Temperature and Meal Size Effects on the Postprandial Metabolism and Energetics in a Boid Snake

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ABSTRACT

We investigated the combined effect of meal size and temperature on the aerobic metabolism and energetics of digestion in *Boa constrictor amarali*. Oxygen uptake rates ($\dot{V}o_2$) and the duration of the digestion were determined in snakes fed with meals equaling to 5%, 10%, 20%, and 40% of the snake's body mass at 25° and 30°C. The maximum $\dot{V}o_2$ values attained during digestion were greater at 30°C than at 25°C. Both maximal $\dot{V}o_2$ values and the duration of the specific dynamic action (SDA) were attained sooner at 30°C than at 25°C. Therefore, the temperature effect on digestion in *Boa* is characterized by the shortening of the SDA duration at the expense of increased $\dot{V}o_2$. Energy allocated to SDA was not affected by meal size but was greater at 25°C compared to 30°C. This indicates that a postprandial thermophilic response can be advantageous not only by decreasing the duration of digestion but also by improving digestive efficiency. Maximal $\dot{V}o_2$ and SDA duration increased with meal size at both temperatures.

Introduction

Snakes are strictly carnivorous animals known for ingesting their prey as a whole without mastication (but see Jayne et al. 2002). Some species characteristically undergo prolonged periods of fasting interspersed with occasional ingestion of very large meals that, in extreme cases, exceed the body mass of the snake (Greene 1992, 1997). These meals lead to dramatic increases in metabolic rate (specific dynamic action; SDA), where the rate of oxygen consumption ($\dot{V}o_2$) can exceed that elicited by forced muscular activity (Andrade et al. 1997; Secor and

Diamond 1997). Ingestion of food is also followed by morphological reorganization of the gastrointestinal tract (Starck and Beese 2001, 2002), changes in lung ventilation, and alterations of arterial blood gases and acid-base status (Overgaard et al. 1999; Wang et al. 2001). All these physiological responses persist for extended periods of time until digestion is completed within 10–20 d (Benedict 1932; Andrade et al. 1997; Wang et al. 2001). Snakes have impaired capacity of locomotion during digestion (Garland and Arnold 1983; Ford and Shuttlesworth 1986), which may constrain their ability to defend themselves against potential predators or to engage in other behavioral activities (Pauly and Benard 2002).

Behavioral observations in many species of reptiles (Huey 1982; Peterson et al. 1993; Dorcas et al. 1998; Sievert and Andreadis 1999), including *Boa constrictor* (Regal 1966; Mcginnis and Moore 1969), report that the preferred body temperature increases during digestion. This postprandial thermophilic response has often been related to the potential benefits associated with increasing the rate of digestion and/or digestive efficiency (Hailey and Davies 1987; Lillywhite 1987; Reinert 1993; Sievert and Andreadis 1999; Wang et al. 2002). As in other ectothermic organisms, the metabolism of snakes is affected by temperature, and the increased metabolic rate during digestion encompasses both the direct effect of digestion and that caused by increased body temperature. Usually, temperature causes digestion to occur faster at the expense of increased rates of metabolism (Hailey and Davies 1987; Wang et al. 2002). Such a pattern and the occurrence of the postprandial thermophilic response suggest some questions about the energetics of digestion in snakes: Is digestion at higher temperatures more energy consuming than at low temperatures so the snakes "pay" the faster digestive process by allocating more energy to it? Or are the snakes rewarded with greater energetic return when digestion occurs at higher temperatures?

Here we describe the postprandial metabolic response of the boid snake, *Boa constrictor amarali*, at 25° and 30°C. Because meal size affects the magnitude and duration of SDA (Andrade et al. 1997; Secor and Diamond 1997), we include a description of the meal size effects at both temperatures.

Material and Methods

Animals

We used 17 juveniles of *Boa constrictor amarali*, with body masses varying from 0.09 to 0.47 kg (mean = 0.18 ± 0.01 kg), collected during an animal rescue operation during the con-

struction of a hydroelectric power plant, "Usina Hidrelétrica—Sérgio Motta," at the municipalities of Porto Primavera and Presidente Epitácio, São Paulo State, southeastern Brazil. The animals were maintained individually in wooden cages (30 × 29 × 27 cm) lined with cardboard paper and provided with lateral holes for ventilation within a temperature-controlled room at 30° ± 3°C, under natural photoperiod. The snakes were fed on mice or rats every other week and had free access to water. Animals were fasted for at least 2 wk before experimentation, and only individuals that seemed healthy and not moulting were used.

