Postprandial Temperature Selection in 
*Crotaphytus collaris*

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I measured temperature selection of male *Crotaphytus collaris* acclimatized to 25 ± 1 °C and an 12L/12D photoperiod over a 24 h period during the summer. I tested nine lizards in each of four different groups: fasting for 5 d, fed immediately before, 24 h before or 48 h before experimentation. Mean 24 h body temperatures (Tₜₜ) did not differ significantly among the four groups. The scotophase Tₜₜ of the group fed immediately before experimentation were significantly higher than scotophase Tₜₜ of the fasting group. The fasting, fed 24 h and fed 48 h before experimentation groups had significantly higher photophase Tₜₜ than scotophase Tₜₜ. I found no difference in Tₜₜ of the group fed immediately before experimentation. The fed groups did not thermoregulate more precisely than the fasting group. Some authors have used: 1) incorrect statistical methods; 2) small sample sizes; 3) no controls; and 4) basking time as a measure of Tₜₜ, and reported thermophilic responses where none were demonstrated.

BODY temperature (Tₜₜ) plays a major role in determining digestive rate (Greenwald and Kanter, 1979; Skoczyk, 1970; Stevenson et al., 1985) and digestive efficiency (Harlow et al., 1976; Troyer, 1987) in reptiles. Reptiles attain a preferred (=selected) Tₜₜ primarily by behavioral means. This preferred Tₜₜ is not a fixed value (Rismiller and Heldmaier, 1982), but varies within individuals over time as a result of environmental conditions such as time of day (Regal, 1967; Sievert and Hutchison, 1988), season (van Damme et al., 1986; Sievert and Hutchison, 1989) and nutritional status (Bradshaw et al., 1980; Slip and Shine, 1988).

Most of the work on the effect of feeding on temperature selection in reptiles has been with snakes. Yet, a few studies have been with lizards. *Lialis burtonis*, a fossorial lizard, selected significantly higher Tₜₜ after feeding (Bradshaw et al., 1980). *Scinella laterale*, *Gerrhonotus multiscutatus* and *Xantusia vigiliis*, oriented to heat sources after feeding, although Tₜₜ were not recorded (Regal, 1966). *Amphibolurus fordi* on a reduced intake consisting of food not normally eaten in the wild, selected lower Tₜₜ than conspecifics in the field (Cogger, 1974). *Amphibolurus nobbi* selected significantly higher Tₜₜ following feeding (Witten and Heatwole, 1978). However, Hammeron (1979) contends that problems with Witten and Heatwole’s methodology may have caused them to come to the wrong conclusion. Unstarved *Sauromalus obesus* had similar Tₜₜ to conspecifics starved for 2 mo (Case, 1976). Bustard (1967) suggested that the nocturnal gecko *Gekya variegata* behaviorally thermoregulated during the day to aid digestive processes, but he did not compare Tₜₜ of fasting and fed lizards.

Because assimilation efficiency of *Crotaphytus collaris* is temperature dependent (Ruppert, 1980), I hypothesized that recently fed lizards would select higher Tₜₜ and thermoregulate more precisely than lizards that were fasting. To test this I determined the effect of feeding vs fasting on: 1) mean Tₜₜ selected over a 24 h period; 2) temporal patterns of temperature selection throughout the 24 h period; and 3) thermoregulatory precision in *C. collaris*, the collared lizard. *Crotaphytus collaris* was used because no work on post-feeding responses in temperature selection has been reported with an iguanid lizard and because much of the thermoregulatory behavior of this species was known (Sievert and Hutchison, 1989).

**Materials and Methods**

I maintained adult male *C. collaris* (23–67 g) collected in central Oklahoma in the laboratory on a 12L/12D photoperiod with a photophase from 0600–1800 h Central Standard Time (CST) and 25 ± 1 °C from several weeks to several years prior to experimental use. A 60 W light bulb over two adjacent cages provided a radiant heat source for basking during photophase (Sievert, 1987). I acclimated lizards on the same 12L/12D photoperiod and a constant 25 ± 1 °C for 5 d before experimental use. The
lizards had water ad lib and no food except as called for by the experimental protocol.

