

Hovering Energetics and Thermal Balance in Anna's Hummingbirds (*Calypte anna*)

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ABSTRACT

We studied the energetics of hover-feeding Anna's hummingbirds, using three different simultaneous techniques: heat loss as estimated via thermal imaging, metabolic rate as measured at a feeder mask using flow-through respirometry, and aerodynamic power estimated from wing-beat kinematic data. These three methods yielded comparable estimates of power output at ambient air temperatures ranging from 18° to 26°C, whereas heat imbalance at higher air temperatures (up to 34°C) suggested loss by mechanisms other than convection and radiation from the body, such as evaporative cooling and enthalpy rise associated with exhaled air and excreted water and convective heat loss from the patagia. Hummingbirds increased wingbeat frequency and decreased stroke amplitude as air temperature increased, but overall muscle efficiency was found to be approximately constant over the experimental range of air temperatures.

Introduction

Among vertebrates, hummingbirds (Trochilidae, Apodiformes) are among the smallest endotherms and exhibit extremely high mass-specific metabolic rates (Weis-Fogh 1972; Suarez 1992). In addition to their small sizes, hummingbirds are the only birds capable of sustained hovering flight, an energetically de-

manding form of locomotion that is associated with high levels of metabolic power input (Bartholomew and Lighton 1986; Suarez et al. 1990; Suarez 1992) and mechanical power output (Lasiewski 1963; Wolf and Hainsworth 1971; Epting 1980; Wells 1993; Chai and Dudley 1996). Because of their small sizes and costly mode of locomotion, hummingbirds represent an important taxon in which to evaluate maintenance of endothermic balance in the face of environmental challenge (Miller 1996).

Despite their high energetic cost of flight and exposure to wide fluctuations in ambient air temperature, hummingbirds maintain energy balance through varied behavioral and physiological mechanisms such as entering nocturnal torpor and altering foraging strategies according to environmental conditions (e.g., Hixon and Carpenter 1988; Gass and Garrison 1999; Fernández et al. 2002). Hummingbirds also economize by substituting heat generated during flight for that required for thermoregulation (Berger and Hart 1972; Chai et al. 1998), although the magnitude of this response may vary with body size (see Welch and Suarez 2008). Variation in wingbeat kinematics in response to variable air temperature may also alter efficiency so as to advantageously augment metabolic heat production (Chai et al. 1998; see also Zerba and Walsberg 1992).

Although hummingbird hovering energetics are now well studied, the quantitative extent of heat dissipation has not been simultaneously evaluated for comparison with estimates of metabolic and mechanical work. For starlings in forward flight, the use of infrared thermography has enabled identification of different modes of heat loss as well as an independent estimate of flight muscle efficiency (Ward et al. 1999). The specific mechanisms of heat retention used by hovering hummingbirds, possibly enabled by variable conductance and the use of thermal windows, may be of broader ecological and evolutionary relevance given the historical patterns of trochilid diversification into colder montane habitats (Altshuler and Dudley 2002; McGuire et al. 2007). To investigate these mechanisms, we analyze simultaneous measurements of surface temperature, metabolic rate, and wingbeat kinematics during hovering flight of Anna's hummingbirds over a range of ambient air temperatures. By evaluating temperature-dependent changes in kinematic, energetic, and efficiency variables, we seek to determine whether elevated surface temperatures and heat dissipation are limiting factors in hot air and whether excess heat loss via convection limits hovering performance in the cold.

Material and Methods

Anna's hummingbirds were captured in the wild in Berkeley, California, and were acclimated to laboratory conditions over several days. Birds were maintained in individual mesh cages

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Table 1: Morphological data for three male Anna's hummingbirds (*Calypte anna*)

Individual	Mass, g	Wing Length, m	Aspect Ratio
Adult male	4.6 ± .3	.050	8.5
Adult male	5.0 ± .0	.050	9.2
Subadult male	4.7 ± .2	.059	8.3

Note. Average body mass was 4.8 g. Wing length and aspect ratio were determined from photographs of the spread wings against a grid. Values represent mean ± 1 SD.

(90 cm × 90 cm × 90 cm) with ad lib. access to a commercial solution designed for nectar-feeding birds (Nektar-plus, Pforzheim, Germany). Morphometric data for the three study individuals (two adult males and one subadult male) are provided in Table 1. At the completion of the experiments, all birds were released into the wild, at the point of capture. Measurements with individual birds were taken in several 4-h periods that were spread over two and 10 d. Data were considered to be from separate flight trials if measurements were separated by at least 15 min of intermittent flight and perching.

