

THERMOPHILIC RESPONSE TO FEEDING OF THE DIAMOND PYTHON, *MORELIA S. SPILOTA* (SERPENTES: BOIDAE)

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Abstract—1. Miniature temperature-sensitive radiotransmitters were implanted surgically into eighteen adult diamond pythons and thermoregulation of these snakes studied in a large thermal gradient in the laboratory.

2. Unfed diamond pythons selected temperatures in the range 26–33°C. Selected body temperature changed after feeding, with mean temperatures generally increasing by 2–5°C, and variances decreasing significantly in most snakes.

3. Selected body temperatures in the laboratory were similar to maximum body temperatures achieved when basking in the field.

4. Pythons without access to a heat source showed no elevation in body temperature after feeding, indicating that the thermophilic response to feeding in this species is achieved behaviorally, not physiologically.

INTRODUCTION

Most ectothermic animals have variable body temperatures which are controlled primarily by behavior. Ectotherms thus have flexibility in temperature selection, with the selected temperature depending on a variety of phylogenetic, physiological and ecological factors. Early notions of an inflexible "preferred" body temperature for a species (e.g. Cowles and Bogert, 1944; Brattstrom, 1965) have been replaced by more dynamic models which emphasize lability in temperature selection, depending upon specific "costs" and "benefits" of different thermal levels (for review see Huey, 1982). One important determinant of the temperature selected by an individual may be its ingestive status. Many reptile species show a positive thermophilic response to feeding although other species do not (for review, see Lillywhite, 1987).

In this study we determine the range of body temperatures selected by eastern Australian diamond pythons (*Morelia s. spilota*) in a thermal gradient, examine the effect of feeding on the selected range of body temperatures and relate this to field measurements of body temperatures. In addition, we investigate a particular aspect of thermoregulation unique to pythons. Most reptiles which select higher temperatures after feeding do so by behavioral thermoregulation (e.g. Regal, 1966; McGinnis and Moore, 1969; Lysenko and Gillis, 1980). However, it has also been suggested that *Python molurus* can elevate its body temperature after feeding in the absence of an external heat source (Benedict, 1932; Van Mierop and Barnard, 1976; Marcellini and Peters, 1982). The method by which this is achieved is unclear. Some heat may be generated by the specific dynamic action of digestion (Benedict, 1932), but Marcellini and Peters (1982) suggested that more heat is generated than can be attributed to digestive

activity. They suggested that as brooding female *P. molurus* can produce endogenous heat through muscular action, a similar form of heat production may occur after feeding. Shivering thermogenesis has been well-documented in *M. s. spilota* (Harlow and Grigg, 1984; Slip and Shine, 1988a). Thus, we investigate the possibility that *M. s. spilota* might, when held at relatively constant low temperatures, raise body temperatures after feeding through the endogenous production of heat. Female snakes which had recently completed incubation were used for this latter experiment, as it seemed likely that these animals (which had been using shivering thermogenesis for months) might be the ones most likely to use this behavior in another context (thermophilic response to feeding).

MATERIALS AND METHODS

Eighteen snakes (12 males and 6 females) were collected from different locations between Nowra and Newcastle, New South Wales, housed for 2–12 months prior to the experiment in glass tanks and supplied with ultra-violet lights for basking. Photoperiod was adjusted to approximate natural photoperiod and temperature maintained at 24–29°C. Some of these animals had previously been radio-tracked in the field (see Slip, 1986; Slip and Shine, 1988a,b,c,d,e). All snakes were kept on identical feeding schedules for 2 months before being introduced into the thermal gradient. Body temperatures were determined from temperature-sensitive radiotransmitters (TT-IU-1000, J. Stuart Enterprises, Grass Valley, California, <4% of snake body weight) surgically implanted into the peritoneal cavity using aseptic surgical technique under halothane anaesthesia. Body temperatures were recorded automatically using a TR-2E miniature telemetry receiver (Telonics Telemetry Consultants, Mesa, Arizona) interfaced with an Oric microprocessor.

The thermal gradient consisted of a wooden box (240 × 120 × 20 cm) with a perspex top, divided into six 20 cm-wide runways. The substratum was left bare. Heat was provided by a green 40-watt globe inserted on the wall

at one end of each of the runways and a heating wire attached under two-thirds of the base of the gradient. This wire was set 1 cm apart at the warm end of the gradient increasing to 15 cm apart 160 cm down the gradient. Both heat sources were left on throughout the experiment. The gradient was in a quiet room with ambient temperatures of 15–17°C, providing a range in substratum temperature within each runway from 17 to >50°C. The room was illuminated with fluorescent lighting for 12 hr per day.