Experimental Protocol

The effects of meal size and temperature on metabolic rate during digestion were determined by measuring rates of oxygen uptake ($\dot{V}o_2$) of snakes before (resting metabolic rate; RMR) and after the ingestion of meals with different relative masses at 25° and 30°C. At each temperature, snakes were fed with a single mouse or rat, so the meal equaled 5%, 10%, 20%, or 40% of the snake's body mass (deviation of ±1% in all cases; groups hereafter referred to as G5, G10, G20, and G40, respectively). The order of meal sizes was random.

After we determined the mass of fasting snakes, they were placed in hermetically closed respirometers with a volume of 1–1.5 L maintained within a climatic chamber kept at the chosen experimental temperature throughout the experiment. Snakes were allowed to acclimate to the experimental temperature for at least 24 h before measurements, and $\dot{V}o_2$ of fasting snakes was monitored for no less than 24 h for determination of RMR. Afterward, the respirometers were opened and the snakes were offered a prey item, which they readily killed by constriction. When the meal had been ingested, the measurements of $\dot{V}o_2$ were continued until it had returned to RMR levels. In each animal, this was judged as the time until post-feeding $\dot{V}o_2$ was within the 95% confidence limit of RMR.

Respirometry

$\dot{V}o_2$ was measured using an intermittently closed respirometry setup (Sable System, TR-RM8). Briefly, a computer controlled pumps and solenoid valves and was programmed to ventilate the respirometers with fresh air (open phase, 200 mL min^{-1}) for 70 min while measuring the rate of oxygen depletion during a 10-min closed phase when the air was recirculated through an oxygen analyzer (Sable System, PA-1). Thus, the system allowed for a $\dot{V}o_2$ measurement at every 80 min. The output from the gas analyzer was collected on a data acquisition system (Sable System, DATACAN V), and $\dot{V}o_2$ was calculated from the rate at which oxygen concentration decreased within the respirometer during the closed phase. The fall in oxygen concentration inside the respirometer was linear, and $\dot{V}o_2$ was calculated as the inclination of the linear regression—minimum

square method—obtained for all the single measurements recorded during the closed phase (600 data points sampled over 10 min). These regressions usually yield r^2 values greater than 0.9.

During digestion, body mass of the snake will increase as food is assimilated. To calculate mass-specific $\dot{V}o_2$, we estimated actual snake body mass each day throughout the SDA response. We assumed that snakes assimilated 50% of the ingested meal mass at a constant rate following ingestion (Overgaard et al. 2002). Based on the temporal profile of the SDA response in boas, we assumed that assimilation occurred over 10 d at 30°C and over 15 d at 25°C (see also Wang et al. 2002). After that, body mass was assumed to be constant.

Data Handling and Analysis

RMR was determined as the mean of the $\dot{V}o_2$ measurements taken before feeding, over a minimum period of 24 h. Maximal $\dot{V}o_2$ during digestion ($\dot{V}o_{2\,peak}$), the time to reach it, and the duration of the SDA were derived by plotting each individual SDA response and tracing the best curve fit using TableCurve 2D (Jandel Scientific). The factorial increment of $\dot{V}o_2$ was calculated as $\dot{V}o_{2\,peak}$/RMR. To analyze digestive energetics, we transformed meal mass into energetic equivalents by assuming a caloric content of the meal (CCM) of 8.95 kJ g^{-1} rodent (Smith 1976). Net energetic cost of digestion (E_d) was calculated under the assumption that O_2 volume used in the aerobic metabolism (after we subtracted the cost of maintenance during this period, calculated from RMR values) was equivalent to 0.0198 kJ mL O_2^{-1} (Gessman and Nagy 1988). Total cost of digestion was calculated under this same assumption but included the maintenance cost (estimated from the RMR). The SDA coefficient (%E_d; see Jobling and Davies 1980) was expressed as the percentage of CCM that is allocated for digestion: %E_d = [(E_d/CCM) × 100].

Given that the different meal sizes were given at random and that most individual snakes were not tested in all combinations of temperature and meal sizes, we employed a two-way ANOVA to evaluate for statistical differences. Whenever this test indicated a significant variance of the data, a post hoc Student-Newman-Keuls test was used to identify which groups differed from each other. In all cases, the metabolic and energetic parameters were tested in relation to two factors: temperature and relative meal size. The relationship between meal size and any measured parameter was envisaged using a least squares linear regression. Statistical procedures followed Sokal and Rohlf (1995), and differences were considered statistically significant at the level of $P \leq 0.05$. All results, unless otherwise noted, are presented as mean ± SEM.