The animals were divided into four treatment groups: 1) fasting through the acclimation and experimental period; 2) fasting through acclimation and fed immediately before the experimental period; 3) fasting during the first 4 d of acclimation and fed 24 h before the experimental period; and 4) fasting during the first 3 d of acclimation and fed 48 h before the experimental period. I placed a single lizard into each thermal gradient late in the photophase of the day before experimentation to allow habitation to the gradient. Each lizard in groups 2–4 was weighed immediately before feeding and given a mass of *Tenebrio molitor* larvae and/or pupae equal to 3.5% of the lizard’s body mass. This was comparable in volume to a typical meal I fed lizards in captivity. Only lizards that voluntarily ate all of the meal were used in the study. Larger masses of mealworms frequently caused the lizards to regurgitate. Nine lizards were used for each treatment.

The linear thigmothermal gradients had aluminum (0.3 cm thick) floors and were 210 cm long, 20 or 22 cm wide, and 22 cm high. Floor temperatures ranged from 10 ± 0.2–50 ± 2 C. The hot end was maintained by a subsurface heater and the cold end was maintained at room temperature (10 C). Broad spectrum fluorescent tubes directly above each gradient provided light, but not heat. The gradient lights provided the only source of light in the room and were on a 12L/12D photoperiod. The gradients are described and diagramed in Sievert and Hutchison (1988). I used thigmothermal gradients rather than photothermal gradients so the lizards could select only for heat and not both heat and light levels.

Thirty minutes before experimentation, I removed the lizard from the gradient and inserted a 30 gauge copper-constantan thermocouple approx. 1 cm into the cloaca and taped the exiting wire to the tail. I monitored body temperatures at 5 min intervals from 0900–0900 h (CST) the next day (Sievert and Hutchison, 1988).

I used a two-way repeated measures ANOVA to examine: 1) differences in *Tb* among the four treatment groups and between pairs of treatment groups; 2) changes in *Tb* over time; and 3) temporal patterns (interaction of treatment vs time). I used a Student’s t-test to compare *Tb* of different groups during portions of the diel cycle. I used a Tukey’s studentized range test (SAS, 1982) on 1 h time blocks within each treatment group to determine if *Tb* of each group varied significantly over time.

I used variance of the mean as a measure of thermoregulatory precision (Sievert and Hutchison, 1988). The variance of the mean of individual lizards from 1200–1800 h, from 2400–0600 h and over the entire 24 h period was computed. I used an Fmax test (Sokal and Rohlf, 1981) to test for differences in variances among the groups.

**Results**

Fed lizards had a slight, but not significant thermophilic response over the entire 24 h period. The mean 24 h *Tb* was 1.6 C higher for the fed groups than for the fasting group. Photophase *Tb* did not differ significantly among the four treatment groups. Scotophase *Tb* of the group fed immediately before experimentation were significantly higher than the scotophase *Tb* of the fasting group (Fig. 1).

The fasting group and the groups fed 24 h and 48 h before experimentation displayed diel *Tc* cycles. *Tb* of these three groups during one or more of the 1 h time blocks during photophase were significantly higher than *Tb* during one or more of the 1 h time blocks during scotophase. The group fed immediately before experimentation lacked significant differences in *Tb* during any portion of the photophase and scotophase. Scotophase *Tb* of this group were similar to photophase *Tb*.

The amplitude of the difference between mean photophase and mean scotophase *Tb* increased with time since feeding. When mean scotophase *Tb* was subtracted from mean photophase *Tb*, the difference was 0.2 C for the 0–24 h group, 2.6 C for the 24–48 h group, 3.7 C for the 48–72 h group and 5.2 C for the fasting group.

I found no significant differences in thermoregulatory precision among the four treatment groups when the groups were compared over the whole 24 h period, from 1200–1800 h or from 2400–0600 h.

**Discussion**

Collared lizards do not select significantly higher postprandial *Tb* over a 24 h period although they show a tendency towards higher *Tb* after feeding. The lizards did show a thermophilic response during scotophase. Data on postprandial thermophilic in lizards are scarce, but, possibly, an elevation of *Tb* following feed-
Fig. 1. Temperature selection of *Crotaphytus collaris* over a 24 h period in a thermal gradient after acclimation to 25 ± 1°C and an 12L/12D photoperiod. The circles represent mean body temperatures over a 1 h interval. Vertical lines represent 1 SE above the mean. \( \bar{x} \) = mean \( T_b \) of the nine lizards over the 24 h period and \( P \) = probability that mean 1 h \( T_b \)s are not significantly different from each other. Horizontal bars represent scotophase.

