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Unusual Metabolic Shifts in Fasting Hummingbirds

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Nectar is the main source of energy for hummingbirds (Suarez et al. 1986). They also prey on small insects, which serve as a protein supplement to their diet, although they can survive long periods feeding only on nectar (Brice and Grau 1991). Hummingbirds are among the smallest living endothermic vertebrates and, as a consequence of their minute body mass, have extremely high mass-specific metabolic rates. At the same time, they have limited space for food and/or energy storage. In addition, hummingbirds are only able to forage during the light phase of the day. Fat as substrate would seem to be the best alternative to address both problems. Fat has the highest energy delivery per unit mass among the different foodstuffs, and it does not need water for storage. Therefore, it is reasonable to expect hummingbirds to transform most of their carbohydrate intake into fat to overcome the starving hours of the night (Blem 1976, Powers 1991). Fat would guarantee not only the night-period survival, but also could be used to support migratory flights in a number of hummingbirds species that migrate (Suarez et al. 1990). Since fat is not the main constituent of hummingbirds food intake, it has to be biosynthesized from another item of the diet. Carbohydrates become the main candidates for this biotransformation.

The respiratory-exchange ratio (RER) is the ratio between carbon dioxide production ($\dot{V}\,CO_2$) and oxygen consumption ($\dot{V}\,O_2$). Under steady-state conditions, RER is equal to the respiratory quotient (RQ), which has specific values for different kinds of substrates metabolized by the animal. A RQ of 1.0 indicates the utilization of carbohydrates, and 0.7 indicates the use of fats. Values between these two extremes are achieved when proteins are used, or when a combination of carbohydrate, fat and protein oxidation represents the animal's overall catabolism. Soon after feeding, hummingbirds have respiratory quotients above 1.0 (Powers 1991). Such RQ values are probably explained by biosynthesis of fat from sugars (Powers 1991, Schmidt-Nielsen 1991), as proposed above. After the last feeding, the RQ drops, reaching values close to 0.7 (Suarez et al. 1990, Powers 1991). The use of fat during fasting conditions is well established among animals (Allen 1976, Schmidt-Nielsen 1991) and is the result of a high specific-energy delivery of this substrate.

Hummingbirds may or may not go into torpor dur-

ing the night, depending on the amount of food stored during the day. The mechanisms that signal whether the bird should go into torpor are still not clear, but there is an apparent inverse correlation between the amount of food stored and the depth/length of the metabolic depression in hummingbirds (Bech et al. 1994). A well-fed hummingbird may spend the whole night without going into torpor, whereas poorly-fed hummingbirds may go into torpor very early. Going into torpor has clear advantages in terms of energy savings, although the process has a nonneglegible energy cost, especially during arousal (Lasiewski 1963). When in torpor the animal becomes much more vulnerable to predators, and this constitutes a major disadvantage in terms of species survival. Thus, remaining awake and alert, if energy reserves permit, would be advantageous to hummingbirds. Our own observations of hummingbirds have shown that they may spend several hours after the last feeding without going into torpor, which means they can fast for long periods of time relying primarily on their food stores. The question then concerns the kinds of substrate used by hummingbirds during these prolonged periods of fasting to sustain their basic energy needs. We attempted to answer this question by measuring the oxygen consumption and carbon-dioxide production of a Brazilian hummingbird species, *Eupetomena macroura*, using an open-flow respirometry system. We were able to calculate its RQ during these prolonged periods of fasting.

Methods.—Hummingbirds were captured in the vicinities of the Biosciences Institute at the University of Sao Paulo (Sao Paulo/SP, Brazil) using a mist net (IBAMA license no. 128/91-DEVIS). The animals were trapped between 0700 and 1000, and were used for the experiments in the same day. They were kept in a 45 × 40 × 52 cm cage with a hummingbird feeder inside containing a 20% sugar solution. Some birds were fed just before the measurements began, and others had the feeder removed 2 to 3 h before the experiments. Fourteen *E. macroura* (body mass $\bar{x} = 8.4$ g, range 6.8–9.7 g) were used throughout the study. All the experiments were carried out from November 1991 to May 1992.

