

The Thermal Biology of Digestion in Rubber Boas (*Charina bottae*): Physiology, Behavior, and Environmental Constraints

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# The Thermal Biology of Digestion in Rubber Boas (*Charina bottae*): Physiology, Behavior, and Environmental Constraints

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## ABSTRACT

Coadaptation predicts a match between the thermal physiology and thermoregulatory behavior of reptiles. We tested this prediction by studying the digestive biology of rubber boas (*Charina bottae*). We measured the thermal dependence of gastric digestive rate and passage rate in rubber boas from 10°C to 35°C. We examined the effect of digestion on their thermal preference by measuring the temperatures of *C. bottae* in a thermal gradient before and after feeding. While the passage rates calculated from the body temperatures of digesting snakes were higher than the passage rates calculated from the body temperatures of nondigesting snakes, there was no difference in calculated digestive rates. These results indicate that the thermoregulatory behavior of *C. bottae* may be more tightly correlated with factors affecting passage rate than with digestive rate alone. Results of simulating the constraints of the thermal environment on the digestive biology of *C. bottae* showed that digestion would take more than twice as long in the spring as in the summer. In addition, during the summer, snakes thermoregulating as digesting snakes would pass food 12% faster than those thermoregulating as nondigesting snakes. These results demonstrate how interpretation of laboratory studies can be improved when combined with measurements of appropriate environmental conditions.

## Introduction

The concept of coadaptation (Huey and Slatkin 1976; Huey and Bennett 1987; Huey et al. 1989; Peterson et al. 1993)

predicts that reptiles should thermoregulate during a certain activity so as to maximize biological functions important to that activity (e.g., gravid reptiles should thermoregulate during gestation so as to maximize the developmental rate and/or phenotypic traits of their offspring). A prevailing view is that the behavioral characteristics of most reptiles match (are coadapted with) their physiological traits (Huey and Slatkin 1976; Stevenson et al. 1985; Huey and Bennett 1987; Huey et al. 1989; Peterson et al. 1993). However, the limited number of species studied and procedures used in measuring thermoregulatory behavior raises concerns that this generalization should be viewed with care.

The most commonly used index of thermoregulatory behavior of reptiles is the thermal preference (selected temperature: the mean body temperature [ $T_b$ ] selected by a reptile in a laboratory thermal gradient; Pough and Gans 1982). To facilitate comparisons among species, thermal preferences are usually measured on reptiles that are fasting, nongravid, and nonmolting, conditions that may have a large effect on thermoregulatory behavior (Dawson 1975; Huey 1982; Gibson et al. 1989). Failure to consider the effects of these factors may result in incorrect evaluations of the extent of coadaptation. For example, an inaccurate evaluation of the extent of coadaptation between the thermal preferences and thermal optima for digesting reptiles could result if only fasted individuals were used in the thermal preference study. It is therefore necessary to conduct thermal preference studies on reptiles with the physiological condition appropriate for the function being studied.

While thermal preference has traditionally been the measure of thermoregulatory behavior most frequently compared with thermal dependencies, this comparison may be misleading because the thermal preference is usually determined in an unconstrained, laboratory thermal gradient. In contrast, many free-ranging reptiles are often constrained from reaching preferred  $T_b$ , especially in extreme environments (Peterson 1987; Dorcas 1995). Consequently, the thermal dependencies of important biological functions should reflect coadaptation with the interaction of thermoregulatory behavior and environmental constraints.

The current data regarding coadaptation in reptiles are also phylogenetically and ecologically biased (Avery 1982; Huey 1982; Lillywhite 1987). Most studies have focused on diurnal lizards because they are abundant and easily observed and their performance (e.g., sprint speed) can be conveniently measured in the laboratory. To better understand the relationship be-

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tween thermoregulatory behavior and thermal physiology, we need to examine species from other taxa and ecological niches, especially reptiles with limited access to heat (e.g., nocturnal, fossorial, aquatic, or forest forms; Peterson 1987).

