Maximum Flight Performance of Hummingbirds: Capacities, Constraints, and Trade-Offs

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ABSTRACT: Flight performance trade-offs and functional capacities of ruby-throated hummingbirds (*Archilochus colubris* L.) were studied using an integrative approach. Performance limits were measured by noninvasively challenging birds with two strenuous forms of flight: hovering in low-density gas mixtures (a lift assay for the capacity to generate vertical force) and fast forward flight in a wind tunnel (a thrust assay for the capacity to generate horizontal force). Functional capacities during hovering were measured by simultaneously collecting metabolic data using respirometry and information on wingbeat kinematics for aerodynamic analysis. Intraspecific differences in flight capacity, presumably reflecting diverse selective forces because of sexual dimorphism, migration, and plumage renewal, were then compared. Birds with shorter wings (adult males) or with increased body weight displayed a reduced hovering capacity, although their maximum flight speed was unaffected by such morphological changes. Birds undergoing molt of their flight feathers exhibited a diminished performance during both hovering and forward flight. Hovering capacities in relation to variation in wing morphology and body mass were congruent with aerodynamic predictions, whereas performance capacities in fast forward flight differed from theoretical models. Kinematically, hovering hummingbirds operate within a narrow range of wing-beat frequencies, and modulation of aerodynamic forces and mechanical power is achieved primarily through variation in wing-stroke amplitude. Although differing in hovering performance, both sexes of nonmolt birds demonstrate similar mechanical and metabolic capacities, whereas molting inflicts high energetic costs. Relatively invariant physiological capacities may thus ultimately constrain the extent of intraspecific trade-offs between morphology and performance, providing mechanistic insights into the multilevel functional design of the hummingbird flight system.

Keywords: flight energetics, hummingbirds, morphology, performance, trade-offs.

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Aerodynamic and energetic concerns of flight strongly mold the body design of flying animals, whereas diverse flight and survival concerns ensure that animal fliers encompass multiple trade-offs in morphology and physiology. For example, flight is energetically expensive, and fliers need to carry fuel loads (e.g., fat) to ensure energy security. Yet such increased loads can be deleterious to flight performance and also increase the energetic costs of flight (Ellington 1984*b*; Rayner 1990; Hedenström 1992; Norberg 1995). Furthermore, small endothermic fliers such as hummingbirds run the risk of energy deficits but must also be sufficiently light as to maintain agility in the face of mass-dependent predation risks (Gosler et al. 1995; Kullberg et al. 1996). Hummingbird wing morphology also reflects an aerodynamic trade-off because the two extreme forms of flight along the airspeed spectrum (hovering and fast forward flight) differ substantially in their mechanical power requirements. During hovering and low-speed flight, flapping wings maximize vertical forces (lift) by moving air downward for weight support. Longer and larger wings can enhance lift production, whereas weight loss and concomitantly lower wing loading (body weight relative to wing area) can reduce the cost of lift generation. During fast forward flight, horizontal force (thrust) increases to offset greater drag forces, primarily on the body and secondarily on the wings. A streamlined body, shorter wings, and higher wing loading should decrease wing and body drag and thereby promote faster flight (Pennycuick 1975; Rayner 1988; Norberg 1990).

Force production by the wings in turn necessitates expenditure of mechanical and metabolic power. Mechanical power production during flight derives from the contractile properties of flight musculature. In general, muscle fibers operate at optimal contractile frequencies and shortening velocities in order to maximize power production (Josephson 1993; Rome 1997). These parameters in turn influence the preferred wing-stroke amplitude and wing-beat frequency. Wing-beat kinematics and muscle mechanics are thus tightly linked during strenuous flight, whereas the duration of such extreme performance is often determined by metabolic flux capacities at the level of the

whole organism (Jones and Lindstedt 1993; Suarez 1996). Overlain on such heterogeneous physical and physiological factors constraining performance are the behavioral and ecological contexts of flight. For example, hummingbirds display unusual physiological capacities that presumably facilitate efficient nectar foraging; hummingbirds are the only group of birds that are capable both of prolonged hovering and of fast forward flapping flight (Greenewalt 1960). Because hovering is highly energy demanding, the physiological functions of hummingbirds relating to oxygen and fuel supply as well as to waste removal are all up-regulated to achieve rates of metabolism and muscle power that are among the highest recorded for vertebrates (Suarez 1992; Hochachka 1994; Chai and Dudley 1995).

Species-specific biology adds further repercussions to flight performance. Intraspecific variation in wing morphology and body mass represents inevitable trade-offs because of diverse flight challenges such as courtship, migration, and plumage renewal. These trade-offs likely reduce safety margins of flight performance and impose fitness costs. Many hummingbirds such as the ruby-throated hummingbird (*Archilochus colubris* L.) are sexually dimorphic. The smaller males possess shorter, more pointed wings and display aerially during courtship; parental care and rearing of young are solely the domain of females (Johnsgard 1997). Based on banding data, wild male ruby-throated hummingbirds have reduced survivorship relative to that of females, probably because of differential mortality, with males suffering greater losses than females during the breeding season (Mulvihill et al. 1992). Both sexes of this species conduct long-distance migratory flight across the Gulf of Mexico in the fall (Lasiewski 1962). Fat loads and associated weight gain before initiating migration are striking, with some birds nearly doubling their mass in this process (Norris et al. 1957). Such mass increase may enhance particular ecological hazards, since studies on small passerines suggest that fat loads can increase the risk of predation (Gosler et al. 1995; Metcalfe and Ure 1995; Kullberg et al. 1996; Lilliendahl 1997). Upon reaching their wintering ground in Central America, ruby-throated hummingbirds accomplish a complete molt prior to the return spring migration (Baltosser 1995). With their reduced wing area and suboptimal wing shapes, molting hummingbirds likely experience impaired flight performance while simultaneously being exposed to increased competition and predation in the Tropics. Indeed, molting by birds can impose substantial fitness costs and increase mortality (e.g., Slagsvold and Dale 1996; Svensson and Nilsson 1997; Swaddle and Witter 1997).

We have noninvasively induced maximum hovering performance in individual ruby-throated hummingbirds using normoxic but hypodense mixtures of air and heliox (21% O_2 and 79% He). Oxygen availability is not limiting in such studies, but the density of heliox is only one-third that of normal air (Chai and Dudley 1995; Dudley and Chai 1996). Hovering in low-density air is analogous to increasing treadmill speeds for runners in that hummingbirds must increase their mechanical power output to generate lift force sufficient to stay airborne. Limits to the locomotor capacity of hovering hummingbirds are unequivocally indicated by aerodynamic failure at low air densities (Chai and Dudley 1995). Thus, manipulation of air density assays the maximum capacity of flapping wings to provide weight support, and we term this method the "lift assay." The other treadmill analogue we have employed is horizontal flight in a variable-speed wind tunnel; horizontal thrust force must be maximized if flight is to be sustained. Airspeed manipulation using a wind tunnel can then be termed the "thrust assay."

By challenging hummingbirds with both kinds of strenuous flight, the first objective of this study is to assess intraspecific variation and possible trade-offs in flight performance (table 1). The second objective is to investigate how different functional levels, including wing morphology, wing-beat kinematics, flight muscle contractile mechanics, and whole-body metabolism, are interrelated during maximum hovering performance. Maximum biomechanical and energetic capacities of hummingbirds with shorter wings (adult males), with increased body weight, and with loss of wing area (during molt) are systematically compared with predictions derived from aerodynamic theory (table 1). The primary constraint during hovering is generation of lift force and production of sufficient mechanical power to overcome induced power requirements associated with the downward momentum flux of air. Birds with reduced wing length and wing area or with increased body weight likely exhibit inferior performance in low-density gas mixtures.

