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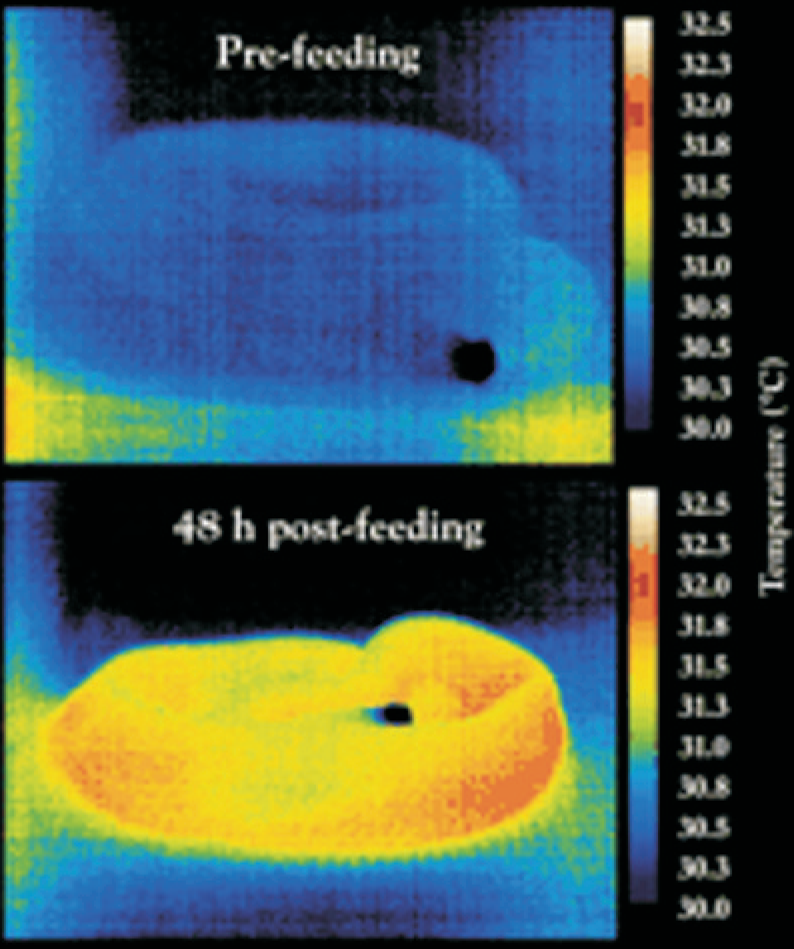

Cover: Infrared thermal image of a South American rattlesnake (*Crotalus durissus*; top) prior to (middle) and 48áh following (bottom) feeding a meal comprising 32% of its body mass (photographs by Glenn Tattersall). The scale bars show a total temperature range of 2.5¡C, where black is the coldest and white the warmest temperature. Note the uniform increase in body surface temperature in the snake following feeding. The darkest spot in each image is the nose, where evaporative cooling leads to a significant reduction in temperature. See paper by G. J. Tattersall, W. K. Milsom, A. S. Abe, S. P. Brito and D. V. Andrade, pp. 579-585.

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# The thermogenesis of digestion in rattlesnakes

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## Summary

**Some snakes have a feeding regime characterized by the infrequent ingestion of relatively large meals, causing impressive increments in post-prandial metabolism. Metabolism remains elevated for many days, while digestion proceeds, resulting in considerable investment of time and energy. Snakes actively adjust thermoregulatory behavior to raise their body temperature during digestion, exhibiting a post-prandial thermophilic response that accelerates digestion at the expense of higher metabolic rates. In the present study, we investigated the possibility that endogenously derived heat, originating as a byproduct of the post-prandial increase in metabolism, could itself contribute to the elevated body temperature during digestion in the South American rattlesnake *Crotalus durissus*. We assessed heat production, at a constant environmental temperature, by taking infrared (IR) images of snakes during fasting and after being fed meals varying from 10% to 50% of their own body masses. Our results show clearly that digesting rattlesnakes have significantly increased body temperatures, even when precluded from adjusting their thermoregulatory behavior. The feeding-derived thermogenesis caused the surface body temperature of rattlesnakes to increase by 0.9–1.2°C, a temperature change that will significantly affect digestive performance. The alterations in body temperature following feeding correlated closely with the temporal profile of changes in post-prandial metabolism. Moreover, the magnitude of the thermogenesis was greater for snakes fed large meals, as was the corresponding metabolic response. Since IR imaging only assesses surface temperatures, the magnitude of the thermogenesis and the changes in deep core temperature could be even more pronounced than is reported here.**

Key words: reptile, rattlesnake, *Crotalus durissus*, specific dynamic action, infra-red imaging, thermogenesis, thermoregulation, endothermy, digestion.

