

Temperature and thermal regime effects on the specific dynamic action of *Bothrops alternatus* (Serpentes, Viperidae)

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Abstract. Metabolic studies in ectothermic vertebrates are, almost always, conducted at a constant temperature, a valid and recommended procedure in most instances. However, for long term measurements, for example during snakes digestion, keeping experimental temperature constant subjects the animals to a condition potentially quite diverse from what animals may experience in nature. Thus, we investigated the influence of constant (20°C, 25°C, and 30°C) and fluctuating (circadian thermoperiod cycles of 20:30°C, 12:12 h) temperatures regimes on the post-prandial metabolic response of the Crossed pit viper, *Bothrops alternatus*. Maximum oxygen consumption rates ($\dot{V}O_{2peak}$) during digestion increased with temperature, while the time to reach these rates (T_{peak}) and the duration of the digestive process decreased as temperature was elevated. Both, scope ($\dot{V}O_{2peak}/RMR$) and SDA coefficient were not influenced by temperature. When compared to the results obtained at constant 25°C (which is equivalent to the average temperature of the fluctuating regime), the fluctuating temperature regime caused a decrease in RMR and $\dot{V}O_{2peak}$ accompanied by an increase in digestion duration. Thermal regime did not affect the energetic cost of digestion in *B. alternatus*.

Keywords: energetics, metabolism, postprandial, snakes, thermoperiod.

Introduction

The extra energy expended in the digestion and assimilation of a meal, known as specific dynamic action (SDA) (Kleiber, 1961), has been described in almost every vertebrate group (McCue, 2006; Secor, 2009) being particularly impressive in some snake species (Andrade et al., 2005; Hansen et al., 2013). With one exception (Jayne, Voris and Ng, 2002), all snakes eat their prey whole and many species experience prolonged periods of fasting, interrupted occasionally by the ingestion of relatively large prey which, eventually, may even exceed the snake's own body mass (Greene, 1992; Rodríguez-Robles, Bell and Greene, 1999). This set of features plus a marked intestinal regulatory response (Secor, 2001; Zerbe et al., 2011) explain the unique postprandial metabolic response of

snakes. In general, the postprandial metabolic increment in snakes varies from 5 to 15-fold the metabolic rate measured in rest and fasting animals (Andrade, Cruz-Neto and Abe, 1997; Secor, 2001; McCue and Lillywhite, 2002), although a very extreme 44-fold increase has been reported (Secor and Diamond, 1997). Moreover, the postprandial scope of $\dot{V}O_{2peak}$ can exceed the levels observed during forced exercise (Andrade, Cruz-Neto and Abe, 1997; Secor, Hicks and Bennett, 2000). Also, SDA in snakes is almost entirely aerobically sustained, which allows for the persistency of elevated rates of metabolism for periods up to 20 days (Benedict, 1932; Andrade, Cruz-Neto and Abe, 1997; Wang, Busk and Overgaard, 2001).

The postprandial metabolic response is known to be affected by many different variables, but most prominently it depends on meal size and composition (Toledo, Abe and Andrade, 2003; McCue, Bennett and Hicks, 2005). Abiotic factors are also known to influence the SDA and, particularly in ectotherms (Huey and Stevenson, 1979; Dorcas, Peterson and Flint, 1997; Angilletta, Niewiarowski and Navas, 2002; Angilletta, 2009), temperature has

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a very important influence, which fomented a number of studies dedicated to the dissection of temperature effects on the SDA response (see reviews in Andrade et al., 2005; McCue, 2006; Secor, 2009). In all of these studies, the different parameters used to evaluate the postprandial metabolic response were compared among groups measured at different temperatures, which were kept constant throughout the digestive process, a valid and straightforward approach in most cases. However, for long term measurements, such as snakes' digestion which can extend for many days, keeping experimental temperature constant constitutes a situation potentially quite diverse to what most snakes may experience in nature. Indeed, although fed snakes tend to become more reclusive, they can still exhibit marked circadian fluctuations in body temperature (Regal, 1966; Greenwald and Kanter, 1979; Huey, 1982; Slip and Shine, 1988; Jaeger and Gabor, 1993; Tattersall et al., 2004). Therefore, in the present study we first examined the effects of temperature variation on the postprandial metabolic response of a neotropical viperid snake, *Bothrops alternatus*, under the classical approach of submitting the animals to constant temperature regimes. Secondly, we investigate whether submitting the snakes to a fluctuating circadian thermal regime would influence any of the parameters associated to the postprandial metabolic response. In an attempt to narrow the gap between physiological measurements and biological reality, our thermoperiod was set to vary from 20 to 30°C during night and daytime, respectively (12:12 h). Since we have measured snakes at constant 20, 25, and 30°C, we were also able to compare parameters measured at 20 and 30°C under the different thermal regimes and, whenever appropriate, averaged values extracted under the fluctuating regime were compared to those obtained under constant 25°C, which corresponded to the mean temperature of the former one.

