FLIGHT AND SIZE CONSTRAINTS: HOVERING PERFORMANCE OF LARGE HUMMINGBIRDS UNDER MAXIMAL LOADING

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Summary

As the smallest birds, hummingbirds are the only birds capable of prolonged hovering. This suggests that hovering locomotion scales unfavourably with size. Is the hovering performance of larger hummingbird species more constrained by size than that of smaller ones? Maximal load-lifting capacities of the two largest species of hummingbirds found in the United States, the blue-throated (*Lampornis clemenciae*, 8.4 g) and magnificent (*Eugenes fulgens*, 7.4 g) hummingbird, as well as the two other local small species, the black-chinned (*Archilochus alexandri*, 3.0 g) and rufous (*Selasphorus rufus*, 3.3 g) hummingbird, were determined under conditions of short-burst performance. The power reserves of hummingbirds are substantial relative to normal hovering performance. The two large species lifted maximal loads close to twice their body mass for a very brief duration of over 0.4 s. The small species lifted maximal loads approximately equal to their own mass with a longer duration of over 0.6 s. For the two large species under maximal loading, estimates of burst muscle mass-specific mechanical power output assuming perfect elastic energy storage averaged 309 W kg^{-1}, compared with 75 W kg^{-1} during free hovering without loading. For the two small species, these values were 228 W kg^{-1} and 88 W kg^{-1}, respectively. The differences in aerodynamic force production and power output between the large and small size classes occur despite their similar wing stroke velocity. This indicates that, during burst performance in these hummingbirds, the larger ones had a higher load-lifting capacity and generated more muscle power. In spite of the twofold difference in body mass, both large and small hummingbirds have evolved to become potent aerial competitors in order to exploit their common food resource, nectar. Both size classes have evolved to cope with the multi-dimensional effects of size constraining their aerodynamics, muscle mechanics, metabolism and ecology.

Key words: aerodynamics, body size, hovering, hummingbird, load-lifting, maximal burst performance, muscle power output, scaling, wing stroke velocity.

Introduction

During flight, wing morphology, wingbeat kinematics, aerodynamic forces and flight muscle mechanics are intricately linked, yet the detailed mechanical foundations and predictions of flight performance are still elusive. Two parameters, wing loading and aspect ratio, grossly quantify the size and shape of the wings and are widely used both in studies of bird flight and in aircraft engineering to characterize flight performance (Norberg, 1990; Tennekes, 1996). The scaling of wing span (length) and wing area with size in hummingbirds is considerably different from that for other flying birds, and the smaller species, which have disproportionately small wings relative to large hummingbirds, are not scaled according to geometric similarity (Greenewalt, 1962, 1975; Rayner, 1988). Wing area of hummingbirds varies with body mass, not with the two-thirds power of body mass predicted by isometric scaling. As a result, wing loading and aspect ratio in hummingbirds are size-invariant. This implies similar flight performance variables, such as flight speed, across the hummingbird size range (Rayner, 1996).

As the smallest birds, hummingbirds are unique in that both forward and backward strokes generate lift during hovering, and they are thus capable of extended hovering to feed on high-energy nectar. Hovering is the most energy-demanding form of locomotion because lift generation comes entirely from the flapping wings to meet the induced power requirement for weight support (Weis-Fogh, 1977). Consequently, prolonged stationary hovering is essentially only achieved by hummingbirds of small masses. This is also in agreement with the common observation that flight performance tends to be degraded with increasing size, although the capacities and constraints in aerodynamic force and muscle power generation as well as their allometric relationships are still unclear (Ellington, 1991; Marden, 1994; Dudley and Chai, 1996). Based on individuals of eleven bird species, Marden (1990)

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established a regression line relating the maximum load lifted to the flight muscle mass in birds, and Marden (1994) concluded that, for flying animals, muscle mass-specific lift scales independently of body size. Hummingbirds, in general, are expected to lift a maximal load approximately equal to their body mass. Do hummingbirds of different sizes have a similar hovering performance resulting from similar wing loading and aspect ratio, or does maximal performance deteriorate with increasing body mass?

