

# An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes *Elaphe obsoleta obsoleta*

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## Summary

1. Most physiological processes are temperature-dependent. Thus, for ectotherms, behavioural control of body temperatures directly affects their physiology. Ectotherms thermoregulate by adjusting habitat use and therefore thermoregulation is probably the single most important proximate factor influencing habitat use of terrestrial reptiles, at least in temperate climates.

2. Snakes have been shown to raise their body temperature following feeding in a laboratory thermal gradient, presumably to enhance digestion. This experiment was exported to the field to explore the link between feeding, habitat selection and thermoregulation in free-ranging snakes.

3. Experimental feeding was conducted in the laboratory and in the field on black rat snakes (*Elaphe obsoleta obsoleta*) that had temperature-sensitive radio-transmitters surgically implanted.

4. Snakes had higher mean body temperatures following feeding than prior to feeding in a laboratory thermal gradient.

5. Some, but not all evidence, indicated that black rat snakes increased their mean body temperature following feeding in the field. Indices of thermoregulation indicated that the snakes thermoregulated more carefully and more effectively after they had eaten.

6. Forest edges provided the best opportunities for thermoregulation in the study area. Black rat snakes were less likely to move following feeding when fed in edges than when fed in the forest and were more likely to be found in edges following feeding, whether they had been fed in the forest or in an edge.

7. Results of this study and one previous study suggest that thermoregulatory behaviour of snakes following feeding in the laboratory is a reliable predictor of their behaviour in the field. A review of 13 studies of the thermoregulatory behaviour of snakes following feeding in the laboratory revealed that not all species behave similarly. However, the quality and number of studies currently available is not adequate for testing hypotheses about which species should change thermoregulatory behaviour in response to eating and which should not.

**Key-words:** Black rat snake, movements, postprandial thermophily, radio-telemetry, supplemental feeding.

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## Introduction

Nearly all physiological processes are temperature-dependent. Thus, because reptiles are ectotherms, variation in their body temperature ( $T_b$ ) affects their development, physiology and behaviour (Arnold & Bennett 1984). Because virtually all aspects of reptile ecology are affected by  $T_b$ ,  $T_b$  ultimately has a significant impact on fitness (Huey & Kingsolver 1989). All ectotherms obtain heat from their environment and  $T_b$  regulation is achieved behaviourally by adjusting habitat selection, body posture and timing of activity (Huey *et al.* 1989). Thermoregulation is probably the single most important proximate factor influencing habitat selection by terrestrial squamates (Reinert 1993), at least in temperate climates (Shine & Madsen 1996). Our general goal in this paper is to investigate the association between foraging, thermoregulation and habitat use in black rat snakes (*Elaphe obsoleta obsoleta* (Say)).

The thermoregulatory behaviour of snakes following feeding provides an ideal opportunity to study thermal ecology. Snakes typically ingest large meals at infrequent intervals and several factors should make hastened digestion through increased thermoregulation advantageous. (1) A large meal might impair locomotion, making the snake more susceptible to predators. (2) Time spent inactive while digesting cannot be spent in other activities, such as searching for mates or for the next meal (Greenwald & Kanter 1979). (3) Slow digestion allows decomposition of the prey item inside the snake, potentially leading to regurgitation of the meal or even death (Naulleau 1983). From a practical perspective, thermoregulatory behaviour following feeding is studied easily because it has a precisely defined start time, unlike other factors that have been reported to increase thermoregulation such as reproduction (Charland & Gregory 1990) or skin shedding (Gibson, Smucny, & Kollar 1989). Also unlike other factors, the association between feeding and thermoregulation is amenable to experimentation through supplemental feeding by the researcher (Brown & Weatherhead 2000).