Table 1: Metabolic and energetic parameters associated with the specific dynamic action (SDA) of *Boa constrictor amarali* fed on meals of different relative size at 25° and 30°C

	5%		10%		20%		40%	
	25°C	30°C	25°C	30°C	25°C	30°C	25°C	30°C
Body mass (g)	258 ± .37	204 ± .32	181 ± .16	194 ± .51	161 ± .22	137 ± .2	221 ± .45	114 ± .08
RMR (mL O_2 h^{-1} kg^{-1})	33.4 ± 9.7	48.9 ± 6.2	35.6 ± 6.1	49.2 ± 4.5	42.2 ± 4.0	78.3 ± 17.2	27.6 ± 1.7	45.5 ± 8.1
SDA duration (h)	104 ± 15.1	57.6 ± 8.1	168.1 ± 15.2	65.5 ± 8.6	230.2 ± 32.1	114.5 ± 19	292.3 ± 11.1	210.4 ± 25.8
$\dot{V}_{O_2 peak}$ (mL O_2 h^{-1} kg^{-1})	89.1 ± 16.2	136.7 ± 9.2	121.2 ± 7.2	187.1 ± 11.9	165.7 ± 4.6	310.5 ± 34.4	247.8 ± 7.9	358.7 ± 21.6
Time to $\dot{V}_{O_2 peak}$ (h)	19.8 ± 3	13.9 ± 1.8	35.8 ± 2.8	16.1 ± 1.7	55.3 ± 9.5	23.2 ± 3.7	71.2 ± 6.6	37.6 ± 5.2
E_d (kJ kg^{-1})	60.2 ± 13.3	52.5 ± 12.6	148.9 ± 17.7	87.3 ± 13.2	378.8 ± 74.1	251.4 ± 24.6	636.7 ± 36.5	472.6 ± 91.9
CCM (kJ kg^{-1})	447.5	447.5	895	895	1,790	1,790	3,580	3,580
E_d (%)	13.5 ± 3	11.7 ± 2.8	16.6 ± 2	9.7 ± 1.5	21.2 ± 4.1	14 ± 1.4	17.8 ± 1	13.2 ± 1.8
Sample size	8	10	6	6	7	5	5	5

　　Note. Mean values ± SE. RMR = resting metabolic rate; CCM = caloric content of the meal.

Results

Mean body mass did not differ between experimental groups ($P = 0.7$), and there was no significant difference in RMR among meal size groups at a given temperature ($P > 0.05$ in both cases; Table 1). At 25°C, RMR averaged 38.3 ± 2.5 mL O_2 h^{-1} kg^{-1}, which is significantly lower than that at 30°C (64.7 ± 4.8 mL O_2 h^{-1} kg^{-1}; $P = 0.0002$); Q_{10} for RMR was 3.4.

　　The temporal profile of the SDA response was characterized by a rapid increment of $\dot{V}_{O_2}$ soon after ingestion; maximum $\dot{V}_{O_2}$ values were reached within 14–71 h after feeding, then metabolic rate gradually returned to RMR in the next 58–292 h (Fig. 1; Table 1). $\dot{V}_{O_2 peak}$, time to reach $\dot{V}_{O_2 peak}$, and SDA

duration increased with meal size at both experimental temperatures (Fig. 2).