Although hummingbirds range in size from approximately 2 to 20 g, only the small (3–4 g) North American species have been investigated for their hovering performance capacities (Wells, 1993; Chai and Dudley, 1995; Chai et al. 1997). Little is known about the aerodynamic capacities of intermediate-sized or large hummingbirds and how they compare with those of the smaller species (a 6 g tropical hummingbird was tested for its load-lifting capacity by Marden, 1987). Through the use of load-lifting manipulations, the present study investigates the maximum flight performance of both small and large (7–9 g) hummingbirds during short-burst activity. Peak performance in hovering is analyzed using detailed morphological and kinematic data and a contemporary aerodynamic model of hovering flight (Ellington, 1984a–f). An earlier load-lifting study with ruby-throated hummingbirds (Archilochus colubris, 3.5 g) indicated that the power reserves of this species were considerable; the maximal artificial load lifted averaged 80 % of body mass but with a brief duration of the order of 1 s. Under maximal loading, estimates of muscle mass-specific mechanical power output assuming perfect elastic energy storage averaged 206 W kg^{-1}, compared with 94 W kg^{-1} during free hovering without loading (Chai et al. 1997). Do larger species exhibit comparable aerodynamic capacities? To our knowledge, this is the first such study investigating the allometric variation in hovering performance of hummingbirds.

Materials and methods

We examined the hovering performance of four hummingbird species. We restricted our study to male specimens because of the potentially confounding sexual dimorphism exhibited by hummingbirds and also because our investigation took place during the breeding season, when female birds were tending eggs or young. Two blue-throated (Lampornis clemenciae Lesson, mean body mass 8.4 g, Table 1), three magnificent (Eugenes fulgens Swainson, 7.4 g), five black-chinned (Archilochus alexandri Bourcier and Mulsant, 3.0 g) and one rufous hummingbird (Selasphorus rufus Gmelin, 3.3 g) were studied during July 1996 at the American Museum of Natural History's Southwestern Research Station in the Chiricahua Mountains, Arizona, USA (31°50′N, 109°15′W). The facility is 1676 m above sea level with an air density of 0.98 kg m^{-3}. Hummingbirds were mist-netted and were housed in screen cages of dimensions 90 cm×90 cm×90 cm for less than 2 days. Hummingbird care was in accordance with federal and state guidelines. Each bird was subjected to loading trials over two consecutive days.

A cylindrical mesh enclosure (perforation diameter 12.7 mm to avoid boundary effect; Rayner and Thomas, 1991) was used in loading trials. Enclosure diameter was 47 cm, while 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. Two video cameras synchronized to within 1 s were used to obtain wing kinematics and loading values. One camera (Sony CCD-FX330), placed laterally, filmed the table immediately beneath the hanging enclosure, whereas the other camera (Sony CCD-TR600) recorded horizontal projections of wingbeat kinematics via a mirror oriented at 45 ° above the hovering birds within the enclosure (filming and subsequent analysis were at 60 fields s^{-1} with a high-speed shutter of 1/4000 s).

The methods used for load-lifting have been described previously (Chai et al. 1997). Briefly, a thread with weight units was used to evaluate the maximal load-lifting capacity of each bird. The thread was 76 cm long with 20 individual weight units evenly distributed along its length. The colour-coded thread of weights was either 4 g in total for the two small species or 16 g in total for the two large species, and the location of each weight unit could be uniquely identified by its own and adjacent colours. A flexible loop of rubber band (0.2 g) was tied to one end of the thread so that the bird would wear it like a necklace. The bird then had to lift 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.