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## Introduction

Snakes are exclusive carnivores that, with few exceptions (Jayne et al., 2002), always ingest their prey whole. Moreover, some species are renowned for their ability to feed on exceedingly large prey, sometimes larger than the snakes themselves (Greene, 1992, 1997). In such cases, ingestion is followed by a dramatic increase in metabolism, usually referred to as the specific dynamic action of digestion, or simply SDA (see Kleiber, 1961). In some cases this can exceed the rise in metabolism elicited by forced muscular activity (Andrade et al., 1997; Secor and Diamond, 1997). Digestion in infrequently feeding snakes is often accompanied by the morphological reorganization of the gastrointestinal tract (Jackson and Perry, 2000; 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). These physiological changes associated with feeding may persist for extended periods while digestion proceeds; in snakes they can last for up to 10–20 days (Benedict, 1932; Andrade et al., 1997; Wang et al., 2001). From an ecological perspective, digestion imposes constraints on the snake's defensive and locomotor abilities (Garland and Arnold, 1983; Ford and Shuttlesworth, 1986), and it is reputed to be the most energetically expensive phase of predation (Andrade et al., 1997; Secor, 2001).

As in other ectothermic organisms, temperature exerts a pervasive influence on all activities in snakes. Different activities, however, are affected differently by changes in body temperature (Stevenson et al., 1985; Van Damme et al., 1991), and thus different activities (e.g. locomotion, digestion) may be optimal at different temperatures. As a consequence, snakes may alter their body temperature in activity specific patterns. For example, if given a choice of environmental temperatures during digestion, snakes (Cowles and Bogert, 1944; Regal, 1966; Walker and Taylor, 1966; Greenwald and Kanter, 1979; Huey, 1982; Slip and Shine, 1988a,b; Jaeger and Gabor, 1993; Sievert and Andreadis, 1999), as well as other reptiles (see

Huey, 1982), behaviorally increase their preferred body temperature, the so-called post-prandial thermophilic response. The primary consequence of such an increase in body temperature, in almost all cases examined, is a shortening of digestion time at the expense of increased rates of metabolism during the period of SDA (Wang et al., 2003; Toledo et al., 2003). Toledo et al. (2003), however, found that the SDA of boas fed different meal sizes was energetically less costly at 30°C than at 25°C. Thus, at least in this one particular case, it seems that the post-prandial thermophilic response was advantageous not only by decreasing the duration of digestion but also by improving the energetic return on the meal.

The post-prandial thermophilic response has always been associated with adjustments in thermoregulatory behavior that would allow animals to alter body temperature by exploring the natural heat sources available in their environment (e.g. Blouin-Demers and Weatherhead, 2001). The possibility of using metabolism as a source of heat to increase body temperature was thought to be of minor importance, perhaps due to the widespread belief that ectothermic vertebrates in general (Pough, 1983), and some snakes in particular, have a relatively low aerobic capacity (Ruben, 1976; Lillywhite and Smits, 1992), that would preclude any considerable heat generation by metabolic means. Such an interpretation, although generally true, ignores the fact that the metabolism of some snakes may increase by up to 17-fold during digestion (Secor and Diamond, 1995, 2000), which will generate a considerable amount of heat (Benedict, 1932; Van Mierop and Barnard, 1976; Marcellini and Peters, 1982). Therefore, in the present study, we investigated whether snakes could use this heat source. Specifically we examined whether the body temperature of the South American rattlesnake *Crotalus durissus terrificus* is affected by the increased metabolic rate experienced during digestion at a constant environmental temperature using infra-red (IR) imaging technology. We took IR pictures from digesting and non-digesting snakes for a period of 7 days, and compared their body surface temperature with the ambient temperature. We also examined the effects of meal size on the magnitude of the thermogenesis in these snakes, since meal size is one of the most influential determinants of the SDA response: the larger the meal, the greater the post-prandial metabolism and the longer the duration of the SDA (Andrade et al., 1997; Toledo et al., 2003). We hypothesized that body temperature following feeding (i.e. thermogenesis) would rise with a similar time course to the SDA that is well characterized in snakes, and that the magnitude and duration of the metabolic, post-prandial thermogenesis would be positively correlated with meal size.