　　At a given temperature, $\dot{V}_{O_2 peak}$ varied significantly among meal size groups ($P < 0.0001$ in both cases). The effect of meal size on $\dot{V}_{O_2 peak}$ differed between the two experimental temperatures (Fig. 2; $P < 0.0001$). At 25°C, $\dot{V}_{O_2 peak}$ increased linearly with meal size over the whole range tested ($r^2 = 0.9$; $F_{1,22} = 185$; $P < 0.0001$). At 30°C, $\dot{V}_{O_2 peak}$ increased progressively at the small meal sizes but tended to level off at larger meals. Accordingly, we divided the data into two sets and applied linear regression on each. This procedure revealed that, at 30°C, $\dot{V}_{O_2 peak}$ varied linearly within the meal size interval of 5%–20% ($r^2 = 0.8$; $F_{1,23} = 77$; $P < 0.0001$), with a slope significantly dif-
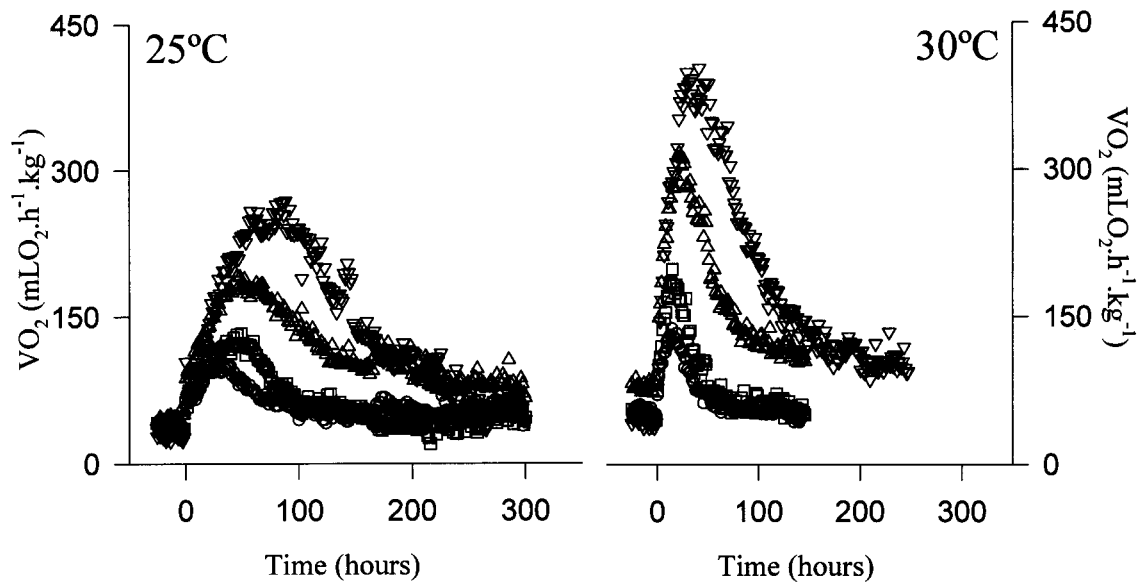