Birds were released from the table area beneath the enclosure. The common escape response of hummingbirds is to fly directly upwards. In the cylindrical enclosure, birds ascended almost vertically while lifting the weighted thread. When the maximal load was carried and the bird could no longer fly upwards, the response was either to land and cling to the enclosure screen or to be pulled downwards by the weights. The bird was allowed to rest for 20 s or more, and was then encouraged to fly again by tapping the wall. Brief hovering at the maximal attained height was chosen for analysis in these cases. Each experiment 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 fly upwards and to reach a maximal height were located. The maximal number of weight units lifted was then determined from the video recording of weights remaining on the table. The flight duration under maximal loading was determined by counting the number of sequential video fields (each lasts 1/60 s) in which the maximal number of weight units was lifted. Erratic dashing flight sequences and flight sequences of brief duration

(less than 1/3 s) were rejected. Sequences of short duration were rejected for two reasons. First, during the initial burst, the vertical velocity and kinetic energy could be converted to potential energy and aid the load-lifting capacity momentarily. Second, it was hard to extract kinematic data reliably from flight sequences of short duration. The mean number of flight sequences chosen for analysis per bird was 6.5, range 2–17 (over 2 days). The maximal load that a given bird could lift was then calculated as the mean value of the maximal number of weight units lifted in all selected flight sequences (a given bird could generally lift a similar amount of load; mean coefficient of variation per trial across birds averaged 10 %). The flight duration under maximal loading was also calculated in the same way.

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 wingbeat kinematic variables measured included wingbeat frequency n and stroke amplitude Φ. Methods of calculating wingbeat frequency and stroke amplitude have been described previously (Chai and Dudley, 1995, 1996). 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. However, because the duration of burst performance was very brief, measurements of wingbeat frequency and stroke amplitude were also taken from images around those at maximal loading (approximately 1 s). Mean values were used to represent the wing kinematics for a given flight sequence, and the mean of these mean values was used to represent the wing kinematics of a given bird across the chosen flight sequences.

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, 1984*a*–*f*). Morphological parameters used in aerodynamic calculations included body mass m, relative flight muscle mass m_{muscle} expressed as a fraction of body mass, relative wing mass m_{wing} of both wings, wing length R, total wing area S (the area of both wings), wing loading p_w (=mg/S, where g is gravitational acceleration) and aspect ratio $Æ\!R$ (=$4R^2/S$). Five male individuals (three blue-throated, one magnificent and one black-chinned hummingbird), different from the study birds, were killed for *post mortem* analysis for another ongoing study. Flight muscle mass as well as wing mass and its spanwise distribution were measured, and mean values were applied to the study birds (values from the single black-chinned hummingbird were also used for the rufous hummingbird). The aerodynamic variables calculated were mean wing tip velocity $\overline{U}_t$ (2$n\Phi R$), mean Reynolds number $\overline{Re}$ and mean lift coefficient $\overline{C_L}$ (see equations in Ellington, 1984*f*). For each flight sequence, the muscle mass-specific mechanical power requirements of flight were estimated by evaluating individual components of profile (P^*_{pro}), induced (P^*_{ind}) and inertial (P^*_{acc}) power during the first half of a half-stroke. Total muscle mass-specific power expenditure for a flight sequence was calculated for the two cases of perfect (P^*_{per}) and zero (P^*_{zero}) elastic storage of wing inertial energy, which represent minimum and maximum estimates of the required mechanical power (Ellington, 1984*f*). Thus, $P^*_{per}=P^*_{pro}+P^*_{ind}$ assuming perfect elastic energy storage, and $P^*_{zero}=1/2(P^*_{pro}+P^*_{ind}+P^*_{acc})$ assuming zero elastic energy storage. A derived variable L/P (N W^{-1}) was calculated as the load lifted per unit power expenditure (for perfect elastic energy storage) and was used to link aerodynamic force generation and power expenditure (Marden, 1994).

Owing to the small sample size (11 individuals), data were pooled to create two size classes in order to assess the effects caused by size differences: the two large species formed the large size class, and the two small species the small size class. The effects of size differences between the two classes were then evaluated for each kinematic, aerodynamic and mechanical variable using the two-sample *t*-test (SAS Institute, 1989). This analysis was conducted separately on the results under maximal loading and on those from unloaded free hovering flight (see Table 2).

