal height for at least 0.5 s. Time of flight was measured using a stop watch; mean number of flight sequences chosen per bird per loading trial was 3.3, range 1–7. Erratic dashing flight sequences were rejected. For each chosen sequence, the number of weight units lifted at maximal height was determined. The maximal load that the bird could lift in a given loading trial was then calculated as the mean value of the maximal number of weight units lifted in all selected flight sequences (a given bird generally lifted similar amount of load; mean coefficient of variation per trial across birds averaged 10%). The other video recording was used to obtain horizontal projections of wingbeat kinematics for the flight sequences from which the maximal load was calculated. The methods used to calculate wingbeat frequency and stroke amplitude have been described previously (Chai and Dudley, 1995, 1996); mean values were used to represent the wing kinematics for a given loading trial. Briefly, wingbeat frequency was derived from the interaction frequency between wing motion and filming rate, and stroke amplitude was derived from video images in which the wings were located at the extreme positions of the wingbeat.

Wingbeat kinematics, together with morphological parameters for individual birds, were used to estimate the mechanical power requirements of flight using a detailed aerodynamic model of hovering flight (Ellington, 1984a–f). Wingbeat kinematics measured included wingbeat frequency  $n$  and stroke amplitude  $\Phi$ . Morphological parameters used in aerodynamic calculations included body mass  $m$ , relative wing mass  $m_w$  for both wing pairs and expressed as a fraction of body mass, wing length  $R$ , total wing area  $S$  (the area of both wing pairs), wing loading  $p_w (=mg/S$ , where  $g$  is gravitational acceleration) and aspect ratio  $\mathcal{A} (=4R^2/S)$ . For humane reasons, none of the experimental birds was killed for *post-mortem* analysis. Wing mass and its spanwise distribution were estimated from one bird of each sex in previous studies with the same species (Chai and Dudley, 1995, 1996). The mechanical power requirements of flight were estimated by evaluating the individual components of profile ( $P_{\text{pro}}$ ) and induced ( $P_{\text{ind}}$ ) power. The total power expenditure for a flight sequence was calculated for the case of perfect ( $P_{\text{per}}$ ) elastic storage of wing inertial energy. Thus,  $P_{\text{per}} = P_{\text{pro}} + P_{\text{ind}}$ .  $P_{\text{per}}$  was expressed in muscle mass-specific form assuming that flight muscle equals 25% of the body mass (Chai and Dudley, 1995).

Table 1. Summary of hovering performance of six individuals of *Archilochus colubris* under maximal loading and during free hovering at air temperatures of 5 and 25 °C

Flight type	<i>T</i> (°C)	Load (%)	Duration (s)	<i>n</i> (Hz)	$\Phi$ (degrees)	$\overline{C_L}$	$(\overline{Re} \times 10^3)$	$P_{ind}$ (W kg <sup>-1</sup> )	$P_{pro}$ (W kg <sup>-1</sup> )	$P_{acc}$ (W kg <sup>-1</sup> )	$P_{per}$ (W kg <sup>-1</sup> )	$P_{zero}$ (W kg <sup>-1</sup> )
Loaded	5	80±17	1.0±0.2	52±4	181±4	1.2±0.1	13.4±1.3	152±21	48±4	807±80	201±24	504±44
	25	81±44	1.0±0.2	53±4	183±4	1.2±0.1	12.2±1.1	160±19	52±5	858±108	211±22	535±59
Free	5	–	–	51±3	128±11	1.4±0.2	9.4±1.0	76±4	20±3	388±79	95±2	242±39
	25	–	–	45±4	149±5	1.4±0.1	8.4±0.8	73±1	21±2	353±74	94±1	223±38

Values are means ± s.d. (*N*=6).

Load indicates maximal load lifted as a percentage of body mass; duration is hovering duration under maximal loading. *n*, wingbeat frequency;  $\Phi$ , stroke amplitude;  $\overline{C_L}$ , mean lift coefficient;  $\overline{Re}$ , mean Reynolds number;  $P_{ind}$ , muscle mass-specific induced power;  $P_{pro}$ , profile power;  $P_{acc}$ , inertial power;  $P_{per}$  and  $P_{zero}$ , total power assuming perfect and zero elastic energy storage, respectively.