Birds were trained to hover at a feeder suspended within a 90 cm × 90 cm × 90 cm nonhermetically sealed Plexiglas chamber. Flight experiments were conducted at each of five nominal air temperatures (mean ± SD: 18° ± 2°, 24.0° ± 0.9°, 26° ± 2°, 30.2° ± 0.2°, and 33.5° ± 0.5°C), with the order of presentation chosen randomly. To obtain air temperatures above 24°C, a small convection heater was used to regulate chamber temperature. Ice baths on the chamber floor were used to cool the chamber below 24°C. Chamber air was mixed regularly via the bird's periodic flight bouts; air temperature was measured at the height of the feeder mask, where metabolic and surface temperature measurements were also obtained. Through the use of moving visual cues, birds were regularly stimulated to fly in order to obtain longer hover-feeding bouts and to reduce transient changes in body temperature at the start of hovering. Relative humidity during our experiments

was 56% ± 9% (mean ± SD); air temperature effects on humidity were nonsignificant ($P = 0.17$). Air temperature was monitored during experiments and varied no faster than 1°C in 10 min.

Rates of oxygen consumption during hover-feeding were obtained with an open-respirometry system (see Bartholomew and Lighton 1986; Chai and Dudley 1995). Expired air was pulled from the nares at a rate of 0.8 L min⁻¹ through a modified syringe (attached to the feeder) that functioned as a respirometry mask. The air was then drawn through a column of desiccant (Drierite, Xenia, OH) to remove water vapor. Oxygen concentration of the airstream was recorded with a portable oxygen analyzer (Foxbox; Sable Systems International, Las Vegas, NV). Oxygen depletion was estimated as the difference between baseline and minimum equilibrium values of oxygen partial pressure, incorporating the rate of airflow and the effect of ambient humidity. The calculated volume of oxygen consumed was divided by the duration of the feeding bout to obtain metabolic rate. A minimum of five hover-feeding bouts per individual bird were obtained at each experimental air temperature; feeding bouts of less than 2 s in duration were discarded. A standard conversion factor of 20.1 J mL⁻¹ O₂ was assumed.

To determine the rate of heat loss from hovering birds, infrared (IR) thermal images of the hummingbirds were obtained using a thermal imaging camera (Fluke, Everett, WA) operated through a window cut in one wall of the flight chamber. Hovering birds were filmed from a lateral perspective while at the feeder (see Fig. 1); orthogonal perspectives were then obtained by rotating the feeder about vertical through 90° and repeating the procedure. An emissivity ϵ of 0.95 for feathers was assumed (Cossins and Bowler 1987). From the thermal images, the region of interest containing the hummingbird was first identified manually. The image was then cropped and an optimal threshold was chosen to segment the background from the foreground (see Otsu 1979). Mean surface temperature was computed as the area-weighted average of temperature pixels in the cropped

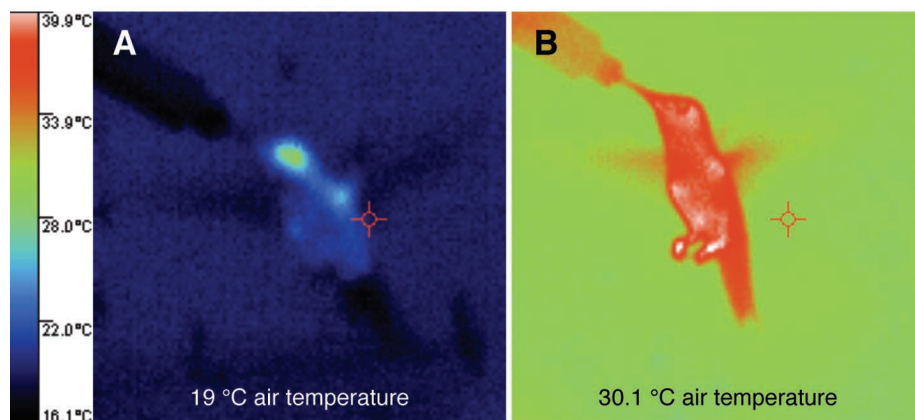


Figure 1. Representative thermal images showing behavioral response to increased air temperatures. At low to midrange air temperatures (A), heat loss is primarily from areas around the head, eyes, and pectoral muscles. At high air temperatures (B), heat loss is evident from the entire body, including the wings. In addition, the feet are extended.