Although several researchers have recognized the experimental potential of thermoregulation following feeding, exploitation of that potential has been limited largely to studies of captive animals. Postprandial thermophily (PPT) in the laboratory has been reported in many snake species, but may not be important in others (Peterson, Gibson, & Dorcas 1993). There is obviously no consensus about the generality of the phenomenon in snakes (Lillywhite 1987), and it is unclear whether this reflects real differences among species or is an artefact of studying captive animals. Only two studies of PPT have been conducted on free-living snakes (Beck 1996; Brown & Weatherhead 2000), and only Brown & Weatherhead (2000) tested simultaneously for the presence of PPT in the laboratory and in the field. They found that northern water snakes (*Nerodia sipedon sipedon* (Linnaeus)) did not increase their  $T_b$  significantly, and did not thermoregulate more carefully

following feeding in either the laboratory or the field. However, their study also revealed that environmental operative temperatures ( $T_e$ s) within the preferred  $T_b$  range ( $T_{set}$ ) of northern water snakes were widely available in the snakes' habitat, thus making it very easy for the snakes to maintain their preferred  $T_b$ . To assess the generality and importance of PPT in the wild, we need information on the postprandial thermoregulatory behaviour of species that face thermally challenging environments. Black rat snakes in eastern Ontario provide such an opportunity. In addition, we are unaware of any study that has formally examined habitat selection in relation to digestion of a meal in snakes, despite the tenet that habitat selection is one of the primary ways in which snakes adjust their  $T_b$  (Reinert 1993). Thus, it is important to study not only PPT in free-living snakes, but also to document the role that habitat selection plays in this phenomenon.

We have three specific objectives. First, we test the prediction that black rat snakes elevate their  $T_b$  following a meal in a laboratory thermal gradient. Secondly, we test the prediction that free-ranging black rat snakes increase  $T_b$ s and/or increase the extent of behavioural thermoregulation following a meal. Thirdly, we test the prediction that free-ranging black rat snakes use habitat selection as the mechanism for behavioural thermoregulation.

Although feeding is amenable to experimentation, several logistical problems need to be overcome to conduct this seemingly simple experiment. First, because snakes are shy and elusive animals, opportunities for experimental feeding are scarce. For example, in a 4-year telemetry study (Blouin-Demers & Weatherhead 2001a), black rat snakes were visible on only 30% of 3715 occasions that they were located. Secondly, one needs to obtain natural prey items of the study species and entice both captive and free-ranging snakes to ingest them voluntarily (force-feeding is not an option because the associated trauma could lead to abnormal behaviour). Thirdly, it is necessary to record  $T_b$ s and habitat use for at least 24 h prior to and following feeding, even if the snakes move following feeding. Obtaining data on  $T_b$  and habitat use prior to feeding allows individual snakes to be used as their own controls. Fourthly, in addition to monitoring  $T_b$ s, one needs to monitor simultaneously  $T_e$ s in all habitats available to the study species prior to and following feeding to allow calculation of thermoregulatory indices (Hertz, Huey, & Stevenson 1993). Finally, one needs to repeat the feeding trials on a sufficient number of individuals to achieve adequate statistical power. The combination of these difficulties probably explains why this experiment has not been performed previously.

## Materials and methods

### STUDY AREA AND STUDY ANIMALS

This study was conducted from 1997 to 1999 at the Queen's University Biological Station, approximately

40 km north of Kingston (Ontario, Canada). The study area was approximately 10 km × 3 km along the north-western shore of Lake Opinicon and was covered mainly by second-growth deciduous forest. Black rat snakes were captured both at communal hibernacula during spring emergence (Blouin-Demers, Prior & Weatherhead 2000) and opportunistically during the active season (Prior, Blouin-Demers & Weatherhead 2001). A subset of individuals was selected and surgically implanted with temperature-sensitive radio-transmitters (Model SI-2T, Holohil Systems Inc., Carp, Ontario, Canada) under isoflurane anaesthesia (Blouin-Demers *et al.* 2000). Transmitters weighed 8.6 g (maximum ratio of transmitter mass: body mass = 0.025) and had 20 months of battery life at 20 °C. Calibration curves relating transmitter pulse rate to temperature were supplied by the manufacturer. Two automated radio-telemetry data loggers (SRX 400, Lotek Engineering Inc., Newmarket, Ontario, Canada) were used to record  $T_b$ s of snakes every 10 min.  $T_b$ s for each individual were then averaged for each hour. From May (1997) to November 1999 17 males and 36 females were followed for periods ranging from 1 to 30 months. Twenty-three snakes (nine males and 14 females) were followed in multiple years and therefore data are available for 79 'snake years' (25 'male years' and 54 'female years'). It was from this group of snakes that subjects for this study were drawn. All experimental procedures were approved by the Carleton University Animal Care Committee (protocol B97-1).