Material and methods

Experimental animals

Eight juvenile *B. alternatus* of undetermined sex and born in captivity from pregnant females collected in several localities of São Paulo state, Brazil, were used in this study. With a large and heavy body, which can exceed 2 m in length, these terrestrial lanceheads are found in tropical, semitropical, and temperate deciduous forests. Also, they occupy open fields and rocky areas, mainly at humid habitats, from the center-west of Brazil to central Argentina, extending into Uruguay and Paraguay, from near sea level to about 700 m (Campbell and Lamar, 2004). For the last 10 years, the average of minimum and maximum temperatures recorded for the area of *B. alternatus* occurrence (Campbell and Lamar, 2004) were found to be 15.0 (SE \pm 0.21°C) and 27.1 (SE \pm 0.25), respectively (R.S.B. Gavira and D.V. Andrade; unpublished data compiled from WORLDCLIM, see Hijmans et al., 2005). Therefore, although we have no detailed information about the field body temperature for *B. alternatus*, we believe that daily temperature changes, as large as the one herein set at the "Fluctuating Temperature Regime", are not an uncommon occurrence in the area where this species is found.

The snakes were kept individually in wooden cages with glass front and side holes for ventilation (30 \times 29 \times 27 cm), lined with corrugated cardboard placed in a temperature-controlled room at approximately 25°C (\pm 5°C). The meal consisted of mice (*Mus musculus*), since *B. alternatus* feeds on endothermic during all phases of its life (Martins, Marques and Sazima, 2002), and the snakes had free access to water. Only animals apparently healthy that were not undergoing ecdysis were used. All experimental animals were used under permission of "Animal Use Ethic Committee", CEUA (protocol number 4587, July 22nd 2009), from Instituto de Biociências, Universidade Estadual Paulista.

Experimental protocol

The post-prandial metabolic response was determined by quantifying the rate of O₂ consumption ($\dot{V}O_2$) of snakes before (Resting Metabolic Rate, RMR) and after meal ingestion. The snakes were subjected to constant 20°C, 25°C, and 30°C and to a fluctuating temperature regime (T°Fluct) composed by a thermoperiod varying from 30°C during daylight (06:00 to 17:59 h) to 20°C overnight (18:00 to 05:59). To control the experimental temperatures, with a \pm 1°C, snakes were kept in a climatic chamber BOD (Fanem, 347CD, and Eletrolab, 122FC) throughout the experiments. Daily transition between temperatures for the T°Fluct regime took less than 20 minutes, with temperature being kept constant at the new level (20 or 30°C) until the next transition (12 hours).

RMR of fasted snakes was measured for a period of 48 hours, being 24 hours for acclimation and 24 hours for effective data collection. Thereafter, snakes were removed from the respirometer and returned to their maintenance cage, where a live mouse with mass equivalent to 30% of snake body mass was offered. When snakes voluntarily captured

and ingested their prey, they were immediately returned to the respirometer and $\dot{V}O_2$ measurements resumed until they return to RMR. All experimental individuals were measured, in a randomized sequence, in all treatments, which took approximately 8 months. Prior to the measurements, all snakes were fasted for at least 20 days.

Respirometry

Rates of oxygen consumption were determined by using an automated system of intermittently closed respirometry. The snakes were placed in hermetically sealed respirometric chambers with appropriated volume for their size (~700 ml). Using the software DATACAN V (Sable Systems), a flow multiple controller (Multiplexer TR-RM8, Sable Systems) was programmed to intercalate periods of 60 minutes in which the chambers were ventilated with outside air to refresh the air contained in respirometers (open phase), with periods of 10 minutes (closed phase) in which the air contained in the chambers was recirculated through an oxygen analyzer (Sable Systems PA-1B). As the system sequentially rotate among 7 different chambers, each of them experienced a closed phase at every 70 minutes. Therefore, since the decline in the fractional concentration of O_2 recorded during the closed phase was used to calculate $\dot{V}O_2$, we were able to obtain a measurement for each snake at every 70 minutes.