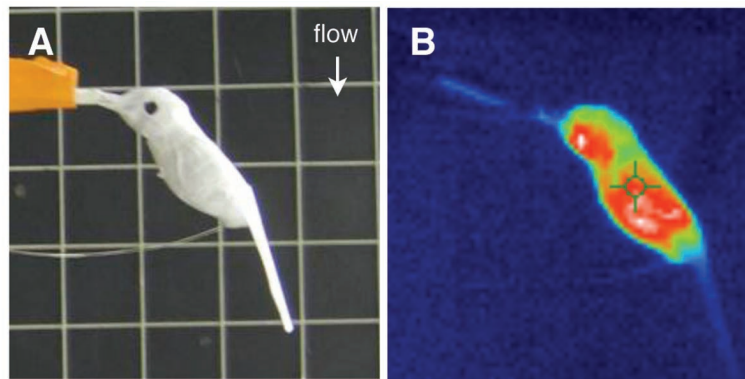


Figure 2. *A*, Life-sized (4-cm-long) physical model was used to obtain heat transfer coefficients at typical induced velocities and surface temperatures. Average surface temperatures were determined using the same thermal imaging camera and algorithm as for the live birds. *B*, Representative surface temperature profile using infrared thermal imaging (red corresponds to 37°C, blue corresponds to 20°C). Variation in the surface temperatures is due primarily to model grazing angle effects, which are identical to those in the live bird because they are in the same position.

image. The wings are ignored in the heat-transfer calculations, as the thermal imaging camera could not reliably resolve the fast-moving wings. In “Discussion,” we bind the potential magnitude of heat loss from the wings on the basis of convection.

The net rate of heat loss to ambient, \dot{Q}_{loss} (in W), was determined from both convective and radiative terms by the following equation (see Incropera and Dewitt 1996; Ward et al. 1999):

$$\dot{Q}_{\text{loss}} = \bar{h}A(T_s - T_a) + \sigma\epsilon A[(T_s + 273)^4 - (T_a + 273)^4], \quad (1)$$

where \bar{h} is the overall average convective heat transfer coefficient, $\sigma = 5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$ is the Stefan-Boltzmann constant, and T_s is the surface temperature and T_a is the ambient air temperature (both temperatures in °C). This formulation ignores evaporative heat loss and assumes that the average surface temperature for radiative heat transfer is the air temperature. Thermal images suggest that surface temperatures are close to ambient air temperatures. In any case, radiative heat transfer makes up only about 5% of the heat loss calculated with equation (1). To estimate the heat transfer coefficient \bar{h} , a life-sized physical model of an Anna’s hummingbird (see Fig. 2) was constructed of a solid piece of polymer clay (Sculpey; Polyform Products, Elk Grove Village, IL) wrapped with 30-gauge nichrome wire and paper tape (Johnson and Johnson, Langhorne, PA) characterized by an emissivity ϵ of 0.95 (Incropera and Dewitt 1996). The model was heated by connecting a power supply to the nichrome wire, yielding an estimated surface heat flux that is based on the model’s surface area and the applied voltage and current within the wire. Convective flow was imposed on the model using a large fan operated at air speeds comparable to estimated values of the induced velocity for hummingbirds (4.4–4.6 m s^{-1} , calculated according to Ellington 1984*b*; values from 3 to 6 m s^{-1} were tested). Flow was measured with a hot-wire anemometer (Kurz Instruments, Monterey, CA) sampling at 25 Hz that was located four body

lengths from the model and parallel within the working section. Flow direction was effectively downward relative to the model oriented in an appropriate feeding position (see Fig. 2*B*). The aforementioned thermal imaging camera was then used to obtain surface temperatures, with the model placed at the feeder in the same orientation as a hovering bird. Measured heat transfer coefficients were within a factor of 2 of that for a sphere, indicating reasonable estimates for the nonstandard hummingbird geometry (Incropera and Dewitt 1996; Ward et al. 1999). The model test results were used to estimate convective heat loss for each hovering trial, using the model’s mean surface temperature and an induced airflow velocity based on aero-

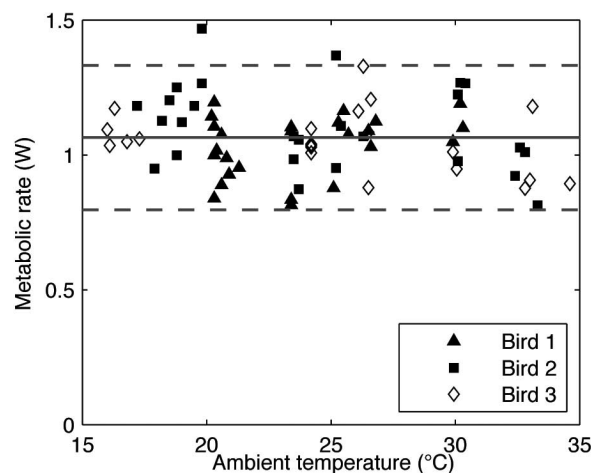


Figure 3. Metabolic rate measurements $\dot{Q}_{\text{metabolic}}$ (in W) for all birds at all temperatures. $\dot{Q}_{\text{metabolic}}$ for all birds is roughly constant at $1.1 \pm 0.1 \text{ W}$, or about $42 \pm 5 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (mixed-mode regression: $P = 0.17$; individual effects not significant: $P = 0.10$). For all remaining results, power is expressed in Watts to allow side-by-side comparison of metabolic rates, rates of heat loss, and mechanical power.