#### FEEDING TRIALS

To determine if PPT occurred in black rat snakes, radio-implanted snakes had to be fed because natural feeding events were rarely observed (Gabriel Blouin-Demers, unpublished data). Black rat snakes were fed by offering them a euthanized rodent (obtained through removal trapping; Blouin-Demers & Weatherhead 2001a) clipped to the end of an extendable pole. Snakes were fed in this manner in the laboratory and in the field. During each trial, snakes were fed as much food as they would ingest voluntarily. Although initially hesitant, the snakes soon learned to recognize this feeding opportunity and started taking food directly from our hands. Rodents included *Tamias striatus* (Linnaeus), *Microtus pennsylvanicus* (Ord) and *Peromyscus maniculatus* (Wagner). Rodents were weighed prior to being fed to snakes, allowing calculation of the total amount of food consumed by an individual for each feeding trial. When attempting feeding in the field, it was not possible to tell if the snake had fed recently, except if it had an obvious food bulge (snakes with obvious bulges were not included in the experiment). However, snakes had substantially more food in their stomach after feeding than before, indicating that they were hungry at the time of feeding if they accepted food. To ensure that snakes had an empty stomach prior to feeding in the thermal preference chamber they

were fasted for a week before testing. Feeding trials were conducted at least 6 weeks after radio-transmitter implantation to allow ample time for healing.

#### PPT IN THE LABORATORY

The presence of PPT was tested in the laboratory using a thermal gradient chamber. Radio-implanted black rat snakes were introduced individually in the chamber under two treatments: post-absorptive and recently fed. The order in which the treatments were administered was randomized and snakes were given 24 h to acclimatize to the setting in each case.  $T_b$ s selected in the gradient were then recorded every 10 min for 24 h using a telemetry data logger. Because food passage time in black rat snakes is approximately 3–4 days, the snakes were in the process of digesting throughout each trial. The bounds of the central 50% of observed  $T_b$ s (Hertz *et al.* 1993) and the mean  $T_b$  selected for each individual under both treatments were compared to determine if  $T_b$  selection varied following feeding. The bounds of the central 50% of observed  $T_b$ s for the fasted snakes were also used to estimate the preferred body temperature ( $T_{set}$ ; Hertz *et al.* 1993) of black rat snakes for use in the field experiments.

#### PPT IN THE FIELD

To determine if PPT occurred in the field, free-ranging radio-implanted black rat snakes were fed and their thermoregulatory behaviour for 24 h preceding feeding was compared to their thermoregulatory behaviour for 24 h following feeding. Three indices of thermoregulation were used to quantify the snakes' thermal behaviour. The simplest method compared the mean  $T_b$  of snakes before and after feeding. The other indices compare the extent to which snakes actually experience  $T_b$ s within their  $T_{set}$  (the accuracy of  $T_b = d_b$ ) to the extent to which the habitat allows  $T_b$ s within the  $T_{set}$  to be reached (the thermal quality of the habitat =  $d_e$ ). Hertz *et al.* (1993) calculated  $d_b$  as the absolute value of the difference between an observed  $T_b$  and the lower (or upper) bound of  $T_{set}$ , and  $d_e$  as the absolute value of the difference between the environmental temperature ( $T_e$ ) and the lower (or upper) bound of  $T_{set}$ . Based on these metrics, they derived an index of the effectiveness of thermoregulation ( $E$ ):  $E = 1 - (\bar{d}_b/\bar{d}_e)$ . However, Blouin-Demers & Weatherhead (2001b) showed that  $d_e - d_b$  is a better index of thermoregulatory effectiveness than  $E$  because it does not use a ratio. Therefore, this latter index was used here. The final index used was  $Ex$  (Christian & Weavers 1996), which determines the extent to which snakes exploit their thermal environment when conditions allow.  $Ex$  is the time an animal spends within its  $T_{set}$  expressed as a percentage of the time that  $T_b$ s within  $T_{set}$  were available (as indicated by  $T_e$ ).