Figure 1. Temporal variation of *Boa constrictor amarali* metabolism following the ingestion of meals equaling 5% (*circles*), 10% (*squares*), 20% (*triangles*), or 40% (*inverted triangles*) of snakes' body masses at 25° and 30°C. Time "0" (zero) depicts the moment of feeding. Each point depicts the mean $\dot{V}_{O_2}$ value measured at every 80 min. Error bars omitted for clarity.
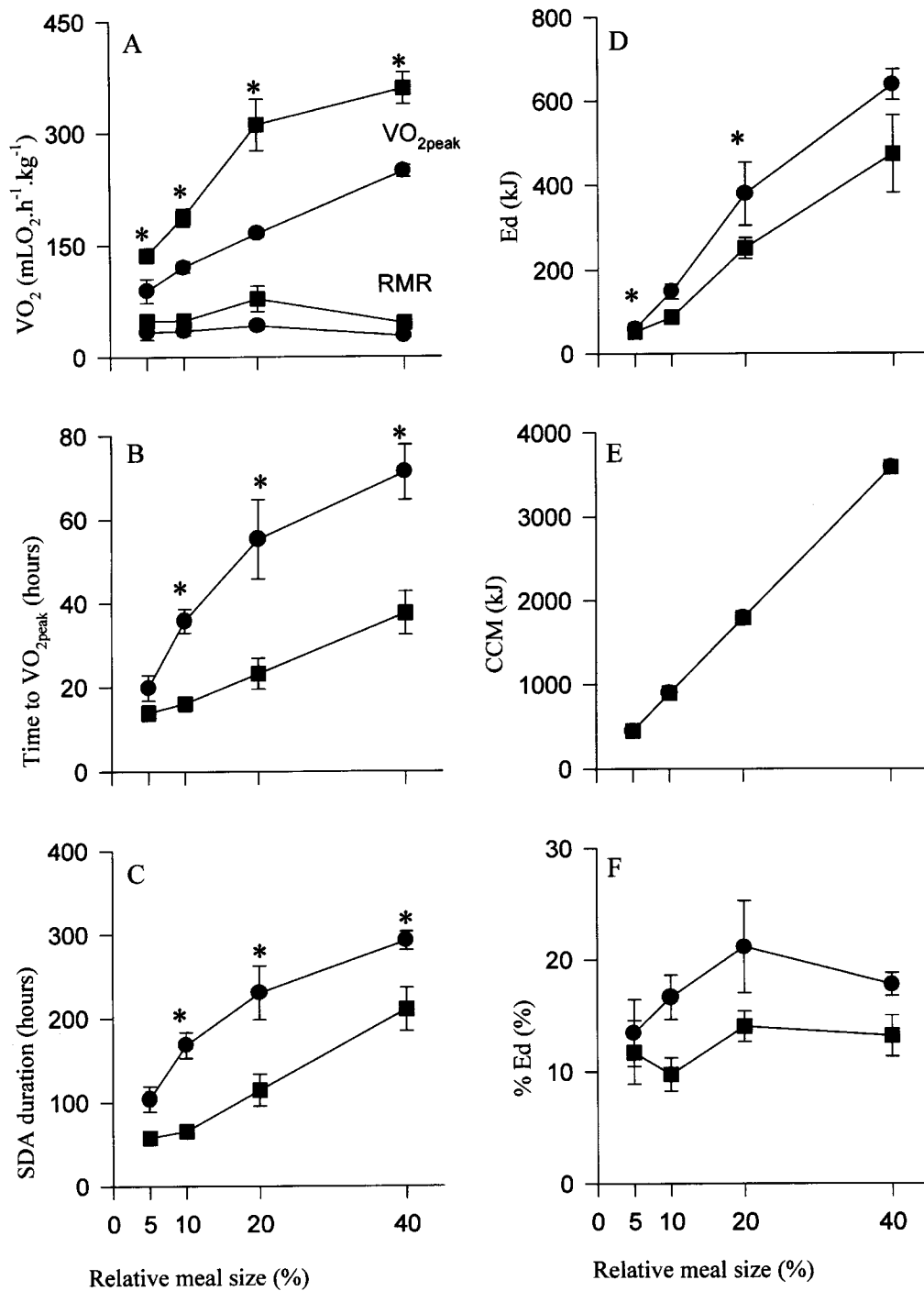
Figure 2. Temperature (25°C = *solid circles*, 30°C = *solid squares*) and meal size effects on metabolic and energetic parameters during the specific dynamic action (SDA) of *Boa constrictor amarali*. A, Resting metabolic rate (RMR) and maximum $\dot{V}O_2$ consumption rate during digestion ($\dot{V}O_{2peak}$). B, Time to reach $\dot{V}O_{2peak}$ after meal ingestion. C, SDA duration. D, Energetic cost of digestion (E_d) calculated for a 1-kg snake. E, Caloric content of the meal (CCM), considering a snake body mass = 1 kg. F, SDA coefficient (%E_d). Mean values are ±SEM. An asterisk indicates a significant difference between temperatures.

ferent from 0 ($t_{1,23} = 4.4$; $P = 0.0002$). However, within the 20%–40% interval, the increase in $\dot{V}o_{2peak}$ did not increase linearly with meal size ($r^2 = 0.2$; $F_{1,12} = 194$; $P = 0.2$), and the slope did not differ from 0 ($t_{1,12} = 1.4$; $P = 0.2$; Fig. 2). For all meal size groups, $\dot{V}o_{2peak}$ was significantly higher at 30°C than at 25°C ($P < 0.0001$; Fig. 2), but the factorial increase in metabolism ($\dot{V}o_{2peak}$/RMR) was not affected by temperature ($P = 0.9$; Table 1).

The time to reach $\dot{V}o_{2peak}$ increased with meal size at both temperatures and was significantly shorter at the higher temperature ($P < 0.0001$). In general, the time to reach $\dot{V}o_{2peak}$ increased linearly with meal size at 30°C, while at 25°C this increase occurred in an asymptotical mode (Fig. 2). SDA duration increased with meal size and decreased with temperature ($P < 0.0001$ in both cases; Figs. 1, 2). At 25°C, SDA duration did not differ significantly between G10 and G20 ($P > 0.05$). At 30°C, SDA duration was significantly greater for G40 and G20 than for G10 and G5 ($P < 0.05$ for all pairwise comparisons).