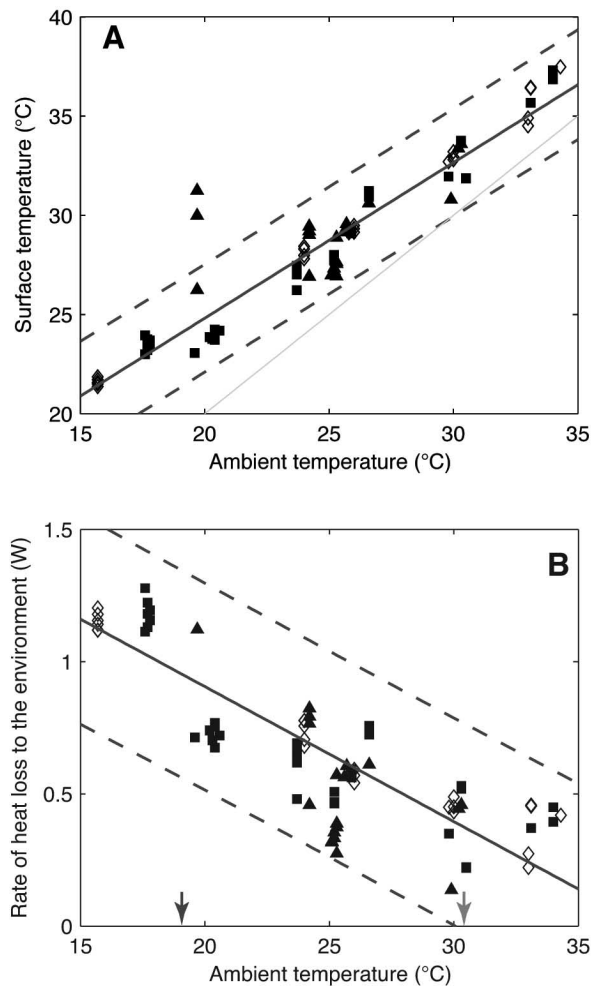


Figure 4. A, Average surface temperature, T_s , determined from thermal images. B, Rate of heat loss, \dot{Q}_{loss} , for all birds and all temperatures. T_s increases significantly with ambient air temperature T_a ($T_s = 0.78T_a + 9.32$, $P \leq 0.0001$; individual effects not significant: $P = 0.17$). \dot{Q}_{loss} declines significantly with ambient air temperature as the driving temperature difference, $T_s - T_a$ is reduced (mixed-mode regression: $\dot{Q}_{\text{loss}} = -0.06T_a + 2.05$, $P < 0.0001$; individual effects not significant: $P = 0.34$). Blue arrow (at $<20^\circ\text{C}$; a color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*) indicates onset of feather fluffing while individual is perched, as observed in bird 2. Red arrow (at $>30^\circ\text{C}$) indicates onset of wing spreading, mouth gaping, and foot extension, as observed in all birds. Symbols are as in Figure 3.

dynamic calculations. For all trials, induced velocity based on kinematics was $4.5 \pm 0.2 \text{ m s}^{-1}$.

To obtain kinematic data for estimates of mechanical power output, hover-feeding hummingbirds were filmed ventrally with a high-speed digital video camera (AOS Technologies, Baden Daettwil, Switzerland) operated at $500 \text{ frames s}^{-1}$. Video sequences were analyzed frame by frame to obtain values of wingbeat frequency and stroke amplitude (see Chai and Dudley 1995, 1996). Air density was determined from measurements of barometric pressure. Body mass of individual birds was measured before and after each experimental series; the mean value

was used in aerodynamic calculations. Outstretched wings of birds were photographed against graph paper and then digitized using ImageJ (National Institutes of Health, Bethesda, MD) to obtain morphological parameters relating to wing planform (see Ellington 1984a).

Kinematic and morphological data were used to calculate the mechanical power output using a standard model of animal hovering (Ellington 1984b) modified to incorporate unsteady drag coefficients as measured on a hummingbird wing in continuous rotation (Altshuler et al. 2004). Stroke plane angle was assumed to equal 0, and simple harmonic motion was assumed for wing movements within the stroke plane (see Chai and Dudley 1995; Altshuler and Dudley 2003).