Snakes were introduced into the thermal gradient, six at a time, one individual per runway and were allowed at least 24 hr in which to acclimate to the thermal gradient before measurements were taken. Body temperatures were recorded at hourly intervals for up to 72 hr. Three individuals were then fed an equivalent amount of either laboratory rats or mice (200–300 g), the remaining three snakes acting as a control group. Body temperatures were then recorded for up to 72 hr after feeding. At the completion of this trial the animals in the unfed group were fed, thus maintaining almost equivalent feeding schedules and all animals were returned to their tanks. These animals were then left unfed for at least 1 month before being reintroduced into the gradient. The experiment was repeated until post-feeding body temperatures were obtained from fifteen snakes; the remaining three snakes refused to feed in the thermal gradient.

The mean body temperature for a snake in a particular nutritional state was taken as its selected body temperature (Pough and Gans, 1982) associated with that state. All individuals were apparently healthy when introduced into the gradient. At least 6 weeks had elapsed since any snakes

had undergone surgery and no individuals were used if they were about to shed.

For analysis of data on selected temperatures the snakes in the thermal gradient were classified into four groups: the experimental snakes in the periods before and after they were fed, and the control snakes in the periods before and after the experimental snakes were fed. There were 14 snakes in each group. Some snakes occur in each group as they were used as control animals on one occasion and experimental animals on another. Twenty-four readings of body temperature were selected randomly from each snake in each group. A Kruskal-Wallis test (Hull and Nie, 1981) was used to test for significant differences among the four groups.

Mean body temperatures were also calculated for each snake in the fed and unfed condition from all data recorded for up to 72 hr before and after feeding. These data were combined to establish a pooled mean body temperature for unfed snakes and a pooled mean body temperature for fed snakes.

A second experiment was run with two female snakes, captured soon after incubating eggs (see Slip and Shine, 1988b). These animals were kept in a glass tank 140 × 60 × 40 cm, with access to water but no heat source. Ambient temperature fluctuated between 19.5 and 21.5°C (as recorded with a transmitter suspended in the centre of the tank 10 cm above the substratum). The snakes were allowed 24 hr to acclimate to the tank before temperatures were measured. Body temperatures and air temperatures were monitored for 24 hr before one snake was removed and fed a laboratory rat (350 g) and then returned to the tank.