$P_{per}$  was used because hummingbirds can probably store kinetic energy elastically during the deceleration phase of the wing stroke (Wells, 1993b). For reference, total power expenditure for a flight sequence was also calculated for the case of zero ( $P_{zero}$ ) elastic storage of wing inertial energy. Thus,  $P_{zero}=(1/2)(P_{pro}+P_{ind}+P_{acc})$ .  $P_{acc}$  is the inertial power during the first half of a half-stroke.  $P_{per}$  and  $P_{zero}$  represent minimum and maximum estimates of required mechanical power respectively (Ellington, 1984f).

The effects of loading and air temperature were evaluated for each kinematic and aerodynamic variable using repeated-measures analysis of variance (ANOVA) (SAS Institute, 1989). The first model concerned the effect of the load (maximal loading versus free hovering) and tested two explanatory variables: load and day of experiment (over 4 days) as within-subject sources of variation for the two temperatures, respectively. The second model concerned the effect of air temperature difference (5 versus 25 °C) and was equivalent to the first model except that the load variable was replaced by the temperature variable.

## Results

Hovering while lifting a weighted thread substantially altered wingbeat kinematics, especially the stroke amplitude (Fig. 1). Amplitude modulation played a far more important role than did frequency modulation in generating the requisite lift force and mechanical power (Table 1). The mean stroke amplitude of the six individual hummingbirds under maximal loading was significantly different from that during free (unloaded) hovering (Table 2), and essentially reached its geometrical limit. Loaded birds often beat their wings so hard that the wingtips at the extreme position of the downstroke crossed one another. At the maximum positional angle of the upstroke, the wing axes were usually parallel. As a result, the stroke amplitude at maximal loading often reached 190°. These kinematic differences between down- and upstroke may reflect the twofold difference in mass between the pectoralis major and the supracoracoideus in hummingbirds (Hartman, 1961).

At an air temperature of 25 °C, wingbeat frequency

increased significantly with loading, compared with that in free hovering (Fig. 1; Table 1). At 5 °C, the wingbeat frequency during free hovering was similar to that at maximal loading, in contrast to the result obtained for stroke amplitude at this air temperature. Under maximal loading, wingbeat frequency was slightly higher for hovering at 25 °C than for hovering at 5 °C. However, air is somewhat denser at 5 °C than at 25 °C (1.26 kg m<sup>-3</sup> versus 1.18 kg m<sup>-3</sup> at 25 °C) and flight should be somewhat facilitated at the lower temperature. Stroke amplitude and wingbeat frequency during free hovering averaged 128±11° (mean ± 1 s.d., *N*=6) and 51±3 Hz at 5 °C,

Table 2. Results from a repeated-measures ANOVA for kinematic, aerodynamic and mechanical variables testing the effect of loading at 5 and 25 °C

Variable	<i>P</i> value		
	Load d.f. = 1, 5	Day d.f. = 3, 15	Load × Day d.f. = 3, 15
At 5 °C			
<i>n</i>	0.480	0.215	0.695
$\Phi$	0.001***	0.013*	0.549
$\overline{Re}$	0.001***	0.593	0.314
$\overline{C_L}$	0.011*	0.780	0.520
$P_{per}$	0.001***	0.062	0.063
$P_{ind}$	0.001***	0.048*	0.134
$P_{pro}$	0.001***	0.916	0.262
At 25 °C			
<i>n</i>	0.001***	0.174	0.003**
$\Phi$	0.001***	0.674	0.430
$\overline{Re}$	0.001***	0.880	0.259
$\overline{C_L}$	0.003**	0.987	0.577
$P_{per}$	0.001***	0.084	0.032*
$P_{ind}$	0.001***	0.230	0.186
$P_{pro}$	0.001***	0.397	0.064

*P* values are from *F*-tests; d.f., degrees of freedom. *n*, wingbeat frequency;  $\Phi$ , stroke amplitude;  $\overline{Re}$ , mean Reynolds number;  $\overline{C_L}$ , mean lift coefficient;  $P_{per}$ , mechanical power output per unit flight muscle mass assuming perfect elastic energy storage;  $P_{ind}$ , induced power;  $P_{pro}$ , profile power. \**P*<0.05; \*\**P*<0.01; \*\*\**P*<0.001.