Results

The power reserves of hummingbirds are considerable relative to normal hovering performance. The maximal experimental load lifted by the two large species was impressive and close to twice their own mass, but with a very brief flight duration of over 0.4 s. The maximal load lifted by the small species was close to or slightly greater than their own mass, but with a longer duration of over 0.6 s (Table 1). In the present study, flight sequences with maximal load-lifting durations of less than 1/3 s were rejected from the analysis. For the two small species, only 12 % of the flight sequences were excluded on the grounds of short duration (when these were included, the mean duration of maximal loading remained similar at over 0.6 s) whereas, for the two large species, 59 % were excluded (when these were included, the mean duration was reduced to over 0.3 s). (In supplemental analysis, when flight sequences of short duration were included, the results were similar and the statistical conclusions remained unchanged.) Despite the differences in load-lifting capacities between the two size classes, their relative flight muscle mass was similar (27–29 %), and 29 % was also the mean value obtained previously for the males of 22 primarily tropical species of hummingbird (Hartman, 1961). Relative mass, size and shape of the wings were also generally similar (Table 1). Except for the male rufous hummingbird, which is well known to have small wings and high wing loading, the other three species showed similar wing loadings. Aspect ratios were also similar, but the large species had relatively longer wings and thus higher values than the smaller species (Table 1).

Hovering while lifting a weighted thread substantially altered wingbeat kinematics (Table 1). Both frequency and amplitude modulation were used to generate the requisite lift force and mechanical power. Both size classes increased their

Table 1. *Load-lifting capacities and morphological, kinematic, aerodynamic and mechanical variables for males of four species of hummingbird*

	Hummingbird species			
Variable	Blue-throated *Lampornis clemenciae* (N=2)	Magnificent *Eugenes fulgens* (N=3)	Black-chinned *Archilochus alexandri* (N=5)	Rufous *Selasphorus rufus* (N=1)
m (g)	8.4±0.3	7.4±0.2	3.0±0.2	3.3
Maximum load (%)	274±33	291±21	204±16	189
Duration (s)	0.43±0.01	0.48±0.12	0.64±0.09	0.65
R (mm)	85±2	79±3	47±1	42
p_w (N m^{-2})	23.5±1.3	24.7±1.0	23.5±0.7	33.6
$A\!R$	8.2±0.1	8.4±0.4	7.1±0.3	7.4
m_{wing} (%)	7.0	7.0	5.1	5.1
m_{muscle} (%)	29.0	27.1	29.0	29.0
n (Hz)	30.7±0.4	31.9±0.9	59.7±3.2	62.2
	23.3±1.9	24.0±0.9	51.2±3.8	51.7
Φ (degrees)	185±1	188±2	162±5	185
	151±7	150±6	126±6	163
$\bar{U}_t$ (m s^{-1})	16.8±0.6	16.5±0.3	15.8±1.0	16.9
	10.4±0.2	9.9±0.4	10.5±0.8	12.3
$\overline{Re}$	18 400±700	16 300±1000	11 100±1200	10 100
	11400±200	9800±700	7400±900	7400
$\overline{C_L}$	1.50±0.04	1.73±0.22	1.28±0.21	1.37
	1.46±0.01	1.67±0.17	1.42±0.28	1.41
P^*_{acc} (W kg^{-1})	721±60	913±57	895±157	959
	209±21	247±30	342±71	430
P^*_{ind} (W kg^{-1})	234±30	277±33	176±18	169
	58±4	63±1	68±2	70
P^*_{pro} (W kg^{-1})	48±5	49±2	53±8	50
	14±1	14±1	19±3	23
P^*_{per} (W kg^{-1})	282±35	327±31	230±22	219
	72±4	76±1	87±4	93
P^*_{zero} (W kg^{-1})	501±48	620±23	562±87	589
	141±37	162±16	215±37	261
L/P (N W^{-1})	0.328±0.003	0.323±0.010	0.306±0.014	0.293
	0.470±0.028	0.474±0.005	0.391±0.018	0.366

The first value of the kinematic, aerodynamic and mechanical variables refers to the value under maximal loading; the second refers to the value during free hovering.

m_{wing} and m_{muscle} are *post mortem* values from different male individuals.

All values are given as mean ± S.D.