Treatment and data analysis

RMR was calculated as the average $\dot{V}O_2$ measured in fasting snakes during the 24 hours immediately before they were fed. $\dot{V}O_{2peak}$ was defined as the maximum oxygen consumption rate observed during the postfeeding metabolic increase, and T_{peak} as the time to reach this level. SDA duration was determined as the time required for the lower limit of the 95% confidence interval of the postprandial period overlapped to the upper limit of the 95% confidence interval calculated during the RMR (see Andrade, Cruz-Neto and Abe, 1997). $\dot{V}O_{2peak}$, T_{peak} , and SDA duration were all extracted from a fourth-degree curve fitted to the temporal variation of $\dot{V}O_2$, before and after feeding using TableCurve 2D (Systat Software). The scope of $\dot{V}O_{2peak}$ was calculated as the ratio between $\dot{V}O_{2peak}$ and RMR.

Meal energy content (ME) was calculated based on Cox and Secor (2007). The energetic cost of digestion (SDA) was calculated by the sum of the total amount of extra oxygen consumed for the duration of elevated metabolic rates, minus the maintenance cost for this period estimated on the basis of the RMR values, assuming that 1 ml of oxygen used in aerobic metabolism results in the expenditure of 0.0198 kJ (Gessman and Nagy, 1988). The SDA coefficient was calculated as the percentage of energy expended in digestion (SDA) in relation to the energy content of the mice being digested (ME).

To examine the effects of temperature on the different parameters associated with the SDA among constant temperature regimes, we used Repeated Measures ANOVA (Oneway). When we observed lack of normality and/or homoscedasticity of variances, data were initially logarithmized and the test was repeated. If the data have not yet

met the necessary assumptions, the nonparametric test of posts with signs of Wilcoxon was used. For the fluctuating temperature regime, the values for some parameters obtained at the two temperatures composing this regime (i.e., 20 and 30°C) were averaged and compared to those obtained at constant 25°C, since this temperature corresponds to the average temperature of the fluctuating regime. In some instances, values measured at the 20 or 30°C phase of the fluctuating temperature regime were compared to those obtained at constant 20 or 30°C, respectively. Comparisons between $T^{\circ}Fluct$ and constant temperatures were done by paired *t*-tests. All data are presented as mean \pm standard error. The level of significance was set at $P < 0.05$.

Results

Snake's body masses (mean for all treatments = 101.4 ± 3.1 g), and meal energy did not differ among temperature treatments (table 1). Resting metabolic rate increased significantly ($P < 0.001$) with increase temperature, however the temperature coefficient (Q_{10}) did not differ between that calculated from 20 to 25°C and that from 25 to 30°C (overall mean $Q_{10} = 2.64 \pm 0.26$) (table 1; fig. 2a).

The postprandial metabolic response of *B. alternatus*, in all temperatures, was characterized by a rapid initial increase in oxygen consumption peaking between 28 and 74 hours post-feeding, followed by a gradual return to the levels recorded before feeding (RMR). In general, the temperature effect on the SDA of *B. alternatus* was characterized by the shortening in duration at the expenses of greater metabolic increases as temperature was elevated (figs 1 and 2d). $\dot{V}O_{2peak}$ differed ($P < 0.001$) among all treatments, with the Q_{10} for the 20 to 25°C interval (3.69 ± 0.48) being significantly higher ($P = 0.003$) than that obtained from 25 to 30°C (2.12 ± 0.13) (table 1; fig. 2b). The scope of $\dot{V}O_{2peak}$ was not affected by temperature averaging 6.23 ± 0.2 (table 1). Both T_{peak} and duration decreased (P values < 0.001) with increasing temperature (table 1; fig. 2c, d). Neither SDA nor SDA coefficient differed among temperature treatments (table 1).

The SDA response under the fluctuating temperature regime was similar to the general pattern observed for constant temperatures, except

Table 1. Metabolic and energetic parameters associated with the SDA of *Bothrops alternatus* (n = 8) fed on meals equaling to 30% of the snake's body mass at different temperatures and thermal regimes (see text for details).