We tested the coadaptation hypothesis by examining the digestive physiology and thermoregulatory behavior of rubber boas (*Charina bottae* Blainville). We compared the thermal dependencies of gastric digestive rate and passage rate in *C. bottae* with their  $T_b$  selection. *C. bottae* is a particularly interesting and convenient species in which to investigate coadaptation for several reasons. Like most snakes, they consume large meals at infrequent intervals, making observation of the digestive process easier. Also, studies of free-ranging *C. bottae* provide environmental measurements that can be combined with  $T_b$  selection data to simulate the interaction between thermoregulatory behavior and thermal constraints (Dorcas 1995). Finally, *C. bottae* is different both phylogenetically (it is a boid) and ecologically (it is often nocturnal) from most other species of reptiles studied thus far. Consequently, studies of *C. bottae* may offer new insights into the prevailing view of coadaptation between  $T_b$  variation and thermal dependencies in reptiles.

## Material and Methods

### Animals

Eight *Charina bottae* (four males and four females; body mass, 40.2–129.6 g) were collected from eastern Washington and southeastern Idaho. We housed snakes individually in 37.8-L aquaria (floor dimensions: 26 × 51 cm) with a substrate of 3–5 cm of aspen bedding uniformly distributed and covered with two layers of newspaper, thus making the entire substrate uniformly dark. All snakes had been in captivity at least 3 mo before the thermal dependence experiments and at least 1 mo before thermal preference experiments began. We provided a photoperiod using fluorescent lighting that matched that of southeast Idaho. During the active season (May–October), the ambient room temperature was kept at approximately 18°C. One end of each cage was placed on heat tapes, which raised the operative temperature (Bakken 1992) at that end of the cage to 38°C. This arrangement allowed the snakes to select  $T_b$ 's between 18°C and 38°C (see Dorcas and Peterson [1997] for more details of the thermal gradient setup). We provided water ad lib.

### Treatment

During the summer (June–August 1992 and 1993) five of the snakes (three females and two males) were fed laboratory mice (*Mus musculus*; 7–12 g; 10%–15% of snake body mass) in their cages with the thermal gradients. Within 1 h of ingestion, snakes were placed in plastic shoe boxes (15 cm × 29 cm × 8 cm) with a paper towel substrate and moved to environmental

chambers (Model I-30BL, Percival Manufacturing, Boone, Iowa) at the appropriate test temperature. To minimize the effects of one experimental temperature on the other, we tested snakes in the following order: 25°, 10°, 30°, 15°, 20°, and 35°C. We tested snakes at 35°C last because we did not know if snakes would be adversely affected by this temperature. Temperatures in the environmental chambers were measured using type-T thermocouples and recorded every second and averaged every 5 min with a data logger (Model CR10, Campbell Scientific, Logan, Utah). The 5-min average within the chambers did not vary more than 0.8°C above or below the test temperatures at any time during the experiment. Each snake was tested once at each test temperature.

### Gastric Digestive Rate

Every 12 h (24 h for 10°C treatment) we removed the snakes from the environmental chambers, restrained them by placing them in plastic tubes slightly larger than their diameter, and then x-rayed them from the side with an x-ray machine in an adjacent building. We used a General Electric DXD-350II, single phase, fully rectified x-ray machine (General Electric, Medical Systems Division, Milwaukee, Wis.) and Kodak Ortho L 14 × 17 cm film (Eastman Kodak, Rochester, N.Y.). We exposed the snakes at 52 kV and 100 mA for 1/40 s. The time the snakes were out of the environmental chamber never exceeded 15 min and typically was only 5–10 min. There was no evidence that disturbing the snakes twice per day for the x-ray affected the completion of digestion. During this time, the snakes'  $T_b$ 's changed slightly toward room temperature (approximately 21°C). This change was greatest at 10°C and 35°C (e.g., at a test temperature of 10°C, the average of the snakes'  $T_b$ 's was 15.8°C when the snakes were returned to the environmental chambers after the x-ray). We defined the completion of digestion as halfway between the time of the x-ray at which mouse bones are no longer visible and the time of the previous x-ray (Stevenson et al. 1985). At the completion of digestion (or upon regurgitation) snakes were returned to their normal cages with the thermal gradients.

