FLIGHT THERMOGENESIS AND ENERGY CONSERVATION IN HOVERING HUMMINGBIRDS

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Summary

As the smallest homeotherms, hummingbirds suffer from low thermal inertia and high heat loss. Flapping flight is energetically expensive, and convective cooling due to wing and air movements could further exacerbate energy drain. Energy conservation during flight is thus profoundly important for hummingbirds. The present study demonstrates that heat produced by flight activity can contribute to thermoregulatory requirements in hovering hummingbirds. The rate of oxygen consumption, as an indicator of metabolic cost, was measured during hover-feeding and compared with that during perch-feeding. In hover-feeding, oxygen consumption increased only moderately between 35 and 5 °C in contrast to the sharp increase during perch-feeding over the same temperature range. This result suggests that heat produced by contraction of the flight muscles substituted for regulatory thermogenesis to accommodate for heat loss during exposure to low temperature. With declining air temperatures, the mechanical power requirements of hovering decreased slightly, but metabolic costs increased moderately. As a result, the mechanical efficiency of the muscle in converting metabolic power to mechanical power was reduced. Changes in wingbeat kinematics also accompanied the reduction in muscle efficiency. Wingbeat frequency increased but stroke amplitude decreased when hovering in the cold, suggesting thermoregulatory roles for the flight muscles. Hovering hummingbirds modulated their wingbeat frequency within a narrow range, reflecting the physical constraints of tuning to a natural resonant frequency with an elastic restoring force. We hypothesize that, by forcing the resonant system of the wings and thorax to oscillate at different frequencies, muscle contraction in the cold generates more heat at the expense of mechanical efficiency. This mechanism of modulating the efficiency of muscle contraction and heat production allows flying hummingbirds to achieve energy conservation at low air temperatures.

Key words: flight energetics, hovering flight, hummingbirds, mechanical power output, metabolic heat production, muscle mechanical efficiency, oxygen consumption, temperature, thermoregulation, *Archilochus colubris*.

Introduction

The small size of hummingbirds results in a high thermal conductance and metabolic rate relative to other birds (Lasiewski, 1963). There thus exists strong selective pressure for hummingbirds to achieve thermal stability and energy balance. To save energy reserves, inactive hummingbirds have the unusual physiological capacity of falling into torpor with a drastically reduced metabolic rate (Wolf and Hainsworth, 1972; Krüger *et al.* 1982; Carpenter and Hixon, 1988; Hiebert, 1990; Calder, 1994). The means by which an active hummingbirds reduces its energy expenditure are still unclear. Flying birds, in general, must allocate energy to meet both thermostatic demands and the requirements of flight. During flight, convective effects should exert greater effects on thermostasis than during rest or inactivity (Bakken, 1991; St-Laurent and Larochelle, 1994). Both the movement of the bird and the resultant wind can disrupt plumage insulation and inflict higher demands for regulatory thermogenesis. However,

heat produced as a by-product of physical activity can substitute for thermoregulatory requirements, and this incidental source of energy has been demonstrated in diving and terrestrial locomotion of several bird species (Pohl and West, 1973; Paladino and King, 1984; Webster and Weathers, 1990; Bevan and Butler, 1992; Zerba and Walsberg, 1992). For flying birds, our understanding of the substitution of exercise thermogenesis for thermoregulatory needs is still unclear (Schuchmann, 1979; Paladino and King, 1984; Webster and Weathers, 1990). This substitution determines the extent of energetic cost associated with flight at different ambient temperatures and thus has important physiological and ecological implications.

As the smallest birds, but practicing energy-demanding hovering flight, flying hummingbirds must couple thermoregulation and energy metabolism closely. Berger and Hart (1972) first noted that, during hovering, a South American