$T_e$  was measured using temperatures from snake models (water-filled pieces of copper tubing the size

and colour of an adult black rat snake) placed in both forest and open habitats. Testing with real snakes confirmed that these models provided highly accurate estimates of a black rat snakes'  $T_b$  in a given habitat under prevailing weather conditions (Blouin-Demers & Weatherhead 2001b). All indices of thermoregulation were calculated for the whole day and for the daytime only (06.00–08.00 h), because opportunities for snakes to achieve  $T_{bs}$  within  $T_{set}$  at night seemed likely to be rare. In addition, the thermoregulatory behaviour of experimentally fed snakes was compared to the thermoregulatory behaviour of snakes radio-tracked during the same time period as part of a larger telemetry study.

#### HABITAT USE BEFORE AND AFTER FEEDING

Blouin-Demers & Weatherhead (2001a) showed that black rat snakes used habitat edges more than expected by chance. This preference was detected both by using a MANOVA on a large set of habitat variables and by simply classifying the snake and random locations into habitat categories. In the latter analysis, it was considered that a snake was in an edge when it was within 15 m of the boundary between the forest and an open habitat such as old hayfields or rock outcrops. The same definition was used here, so snake locations prior to feeding and following feeding were simply classified as being in an edge or not in an edge based on the 15 m criterion. The behaviour of experimentally fed snakes was also compared to the behaviour of snakes radio-tracked as part of a larger telemetry study. Specifically, their behaviour when relocated (classified as basking/resting or other) and their frequency of movement (where no movement was defined as a displacement  $\leq 5$  m between relocations) were compared to test two predictions. First, snakes should bask more following feeding and, secondly, if edges are used for thermoregulation, snakes should travel more following feeding in the forest than following feeding in an edge.

#### STATISTICAL ANALYSES

Series of  $T_b$ s recorded from a single individual are not independent. Therefore, all analyses were performed on data ( $T_b$ ,  $d_e - d_b$ , or  $Ex$ ) averaged for each individual over the period before and after feeding. Paired  $t$ -tests (one-tailed because the hypothesis being tested was that snakes thermoregulate more carefully following feeding) were used to compare thermoregulatory behaviour of individuals prior to and following feeding, except when

comparing mean  $T_b$ , where ANCOVA was used to control for the effect of measuring  $T_b$ s under different  $T_e$ s. The thermoregulatory behaviour of experimentally fed snakes was compared to the thermoregulatory behaviour of snakes radio-tracked as part of a larger telemetry study using  $t$ -tests. Habitat use prior to and following feeding was compared using a binomial test (Zar 1984). The behaviour of snakes and their frequency of movement was compared using chi-square tests.

Analyses were conducted on JMP Version 3.2 (SAS Institute 1997) and GPower Version 2.1 (Buchner, Faul & Erdfelder 1997) on a Macintosh desktop computer. Box plots were inspected to determine if the assumptions of normality and homogeneity of variance were upheld. No significant departures from these assumptions were detected. All means are reported  $\pm$  one standard error.

## Results

#### PPT IN THE LABORATORY

Thirteen individual snakes were fed an average of  $101.6 \pm 8.0$  g of food in the thermal preference chamber. This mean meal size represents  $17.3 \pm 1.9\%$  of the snakes' mean fasted mass and the minimum meal size was greater than 10% of the snake's fasted mass in all trials. In total, 3744  $T_b$ s were recorded and reduced to 624 individual hourly mean  $T_b$ s from these 13 snakes. Their  $T_b$  selection for 24 h while fasted was compared to their  $T_b$  selection for 24 h following a large meal. Paired  $t$ -tests revealed that, after feeding, snakes had significantly higher mean  $T_b$ s and 25% quartiles, but had 75% quartiles that were not significantly different at  $\alpha = 0.05$  (Table 1). Thus, black rat snakes exhibited PPT in the laboratory and shifted the lower end of their  $T_{set}$  range (the 25% quartile) upward after feeding. This increased the snakes' mean  $T_b$ , even though the upper end of  $T_{set}$  remained unchanged.