### Passage Rate

To determine passage rate, we checked the plastic shoe box of each snake for fecal masses at the time of each x-ray. The time of the appearance of the first fecal mass from the latest feeding was used to calculate the passage rate. We injected all mice, before feeding, with approximately 0.1 mL of 1- $\mu$ m fluorescent, latex FluoSpheres (Molecular Probes, Eugene, Oreg.; Waldschmidt et al. 1986). Snake feces were later examined with a fluorescent microscope (Zeiss Model WL with epifluorescence, Oberkochen/Wuett, West Germany) for the Fluo-Spheres. By alternating the colors of the FluoSpheres at alternate feedings (either red or yellow-green), we were able to determine which

fecal mass came from which mouse. Snakes were not returned to their cages before their first defecation.

### Body Temperature Selection

To determine the effects of digestion on  $T_b$  selection in *C. bottae*, we measured the cloacal temperatures of all eight snakes in the thermal gradient once per day for 2 d before and 2 d after feeding. Snakes were fed approximately every 2 wk. All measurements were made during the summers (June 1–August 31) of 1990 and 1991 between 1100 and 1400 hours. To make the measurements while disturbing the snakes as little as possible, we carefully lifted the tip of each snake's tail with one hand and inserted a thermocouple approximately 1 cm into its cloaca. There was no evidence that our measurements disturbed the snakes in any substantial way (i.e., the snakes usually would not move to another part of the cage after the measurements). We used a thermocouple thermometer (Model HH23, Omega, Stamford, Conn.) with a type-T thermocouple (36 gauge).

### Data Analysis

Gastric digestive rate data were converted to number of mice per day and passage rate was calculated by taking the reciprocal of the number of days until first defecation. We log transformed the dependent variables to correct for heterogeneity of variance. Because all snakes regurgitated at 10°C and 35°C, only data for 15°–30°C were used in the statistical analyses (conducted using SYSTAT 5.02; Wilkinson 1990). We used repeated-measures ANOVA to test separately gastric digestive rate and passage rate for significant trends and a post hoc test with a Bonferroni correction to test for differences in gastric digestive rate between 25°C and 30°C. We used MANOVA to test for any difference in the relationships of gastric digestive rate and passage rate with temperature. An alpha level of 0.05 was used throughout the study.

All of the original (untransformed) data (including 10°C and 35°C) for both gastric digestive rate and passage rate were fitted to linear regression equations using a curve-fitting pro-

gram (TableCurve ver. 2.12, Jandell Scientific, Corte Madera, Calif.). Polynomials were chosen that minimized the sums of squares per temperature, had the fewest free parameters, and accurately represented patterns in the data (Table 1). These regressions were used to predict the temperature of maximal performance and the thermal performance breadth (the range of temperatures over which performance is  $\geq 80\%$  of maximal performance; Huey and Stevenson 1979) for gastric digestive rate and passage rate (Table 2). In addition, we fit the digestive rate data and passage rate data for each individual *C. bottae* to linear regression equations (i.e., calculated an equation for each snake) and used these to predict the  $T_b$  of maximal performance for each snake. We then used a paired *t*-test to test for a difference in the  $T_b$  of maximal performance of gastric digestive rate and the  $T_b$  of maximal performance of passage rate.

Body temperature selection data were divided into 4 d (groups): 2 d before feeding, 1 d before feeding, 1 d after feeding, and 2 d after feeding. We tested for differences among days using a one-way ANOVA. Paired comparisons, with a Bonferroni alpha adjustment, were used to test for differences between specific days.

To determine the effects of thermoregulatory behavior on gastric digestive rate and passage rate, we used the regression equations to calculate predicted gastric digestive rates and predicted passage rates for each  $T_b$  measured during the temperature selection experiment. This was done for both digesting and nondigesting snakes. We then compared the predicted gastric digestive rates and predicted passage rates calculated from the  $T_b$  distributions of digesting and nondigesting snakes with *t*-tests.

### Simulation of Free-Ranging Snakes

We simulated the  $T_b$ 's of digesting and nondigesting snakes at 15-min intervals for an entire day by randomly selecting 96 (15 min  $\times$  96 = 24 h) samples from the  $T_b$  distributions (generated from the  $T_b$  selection experiment) of both digesting and nondigesting snakes. To smooth out the daily  $T_b$  patterns, we repeated this seven times and then averaged the seven samples for each 15-min interval. This generated a  $T_b$  every 15

Table 1: Regression equations and parameters for gastric digestive rate and passage rate

Function	Parameters					$R^2$
	$a$	$b$	$c$	$d$	$e$	
Digestive rate .....	.571009	-.128156	.008749	-.000158	. . .	.96
SE .....	.134227	.021039	.001001	.000014	. . .	. . .
Passage rate .....	-4.292291	.946681	-.073441	.002457	-2.9E-05	.87
SE .....	1.070450	.229322	.017113	.000533	5.9E-06	. . .

