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S22-2 Metabolic aspects of torpor in hummingbirds

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Abstract Tropical species of hummingbirds generally use nightly torpor during which they defend body temperatures (T_b) of between 12 and 20°C. We review metabolic aspects in several Brazilian species covering the three phases of the torpor cycle: entrance, basic state and arousal. The entrance phase is characterized by initial rapid decline in metabolic rate (MR), apparently related to abandonment of cold-induced shivering. This drop is then followed by a much slower decrease in MR, possibly due to a Q10-effect of the lowered body temperature. Hence, active metabolic depression does not seem to be involved. During the basic state phase of torpor, hummingbirds will respond to low ambient temperatures by an increased MR, often to values which exceed their basal metabolic rates. At the circulatory level, changes in blood oxygen transport are accommodated mainly by an increase in stroke volume rather than in heart rate. During the arousal phase, the metabolic rate increases noticeably, reaching peak rates of oxygen consumption nearly indistinguishable from those values measured during hovering flight. The achievement of such high levels of MR during arousal is even more remarkable considering that the peak rates of MR occur at T_b of about 32–35°C, considerably below T_b during active flight (>40°C). These results clearly demonstrate the very high degree of expansibility in the rate of oxygen consumption in hummingbirds.

Key words Energy expenditure, Flight, Hummingbirds, Temperature regulation, Torpor

1 Introduction

The majority of hummingbirds (Trochilidae) are very small, some weighing just two grams and over 90% of species with body masses less than 8 grams (Dunning, 1993). Hummingbirds thus include some of the smallest homeotherms known. Small body size is generally associated with high metabolic costs, and so also with the potential danger of negative energy balance. As a consequence, hummingbirds are renowned for their use of nightly torpor, during which they regulate their body temperature at levels just a few degrees above ambient temperature (Bicudo, 1996; Bech et al., 1997). This in turn greatly reduces nightly energy expenditure. When one considers the high costs of energy expenditure during flight, thermoregulatory needs in the cold and low metabolism during torpor, it is clear that hummingbirds must be able to adjust their energy expenditure across a very large range of values (Bicudo and Chaui-Berlinck, 1998). Hence, both the respiratory and the circulatory systems must show considerable flexibility.

Here we review several aspects of the use of torpor in hummingbirds, focusing on those metabolic characteristics concerned with changes in oxygen consumption during nightly torpor.

2 Materials and methods

The study was carried out at the Museu de Biologia, at Santa Teresa in Espirito Santo, Brazil (19°55'S, 40°36'W), at about 700 m a.s.l., on the following species: frilled coquette *Lophornis magnifica* (~ 2.7 g), amethyst woodstar *Calliphlox amethystina* (~ 2.7 g), versicolored emerald *Amazilia versicolor* (~ 4.1 g), Planalto hermit *Phaethornis pretrei* (~ 5.2 g), white-throated hummingbird *Leucochloris albicollis* (~ 5.4 g), black jacobin *Melanotrochilus fuscus* (~ 7.5 g), Brazilian ruby *Clytolaema rubricauda* (~ 7.7 g), and swallow-tailed hummingbird *Eupetomena macroura* (~ 8.7 g). All species were common breeding birds in the study area (Ruschi, 1982), where they were accustomed to feed at artificial feeders. Individuals of all species studied were easily caught at these feeders.

Rates of oxygen consumption (VO_2) were measured by flow-through respirometry: an individual hummingbird was placed in the respirometry chamber during the evening and was taken out again the next morning. The volume of the metabolic chamber was 650 ml for the smaller species or 1 880 ml for the larger. Airflow rate was kept at approximately 70 ml min^{-1}. Because of low rates of oxygen consumption during torpor, we were obliged to use a low flow-to-volume ratio. When calculating values of oxygen

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consumption, however, we corrected for the washout-characteristics of the system with the method described by Niimi (1978). Hence we obtained the instantaneous rate of oxygen consumption at any time. Changes in ambient temperature were created by circulating water from a thermostatically-controlled water-bath around the chamber.

VO_2 during hovering flight was measured by the method described by Berger and Hart (1972). Air was sucked continuously through a small tube attached to the top of an artificial flower connected to a small glass container of liquid sugar solution. When the hummingbirds were feeding, we were able to collect all expired air, and VO_2 during hovering flight was calculated by integrating the output signal. Total time feeding was recorded by an infrared detector placed above the artificial flower. All measurements of hovering VO_2 were recorded at "room" temperature (22–25 °C).

Body temperature (T_b) was measured with a copper-constantan thermocouple (California fine wire, type 00) placed subcutaneously and laterally on the pectoral muscle. The thermocouple was fixed in place with small pieces of adhesive tape. During measurement, the wing covered the subcutaneously placed tip of the thermocouple. Control experiments showed that such measurements of pectoral temperature did not differ by more than 0.2–0.3°C from simultaneously measured rectal temperature (Bech et al., 1997). Ambient temperature (T_a) was measured using a similar thermocouple. All thermocouples were connected to a Data Translation (DT 2805) A/D converter, via a DT-757 Terminal board, and processed by a computer using a Labtech Notebook data acquisition program.