	Constant			T°Fluct
	20°C	25°C	30°C	
Body mass (g)	110.6 ± 8.6	101.2 ± 6.5	94.8 ± 4.4	98.9 ± 4.1
ME (kJ/meal)	2389.6 ± 11.8	2383.8 ± 7.8	2376.3 ± 7.3	2380.2 ± 4.5
RMR (ml O ₂ · g ⁻¹ · h ⁻¹)	0.0211 ± 0.0018 ^a	0.0333 ± 0.0014 ^b	0.0514 ± 0.0021 ^c	Mean = 0.0275 ± 0.0026* 20°C = 0.0151 ± 0.0023* 30°C = 0.0420 ± 0.0031
ṠO _{2peak} (ml O ₂ · g ⁻¹ · h ⁻¹)	0.1176 ± 0.0039 ^a	0.2212 ± 0.0117 ^b	0.3195 ± 0.0152 ^c	Mean = 0.1883 ± 0.0100 20°C = 0.1020 ± 0.0058 30°C = 0.2745 ± 0.0144*
Scope of ṠO _{2peak} (ṠO _{2peak} /RMR)	5.8 ± 0.4	6.6 ± 0.2	6.2 ± 0.3	Mean = 7.0 ± 0.4 20°C = 7.3 ± 0.6* 30°C = 6.6 ± 0.3
T _{peak} (h)	74.5 ± 4.5 ^a	41.7 ± 1.7 ^b	28.7 ± 0.6 ^c	41.7 ± 6.8
Duration (h)	502.7 ± 16.3 ^a	217.7 ± 12.8 ^b	153.7 ± 9.9 ^c	287.2 ± 19.4*
SDA (kJ · kg ⁻¹)	467.4 ± 16.5	444.2 ± 21.9	433.6 ± 32.3	420.9 ± 22.0
SDA coefficient (%)	19.5 ± 0.6	18.6 ± 0.8	18.2 ± 1.3	17.6 ± 0.9

ME, meal energy content; RMR, resting metabolic rate; ṠO_{2peak}, maximum oxygen uptake during digestion; T_{peak}, time taken to reach the ṠO_{2peak}; SDA, energetic cost of digestion. Different letters indicate significant differences among constant temperature regimes. An asterisk denotes significant differences for comparisons between constant temperatures (20°C, 25°C and 30°C) and T°Fluct (20°C, mean and 30°C, respectively).

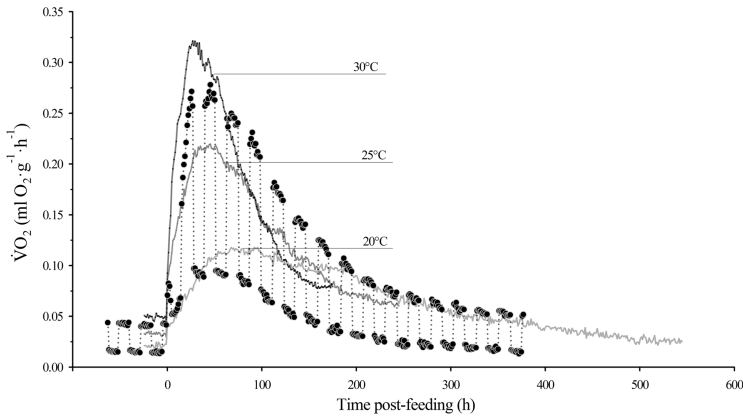


Figure 1. Time course variation in oxygen consumption rates ($\dot{V}O_2$) during the digestion of *Bothrops alternatus* fed on meals equaling to 30% of the snake's body mass at 20°C, 25°C, 30°C (solid lines) and T°Fluct (circles). The time “0” (zero) indicates the time of feeding. The interval between two consecutive points is 70 minutes; each point represents the mean of eight snakes. Dotted lines denote the thermoperiod change (20°C and 30°C every 12 hours). Standard error bars omitted for clarity of data.

for the superposition of a marked variation associated with the thermoperiod, both pre- and post-feeding (fig. 1). In general, the SDA response obtained for T°Fluct, composed by the

alternation of 12 hours periods at 20 and 30°C, can be characterized as an acceleration/delay in comparison with the SDA registered at constant 20 and 30°C, respectively.