#### PPT IN THE FIELD

In the field, 23 individuals were fed an average of  $132.3 \pm 8.9$  g of food a total of 37 times. This mean meal size represents  $19.6 \pm 1.4\%$  of the snakes' mean mass and the minimum meal size was greater than 10% of the snake's mass in all trials, where mass was determined from the most recent capture (maximum time since capture = 2.5 months). Because fed snakes were often out of range of the automated data loggers for part of

**Table 1.** Summary of the thermoregulatory behaviour of black rat snakes prior to and after feeding in the laboratory thermal gradient

Thermoregulation variable	Before feeding	After feeding	Significance
Mean $T_b$	$27.4 \pm 0.7$ °C	$29.2 \pm 0.8$ °C	Paired $t_{12} = 2.289$ $P = 0.021$
25% quartile	$25.6 \pm 0.8$ °C	$27.8 \pm 0.9$ °C	Paired $t_{12} = 2.713$ $P = 0.009$
75% quartile	$29.5 \pm 0.8$ °C	$30.6 \pm 0.7$ °C	Paired $t_{12} = 1.238$ $P = 0.12$

**Table 2.** Summary of the thermoregulatory behaviour of black rat snakes prior to and after feeding in the field

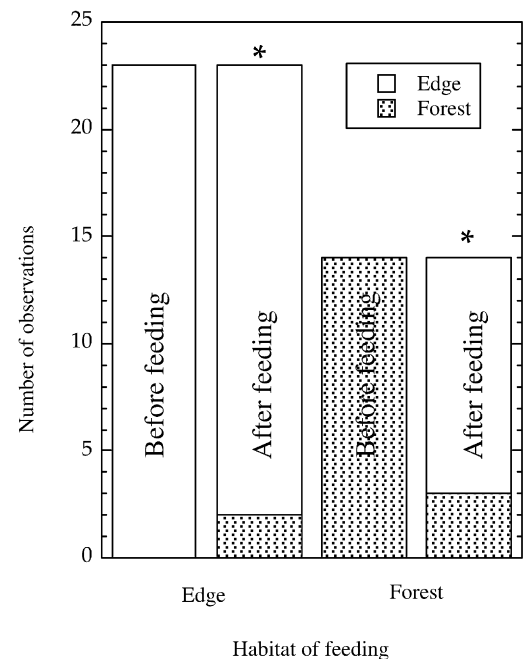
Thermoregulation index	Period	Before feeding	After feeding	Significance
Mean $T_b^*$	Whole day	26.5 ± 0.5 °C	26.7 ± 0.5 °C	$F_{1,13} = 0.013$ $P = 0.91$
	Day only	26.8 ± 0.6 °C	27.2 ± 0.6 °C	$F_{1,13} = 0.239$ $P = 0.63$
$d_e - d_b$	Whole day	3.3 ± 0.7 °C	4.4 ± 0.8 °C	Paired $t_7 = 1.255$ $P = 0.12$
	Day only	3.1 ± 0.8 °C	4.1 ± 0.6 °C	Paired $t_7 = 0.891$ $P = 0.20$
$Ex$	Whole day	32 ± 12%	52 ± 5%	Paired $t_7 = 0.775$ $P = 0.23$
	Day only	31 ± 13%	51 ± 8%	Paired $t_7 = 1.220$ $P = 0.13$

\*Mean  $T_b$  was adjusted for differences in mean  $T_e$  by using least-square means.