The mechanical power output required to hover is the sum of the power required to overcome profile drag and the induced power required for weight support. Net inertial power to accelerate the wings is taken to be 0 on the basis of the assumption that the hummingbird flight apparatus exhibits full elastic storage of wing inertial energy (Ellington 1984c). Drag on the body during hovering flight was similarly assumed to be small compared with profile power lost to drag on the fast-moving wings (Ellington 1984c). Induced power, the power required to support body weight, follows from momentum balance and was calculated following Ellington (1984), as was profile power using a wing drag coefficient $\bar{C}_{D,\text{pro}} = 0.139$ (see Altshuler et al. 2004).

Heat balance for the hovering hummingbird at thermal equilibrium is given by

$$\dot{Q}_{\text{metabolic}} = \dot{Q}_{\text{loss}} + \dot{W}_{\text{mechanical}} \quad (2)$$

where positive $\dot{Q}_{\text{metabolic}}$ is the rate of metabolic heat production (as measured via respirometry), positive \dot{Q}_{loss} is the rate of heat

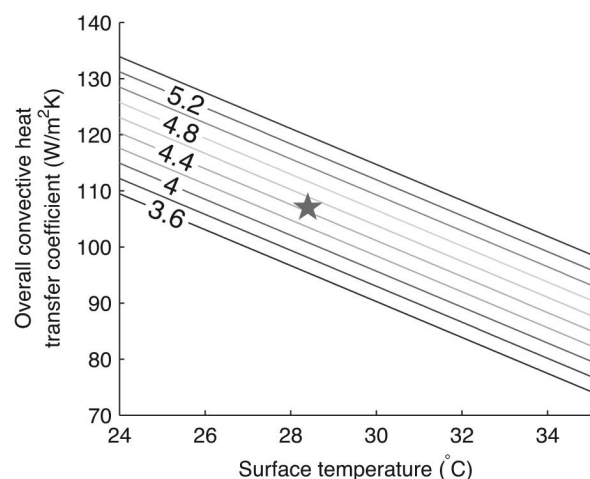


Figure 5. Overall average heat transfer coefficient, \bar{h} , for the physical model of *Calypte anna* is shown as a function of surface temperature, T_s , and airflow velocity ($\bar{h} = 137 - 3T_s + 13.5u_{\text{ind}}$, $P = 0.018$). The star indicates the average of all values used in calculations for hovering hummingbirds (see text). A color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*.

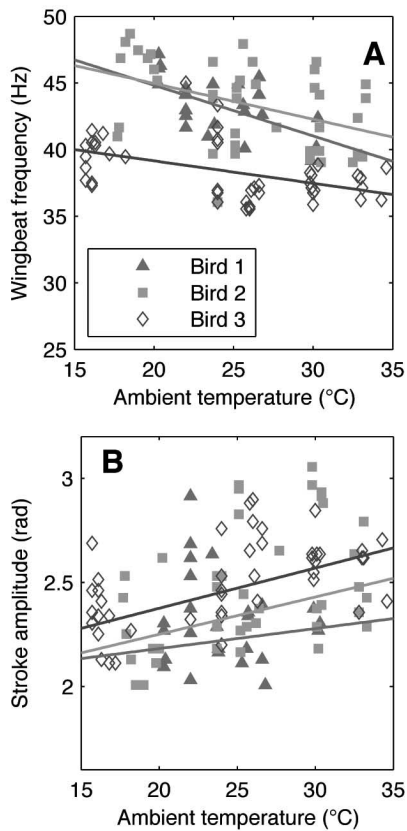


Figure 6. A, Wingbeat frequency decreases with ambient air temperature T_a (individual effects significant: $P < 0.001$). B, Stroke amplitude increases with ambient air temperature (individual effects significant: $P < 0.001$). A color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*.

loss to the surrounding air, and positive $\dot{W}_{\text{mechanical}}$ is the mechanical work output as estimated aerodynamically. We represent the overall efficiency η (Josephson et al. 2001) as

$$\eta_1 = \frac{\dot{W}_{\text{mechanical}}}{\dot{Q}_{\text{metabolic}}}, \quad (3)$$

where η_1 is efficiency based on mechanical power estimates and respirometric measurements of metabolic power. Alternatively, we compute η_2 as follows using equation (2) for metabolic power estimates:

$$\eta_2 = \frac{\dot{W}_{\text{mechanical}}}{\dot{W}_{\text{mechanical}} + \dot{Q}_{\text{loss}}}. \quad (4)$$

Purely on the basis of thermodynamics, η_2 can be viewed as an “efficiency,” but measurements of \dot{Q}_{loss} may miss some heat loss terms. Discrepancies between these two estimates indicate supplemental avenues of heat dissipation (such as evaporative loss) not represented in equation (1).