For each individual, flight sequences in which the duration of maximal load lifting was less than 0.33 s are excluded.

m, body mass; maximum load, maximum load lifted relative to the bird's mass (bird's own mass included); duration, duration of lifting maximum load; R, wing length; p_w, wing loading; $A\!R$, aspect ratio; m_{wing}, relative wing mass of both wings; m_{muscle}, relative flight muscle mass; n, wingbeat frequency; Φ, stroke amplitude; $\bar{U}_t$, mean wing tip velocity; $\overline{Re}$, mean Reynolds number; $\overline{C_L}$, mean lift coefficient; P^*_{acc}, muscle mass-specific inertial power; P^*_{ind}, muscle mass-specific induced power; P^*_{pro}, muscle mass-specific profile power; P^*_{per} and P^*_{zero}, total mechanical power output per unit flight muscle mass assuming perfect or zero elastic energy storage, respectively; L/P, load lifted per unit power expenditure (assuming perfect elastic energy storage).

wingbeat frequency under maximal loading relative to unloaded free hovering (Tables 1, 2). Wing stroke amplitude also increased under maximal loading. At the downward (forward) stroke, individuals of all four species beat their wings so hard that the wing tips at the extreme position of the downstroke touched or even crossed one other. (The birds, especially the large species, usually became immobilized, hyperventilating and exhausted after a bout of maximal burst performance.) At the maximal positional angle of the upward (backward) stroke, the wing axes were usually parallel. As a result, the stroke amplitude at maximal loading often reached 190°, essentially at its geometrical limit. However, the black-

Table 2. *Results from two sample* t-*tests for kinematic, aerodynamic and mechanical variables testing the effect of body size under maximal loading or for unloaded free hovering*

Variables	*P* value Under maximal loading	*P* value Unloaded free hovering
Maximum load (%)	0.001***	–
Duration (s)	0.006**	–
n (Hz)	0.001***	0.001***
Φ (degrees)	0.002**	0.035*
$\bar{U}_t$ (m s^{-1})	0.240	0.176
$\overline{Re}$	0.001***	0.001***
$\overline{C_L}$	0.017*	0.229
P^*_{acc} (W kg^{-1})	0.409	0.006**
P^*_{ind} (W kg^{-1})	0.001***	0.002**
P^*_{pro} (W kg^{-1})	0.278	0.005**
P^*_{per} (W kg^{-1})	0.001**	0.001***
P^*_{zero} (W kg^{-1})	0.899	0.005**
L/P (N W^{-1})	0.015*	0.001***

Two size classes were used (large size, two individual blue-throated hummingbirds and three magnificent; small size, five black-chinned and one rufous hummingbird) and nine degrees of freedom.

n, wingbeat frequency; Φ, stroke amplitude; $\bar{U}_t$, mean wing tip velocity; $\overline{Re}$, mean Reynolds number; $\overline{C_L}$, mean lift coefficient; P^*_{acc}, muscle mass-specific inertial power; P^*_{ind}, muscle mass-specific induced power; P^*_{pro}, muscle mass-specific profile power; P^*_{per} and P^*_{zero}, total mechanical power output per unit flight muscle mass assuming perfect and zero elastic energy storage, respectively; L/P, load lifted per unit power expenditure assuming perfect elastic energy storage. *$P<0.05$, **$P<0.01$, ***$P<0.001$.

chinned hummingbirds did not reach such high stroke amplitudes because the contralateral wing axes at the maximal upstroke for this species were never parallel (Table 1).

The large species, which have longer wings, beat their wings at a lower n than the small species. As a result, both size classes exhibit similar wing stroke velocity as indicated by the mean flapping velocity of the wing tip (Table 1), and no size effect was found either under maximal loading or for unloaded free hovering (Table 2). Because wing stroke velocities were similar, the greater wing chords of the large species resulted in higher mean Reynolds numbers (Tables 1, 2). Under maximal loading, the mean lift coefficient was also higher for the large size class primarily because, with a similar wing stroke velocity, this size class could transiently lift much heavier loads than the small one.