## Materials and methods

### Animals

Juvenile rattlesnakes *Crotalus durissus* L. were born in captivity from females collected in São Paulo state, south-eastern Brazil. They were housed in individual wood cages (25 cm×26 cm×26 cm) with lateral holes for ventilation and a glass-front sliding door in a temperature controlled room (30±2°C). Snakes were fed every other week with mice and rats (meal mass approximately 30% of snake body mass $M_b$) and were given free access to water. In total, 18 animals were used in this study (mean $M_b$ 341±21 g). Animals were fasted for 2 weeks before experimentation, and only individuals that seemed healthy and that were not moulting were used.

Table 1. *Feeding variables in the three groups of snakes*

| | Snake mass $M_b$ (g) | Meal size (%$M_b$) | No. of mice eaten |
|---|---|---|---|
| Fasted | 333±44 | 0 | 0 |
| Small meal | 351±37 | 19.4±2.0 | 1.5±0.2 |
| Large meal | 336±34 | 33.7±2.6 | 2.5±0.2 |

### Experimental protocol

Three groups of snakes were used in this study. The control group (*N*=4) was fasted throughout all measurements. The remaining snakes were fed varying numbers of mice (either 1, 2 or 3) to create a small meal group and a large meal group. The small meal group (*N*=6) was fed enough mice to produce a meal ranging from 10–25% (average 19.4%) of the snake's pre-meal $M_b$. The large meal group (*N*=8) was fed enough mice to produce a meal ranging from 26–50% (average 33.7%) of the snake's pre-meal $M_b$ (see Table 1 for details of snake body masses and meal masses). These mice were consumed within 30 min of presentation to the snakes. Prior to feeding, an IR thermal image was taken of each snake, serving as the fasted (time 0) value. Immediately following this, snakes were either allowed to continue to fast, or fed the appropriate number of mice, and thermal images were taken again 3, 16, 24, 36, 48, 64, 72, 96, 120, 144 and 168 h later. These images allowed the precise determination of both snake surface temperature and local ambient temperature within the individual animal's cage.

### Infrared imaging

IR thermal images were taken with a MikroScan 7515 Thermal Imager (Mikron Infrared®, Oakland, NY, USA). This device produces a 12-bit image (320×240 pixels) and stores the temperature information of each pixel at a resolution of 0.1°C. All temperature readings are automatically corrected for non-blackbody properties by assuming an emissivity of 0.95, which is a reasonable estimate for biological tissues. We assessed the validity of this assumption by examining the IR from black electrical tape (known emissivity = 0.95) held at the same temperature as snake skin. Both the tape and the skin were found to radiate the same degree of IR, suggesting that an emissivity of 0.95 is a safe assumption. The procedure for taking IR images involved briefly opening the glass front of the cage and taking an image at a distance of 30–45 cm from the snake. The snakes were well accustomed to this procedure by the time the experiment started, and most individuals simply remained coiled and passive as the image was taken. No changes in body surface temperatures associated with agitation were observed.

### Data analysis and statistics

IR images were analyzed using MikroSpec RT (Mikron Infrared®) software. Regions of interest on the body were outlined and the average surface temperature determined. Since there was little variability in the surface temperature of the body (except for the head region), random regions (comprising approximately 10% of the body surface area) were used to determine body surface temperature (hereafter referred to as body temperature, $T_b$). The background temperature of the wooden cage was also determined, and served as a local ambient temperature comparison. The difference between body temperature and ambient temperature ($\Delta T$) was determined for every snake at every time point. To aid in the analysis, the maximum $\Delta T$ during SDA, the time at which the maximum $\Delta T$ occurred, and the area under the $\Delta T$ curve during SDA were determined for each individual snake. A one-way ANOVA using a Bonferroni *post-hoc* comparison was used to test the significance of all changes in these three variables (max. $\Delta T$, time of max. $\Delta T$, and area under the $\Delta T$ curve). The comparison between pre- and post-feeding values of $\Delta T$ were made using a one-way repeated measures analysis of variance (ANOVA), followed by the *post-hoc* Dunnett's test, which tested for differences between post-feeding values against a control value (pre-feeding value). Differences were considered significant when $P<0.05$.