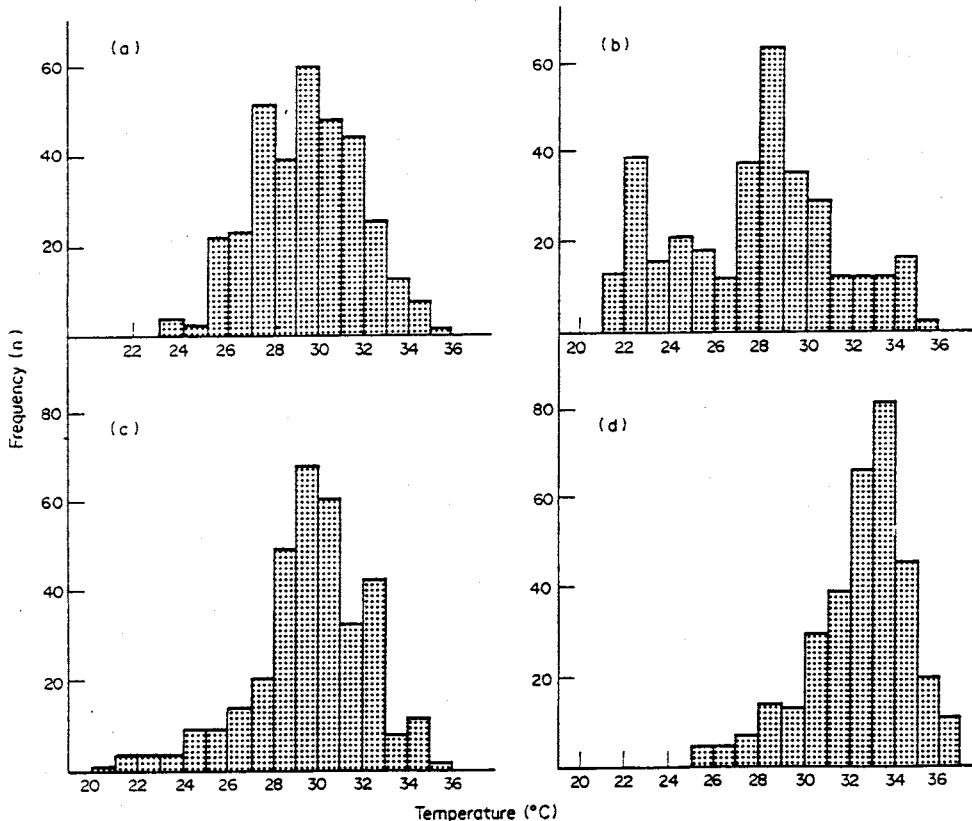


Fig. 1. Frequency distributions of body temperatures of diamond pythons before and after feeding. (a) shows the control group (unfed) at a time period one, mean = 29.9 ± 2.34 (SD); (b) shows the control group (unfed) at time period two, mean = 28.2 ± 3.54 (SD); (c) shows the experimental group at time period 1 (unfed), mean = 30.1 ± 2.59 (SD); (d) shows the experimental group at time period 2 (fed), mean = 32.9 ± 2.27 (SD). Each distribution consists of 24 randomly selected body temperatures from each of 14 individuals over a 72-hr period.

Body temperatures and air temperatures were then monitored for 40 hr after feeding. After 10 days the experiment was repeated, feeding the other snake.

RESULTS

There were significant differences in mean body temperatures among the four groups of snakes ($H = 389.048$, $v = 3$, $P < 0.001$). Multiple range testing revealed that, after feeding, the mean body temperature of the experimental group was significantly higher than that of the unfed (control) group. There was no significant difference between the two groups before feeding. While the mean body temperature of the experimental group increased significantly in the period after feeding, the control group significantly decreased mean body temperature over the corresponding period. The frequency distributions of body temperatures for each group are shown in Fig. 1.

The mean body temperatures of individual snakes while in the thermal gradient ranged from 26.3 to 32.4°C when unfed and from 30.8 to 35.3°C when recently fed (Table 1). Most snakes showed an increase in mean body temperature of 2–5°C when fed. Only two snakes failed to show a significant increase after feeding (No. 4 and No. 23) and these snakes maintained the same mean body temperature before and after feeding. The variances associated with the

total mean body temperature before and after feeding were heterogeneous ($F_{4243.1854} = 1.778$, $P < 0.001$, Table 1). There was no evidence of photoperiod effects on preferred body temperature: mean body temperatures at night were not significantly different from those in the day ($F_{1.1342} = 1.07$, $P > 0.25$).

Figure 2 shows the fluctuations in body temperature of females No. 2 and No. 4 after feeding in a relatively homogeneous thermal environment. There was no obvious rise in body temperature from either snake after feeding. Body temperatures remained a little above air temperature. There was no significant difference in mean body temperature between the control snake and the fed snake before or after feeding ($H = 3.93$, $v = 3$, $P > 0.25$), suggesting that shivering thermogenesis was not employed by either snake.

DISCUSSION

Thermophilic response to feeding

After feeding, captive specimens of *Morelia spilota* exhibited a positive thermophilic response, with most individuals maintaining mean body temperatures about 2–5°C above fasting levels. Possible advantages in selecting higher temperatures after feeding include increases in digestive rate and perhaps digestive

Table 1. Body temperatures (°C) of diamond pythons in a thermal gradient when unfed and fed. Means and standard deviations are given, with range and number of readings in parentheses. Snakes Nos 3, 20 and 27 could not be induced to feed