For the large size class under maximal loading, estimates of muscle mass-specific mechanical power output for P^*_{per} averaged 309 W kg^{-1}, compared with 75 W kg^{-1} during free hovering without loading. For the small size class, these values are 228 W kg^{-1} and 88 W kg^{-1}, respectively (Table 1). P^*_{per} may be more representative than P^*_{zero} because hummingbirds can probably store kinetic energy elastically during the deceleration phase of the wing stroke (Greenewalt, 1975;

Wells, 1993; Dickinson and Lighton, 1995). During hovering, the major component of P^*_{per} was P^*_{ind}, representing the cost of generating lift for weight support (Table 1). Under maximal loading, the large species transiently lifted higher loads and had higher P^*_{ind} and P^*_{per} (Table 2). The major component of power, P^*_{ind}, is directly correlated with wing disk loading ($=mg/\Phi R^2$; Ellington, 1984*e*). Small hummingbirds have disproportionately shorter wings and higher wing disk loading. Consequently, during unloaded free hovering, the small size class exhibited higher P^*_{ind} and P^*_{per} (Table 1). Finally, the derived variable L/P, linking aerodynamic force and mechanical power (P^*_{per}), indicated that the large size class was better at producing maximal load-lifting per unit power expenditure. (A supplemental analysis that excluded the data derived from the single rufous hummingbird, because of its very different wing size and loading, yielded similar contrasts between the large and small size classes).

Discussion

Both large and small hummingbirds demonstrated impressive aerodynamic capacities and power reserves. The maximal artificial load lifted and the burst power output (P^*_{per}) by the two large species were greater than those attained by the two small species (184 *versus* 101 % of body mass and 309 *versus* 228 W kg^{-1}, respectively), but the duration of maximal loading was much shorter (mean at 0.46 *versus* 0.64 s). These results are in agreement with an earlier study on the maximal load-lifting performance of ruby-throated hummingbirds *Archilochus colubris*, which showed a lower burst power but a longer flight duration (maximum load 80 % of body mass, P^*_{per} 206 W kg^{-1} and duration 1.0 s; unlike the birds in the present study, the ruby-throated hummingbirds had been kept in captivity for 4 months; Chai *et al.* 1997). Our maximal power estimates from burst hovering performance are also similar to values of maximum instantaneous power output measured from a variety of animals (i.e. 200–300 W kg^{-1} from fish, scallop and mouse muscles; Franklin and Johnston, 1997). However, the flight muscles of hummingbirds are highly aerobic, with a reduced proportion of myofibrils (see below). The differences in aerodynamic force production and power output between the large and small size classes occur despite their similar wing stroke velocity (16.6 *versus* 16.0 m s^{-1}, respectively, at maximal load-lifting).

Under short-burst maximal loading, birds beat their wings so hard that the wing tips at the extreme position of the downstroke touched or even crossed one other (Weis-Fogh, 1973). At the extreme upstroke position, the wings were usually parallel or separated by a larger angle. This is especially true for the black-chinned hummingbirds, for which the maximal stroke amplitude averaged only 162 °. The kinematic differences between the down- and the upstroke may reflect the twofold difference in muscle mass between the pectoralis major and the supracoracoideus in hummingbirds (Hartman, 1961).

The differences in burst performance between the large and

small hummingbirds could be confounded by their responses to the loading manipulation in the present experiments. In order to restrict the bird's movement so as to record hovering flight within the enclosure, the enclosure diameter was 47 cm. With wing spans of 17–19 cm, the large species were more confined than the small species, with wing spans of 10–11 cm. Nevertheless, both large and small sizes showed comparable burst capacities. This generalization is based on four species (eleven individuals) with unclear phylogenetic relationships, but recent DNA hybridization evidence indicates that the taxon that includes the genera *Archilochus* and *Selasphorus* and the taxon that includes the genera *Eugenes* and *Lampornis* are sister taxa (Bleiweiss *et al.* 1997).

