

Hovering and Forward Flight Energetics in Anna's and Allen's Hummingbirds

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ABSTRACT

Aerodynamic theory predicts that the mechanical costs of flight are lowest at intermediate flight speeds; metabolic costs of flight should trend similarly if muscle efficiency is constant. We measured metabolic rates for nine Anna's hummingbirds (*Calypte anna*) and two male Allen's hummingbirds (*Selasphorus sasin*) feeding during flight from a free-standing mask over a range of airspeeds. Ten of 11 birds exhibited higher metabolic costs during hovering than during flight at intermediate airspeeds, whereas one individual exhibited comparable costs at hovering and during forward flight up to speeds of $\sim 7 \text{ m s}^{-1}$. Flight costs of all hummingbirds increased at higher airspeeds. Relative to Anna's hummingbirds, Allen's hummingbirds exhibited deeper minima in the power curve, possibly due to higher wing loadings and greater associated costs of induced drag. Although feeding at a mask in an airstream may reduce body drag and, thus, the contributions of parasite power to overall metabolic expenditure, these results suggest that hummingbird power curves are characterized by energetic minima at intermediate speeds relative to hovering costs.

Introduction

Understanding how the energetic costs of flight vary as a function of airspeed (i.e., the shape of the metabolic power curve) has important implications for avian behavior and ecology. Aerodynamic models suggest that both slow and fast forward flight require elevated power expenditure relative to flight at intermediate airspeeds (Pennycuick 1969, 1989; Tucker 1973; Greenewalt 1975; Rayner 1979, 1994, 1999, 2001). High levels

of induced drag make hovering and slow flight costly, whereas parasite drag and profile drag on flapping wings increase disproportionately at high speeds to yield a high cost of fast forward flight. At intermediate speeds, none of these components dominate and net aerodynamic costs are lower. Direct measurements of mechanical power required for flight as measured in vivo for the pectoralis major are consistent with the hypothesis of decreasing mechanical power with increasing speed (Dial et al. 1997) and of a minimum mechanical power at intermediate flight speeds (Tobalske et al. 2003), although the contributions of the smaller flight muscles are not known.

Metabolic measurements of the cost of flight, as measured by either mask respirometry or volumetric depletion of oxygen within closed-circuit tunnels, has yielded a range of shapes for the power curve (reviewed in Ellington 1991; Rayner 1994, 1999). In some studies, the cost of flight is clearly lowest at intermediate speeds (Tucker 1968; Bundle et al. 2007). Other studies have reported essentially flat power curves over the airspeed range in question (Bernstein et al. 1973; Torre-Bueno and Larochelle 1978; Rothe et al. 1987; Ellington et al. 1990; Ward et al. 2002, 2004; Engel et al. 2006), linearly increasing costs of flight (Tucker 1972), and flat curves at low speeds but then substantial increases at higher speeds (Berger 1985). Given the ranges of airspeed, different animal taxa, and multiple methods of physiological measurement used in these studies, together with possibly variable muscle efficiencies (Rayner 1999, 2001), such diversity in the shape of the power curve is perhaps not surprising.

Moreover, the standard mechanical model of forward flight (Pennycuick 1969, 1989; Tucker 1973; Greenewalt 1975; Rayner 1979, 1994, 1999, 2001) employs steady-state aerodynamic assumptions similar to those for fixed-wing aircraft, under which induced power scales as speed^{-1} and parasite power scales as speed^3 (Rayner 1999). However, this mechanical model is incomplete at slow flight speeds and for hovering, and at these speeds it may overestimate the mechanical power required to fly. Hovering flight has been modeled with blade-element (propeller) models investigating the forces on flapping wings, including such unsteady aerodynamic effects as wing rotation and wake recapture (Weis-Fogh 1972; Ellington 1984; Dickinson et al. 1999; Sane 2003). It may be that unsteady aerodynamic effects, which are possibly more prevalent at low flight speeds, flatten the low-speed portion of the power curve, resulting in curves that are statistically flat at low speeds and then rise at high speeds (Ellington 1991). In addition to these theoretical concerns, forward flight as mimicked in a wind tunnel may not realistically simulate natural free flight if the animal adopts atypical kinematics or intermittent behaviors or if it flies near the boundaries of the working section (see Rayner 1994).

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Hummingbirds readily fly in wind tunnels with minimal training, making them well suited for use in testing theories of flight energetics over a range of airspeeds. Using an attached respirometry mask method, Berger (1985) measured metabolic power curves for two species of hummingbird (sparkling violetear *Colibri coruscans* and green violetear *Colibri thalassinus*). However, data for hovering were obtained from only one sparkling violetear, and sample sizes at slow speeds were modest. Moreover, the mask's weight and drag potentially influenced the metabolic expenditure of the hummingbirds. Nonetheless, Berger's data have been specifically cited as evidence that hummingbird power curves are essentially flat up to speeds of $\sim 8 \text{ m s}^{-1}$, and then they increase sharply (Ellington et al. 1990; Ellington 1991; Rayner 1994, 1999, 2001; Alexander 1997).