the trial, these 37 trials produced only 10 complete observations on eight individuals (an observation was considered complete if temperatures were recorded for ≥ 90% of the 24-h period prior to and following feeding. The 10 complete trials consisted of 2052  $T_b$  readings that reduced to 355 individual hourly mean  $T_b$ s. The values for  $T_{set}$  (26.5 °C to 29.8 °C) used to calculate thermoregulation indices in the following analyses come from data for 32 post-absorptive individuals tested in the thermal preference chamber (Blouin-Demers & Weatherhead 2001b). For each of the eight snakes, a mean  $T_b$ ,  $T_e$ ,  $d_b$ ,  $d_e$  and  $Ex$  (for the whole day and for daytime only) were calculated for the 24 h prior to feeding and the 24 h following feeding. To test whether or not snakes increased their  $T_b$  following feeding in the field, mean  $T_e$  and feeding status were used as independent variables and mean  $T_b$  as the dependent variable in an ANCOVA. Least square mean  $T_b$ s (corrected for  $T_e$ s) of snakes following feeding for the whole day or daytime only were not significantly different from  $T_b$ s maintained prior to feeding at  $\alpha = 0.05$  (Table 2). However, the indices of thermoregulation were higher following feeding. The index  $d_e - d_b$  was ≈ 1 °C higher following feeding and  $Ex$  was ≈ 18% higher following feeding. However, paired  $t$ -tests indicated that none of these differences was statistically significant at  $\alpha = 0.05$  (Table 2).

*Post-hoc* analyses indicated that, despite large effect sizes (all  $d$ s were ≥ 0.75), power was ≤ 0.25 for all tests and that a sample size of ≥ 55 would have been necessary to achieve acceptable power (≈ 0.80; Stevens 1996). Given the difficulties involved in collecting this type of data, it is highly unlikely that such a substantial data set will become available in the near future. Under conditions of large effect sizes and low power due to small sample sizes, Cohen (1977) and Stevens (1996) have suggested adopting a more lenient  $\alpha$  level (0.10 or 0.15) to improve power sharply, particularly if the consequences of making a Type I error are not serious, such as in the present case. At  $\alpha = 0.15$ , several effects are significant ( $d_e - d_b$  whole day and  $Ex$  day only; Table 2).

Another source of data to assess the effect of feeding on thermoregulation comes from unfed snakes tracked during the same time period as part of a larger telemetry study (Blouin-Demers & Weatherhead 2001b). This analysis lacks the paired feature of the previous analysis, but provides more extensive data from snakes



**Fig. 1.** Number of observations of black rat snakes in forest or edges before and after being fed in either edge or forest habitat. Statistically significant differences based on the proportions of the binomial distribution are indicated by an asterisk.

that we assume were primarily doing things other than digesting meals. Snakes that had been fed thermoregulated more carefully and at higher  $T_b$ s. Fed snakes had significantly higher  $T_b$  (26.7 ± 1.1 °C vs. 23.9 ± 0.4 °C,  $t_{59} = 2.43$ ,  $P = 0.018$ ), significantly higher  $d_e - d_b$  (4.4 ± 0.8 °C vs. 2.6 ± 0.3 °C,  $t_{59} = 1.96$ ,  $P = 0.050$ ) and significantly higher  $Ex$  (51.8 ± 4.5% vs. 24.8 ± 1.7%,  $t_{59} = 5.60$ ,  $P < 0.001$ ) than unfed snakes.

#### HABITAT USE AND MOVEMENT BY SNAKES BEFORE AND AFTER FEEDING

A total of 23 free-ranging individuals was fed a total of 37 times (23 times in edges and 14 times in the forest). We considered that a snake was faced with a binomial choice following feeding: to be in an edge or not. After being fed in an edge (23 times), snakes were relocated in an edge the following day 21 times (Fig. 1), which deviates significantly from random ( $P < 0.001$ ) based on the proportions of the binomial distribution. After

being fed in the forest 14 times, snakes were relocated in an edge the following day 11 times (Fig. 1). This again was more often than expected by chance ( $P = 0.022$ ). In addition, snakes travelled shorter distances between feeding and relocation the following day when fed in edges (mean =  $78.4 \pm 19.4$  m) than when fed in the forest (mean =  $139.2 \pm 24.8$  m;  $t_{35} = 1.931$ ,  $P = 0.06$ ). When movement is considered as simply whether or not the snakes moved, the effect of habitat is more obvious. Snakes were significantly more likely to move when fed in the forest than when fed in edges ( $N = 37$ ,  $\chi^2 = 7.63$ ,  $P = 0.006$ ). Snakes fed in forest moved  $> 5$  m between relocations in 100% of trials compared to only 69.6% for snakes fed in edges.