The effects of variable air temperature on rate of heat loss, metabolic rate, wingbeat kinematics, mechanical power, heat

balance, and muscle efficiency were evaluated using mixed-model regression in JMP (SAS Institute, Cary, NC) unless otherwise noted. In all analyses, individual effects and interactions (for example, metabolic rate as a function of bird, bird \times temperature, and temperature) were checked by ANOVA. In all cases except wingbeat frequency and stroke amplitude, which are discussed below, individual effects were found to be non-significant and so data were pooled in subsequent analyses.

Results

Metabolic rates of hover-feeding hummingbirds averaged 1.1 ± 0.1 W (mean \pm SD) and were independent of ambient air temperature ($P = 0.17$; see Fig. 3; individual effects not significant: $P = 0.10$). The measured metabolic rates correspond to a mass-specific metabolic rate of 42 ± 5 mL O_2 g^{-1} h^{-1} . By contrast, surface temperature (T_s) of hovering *Calypte anna* increased significantly with ambient air temperature T_a (Fig. 4A; $T_s = 0.78T_a + 9.32$, $P \leq 0.0001$; individual effects not significant: $P = 0.17$). Correspondingly, the estimated rate of heat loss to the environment by convective and radiative heat transfer declined significantly with air temperature (Fig. 4B; $\dot{Q}_{\text{loss}} = -0.06T_a + 2.05$, $P < 0.0001$; individual effects not significant: $P = 0.34$).

The overall average heat transfer coefficient, \bar{h} , as measured on the physical model of a hummingbird, varied with both surface temperature and airflow velocity (Fig. 5; $\bar{h} = 137 - 3.0T_s + 13.5u_{\text{ind}}$, $r^2 = 0.63$, $P = 0.018$). The model test results were used to estimate convective heat loss for each hovering trial on the basis of mean surface temperature of the bird and an induced airflow velocity on the basis of aerodynamic calculations. To determine whether the small changes in \bar{h} underlay observed trends, we also calculated convective heat loss with a constant \bar{h} ; estimates differed slightly but do not alter

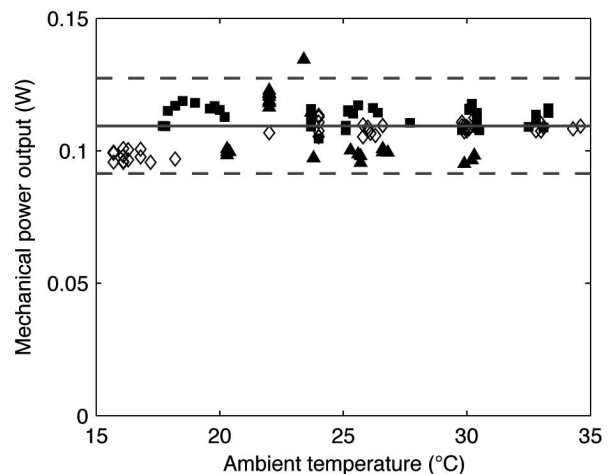


Figure 7. Mechanical power output required to hover, $\dot{W}_{\text{mechanical}}$, is roughly constant at 0.11 ± 0.01 W (mixed-mode regression: $P = 0.2611$; individual effects not significant: $P = 0.17$). Mass-specific mechanical power is approximately 4.1 mL O_2 g^{-1} . Symbols are as in Figure 3.

Table 2: Heat balance terms as a function of air temperature

T_a (°C)	$\dot{Q}_{\text{metabolic}}$	$\dot{W}_{\text{mechanical}}$	\dot{Q}_{loss}
18 ± 2	1.0 ± .1	.11 ± .01	.9 ± .3
24.0 ± .9	1.0 ± .1	.12 ± .01	.5 ± .2
26 ± 2	1.1 ± .1	.11 ± .01	.6 ± .2
30.2 ± .2	1.1 ± .1	.11 ± .01	.5 ± .1
33.5 ± .5	1.0 ± .1	.111 ± .003	.4 ± .2

Note. All values are in Watts unless otherwise noted, and are means ± SD. In mass-specific form, metabolic rates are approximately $42 \pm 5 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-1}$ and mechanical power estimates are about $4.1 \pm 0.5 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-1}$.

our conclusions. For all trials, the average heat transfer coefficient was $107 \text{ W m}^{-2} \text{ K}^{-1}$ on the basis of average surface temperatures of $29^\circ \pm 4^\circ\text{C}$ and average induced airflow velocities of $4.5 \pm 0.2 \text{ m s}^{-1}$.

Wingbeat frequencies decreased with ambient air temperature by about 10% over the experimental range (Fig. 6A; significant individual effects: $P < 0.001$). By contrast, stroke amplitudes increased with ambient air temperature by about 10% over the same range (Fig. 6B; significant individual effects: $P < 0.001$). Mechanical power output was, however, independent of air temperature (Fig. 7; $P = 0.26$, individual effects not significant: $P = 0.17$), and it averaged $0.11 \pm 0.01 \text{ W}$ (or, in mass-specific form, $4.1 \pm 0.5 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$).