Note. The model for digestive rate is  $y = (a + bT_b + cT_b^2 + dT_b^3)$ . The model for passage rate is  $y = (a + bT_b + cT_b^2 + dT_b^3 + eT_b^4)$ .

Table 2: Maximal rate,  $T_b$  at maximal rate, and the thermal performance breadth for gastric digestive rate and passage rate

Function	Maximal Rate <sup>a</sup>	$T_b$ at Maximal Rate (°C)	Thermal Performance Breadth (°C)
Digestive rate .....	.36	26.7	21.9–30.6 (8.7)
Passage rate .....	.48	29.6	25.9–32.3 (6.4)

Note. All values are calculated from the regression equations in Table 1. The thermal performance breadth is the range of  $T_b$ 's over which performance is greater than or equal to 80% of maximum; numbers in parentheses are SEs.

<sup>a</sup> Units: digestive rate, number of mice per day; passage rate, the reciprocal of the number of days until first defecation.

min for an entire day for both “digesting” and “nondigesting” snakes (for the remainder of this article, quotation marks will be used to indicate simulated “digesting” and “nondigesting” snakes).

To simulate the  $T_b$ 's of “digesting” and “nondigesting” snakes in the field, we constrained the simulated  $T_b$ 's with the minimal and maximal operative temperatures (Bakken and Gates 1975; Bakken 1992) measured at our study site in southeast Idaho for a typical spring day (May 25, 1991) and a typical summer day (July 15, 1991) (see Dorcas [1995] for a complete description of the operative temperature measurements). The representative spring and summer days were chosen by visually inspecting yearly plots of daily minimal and maximal operative temperatures and selecting days that were typical. Because some free-ranging snakes (i.e., pregnant females with temperature sensitive radiotransmitters) were able to maintain  $T_b$ 's considerably warmer than our operative temperature measurements at night (Dorcas 1995), we corrected our maximal operative temperature measurements by using the warmest snake's  $T_b$  as the maximal operative temperature at those times. After determining the minimal and maximal operative temperature at 15-min intervals for both days, we constrained the simulated  $T_b$ 's of “digesting” and “nondigesting” snakes with the minimal and maximal operative temperature for each 15-min interval for both the spring and summer days (e.g., if the simulated  $T_b$  at a certain time was higher than the maximal operative temperature, then we reduced that simulated  $T_b$  to the value of the maximal operative temperature). We then calculated the predicted gastric digestive rates and passage rates for “digesting” and “nondigesting” snakes at 15-min intervals on both days using the regression equations.

## Results

Both gastric digestive rate and passage rate of *Charina bottae* were greatly affected by changes in  $T_b$ . All snakes regurgitated at 10°C (mean time in test chamber, 11.6 d; range, 10–14 d) and 35°C (mean time in test chamber, 1.4 d; range, 1–2 d). Regurgitated mice were mostly intact, indicating that little digestion had occurred. Gastric digestive rates rose steadily in snakes kept at temperatures increasing from 15°C to 25°C and

then leveled off or decreased slightly for snakes kept at 30°C (Fig. 1A). Passage rates were lowest in snakes kept at 15°C, about the same for those kept at both 20° and 25°C, and were highest in those kept at 30°C (Fig. 1B). Trend analysis revealed significant linear ( $F = 126.08$ ,  $P < 0.001$ ) and quadratic trends ( $F = 155.64$ ,  $P < 0.001$ ) for gastric digestive rate and significant linear ( $F = 58.25$ ,  $P < 0.002$ ) and cubic trends ( $F = 11.97$ ,  $P < 0.03$ ) for passage rate. There was no difference in gastric digestive rate between 25°C and 30°C ( $F = 0.11$ ,  $df = 4$ ,  $P > 0.05$ ). Gastric digestive rate and passage rate were affected differently by  $T_b$  ( $F = 39.12$ ,  $df = 12$ ,  $P < 0.025$ ; Fig. 2). The