Metabolic rates of hovering hummingbirds can be readily obtained through an alternate technique: the use of a free-standing respirometry mask into which birds voluntarily insert their heads to obtain nectar (Bartholomew and Lighton 1986; Wells 1993; Chai and Dudley 1996; Welch and Suarez 2008). By placing such a mask in a wind tunnel, metabolic rates of feeding hummingbirds can be obtained at different airspeeds, although some aerodynamic interference will necessarily derive from the presence of the mask within the airflow. We (Clark and Dudley 2009) used this method to investigate effects of tail length on forward-flight energetics of five male and one female Anna's hummingbirds (*Calypte anna* Lesson). Because the focus of Clark and Dudley (2009) was specifically the effects of tail length on forward flight performance, analyses in that article did not include hovering data for a comparison with Berger (1985) or an assessment of possible sources of variation in curve shape. Here we consider energetic data over a full airspeed range for the six individual hummingbirds examined in Clark and Dudley (2009) and for an additional five birds, yielding power curves from a total of six male Anna's hummingbirds, three female Anna's hummingbirds, and two male Allen's hummingbirds (*Selasphorus sasin* Lesson).

Because of the high induced power costs of hovering, we hypothesized that the power curve of all hummingbirds exhibits a minimum at intermediate flight speeds. Moreover, the species-sex classes studied here show some variation in wing loading, with male Allen's hummingbirds having higher values than Anna's hummingbirds; both of these species have wing loading values that are higher than that of the sparkling violetear as measured by Berger (1985). We predicted a priori that species-sex classes with greater wing loading would demonstrate higher hovering flight costs relative to costs at intermediate flight speeds, given relatively increased induced power requirements during hovering flight. Finally, we also report patterns of intra- and interindividual variation to assess additional factors that potentially influence the shape of the power curve.

Material and Methods

Study Animals and Respirometry

This research was conducted in compliance with the University of California, Berkeley's Animal Use Protocol R282-0310. Six

male and three female Anna's hummingbirds and two male Allen's hummingbirds were captured in the wild between 2003 and 2006 under California Fish and Game permit SC-006598. Metabolic measurements were conducted within the working section of an Eiffel-style open-circuit wind tunnel (model 404, Engineering Laboratory Design, Lake City, MN). The tunnel had a 6.25 : 1 contraction section and a working section measuring 45.5 cm \times 45.5 cm \times 91.5 cm.

Some details of the respirometry mask suspended within the tunnel are given in Clark and Dudley (2009; see their Fig. 2). Mask size was reduced as much as possible given the constraints of the setup, but it did obstruct free-stream flow in the region of the body (see particle image velocimetry of the mask's wake in the supplemental materials of Clark and Dudley 2009). The mask and nectar reservoir were approximately the same width as the hummingbirds' bodies ($\sim 2 \text{ cm}$), and no part of the mask was directly upstream of the flapping wings. Therefore, it is likely that the mask had minimal effects on the aerodynamic conditions experienced by the birds' wings.

The three species-sex categories of birds varied in bill length, and birds tended to insert their heads only as far as necessary into the mask to obtain food. So as to induce all of the birds to insert their heads with the nares directly below the tube leading to the oxygen sensor (Fig. 2 in Clark and Dudley 2009), three different masks that varied in distance to the nectar reservoir were used. The masks did not otherwise significantly vary in shape (i.e., they had a constant diameter), so all three masks likely had similar aerodynamic effects on the birds. Mask orientation varied slightly every time we refilled the nectar reservoir, and occasionally the mask's orientation was adjusted by slightly tilting it up or down so as to facilitate feeding (usually at high airspeeds). Nectar was available ad lib., which yields a nominal respiratory quotient of 1 (Welch et al. 2007), and the solution was weak ($\sim 10\%$ sucrose) to induce frequent feeding. Following acclimation to captivity for 2 d, birds were trained to feed from the mask at a range of airspeeds (typically 0–10 m s^{-1}).

In all experiments, the flow rate through the mask was set at 3.9 L min^{-1} . Laboratory humidity averaged 27% (20°C), with little variation, and water was not scrubbed from the main line. At low tunnel speeds, essentially any flow rate through the mask would have sufficed, but at high tunnel speeds, turbulent mixing in the wake of the mask risked some of the bird's breath being lost if the flow rate through the mask was too low. A flow rate of 3.9 L min^{-1} was selected on the basis of the results of the following procedure: With the tunnel speed set to 10 m s^{-1} (the highest speed at which the birds could feed with little apparent effort), flow rate through the mask was varied from 0.3 to 4.5 L min^{-1} and the bird's apparent metabolic rate was calculated. At values greater than $\sim 3 \text{ L min}^{-1}$, the bird's calculated metabolic rate was independent of the mask flow rate. This procedure was repeated with each of the three aforementioned masks used in the study, with similar results.