The animal chamber for the open-flow respirometry system consisted of a PVC tube (2.54 cm internal diameter and 20 cm length). The ends of the tube had threads allowing two lids to be screwed in. One end had an ambient-air inlet, and the other a mixed-air outlet connected to the sensors by polyethylene tubing. The mixed air was dried (in a silica-gel chamber) and then passed through the CO_2 analyzer (AMETEK CD-3A), O_2 analyzer (AMETEK S-3A/I), pump (AMETEK R2), and flow meter (Omega Engineering Inc., FL-1495-G). Body temperature (T_b) was measured by means of a thermocouple (TT-T-40, copper/constantan, Omega Engineering Inc.) placed on the lateral thorax of the animal under the wing, and fixed by common surgical tape. Another thermocouple (TT-T-30) was placed through one of the ends of the chamber to read ambient temperature. The thermocouples were connected to a digital thermometer (Omega Engineering Inc., model 199) previously calibrated (±0.2°C accuracy). Air flow was set to 267 ml/min (outlet), maintained constant throughout the experiment, and corrected to STPD before the final calculations. Before each experiment, the oxygen sensor was calibrated with dried ambient air to a reading of 20.94% (Hill 1972, Withers 1977, Bartholomew and Lighton 1986, Powers 1991; 0.2094 is value for room air without carbon-dioxide absorption). It was always rechecked after this procedure, and the reading was never more than 0.03% from the calibrated value. The CO_2 analyzer was calibrated against 11.92 and 5.34% carbon-dioxide mixtures (AGA S/A) and its zero was 0.03%. Zero and span calibrations for both CO_2 and O_2 sensors were performed strictly in accordance with manufacturer instructions. Both sensors showed linear responses within the above ranges.

For seven experiments with *E. macroura*, ambient temperature was lowered from room temperature to between 10° and 14°C. This was achieved by placing the respirometry chamber inside a temperature-controlled water bath. The temperature changing rate was about 1.5° to 2.0°C per hour to induce torpor. The other seven were held at room temperature throughout the entire experiments. After the bird had been placed inside the chamber, we waited 15 to 25 min before attempting any gas measurement or inducing any temperature change. This period permitted both stabilization of the sensor readings and adjustment by the bird to the chamber. All values used in the calculations were the mean values obtained during periods of stable readings of at least 2 min (stable periods of several minutes were the rule, with readings varying no more than ±0.03% from a mean value). $\dot{V}O_2$ was calculated based on equation 3a given by Withers (1977) and RQ by the formula in Snapp and Heller (1981) for dependent measurements of fractional oxygen and carbon-dioxide concentrations. Results were checked by converting the oxygen readings into CO_2-free readings and calculating RQ values as independent measurements. The results were exactly the same.

Results.—All data presented were obtained from animals out of torpor. We define torpor as a combination of lowered oxygen consumption (at least fivefold decrease from a mean resting value of 4 ml $O_2 \cdot g^{-1} \cdot h^{-1}$; pers. obs.) and lowered body temperature (since superficial temperatures were measured, we did not accept them alone as an indicator of metabolic depression).

Time 0 for all experiments was set as the moment of the last feeding (known or supposed, when feeder was removed from cage). The two groups of *E. macroura* behaved in a similar manner. Initially, after the last feeding, they presented RQ values above 1.0. During the second hour, RQ values varied around 0.8

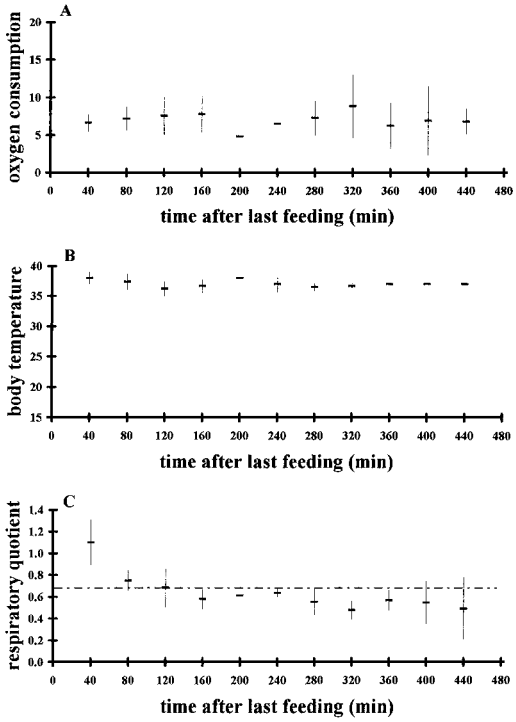

Fig. 1. (A) Oxygen consumption ($ml \cdot g^{-1} \cdot h^{-1}$), (B) body temperature (°C), and (C) respiratory quotient (dashed line indicates RQ of 0.70) as function of time for seven specimens of *Eupetomena macroura*. Ambient temperature ranged from 24° to 27°C. Time 0 set when hummingbirds had their last feeding. Values $\bar{x} \pm$ SD.