At low air temperatures, metabolic heat generation was approximately equal to the summed rate of heat loss via radiation and convection and the estimated mechanical power output (Table 2). At midrange and high temperatures, however, the terms did not balance, demonstrating additional modes of heat loss, such as evaporative cooling, enthalpy rise of excreted water, and avenues of convective heat, that were not included in equation (1). Overall efficiencies calculated for hover-feeding on the basis of either aerodynamic power estimates and respirometry (η_1) or aerodynamic power and radiative and convective heat loss (η_2) at low temperatures were about 10% (Table 3). The η_1 efficiencies of 10% are comparable to results from other studies of hovering hummingbirds (9%–11%; see Wells 1993; Chai et al. 1998). At high air temperatures, η_2 estimates (15%–20%) are somewhat higher than efficiencies based on aerodynamic power (η_1), indicating unaccounted modes of heat dissipation in the overall energy balance (eq. [1]).

We observed several behaviors corresponding to the loss of the driving temperature differential at higher air temperatures. At air temperatures of $18^\circ\text{--}24^\circ\text{C}$, the main areas of heat loss were found around the head, eye, and pectoral muscles (Fig. 1A). Above 30°C , these regions expanded to include the entire body, as seen in thermal images (see Fig. 1B), potentially corresponding to an increase in blood perfusion over the entire body. Above 30°C , all birds exhibited bill gaping while perched and one bird exhibited wing spreading while perched. Birds were also observed to extend their feet while hovering at high air temperatures (see Fig. 1B).

Discussion

At low air temperatures, application of thermal imaging, aerodynamic estimates, and respirometric measurements yielded consistent results for the energetics of hovering flight. By contrast, use of infrared thermography at higher ambient air temperatures underestimated heat lost to the environment because of unaccounted modes of heat transfer. At higher air temperatures, the primary mechanisms available for dissipating heat are evaporative cooling and enthalpy rise in either exhaled air or excreted water (Lasiewski 1964; Powers 1992; Lotz et al. 2003). In addition, heat loss from the wings, which have relatively large surface areas and higher convective heat transfer coefficients due to high flapping velocities, may become relatively more important at higher temperatures.

As ambient air temperatures approach body temperature, the driving thermal gradient ($T_s - T_a$) for convection and radiative loss is progressively diminished. At high ambient air temperatures, flight performance may then become thermally limited, as is suggested by estimated rates of convective and radiative heat loss that extrapolate to zero heat loss at approximately 40°C (Fig. 4). This diminished shedding of heat is further compounded by a slight decline in the heat transfer coefficient with increased air temperature (Fig. 5). At temperatures higher than its thermal neutral zone, *Calypte anna* may become slightly hyperthermic, which could augment heat transfer by increasing the $T_s - T_a$ gradient (Powers 1992).

Whereas our calculations do not include such heat transfer modes as evaporative cooling, enthalpy rise, and convection from the wings, the measurements taken here provide an indirect way to estimate these terms. At low temperatures, these additional heat loss terms, taken as the sum of $\dot{Q}_{\text{metabolic}} - \dot{W}_{\text{mechanical}} - \dot{Q}_{\text{loss}}$, are negligible ($0.0 \pm 0.3 \text{ W}$). At the highest air temperature, these additional terms would have to be $0.5 \pm 0.2 \text{ W}$, almost half of the metabolic rate; it is interesting to consider how this could be split among evaporative water loss, enthalpy rise of ingested liquid, and wing convection. Powers (1992) and Lasiewski (1964) give evaporative water loss rates for hummingbirds of around $20 \text{ mg g}^{-1} \text{ h}^{-1}$. Assuming that 2,257 kJ is needed to vaporize 1 kg of water, the associated evaporative heat loss would be about 0.06 W, corresponding to 6% of the metabolic rate measured here. The energy needed to warm ingested nectar could also be significant (Lotz et al.

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Table 3: Efficiency estimates as a function of air temperature

T_a (°C)	η_1	η_2	$\eta_1 - \eta_2$
18 ± 2	.11 ± .02	.109	.001
24.0 ± .9	.12 ± .02	.194	-.074
26 ± 2	.10 ± .02	.155	-.055
30.2 ± .2	.10 ± .02	.180	-.080
33.5 ± .5	.10 ± .01	.217	-.117

Note. η_1 efficiencies are computed using $\eta_1 = \dot{W}_{\text{mechanical}}/\dot{Q}_{\text{metabolic}}$. η_2 estimates are computed using $\eta_2 = \dot{W}_{\text{mechanical}}/(\dot{W}_{\text{mechanical}} + \dot{Q}_{\text{loss}})$.

