Comparative Biochemistry and Physiology, Part A 157 (2010) 291–296

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Metabolic rate and specific dynamic action of the Red-legged Honeycreeper, a nectar-feeding Neotropical passerine

Astolfo Mata *

Laboratorio de Biología de Organismos, Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC) Apdo. 20632, Caracas 1020-A, Venezuela

ARTICLE INFO

Article history:
Received 1 March 2010
Received in revised form 19 July 2010
Accepted 24 July 2010
Available online 30 July 2010

Keywords:
Oxygen consumption
Carbon dioxide production
Respiratory quotient
Specific dynamic action
Nectar-feeding
Cyanerpes cyaneus

ABSTRACT

Rate of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) were measured in the Red-legged Honeycreeper (*Cyanerpes cyaneus*, mean body mass 14.0±0.1 g) at ambient temperatures (T_a) between 15 °C and 35 °C to determine the basal metabolic rate (BMR). $\dot{V}O_2$ in response to the light–dark cycle and the specific dynamic action (SDA) effect was also investigated. BMR was estimated to be 2.9 mL O_2 g^{-1} h^{-1}, 10% lower than expected according to the Aschoff–Pohl relationship for passerines and 12% higher than expected following Mckechnie and Wolf's (2004) equation. Below 25 °C, $\dot{V}O_2$ was linearly related to T_a. Body temperature averaged 40.2 °C and was not affected by T_a over the range of temperature tested. The SDA was demonstrated at 20 °C by a two fold increase in $\dot{V}O_2$ compared to pre-feeding levels. The honeycreepers showed a marked light–dark $\dot{V}O_2$ cycle, with a mean reduction of 46% at night. During the night, birds rely on their body reserves as deduced from the respiratory quotient (RQ) values. Honeycreepers show a metabolic rate higher than predicted by allometry, marked diel fluctuations in their metabolic rates and a moderate SDA effect despite of the simplicity of nectar as food.

1. Introduction

Although at tropical latitudes seasonal changes in environmental temperatures and photoperiod were not as drastic as those experienced in temperate climes, individuals of endothermic species living year-round in the tropics must face pronounced dry and wet seasons (Leigh *et al.*, 1996). This seasonality causes variations in the quality and availability of food and thus in foraging habits. Considering the huge diversity of bird species and the wide variety of food habits, studies on the physiological and behavioral responses of Neotropical birds to changes in environmental temperature are scarce and restricted to lowland tropical forest species (Weathers, 1997; Wiersma *et al.*, 2007a, b).

Energy is thought to play an important role in shaping behavior, ecology and physiology in animals (Berteaux *et al.*, 1996). Metabolism reflects the cost of living of an organism. Basal metabolic rate (BMR) is one of the most commonly measured physiological traits in endotherms (Burness *et al.*, 1998; Kvist and Lindström, 2001) and varies greatly both inter- and intra-specifically. BMR is defined as the rate of energy transformation in an endothermic organism at rest in a post-absorptive state, measured within its thermoneutral zone (Robbins, 1993). Exogenous factors influencing BMR include time of day, temperature, rainfall, season, length of time in captivity, diet, and habitat (Pohl, 1969; Weathers and Caccamise, 1978; Weathers, 1979; McNab, 1988; Warketin and West, 1990; Weathers, 1997; Cooper *et al.*, 2002; McNab, 2009).

Small birds have a large surface area to volume ratio, which means that they show a high rate of heat loss to the environment (Calder, 1984). To compensate for this heat loss, small birds have high mass-specific metabolic heat production (Calder, 1984). The metabolic rate values reported for most tropical species investigated so far are low, which have led to the conclusion that a low metabolic rate is characteristic of tropical birds as a whole (Vleck and Vleck, 1979; Hails, 1983; Bosque *et al.*, 1999; Wiersma *et al.*, 2007b). However, some studies have found that certain species of tropical birds have higher metabolic rate values than expected (Vleck and Vleck, 1979). To meet maintenance costs related to daily functions and metabolism, small birds must feed frequently on high quality foods. After the ingestion of a meal occurs a rise of the metabolic rate of a resting animal. This process is referred to as specific dynamic action (SDA) and reflects numerous processes involved in the breakdown, absorption, and post-absorptive processing of food (McCue, 2006). However, in Neotropical nectar-feeding birds this relationship has not been studied.