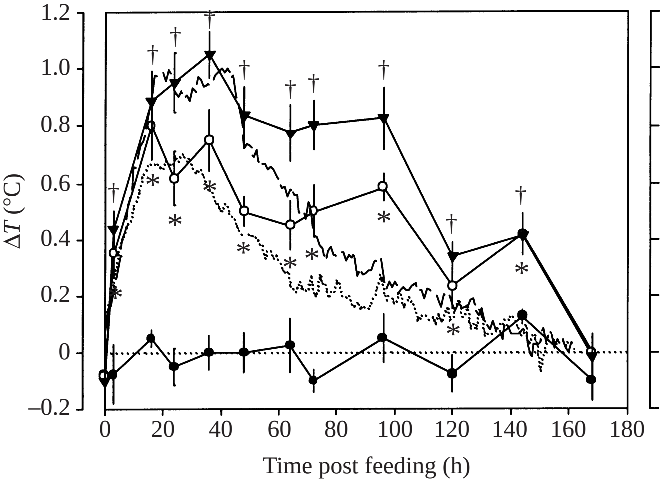

Fig. 1. The difference between body surface temperature and the ambient temperature ($\Delta T$) during the 168 h following feeding. Filled circles represent the fasted group of snakes, open circles represent the snakes fed a small meal (10–25%$M_b$), and the filled triangles represent the snakes fed a large meal (26–50%$M_b$). *Significant difference between the small meal value and its pre-feeding value (time 0); †significant difference between the large meal value and the pre-feeding value (time 0). The dotted line represents the oxygen uptake for snakes fed a diet of 20%$M_b$, and the broken line represents the oxygen uptake for snakes fed a diet of 30%$M_b$ (taken from Andrade et al., 1997).

## Results

### Meal size

Feeding variables are summarized in Table 1. There were no significant differences between the masses of snakes used in each group.

### Thermal increment of feeding

Fasted snakes did not show any significant changes in $\Delta T$ throughout their fasting period (Fig. 1), although $\Delta T$ did fluctuate over time by approximately –0.1°C to +0.1°C.

Snakes fed both small and large meals demonstrated significant and sustained increases in $T_b$ following feeding (Table 2; Figs 1, 2). Within 3 h of being fed a meal, both the small and the large meal group exhibited a significant rise in $\Delta T$, which remained above the pre-feeding value for up to 6 days (144 h; Fig. 1). The maximum $\Delta T$ of 0.93±0.11°C in the small meal group occurred on average 23±4 h post-feeding, whereas the maximum $\Delta T$ of 1.3±0.04°C in the large meal group occurred 42±7 h post-feeding. Both the maximum $\Delta T$ and the time at which maximum $\Delta T$ occurred were significantly higher in the large meal than in the small meal group. Furthermore, the total area under the $\Delta T$ curve during the SDA period was significantly higher in the large meal group than in the small meal group (Table 2). Interestingly, the rate of rise of $\Delta T$ was identical in both groups. Slight regional variations in surface temperature did exist in some snakes (Fig. 2), however, most surface temperatures over most of the snake's body were relatively uniform (<0.2°C difference).

Table 2. *Thermal variables in the three groups of snakes*

| | Maximum $\Delta T$ during SDA (°C) | Time of peak $\Delta T$ during SDA (h) | SDA area (°C×h) |
|---|---|---|---|
| Fasted | 0.25±0.03 | – | –1.3±4.3 |
| Small meal | 0.93±0.11* | 23±4 | 76.2±7.6* |
| Large meal | 1.2±0.04*,† | 42±7† | 105.7±5.0*,† |

SDA, specific dynamic action of digestion.

*Significant difference from the fasted value; †significant difference between the two diets.