On the other hand, the major constraint during fast forward flight is generation of sufficient power to satisfy the requirements associated with overcoming body (parasite) drag and wing (profile) drag. Adult males with shorter, smaller wings and higher wing loadings are predicted to exhibit better speed performance in the wind tunnel. Assuming that the capacity for power production scales isometrically, heavier birds should be comparable in maximum speed performance. However, weight gain may still impair forward flight because of an increased induced power requirement, although this component is small relative to parasite power at high airspeeds (Norberg 1990). Parasite power requirements may also increase because of the additional frictional drag associated with an increased cross-sectional area of the transiently fattened body (Hedenström 1992; Hedenström and Alerstam 1995; Norberg 1995). The maximum speed performance of molting birds is difficult to predict. Such birds have reduced wing area

Table 1: Aerodynamic predictions on maximum flight performance because of variation in wing morphology and body mass

Context of flight	Morphological responses	Maximum flight performance	
		Hovering	Fast forward
Sexual dimorphism	Reduced male wing length for increased flight speed and agility	Decreased	Increased
Migration	Weight gain because of carrying fuel load	Decreased	Decreased
Molt	Loss of wing area because of plumage renewal	Decreased	Increased

Note: Predictions assume physiological equivalence (equal amount of mechanical and metabolic energy available for flight).

and presumably reduced wing drag, possibly enhancing speed performance because of reduced profile power requirements. But molting birds also possess suboptimal wing shapes, possibly interfering with neuromuscular coordination (see Ellington 1984*a*; Chai 1997). Furthermore, molting can inflict multiple energetic costs, including the loss of plumage insulation and an increase in basal metabolism (Walsberg 1983; Lindström et al. 1993; Jenni and Winkler 1994; Murphy 1996).

Energy demands associated with maximum flight activity can be estimated using aerodynamic models, but the maximum rate of energy supply by flight muscles cannot be predicted. In fact, the reserve capacity or safety margin of multiple functional systems of kinematics, mechanics, and metabolism revealed during such maximum performance is a likely target of natural selection (see Arnold 1983; Bennett 1991; Diamond and Hammond 1992; Wainwright 1994). Reserve capacities reflect the overall design of the flight machinery as shaped by both physical laws and natural selection. How much reserve capacity is built into each functional level, and what are the invariant versus malleable elements of design? The goal of this study is thus to explore links between aerodynamics and energetics of hummingbird flight on the one hand, and on the other hand to evaluate potential implications of these factors for maximum performance in different behavioral and ecological contexts.

Material and Methods

Lift Assay

Ruby-throated hummingbirds (*Archilochus colubris* L.) were mist netted in the vicinity of Austin, Texas, and were housed in screen cages (90 cm × 90 cm × 90 cm). Hummingbird care was in accordance with federal and state guidelines; birds were housed two to one cage. Experimental procedures for manipulating air densities have been described previously (Chai and Dudley 1995; Dudley 1995). Flight experiments were implemented within an airtight Plexiglas cube of dimensions equal to those of screen cages used for housing. The bird was trained to hover feed approximately every 20 min through a mask, which allowed for the collection of respiratory gases and the measurement of rates of oxygen consumption (Chai and Dudley 1995). At the same time, wing-beat kinematics were videorecorded (Sony CCD-TR600 at 60 fields s^{-1} with a high-speed shutter of 1/4,000 s). Data were collected initially from birds hover-feeding in unmanipulated sea-level air (density 1.20 kg m^{-3}). Air within the cube was then gradually replaced by filling with normoxic heliox (21% O$_2$ and 79% He, density 0.40 kg m^{-3}). Density reduction associated with replacement of normal air by heliox was monitored acoustically. Prior to each filmed episode of hover-feeding, a tube whistle within the cube was remotely activated, generating an acoustic monotone. Because the resonant frequency of a simple tube increases in heliox, the change in dominant whistle frequency following heliox substitution can be used to derive the air density within the flight chamber (Beranek 1949). As the air became thinner and hovering flight became more strenuous, the bird gradually reduced its hover-feeding duration (see also Chai and Dudley 1995). Heliox filling was terminated after the bird showed aerodynamic failure while hover-feeding in hypodense air. The bird drastically descended to the chamber floor and momentarily lost the ability to fly. Maximum transient hovering performance was taken as the short hover-feeding sequence recorded immediately prior to aerodynamic failure. Wing-beat kinematics (i.e., wing-beat frequency n and stroke amplitude Φ) and morphological parameters of individual birds then were used

to estimate the mechanical power requirements at maximum hovering performance (see Ellington 1984b). Wing-beat frequency was derived from the interaction frequency between wing motions and the filming rate of the video camera (the accuracy of this method was verified through comparision with high-speed video films at 1,000 frames s^{-1}). A time-averaged wing-beat frequency was determined from the last 2 s of a hovering flight in which the bird was continuously feeding through the mask; this period was chosen because the hover-feeding duration prior to aerodynamic failure was very brief. For normal hover-feeding durations (>20 s), the wing-beat frequency at the beginning of a sequence was not noticeably different from that at the end. Stroke amplitude represents the angular extent of wing tip motion in the stroke plane to which wing motions are nominally confined and was derived from video images in which the wings were located at the extreme positions of the wing beat. Mean values of stroke amplitude were determined from three to five separate measurements within each bout of maximal hovering.

Morphological parameters used in aerodynamic calculations included body mass m, wing length R, total wing area S (the area of both wings), wing loading p_w ($=mg/S$, where g is gravitational acceleration), wing disk loading p_d [$=mg/(\Phi R^2)$, where Φ is expressed in radians], and aspect ratio AR ($=4R^2/S$). Kinematic and aerodynamic calculations included mean flapping velocity of wing tips $\overline{U_t}$ ($=2n\Phi R$), mean Reynolds number $\overline{Re}$ (based on the mean wing chord $\bar{c}$ and mean flapping velocity $\overline{U_t}$, assuming simple harmonic motion of the wings), and the mean lift coefficient $\overline{C_L}$ (derived by assuming that vertical force production averaged over the wing-beat period equals the bird's body weight; see Ellington 1984b). The coefficient $\overline{C_L}$ is a dimensionless measure of the lift-generating capacity of a wing. The Re is the ratio of inertial forces to viscous forces in a flow and is directly proportional to air density (Vogel 1994). Mechanical power requirements were estimated by evaluating individual components of body mass–specific profile (P_{pro}^*) and induced (P_{ind}^*) power requirements (the parasite power requirement P_{par}^* is negligible in hovering flight). The variable P_{pro}^* represents energetic expenditure to overcome frictional drag forces on the flapping wings, and P_{ind}^* is the power needed to generate downward momentum to the surrounding air so as to offset the body weight (for ruby-throated hummingbirds, P_{ind}^* is three to four times greater than P_{pro}^*; Chai et al. 1997). Total power expenditure (P_{per}^*) was calculated assuming perfect elastic storage of wing inertial energy, representing the minimum estimate of required mechanical power. Thus, P_{per}^* ($=P_{pro}^* + P_{ind}^*$) is equal to the aerodynamic power requirements (i.e., to the power required to overcome profile and induced drag forces on the wings). Hummingbirds can likely store kinetic energy elastically during the deceleration phase of the wing stroke, so that inertial power requirements are probably negligible (see Greenewalt 1975; Ellington 1984b; Wells 1993). Whole-bird mechanical power output (P_{OUT}) is given by the product of body mass and the calculated mass-specific mechanical power requirement (P_{per}^*).

Whole-bird metabolic power input (P_{IN}) was derived from rates of oxygen consumption ($\dot{V}o_2$). As hovering became more strenuous because of the reduction in air density, birds gradually reduced their feeding duration. Near maximum hovering, oxygen consumption rates at aerodynamic failure could not be reliably obtained given the short duration of hover-feeding. Instead, measurements were taken from hover-feeding bouts greater than 5 s in duration but at air densities slightly higher than the values at which birds failed aerodynamically. Flight efficiency was then taken as the ratio of mechanical power output to metabolic power input for the same hover-feeding sequence (i.e., P_{OUT}/P_{IN}). Furthermore, reserve capacities of wing-beat frequency, stroke amplitude, wing flapping velocity, lift capacity of the wings, mechanical power output, and rates of oxygen consumption were expressed as the percentage increase in these parameters relative to values obtained for hovering in unmanipulated sea-level air.

