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Thermogenic capacity of three species of fruit-eating phyllostomid bats

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ABSTRACT

This study evaluated the thermogenic capacity of three species of fruit-eating phyllostomid bats (*Carollia perspicillata*, *Sturnira lilium* and *Artibeus lituratus*) during the dry-cool and wet-warm seasons, by measuring changes in body mass, basal metabolic rate (BMR), maximal metabolic rate (MMR), nonshivering thermogenesis and shivering thermogenesis. Body mass was lower, on average, during the dry-cool season and all species of fruit-eating bats showed an increase in oxygen consumption after noradrenaline injection and after exposure to a He–O_2 atmosphere. However, the magnitude of this increase was similar in both seasons. BMR also did not vary between seasons. Although, our results showed for the first time that all three species studied were able to increase thermogenesis by both nonshivering and shivering thermogenesis, we did not find significant differences in any thermoregulatory variable measured when comparing data from the two different seasons. Probably the difference in the mean and variance of the temperature profile between seasons were not strong enough to alter the thermogenic capacity of these species. Furthermore, the use of alternative physiological (torpor) or behavioral (huddling) strategies might have alleviated the need to trigger energetic-costly thermogenic responses.

1. Introduction

All processes of combustion in the body result in heat production and can, therefore, be called thermogenic (Cannon and Nedergaard, 1998). In mammals these processes involve continuous and obligatory heat production (obligatory thermogenesis) by many organ systems. The basal rate of metabolism (BMR) is a reflection of the obligatory thermogenesis in resting mammals within the thermoneutral zone, with the heat generated being enough to sustain a constant internal body temperature (T_b). As ambient temperature (T_a) decreases below the lower critical temperature, the extra heat needed to maintain a constant T_b is supplied by the so-called thermoregulatory thermogenesis. These processes involve shivering thermogenesis, where heat is generated by the contraction of skeletal muscles, and nonshivering thermogenesis, where extra heat is mostly generated by cellular processes in the brown fat under the control of catecholamines (noradrenaline) released by the sympathetic nervous systems (Cannon and Nedergaard, 2004). The maximum amount of heat that a mammal can produce to maintain a constant T_b can be measured as the maximum metabolic rate (MMR) during cold exposure, which is the result of the addition of BMR, nonshivering and shivering thermogenesis (Wunder and Gettinger, 1996; Nespolo et al., 2001a). Therefore, MMR may vary because of changes in any of the former variables. Thus, quantifying how these variables are modulated is essential to understand the diversity in thermoregulatory strategies displayed by mammals to cope with changes in their thermal environment.

Bats (Mammalia: Chiroptera) are one of the most diverse group of mammals, and this diversity can be noticed by their remarkable array of thermoregulatory strategies (Speakman and Thomas, 2003). However, analyses of this diversity in terms of thermogenic capacity have only been assessed by the quantification of the relationships between air temperature (T_a), T_b and metabolic rate (for a recent review see (Speakman and Thomas, 2003)). Although the obligatory component of the thermogenic capacity (BMR) can be quantified with this protocol, it is uncertain to the extent by which the MMR obtained in such analysis reflects the maximum thermogenic capacity, as measured by more efficient protocols such as exposure to a Helium–Oxygen (He-O_2) atmosphere (Rosenmann and Morrison, 1974). We are aware of only a single study in bats that assessed MMR using this protocol (Canals et al., 2005), but this study did not separate the components responsible for MMR. Alternatively, few studies that provided indirect or direct evidences of shivering and nonshivering thermogenesis in bats (Heldmaier, 1989; Leitner and Nelson, 1967; Noll, 1979; Trayhurn et al., 1991) did not provide data on MMR. Thus, notwithstanding the wide literature about thermal biology of bats, and the vast amount of data on the obligatory component of the thermogenic capacity for these mammals (BMR (Speakman and Thomas, 2003; Cruz-Neto and Jones, 2006)), there is still a lag on the knowledge about the magnitude of the maximum

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thermogenic capacity of bats, and the relative contribution of nonshivering, shivering and BMR for this capacity. In this study, our first aim is to fill this gap by measuring the maximum thermogenic capacity, and its components, in 3 species of fruit-eating bats from the Family Phyllostomidae: *Carollia perspicillata*, *Sturnira lilium* and *Artibeus lituratus*. These 3 species of bats occurs syntopically, but differs widely in body mass (Nowack, 2004) and, thus, one might expect variations in the magnitude of their thermogenic capacity and use of thermoregulatory strategies.

Laboratory studies on rodents showed a high degree of phenotypic plasticity in the maximum thermogenic capacity after cold exposure, usually mediated by changes in nonshivering thermogenesis (Li and Wang, 2005; Wang et al., 2006; Zhang and Wang, 2007), but see also (Nespolo et al., 1999). Albeit being equally flexible, changes in BMR due to acclimation to cold conditions, on the other hand, have not been reported as a universal response (Wunder and Gettinger, 1996). It is important to emphasize that most of these studies have analyzed the thermogenic plasticity to thermal stresses induced during acclimation, which may or may not be similar to the animals' responses in their natural habitat (acclimatization). Lovegrove (2005) reviewed the acclimatization responses of mammals and found that a reduced BMR and body mass (Dehnel effect), and an increased thermogenic capacity (due to changes in nonshivering thermogenesis), are the most common responses observed to cold acclimatization. We are not aware of any study that measured the phenotypic plasticity of the thermogenic capacity of bats, and/or its components. Thus, the second aim of this study is to determine the extent by which the thermogenic capacity and its main components vary when measured during two different periods of the year (dry-cool season and wet-warm season).