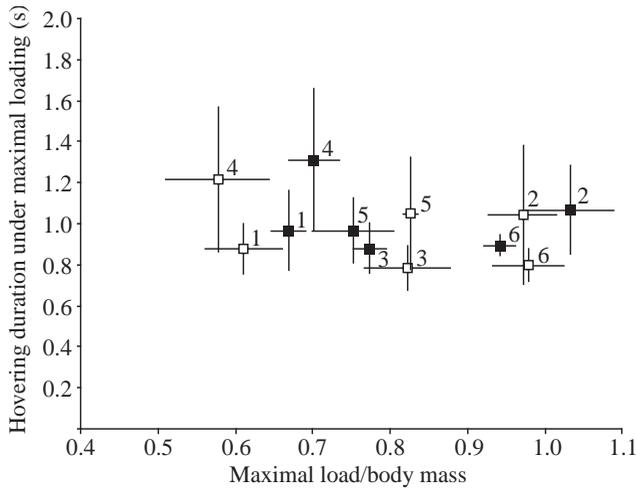


Fig. 2. Hovering duration under maximal loading versus maximal load lifted as a fraction of body mass for individual hummingbirds at 5 and 25 °C (symbols as in Fig. 1).

respectively, compared with  $149 \pm 5^\circ$  and  $45 \pm 4$  Hz at 25 °C. Thus, stroke amplitude declined while wingbeat frequency tended to increase at the lower temperature.

At 5 and 25 °C, the maximal load lifted was similar and the duration of load-lifting was almost identically brief (Fig. 2; Table 1). The increased flapping velocity under maximal loading resulted in an increase in the mean Reynolds number of the wing chord (Fig. 3; Table 1). Under maximal loading and at higher Reynolds number, the mean lift coefficient was lower than that for free hovering (Fig. 3; Table 1). Except for the wingbeat frequency at 5 °C, the effects of loading on all kinematic and aerodynamic variables were statistically significant (summarized in Table 2).

The total power requirements assuming perfect elastic energy storage, as well as the individual components of power, showed a more than twofold increase under maximal loading (Fig. 4; Tables 1, 2). Interestingly, although stroke amplitude and wingbeat frequency in free hovering varied in inverse

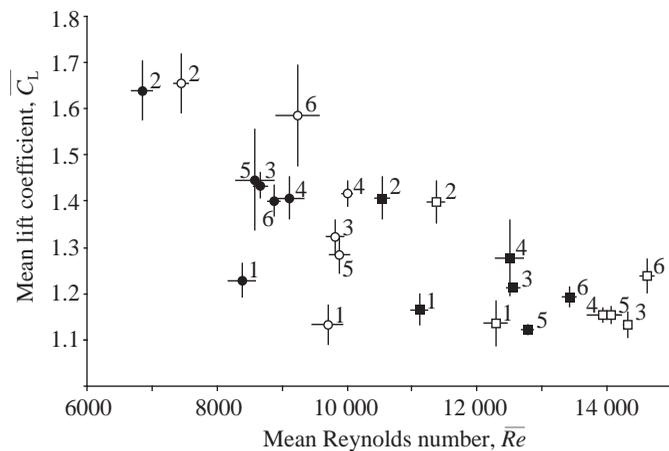


Fig. 3. Mean lift coefficient versus mean Reynolds number for individual hummingbirds under maximal loading and during free hovering flight at 5 and 25 °C (symbols as in Fig. 1).

proportion between 5 and 25 °C, their effects combined to yield similar aerodynamic power estimates (see Figs 1, 4). The statistical results assessing the effects of temperature on the kinematic, aerodynamic and mechanical variables were less uniform (Table 3).