ANCOVA was conducted on kinematic, aerodynamic, mechanical, and metabolic variables derived from maximum hovering performance in hypodense gas mixtures. ANCOVA was also used to assess effects of body mass and bird group. Four bird groups were identified given gender and plumage differences: molting birds, nonmolt females, juvenile males (with wing lengths between those of females and adult males), and adult males. Least-squares means adjusted for the covariate effect of body mass as well as for unbalanced sample sizes were calculated to indicate the expected mean and estimated standard error for each bird group (SAS PROC GLM, SAS Institute 1989). Least-squares means (i.e., population marginal means) are the expected value of bird group means in a balanced design involving bird groups with the body mass covariate set at its mean value (Milliken and Johnson 1992).

Thrust Assay

Maximum transient flight speeds were measured in a wind tunnel (Aerovent, Piqua, Ohio). The Plexiglas test section was square in cross section and of dimensions equal to 61 cm × 30 cm × 30 cm (by comparison, the wing length of ruby-throated hummingbirds ranges from 4 to 5 cm). Ends of the test section were covered by thin mesh screen with a perforation diameter of 12.7 mm. Wind speed was monitored with an anemometer (VelociCalc Plus 8360, TSI, St. Paul, Minn.), itself calibrated using a Pitot probe (see Vogel 1994). Temporal and spatial variations in wind

Table 2: Statistical results of ANOVA assessing effect of bird group on morphological parameters

Variable	P value (F-test)	Group 1: females ($n = 11$)	Group 2: juvenile males ($n = 5$)	Group 3: adult males ($n = 9$)	Group 4: molting birds ($n = 9$)	Pairwise comparisons (t-test)
m (g)	$<.001^{***}$	$4.0 \pm .1$	$3.9 \pm .2$	$3.6 \pm .1$	$3.2 \pm .1$	12, 23
R (mm)	$<.001^{***}$	48 ± 1	45 ± 1	42 ± 1	46 ± 1	24
S (cm²)	$<.001^{***}$	$12.0 \pm .3$	$10.4 \pm .4$	$9.4 \pm .3$	$8.7 \pm .3$	34
AR	$<.001^{***}$	$7.8 \pm .3$	$7.7 \pm .3$	$7.4 \pm .2$	$9.9 \pm .2$	123
p_w (N m⁻²)	$.039^{*}$	33 ± 1	37 ± 2	38 ± 1	36 ± 1	12, 14, 234
p_d (N m⁻²)	$<.001^{***}$	$5.5 \pm .2$	$6.2 \pm .3$	$6.9 \pm .3$	$4.8 \pm .3$	12, 14, 23

Note: Least squares means (means $\pm$ SE) in groups 1–4 adjusted for unbalanced sample size are used to show the mean and estimated standard error for each bird group. Results of pairwise comparisons of least-squares means between groups (H_0: least squares means $[i]$ = least squares means $[j]$) are indicated (groups that are not significantly different from each other are listed together). Molting birds include five females, three juvenile males, and one male. Molting birds on average possessed 78% $\pm$ 8% of nonmolt wing area. Their wing length did not change because two to three old outer primaries still remained: m, body mass; R, wing length; S, wing area; AR, aspect ratio; p_w, wing loading; p_d, wing disk loading.

* $P < .05$.

*** $P < .001$.

speed averaged 4% of the set value. Each experimental bird was first trained for several days to fly in the tunnel over a range of airspeeds. At the beginning of each experimental trial, each bird was flown for at least 30 s, first at 8 m s⁻¹ and then at 10 m s⁻¹. After the bird rested on a perch for 20 min, the tunnel speed was set at 11 m s⁻¹ and the bird was stimulated to fly. The tunnel wind speed was then gradually increased by approximately 1 m s⁻¹ every 5 s until the flying bird could no longer hold its position at the front end of the test section and slowly drifted to the rear of the test section. Wind speed in the tunnel was then measured with the anemometer and assumed to represent the maximum airspeed during flight. After a 20-min break, a second test was repeated commencing at 11 m s⁻¹, and each bird's maximum flight speed was taken as the average of the two maximum measurements.

Birds were measured at four stages: premolt, peak molt, 1 wk postmolt, and 2 wk postmolt. Premolt birds were studied 1–3 wk before molt. Postmolt birds increased body mass shortly after finishing the molt. After measurement of maximum flight speed (1 wk postmolt), postmolt birds were forced to lose weight through curtailment of their artificial diet for 1 wk (previously the birds were maintained with food ad lib.; see Chai and Dudley 1996). Maximum flight speed was then measured for each individual (2 wk postmolt). In the statistical analysis of maximum flight speed, repeated-measures ANOVA was used to model gender factor as between-subject source of variation and four molting stages (with weight differences) as a within-subject source of variation (SAS PROC GLM, SAS Institute 1989). If the repeated-measures effect of the stages was found to be significant, then contrast transformation was used to compare each molting stage against the others.

Sample size was small because only five birds (three males and two females) out of a total of eight were measured at each stage of the pre- and postmolt sequence.

Results

Lift Assay

We conducted a total of 34 density reduction experiments on 18 individual hummingbirds with varying body mass and wing condition. Each individual bird received one to three density reduction trials either with unimpaired wings (premolt and postmolt) or during the annual molt (measured during peak molt of flight feathers in the spring). The highly dissimilar plumage during molt justifies treating performance capacity measured from each density reduction trial as an independent observation (i.e., $n = 34$). Adult males had the shortest and smallest wings; wing loading and wing disk loading were correspondingly higher than those of juvenile males and females (table 2). Juvenile plumage became identical to that of the adults after the first molt (the wing morphology of juvenile and adult females is indistinguishable). Nonmolting birds were thus divided into three groups (table 2). Wing morphological parameters of juvenile males were intermediate to those of females and adult males. Molting birds still possessed two to three outer primaries (and thus exhibited constant wing length) but, on average, retained only 78% $\pm$ 8% ($\overline{X} \pm 1$ SD) of nonmolt wing area (see Chai 1997).

Maximum hovering performance in low-density gas mixtures was transient and only lasted 2–4 s, whereas an episode of normal hover-feeding in sea-level air generally lasted more than 20 s (table 3). The capacity to hover in hypodense air varied inversely with body mass, with heav-

Table 3: Results of ANCOVA assessing effects of body mass and bird group on kinematic, aerodynamic, and mechanical parameters relating to maximum hovering performance in hypodense air (see text for explanation of parameters)