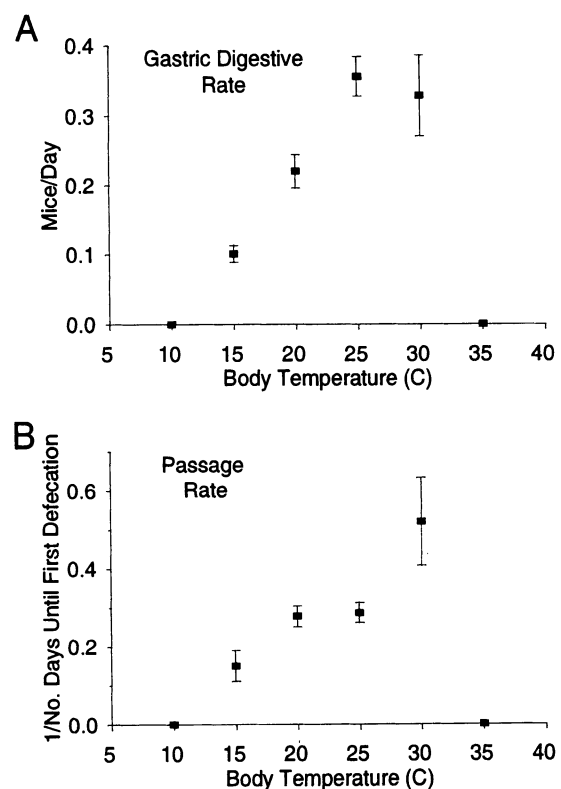


Figure 1. The thermal dependence of gastric digestive rate (A) and passage rate (B) in *Charina bottae*. Five different individuals were tested at 5° increments between 10°C and 35°C. All individuals regurgitated at 10°C and 35°C. Filled squares represent means. Bars represent ±1 SE.

$T_b$  of maximal gastric digestive rate was significantly lower than the  $T_b$  of maximal passage rate ( $t = 3.752$ ,  $df = 4$ ,  $P < 0.05$ ).

There was a significant effect of digestion on  $T_b$  selection ( $F = 10.52$ ,  $df = 117$ ,  $P < 0.001$ ). Comparisons among days showed that there was no significant difference between the 2 d prior to feeding ( $P > 0.99$ ; power  $> 0.9$ ) nor between the 2 d after feeding ( $P > 0.284$ ; power  $> 0.9$ ). However, there were significant differences between all possible pairs of the 2 d before feeding with the 2 d after feeding ( $P < 0.05$ ). Consequently, we pooled data for the 2 d prior to feeding and for the 2 d after feeding and tested for an effect of digestion on  $T_b$  selection using a  $t$ -test. Results showed that digesting snakes exhibited  $T_b$ 's  $2.3^\circ\text{C}$  higher than nondigesting snakes ( $t = 27.07$ ,  $P < 0.001$ ; Fig. 3). We found no evidence that snakes chose a location within their thermal gradients due to any factor other than temperature (e.g., light levels were uniform beneath the newspaper and there was no evidence that snakes preferred to be at either end of the cage, as demonstrated by a normally distributed dataset; Fig. 3).

Predicted gastric digestive rates calculated from the  $T_b$ 's of digesting snakes were not significantly different from those calculated from the  $T_b$ 's of nondigesting snakes ( $t = 1.84$ ,  $P > 0.06$ ; note, however, that this result could be considered marginally significant). However, predicted passage rates calculated from the  $T_b$ 's of digesting snakes were significantly higher than those of nondigesting snakes ( $t = 4.48$ ,  $P < 0.001$ ).

## Discussion

### Thermal Dependencies

Like other reptiles, temperature greatly affects gastric digestive rate in *Charina bottae* (Skoczylas 1970, 1978; Diefenbach 1975a,