Nectarivorous birds play an important role in the ecology of rain forests as they contribute to the pollination of trees and shrubs (Snow and Snow, 1971; Feinsinger, 1978). Although in the American tropics, hummingbirds are the main avian floral visitors, some passerine birds belonging to different families [Traupidae (tanagers, honeycreepers, Bananaquit), Emberezidae (flowerpiercers), and Icteridae (blackbirds)] show varying degrees of dependence on nectar (Stiles, 1981). As nectar supplies vary over time, spatially, and with respect

* Tel.: +58 212 504 1840; fax: +58 212 504 1088.
E-mail addresses: amata@ivic.gob.ve, astolfomata@gmail.com.

1095-6433/$ – see front matter © 2010 Elsevier Inc. All rights reserved.
doi:10.1016/j.cbpa.2010.07.018

to their nutritional value, passerine nectarivores often need to forage for other food sources such as fruits and insects. Nectar is a sugar rich liquid food source that provides large amounts of energy to those birds able to harvest it. The most common nutrients in nectar are sucrose, fructose, and glucose but the concentration and ratio of these sugars vary widely between flower species (Baker and Baker, 1983; Martínez del Río *et al.*, 1992).

The Red-legged Honeycreeper, *Cyanerpes cyaneus*, is a Neotropical nectar-feeding bird distributed throughout northern South America (from the Brazilian Amazon upwards), the Guyanas, and Central America. Its diet includes varying proportions of nectar, fruits, and arthropods (Isler and Isler, 1990; Hilty, 2002) with nectar being the most important energy source. This species is distributed throughout the tropics and subtropics, over a wide altitudinal range, and has to cope with energetically challenging environmental conditions. In this study I report on the basic metabolic and thermoregulatory parameters for the Red-legged Honeycreeper inhabiting north east Venezuela and investigate the effect of food ingestion on metabolic rate.

The BMR, body temperature (T_b), RQ and SDA were determined in long-term captive Red-legged Honeycreepers.

2. Materials and methods

2.1. Birds and their maintenance

Nine honeycreepers (*Cyanerpes cyaneus*) (two females and seven males) were captured in mist nets in the Turimiquire mountain range in Sucre state (northeastern Venezuela) in November 2004, May 2005 and March 2007. Birds were color-banded and weighed to the nearest 0.01 g with an electronic balance (Ohaus Scout II). They were housed in cages measuring 70×50×40 cm. Each cage had several perches, feeders and water in a dish for bathing and drinking. Birds were exposed to natural light conditions. Ambient temperature varied between 18 and 22 °C during the experimental period (end of January–beginning of May, 2008). They were fed *ad libitum* with artificial food (CEDE, Belgium), a sucrose solution and water. Birds were very active in captivity; flying and hopping constantly.