Heart rates were measured with thin electrodes made from 0.4 mm insect needles that were inserted subcutaneously at the neck and the caudal part of the sternum. The signals were amplified using a Grass amplifier and the electrocardiograms recorded on a Brush pen recorder.

3 Results and discussion

3.1 The entrance phase of torpor

A central topic, which has been widely debated, is whether homeotherms enter torpor by active metabolic down-regulation. Is the drop in metabolic rate caused by active metabolic depression or is it caused only by a passive Q_{10}-effect of a lowered body temperature? Several studies, both empirical and theoretical, have addressed this question, and there have been arguments both for and against an active component (Geiser, 1988; Snyder and Nestler, 1990; Malan, 1993; Song et al., 1996).

We obtained simultaneous measurements of T_b and VO_2 during complete torpor bouts from six of the studied species. For these species we also obtained measurements of basal metabolic rate (BMR) at thermoneutral conditions. All entries into torpor were qualitatively alike and showed a two-step pattern (Fig. 1: Brazilian Ruby). First there is a sharp drop in oxygen consumption until it reaches the predicted BMR-level; this is probably related to an abandonment of cold-induced thermogenesis (i.e., shivering). Through the second step, VO_2 changes at a much slower rate, generally following the predicted changes in the BMR. The predicted change in BMR was calculated using the actual measured changes in T_b, the measured values of BMR and assuming a Q_{10}-effect of 2.5. It is obvious from the results (Fig. 1), that the overall change in metabolic rate from normothermia to torpor, need not involve active depression of metabolism, for VO_2 is not at any time substantially below the BMR-level.

The same general two-step entry is also manifested when individual hummingbirds are exposed to such low ambient temperatures that a regulated torpor is induced. In such cases, metabolic rate will first fall quickly to a low level and, as the defended body temperature is approached, then secondarily increase once more to the level required for maintaining T_b during torpor. Overall results thus indicate that no active metabolic depression is necessary for hummingbirds to enter torpor, at least in the species studied. A similar conclusion was reached by Song et al. (1996) for

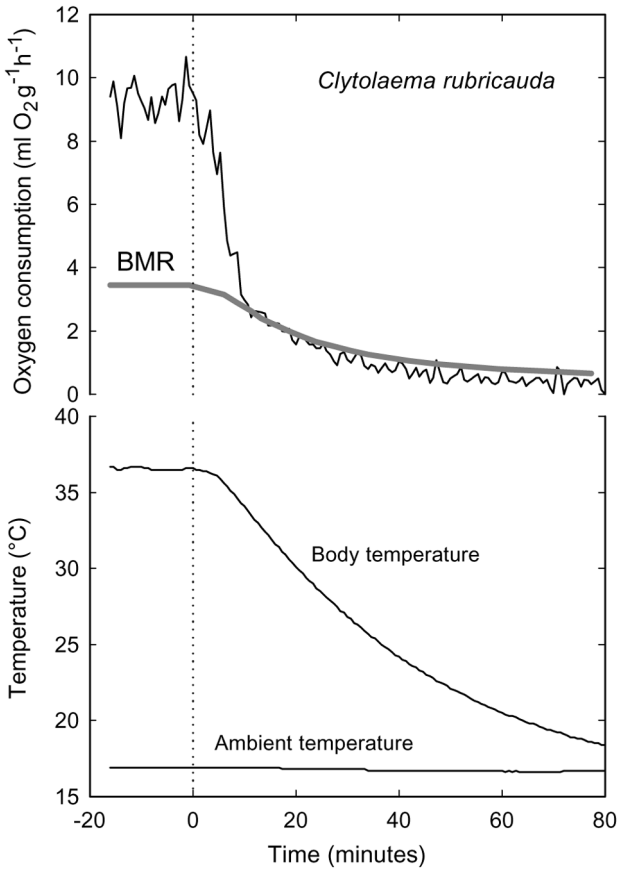


Fig. 1 Changes in oxygen consumption, and body and ambient temperature during entry into torpor in *Clytolaema rubricauda*

The thick line denotes the level of BMR during both normothermia (measured value) and during the entrance phase (based on the measured body temperature and assuming a Q_{10} of 2.5). The vertical stippled line indicates the initiation of body temperature decrease.

small mammals entering torpor, also with a two-step entry.

3.2 The basic state of torpor

In the tropics, species of hummingbirds employ nightly torpor to conserve energy, during which they defend body temperatures between 12 and 20°C (Bech et al., 1997). This implies that exposure to lower ambient temperatures will induce regulatory thermogenesis: torpid hummingbirds must necessarily increase their metabolic heat production during exposure to low T_as. The corresponding high values of VO_2 may actually reach values that exceed its thermoneutral value. An important question then arises: does the low body temperature constrain oxygen transport mechanisms?

The regulation of T_b during torpor is brought about by a several-fold increase in heat production to compensate for the increased body-to-ambient temperature gradient and hence increased heat loss. During this regulation, heart rate changes only slightly (Fig. 2). As a consequence, however, the stroke volume, and hence the oxygen pulse (the amount of oxygen transported per heart beat), must increase considerably. In such situations, the oxygen pulse may reach values of up to 0.7 µl g^{-1} $beat^{-1}$, which otherwise only occurs during flight (Fig. 2).