...ing is most prominent in lizards such as *Lialis burtonii* (Brashaw et al., 1980) that normally prefer cool \( T_b \)s. Regal's (1966) observations are in agreement with this, but specific \( T_b \) data are not available. Diurnal heliotherms such as *C. collaris* and *Amphibolurus nobbi* only show slight increases in \( T_b \) following feeding. *Amphibolurus nobbi* had a small (approx. 0.6°C) increase in \( T_b \) following feeding on day 1 in a thermal gradient. On day 2 the difference between fasting and fed animals was greater (approx. 2.8°C), but fasting lizards on day 2 had \( T_b \)s that were 5°C lower than fasting lizards on day 1 (Witten and Heatwole, 1978). Hammerson (1979) suggested that reptiles with high preferred \( T_b \)s, such as the striped racer, *Masticophis lateralis*, did not need to elevate \( T_b \)s after feeding to digest efficiently.

The only significant elevation of \( T_b \) in *C. collaris* occurred during scotophase. The 0–24 h group maintained normal activity \( T_b \)s throughout scotophase when they were inactive (Fig. 1). If normal daytime \( T_b \)s are sufficient for efficient digestion, then this group prolonged efficient digestion by not selecting cooler scotophase \( T_b \)s. Possibly, higher diurnal \( T_b \)s after feeding would not be helpful to collared lizards or could be detrimental because of the increase in metabolic rate. If this were true then *C. collaris* could only enhance digestion by increasing the time spent at preferred \( T_b \)s, not by increasing the preferred temperature. Another possibility is that it would be disadvantageous for fasting collared lizards to select lower \( T_b \)s during the day since other bodily functions such as hearing (Werner, 1972) and running ability (Crowley, 1985) are also affected by body temperature.

Contrary to my prediction, fed collared lizards did not thermoregulate more precisely than fasting conspecifics, although there was a non-significant tendency for the fasting group to be less precise. Fasting crocodilians, *Alligator mississippiensis* and *Crocodylus acutus* (Lang, 1979) had more variable \( T_b \)s than fed crocodilians, but the differences were not analyzed statistically. Fed juvenile New Guinea crocodiles, *C. novae-guineae*, did not thermoregulate more precisely than fasting individuals (Lang, 1981). Fed *Masticophis lateralis* tended to have less variable \( T_b \)s than fasting snakes (Hammerson, 1979) but the differences were not statistically analyzed. Fed diamond pythons, *Morelia spilota*, thermoregulated significantly more precisely than fasting snakes (Slip and Shine, 1988).