hummingbird species reduced its wingbeat frequency as ambient temperature increased, whereas oxygen consumption increased moderately with declining air temperature. They proposed that heat generated by contraction of the flight muscles contributed to thermoregulation at low temperatures. However, Schuchmann (1979) found that rates of oxygen consumption during hovering by two other hummingbird species increased linearly with decreasing ambient temperature, showing slopes similar to those measured in resting birds. Thus, his results did not support the idea that heat produced by contraction of the flight muscles could significantly substitute for thermoregulatory heat production during cold exposure. Our previous study with ruby-throated hummingbirds (*Archilochus colubris*) also recorded an increase in wingbeat frequency in the cold and further identified an inverse relationship between wingbeat frequency and stroke amplitude at 5 and 25 °C. As a result, mechanical power output remained similar during free hovering (Chai *et al.* 1997). The present study measures metabolic rates, wingbeat kinematics and mechanical power during hovering flight at different air temperatures to investigate further the substitution hypothesis that flight-generated heat contributes to thermostatic requirements. This work thus sheds light on the discrepancy between the results of Schuchmann (1979) and those of Berger and Hart (1972) and Chai *et al.* (1997). Experimental measurements in the present study allow us to ascertain whether heat production reflects an increase in the intensity of mechanical power output or a change in the mechanical efficiency of the muscle in converting metabolic power to mechanical power.

Materials and methods

Ruby-throated hummingbirds (*Archilochus colubris* L.) were mist-netted in the vicinity of Austin, Texas, USA, during the autumn migratory season of 1996 and were housed in screen cages of dimensions 90 cm×90 cm×90 cm. Hummingbird care was in accordance with federal and state guidelines. Two birds were housed within a single cage. Five individual hummingbirds with intact flight feathers (two juvenile males and three females) were studied under various ambient temperatures, T_a. All experimental trials were conducted within a large environmental chamber at each of four temperatures (5, 15, 25 and 35 °C). A cylindrical enclosure made of nylon screen was used to confine the movements of the bird. Enclosure diameter was 47 cm (more than four times the wingspan of the bird), while enclosure length was 91 cm. Uniform perforations of the mesh enclosure (perforation diameter of 1.3 mm) permitted the passage of air and alleviated boundary effects associated with flight in small enclosures. These effects were in any event small given the large enclosure dimensions relative to hummingbird wing span (see Rayner and Thomas, 1991).

Each bird was subjected to two trials, with one trial implemented per day over two consecutive days. Within each trial, the bird was exposed to progressively increasing or decreasing temperature treatments. During the experiment, the bird was allowed to feed every 20 min to ensure that it was hungry and responsive. At each temperature setting, two feedings (hover-feeding and perch-feeding) were examined. By providing a twig in front of the feeder mask, the bird could perch while feeding (ruby-throated hummingbirds prefer perch-feeding to hover-feeding; P. Chai, unpublished data). Birds were trained to feed through a cylindrical mask attached to a hanging syringe that allowed collection of expired gases. This open-flow feeder-mask respirometry system permitted measurements of rates of oxygen consumption ($\dot{V}_{O_2}$) during hover-feeding and perch-feeding (see Chai and Dudley, 1995, 1996, for detailed accounts of experimental procedures). Rates of oxygen consumption were expressed at STP.

Horizontal projections of wingbeat kinematics of each hover-feeding sequence were video-recorded (Sony CCD-TR600) from a mirror oriented above the bird at 45 ° to the horizontal (filming and subsequent analysis were at 60 fields s^{-1} with a high shutter speed of 1/4000 s). Wingbeat kinematics measured for each hovering sequence included wingbeat frequency n and stroke amplitude Φ. Wingbeat frequency and stroke amplitude were calculated by the methods described previously (Chai and Dudley, 1995, 1996). Briefly, wingbeat frequency was derived from the interaction frequency between wing motion and filming rate, whereas stroke amplitude was derived from video images in which the wings were located at the extreme position of the wingbeat. Wingbeat kinematics, together with morphological parameters for individual birds, were used to estimate the mechanical power requirements of flight using a detailed aerodynamic model of hovering flight (Ellington, 1984*a–f*). Morphological parameters used in aerodynamic calculations included body mass m, relative wing mass m_w for both wing pairs and expressed as a fraction of body mass, wing length R, total wing area S (the area of both wing pairs, body area not included), wing loading p_w ($m\mathbf{g}/S$, where $\mathbf{g}$ is gravitational acceleration) and aspect ratio $\mathscr{R}$ ($4R^2/S$). For humane reasons, none of the experimental birds was killed for *post mortem* analysis. Wing mass and its spanwise distribution were estimated from one bird of each sex in previous studies with the same species (Chai and Dudley, 1995, 1996).