Snake no.	Sex	SVL (cm)	Mass (kg)	Mean body temperature (°C)	
				Unfed	Fed
2	F	184	1.58	28.2 ± 4.51 (20.9 – 36.0) (317)	31.5 ± 1.73 (24.8 – 35.8) (113)
3	F	182	2.70	28.0 ± 3.56 (22.0 – 35.5) (317)	—
4	F	190	1.88	30.5 ± 1.72 (27.0 – 35.8) (317)	30.8 ± 1.77 (26.7 – 33.1) (166)
5	F	184	2.33	30.3 ± 1.71 (23.5 – 34.3) (144)	32.9 ± 2.98 (25.6 – 37.5) (166)
6	F	230	3.70	30.1 ± 1.79 (23.5 – 33.3) (317)	34.1 ± 2.22 (26.7 – 36.7) (166)
7	F	190	2.95	29.4 ± 1.40 (25.8 – 33.5) (144)	34.0 ± 2.06 (26.2 – 37.1) (113)
14	M	182	2.84	29.7 ± 2.01 (24.4 – 33.7) (242)	35.3 ± 0.94 (32.7 – 37.2) (141)
17	M	150	1.25	28.5 ± 2.51 (22.6 – 31.4) (206)	33.5 ± 0.67 (30.7 – 35.0) (100)
18	M	175	1.86	30.1 ± 1.94 (27.2 – 36.7) (242)	33.7 ± 1.39 (31.3 – 35.1) (95)
20	M	182	2.06	31.8 ± 2.27 (26.3 – 35.7) (242)	—
22	M	185	2.10	31.4 ± 2.40 (25.0 – 35.6) (242)	33.3 ± 0.94 (31.7 – 35.8) (123)
23	M	175	1.80	31.6 ± 1.96 (25.9 – 35.1) (242)	31.3 ± 2.04 (26.9 – 35.9) (141)
24	M	176	1.90	26.3 ± 2.50 (21.7 – 31.7) (242)	33.5 ± 1.14 (31.1 – 36.0) (141)
25	M	160	1.10	30.7 ± 3.32 (27.0 – 35.6) (206)	33.6 ± 1.78 (30.9 – 35.7) (95)
26	M	155	0.90	31.7 ± 1.25 (29.3 – 36.0) (206)	33.0 ± 1.42 (29.5 – 37.6) (100)
27	M	150	1.10	32.4 ± 1.52 (29.9 – 35.9) (206)	—
28	M	142	0.99	28.9 ± 2.17 (25.5 – 33.3) (206)	32.1 ± 2.73 (25.0 – 35.1) (100)
29	M	140	0.72	30.2 ± 2.17 (27.3 – 35.1) (206)	33.9 ± 0.58 (32.4 – 35.1) (95)
Total				29.9 ± 2.92 (20.9 – 36.7) (4244)	33.1 ± 2.19 (24.8 – 37.6) (1855)