A comparison of experimentally fed snakes to unfed snakes tracked during the same time period as part of a larger telemetry study (Blouin-Demers & Weatherhead 2001a) indicated that snakes that had been fed were significantly more likely to be found basking than unfed snakes ( $N = 1353$ ,  $\chi^2 = 4.75$ ,  $P = 0.029$ ). Fed snakes were significantly more likely than unfed snakes to have moved ( $N = 1353$ ,  $\chi^2 = 18.21$ ,  $P < 0.001$ ), where movement data for unfed snakes was the frequency of movement between two successive relocations.

## Discussion

We found that black rat snakes exhibited PPT in the laboratory. When comparing the behaviour of snakes in the field for 24 h before and after feeding, we found that black rat snakes did not elevate their  $T_b$  following feeding. However, we did find that they thermoregulated more carefully after a meal and that habitat selection was the means by which more careful thermoregulation was achieved. Comparison of fed snakes with other snakes followed as part of a larger telemetry study revealed that fed snakes basked more and thermoregulated more carefully. Snakes were also more likely to move after being fed relative to the movement frequency of unfed snakes. Thus, our results support both the hypothesis that snakes increase their thermoregulation to facilitate digestion, and the hypothesis that habitat selection is the mechanism used to achieve, or at least allow, increased thermoregulation. More generally, our results are consistent with the view that habitat selection is an important component of behavioural thermoregulation (Huey *et al.* 1989).

Our study rested on two assumptions regarding the feeding status of black rat snakes in the field. First, we assumed that prior to being fed, the snakes in our field experiment were not digesting a meal. The comparison of snakes fed in captivity with those fed in the field suggests this assumption was valid. Captive snakes were fasted for a week before being fed, and with *ad libitum* feeding they consumed meals equivalent to 17% of their body weight on average. Snakes in the field consumed meals equivalent to 20% of their body weight on average, indicating that they were just as hungry as snakes that had been fasted for at least a week.

Secondly, we also assumed that snakes that were monitored as part of the larger telemetry study, and whose behaviour was compared with that of snakes fed experimentally in the field, were generally not digesting meals at that time. While that seems unlikely to have been true for some individuals, the validity of the assumption requires only that it was true for most of the snakes. We have no data on feeding frequency by free-living black rat snakes. However, in general snakes appear to feed relatively infrequently (Shine 1986; Mushinsky 1987). In a review of published studies, Shine (1986) found that for many snake species, a substantial proportion of freshly captured individuals had no food in their stomachs. Furthermore, depending on how they were captured, the snakes in the studies reviewed by Shine (1986) may not be a random sample in terms of feeding status. If most snakes bask more when digesting they should be more visible to researchers, and a large meal may make them easier to capture. Thus, snakes may feed even less frequently than current evidence suggests.

Before the more general implications of our results for PPT are considered, one specific result needs to be addressed. Although snakes that were fed in edge habitat nearly always remained in edges, they none the less moved an average of almost 80 m between feeding and starting digestion. It is possible that the snakes were often fed in parts of the edge that did not offer ideal basking opportunities. However, edges only extended 15 m into the forest, so a snake should not have had to move far just to find a more exposed location. An alternative explanation is that snakes look for a site that allows both basking and safe retreat when digesting a meal. If that combination of features was not readily available, then most often snakes may have had to move some distance after being fed.

Brown & Weatherhead's (2000) study of northern water snakes, and this study of black rat snakes, are the only studies that have investigated PPT simultaneously in the field and in the laboratory using the same study population. Northern water snakes were consistent in not demonstrating PPT in either the lab or the field. Black rat snakes were consistent in demonstrating PPT in both situations. Thus, based on these two studies, the response of snakes following feeding in a laboratory thermal gradient may predict reliably their response to feeding in the wild. If so, then it should be possible to use studies of captive snakes to determine whether any ecological factors consistently differentiate snakes that exhibit PPT from those that do not. Potential factors include the size and frequency of meals (Touzeau & Sievert 1993), the type of food ingested or the thermal environment faced by the species.