A subsample was drawn from the main airstream at 0.3 L min^{-1} and consecutively passed through a 1.5-mL desiccation chamber (filled with Drierite) and an oxygen analyzer (Applied

Electrochemistry S-3A/II). Partial pressure of the oxygen in the subsample was digitized using a National Instruments 6052E 16-bit DAC card and sampled at 240 Hz using Labview. Sets of 12 consecutive data points were averaged to reduce electrical noise, resulting in an effective sampling rate of 20 Hz. When a hummingbird fed from the respirometry mask, equilibrium (minimum) values for oxygen concentration were attained in less than 2 s from the onset of a feeding bout. Metabolic rates were calculated from the associated change in oxygen partial pressure multiplied by the total flow rate through the mask. Feeding bouts were rejected if they were of insufficient duration to reach equilibrium or when respirometric airflow was perturbed via motions of the bird's head within the mask. For example, small-amplitude lateral, dorsoventral, or longitudinal motions of the bird's head sometimes altered respirometric airflow, causing pressure fluctuations that resulted in spurious readings. Feeding bouts in which the bird repeatedly inserted and removed its head from the mask in quick succession were used if at least one head insertion was of sufficient duration to reach equilibrium.

In-flight metabolic measurements were obtained at wind-tunnel settings of 0, 2, 4, 6, 8, 10, and 12 m s⁻¹ presented in haphazard order. Measurements obtained within 30 s of a change in the tunnel's airspeed were not used, in case the bird's instantaneous oxygen consumption lagged behind its instantaneous flight speed. Some birds were capable of feeding from the mask while flying at 13 or 14 m s⁻¹; measurements at these speeds were always taken near the end of a series of measurements. For any given bird, a series of metabolic measurements for the entire speed range was collected over the course of several hours. Body mass was measured before and after each experiment, and it is reported as the average value (Table 2), as is the value for wing loading (the ratio of body weight to the total area of the wing pair). Body mass fluctuated over the course of the experiment with each ingested meal and with defecation. It was not possible to measure changes in body mass continuously over the course of the experiments, and average body mass was used instead in all calculations. A perch was provided downstream of the respirometry mask.

For five male and one female Anna's hummingbirds, two measurement series were taken to represent the control treatments of Clark and Dudley (2009): (1) a normal unmanipulated series, and (2) performed on a subsequent day, a series for which the fourth rectrices were cut and then reattached. This sham manipulation had no systematic effect on flight metabolic rate (see Clark and Dudley 2009), and both sets of data are presented here as two series of metabolic measurements taken from individual birds. Wingbeat frequencies were obtained from high-speed videos (500 frames s⁻¹) that were taken of four male Anna's hummingbirds while they were feeding and in free flight over the experimental range of airspeeds.

Statistical Analysis

The high-speed portion of the power curve is hypothesized to be dominated by parasite drag, which increases in proportion

to the cubed value of the airspeed. Moreover, induced power varies in inverse proportion to speed; thus, a model for a curvilinear metabolic power curve is as follows (Rayner 2001):

$$\dot{V}_{O_2} m^{-1} = \beta_0 + \beta_1 v^{-1} + \beta_2 v^3, \quad (1)$$

where $\dot{V}_{O_2} m^{-1}$ is the body mass-specific metabolic rate, v is air velocity, and β_0 , β_1 , and β_2 are statistically estimated parameters. However, to fit Equation (1) to the data, the values for flying at 0 m s⁻¹ (i.e., hovering) were excluded, because this speed has an undefined inverse. An alternative model, for which it is not necessary to exclude values for hovering, is as follows:

$$\dot{V}_{O_2} m^{-1} = \beta_0 + \beta_1 v + \beta_2 v^3. \quad (2)$$

Note that all references to v are specific to the v term in Equation (2), while v^{-1} refers to Equation (1).

We analyzed the shape of the power curve in a general linear model (GLM) using v and v^3 as covariates, bird ID as a random factor, species-sex category as a fixed factor, measurement series as a random factor, and a measurement series \times bird ID interaction term (to test for changes in the power curve for particular individual birds). Also included was a $v \times$ species-sex category interaction to test the hypothesis that different species-sex categories exhibited different shapes of the low-speed portion of the power curve. Similarly, a $v^3 \times$ species-sex category interaction tested the hypothesis that the different species-sex categories exhibited different shapes for the high-speed portion of the power curve. This model was implemented a second time using v^{-1} in place of v .

A priori, we hypothesized that the shape of the power curve varied with species-sex category. However, both the results of the full GLM and inspection of the data suggested that a posteriori examination of three levels of variation of power curve shape was warranted. Those levels are as follows: (1) between-bird variation (within each species-sex category), (2) within-bird variation (between measurement series), and (3) variation among species-sex categories. Within-bird variation was indicated by significant bird ID \times measurement series interactions in the GLM, whereas visual inspection of the data for the female Anna's hummingbird individual 8 suggested notable between-bird variation. It was not possible to statistically assess all of these sources of variation within a single GLM because our data set lacked the high number of degrees of freedom that would be necessary to include three-way interactions.

To explore these sources of variation, we performed two post hoc analyses of the shape of the power curve. The first analyzed each individual bird measurement series separately, using an ANCOVA with v and v^3 as covariates. In the second analysis, we averaged all replicate measurements for each individual within each speed and then performed an ANCOVA with v and v^3 as covariates and species-sex category as a factor. This ANCOVA was performed both with and without female Anna's hummingbird individual 8. Regressions for which values of

both β_1 and β_2 were statistically significant were interpreted to indicate minimum costs at intermediate speeds, whereas statistical insignificance for values of either β_1 or β_2 were interpreted to indicate the absence of such a minimum.