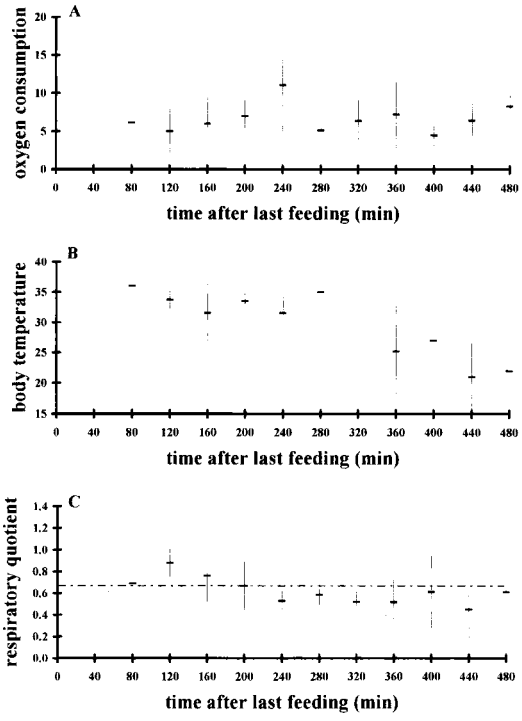

Fig. 2. (A) Oxygen consumption ($ml \cdot g^{-1} \cdot h^{-1}$), (B) body temperature (°C), and (C) respiratory quotient (dashed line indicates RQ of 0.70) as function of time for seven specimens of *Eupetomena macroura*. In this experiments, ambient temperature lowered to 10°–14°C. Although hummingbirds had a decrease in body temperature, there was no decrease in oxygen consumption and, thus, torpor was not elicited. Values $\bar{x} \pm$ SD.

and, during the third hour, unusually low RQ values (i.e. <0.67) were observed. These low RQ values were predominate during subsequent hours of the experiments and were not correlated to entry into torpor.

Figure 1 shows oxygen consumption, body temperature, and respiratory quotient as a function of time from last feeding for the seven experiments at room temperature. Figure 2 summarizes data for the seven *E. macroura* that were exposed to decreasing ambient temperatures.

Discussion.—References to low RQ values (below 0.70) are uncommon in the literature. Kleiber (1961) cited several papers dealing with the problem. Those studies are basically contradictory, and provide no firm answers. Possible explanations for low RQ values, such as protein metabolism in birds, were not considered plausible by Kleiber. Also, theoretical estimates of ATP and muscle protein breakdown, leading to uric acid production in order to lower RQ to the values presented in this study, reveal the unfeasibility of such a mechanism. In fact, the change from urea to uric acid as the final nitrogen waste product in birds will result in RQ values close to 0.667 (Kleiber, 1961), which are well above those we describe.

Fat catabolism results in respiratory quotients around 0.70 as a consequence of the release of NADH and $FADH_2$ molecules during beta-oxidation without CO_2 production. The exact RQ value reached depends on the number of carbon atoms in the fatty-acid chain but, as an average number, 0.70 is a very good estimate. This is the lowest value expected for animals in general that use fat stores as their only source of energy. Brief periods of RQ drops have been described in mammals prior to daily torpor or hibernation (Snapp and Heller 1981, Malan et al. 1985, McArthur et al. 1990, Nestler 1990). However, these drops are of small amplitude (ca. 0.08), short duration (12 to 16 min), and terminated with the onset of a metabolic depression. On such occasions, the fall in

RQ is not due to a metabolic change, but rather to a decrease in ventilation causing a respiratory acidosis as a result of CO_2 retention. We see no reason to suppose that a respiratory acidosis is the explanation for low RQ values observed in hummingbirds. Metabolic depression (torpor), when it occurred, began long after a fall in RQ, which in turn were of great amplitude and duration. As an example, we calculated an arterial CO_2 tension around 900 torr as a consequence of CO_2 retention during 1 h at a $\dot{V}\,O_2$ of 4 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ (mean value measured during such periods). Such a level of arterial CO_2 tension would be totally unbearable. Recent evidence from total body plethismography (Chaui-Berlinck unpubl. data) reveals no significant changes in minute volume ventilation in hummingbirds during periods of low RQ. Furthermore, during metabolic depression, low RQ values still persisted (see Results).

In order to attain RQ below 0.70 during beta-oxidation, acetyl-CoA must be formed, but somehow not enter into the Krebs cycle. Thus, there will be a diminished CO_2 delivery, lowering the RQ. Ketone-body formation shunts acetyl-CoA from the Krebs cycle and could perhaps explain our results. It is well established that the appearance of ketone bodies during fasting conditions is a common pattern observed in mammals and birds (Lehninger 1972, Swain 1992). However, although ketone-body formation might appear as a reasonable explanation for our results, its use restores the RQ to the original value for fatty-acid oxidation (i.e. 0.70) and, therefore, provides no support for the above hypothesis.