Variable	P value (F-test) Bird group	P value (F-test) Body mass	Group 1: females ($n = 11$)			Group 2: juvenile males ($n = 5$)			Group 3: adult males ($n = 9$)			Group 4: molting birds ($n = 9$)			Pairwise comparisons (t-test)
ρ_{fail} (kg m^{-3})	$<.001^{***}(+)$	$<.001^{***}$	.50	±	.02	.59	±	.03	.68	±	.02	.79	±	.02	...
t (s)	.868	.479	2.4	±	.5	3.4	±	.7	3.4	±	.5	3.2	±	.6	1234
t (value in normal air)	$.015^{*}(-)$	.389	24.5	±	2.3	25.8	±	3.1	21.5	±	2.2	18.6	±	2.8	1234
n (Hz)	.711	$<.001^{***}$	47	±	1	53	±	1	59	±	1	49	±	1	14
n reserve (%)	.271	.689	6	±	1	4	±	2	4	±	1	6	±	2	1234
Φ (degrees)	.342	.155	177	±	1	178	±	2	174	±	1	172	±	2	1234
Φ reserve (%)	$.010^{*}(-)$	$.016^{*}$	25	±	3	20	±	4	15	±	3	10	±	3	12, 23, 34
$\overline{U}_t$ (m s^{-1})	.199	$.003^{**}$	13.9	±	.2	14.6	±	.3	14.8	±	.2	13.9	±	.2	14, 23
$\overline{U}_t$ reserve (%)	$<.001^{***}(-)$	$.001^{**}$	32	±	2	24	±	3	20	±	2	17	±	3	234
$\overline{Re}$	$<.001^{***}(+)$	$<.001^{***}$	4,000	±	150	4,800	±	200	5,600	±	150	5,400	±	200	34
$\overline{C}_L$	.055	$<.001^{***}$	2.0	±	.1	1.8	±	.1	1.7	±	.1	1.5	±	.1	23
$\overline{C}_L$ reserve (%)	.644	$.002^{**}$	33	±	3	31	±	5	23	±	3	8	±	4	12, 23
P^{*}_{per} (W kg^{-1})	.457	$<.001^{***}$	32.2	±	.5	32.6	±	.6	32.5	±	.5	28.9	±	.6	123
P^{*}_{per} reserve (%)	$<.001^{***}(-)$	$<.001^{***}$	38	±	2	31	±	2	25	±	2	18	±	2	...
$\dot{V}o_2$ (mL O$_2$ g^{-1} h^{-1})	$.009^{**}(-)$	$.003^{**}$	53.2	±	1.7	56.1	±	2.3	56.0	±	1.7	65.3	±	2.1	123
$\dot{V}o_2$ reserve (%)	.264	.997	24	±	4	24	±	5	23	±	3	23	±	4	1234
P_{IN} (W)	$.003^{**}(+)$	$.013^{*}$	1.13	±	.04	1.21	±	.05	1.20	±	.04	1.36	±	.05	123
P_{OUT} (W)	$<.001^{***}(+)$	$.002^{**}$	.118	±	.002	.120	±	.002	.119	±	.002	.107	±	.002	123
P_{OUT}/P_{IN} (%)	$.031^{*}(+)$	$<.001^{***}$	9.5	±	.3	9.5	±	.3	9.6	±	.3	7.3	±	.3	123
P_{OUT}/P_{IN} (value in normal air)	$<.001^{***}(+)$	$.001^{**}$	9.3	±	.2	9.4	±	.3	9.8	±	.2	8.1	±	.3	123

Note Least-squares means (means ± SE) for groups 1–4 adjusted for the covariate effect of body mass as well as unbalanced sample size are used to show the mean and estimated standard error at maximum performance for each bird group. Results of pairwise comparisons of least-squares means between groups (H$_0$: LSM[i] = LSM[j]) are indicated (groups that are not significantly different from each other are listed together). All values are at maximum hovering performance: ρ_{fail}, air density at aerodynamic failure; t, hover-feeding duration; n, wing-beat frequency; n reserve, percentage increase of n at maximum performance relative to that in normal, unmanipulated air prior to filling with heliox; Φ, stroke amplitude; Φ reserve, percentage increase of Φ at maximum performance; $\overline{U}_t$, mean wing-tip velocity; $\overline{U}_t$ reserve, percentage increase of $\overline{U}_t$ at maximum performance; $\overline{Re}$, mean Reynolds number; $\overline{C}_L$, mean lift coefficient; $\overline{C}_L$ reserve, percentage increase of $\overline{C}_L$ at maximum performance; P^{*}_{per}, body mass–specific mechanical power output assuming perfect elastic energy storage (=aerodynamic power output); P^{*}_{per} reserve, percentage increase of P^{*}_{per} at maximum performance; $\dot{V}o_2$, body mass–specific rate of oxygen comsumption; $\dot{V}o_2$ reserve, percentage increase of $\dot{V}o_2$ close to aerodynamic failure; P_{IN}, whole-bird metabolic power input derived from $\dot{V}o_2$; P_{OUT}, whole-bird mechanical power output derived from P^{*}_{per}; and P_{OUT}/P_{IN}, overall flight efficiency. The symbols + and − indicate positive or negative correlation with body mass when P value is statistically significant.

* $P < .05$.
** $P < .01$.
*** $P < .001$.

ier birds displaying aerodynamic failure at higher air densities (fig. 1). Weight effects were however confounded by variation in wing morphology. For nonmolt birds, adult males were the least capable of hovering, whereas females were most capable. Molting birds with reduced wing area also lost weight, yielding values of wing loading similar to those of nonmolt birds (table 2). Despite such presumably adaptive weight loss, molting birds still failed at higher air densities relative to nonmolt birds (fig. 1).

Hovering birds met the challenge of low-density air by modulating wing-beat kinematics. However, wing-beat frequency varied by only 4%–6%, and modulation of wing-stroke amplitude was a more important means of generating requisite mechanical power. Maximum power was attained at a stroke amplitude near 180° (table 3). Wing length and wing-beat frequency were inversely correlated, and adult males actually achieved slightly higher flapping velocities at the wing tip (U_t) than the females. Nonetheless, males showed inferior lift performance from the wings (lower $\overline{C_L}$) and failed at higher air densities, yielding higher $\overline{Re}$. Molting birds showed the least capacity for lift generation (table 3).

Despite variable hovering capacity in hypodense gas mixtures among bird groups (fig. 1), mass-specific mechanical power outputs (P^*_{per}) of nonmolt bird groups were actually similar (table 3). On average, P^*_{ind} was more than three times greater than P^*_{pro} ($=P^*_{per} - P^*_{ind}$; see fig. 2). Neither P^*_{ind} or P^*_{per} varied with body mass. Mass-invariant P^*_{per} indicates mass dependence of P_{OUT}, with the absolute value of mechanical power output increasing linearly with body mass (cf. P^*_{per} and P_{OUT}; fig. 2 and table 3). No statistical differences in power output were found among nonmolt bird groups, and the molting bird group was again the least capable of producing useful mechanical power (table 3). Relative to hovering in normal air, heavier birds at maximum performance exhibited proportionally less power reserve (table 3). Male birds also suffered from a reduced power reserve, while females showed the highest margin for excess power. Molting birds during hovering also showed the least power reserve (table 3).

Maximum rates of oxygen consumption also indicated a significant weight effect. Both metabolic power input and mechanical power output increased with body mass (cf. P_{IN} and P_{OUT}; table 3). No statistical differences existed
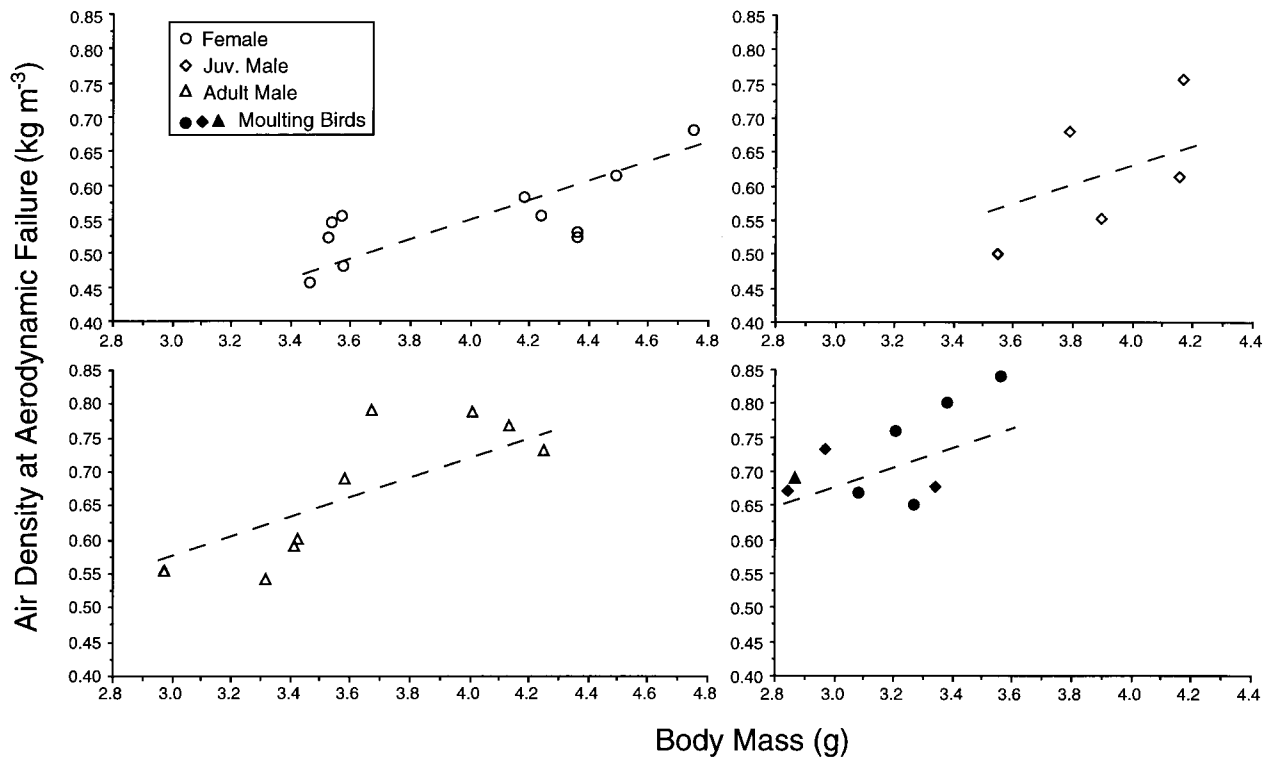