For each hover-feeding flight sequence, the mechanical power requirements of flight were estimated by evaluating individual components of profile (P^*_{pro}), induced (P^*_{ind}) and inertial power during the first half of a half-stroke (P^*_{acc}). Total power expenditure for a flight sequence was calculated for the two cases of perfect (P^*_{per}) and zero (P^*_{zero}) elastic storage of wing inertial energy, which represent the minimum and maximum estimates of required mechanical power respectively (Ellington, 1984*f*). Thus, $P^*_{per}=P^*_{pro}+P^*_{ind}$ assuming perfect elastic energy storage, and $P^*_{zero}=(P^*_{pro}+P^*_{ind}+P^*_{acc})/2$ assuming zero elastic energy storage. P^*_{per} and P^*_{zero} are expressed in muscle mass-specific form, assuming that flight muscle makes up 25 % of the body mass (Chai and Dudley, 1995). Muscle mechanical efficiencies η_m for P^*_{per} and P^*_{zero} were, respectively, estimated as $P^*_{per}/(0.9{\times}P^*_{IN})$ and $P^*_{zero}/(0.9{\times}P^*_{IN})$, where P^*_{IN} is metabolic power input assuming a 90 % direct energy

expenditure by flight muscle (Lasiewski, 1963; Wells, 1993a). P_{IN}^* was derived from measured rates of oxygen consumption.

The effects of air temperature manipulation were evaluated for each kinematic, aerodynamic and mechanical variable using repeated-measures analysis of variance (ANOVA) (SAS Institute, 1989) modelling the temperature effect as the within-subject source of variation. Data points used in the ANOVA were mean values of each bird and temperature combination averaged across 2 days because progressively increasing or decreasing temperature treatments did not change the behavior of the bird (P. Chai, unpublished data).