There is no consensus on the thermophilic effect of feeding on reptiles (Lillywhite, 1987) and there are no clear-cut trends in which taxonomic groups display postprandial thermophily (Table 1). More confounding than a lack of clear-cut trends is the fact that many authors are
<table>
<thead>
<tr>
<th>Species</th>
<th>Thermophilic effect</th>
<th>Sample size used for statistics</th>
<th>Number of individuals</th>
<th>Difference between pre- and post-feeding $T_a$ (°C)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Crocodilians</strong></td>
<td></td>
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<tr>
<td><em>Alligator mississippiensis</em></td>
<td>S(^1)</td>
<td>270 ?*</td>
<td>10</td>
<td>≈3.4</td>
<td>Lang, 1979</td>
</tr>
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<td><em>Crocodylus acutus</em></td>
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<td>270 ?*</td>
<td>10</td>
<td>≈1.5</td>
<td>Lang, 1979</td>
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<td><em>C. novaeguineae</em></td>
<td>NS(^3)</td>
<td>20 ?</td>
<td>8</td>
<td>0.2 (18–27 d old)</td>
<td>Lang, 1981</td>
</tr>
<tr>
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<td>Unstated</td>
<td>12</td>
<td>None</td>
<td>Diefenbach, 1975</td>
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<td><strong>Turtles</strong></td>
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<td><em>Trachemys scripta</em></td>
<td>S</td>
<td>500</td>
<td>10</td>
<td>4.5</td>
<td>Gatten, 1974</td>
</tr>
<tr>
<td><em>Terrapene ornata</em></td>
<td>S(^2)</td>
<td>500</td>
<td>10</td>
<td>1.5</td>
<td>Gatten, 1974</td>
</tr>
<tr>
<td><strong>Lizards</strong></td>
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<tr>
<td><em>Amphibolurus nobbi</em></td>
<td>S(^2)</td>
<td>42–282</td>
<td>?</td>
<td>Day 1 0.6</td>
<td>Witten and Heatwole, 1978</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Day 2 2.8</td>
<td></td>
</tr>
<tr>
<td><em>Lialis burtonis</em></td>
<td>S</td>
<td>Unstated</td>
<td>5</td>
<td>2.5 (fasted 7–8 d)</td>
<td>Bradshaw et al., 1980</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5.1 (starved 3–4 wk)</td>
<td></td>
</tr>
<tr>
<td><em>Gymnophyes collaris</em></td>
<td>NS (24 h)</td>
<td>9</td>
<td>9</td>
<td>1.6</td>
<td>Present study</td>
</tr>
<tr>
<td></td>
<td>S (scotophase)</td>
<td>9</td>
<td>9</td>
<td>4.1</td>
<td></td>
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<td><strong>Snakes</strong></td>
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<td><em>Thamnophis s. sirtalis</em></td>
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<td>Unstated</td>
<td>3</td>
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<td>Kitchell, 1969</td>
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<td><em>T. s. parietalis</em></td>
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<td>4</td>
<td>4</td>
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<td>0.7</td>
<td>Lysenko and Gillis, 1980</td>
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<td><em>N. tobii</em></td>
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<td>1</td>
<td>1.4</td>
<td>Goodman, 1971</td>
</tr>
<tr>
<td><em>Heterodon platyrhinos</em></td>
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<td>Unstated</td>
<td>3</td>
<td>0.4</td>
<td>Kitchell, 1969</td>
</tr>
<tr>
<td><em>Boa constrictor</em></td>
<td>NS</td>
<td>Unstated</td>
<td>3</td>
<td>9–14</td>
<td>Kitchell, 1969</td>
</tr>
<tr>
<td></td>
<td>No stats</td>
<td>—</td>
<td>1</td>
<td>3.8</td>
<td>Regal, 1966</td>
</tr>
<tr>
<td><em>Morelia spilota</em></td>
<td>S</td>
<td>14</td>
<td>14</td>
<td>2.5</td>
<td>McGinnis and Moore, 1969</td>
</tr>
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<td><em>Masticophis lateralis</em></td>
<td>NS</td>
<td>101 ? (Snake B)</td>
<td>2</td>
<td>None</td>
<td>Slip and Shine, 1988</td>
</tr>
<tr>
<td></td>
<td>135 ? (Snake D)</td>
<td></td>
<td></td>
<td></td>
<td>Hammerson, 1979</td>
</tr>
<tr>
<td><em>Coluber constrictor</em></td>
<td>NS</td>
<td>Unstated</td>
<td>3</td>
<td>Not given</td>
<td>Hammerson, 1987</td>
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<tr>
<td><em>Python molurus</em></td>
<td>S(^2)</td>
<td>55–82</td>
<td>3</td>
<td>1.8 (for one snake)</td>
<td>Marcellini and Peters, 1982</td>
</tr>
<tr>
<td></td>
<td>No stats</td>
<td>—</td>
<td>1</td>
<td>≈3</td>
<td>van Mierop and Barnard, 1976</td>
</tr>
<tr>
<td><em>Vipera aspis</em></td>
<td>No stats</td>
<td>Unstated</td>
<td>2</td>
<td>Not given—not effect found</td>
<td>Naulleau, 1979; Naulleau and Marques, 1973</td>
</tr>
</tbody>
</table>

\(^1\) S results are significant at $P \leq 0.05$.  
\(^2\) S\(^2\) author states results are significant at $P \leq 0.05$, but methodology employed in the research or analysis makes this questionable.  
\(^3\) NS results are not significant at $P \leq 0.05$.  
\(^?\) ? refers to ambiguity in sample size used for statistics.
uncritical in their acceptance of this phenomenon and incorrectly cite examples of thermophilic responses (Hammerson, 1979). For example, Kitchell (1989) has been cited as both demonstrating a thermophilic response (Hammerson et al., 1988; Lang, 1979: Witten and Heatwole, 1978) and not showing a significant response (Hammerson, 1979: Lillywhite, 1987; Lysenko and Gillis, 1980). Kitchell (1989) stated that the post-feeding Tₚₛ of the snake species he studied were "consistently, though not significantly, higher than the normal means."