Figure 1: Air density at aerodynamic failure in low-density gas mixtures (density of sea-level air $= 1.20 \text{ kg m}^{-3}$) by individual hummingbirds in relation to body mass and bird group. Measurements on molting birds were taken at the peak of their wing molt when the bird had lost most of its primary flight feathers and was flying with the smallest wing area and presumably the lowest lift-generating capacity. Fitted lines come from ANCOVA results modeling effects of body mass and bird group.
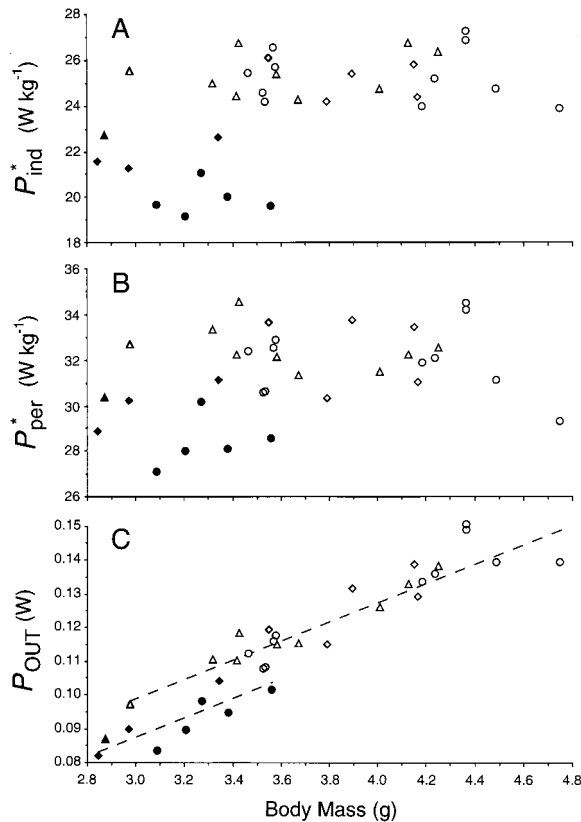
Figure 2: Estimated maximum body mass–specific induced power (A, P_{ind}^*), body mass–specific power (B, P_{per}^*), and whole-bird power (C, $P_{OUT} = P_{per} \times$ body mass) of individual hummingbirds in relation to body mass and bird group (symbols as in fig. 1). Fitted lines in C derive from ANCOVA results modeling effects of body mass and bird group. Fitted lines for nonmolt birds are graphically close and are thus combined.

among nonmolt bird groups in metabolic expenditure, whereas molting birds showed a significant increase in metabolism ($\dot{V}_{O_2}$ and P_{IN}; table 3). Reserve capacity in mechanical power output (P_{per}^* reserve) varied significantly among bird groups, yet metabolic reserve capacities ($\dot{V}_{O_2}$ reserve) were similar (table 3). Increased mechanical power requirements because of weight gain were accompanied by an increased rate of oxygen consumption, but this increase was not commensurate with the rise in mechanical power. Overall flight efficiency (P_{OUT}/P_{IN}) also improved with weight gain (table 3). During strenuous hovering performance, molting birds were the least capable of generating mechanical power and also displayed the highest metabolic costs, thereby yielding the lowest flight efficiency. Flight efficiency did not significantly vary among nonmolt birds.

Thrust Assay

Maximum flight speeds averaged 14.4 ± 0.3 m s^{-1} ($\overline{X} \pm$ 1 SE) and were independent of body mass (fig. 3). Gender effects were nonsignificant ($P = .072$), although males generally flew faster. The small sample size of five birds with the complete measurements necessary for repeated-measures ANOVA precludes a more definite conclusion. Molting birds displayed reduced maximum flight speeds and averaged 12.4 ± 0.2 m s^{-1} ($P < .001$). Further pairwise comparisons using statistical contrast indicate that flight speeds at the two postmolt points were significantly different from those at premolt and molt points. The highest maximum flight speed was attained by postmolt birds, whose plumage was least affected by wear.

Discussion

The expression of flight requires generation of two orthogonal forces: lift and thrust. By noninvasively challenging ruby-throated hummingbirds with two strenuous but biomechanically distinct assays of performance (fast forward flight and hovering in hypodense gas), this study identified different limits relating to production of lift and thrust forces. Congruent with aerodynamic predictions, hummingbirds with shorter wings (adult males), with increased body weight, and with loss of wing area (during molt) exhibited inferior hovering capacities (cf. fig. 1 and table 1). In contrast, performance limits of fast forward flight did not follow theoretical predictions: heavier birds demonstrated equivalent maximum flight speeds, whereas molting birds showed the slowest speed (cf. fig. 3 and table 1). Aerodynamic predictions were based exclusively on parameters of wing and body morphology, whereas hummingbirds of different sexes and molt stages may also have differed physiologically and behaviorally. Predictions based on the energetic costs of flight may also be unsatisfactory because reserve capacities of energy supply from the flight muscles are largely unknown. To evaluate the extent of such reserves, however, we examined wing-beat kinematics and muscle mechanical and metabolic capacities either at or near maximum hovering performance.