**Discussion**

The most impressive outcome of load-lifting is the transiently elevated mechanical power output of the flight muscles (overall mean for both temperatures  $206 \text{ W kg}^{-1}$  muscle mass), more than double that in normal hovering ( $94 \text{ W kg}^{-1}$ ). This transient level is substantially higher than the largest power output yet measured on vertebrate muscle using the work loop technique ( $154 \text{ W kg}^{-1}$  muscle mass for the anaerobic locomotor muscle of a lizard; Swoap *et al.* 1993, see also review in Josephson, 1993). However, this result is similar to estimates of maximum anaerobic power output ( $200\text{--}250 \text{ W kg}^{-1}$ ) reported in two other studies (Ruben, 1991; Marden, 1994). In ruby-throated hummingbirds, the work per wingbeat under maximal loading averages only  $4 \text{ J kg}^{-1}$  muscle mass, substantially less than the  $7 \text{ J kg}^{-1}$  muscle mass of starlings in fast forward flight

Table 3. Results from a repeated-measures ANOVA for kinematic, aerodynamic and mechanical variables testing the effect of temperature (5 or 25 °C) under maximal loading or for unloaded free hovering

Variable	P value		
	Temperature d.f. = 1, 5	Day d.f. = 3, 15	Temperature × Day d.f. = 3, 15
<b>Under maximal loading</b>			
<i>n</i>	0.009**	0.027*	0.275
$\Phi$	0.091	0.001***	0.714
$\bar{Re}$	0.001***	0.595	0.774
$\bar{C}_L$	0.336	0.742	0.589
$P_{per}$	0.048*	0.001***	0.714
$P_{ind}$	0.118	0.001**	0.691
$P_{pro}$	0.026*	0.086	0.556
% Maximum load	0.684	0.001**	0.698
Duration	0.137	0.180	0.102
<b>During free hovering</b>			
<i>n</i>	0.005**	0.807	0.051
$\Phi$	0.005**	0.391	0.134
$\bar{Re}$	0.002**	0.276	0.888
$\bar{C}_L$	0.620	0.759	0.682
$P_{per}$	0.130	0.888	0.091
$P_{ind}$	0.089	0.947	0.264
$P_{pro}$	0.248	0.741	0.842

See Table 2 for symbols.

% Maximum load is maximal load lifted as a percentage of body mass; duration refers to hovering duration under maximal loading.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

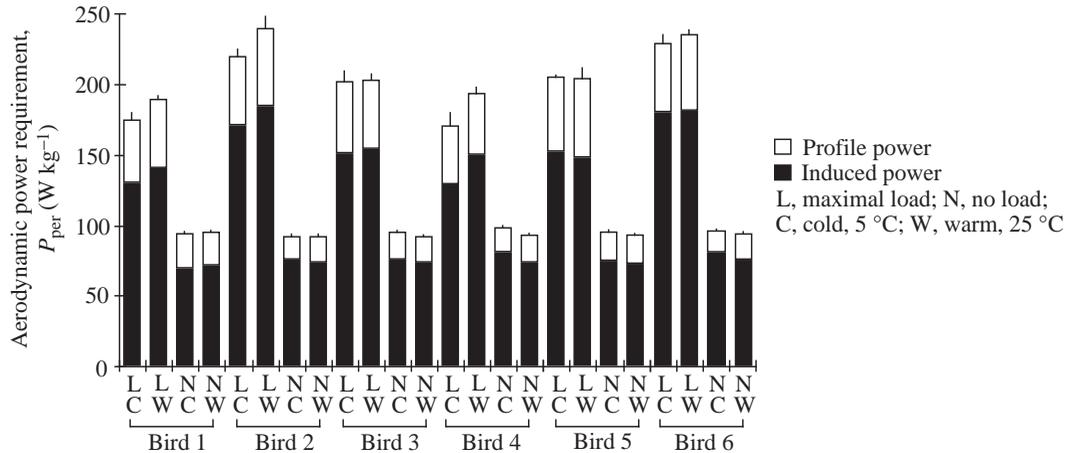


Fig. 4. Total mechanical power output assuming perfect elastic energy storage (induced power plus profile power) under maximal loading and during free hovering flight at 5 and 25 °C. Error bars indicate 1 S.E.M.

(Biewener *et al.* 1992). The volume fraction of mitochondria in hummingbird muscle is approximately 35%, while the contractile myofibrils account for only 50–60% of the muscle volume (Suarez *et al.* 1991). The high power output of ruby-throated hummingbirds is attained by the fast intrinsic speed of muscle contraction at operating frequencies around 52 Hz. The twofold increase in transient mechanical power output at maximal loading is probably essential for the ecological and behavioral repertoire of hummingbirds.