The effect of diet size is further demonstrated in the correlations between maximum $\Delta T$ and the SDA area *versus* meal size for individual animals (Fig. 3). Significant positive correlations exist between maximum $\Delta T$ and meal size (%$M_b$) ($r^2=0.83$) and between SDA area and meal size (%$M_b$) ($r^2=0.83$), suggesting tight correlations between these variables, although there was a tendency for the relationships to asymptote at the largest meal sizes, suggesting that diet-induced thermogenesis does not continue to increase linearly with meal size.

## Discussion

### Critique of methods

Although IR thermography has not seen widespread use in physiology, its non-invasive nature makes it an ideal method

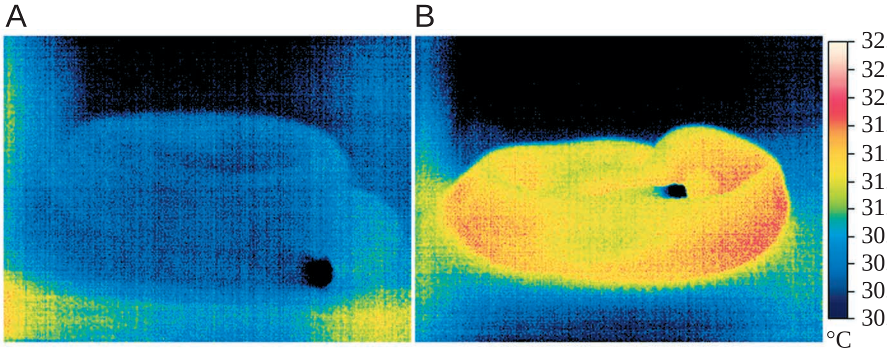

Fig. 2. Infrared thermal image of a rattlesnake (A) prior to feeding and (B) 48 h following feeding a meal comprising 32% $M_b$. The scale bar shows a total range of 2.5°C, where black is the coldest temperature and white is the warmest temperature. Note the uniform increase in body surface temperature in the snake following feeding. The darkest spot in each image is the nose, where evaporative cooling leads to a significant reduction in temperature.

for rapidly assessing multiple surface temperatures in a large number of animals. The technology has reached the stage where resolution and the accuracy rival that of other temperature recording devices. The largest error in using this technique occurs in knowing the emissivity of the target. Most biological tissues exhibit an emissivity of 0.95, which implies that they emit 95% of the radiation emitted by an ideal blackbody radiator at the same temperature (Speakman and Ward, 1998). The emissivity of snake skin is unknown; however, when IR image comparisons were made between the snakes' surface temperatures and the surface temperature of a substance of known emissivity, there were no discernable temperature differences, inferring that we have used a valid emissivity correction factor in the determination of surface temperatures.

### *Specific dynamic action and meal size effects on thermogenesis*

By overlapping the thermal increment associated with feeding (present study) with the post-prandial metabolic response of rattlesnakes (Andrade et al., 1997), a clear correlation emerges between both variables (See Fig. 2). While digesting meal sizes 10–50% of their own body masses, this species experiences peaks in metabolism between 15 h and 33 h post-feeding, at values 3.7- to 7.3-fold higher than the values measured during fasting (Andrade et al., 1997). Similarly, we have found that thermogenesis attained greater magnitude in those snakes fed with larger meals and that the attainment of peak values in $T_b$ occur in accordance with the peak in metabolism. It thus appears that the thermal effect of feeding that we recorded reflects a total body temperature increment arising from the SDA, as previously conjectured by Benedict (1932).

There are other possible explanations for the source of this heat production. Marcellini and Peters (1982) conjectured that undetectable muscular contractions and chemical decomposition of food may have contributed substantially to the post-prandial thermogenesis of snakes. Our data, however, suggest that the latter is unlikely. Indeed, we observed that a decaying, uneaten mouse produced no significant heat under the same experimental conditions (G. J. Tattersall, unpublished data). Further, the only increase in muscular activity that could be anticipated for digesting snakes is an increase in gut motility, since activity in general is decreased in fed snakes (Beck, 1996). This renders it improbable that an undetectable increase in muscular activity might have been involved in the increase in heat production after feeding. The maintenance of all snakes in a temperature-controlled room, with no possibility of changing heat exchange rates by behavioral means, excludes the possibility that the increment in body temperature exhibited by fed rattlesnakes is the result of an adjustment in thermoregulatory behavior, i.e. a post-prandial thermophilic response. Finally, the rattlesnakes' body temperatures returned to fasting levels with a time course that is in good agreement with the duration of the metabolic SDA response recorded for this species (Andrade et al., 1997).