Hovering in variable-density gas mixtures requires alteration of wing-beat kinematics to attain the requisite aerodynamic force balance and associated mechanical power output. Wing-beat kinematics likely reflect constraints in flight muscle mechanics for optimal contraction frequency and strain amplitude. Constraints on the rate of muscle contraction are particularly implicated by the limited range of values for wing-beat frequency, with the frequency reserve averaging only 5%. Also, a strong inverse correlation exists between wing length and wing-beat frequency (table 3). Such variation in wing-beat frequency
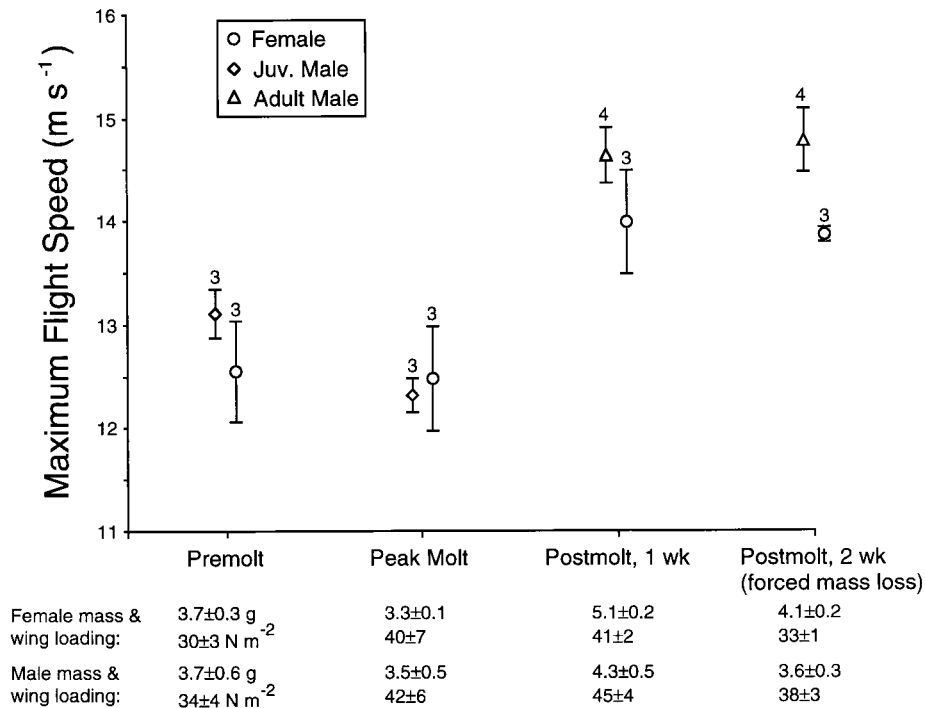
Figure 3: Maximum flight speeds ($\overline{X} \pm 1$ SE) measured in the wind tunnel by bird group under different body mass and wing condition. Juvenile males attained adult male plumage after the molt. Number of individual birds tested are indicated (out of a total of eight birds). Birds at 2 wk postmolt (2 wk after the completion of wing molt) were forced to lose mass through acute food deprivation for a week (previously the birds were fed ad lib.).

(remaining relatively constant within individuals and being inversely related to wing length among individuals) is typical of hummingbirds (Greenewalt 1962) as well as of other flying birds (Pennycuick 1996). This result suggests that the flight muscles of hummingbirds probably work at a particular resonant frequency that optimizes mechanical power output of wing flapping (Greenewalt 1975). The existence of elastic energy storage in such a resonant system should also be favored because the mechanical power expenditure in absence of such storage of wing inertial energy is more than doubled (Wells 1993; Chai and Dudley 1995).

Modulation of wing-stroke amplitude is the primary means of varying mechanical power during hovering, with maximum power output attained near a geometrical limit of 180°. Stroke amplitude in normal air thus serves as a useful index for reserve hovering capacity because changes in wing-beat amplitude are the primary means for ruby-throated and other hummingbirds to modulate mechanical power output and force production (Chai and Dudley 1995; Chai and Millard 1997; Chai et al. 1997). Such reserve capacity is also necessary for carrying supplemental loads (e.g., nectar, fat, and eggs). Furthermore, an inverse relationship exists between magnitude and duration of me-

chanical power production, indicating limits to the aerobic capacity for sustainable performance (Josephson 1993; Chai and Dudley 1995). The duration of maximum hovering performance is correspondingly brief.

Data are not presently available to assess the potential roles of wing-beat frequency and stroke amplitude in constraining performance during maximum fast forward flight. The flight muscles of hummingbirds are unusual in that the ratio of the mass of the main downstroke muscle (the pectoralis major) to that of the main upstroke muscle (the supracoracoideus) is roughly $2:1$, as compared to approximately $10:1$ in other birds (Hartman 1961; Greenewalt 1962). High-speed videography reveals that wing motions are highly symmetrical during hovering. The down- and upstrokes are thus probably equivalent aerodynamically, and both the pectoralis major and the supracoracoideus likely contribute equally to power production. If these two muscles are also mechanically and physiologically equivalent, the $2:1$ ratio of the corresponding muscle masses suggest a supplemental component of the pectoralis major that may be used only in forward flight or during maneuvers (see also Greenewalt 1960). Maximum mechanical and metabolic power output

may thus differ in fast forward flight relative to hovering in hypodense gas media.

Air densities at aerodynamic failure were significantly different among the four bird groups. Of the nonmolt bird groups, females with the longest wings and lowest wing loadings were the most capable of hovering, whereas adult males with the shortest wings and highest wing loadings were the least capable (table 2). However, these data were derived from captive hummingbirds with food provided ad lib. during captivity. Indeed, body masses of our study birds were higher than those of wild ruby-throated hummingbirds (e.g., wild-caught males in September: 3.3 ± 0.2 g [$\overline{X} \pm 1$ SD]; males of this study: 3.6 ± 0.4 g; wild-caught females: 3.5 ± 0.4 g; females of this study: 4.0 ± 0.5 g; see Robinson et al. 1996). Furthermore, if our adult males had not substantially gained weight in captivity, their hovering capacity would likely have been higher. Presumably to improve aerial display and territorial defense, wild ruby-throated males showed a reduced body mass during the June breeding season (2.8 ± 0.3 g relative to 3.4 ± 0.3 g in females). However, males with fewer energy reserves may experience more stress than females, a factor that has been suggested to cause greater male mortality during breeding (Mulvihill et al. 1992). Despite the differences in hovering performance, maximum generation of mechanical power by the two sexes was approximately equivalent (i.e., similar P^*_{per} and P_{OUT}; table 3). The major component of P^*_{per} is P^*_{ind} (fig. 2), which varies in approximate proportion to the square root of wing disk loading (see Ellington 1984*b*). Energetic costs of hovering are thus highest in adult males, and this group displayed the lowest mechanical power reserve (P^*_{per} reserve) among nonmolt birds.

The reserve of mechanical power during hovering varied between sexes, with females displaying the highest reserve capacity (table 3). Females were most effective in generating lift force in low-density gas mixtures (highest $\overline{C}_L$ and $\overline{C}_L$ reserve) but incurred metabolic costs similar to other bird groups ($\dot{V}o_2$ and P_{IN}, table 3). In spite of dissimilar hovering capacities, maximum values of mechanical power output and metabolic power input by the two sexes were surprisingly similar. In contrast to variable mechanical power reserves, the reserve capacity of the metabolic machinery ($\dot{V}o_2$ reserve) was invariant among bird groups, implying a similar underlying constraint in metabolic flux capacity. Given equivalent muscle mechanical and metabolic potential, the reduced hovering performance by males probably reflects a trade-off in wing morphology for increased speed and agility.

Probably because of a lack of statistical power due to the small number of birds tested in the wind tunnel, gender differences in maximum flight speed were not statistically significant (fig. 3). Contrary to the expectation that heavier birds should display reduced maximum flight speeds (Hedenström 1992), study birds with substantially different body masses showed almost identical top flight speeds. Weight gain is associated with reduced hovering performance but not with decreased performance in fast forward flight. An aerodynamic explanation for this effect is currently unavailable, primarily because of a lack of empirical measurements of relevant mechanical variables. Body lift and drag are particularly difficult measurements to obtain reliably for birds (see Pennycuick et al. 1996). If extra lift force is generated by the body during fast forward flight, the already low induced power requirements may be further reduced.

The maximal horizontal flight speed (14.4 m s^{-1}) of ruby-throated hummingbirds in the wind tunnel was impressively high. However, this level of performance was not sustainable and may not be comparable with the few published data on hummingbird flight speeds. The top speed for a female ruby-throated hummingbird in an outdoor wind tunnel was 12.1 m s^{-1}, although the duration of flight at this speed is unknown (Greenewalt 1960). Maximum flight speeds of wild hummingbirds of other species generally fall between 10 and 12 m s^{-1} (e.g., Pearson 1961; Gill 1985). Despite their small size, the speeds of ruby-throated hummingbirds are comparable to speeds of much larger birds studied in wind tunnels, such as the crow *Corvus ossifragus* (Bernstein et al. 1973), the magpie *Pica pica* (Tobalske and Dial 1996), the gull *Larus atricilla* (Tucker 1972), and the budgerigar *Melopsittacus undulatus* (Tucker 1968). The distinctive wing morphology and wingbeat kinematics of hummingbirds relative to all other birds clearly deserve further biomechanical attention, particularly in light of the extensive morphological variation evident among the >300 extant hummingbird species.