In order to exploit their common food resource of nectar, both large and small hummingbirds have evolved to become potent aerial competitors in their shared habitat (Carpenter, 1978). As the most northerly distributed species, rufous hummingbirds are only transient migrants in southeastern Arizona (Calder, 1987). Among hummingbirds, this species has unusually small wings and high wing loadings, presumably to achieve fast flight speeds during long-distance migration (Feinsinger and Chaplin, 1975; Hixon and Carpenter, 1988). The other three species are local breeders with closer ecological ties and presumably more severe interspecific competition (Pimm, 1978; Pimm *et al.* 1985; Powers and McKee, 1994). Their numerous similarities in body and wing designs, e.g. wing loading, relative flight muscle mass and wing stroke velocity, are consistent with convergent flight performance.

However, owing to the more than twofold difference in body size, these species were constrained in different ways. Although wing stroke velocities were similar among species, patterns of aerodynamic force production and mechanical power output were dissimilar. Because the lift-to-drag ratio and mean lift coefficient tend to scale favourably with size or Reynolds number (Vogel, 1994), the large species were capable of lifting closer to twice their own body mass. In contrast, aerobic capacity tends to scale unfavourably with size (Jones and Lindstedt, 1993), and this may explain the shorter duration of maximal load-lifting by the large species. Mitochondrial volume densities (indicating aerobic capacity) ranged from 35 to 37 % in the flight muscles of two North American *Selasphorus* hummingbird species with body masses of 3–4 g (Wells, 1990; Suarez *et al.* 1991), whereas these values were only 28 % for a 10 g South American species and 33 % for another 5 g species (Zerbinatti *et al.* 1991). The large hummingbird species may have difficulty in keeping up with the small species in prolonged aerobic performance (e.g. aerial pursuit). However, little is known about the sustainable performance capacity of large hummingbirds.

All hummingbirds use aerial fights and chases for aggressive interactions; flight speed and agility are important for using and defending nectar resources. For the small hummingbirds to match the large species in forward flight, the smaller species are constrained to have disproportionately small wings because flight speed tends to scale adversely with size (Rayner, 1988, 1996). As a result, the muscle mass-specific mechanical power

requirement during free unloaded flight was relatively high in the small species compared with the large ones (88 *versus* 75 W kg^{-1}). However, in terms of absolute power expenditure, the more expensive metabolic requirement of large hummingbirds could constrain the hummingbird size range as a result of the simple ecology of finding enough high-energy nectar. Indeed, the presence of small hummingbirds may exacerbate and cause even higher metabolic power expenditure in the large species owing to the need to defend the nectar resources and to chase off competitors (Powers and McKee, 1994). Using the doubly labelled water technique, Powers and Conley (1994) found that body mass-specific field metabolic rate in the large dominant blue-throated hummingbirds under conditions of abundant food (feeders) was higher than in the small subordinate black-chinned hummingbirds, presumably as a result of the high costs associated with aggressive territorial defence. Overall, oxygen consumption in hummingbirds showed more positive scaling with size than that of all other birds, suggesting that larger hummingbird species try to maintain aerobic flight performance (Bishop and Butler, 1995).

The effects of size are multidimensional and can constrain the aerodynamics, muscle mechanics, metabolism and ecology of birds. Depending on their lifestyles, different bird species integrate and optimize these multiple constraints and respond with unique patterns of body and wing design. Because of the need to exploit the common food resource (nectar), local hummingbirds are forced to share closer ecological ties. Thus, compared with other birds, hummingbirds display more homogeneity in flight-related traits, presumably reflecting the strong selective pressures from severe competition and aerial interactions which essentially determine a hummingbird's access to flowers. Because of their similarities in aerodynamic and ecological adaptations, hummingbirds are ideal study subjects with which to investigate the effects of size on flight biomechanics and energetics. The present study measuring load-lifting capacities and power output during short-burst hovering performance did not indicate an adverse scaling of aerodynamic force and muscle power production with increasing size among the four sympatric hummingbird species (see Ellington, 1991; Marden, 1994). The next logical step is to investigate allometric capacities in lift and power production during sustainable hovering performance, such as hovering in hypodense gas mixtures (Chai and Dudley, 1995). Comparative studies on flight performance and aerobic capacity in hummingbirds will shed light on and provide an integrative understanding of the roles of physiological specialization and the constraints in shaping their feeding strategies and ecological niches.

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