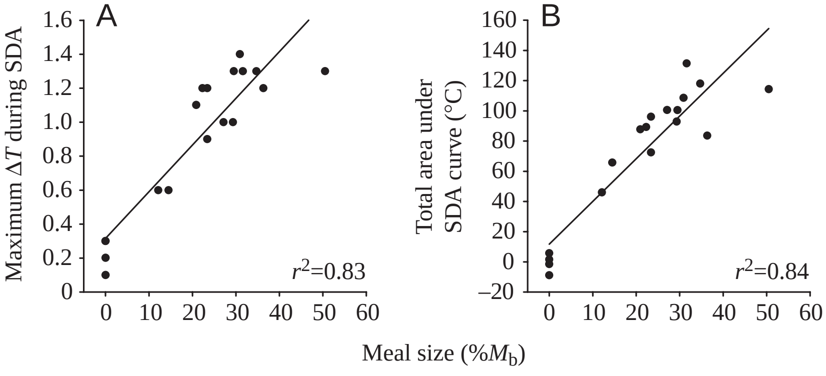

Fig. 3. (A) Individual values for the peak thermal increment ($\Delta T$) following feeding at different meal sizes as a function of snake body mass. (B) Individual values for the total area under the SDA temperature curve following feeding at different meal sizes. Pearson's coefficients are shown in both graphs.

### *Temperature effects on digestion and significance of thermogenesis*

The benefits often associated with the post-prandial thermophilic response in reptiles include an increased rate of digestion and/or digestive efficiency (Stevenson et al., 1985; Lillywhite, 1987; Hailey and Davies, 1987; Reinert, 1993; Sievert and Andreadis, 1999) and an increase in gastrointestinal motility, secretion and absorption (Dandrifosse, 1974;

Skoczylas, 1978; Mackay, 1968; Diefenbach, 1975a,b; Skoczylas, 1970a,b). Moreover, temperature may affect chemical digestion more directly, since some digestive enzymes have maximal activity at higher temperatures (Licht, 1964). The general consequence of such temperature effects on digestion may be characterized by the shortening of the SDA duration at the expense of increased rates of metabolism (see Toledo et al., 2003; Wang et al., 2003). For snakes that ingest large meals and have their locomotor and defensive ability temporarily impaired, speeding up the digestive process through an increase in temperature may be especially relevant since it would reduce the risk of predation (Garland and Arnold, 1983; Ford and Shuttlesworth, 1986). Higher temperatures and faster digestion may also be accompanied by increased rates of food intake, as documented in skinks (Du et al., 2000), which will result in better body condition, growth and perhaps an increased fitness. Finally, the energetic cost of digestion itself seems to decrease at higher temperatures (Toledo et al., 2003).

For rattlesnakes, our results suggest that all beneficial consequences associated with the post-prandial thermophilic response listed above may be achieved not only by altering thermoregulatory behavior, but also through the thermogenic consequences of the elevated metabolism during digestion. In *C. durissus*, we have found that thermogenesis alone may account, on average, for a 0.9–1.2°C increase in body temperature during the first 2–3 days after feeding. The important question is whether such an increase would be of any physiological significance to the rattlesnake's digestion. We tried to address this issue by calculating the effect of a 1°C change in body temperature on the digestion of snakes, by regressing SDA duration and SDA cost (expressed as a percentage of the calorific content of the meal, i.e. SDA coefficient; see Toledo et al., 2003) against body temperature, using a set of data obtained for *C. durissus* at 25° and 30°C (S. P. Brito, A. S. Abe and D. V. Andrade, unpublished data). This procedure revealed that a 1°C increase in body temperature, under the conditions in which we performed the experiments, may account for a 19 h decrease in SDA duration and a 0.3% decrease in the SDA coefficient. Thus, the thermogenic effect of feeding, *per se*, may, indeed, affect the digestive performance and the duration of digestion in rattlesnakes. Moreover, the ability to increase body temperature after feeding by thermoregulatory behaviors is reported to be constrained in rattlesnakes by the availability of adequate thermal microhabitats, reduced mobility and reclusive behaviors (Beck, 1996). Thus, it seems possible that the beneficial effects of metabolic thermogenesis on digestion may assume a greater importance during the night, on cloudy days, or whenever behavioral thermoregulation and the achievement of the post-prandial thermophily are constrained. Finally, by using the infrared imaging technique, we assessed only body surface temperature and, therefore, differences in deep core body temperature due to digestion associated thermogenesis may be even larger. Indeed, in experiments performed with pythons fed with meals containing temperature data loggers, Marcellini and Peters (1982) were able to detect increases in body temperature up to 4°C (see also Benedict, 1932; Van Mierop and Barnard, 1976). Moreover, digesting pythons experience metabolic responses that are far larger than those observed in rattlesnakes (Andrade et al., 1997; Secor and Diamond, 2000), which could also contribute to the larger thermogenic effect of feeding exhibited by this species (Benedict, 1932; Van Mierop and Barnard, 1976; Marcellini and Peters, 1982).