2. Material and methods

2.1. Animals: source and Husbandry

Fifty-five adult males of 3 species of phyllostomid bats, *Carollia perspicillata* ($n=6$ for dry-cool season and $n=7$ for wet-warm season), *Sturnira lilium* ($n=9$ for dry-cool season, and $n=12$ for wet-warm season) and *Artibeus lituratus* ($n=9$ for dry-cool season and $n=12$ for wet-warm season), were mist-netted at a semideciduous forest fragment located in the border of the municipality of Rio Claro and Araras, São Paulo State, southeast of Brazil (22°21′S and 47°28′W). This fragment is immersed amidst extensive areas of sugar-cane plantation and urban settlements and the nearby fragment, which has the same climatic and physiographic characteristics, is located ca. 70 km. Thus, migration between these fragments is an unlike event and, even if it did occur, individuals would have came from areas with similar climatic conditions.

After capture, bats were transferred and housed at large outdoor enclosures ($2\times4\times4$ meters) at the São Paulo State University at Rio Claro, southeast Brazil (22°23′S; 47°32′W), and exposed to natural regimes of photoperiod and T_a. Bats were kept in captivity for no more than three days and were fed with banana and papaya. During this period the bats appeared healthy and maintained body mass. All animals were captured with permission from *Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis* (IBAMA - authorization # 11321-1 to APCN).

Captures and metabolic measurements were carried out at two different seasons, a dry-cool season (from June 25th to August 10th 2007) and a wet-warm season (from November 20th to December 30th 2007). These seasons were chosen by an analysis based on the climate profile (maximum temperature: T_{max}, minimum temperature: T_{min}, mean air temperature: T_a, and precipitation) from previous years (2001–2006) obtained from a meteorological station (*Centro de Estudos e Planejamento de Rio Claro* - CEAPLA) located 10 km distant from the capture site. The mean of T_a, T_{max}, T_{min} and precititation recorded for June–August and November–December, during this 5 year-period, is presented in Table 1. Using these data, we further calculated the mean aridity index (Q) for both seasons, following Bozinovic et al. (2007). This index, which we used as a proxy for productivity, had a mean value for the period June–August equal to 1.07 ± 0.97, and a mean value for the period November–December equal to 2.5 ± 0.18.

Table 1
Mean values ($\pm$1SE) for average air temperature (T_a), maximum temperature (T_{max}), minimum temperature (T_{min}), precipitation and aridity index (Q) obtained from years 2001 to 2006 by the meteorological station (Centro de Estudos e Planejamento de Rio Claro — CEAPLA) located 10 km distant from the capture site.

	June–August	*November–December*
T_a (°C)	20.8 ± 3.1	25.4 ± 4.2
T_{max} (°C)	26.4 ± 0.9	34.7 ± 1.1
T_{min} (°C)	9.6 ± 2.8	14.8 ± 3.0
Precipitaion (mm)	43.4 ± 30.2	230.2 ± 101.3
Q	1.07 ± 0.97	2.5 ± 0.18

2.2. General protocols for metabolic and thermal measurements

Metabolic rates, inferred from rates of oxygen consumption (VO_2), were quantified by an open flow-system (Voigt and Cruz-Neto, 2003). Animals were fasted for 12 hours prior to measurements, weighed and placed in a PVC chamber (150 ml for *S. lilium* and *C. perspicillata*, and 700 ml for *A. lituratus*), fitted with a plastic mesh in the top where the bat could hang. The chamber was then placed in a controlled-temperature cabinet, and was ventilated with air scrubbed from water through a tube containing silica-gel, at a flow of 500–1000 ml/min for *A. lituratus* and 300–450 ml/min for *S. lilium* and *C. perspicillata*, depending on the experimental T_a. Airflow was controlled by a mass-flowmeter (Sierra Mass Flow Meter Side-Track 860) coupled to a mass-flow controller (Sable System Mass Flow Controller). Air leaving the chamber was scrubbed from water through a tube containing silica-gel and an aliquot of 50–200 ml/min was sent to an O_2 analyzer (FC-1B O_2 Analyzer, Sable Systems, USA) and then to a CO_2 analyzer (CA-2A Analyzer, Sable System, USA). These analyzers were plugged to an A/D converter interface (Sable Systems International Universal Interface II, Sable Systems, USA), which sent all the signals to a laptop computer. Sampling rates were set at 10 s and all data acquisition routines were programmed and controlled by a *Visual Basic* based custom-written software. All metabolic calculations were made using this same software, and were based on equation 4 of Withers (1977). A further measurement of body mass was taken after the end of each metabolic run, and a mean value used for subsequent calculations.

Rectal temperature (T_b) was measured by inserting a thermocouple (1.2 mm OD) into the animal's rectum before and after each metabolic run; air temperature (T_a) was measured by placing a thermocouple in the outlet port of the chamber. Both thermocouples were plugged into a thermometer (TC-1000 thermometer, Sable System), which sent the signals with a frequency of 1 s (for T_b) and 10 s (for T_a) to a laptop computer through an A/D converter interface (Sable System International Universal Interface II, Sable Systems, USA). Recordings from the thermocouple were monitored by the same software described above.

2.3. BMR and nonshivering thermogenesis measurements

BMR and nonshivering thermogenesis were measured according to the protocol described by Rezende et al. (2004). Briefly,