The energetic parameters associated with digestion in *Boa constrictor amarali* are given at Table 1. Total energetic expenditure during digestion, that is, E_d plus the maintenance cost (estimated from the RMR), was significantly higher at 25°C than at 30°C only for G20 ($P > 0.05$). The net energetic cost of digestion increased with meal size at both temperatures ($P < 0.0001$) and did not reach statistical significance only between G20 and G40 at 30°C ($P > 0.05$). The net energetic cost of digestion, independent of meal size, tended to be higher at 25°C than at 30°C ($P = 0.02$; Fig. 2). The SDA coefficient varied between 9.7% and 21.2% (Table 1) and was not affected by meal size at both temperatures ($P > 0.05$). The SDA coefficient was 55% higher at 25°C than at 30°C (see Fig. 2), and this difference was statistically significant ($P = 0.03$).

Discussion

Metabolic rate following feeding in *Boa* attained a maximal value that was ninefold above RMR for the snakes that fed meals equal to 40% of their body mass at 30°C. This factorial increase is greater than that measured during prey constriction (Canjani et al. 2002) or during forced muscular activity (D. V. Andrade, W. Klein, L. F. Toledo, S. P. Brito, and T. Wang, unpublished data). Differences in metabolic scope between different activities have been reported before (Andrade et al. 1997; Secor and Diamond 1997; Wang et al. 2001) and may reflect differences in the oxidative capacities of systems involved in distinct physiological functions (Secor et al. 2000; Bennett and Hicks 2001). In general, the SDA response observed in our study fits within the range reported by other studies in snakes (Wang et al. 2001; McCue and Lillywhite 2002). Our values are, however, considerably lower than the approximate 17–18-fold factorial increase reported by Secor and Diamond (1995,

2000) for *Python* and *Boa* after ingestion of meals equaling 25% of their body mass at 30°C.

At 25°C, $\dot{V}o_{2peak}$ increased linearly with meal size. Similarly, at 30°C, snakes digesting meals with relative masses between 5% and 20% also exhibited a linear increase in $\dot{V}o_{2peak}$. However, when digesting larger meals (20%–40%) at 30°C, there was no further increase in $\dot{V}o_{2peak}$. This implies that the $\dot{V}o_{2peak}$ during digestion of large meals at high temperature may have approached the maximum capacity of the boa's cardiorespiratory system.

At both experimental temperatures, SDA duration increased with meal size, which may reflect that larger meals require a longer time to be digested by enzymatic action before absorption (Pough and Groves 1983). SDA duration was also strongly affected by temperature. Independent of meal size, digestion occurred faster at higher temperatures. Moreover, for a given meal size, $\dot{V}o_{2peak}$ was always higher at 30°C than at 25°C at any given time of the SDA. Thus, the temperature effect on the digestion of *Boa* is characterized by a shortening in SDA duration at the expense of increased $\dot{V}o_{2peak}$. This agrees with previous observations in pythons (Wang et al. 2002) and in other ectothermic organisms (Jobling 1981; Powell et al. 1999). By decreasing the time allocated to digestion, snakes can maximize the time spent for other activities, such as reproduction, and increase the rate of food consumption and growth when food availability is high. Moreover, recently fed snakes have impaired locomotor capacity (Garland and Arnold 1983; Ford and Shuttlesworth 1986), which could lead to increased risk of predation and/or inability to find an appropriate shelter (see Pauly and Benard 2002). This ecological cost associated with feeding may be decreased by faster digestion at a higher body temperature.

Considering that higher body temperatures result in higher rates of metabolism accompanied by shorter digestion duration, it is not surprising that the SDA coefficient has usually been reported as not affected by temperature (see Wang et al. 2002). This general pattern, however, appears to vary considerably among species. For example, in the horned frog *Ceratophrys cranwelli* (Powell et al. 1999) and in the snake *Natrix maura* (Hailey and Davies 1987), the SDA coefficient tended to increase with temperature. Our results on *Boa* show that the SDA coefficient was lower at 30°C compared to 25°C. Such differences may have an even greater magnitude since we did not measure assimilation efficiency, which usually increases with temperature (Greenwald and Kanter 1979; Lillywhite 1987), and, therefore, we have expressed the relative cost of digestion as a ratio of CCM rather than of the energy content effectively assimilated from the meal. Thus, our data on *Boa* point to the postprandial thermophilic response, often reported in reptiles (Regal 1966; Mcginnis and Moore 1969; Huey 1982; Peterson et al. 1993; Dorcas et al. 1998; Sievert and Andreadis 1999), as being beneficial not only by shortening SDA duration but also by improving the energetic yield associated with digestion.

Acknowledgments

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