Results

The highest flight speed at which all birds were able to feed from the mask was 12 m s^{-1} . Five birds successfully fed at 13 m s^{-1} , and two male Anna's hummingbirds also learned to feed at 14 m s^{-1} . The inability of birds to feed at higher speeds seemed to be behavioral, and it was possibly a control problem: they would either fail to fully insert their head into the mask or they would do so for unsuitably short durations; this latter action would often be accompanied by excessive head movement. To avoid depriving the birds of food, individuals that were unable to feed were only flown at a given high speed for a few (<10) minutes. We observed no indirect evidence of burst (anaerobic) performance when birds flew at these high speeds.

The hummingbirds tended to fly near the top of the working section, at or above the vertical position of the respirometry mask. At low flight speeds and while hovering ($0\text{--}4 \text{ m s}^{-1}$), the birds tended to either perch or repetitively fly back and forth just below the top of the working section, on the side opposite the experimenter. At higher flight speeds ($>4 \text{ m s}^{-1}$), the birds usually perched less frequently, and they typically flew near the top of the upstream end of the tunnel while making individual-specific repetitive flight circuits. In all, 613 individual metabolic estimates were included in the analyses.

The statistical results of the GLM are shown in Table 1. Bird ID, v^{-1} , v , and v^3 were highly statistically significant in the respective GLMs. Moreover, there was a highly significant interaction between either v or v^{-1} and species-sex category ($P < 0.002$), whereas interactions between v^3 and the species-sex category were either nonsignificant or not highly significant ($P > 0.01$). There was also a significant bird ID \times measurement series interaction (see Table 1).

Between-Bird Variation

The GLM indicated that bird ID was a significant source of variation (Table 1). The metabolic power curves obtained for six male Anna's hummingbirds (Fig. 1A), two of three female Anna's hummingbirds (Fig. 1B), and two male Allen's hummingbirds (Fig. 1C) yielded power curves with statistically significant minima at intermediate flight speeds. The ANCOVA for each individual bird and measurement series is presented in Table 2. Ten of eleven birds had highly significant ($P < 0.001$) β_1 values in at least one measurement series, whereas this parameter was not statistically significant for female Anna's hummingbird individual 8 (Fig. 1B; $P = 0.22$). Moreover, mass-specific metabolic rates at all airspeeds were higher for this individual relative to the two other female Anna's hummingbirds (Fig. 1B).

Table 1: Results of a general linear model for variation in hummingbird metabolic rates

Variable	F (df)	P
Equation (1): ^a		
Bird ID	9.91 (10)	<.0001
v^{-1}	104 (1)	<.0001
v^3	147 (1)	<.0001
$v^{-1} \times$ species-sex category	6.84 (2)	.0012
$v^3 \times$ species-sex category	.117 (2)	.889
Bird ID \times measurement series	6.61 (5)	<.0001
Equation (2): ^b		
Bird ID	11.3 (10)	<.0001
v	354 (1)	<.0001
v^3	307 (1)	<.0001
$v \times$ species-sex category	18.3 (2)	<.0001
$v^3 \times$ species-sex category	4.33 (2)	.014
Bird ID \times measurement series	6.34 (5)	.0001

Note. Results are obtained with Equations (1) and (2). Variables that are statistically marginal to their interaction terms are not shown.

^a df = 528.

^b df = 613.

Within-Bird Variation

The GLM analysis indicated that measurement series for the same bird was a significant source of variation (Table 1). When analyzed individually, all of the birds had statistically significant parameters for β_2 (corresponding to v^3) in at least one of their measurement series, and most of the parameters were highly statistically significant (Table 2; $P < 0.001$). However, one male Anna's hummingbird (individual 5) exhibited different shapes for the power curve between the two different measurement series (Fig. 2; series 1: β_1 , $F_{1,28} = 6.78$, $P = 0.015$; β_2 , $F_{1,28} = 4.48$, $P = 0.043$; series 2: β_1 , $F_{1,31} = 150$, $P < 0.001$; β_2 , $F_{1,31} = 218$, $P < 0.001$). As a result, the power curve of the first series was essentially flat, whereas that of the second series exhibited an unambiguous minimum (Fig. 2).