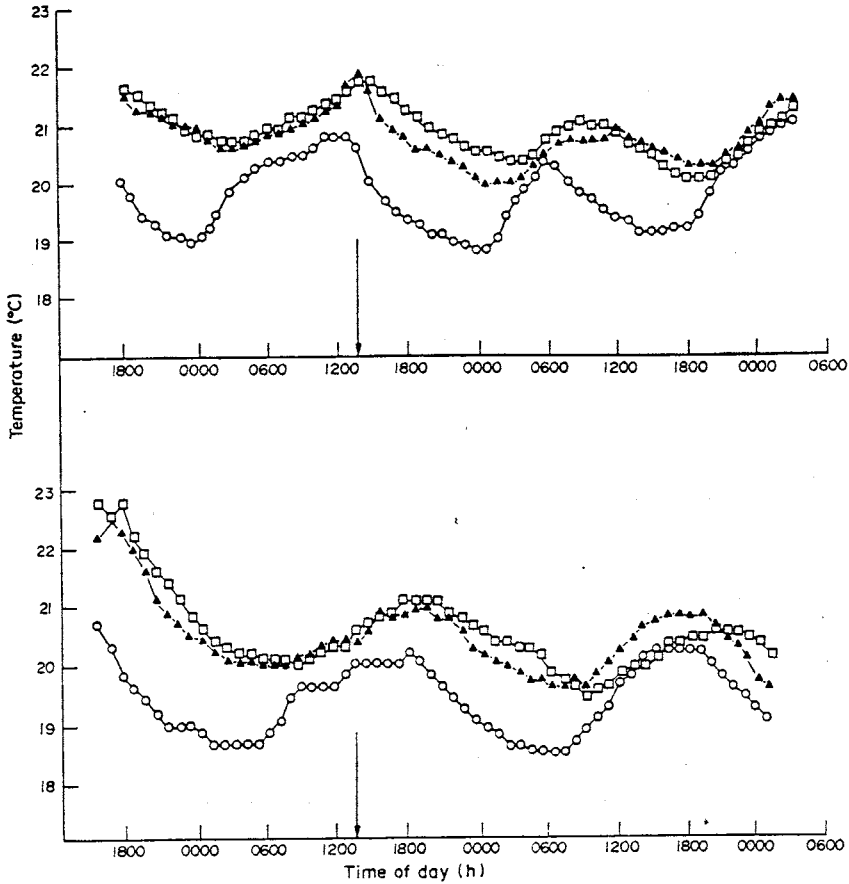


Fig. 2. Fluctuations in body temperatures of two female diamond pythons in the laboratory with no access to an external heat source. (a) Female No. 4 fed (\blacktriangle), female No. 2 unfed (\triangle); (b) Female No. 2 fed (\blacktriangle), female No. 4 unfed (\triangle). The arrow indicates time of feeding (1300 hr); (\circ) = air temperature.

efficiency (Greenwald and Kanter, 1979; Naulleau, 1983; Christian, 1986) and avoidance of any problems from low gastric motility and low digestive rates resulting in putrefaction of food in the stomach (Regal, 1966; Skoczylas, 1970; Harlow *et al.*, 1976). A positive thermophilic response to feeding has been observed in many reptiles. Regal (1966) reported increased body temperatures after feeding in some species of lizards and observed that a recently fed *Boa constrictor* would bask with the food bolus directly under the light source. We have observed similar behavior in *M. s. spilota* in captivity, particularly in juvenile snakes where the prey item can represent 50% or more of snake body weight. Snakes will bask with the bolus under a heat lamp and will also coil such that the stomach is over a heating pad. However, a positive thermophilic response to feeding is not universal among snakes (see Lillywhite, 1987).

The significant lowering of body temperature in the control group after the experimental group was fed is puzzling. Even mild food deprivation may lower the body temperature at which some lizards become active (Cogger, 1974) but it seems unlikely that 48 hr of food deprivation would have such an effect in the present study, given that neither the control group nor the experimental group were fed for at least 14 days prior to their introduction into the thermal gradient. The drop in body temperature may be an

artefact of the method by which snakes were fed. To avoid disturbance from excessive handling, the snakes were fed in the thermal gradient. The action of feeding snakes in the adjacent runway, together with odours from the food items, may have caused snakes in the control group to become more active, possibly lowering body temperatures as they moved to the cooler end of the gradient in search of food.

The wide variation in mean body temperatures of individual snakes, both fed and unfed, is perhaps surprising, given that many studies of reptilian thermoregulation in the past have assumed that reptiles thermoregulate towards a "preferred" temperature which is optimal for activity or some physiological function. The realization that some reptiles elevate body temperature after feeding has led to speculation that reptiles may have multiple physiological optimal temperatures (Bustard, 1967; Lang, 1979; Pough, 1980), although this has only been inferred from behavioral data. Although this hypothesis explains the behavioral observations, there is another possible explanation which does not involve multiple optimal temperatures (Greenwald and Kanter, 1979). This hypothesis (reviewed in Huey, 1982) suggests that reptiles thermoregulate towards the temperature which will maximize net energy gain per unit time (energy gained from food less metabolic cost). As metabolic cost varies with temperature, the tem-

perature which maximizes net energy gain can change as a result of the amount of food ingested (Huey and Slatkin, 1976; Greenwald and Kanter, 1979; Huey, 1982). However, as Huey (1982) suggests, these views may oversimplify reptilian thermoregulation.

In addition to the significant increase in body temperature after feeding, there was also a reduction in the total variance (Table 1). Less variability associated with increased body temperatures after feeding has also been found in other studies (Gatten, 1974; Lang, 1979) and has generally been interpreted as an increase in the precision of thermoregulation. Huey (1982) has discussed the problems associated with measuring precision of thermoregulation and suggests that the variance in body temperature may be a statistically inappropriate measure as reptiles do not regulate their body temperature around a set mean but change between upper and lower set points. Also, variance in body temperature depends on body size (McNab and Auffenberg, 1976) and the degree of thermal heterogeneity of the environment (Heath, 1964). A thermal gradient is by design a thermally heterogeneous environment and animals which were highly mobile within the gradient should have more variable body temperatures than sedentary animals. Thus, the reduced variance in body temperature after feeding may reflect a change in mobility, rather than more precise thermoregulation, as feeding results in reduced mobility in some snakes (Garland and Arnold, 1983).