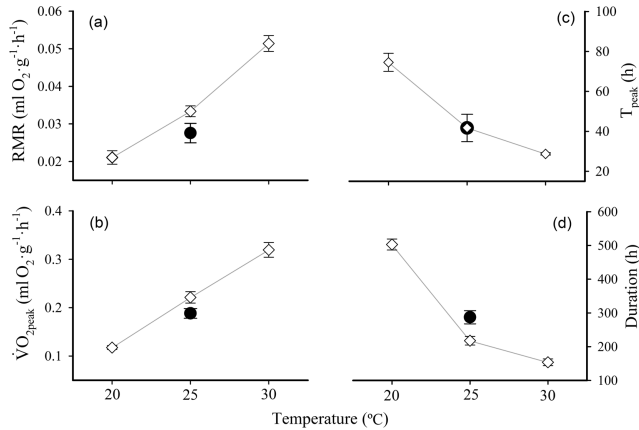


Figure 2. Parameters associated with the digestion of *Bothrops alternatus* fed on meals equivalent to 30% of snakes' body mass, as a function of temperature. (a) Resting metabolic rate; (b) maximum O₂ consumption; (c) time taken to reach the $\dot{V}O_{2peak}$; and (d) duration of digestion. Open diamonds indicate constant temperatures and the circles indicate the average temperature for the T°Fluct regime.

The average RMR of T°Fluct was significantly lower ($P = 0.024$) than that measured at constant 25°C (table 1; fig. 2a). This difference was caused by a decrease in RMR values at both temperatures composing T°Fluct (20 and 30°C) compared to those measured at constant 20 and 30°C, respectively, although only the difference observed at 20°C reached statistical significance ($P = 0.011$).

No significant difference was found for $\dot{V}O_{2peak}$, T_{peak} , and $\dot{V}O_{2peak}$ scope between the average temperature of T°Fluct and constant 25°C (table 1; fig. 2b, c). However, $\dot{V}O_{2peak}$ measured at 30°C in T°Fluct was significantly lower ($P = 0.018$) than at constant 30°C, with no difference for the same kind of comparison at 20°C. The scope of $\dot{V}O_{2peak}$ was significantly different ($P = 0.032$) for the comparison made at 20°C, but not at 30°C. Duration was significantly longer ($P = 0.007$) for T°Fluct compared to 25°C (fig. 2d). Both SDA and SDA coefficient for T°Fluct did not differ from those estimated at constant 25°C (table 1).

Discussion

As usually reported for other snakes (McCue and Lillywhite, 2002; Toledo, Abe and An-

drade, 2003; Wang et al., 2003; Zaidan and Beaupre, 2003; Chu et al., 2009; Bessler et al., 2010), the postprandial metabolic response of *B. alternatus* proceeded faster at the expenses of higher metabolic rates, as temperature was elevated. $\dot{V}O_{2peak}$ attained by *B. alternatus* were comparable to those found for other viperid snakes measured under similar conditions (Andrade, Cruz-Neto and Abe, 1997; McCue and Lillywhite, 2002; Zaidan and Beaupre, 2003). In general, this increment was not affected by temperature (see also Hailey and Davies, 1987; Toledo, Abe and Andrade, 2003; Wang et al., 2003; Andrade et al., 2005) or thermal regime. However, while the change in RMR with temperature (i.e., Q_{10}) did not vary with temperature interval (20–25°C and 25–30°C), the change in $\dot{V}O_{2peak}$ was considerably higher from 20 to 25°C than from 25 to 30°C. Therefore, as the extra metabolic load associated to the SDA was added to RMR, snakes exhibited proportional metabolic increments for the 20–25°C interval, but not for the 25 to 30°C interval. Indeed, while the postprandial scope of $\dot{V}O_{2peak}$ increased in the lower temperature interval, compared to the resting metabolic rates observed before feeding, it decreased at the higher temperature interval, a pattern also found for the Chinese green tree

viper, *Trimeresurus stejnegeri stejnegeri* (Tsai et al., 2008). Thus, the digestion of *B. alternatus*, at least in terms of aerobically sustained metabolism, seemed to have approached a thermal optimum around 25°C, tending to deteriorate towards 30°C. In agreement with this difference, SDA duration was considerably more reduced from 20 to 25°C (ca. 56%) than from 25 to 30°C (ca. 30%).