Despite wing loadings similar to those of nonmolt birds, molting birds exhibited the lowest capacities for hovering and for fast forward flight. Furthermore, molting birds generated less mechanical power at higher metabolic cost relative to nonmolt hummingbirds. Molting birds thus displayed the lowest flight efficiency among the four bird groups (table 3). Molt involves complex morphophysiological changes (see the introduction), and high metabolic costs of hovering for molting birds may be attributed to multiple causes. Molting and associated reduction in flight performance is however only transient. Since this study examined birds at their peak molt, when wing area was at its minimum, biomechanical parameters described for this condition likely reflect the worst possible performance in this species.

Locomotor characteristics underpin an animal's ecology and behavior and also reflect the design and matching of complex morphological structures with physiological functions. Through intraspecific comparisons on humming-

birds with shorter wings (adult males), with increased body weight, and with wing area reduction (during molt), this study measured performance limits and trade-offs that presumably reflect diverse, often conflicting selective forces because of breeding behavior, migration, and feather renewal. The integrated responses of multilevel functional features such as wing morphology, flight kinematics, muscle mechanics, and metabolic scope define the range of flight activities that a hummingbird enjoys. This study has delineated maximum and reserve capacities of such functional systems during hovering and (partially) for forward flight in ruby-throated hummingbirds.

Comparative exercise physiology often focuses on the study of maximum capacities and limiting traits in order to reach mechanistic understanding of physiological performance (Taylor and Weibel 1981). This study used such an approach to analyze constraints and characteristics in the hummingbird locomotor design. Important findings include versatile flight capacities correlated with variation in wing morphology and body mass, fixed wing-beat frequencies but flexible stroke amplitudes, an inverse relationship between magnitude and duration of available mechanical power, similar muscle mechanical and metabolic capacities among nonmolt bird groups, low flight efficiencies (<10%), and high energetic costs associated with molting.

One fundamental question in evolutionary physiology concerns the relationship between functional reserve capacities and natural loads (Diamond 1998). Ruby-throated hummingbirds demonstrate highly up-regulated but also variable hovering capacities. Which functional components are invariant and which are more variable with respect to differing demands (i.e., lower air density, increased body mass, and reduced wing area) on the flight system? Reduced variation in functional performance presumably reflects design constraints, whereas substantial excess capacity illustrates adaptive flexibility. For the flight system of ruby-throated hummingbirds, reserve capacities in stroke amplitude (10%–25% maximum increase relative to hovering flight) exceeded those of wing-beat frequency (4%–6% maximum increase). Similarly, the reserve in mechanical power output (P_{per}^* reserve of 18%–38%) exceeded the potential scope for increasing rates of oxygen consumption ($\dot{V}O_2$ reserve of 23%–24%; table 3). Reserves in mechanical power varied with body mass and additionally differed among experimental groups, whereas reserve capacity in the rate of oxygen consumption was invariant. Species-specific physiological constraints in generating the metabolic energy needed for flight may thus ultimately determine the extent of intraspecific performance trade-offs. For example, the ratio of adult male to adult female wing length averages 0.87 in ruby-throated hummingbirds and is near the lower extreme for all hummingbird species

(Payne 1984). The highest mass-specific rates of oxygen consumption measured in vertebrates are found in hovering hummingbirds, a taxon that may demonstrate upper limits to the vertebrate locomotor capacity (Suarez et al. 1997). The extent of $\dot{V}O_2$ reserves in ruby-throated hummingbirds is accordingly of substantial evolutionary as well as physiological interest.

Flight characteristics of an individual hummingbird are manifested through its behavior and ecology, organismal features that more directly influence fitness (e.g., Garland and Losos 1994). Differences in hummingbird flight performance suggested by variation in wing form and body mass can directly affect strategies of intraspecific competition in the field (e.g., breeding: Calder et al. 1990; Mulvihill et al. 1992; foraging: Kodric-Brown and Brown 1978; Carpenter et al. 1993a, 1993b; migration: Carpenter et al. 1983). For example, male hummingbirds with shorter and smaller wings are more aggressive and exhibit better territory-holding abilities, presumably reducing energetic efficiency of flight but enhancing aerial display and combat abilities (see Norberg 1990). However, in addition to flight-related morphological traits, hummingbirds in the aforementioned field studies also differed in sex and age, with correlated differences in coloration, experience, and hormonal state. Future field studies should link flight-related biomechanical and physiological capacities with behavioral and ecological traits (foraging, reproductive, and antipredatory behaviors) to gain an integrative understanding of phenotypic contributions to fitness (i.e., to understand both limiting traits and optimal behavior; Sih and Gleeson 1995). Our approach of measuring maximum and reserve capacities in flight-related performance should be even more fruitful for interspecific comparisons evaluating design constraints and adaptive trade-offs in hummingbird biology.

Literature Cited

Arnold, S. J. 1983. Morphology, performance and fitness. American Zoologist 23:347–361.

Baltosser, W. H. 1995. Annual molt in ruby-throated and black-chinned hummingbirds. Condor 97:484–491.

Bennett, A. F. 1991. The evolution of activity capacity. Journal of Experimental Biology 160:1–23.

Beranek, L. L. 1949. Acoustic measurements. Wiley, New York.

Bernstein, M. H., S. P. Thomas, and K. Schmidt-Nielsen. 1973. Power input during flight of the fish crow, *Corvus ossifragus.* Journal of Experimental Biology 58:401–410.

Calder, W. A., L. L. Calder, and T. D. Frazier. 1990. The hummingbird's restraint: a natural model for weight control. Experientia (Basel) 46:999–1002.

Carpenter, F. L., D. C. Paton, and M. A. Hixon. 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. Proceedings of the National Academy of Sciences of the USA 94:7065–7069.

Carpenter, F. L., M. A. Hixon, C. A. Beuchat, R. W. Russell, and D. C. Paton. 1993a. Biphasic mass gain in migrant hummingbirds: body composition changes, torpor, and ecological significance. Ecology 74:1173–1182.

Carpenter, F. L., M. A. Hixon, E. J. Temeles, R. W. Russell, and D. C. Paton. 1993b. Exploitative compensation by subordinate age-sex classes of migrant rufous hummingbirds. Behavioral Ecology and Sociobiology 33: 305–312.

Chai, P. 1997. Hummingbird hovering energetics during moult of primary flight feathers. Journal of Experimental Biology 200:1527–1536.

Chai, P., and R. Dudley. 1995. Limits to vertebrate locomotor energetics suggested by hummingbirds hovering in heliox. Nature (London) 377:722–725.

———. 1996. Limits to flight energetics of hummingbirds hovering in hypodense and hypoxic gas mixtures. Journal of Experimental Biology 199:2285–2295.

Chai, P., and D. Millard. 1997. Flight and size constraints: hovering performance of large hummingbirds under maximal loading. Journal of Experimental Biology 200: 2757–2763.

Chai, P., J. S. C. Chen, and R. Dudley 1997. Transient hovering performance of hummingbirds under conditions of maximal loading. Journal of Experimental Biology 200:921–929.

Diamond, J. M. 1998. Evolution of biological safety factors: a cost/benefit analysis. Pages 21–27 in E. R. Weibel, C. R. Taylor, and L. Bolis, eds. Principles of animal design: the optimization and symmorphosis debate. Cambridge University Press, Cambridge.

Diamond, J. M., and K. A. Hammond. 1992. The matches, achieved by natural selection, between biological capacities and their natural loads. Experientia (Basel) 48: 551–557.

Dudley, R. 1995. Extraordinary flight performance of orchid bees (Apidae: Euglossini) hovering in heliox (80% He/20% O_2). Journal of Experimental Biology 198: 1065–1070.