2003). Fernández et al. (2002) give fluid ingestion rates of up to 0.03 g min^{-1} for a 6-g green-backed firecrown hummingbird (*Sephanooides sephanooides*). The energy required to raise the temperature of such nectar volumes from 20°C to typical body temperatures would be about 0.04 W , or 4% of the measured metabolic rate for Anna's hummingbirds. To estimate wing convection, we assume a convective heat transfer coefficient for the wings of $200 \text{ W m}^{-2} \text{ }^\circ\text{K}$ on the basis of forced convection in air on a flat plate at a local velocity of 15 m s^{-1} (Incropera and Dewitt 1996). The patagia are the main vascularized areas of the wings, and the heat transfer surface areas for the dorsal and ventral surfaces of both patagia are approximately $2.6 \times 10^{-4} \text{ m}^2$. For wing temperatures equal to the observed body surface temperatures, convective heat loss from the wings would be about 0.4 W . As with the body, heat loss from the wings will become restricted as ambient air temperature increases.

Limited heat dissipation in high air temperatures may impose constraints on hovering performance. Hummingbirds in hot, humid conditions in the tropics may raise their body temperatures in order to increase convective heat transfer when evaporative cooling is limited (see Powers 1992), although further ecological and behavioral data are needed. Field observations of the giant Andean hummingbird (*Patagona gigas*) indicate decreased activity on hot days (M.J. Fernández, personal observation). Mechanisms of heat dissipation will be further limited under humid conditions, as enthalpy rise associated with exhalation declines with increasing water content of inhaled air. For hummingbirds with relatively high ventilatory frequencies, the magnitude of respiratory cooling is potentially substantial. The fraction of metabolic heat dissipated by evaporation in Anna's hummingbirds is lower than that of other birds in dry air, but it exceeds that of other birds at high humidities when air temperature is less than 33°C (Powers 1992). Experimental manipulation of both air temperature and relative humidity for hovering hummingbirds would definitively test the role of thermal constraints on flight performance.

Convection is expected to be the dominant mode of heat loss at low and midrange air temperatures. However, variation in wingbeat frequency and stroke amplitude at low ambient air temperature (see Fig. 6) does not significantly alter either induced velocity or wing relative velocity, which otherwise might change the convective heat transfer coefficient. Variation in estimated rates of heat loss with air temperature (Fig. 4B) suggests that metabolic rates must increase to compensate for increased heat loss below 15°C , as is observed for ruby-throated hummingbirds hovering at $5^\circ\text{--}15^\circ\text{C}$ (Chai et al. 1998). At even lower air temperatures, below the thermal neutral zone, heat loss becomes large compared with rates of metabolic heat production. For example, we observed substantial feather fluffing by perched birds in very cold air. Studies of other hummingbird species have documented increases in foraging and food intake to maintain energy balance at low air temperatures (Gass et al. 1999). At high elevations in the Andes, hummingbirds often fly and forage at near-freezing air temperatures; associated physiological responses may have been an important factor influencing montane colonization by this lineage.

In spite of significant changes in wingbeat frequency and stroke amplitude over the experimental range of air temperatures (Fig. 6), we observed no significant changes in hovering metabolic rates or mechanical power expenditure at the lowest temperatures used in our experiments (Fig. 3; Table 2). Altered kinematics could potentially generate more heat at the expense of mechanical efficiency (Ivanov 1989; Full et al. 1998; Josephson et al. 2001; Bicudo et al. 2002). Some indication of this effect was evident at the lowest tested air temperatures, for which heat loss approached metabolic rate (see Figs. 3, 4B; see also Chai et al. 1998). Flight efficiency, however, remained remarkably constant at about 10% (see Table 3). These efficiency estimates are comparable to those derived in other studies of hovering hummingbirds (9%–11%; see Wells 1993; Chai et al. 1998). Kinematic variation without reduction in efficiency of hovering may also be of benefit when hummingbirds visit different floral morphologies (Wells 1993).

The thermal limits on flight performance suggested here likely influence hummingbird evolution across altitudinal gradients (McGuire et al. 2007), and they may also impinge on size-based trade-offs in flight performance (see Chai and Dudley 1999; Altshuler and Dudley 2002). The most thermally challenging conditions for trochilids are likely to involve hovering in hot and humid air (resulting in insufficient heat dissipation), as well as forward flight in cold, dry air (which may result in excess heat loss). Fieldwork assessing flight behaviors in relation to microclimatic data would enable assessment of the specific role of thermal limits in influencing ecological distributions of hummingbirds. Similarly, comparative work on thermal responses by differently sized species would assess the allometry of heat production and loss during hovering flight.

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