The preferred body temperature of *B. alternatus* is unknown, as well as the possible occurrence of a postprandial thermophilic response. However, this species occurs in subtropical to temperate zones occupying areas with temperatures typically colder than most congeneric species (Campbell and Lamar, 2004). Furthermore, *B. alternatus* has been found active at temperatures as low as 13°C (Nogueira, Sawaya and Martins, 2003), whereas most other *Bothrops* are active only at higher temperatures (Oliveira and Martins, 2001; Nogueira, Sawaya and Martins, 2003). Also, *B. alternatus* was able to feed voluntarily and complete digestion at constant 20°C (present study) while tropical snakes usually refuse to feed (D.V. Andrade, pers. observ.) or fail to complete digestion at this temperature (Wang et al., 2003). Based on these observations, thermal differences in habitat occupancy, at least within the *Bothrops* genus, may be correlated with digestive performance at different temperatures. However, a comparative study would be necessary to test the validity of this idea.

Temperature did not affect the energetic of meal digestion in *B. alternatus*, indicating that changes in SDA duration were entirely proportional to the variation in metabolism (see also Toledo, Abe and Andrade, 2003; Wang et al., 2003; Tsai et al., 2008; Bessler et al., 2010). Thus, the elevation of body temperature does not provide any energetic benefit to *B. alternatus*. From an ecological perspective, however, the shortening in digestion duration diminishes the time in which the snakes have their locomotion and possibly defense abilities compromised by having a bulky food item in the stom-

ach (Garland and Arnold, 1983; Ford and Shuttlesworth, 1986; Shine and Shetty, 2001; Mehta, 2006; Willson and Hopkins, 2011). Moreover, the acceleration of the digestive process can facilitate the engagement of snakes in new feeding episodes or in other ecologically relevant activities (Wang et al., 2003).

Thermoperiodicity did not alter the general pattern of the postprandial metabolic response in *B. alternatus*, except by the cyclic oscillations in metabolism associated to the cyclic changes in temperature. Indeed, the examination of fig. 1 reveal that the SDA curve obtained under the fluctuating temperature regime can be decomposed into “two” curves, one formed by the higher rates obtained at 30°C, and another with the lower rates measured at 20°C. Therefore, in summary, the effects of the fluctuating temperature regime on the SDA of *B. alternatus* can be described as an acceleration/delay of the response in comparison with constant 20 and 30°C, respectively. While the average rate of oxygen consumption in T°Fluct were lower than at constant 25°C, SDA duration was proportionally extended. As a result, the energetic cost of digestion in T°Fluct also did not differ from constant 25°C. Consistent with these results, Michel and Bonnet (2010) found that growth rate and possibly assimilation efficiency were not affected by contrasting thermal regimes in *Vipera aspis*. However, while these authors proposed that the increase in the digestive tract’s performance associated to periodical body temperature elevation would be cancelled by the concurrent increment of whole-body energetic expenditure, herein, we clearly show that digestive performance itself, in terms of energy return, is not affected by thermal regime.

Besides energetic considerations, the ability to complete meal digestion under a fluctuating thermal regime might bear other important benefits. For example, the South-American rattlesnake (*Crotalus durissus*) refuses eating and seldom complete meal digestion at constant 20°C, however, data obtained from temperature data loggers implanted in snakes kept

in outdoor pens in southeastern Brazil revealed that they can withstand temperatures as low as 6°C overnight and still complete meal digestion (D.V. Andrade, pers. observ.). Thus, the ability to cope with a fluctuating temperature regime might be particularly relevant in allowing meal digestion to proceed even when snakes are experiencing intervenient periods of low temperatures that would, otherwise, disrupt the process.

We found that *B. alternatus* RMR measured at 20 and 30°C under constant temperatures were 28 and 18% greater than the rates measured in T°Fluct at the same temperatures, respectively. For fed animals, the $\dot{V}O_{2\text{peak}}$ under constant temperatures were approximately 13.5% greater than rates measured under T°Fluct, both at 20 and 30°C. Therefore, metabolic rate was considerably reduced when measured under a thermoperiodical regime as compared to measurements done, at the same temperature, under constant temperature regimes. Although the causal factors underlying this disparity are uncertain and remain to be investigated, part of this difference may be related to the influence of thermal conditions experienced by the animals previously to the metabolic measurements (i.e., acclimation), as observed by Carey (1979) in toads. Ectothermic organisms usually experience circadian changes in body temperature, and our study shows that submitting them experimentally to a constant temperature regime may result in some important and unsuspected consequences.

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