Hummingbird flight muscles are exclusively aerobic. Hummingbirds possess little capacity for glycolytic phosphorylation, yet retain the potential for burst performance as indicated by high activities of creatine kinase in the flight muscles (Suarez *et al.* 1986; Hochachka, 1994). Thus, brief hovering at maximum load may have been supported by the creatine kinase/phosphocreatine system, which provides high-powered ATP generation. At burst performance, phosphagen will quickly be depleted. This large but short-term power reserve allows for effective acceleration and maneuverability

to escape predators and to compete intraspecifically for nectar resources and for mates. Although hummingbirds are well known for sustained aerobic flight, the mechanics and biochemistry of their burst performance clearly merit further attention.

High mechanical power must be transduced *via* wing morphology and kinematics to yield high lift force. It is generally believed that hummingbirds, and birds in general, have only a limited capacity for the modulation of wingbeat frequency (Greenewalt, 1962, 1975; Hagiwara *et al.* 1968; Rayner, 1985; Pennycuik, 1990, 1992). The stable wingbeat frequency reflects the physical constraints of tuning to a natural resonant frequency. However, wingbeat frequency is significantly lowered during free hovering at 25 °C compared with that at 5 °C (Fig. 1; Table 1). Berger and Hart (1972) first noted that the South American hummingbird (*Amazilia fimbriata*) reduced its wingbeat frequency as air temperature increased, and they proposed that the heat generated by contraction of the flight muscles contributed to

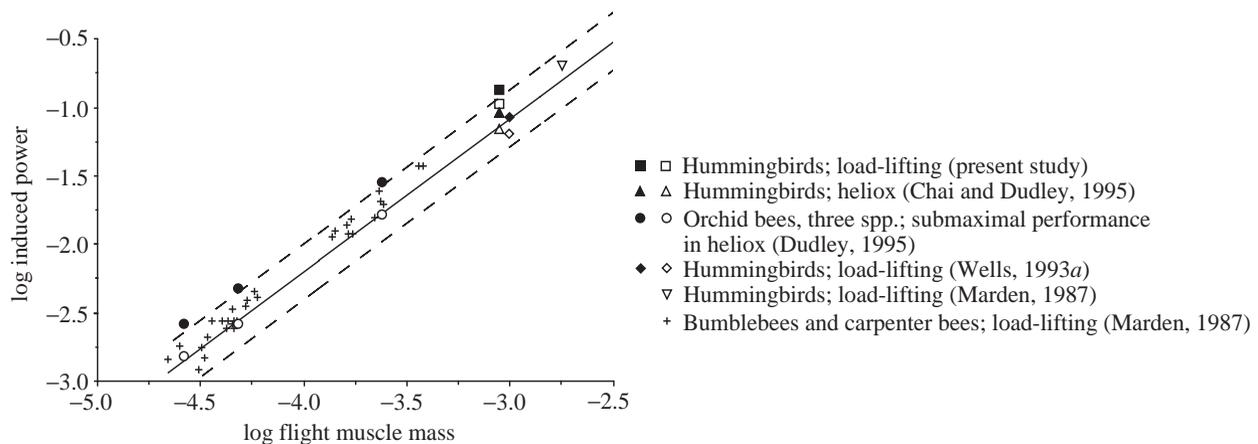


Fig. 5. Regression line ( $y=1.123x+2.292$ ,  $P<0.0001$ ) and 95% confidence band based on 121 individual flyers with conventional wingbeat (Marden, 1987) showing the scaling relationship between flight muscle mass (in kg) and maximum induced power (in W) calculated using the actuator disk equation. The results of the present study and two earlier hummingbird studies (Wells, 1993a; Chai and Dudley, 1995) on maximum performance induced by load-lifting or by hypodense flight media are overlaid, as are submaximal data for orchid bees of Dudley (1995). Filled symbols represent values calculated using Ellington's (1984f) vortex model; open symbols are for values calculated using the actuator disk equation (Marden, 1990).

thermoregulation at low temperatures. Exercise-generated heat also contributes to the thermoregulatory balance of Gambel's quail (*Callipepla gambelii*) running in the cold (at 0, 10 and 20 °C; Zerba and Walsberg, 1992). For ruby-throated hummingbirds, the inverse variation between stroke amplitude and wingbeat frequency at 5 and 25 °C, but maintenance of constant mechanical power, may indicate thermoregulatory contributions from muscle contraction during normal hovering. Presumably, at 5 °C, faster muscle contraction should generate more heat at the expense of mechanical efficiency.