Species-Sex Category Variation

The GLM analysis indicated that species-sex category was a significant source of variation manifested as an interaction effect with v or v^{-1} . The among-individual post hoc analysis revealed that, with the inclusion of female Anna's hummingbird individual 8, the three species-sex classes differed significantly (ANCOVA, $F_{2,80} = 3.96$, $P = 0.023$). In particular, male Anna's hummingbirds and the other two species-sex classes did not differ significantly ($t = -1.69$, $P = 0.09$), whereas male Allen's hummingbirds did differ significantly from female Anna's hummingbirds ($t = -2.80$, $P = 0.006$). This outcome was associated with higher metabolic rates for Allen's hummingbirds at lower airspeeds (Fig. 3). When the data from female Anna's hummingbird 8 were excluded, differences among the three species-sex classes were highly significant (ANCOVA, $F_{2,73} = 23.0$, $P < 0.0001$), including the difference between male and female Anna's hummingbirds ($t = -5.67$, $P < 0.001$). In both

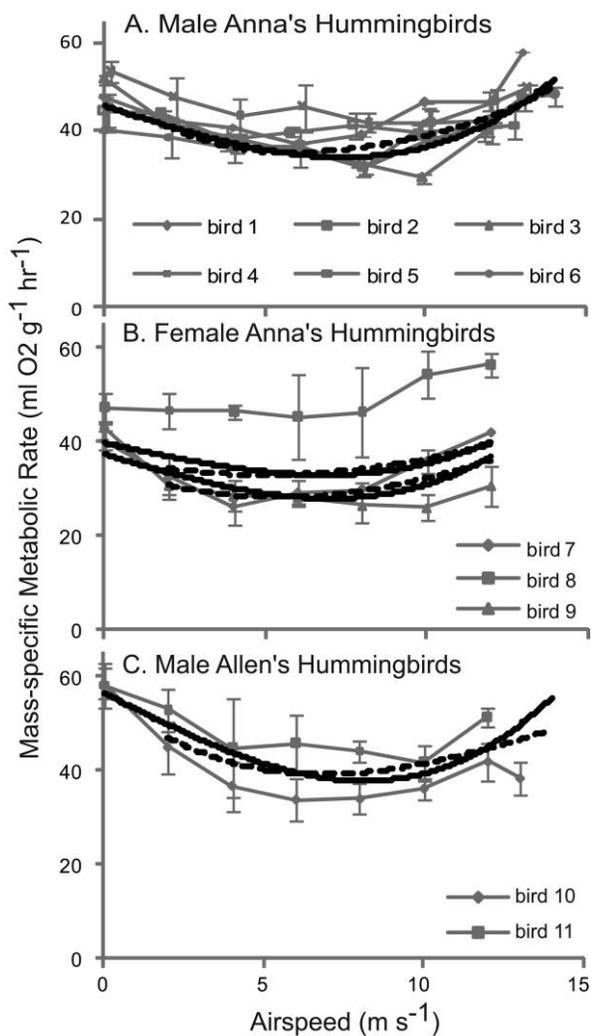


Figure 1. Individual variation in the metabolic power curves for Anna's and Allen's hummingbirds feeding from a stationary mask within a variable-speed airstream. Data from individual birds are in gray. Best-fit lines for each species-sex category were estimated from a general linear model using equations 1 (dashed black line) and 2 (solid black line). Error bars represent ± 1 SD; points without error bars correspond to speeds at which only one sample was collected. Data were collected at 0, 2, 4, 6, 8, 10, 12, 13, and 14 m s^{-1} ; points for male Anna's hummingbirds have been slightly offset. Data refer to average values for either a given set of measurements or two measurement sets for any given individual (see Table 2). The equations for the best-fit lines in (A) are as follows: $\dot{V}\text{O}_2 \text{ m}^{-1} = 30.1 + 23.1v^{-1} + 0.00653v^3$ and $\dot{V}\text{O}_2 \text{ m}^{-1} = 45.7 - 2.38v + 0.0144v^3$. In (B), the equations for the upper lines (including data from bird 8) are as follows: $\dot{V}\text{O}_2 \text{ m}^{-1} = 30.9 + 7.22v^{-1} + 0.00470v^3$ and $\dot{V}\text{O}_2 \text{ m}^{-1} = 39.7 - 1.48v + 0.0105v^3$. In (B), the equations for the lower lines (excluding data from bird 8) are as follows: $\dot{V}\text{O}_2 \text{ m}^{-1} = 25.0 + 12.3v^{-1} + 0.00594v^3$ and $\dot{V}\text{O}_2 \text{ m}^{-1} = 37.3 - 2.01v + 0.0137v^3$. In (C), the equations for the best-fit lines are as follows: $\dot{V}\text{O}_2 \text{ m}^{-1} = 33.5 + 29.8v^{-1} + 0.00491v^3$ and $\dot{V}\text{O}_2 \text{ m}^{-1} = 37.3 - 3.44v + 0.0172v^3$.

cases, the power curve for female Anna's hummingbirds was substantially flatter than the curves for males of either species (Fig. 3).

Wingbeat frequency in free flight did not vary with airspeed,

assuming a linear relationship between the two variables (Fig. 4; ANCOVA with individual bird and airspeed as factors: $F_{1,65} = 0.85$, $P = 0.36$), but it did vary significantly when modeled using the linear and cubic terms of Equation (2) (ANCOVA, β_1 : $F_{1,64} = 5.38$, $P = 0.024$; β_2 : $F_{1,64} = 9.18$, $P = 0.0035$), and it exhibited a slight minimum between 4 and 6 m s^{-1} (Fig. 4). Wingbeat frequency was not significantly different in free flight compared with in flight while feeding from the mask at the same airspeed (paired t -test, $N = 35$, $P = 0.2$). Wing loading (Table 2) varied between the three species-sex categories of the birds in the study (one-way ANOVA, $N = 11$, $P = 0.003$).