A literature survey yielded 13 studies (including the present one) of PPT in captive snakes (Table 3). Most of these studies have been cited in reviews of snake thermal ecology as providing evidence for or against PPT. However, only four of the studies were based on more than five animals (Table 3). Furthermore,  $T_b$ s of snakes in seven of the studies were measured using techniques that are

**Table 3.** Summary of the published literature on the presence or absence of laboratory postprandial thermophily (PPT) in snakes indicating the number of experimental animals involved and the type of food fed to the experimental animals. The methods column indicates whether a thermal preference chamber (TPC) was used and how the body temperatures of snakes were determined

Reference	Species	N	Food	Methods
PPT present				
Regal (1966)	<i>Coluber constrictor</i> (Linnaeus)	1	Mice	TPC + gastric probes
McGinnis (1969)	<i>Boa constrictor</i> (Linnaeus)	1	Rats	TPC + gastric transmitters
Lysenko & Gillis (1980)	<i>Thamnophis sirtalis</i> (Linnaeus)	4	Fish	TPC + substrate temperatures
Slip & Shine (1988)	<i>Morelia spilota</i> (Lacepede)	15	Mice + rats	TPC + coelomic transmitters
Bozinovic & Rosenmann (1988)	<i>Phyllodryas chamissonis</i> (Wagler)	3	Mice + lizards	TPC + cloacal probes
Gibson, Smucny, & Kollar (1989)	<i>Thamnophis sirtalis</i>	5	Fish	Choice of hot + warm shelters
Lutterschmidt & Reinert (1990)	<i>Nerodia sipedon</i>	5	Fish	TPC + substrate temperatures
Touzeau & Sievert (1993)	<i>Opheodrys aestivus</i> (Linnaeus)	7	Crickets	TPC + cloacal probes
Present study	<i>Elaphe obsoleta</i>	13	Chipmunks	TPC + coelomic transmitters
PPT absent				
Kitchell (1969)	<i>Heterodon platyrhinos</i> (Latreille)	1	unknown	TPC + cloacal probes
	<i>Thamnophis sirtalis</i>	3		
	<i>Nerodia sipedon</i>	3		
Lysenko & Gillis (1980)	<i>Thamnophis sirtalis</i>	4	Fish	TPC + substrate temperatures
Hammerson (1989)	<i>Masticophis flagellum</i> (Shaw)	3	Mice + lizards	TPC + gastric transmitters
Tu & Hutchison (1995)	<i>Nerodia rhombifera</i> (Hallowell)	5	Fish	TPC + cloacal probes
Brown & Weatherhead (2000)	<i>Nerodia sipedon</i>	7	Fish	TPC + coelomic transmitters

The Lysenko & Gillis (1980) study involved two subspecies of *Thamnophis sirtalis*. PPT was present in *Thamnophis sirtalis parietalis*, but absent in *Thamnophis sirtalis sirtalis*.

likely to have affected the snakes' behaviour, such as cloacal and gastric probes taped to the animal or large ingested transmitters. These shortcomings mean that, even for captive snakes, there is less reliable information available on PPT than might initially appear to be the case.

If we consider only the five studies where researchers used at least five study subjects and benign methods to record  $T_b$  (i.e. Slip & Shine 1988; Gibson *et al.* 1989; Lutterschmidt & Reinert 1990; Brown & Weatherhead 2000; this study), four found evidence of PPT and a single one did not (Table 3). Interestingly, the one exception was Brown & Weatherhead's (2000) study of northern water snakes, the same species for which Lutterschmidt & Reinert (1990) found evidence of PPT. Subtle differences in research protocols might explain the different outcome in these two studies (Brown & Weatherhead 2000). Alternatively, ecological differences between the two populations that were studied could be responsible. The one thing that is apparent from our review of the literature is that we currently lack the information necessary to make any generalizations about PPT in snakes, even when relying on studies of captive animals. Our study of black rat snakes demonstrated that investigating PPT can provide insights into the links between thermal ecology and habitat selection in snakes. Only when that opportunity is pursued more widely will the data become available that will allow comparative analyses to test hypotheses regarding variation within and among species.

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