Schuchmann (1979) found that the rates of oxygen consumption during hovering by two hummingbird species decreased linearly with increasing ambient temperature over the range 5 to 40 °C. This result suggests that heat production by the flight muscles cannot completely substitute for heat generation at low temperatures (Schuchmann, 1979), although contributions from convective cooling were unclear. This study may have had methodological complications, however, as the measured rates of oxygen consumption during hovering were unusually low (see Bartholomew and Lighton, 1986). Further studies measuring oxygen consumption and metabolic power input at 5 and 25 °C are needed.

For ruby-throated hummingbirds, similar wingbeat frequencies under maximal loading at 5 and 25 °C, and during free hovering at 5 °C, suggest the existence of a physical limit on wingbeat frequency similar to the geometrical limit on stroke amplitude. It will be of interest to determine whether ruby-throated hummingbirds can lift even greater loads in hyperdense but normoxic gas mixtures (see Dudley and Chai, 1996), mixtures for which lift production, and presumably limits to wingbeat kinematics, should become less constraining.

#### *Maximum performance induced by loading and by hypodense flight media*

The present loading study and the earlier density manipulation (heliox experiments) by Chai and Dudley (1995) were similar in that both studies investigated the hovering performance of hummingbirds. The former measured transient burst performance, whereas the latter required the bird to hover-feed for a minimum of several seconds. Five of the same hummingbirds were studied in both loading and heliox experiments, and their flight performance can be compared using the loading results at 5 °C and heliox results at 25 °C. However, the heliox measurements were made in November–December 1995 prior to the loading measurements in February 1996. Birds at this time were heavier, with an associated increase in wing loading. Presumably as a response to their pre-migratory molt, which occurred shortly following the present study, the birds were more aggressive and weighed less (P. Chai, personal observation; see also Wells, 1990; Hiebert, 1993). The mean body mass and wing loading of these individuals averaged 3.5±0.6 g (mean ± 1 s.d.,  $N=5$ ) and 30±2 N m<sup>-2</sup>, respectively, for the loading study compared with 4.2±0.3 g and 37±4 N m<sup>-2</sup>, respectively, in the heliox study.

Total power as well as both the induced and profile power

components were much greater for maximal loading conditions than in heliox, in contrast to the similarity in wingbeat kinematics between the two studies. Total power in the loading study averaged 195±21 W kg<sup>-1</sup>, compared with 131±7 W kg<sup>-1</sup> in heliox. Birds were able to lift and hover with loads equal to 76±16% of body mass for only 1.0±0.2 s. In the heliox study, the same birds hovered for 4.2±1.0 s in gas densities 47±9% lower than that of sea-level air. Thus, this comparison between individual birds in the loading and heliox experiments illustrates the inverse relationship between maximal power and its duration, and is consistent with rapid anaerobic phosphagen depletion. In contrast, wingbeat frequency and amplitude were generally comparable, averaging 52±4 Hz and 180±4° under maximal loading, respectively, compared with values in heliox of 53±5 Hz and 175±6°. The large difference in power expenditure but similar wingbeat kinematics probably reflect the dissimilar aerodynamic conditions arising from different air densities between the two manipulations. The mean Reynolds number and mean lift coefficient were also very different: 13 200±1300 and 1.2±0.1, respectively, for the loading study compared with 5400±700 and 1.7±0.1, respectively, in the heliox study. This result suggests that lift production was not limiting load-lifting capacity, but probably plays a constraining role in flight at reduced air densities.

#### *Comparison of the actuator disk model and Ellington's (1984f) vortex model*

Numerous studies have estimated the mechanical power output of hummingbirds and other flying animals through the application of a simplified actuator disc model without knowledge of wingbeat frequency and stroke amplitude (see Hainsworth and Wolf, 1972; Epting and Casey, 1973; Feinsinger and Chaplin, 1975; Feinsinger *et al.* 1979; Ellington, 1991; Marden, 1990, 1994). By progressively attaching weights of increasing mass to various volant animals, Marden (1987) determined the heaviest weight that test animals could lift in a vertical take-off. Using these load-lifting data, Marden (1990, 1994) and Ellington (1991) estimated the induced power during presumed hovering under maximal loading and concluded that the mass-specific power of flight muscle scales slightly positively with increasing body mass.