Discussion

Metabolic power curves for feeding hummingbirds typically exhibited shallow minima at intermediate air speeds (Figs. 1–3). However, the curves did show some variation in shape between individual birds within a species-sex category (Fig. 1), between sets of measurements of the same individual collected on different days (Fig. 2), and among species-sex classes (Fig. 3). A minority of the power curves we measured from individual birds were not different in shape from the J -shaped curves reported by Berger, who was using a substantially different method (Berger 1985; Fig. 3). We suggest that the shape of the hummingbird power curve can vary substantially for reasons of both experimental error and true variation that are addressed below.

Sources of Experimental Error

Experimental error could potentially cause measured power curves to systematically vary from the actual shape of the power curve. Mask effects fall into this category. For instance, when in flight at low airspeeds ($< 6 \text{ m s}^{-1}$) but not feeding, our birds spent most of the time flying at a typical speed of a few meters per second. Hovering occurred primarily when the birds were actually feeding from the feeder. We hypothesize that hummingbirds with an attached respiratory mask would show similar behavior when the nominal speed of the wind tunnel is 0. Berger's (1985) measurements at an airspeed of 0 may have been more representative of low-speed flight, potentially flattening the lower-speed portions of the power curve. Use here of a free-standing mask from which birds fed at different airspeeds imposed a constant position within the tunnel on the bird; at this position, the bird's airspeed exactly matched that of the set airspeed for all individuals. This effect may have reduced behavioral variation among birds. At low airspeeds, this outcome would appear to represent a clear advantage of the use of a free-standing mask over that of an attached one.

At high airspeeds, advantages of our technique are less clear. One limitation to the method used here is the potential cost of station-keeping at the feeder mask relative to free flight at equivalent airspeeds; maintenance of stability while feeding may

impose greater aerobic demands even though wingbeat frequencies at least were unchanged. Hummingbirds appeared to be limited from feeding at even higher speeds by their ability to insert their head into the mask. Moreover, the attached-mask method of Berger (1985) would be expected to increase parasite drag at high airspeeds. The mask likely disrupts the streamlined form of the bird's body, and both drag and associated torque on the attached respiratory tubing may be significant. These effects may be primarily manifested at higher airspeeds and may explain why Berger's metabolic curves begin to rise at much lower speeds ($\sim 6 \text{ m s}^{-1}$) than our curves do ($\sim 10 \text{ m s}^{-1}$; Fig. 3).

When our birds had their head inside the mask, the wings were exposed to free-stream flow but the head and body experienced altered flowfields that had lower-than-free-stream velocities. Parasite drag and associated mechanical power expenditure for flight behind the mask is therefore reduced while the bird is feeding. However, oxygen consumption likely lags behind instantaneous mechanical power output. If this lag were small (shorter than the timescale required for our system to come to equilibrium), then our metabolic measurements may have underestimated the cost of flight at high speeds given reduced parasite drag behind the mask. Accordingly, the true

shape of power curves in the absence of a mask might rise more sharply at higher speeds. Alternately, if the lag is significant (e.g., $>1 \text{ s}$), then our metabolic measurements may have been more representative of the bird's energetic expenditure in the seconds before feeding, during its approach to the feeder. Because the duration of the metabolic lag relative to mechanical power output is unknown, it is unclear which of these two alternatives is more likely.

In addition to these potential systematic errors, several additional sources of variation could cause individual curves to vary. For example, approach behavior to the mask varied qualitatively among individuals and at different tunnel airspeeds, although such variation would be expected to be random between individuals. Within- and among-individual variation in metabolic rates might also derive from short-term fluctuation in body mass, which was measured before and after each experimental series. Food with a weak sugar concentration was available ad lib. at the feeder; an ingested meal can increase body mass by 10%, and subsequent defecation similarly reduced it. Tunnel airspeed, however, was presented haphazardly, so effects such as these could be responsible for differences in the shape of individual curves (e.g., Fig. 2) but seem unlikely to alter the power curve systematically.

Table 2: Morphology and statistical results for the shape of the power curves for individual hummingbirds

Species, Bird ID, Measurement	<i>N</i>	Sex	Body Mass (g)	Wing Loading (N m^{-2})	<i>F</i> (<i>v</i>)	<i>F</i> (<i>v</i> ³)
<i>Calypte anna</i> :						
1	13	M	4.5	32	12.0	21.9
2:						
Series 1	28	M	4.7	35	79.6	53.4
Series 2	21				101.6	52.0
3:						
Series 1	69	M	4.3	32	127	62.9
Series 2	20				56.1	16.1
4:						
Series 1	46	M	4.5	33	57.8	47.8
Series 2	38				104	130
5:						
Series 1	31	M	4.9	34	6.78*	4.48*
Series 2	34				150	218
6:						
Series 1	46	M	4.4	33	16.3	41.4
Series 2*	46				7.03*	29.4
7:						
Series 1	41	F	4.7	32	50.4	63.1
Series 2	35				9.59	21.8
8	42	F	4.0	28	1.58**	7.18
9	58	F	4.2	28	37.8	31.0
<i>Selasphorus sasin</i> :						
10	37	M	3.2	37	32.6	22.5
11	38	M	3.7	46	86.4	53.5

Note. *N* is the number of metabolic measurements over all airspeeds. Values in italics indicate $P < 0.01$.