2.2. Basal metabolic rate

To determine basal metabolic rate (BMR); oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) of nine honeycreepers in relation to the ambient temperature (T_a) were measured. Briefly, birds were introduced into small cylindrical wire mesh cages to ensure restricted locomotor activity. The base was 1 cm above the bottom of the chamber which was supplied with a perch. Birds were fasted for at least 3 h before being placed in a 700 mL Plexiglas metabolism chamber fitted with inlet and outlet ports. Birds were weighed at the start and the end of each experiment. To maintain a constant temperature, the metabolic chambers were placed inside a 15 L, temperature-controlled cabinet (± 0.5 °C). The temperature inside the cabinet was measured continuously using a thermocouple. BMRs were determined when birds were in a post-absorptive state and during the non-active period of their daily cycle. Metabolic measurements were made between 1800 and 0600 h. $\dot{V}O_2$ and $\dot{V}CO_2$ rates were measured at 15, 20, 25, 30 and 35 °C with a flow-through system using a Sable Systems FOXBOX (Las Vegas, Nevada). Each bird was measured at a different T_a on each occasion before T_a was changed after about 3 days that took to record all 9 birds at each T_a. A four channel Sable System multiplexer (Model TR-RM4) was used to control the flow of air to each of the three chambers holding individual birds, and to the chamber used for baseline recordings. The air flow rate was 200–300 mL min^{-1} and was maintained by the mass-flow controller of the FOXBOX (2% accuracy of reading). Water vapor and carbon dioxide were removed from the air using Drierite® and soda lime, respectively. Airflow through the chambers was maintained even when the metabolic rates were not being measured by the multiplexer. Measurements were recorded sequentially every other 33 min for each bird during each of the 120-min long experiments. Baseline samples (5 min) were taken from an empty chamber before and after sampling each experimental chamber. This cycle was repeated throughout the night. Measurements commenced at 1800 h and lasted 2, 4 or 6 h (at $T_a = 30$ °C and 35 °C the birds were only measured for 2 h to reduce the possibility of hyperthermia). Data were recorded using the ExpeData software package (Sable Systems, Las Vegas, NV, US). $\dot{V}O_2$ at each experimental T_a was calculated as the lowest five-min mean value of instantaneous oxygen consumption. The respiratory quotient was determined as $RQ = \dot{V}CO_2 / \dot{V}O_2$. The gas analyzers were calibrated before each trial using 99.995% pure N_2, 0.95% CO_2 (PraxAir, Caracas, Venezuela) and dry outside air (set to 20.95% O_2 and 0.03% CO_2). Metabolic rates were expressed as mL O_2 g^{-1} h^{-1}.

2.3. Body temperature

Body temperature (T_b, to 0.1 °C accuracy) of all birds was recorded after each sampling. T_b was recorded with a digital thermometer (Digi-Sense) with a copper-constant thermocouple inserted into the cloaca at a depth of 0.5 cm.

2.4. Daily fluctuation of oxygen consumption and carbon dioxide production

Daily variations in $\dot{V}O_2$ and $\dot{V}CO_2$ were measured at an ambient temperature of 20 °C (mean T_a of natural habitats of *C. cyaneus*) for both fasted and fed birds. In the experiment with fasted birds, individual birds were weighed and immediately placed inside a wire mesh cage and the BMR was measured as described above. Measurements started between 1400 and 1500 h. For the experiments with fed birds, the birds were first introduced into a 3 L wire cage with a 5 mL feeder containing a 980 mM sucrose solution and a perch. The size of the cage allowed the birds to change position but impeded flight. The wire cage was then placed inside a 3 L Plexiglas metabolism chamber fitted with a thermocouple. The sucrose solution was available *ad libitum* during all experimental runs, but birds did not feed during the dark period. Each experiment lasted between 12 h and 24 h and included the whole dark phase of the daily cycle and part of the light phase. The metabolic chamber was introduced into the temperature controlled cabinet at 1100 h. The roof of the cabinet was made of transparent Plexiglas to allow natural light into the chamber, thus ensuring a natural photoperiod. The resultant values of the simultaneous measuring of $\dot{V}O_2$ and $\dot{V}CO_2$ were then used to calculate the RQ for each individual.

2.5. Specific dynamic action (SDA)

I measured the SDA for five of the honeycreepers, after a nocturnal fast. Birds were placed in a 3 L metabolic chamber between 0800 h and 0900 h and $\dot{V}O_2$ and $\dot{V}CO_2$ were measured during 4 h after which a 5 mL glass pipette with a 876 mM sucrose solution was introduced and kept in place for 60 min. Evaluations began 10 min after introducing the pipette inside the metabolic chamber. At 1400 h the feeder was removed and measurements were taken during another 3 h. $\dot{V}O_2$ and $\dot{V}CO_2$ rates were determined for each bird at 5-min intervals. All of these measurements were made at 20 °C under natural photoperiod. Honeycreepers were weighed before and after the experiment. The amount of food consumed was calculated after removal of the feeder; the volume of sucrose solution ingested was determined by the difference in contents before and after feeding time. I measured one bird per day, and the five birds were measured sequentially. All metabolic measurements were performed at 20 °C, which is within the normal range of temperatures found in the natural habitat of