Comparison with field temperatures

Although thermal gradients may be useful in determining behavioral responses of reptiles under controlled conditions, and hence examining thermoregulatory responses to specific events such as feeding, the relationship between gradient temperatures and field temperatures may be obscure, as acclimation to laboratory temperatures may occur and it is often difficult to determine the physiological state of animals in the field. Heatwole (1976) compared data on body temperatures of a number of Australian reptiles determined from laboratory studies with analogous data from field studies. He found that in some species similar temperatures are reported, while for others, field and laboratory temperatures were quite different.

The mean body temperatures of unfed diamond pythons in the thermal gradient fell within the range of the daily plateau of diamond python body temperatures measured by radiotelemetry in the field on clear days in spring, summer and autumn (Slip, 1986). The mean midday body temperatures in those seasons were also very close to the gradient temperatures selected by unfed snakes. However, most body temperatures recorded in the field were lower than those selected in the laboratory: midday temperatures in winter were about 3°C lower and mean daily body temperatures (1000 to 1800 hr) were about 2°C lower in spring, summer and autumn, and about 5°C lower in winter (Slip, 1986). This discrepancy suggests that the body temperature maintained in the gradient may represent the body temperature which snakes in the field achieve through basking in spring, summer and autumn. Mean body temperature of unfed snakes in the thermal gradient (29.9 ± 2.92 , Table 1) are very

similar to field measurements of mean maximum body temperature achieved through basking (29.2 ± 3.33 , Slip, 1986). As snakes generally bask only once each day and then use postural changes to reduce heat loss (Slip and Shine, 1988c), one would expect the mean body temperature in the field, taken over a larger part of the day, to be lower than that found in the thermal gradient.

The maximum body temperature recorded in the thermal gradient (analogous to the voluntary maximum) was 37.6°C in fed snakes and 36.7°C in unfed snakes, while the highest body temperature recorded from diamond pythons in the field was 35.5°C. One snake in the thermal gradient had a post-feeding mean body temperature of 35.3°C, which is close to the maximum temperatures tolerated in the field. Whether or not diamond pythons in the field elevate body temperature after feeding is difficult to determine as feeding is observed so rarely (Slip and Shine, 1988d). However, the range of field body temperatures suggests that free-ranging diamond pythons are capable of achieving body temperatures comparable to post-feeding gradient body temperatures, although these may be maintained for only a short time.

Response to feeding with no external heat source

Recently fed *Python molurus* have been reported to raise body temperature above ambient temperature in the absence of an external heat source (Benedict, 1932; Van Mierop and Barnard, 1976; Marcellini and Peters, 1982). Because female pythons are capable of heat production through muscular twitching (Hutchinson *et al.*, 1966; Vinegar *et al.*, 1970; Van Mierop and Barnard, 1976, 1978; Harlow and Grigg, 1984) it has been tentatively suggested that body temperatures are elevated above ambient temperature after feeding through some kind of muscular action (Marcellini and Peters, 1982). Unfortunately none of the studies reporting elevations above ambient temperatures compare the body temperature of the fed snake to that of an unfed snake at the same time. Benedict (1932) realized the difficulties involved in measuring ambient temperatures as regional differences may go unnoticed. It is often difficult to maintain a homogeneous thermal environment and snakes appear to be able to utilize even slight heterogeneity in environmental temperature to increase body temperature. They can then reduce heat loss through tight coiling. In the present study a gradient of slightly less than 1°C was measured in the tank of the female snakes. Nevertheless, the snakes spent most time coiled at the warmer end of the tank. The act of coiling tightly has been suggested as a possible cause of heat production (Marcellini and Peters, 1982).

If digestive rate is increased at higher temperatures, and hence leads to a faster growth rate, it would be of benefit to females which had completed brooding to maximize their rate of food intake. Females finish brooding around mid-February to mid-March (Slip and Shine, 1988b) and would be faced with about 8–12 weeks before air temperatures dropped enough to significantly reduce opportunities to feed. As egg production and incubation are metabolically expensive, it would be an advantage to the female to

gain weight as quickly as possible, in order to reproduce again at the earliest opportunity. Endogenous heat production may be a way of increasing digestive rate and food intake. However, although the body temperatures of the captive snakes in this experiment were often slightly above air temperatures, there is no evidence that the recently-fed snakes used endogenous heat production to elevate their body temperatures above air temperature, or above the body temperature of the unfed snakes. The metabolic cost of shivering thermogenesis is very high (Harlow and Grigg, 1984) and probably so high that it would overshadow any benefits arising from more rapid digestion.

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