Results

Wingbeat frequency varied within a narrow range (mean 47–50 Hz) and increased linearly with declining ambient temperatures, while stroke amplitude decreased (Fig. 1). Thus, wingbeat frequency and stroke amplitude varied inversely between 5 and 35 °C. Air density at 5 °C is approximately 10 %
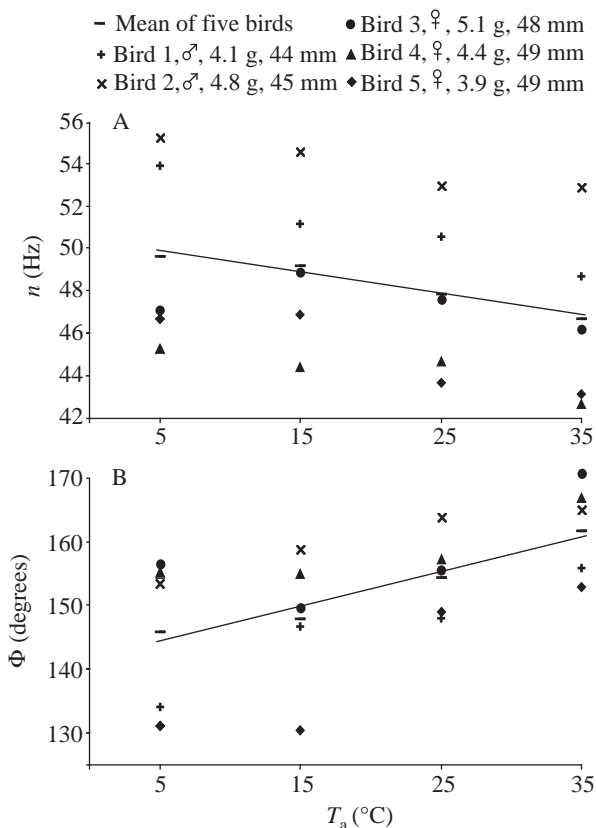
higher than at 35 °C (1.26 *versus* 1.14 kg m^{-3}), and flight should be somewhat facilitated in the colder and denser air. The mean Reynolds number of the wing chord decreased slightly in warmer but less dense air, whereas the mean lift coefficient did not vary with air temperature (Fig. 2). Mechanical power requirements increased only slightly from 98 W kg^{-1} at 5 °C to 101 W kg^{-1} at 35 °C for P_{per}^*, and from 236 to 239 W kg^{-1} for P_{zero}^* (Fig. 3). Because the birds were periodically denied access to the feeder, hovering behavior in an attempt to obtain sugar water usually lasted more than 20 s. On the basis of the asymptotic behavior of the respiratory traces, oxygen consumption rates measured using open-flow respirometry from the feeder mask clearly reached steady-state values during the measurement period. It is probable, but not proven, that body temperature and external heat flux reached equilibrium during this period of hovering. Rates of oxygen consumption were always higher during hover-feeding than during perch-feeding (Fig. 4). However, rates of O$_2$ consumption increased moderately during hover-feeding but rose sharply during perch-feeding between 35 and 5 °C. As a result, the difference in metabolic costs between the two types of feeding methods was progressively reduced with declining air temperature. Since hovering mechanical power output decreased slightly but metabolic power input increased
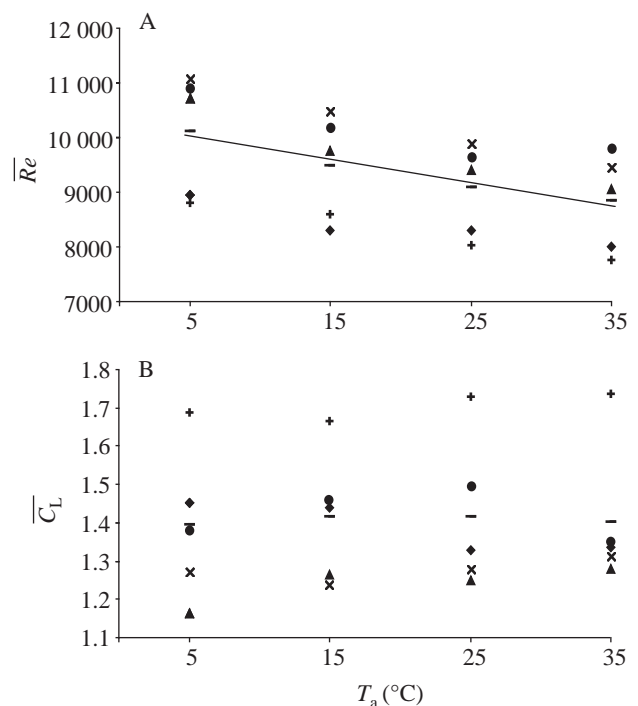

Fig. 1. Wingbeat frequency *n* (A) and stroke amplitude Φ (B) in relation to ambient temperature T_a for five individual *Archilochus colubris*. Bird identification number, sex, body mass and wing length are also given. For wingbeat frequency, repeated-measures ANOVA results indicate a significant temperature effect ($P=0.003$) and a significant linear trend ($P=0.013$). The fitted least-squares regression line is: $y=-0.1x+50.4$. For stroke amplitude, repeated-measures ANOVA results indicate a significant temperature effect ($P=0.001$) and a significant linear trend ($P=0.004$). The fitted least-squares regression line is: $y=0.54x+141.7$.