We think that the low RQ obtained is the result of true changes in catabolism. Since hummingbirds store fat and seem to depend on this substrate to overcome periods of food deprivation, changes in fat beta-oxidation might be a possible explanation for the observed pattern. At present, the biochemical pathway that could result in the low RQ observed in fasting hummingbirds is not known. There is a broad range of low RQ variation within and among individuals. This could be pointing to a mixed metabolism resulting in nonstable and imprecise low RQ values. Further biochemical studies providing measurements of ketone-body formation and concentration, amino acid turnover, lipid composition, etc., should be performed during these periods of low RQ.

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Consumption and Caching of Food in the Northwestern Crow (*Corvus caurinus*)

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Foraging behavior can be divided into two distinct types. When "feeding," a forager ingests all the food it captures. When "provisioning," the resources are delivered to a mate, to a cache site, or to offspring. These foraging modes are distinct because the costs and benefits differ (Ydenberg et al. 1994). Unlike feeders, provisioners pay time and energy costs for delivery and travel to and from the foraging site, and only some of the food they collect is consumed. The remainder is delivered to others, or is stored for later consumption. Thus, provisioners share (or defer) the benefits of foraging, but bear all the costs. Due to these differences, the relative profitability of food items or feeding sites depends on the foraging context.

The Northwestern Crow (*Corvus caurinus*) exhibits a natural daily rhythm in foraging mode, feeding at high tide when food is less available, and provisioning food to cache sites at low tide (James and Verbeek 1983). We simultaneously presented crows with two experimental foraging sites (patches) offering different feeding rates. We predicted that when feeding at high tide, crows would prefer the patch with the higher feeding rate. However, the provisioning rates attainable from the patches were nearly identical, and we predicted that when provisioning at low tide, the crows would be indifferent between the two.

Methods.—The study was carried out during May and June of 1993, on Diana Island near the Bamfield Marine Station, British Columbia, Canada (125°11.5′W, 48°51′N). The two patches were planks of driftwood placed 9 m apart high up on the beach so that they were accessible at all tides. We placed 120 empty mussel valves in a regular array at a density of about 25 valves/m^2 in each patch. Patch type A had one piece of Purina Puppy Chow hidden under each valve, while patch type B had three pieces under one-third of the valves (chosen randomly). Crows foraged by turning each valve over and picking up the puppy chow pieces one by one. Due to the different dispersion of Puppy Chow pieces under the mussel valves, crows could find food slightly faster in patch A (1 s of search per piece) than in patch B (1.25 s of search per piece). Crows ingested these pieces when feeding, but when provisioning held them in the beak and throat, transporting them into the nearby forest where the pieces were cached.

We calculated the feeding rates attainable in the two patch types as the net energy gain per piece (energy per piece minus the energy costs of search and handling) divided by the time required to search for (1.0 s in patch A and 1.25 s in patch B) and handle (0.5 s) each piece. We estimated the cost of search as 14.4 W (4 × BMR, using 3.6 W as BMR; see Richardson and Verbeek 1986), and the cost of handling as 7.2 W (2 × BMR). The advertised energy content of Purina Puppy Chow is 8 kJ per piece. These calculations revealed that crows could feed at a rate of 5.3 W in patch A, and 4.3 W in patch B.

Provisioning crows gathered a load of (almost always) three pieces and made a trip to the forest to cache the pieces before returning to collect another load. We calculated the provisioning rate attainable from each of the patch types as the net energy gain per provisioning trip: energy in three pieces minus the energy costs of search (3 s in patch A and 4 s in patch B at 14.4 W), handling (1.5 s at 7.2 W) and delivery (30 s at 9 × BMR, or 32 W), divided by the time to collect and store each load. The long duration of the caching trip (30 s) relative to the load collection time so diluted the impact of the slight differences in collection time between the patches that the attainable provisioning rates were effectively equal at 0.65 kW, differing by less than 3%.

A group of 9 to 12 crows, very likely the same individuals, frequented the beach and quickly learned the experimental procedure, often waiting nearby for trials to begin. A trial was conducted by preparing both patches and, from a viewing site 50 m away, counting at 5-s intervals the number of crows foraging in each patch, until one of the patches was exhausted. Individual crows often moved between patches during trials. The average number of crows was scored for both patches for each trial. Each trial took between 15 and 30 min to complete and several