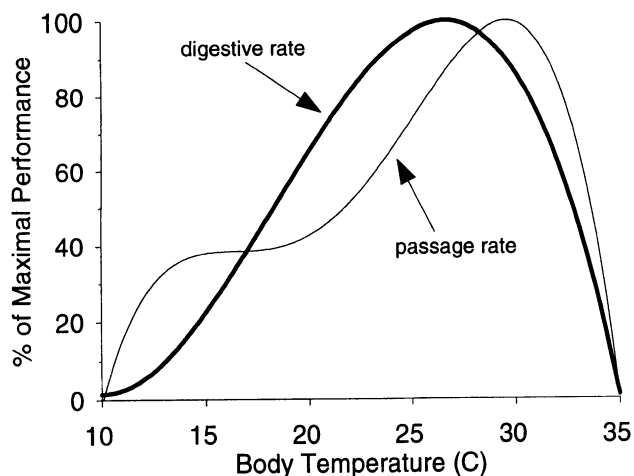


Figure 2. Percentage of maximum of gastric digestive rate and passage rate as a function of  $T_b$ , calculated from the regression equations in Table 1. Note that the relationships of gastric digestive rate and passage rate with temperature are significantly different (MANOVA,  $F = 39.12$ ,  $df = 12$ ,  $P < 0.025$ ).

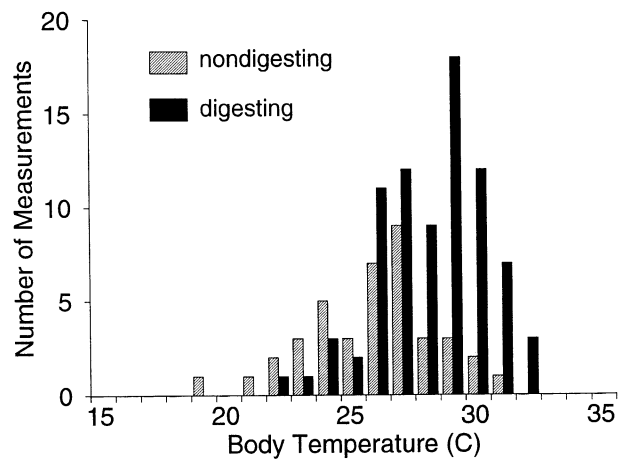


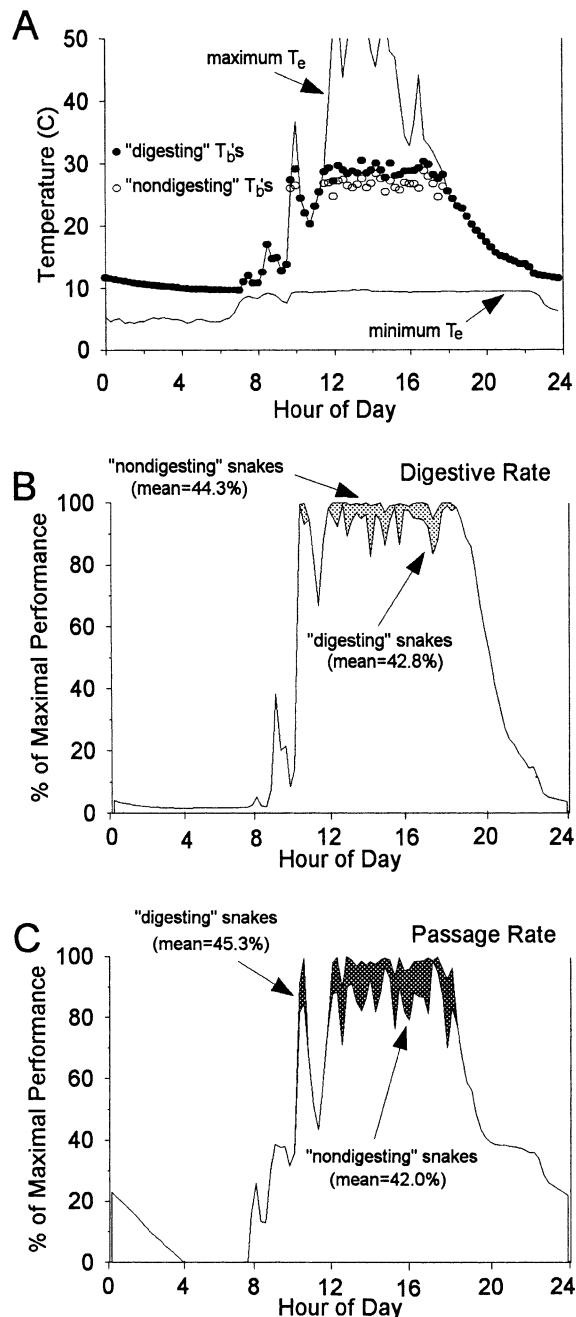
Figure 3. The effect of digestion on  $T_b$  selection in *Charina bottae*. Measurements were made once a day for 2 d before and 2 d after ingestion of a mouse. Forty measurements were made on eight snakes 1 or 2 d before ingesting a mouse, and 79 measurements were made on the same eight snakes 1 or 2 d after ingesting a mouse. Note that digesting snakes select higher temperatures than nondigesting snakes ( $t = 27.07$ ,  $P < 0.001$ ).