Fig. 2. Mean Reynolds number $\overline{Re}$ (A) and mean lift coefficient $\overline{C_L}$ (B) in relation to ambient temperature T_a (symbols as in Fig. 1). For mean Reynolds number, repeated-measures ANOVA results indicate a significant temperature effect ($P<0.001$) and a significant linear trend ($P=0.001$). The fitted least-squares regression line is: $y=-42.4x+10239$. For mean lift coefficient, repeated-measures ANOVA results indicate neither a significant temperature effect ($P=0.905$) nor a significant linear trend ($P=0.849$).
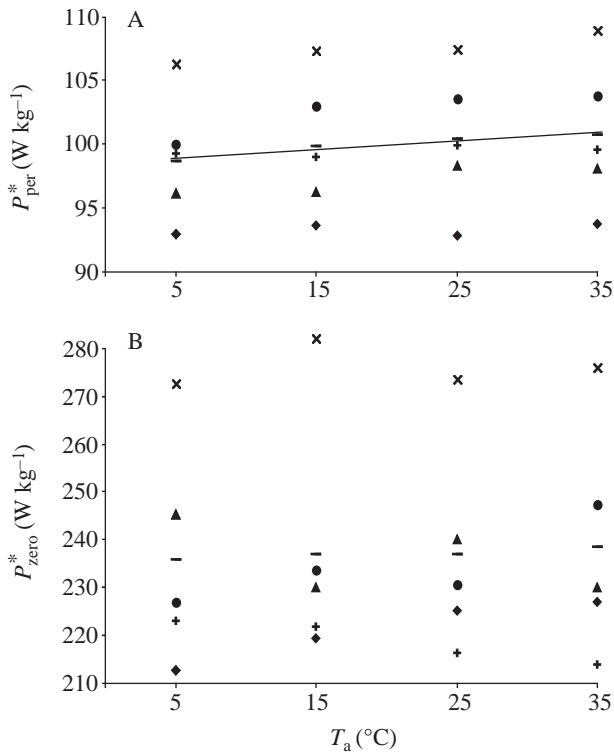
Fig. 3. Muscle mass-specific power output assuming perfect (P^*_{zero}, A) and zero (P^*_{zero}, B) elastic energy storage in relation to ambient temperature T_a (symbols as in Fig. 1). P^*_{per} and P^*_{zero} were calculated assuming that flight muscle is equal to 25% of the body mass. For P^*_{per}, repeated-measures ANOVA results indicate a significant temperature effect ($P=0.017$) and a significant linear trend ($P=0.039$). The fitted least-squares regression line is: $y=0.07x+98.5$. For P^*_{zero}, repeated-measures ANOVA results indicate neither a significant temperature effect ($P=0.946$) nor a significant linear trend ($P=0.701$).

moderately between 35 and 5 °C, muscle mechanical efficiency dropped from 13 to 11% for P^*_{per} and from 30 to 26% for P^*_{zero} in this temperature range (Fig. 5).

Discussion

No animals were killed for this study; instead, mean values for flight muscle mass, wing mass and the spanwise wing mass distribution were taken from previous studies (Chai and Dudley, 1995, 1996). The use of mean values is likely to increase uncertainty in estimates of muscle mechanical power output (Fig. 3; P^*_{per} was affected by uncertainty only in the estimate of flight muscle mass and not wing mass-related variables). The assumption that flight muscle mass is equal to 25% of the body mass will decrease among-subject variation and will also increase the possibility of false statistical significance. However, other derived variables (e.g. mean Reynolds number and mean lift coefficient; Fig. 2) do not incorporate values for muscle or wing mass and are thus not affected. Muscle mechanical efficiency was estimated by assuming that 90% of metabolic power input is expended by the flight muscle (Fig. 5). This assumption will estimate
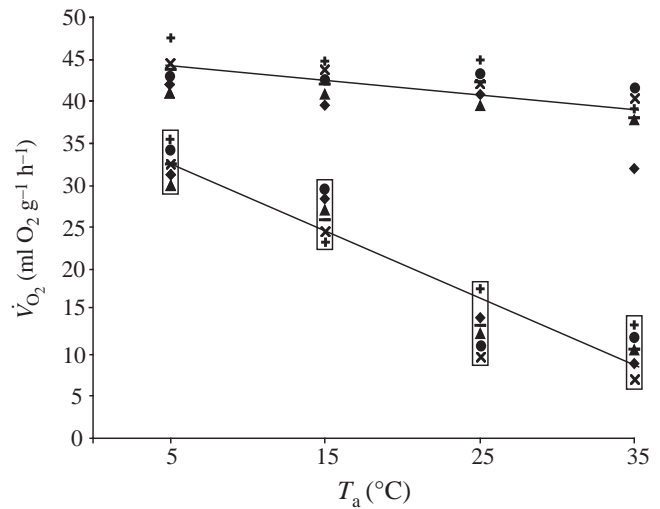