It should be noted that take-off flight is not mechanically equivalent to hovering flight because of changes in potential energy and the energetic costs of vertical acceleration; ground effects may also have influenced estimates of maximal performance (see Ellington, 1991). The present load-lifting data for ruby-throated hummingbirds provide an opportunity to assess possible differences between the use of a simple actuator disk model and the more accurate vortex approach (Ellington, 1984f) in estimating induced power and total power.

Based on 121 individual flyers with conventional wingbeat from Marden's (1987) data set, the regression line and 95% confidence band for individual predicted values were plotted (Fig. 5). The results of the present study and two earlier hummingbird studies (Wells, 1993; Chai and Dudley, 1995) on

maximum performance induced by loading or by hypodense flight media were then overlaid, as were submaximal data for orchid bees from Dudley (1995). Maximum induced power estimated using the actuator disk model was lower than estimates using Ellington's (1984*f*) vortex model. Application of the actuator disc equation to the data of Dudley (1995) and Chai and Dudley (1995) and to the present load-lifting data yields estimates of induced power comparable with those of Marden (1990; see Fig. 5). Differences in induced power estimates between the aforementioned studies and those of Marden (1990) appear to result primarily from the aerodynamic analysis employed. Using only estimates from the actuator disk method, the scaling relationship between flight muscle mass and maximum induced power clearly holds (Fig. 5). The present load-lifting results, together with actuator disc estimates of maximum induced power derived from Chai and Dudley (1995) and Dudley (1995), are congruent with the maximum lifting performance reported by Marden (1987). Resolution of possible biomechanical differences between the various methods that evaluate maximum performance should be implemented on a single taxon so as to preclude confounding phylogenetic associations.

Previous use of the actuator disk model systematically underestimated induced power during load-lifting in three ways: (1) wing span and not wing length was used to estimate actuator disc area, (2) stroke amplitude was assumed to be 180°, and (3) the effects of wing tip vortices were not considered, even though such effects can be substantial (Ellington, 1984*e*). For six ruby-throated hummingbirds, the wing semi-span (half the distance between the fully extended wing tips) was 13±1% greater than the wing length. The use of an actuator disc area with radius equal to half the wing span, together with the assumption of a 180° stroke amplitude rather than the actual area swept out by the beating wings, would underestimate induced power for maximally loaded ruby-throated hummingbirds by 11±1%. The discrepancy between the two estimates was somewhat reduced under maximal loading, because stroke amplitudes were approximately 180° as assumed by the actuator disk equation.

In addition, spatial and temporal fluctuations in the vortex wake can substantially increase the induced power requirements above the Rankine–Froude minimum estimate (Ellington, 1984*e*). For the six individual hummingbirds used in the present study, these effects increase the Rankine–Froude actuator disk estimate by 13±1%. Modifications to the wing area and vortex effects together increase the induced power by 27±2% above that estimated from the actuator disc equation and use of the wing semi-span (Marden, 1990). In Ellington (1991) and Marden (1994), the total power for the case of perfect elastic energy storage was estimated by assuming that the profile power was a constant 25% of the induced power requirement at maximal performance. In the present study, the profile power was 32±3% of the induced power under maximal loading; this effect arose primarily from the increased flapping velocity of the wings. Consequently, the total aerodynamic power ( $P_{\text{per}}$ ) generated by the six individual

ruby-throated hummingbirds averaged 34±3% more than estimates based on the approximations implemented by Marden (1990, 1994) and Ellington (1991). The allometric implications of these findings are presently being investigated for hummingbirds over a range of body masses (P. Chai, in preparation). In general, the use of the simple actuator disc equation without detailed kinematic and morphological data can substantially underestimate the maximal power produced by the flight muscles in hovering flight. Moreover, the accuracy of power estimates in the present study is still limited by a lack of information on additional variables, e.g. the geometrical angle of attack of the wing, the proportion of flight muscles relative to body mass and the contractile properties of the flight muscles. Further resolution is necessary to elucidate the interplay of mechanical power output, aerodynamic force production and allometry within the constraints of wing morphology and kinematics.

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