There are clear demonstrations of post-feeding thermophily (Bradshaw et al., 1980: Lysenko and Gillis, 1980; Slip and Shine, 1988), but there are also well-cited references that claim a thermophilic effect of feeding where none exists. One source of confusion is that researchers (Gatten, 1974: Marcellini and Peters, 1982: Witten and Heatwole, 1978) used the number of observations, rather than the number of individuals in a repeated measures experiment, as the sample size. Mathur and Silver (1980) described in detail why this is statistically unacceptable. Measurement of Tₚₛ at smaller and smaller time intervals increases the number of observations taken from a few individuals to a very large number. If this inflated number is used as a sample size, then very small differences may become significant. By sampling at very frequent intervals, one can often be assured of finding significant differences in the data. Unfortunately, this statistical error was prevalent in studies prior to 1980.

A second problem is that some researchers (McGinnis and Moore, 1969; Regal, 1966; van Mierop and Barnard, 1976) used small sample sizes, in some cases n = 1. Although these authors did not claim to demonstrate statistically an elevated Tₚ after feeding, their work is often cited as though it showed such an effect (Lang, 1981: Marcellini and Peters, 1982: Slip and Shine, 1988); care should be taken when citing these studies to make clear the fact that statistical analyses were not done.

A third problem is lack of appropriate controls of fasting animals. Greenwald and Kanter (1979) measured Tₚ only from snakes that had eaten. Rather than showing a thermophilic effect caused by feeding, these authors showed that Elaphe guttata appeared to thermoregulate after feeding in the fall but not in the winter. Saint Girons (1975) had only one fasted control (on the 5th day following ingestion of a rodent equal to 6% of the snake's body mass). This control Tₚ for Vipera ammodytes was compared to post-feeding Tₚₛ of 10 individuals belonging to four species of Vipera.

A fourth problem involves the use of basking time as a measure of relative Tₚ. Although some authors did not claim that an increase in basking time following feeding caused a significant increase in Tₚ (Boyer, 1965; Hammerson et al., 1988; Moll and Legler, 1971), others have interpreted their data in this manner (Lang, 1981; Marcellini and Peters, 1982). Although this may be a reasonable inference, Tₚ data are required to test the hypothesis and none are available. In addition to time of exposure to the sun, evaporative heat loss, wind speed, conductive cooling, posture and orientation and other environmental factors might influence the rate of heat exchange and thus the Tₚ of a basking animal.

The purpose of this discussion is not to dismiss the phenomenon of postprandial thermophily: some crocodilians, turtles, snakes and lizards clearly show postprandial thermophily (Table 1). The postprandial thermoregulatory strategy of reptiles probably varies with their natural history. Reptiles that maintain high activity Tₚₛ, such as Crotaphytus collaris, may not need an elevation of Tₚ after feeding or may only elevate Tₚₛ during scotophase. Those species that prefer cooler or variable Tₚₛ, or are aquatic, may need to elevate Tₚₛ after feeding. Reptiles that are less mobile after ingesting a large meal may seek shelter (and therefore low Tₚₛ) instead of basking to avoid predation (Hammerson, 1987).

Studies need to be done throughout an entire 24 h period. If I had confined this study to data gathered during photophase, I would have concluded that feeding had no effect on thermoregulatory behavior of collared lizards. Clearly more studies are needed before a thorough understanding of postprandial thermophily in reptiles can emerge.

Acknowledgments

I thank G. Sievert for assistance capturing the lizards; J. Horrell, A. Schwartzkopf, and A. Nicewander for aid in data analysis; J. Redman for computer assistance; D. Willis and W. Porter for construction and maintenance of the equipment; V. H. Hutchison, H. Haines, C. Carpenter, F. Sonleitner and J. R. Estes for critical review of this manuscript. This work was partially funded by a grant from the Graduate Student Association of the University of Okla-
homa. Support and facilities were also provided by the Zoology Department of the University of Oklahoma.

**Literature Cited**


Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019. Accepted 8 March 1989.