Fig. 4. Body mass-specific rate of oxygen consumption $\dot{V}_{O_2}$ during hover-feeding and during perch-feeding (framed values) in relation to ambient temperature T_a (symbols as in Fig. 1). For hover-feeding, repeated-measures ANOVA results indicate a significant temperature effect ($P=0.002$) and a significant linear trend ($P=0.017$). The fitted least-squares regression line is: $y=-0.17x+45.1$. For perch-feeding, repeated-measures ANOVA results indicate a significant temperature effect ($P<0.001$) and a significant linear trend ($P<0.001$). The fitted least-squares regression line is: $y=-0.79x+36.5$.

muscle efficiency inaccurately if other physiological costs of heightened metabolism (including thermoregulatory costs) vary systematically with ambient temperature during hovering.

The striking contrast between the slopes of rates of oxygen consumption of hover-feeding *versus* perch-feeding in the temperature range from 35 to 5 °C clearly suggests that flight thermogenesis contributes to thermoregulatory heat production during hover-feeding under cold exposure. In contrast, the sharp increase in oxygen consumption during perch-feeding was undoubtedly due to an increase in the metabolic heat production needed to thermoregulate over the same temperature range. As in the results of Berger and Hart (1972), which came primarily from one bird, the rate of oxygen consumption of hover-feeding increased moderately with a negative slope of −0.2 (mlO_2 g^{-1} h^{-1} °C^{-1}) as air temperatures decreased (Fig. 4). This slope, however, was very different from those of Schuchmann (1979), which were more negative, in the range −0.6 to −0.7, and were similar to those measured for resting birds under decreasing air temperatures, i.e. their thermal conductance. Schuchmann's (1979) study may have methodological complications, however, as the rates of oxygen consumption measured during hovering were unusually low (see Bartholomew and Lighton, 1986). The slope of −0.8 for perch-feeding was lower than the value of −0.5 to −0.6 of the thermal conductance measured for resting hummingbirds of similar size (Lasiewski *et al.* 1967). This indicates a higher heat loss and a reduction in insulation during perch-feeding in the cold, presumably as a result of a disruption of the optimal posture for heat conservation.
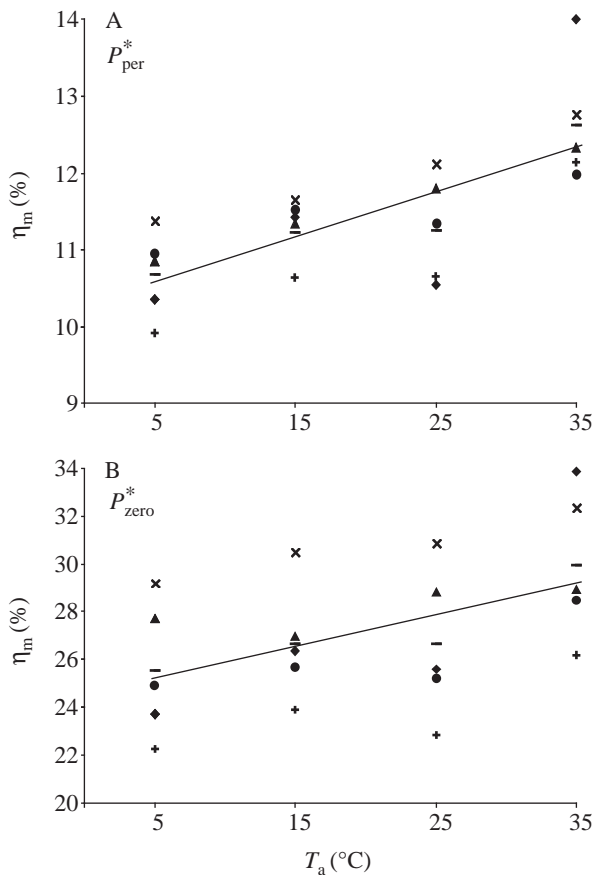
Fig. 5. Muscle mechanical efficiency η_m assuming perfect (A) and zero (B) elastic energy storage in relation to ambient temperature T_a (symbols as in Fig. 1). For η_m (P^*_{per}), repeated-measures ANOVA results indicate a significant temperature effect ($P=0.001$) and a significant linear trend ($P=0.008$). The fitted least-squares regression line is: $y=0.06x+10.3$. For η_m (P^*_{zero}), repeated-measures ANOVA results indicate a significant temperature effect ($P=0.005$) and a significant linear trend ($P=0.035$). The fitted least-squares regression line is: $y=0.13x+24.6$.