Dudley, R., and P. Chai. 1996. Animal flight mechanics in physically variable gas mixtures. Journal of Experimental Biology 199:1881–1885.

Ellington, C. P. 1984a. The aerodynamics of hovering insect flight. II. Morphological parameters. Philosophical Transactions of the Royal Society of London B, Biological Sciences 305:17–40.

———. 1984b. The aerodynamics of hovering insect flight. VI. Lift and power requirements. Philosophical Transactions of the Royal Society of London B, Biological Sciences 305:145–181.

Garland, T., Jr., and J. B. Losos. 1994. Ecological morphology of locomotor performance in squamate reptiles. Pages 240–302 in P. C. Wainwright and S. M. Reilly, eds. Ecological morphology, integrative organismal biology. University of Chicago Press, Chicago.

Gill, F. B. 1985. Hummingbird flight speeds. Auk 102: 97–101.

Gosler, A. G., J. J. D. Greenwood, and C. Perrins. 1995. Predation risk and the cost of being fat. Nature (London) 377:621–623.

Greenewalt, C. H. 1960. Hummingbirds. Doubleday, New York.

———. 1962. Dimensional relationships for flying animals. Smithsonian Miscellaneous Collections 144:1–46.

———. 1975. The flight of birds. Transactions of the American Philosophical Society 65:1–67.

Hartman, F. A. 1961. Locomotor mechanisms of birds. Smithsonian Miscellaneous Collections 143:1–91.

Hedenström, A. 1992. Flight performance in relation to fuel load in birds. Journal of Theoretical Biology 158: 535–537.

Hedenström, A., and T. Alerstam. 1995. Optimal flight speed of birds. Philosophical Transactions of the Royal Society of London B, Biological Sciences 348:471–487.

Hochachka, P. W. 1994. Muscles as molecular and metabolic machines. CRC, Boca Raton, Fla.

Jenni, L., and R. Winkler. 1994. Moult and aging of European passerines. Academic Press, London.

Johnsgard, P. A. 1997. The hummingbirds of North America, 2d ed. Smithsonian, Washington, D.C.

Jones, J. H., and S. L. Lindstedt. 1993. Limits to maximal performance. Annual Review of Physiology 55:547–569.

Josephson, R. K. 1993. Contraction dynamics and power output of skeletal muscle. Annual Review of Physiology 55:527–546.

Kodric-Brown, A., and J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbird. Ecology 59:285–296.

Kullberg, C., T. Fransson, and S. Jakobsson. 1996. Impaired predator evasion in fat blackcaps (*Sylvia atricap-*

illa). Proceedings of the Royal Society of London B, Biological Sciences 263:1671–1675.

Lasiewski, R. C. 1962. The energetics of migrating hummingbirds. Condor 64:324.

Lilliendahl, K. 1997. The effect of predator presence on body mass in captive greenfinches. Animal Behaviour 53:75–81.

Lindström, Å., G. H. Visser, and S. Daan. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiological Zoology 66:490–510.

Metcalfe, N. B., and S. E. Ure. 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. Proceedings of the Royal Society of London B, Biological Sciences 261:395–400.

Milliken, G. A., and D. E. Johnson. 1992. Analysis of messy data. Von Nostrand Reinhold, New York.

Mulvihill, R. S., R. C. Leberman, and D. S. Wood. 1992. A possible relationship between reversed sexual size dimorphism and reduced male survivorship in the ruby-throated hummingbird. Condor 94:480–489.

Murphy, M. E. 1996. Energetics and nutrition of molt. Pages 158–198 *in* C. Carey, ed. Avian energetics and nutritional ecology. Plenum Press, New York.

Norberg, U. M. 1990. Vertebrate flight: mechanics, physiology, morphology, ecology and evolution. Springer, Berlin.

———. 1995. How a long tail and changes in mass and wing shape affect the cost of flight in animals. Functional Ecology 9:48–54.

Norris, R. A., C. E. Connell, and D. W. Johnston. 1957. Notes on fall plumages, weights, and fat condition in the ruby-throated hummingbird. Wilson Bulletin 69:155–163.

Payne, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. Ornithological Monograph no. 33. American Ornithologists' Union, Washington, D.C.

Pearson, O. P. 1961. Flight speeds of some small birds. Condor 63:506–507.

Pennycuick, C. J. 1975. Mechanics of flight. Pages 1–75 *in* D. S. Farner and J. R. King, eds. Avian biology, vol. 5. Academic Press, New York.

———. 1996. Wingbeat frequency of birds in steady cruising flight: new data and improved predictions. Journal of Experimental Biology 199:1613–1618.

Pennycuick, C. J., M. R. Fuller, J. J. Oar., and S. J. Kirkpatrick. 1996. Wingbeat frequency and the body drag anomaly: wind tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). Journal of Experimental Biology 199:2757–2765.

Rayner, J. M. V. 1988. Form and function in avian flight. Pages 1–66 *in* R. F. Johnston, ed. Current ornithology. Vol. 5. Plenum, New York.

———. 1990. The mechanics of flight and bird migration performance. Pages 283–299 *in* E. Gwinner, ed. Bird migration: physiology and ecophysiology. Springer, Berlin.

Robinson, T. R., R. R. Sargent, and M. B. Sargent. 1996. Ruby-throated hummingbird (*Archilochus colubris*). The Birds of North America, eds. A. Poole and F. Gill. No. 204. Academy of Natural Sciences, Philadelphia; and the American Ornithologists' Union, Washington, D. C.

Rome, L. C. 1997. Testing a muscle's design. American Scientist 85:356–363.

SAS Institute. 1989. SAS/STAT User's Guide, version 6, 4th ed. SAS Institute, Cary, N.C.

Sih, A., and S. K. Gleeson. 1995. A limits-oriented approach to evolutionary ecology. Trends in Ecology & Evolution 10:378–382.

Slagsvold, T., and S. Dale. 1996. Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced molt. Ecology 77:461–471.

Suarez, R. K. 1992. Hummingbird flight: sustaining the highest mass-specific metabolic rates among vertebrates. Experientia (Basel) 48:565–570.

———. 1996. Upper limits to mass-specific metabolic rates. Annual Review of Physiology 58:583–605.

Suarez, R. K., J. F. Staples, J. R. B. Lighton, and T. G. West. 1997. Relationships between enzymatic flux capacities and metabolic flux rates: nonequilibrium reactions in muscle glycolysis. Proceedings of the National Academy of Sciences of the USA 94:7065–7069.

Svensson, E., and J. Nilsson. 1997. The trade-off between molt and parental care: a sexual conflict in the blue tit. Behavioral Ecology 8:92–98.

Swaddle, J. P., and M. S. Witter. 1997. The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. Canadian Journal of Zoology 75:1135–1146.

Taylor, C. R., and E. R. Weibel. 1981. Design of the mammalian respiratory system. Respiration Physiology 44:1–164.

Tobalske, B. W., and K. P. Dial. 1996. Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. Journal of Experimental Biology 199:263–280.

Tucker, V. A. 1968. Respiratory exchange and evaporative water loss in the flying budgerigar. Journal of Experimental Biology 48:67–87.

———. 1972. Metabolism during flight in the laughing gull, *Larus atricilla*. American Journal of Physiology 222:237–245.

Vogel, S. 1994. Life in moving fluids. Princeton University Press, Princeton, N.J.

Wainwright, P. C. 1994. Functional morphology as a tool in ecological research. Pages 42–59 *in* P. C. Wainwright and S. M. Reilly, eds. Ecological morphology, integrative

organismal biology. University of Chicago Press, Chicago.

Walsberg, G. E. 1983. Avian ecological energetics. Pages 161–220 *in* D. S. Farner, J. R. King and K. C. Parkes, eds. Avian biology. Vol. 7. Academic Press, New York.

Wells, D. J. 1993. Muscle performance in hovering hummingbirds. Journal of Experimental Biology 178:39–57.