* $0.05 > P > 0.01$.

** Nonsignificant *F* statistic.

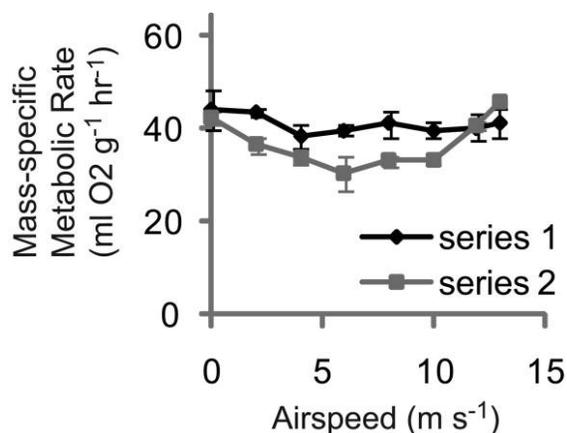


Figure 2. Within-individual variation in the metabolic power curve for a male Anna's hummingbird (bird 5) obtained in two measurement series on different days (Tables 1, 2).

True Variation with Airspeed

According to the fixed-wing theory for forward flight (Pennycuik 1969, 1989; Rayner 1999, 2001) and aerodynamic models of hovering (Weis-Fogh 1972; Ellington 1984), the low-speed portion of the power curve will flatten with lower wing loading because of a relative reduction in induced power requirements. Our data support this hypothesis. Of the three species-sex classes tested here, male Allen's hummingbirds have the highest values for wing loading, whereas female Anna's hummingbirds

have the lowest (Table 2). At lower airspeeds and during hovering, expenditure of metabolic power was higher for the male Allen's hummingbirds relative to Anna's hummingbirds of either sex, whereas all three species-sex classes exhibited similar metabolic rates at higher flight speeds (Table 1; Fig. 3). Moreover, data from Berger (1985) are also consistent with the wing-loading hypothesis: sparkling violetears have an average wing loading of 21 N m^{-2} (Altshuler 2001), which is even lower than that of female Anna's hummingbirds (Table 2). Power curves that are flat at low speeds may be typical of hummingbirds with low wing loading, whereas curves exhibiting minima at intermediate speeds typify birds with moderate to high wing loading (Fig. 3). That being said, the low sample sizes of hummingbirds with both the highest ($n = 2$; male Allen's hummingbird) and lowest ($n = 1$; sparkling violetear; Berger 1985) wing loading, coupled with the additional sources of variation and methodological differences already discussed, render this conclusion only tentative.

In addition to wing loading, other possible variables that could cause differences in the shape of the power curve to arise include differences in muscle morphology, sex differences, or individual differences in flight style. These variables could all contribute to variation in muscle efficiencies that would cause the shape of the metabolic power curve to differ among individuals. However, we identified neither differences in wing-beat frequency (Fig. 4) nor dramatically varying flight styles between our study birds that would suggest any such contributions.