Our data indicate that use of an increased oxygen pulse for altering oxygen uptake is especially important in two situations: during hovering flight and during regulated torpor. During flight, the very high levels of oxygen consumption (more than 10-times the resting thermoneutral rate) apparently cannot be met solely by an increased heart rate (only 3-fold increase). With the heart beating at its maximum, the birds need to increase the oxygen pulse as well. During regulated torpor, constant low body temperature apparently limits increases in heart beat; and so the birds are forced to increase the oxygen pulse instead. In this context, it is noteworthy that hummingbirds have much larger relative heart masses than other birds (Bishop and Butler, 1995). A larger heart mass would presumably provide a relatively much larger stroke volume, and in turn confer advantages in terms of enlarged cardiac output and aerobic capacity. This may be especially important during regulated torpor, when low body temperature may constrain the use of heart rate in oxygen transport.

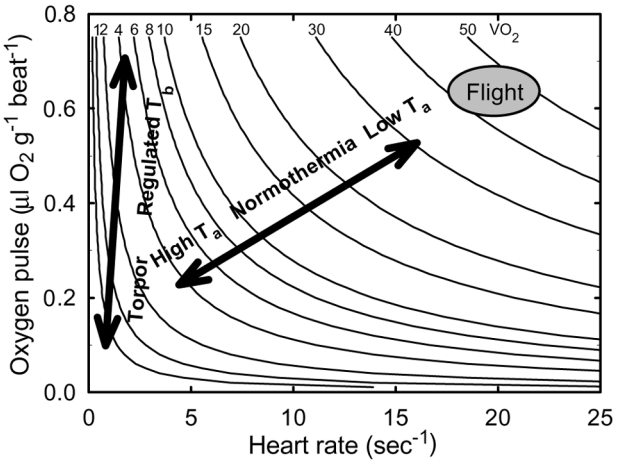


Fig. 2 Normogram showing the combinations of heart rate (HR) and oxygen pulse (OP) for the two smallest species studied The amount of oxygen taken up per heart beat is calculated as VO_2/HR. Isopleths show the resulting values of VO_2 expressed in ml O_2 g^{-1} h^{-1}. The two arrows indicate the combinations of HR and OP during torpor (left) and during normothermia (right).

3.3 The arousal phase of torpor

During arousal, metabolic rate increases sharply to a peak value which may be much higher than that during daytime homeothermy. Earlier reported magnitudes of these peaks have varied a great deal, probably because different methods have been used for calculating rates of oxygen consumption; some early studies made no attempt to account for the rapid changes when calculating it by the flow-through method. We accounted for washout characteristics when calculating the instantaneous level of oxygen consumption and found peak rates to vary between 17 and 41 ml O_2 $g^{-1}h^{-1}$ (species-specific mean values; Fig. 3). In some of our species, peak rates reached actually correspond to an increase in oxygen consumption of about 100 times the lowest level recorded during the torpid state.

To compare these values to values of VO_2 during flight, we measured VO_2 during hovering flight as well, finding little difference in peak rates during either activity (Fig. 3). The achievement of such high rates of oxygen consumption during arousal is even more remarkable considering that the peak values of VO_2 occur at a time when body temperature is still increasing and, at between 32 to 34°C, well below body temperature during active flight.

4 Conclusions

These results demonstrate a very high degree of expansibility in the rate of oxygen consumption in hummingbirds. Hummingbirds can operate at levels equal to basal metabolic rate, whether they are at thermoneutral

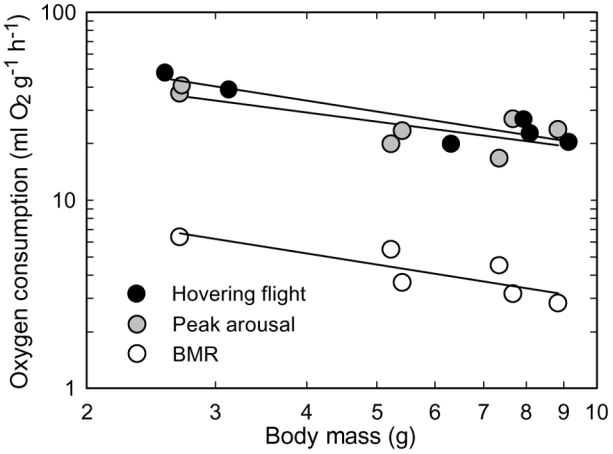


Fig. 3 BMR, peak VO_2 during arousal from torpor, and VO_2 during hovering flight, as a function of body mass in some Brazilian hummingbirds

condition and maintaining a high T_b, or are exposed to very cold ambient conditions and defending torpid T_b by regulated thermogenesis. Additionally, they may generate equally high VO_2 values whether hovering for food or just sitting quietly at low T_b and warming up. There also appears to be a possible temperature constraint on the circulatory system, which torpid hummingbirds overcome by increasing their VO_2 to defend body temperature. In such circumstances, low body temperature may constrain the heart rate, making an increase in oxygen transport necessary.

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