The thermogenic effect of feeding has been examined in one lizard species by Bennett et al. (2000) who found that digesting *Varanus* at 32 and 35° C tripled and quadrupled metabolic rate, respectively, but the resulting heat generated by such increases accounted for increases in body temperature of less than 1°C. This was mainly caused by the fact that the increased heat production was accompanied by increases in thermal conductance attributed to the greater ventilatory rates needed to support the higher rates of metabolism (Bennett et al., 2000). Although the same phenomenon may have prevented further increases in body temperature in *C. durissus*, the magnitude of this process in rattlesnakes most likely was smaller than that recorded in *Varanus*. Reptiles are known to exhibit a relative hypoventilation during digestion (Wang et al., 2001), but while the air convection requirement for $O_2$ in *Python* was reduced by 46% (Secor et al., 2000), in *Varanus* this reduction was only 21.4% (Hicks et al., 2000). Thus, the heat loss due to the changes in conductance associated with the increased total ventilatory rates during digestion should have been greater for *Varanus* compared to *C. durrisus*. Finally, the larger thermogenic effect of feeding in rattlesnakes compared to *Varanus* may also be related to the larger metabolic response to feeding in *C. durissus*; metabolism increases from 4- to 7-fold (Andrade et al., 1997), compared to a 3- to 4-fold change seen in *Varanus* (Bennett et al., 2000).

In brooding pythons *Python molurus* body temperature can increase up to 7.3°C above ambient temperature by endogenous heat production, due to increased metabolic rates associated with the spasmodic contractions of the body musculature (Hutchison et al., 1966). This figure is far more impressive than the thermogenic effect of feeding found in rattlesnakes (present study) and in varanid lizards (Bennett et al., 2000). Interestingly, however, brooding pythons showing such a large increase in body temperature experience metabolic rates that are only 9.3 times higher than non-brooding females under the same environmental conditions (Hutchison et al., 1966). Thus, the discrepancy between the increase in metabolism and body temperature among brooding pythons and digesting rattlesnakes and lizards indicates that other factors may affect the thermoregulatory ability of brooding pythons. One likely factor is posture; by remaining coiled around the eggs, brooding pythons decrease the surface area, which otherwise would serve as an avenue for heat loss (see Vinegar et al., 1970). Other possibilities are changes in conductance associated with circulatory adjustments, however, changes in heat transport *via* the circulatory system remain to be investigated.

### *Concluding remarks*

Endotherms may use SDA or exercise-generated heat for thermogenesis, saving a substantial amount of energy that would otherwise be used for this purpose (Costa and Kooyman, 1984). For an ectotherm, the general notion is that the heat generated during digestion is a wasteful byproduct generated from the metabolic increment (Hailey and Davies, 1987) since they naturally do not use metabolism to generate heat for thermoregulation. However, thermogenesis in snakes may act in concert with the behavioral post-prandial thermophilic response to achieve the suite of ecological and energetic benefits of increased body temperature during digestion. Particularly poignant in the case of snakes is the long, protracted digestion process. So, although the magnitude of the thermal increment following feeding may seem negligible, the duration of this sustained increase in body temperature is sufficient to suggest that digestion-derived heat in this ectotherm is a physiologically and ecologically important phenomenon.

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