For technical reasons, body temperature was not monitored during either hover- or perch-feeding episodes. The body temperature of hovering hummingbirds may change systematically with ambient temperature, but no relevant data are available. In the hummingbird *Amazilia fimbriata*, post-flight body (cloaca) temperatures measured at variable durations (<1 min) after landing increased on average from 40.4 to 42.5 °C over an ambient temperature range of 0–35 °C (Berger and Hart, 1972). This result may suggest a small increase in body temperature at higher air temperatures. However, the measurements made by Berger and Hart (1972) are confounded by the potential temperature-dependence of post-flight cooling rates. Possible variability in thermal conductance over the same temperature range confounds any analysis of heat loss during hovering flight. Nevertheless, body temperature during hovering across a wide range of ambient temperatures is likely to be fairly stable. Similarly, excluding torpor, non-flying hummingbirds also show a fairly constant body temperature at different air temperatures (Lasiewski, 1964; Prinzinger *et al.* 1991).

The achievement of energy balance and homeothermy by hummingbirds that hover in the cold overcomes two challenges. First, hovering flight is energy-expensive (Weis-Fogh, 1972; Norberg, 1990). Second, convective cooling induced by wing movements and low thermal inertia as a consequence of small body size further exacerbate this energy drain. The use of heat by-products from hovering flight appears to be the mechanism by which flying hummingbirds effect thermoregulation while minimizing energy expenditure at low air temperatures. Because cold air is denser than warm air and the mechanical power requirements of hovering decrease slightly, whereas the metabolic costs increase moderately, between 35 and 5 °C, the muscle mechanical efficiency of converting metabolic power to mechanical power is reduced. We hypothesize that variation in flight thermogenesis is achieved through modulation of the efficiency of contraction of the flight muscles.

Several lines of evidence suggest that the flight apparatus of hummingbirds facilitates metabolic heat production, with the wings and thorax acting as a resonant system. In hovering ruby-throated hummingbirds, mechanical power requirements with perfect elastic energy storage (P^*_{per}) were less than half of those with no such storage (P^*_{zero}, Fig. 3). Natural selection should strongly favor the elastic storage of wing inertial energy. It is well known that hovering hummingbirds modulate their wingbeat frequency within a narrow range (Greenewalt, 1962, 1975; Hagiwara *et al.* 1968; Wells, 1993*a,b*; Chai and Dudley, 1995). The constancy of wingbeat frequency in hummingbirds and the close relationship between wing length and wingbeat frequency suggest that the wings and thorax work as a tuned oscillator with an elastic restoring force (Greenewalt, 1975; Corben, 1983; Turvey *et al.* 1988). The flight muscles of hummingbirds probably adapt to work at a particular resonant frequency and this, in turn, confines the strain rate within a particular range. In the present study, changes in wingbeat kinematics were accompanied by a reduction in muscle efficiency: wingbeat frequency increased but stroke amplitude decreased when hovering in the cold (stroke amplitude changes in the opposite direction to keep the mechanical power output approximately constant). By forcing the resonant system of the wings and thorax to oscillate at frequencies other than the resonant frequency, faster muscle contraction in the cold could generate more excess heat at the expense of mechanical efficiency (Ivanov, 1989). Moreover, hummingbird flight muscles are formed exclusively of one fiber type (fast-twitch oxidative glycolytic, FOG), with noticeable cell-to-cell homogeneity (Rosser and George, 1986; Hochachka, 1994). This fiber ultrastructural homogeneity implies homogeneity in biochemistry and physiology. Rayner (1985) suggested that such homogeneity of fiber types may constrain the flight muscles to function as a 'fixed gear' during flapping flight, and it may also suggest an adaptation to a resonant mechanical system (Hill, 1950; Pennycuick, 1990). In conclusion, deviation from preferred resonant frequencies represents a plastic behavioral response to thermal demands in hovering hummingbirds.

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