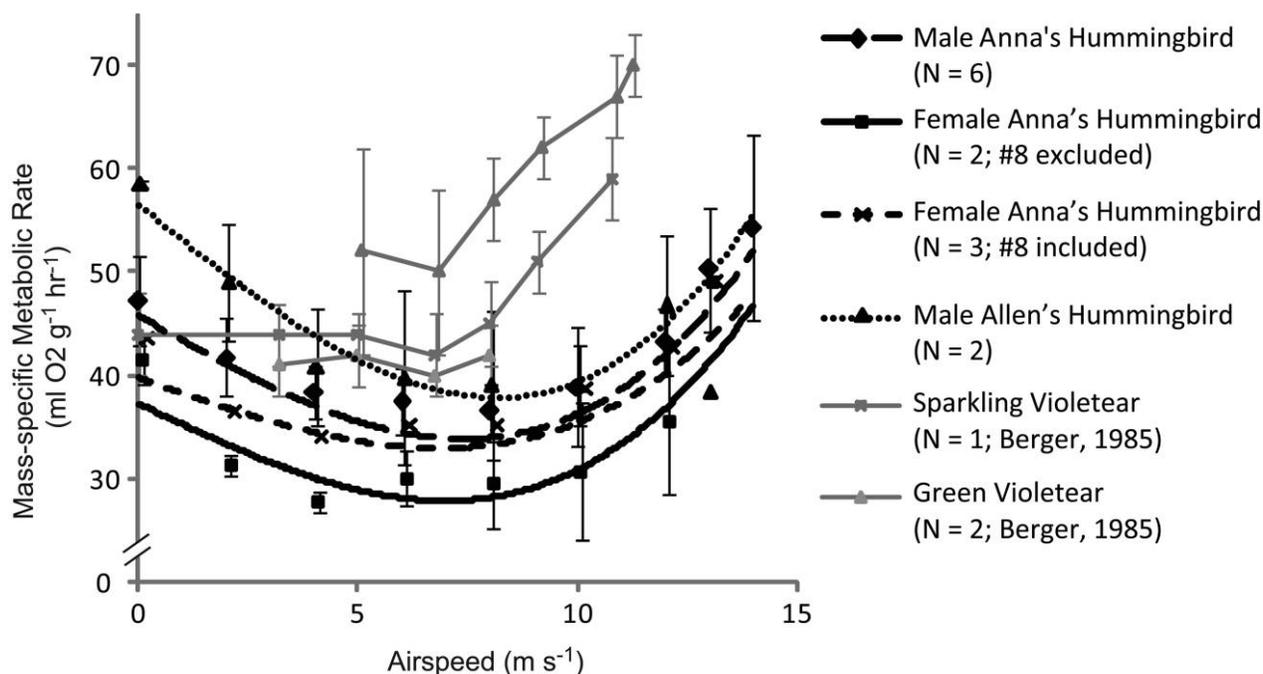


Figure 3. Variation in the metabolic power curve between species-sex categories and between this study and that of Berger (1985). Data from this study are in black. Measurements for a given individual at each speed were averaged; depicted data correspond to averages of different individuals within any given species-sex class. Error bars represent ± 1 SD; for purposes of clarity, they are omitted for the curve of female Anna's hummingbirds that includes individual 8. The curves fitted to the data are the same as those in Figure 1. Data in gray are from Berger (1985) for three individual birds.

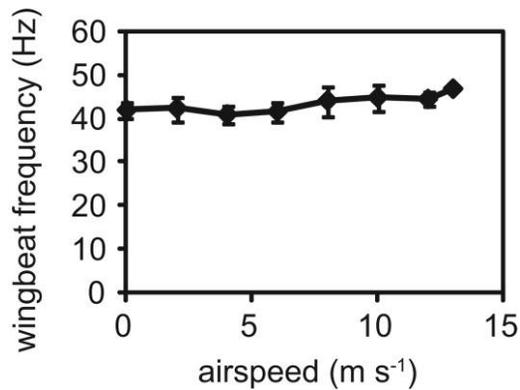


Figure 4. Wingbeat frequency of four male Anna's hummingbirds as a function of flight speed. Bars are ± 1 SD.

The shape of the aerodynamic power curve of flight is determined by the profile and induced powers required to flap the wings and offset body weight and the parasite power necessary to overcome body drag (Pennycuick 1969, 1989; Tucker 1973; Greenewalt 1975; Rayner 1979, 1994, 1999, 2001). Estimating these components of the power curve from the data presented here would be difficult. Muscle efficiency may vary as a function of speed, causing the underlying functional form of the aerodynamic power curve to correspond nonlinearly with the metabolic power curve (Rayner 1999, 2001). Similarly, the statistics of nonlinear functions used to analyze the metabolic data are not straightforward. For example, parasite power is hypothetically proportional to the cube of forward airspeed (i.e., v^3) and could be estimated from β_2 . Quantitative estimates of β_2 , however, are sensitive to the underlying statistical model, as can be seen by the values of β_2 that vary by a factor of approximately 2 between the GLM analyses using either Equation (1) or Equation (2) (see Fig. 1). Metabolic measurements at airspeeds higher than those measured here might improve these statistical estimates, but the value of β_2 would remain cross-correlated with and therefore be contingent on estimates of β_1 , which in turn depends on the assumed statistical model.

As previously mentioned, Equation (1) is clearly inadequate to describe fully the dynamics and energetics of hummingbird flight, as hummingbirds can hover. Similarly, Equation (2) was used here for the pragmatic reason that it generates a fit to all of the empirical data but it does not have a theoretical basis, as induced and profile power are unlikely to scale linearly with v (Rayner 2001). Obtaining statistical estimates in a model with three or more velocity parameters that were not confounded by cross-correlation would require more individuals, denser sampling of the independent variable, and a better understanding of sources of experimental error.

Many studies of flight metabolism using mask respirometry have evaluated only a subset of possible airspeeds for the study taxon, typically from 6–12 m s⁻¹ (e.g., Tucker 1968, 1972; Bernstein et al. 1973; Thomas 1975; Carpenter 1985). For the hummingbirds studied here, metabolic rates varied little for airspeeds between 4 and 10 m s⁻¹ (Figs. 1–3) but they exhibited

clear minima when the full airspeed range of 0–14 m s⁻¹ was considered. Similarly, Bundle et al. (2007) measured metabolic rates of parrots over a wider range of flight speeds (5–15 m s⁻¹) and also obtained energetic minima at intermediate speeds. Clearly, power curves of free-flying animals may vary substantially according to variable morphologies, kinematics, and aerodynamic regime (see Dudley 2000; Tobalske et al. 2003). Results presented here for hummingbirds, in conjunction with measurements of mechanical power output for other birds flying over wide airspeed ranges (e.g., Tobalske et al. 2003; Askew and Ellerby 2007), are nonetheless consistent with a general concave shape of the avian power curve.

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