1975b; Stevenson et al. 1985; Avery 1988). Gastric digestive rate in *C. bottae* is slow at low temperatures, increases at intermediate temperatures, and then decreases again at higher temperatures (Figs. 1A, 2). The slow gastric digestive rate at low temperatures may be due to several synergistic factors, including the slow secretion and action of digestive enzymes and slow gut motility (Skoczylas 1978). As  $T_b$  increases, secretion of digestive enzymes increases as does the secretion of HCl (Skoczylas 1978). At even higher  $T_b$ 's (e.g.,  $30^\circ\text{C}$  and  $35^\circ\text{C}$ ), HCl secretion may decrease, resulting in a pH above optimal for the action of pepsin, thus accounting for the decrease in gastric digestive rate (Skoczylas 1978).

Several investigators have used passage rate as an indirect indicator of overall digestive rate (Henderson 1970; Greenwald and Kanter 1979; Naulleau 1983). Comparison of the thermal dependence of passage rate in *C. bottae* with the thermal dependence of gastric digestive rate reveals significantly different relationships (Figs. 1, 2). Passage rate integrates several processes including gastric digestion, intestinal digestion, gut motility, and intestinal absorption, all of which may have different thermal optima (Skoczylas 1978). It is interesting that the cooler portion of the thermal dependence curve for passage rate is plateau shaped (i.e., flat; Figs. 1B, 2). This has a similar shape to the thermal dependence of metabolic rate in *C. bottae*, which is also plateau shaped (Dorcas 1995). It may be that the many processes that affect passage rate are directly affected by metabolic rate and thus reflected in the overall shape of the passage rate curve. In any case, it is clear that in *C. bottae*, gastric digestive rate and passage rate are affected differently by  $T_b$  variation.

## Body Temperature Selection

Our results were similar to other studies of  $T_b$  selection and showed that digesting snakes selected  $T_b$ 's higher than those of nondigesting snakes. The results of several studies using a variety of techniques provide confirming evidence that digesting snakes select higher  $T_b$ 's than nondigesting snakes (Regal 1966; Kollar 1988; Slip and Shine 1988; Gibson et al. 1989; Lutterschmidt and Reinert 1990; Peterson et al. 1993). While this study provides additional support for this phenomenon as a general principle among snakes, more studies are needed,



especially from ecologically diverse taxa. In addition, the effects of meal size and feeding frequency raise particularly interesting questions. For example, is postfeeding thermophily reduced in snakes that frequently eat small meals? Or, is time since last meal proportional to the difference in  $T_b$  selection?

## Integration of Physiology and Behavior

Perhaps one of the most interesting findings of this study was that predicted gastric digestive rates calculated from the  $T_b$ 's of digesting snakes were not significantly higher than those calculated from nondigesting snakes. In fact, the opposite is nearly true. The predicted gastric digestive rates calculated from the  $T_b$ 's of digesting snakes were borderline significantly lower than those of nondigesting snakes. In contrast, predicted passage rates calculated from the  $T_b$ 's of digesting snakes were significantly higher than those calculated from nondigesting snakes. These results may indicate a higher degree of coadaptation between the thermoregulatory behavior of *C. bottae* during digestion and the thermal dependence of passage rate than with the thermal dependence of gastric digestive rate alone.

While the coadaptation hypothesis predicts a single optimal temperature for all components of the digestive process, multiple physiological optima may be present (Huey 1982). One important factor to consider, and one we did not examine, is digestive efficiency. It may be that *C. bottae* behave in such a way as to optimize the efficiency of digestion (i.e., amount of energy extracted from food) rather than the digestive rate. However, previous studies of digestive efficiency in snakes have revealed minimal sensitivity to temperature (Harlow et al. 1976; Greenwald and Kanter 1979).

Recent studies by Secor et al. (1994) may shed light on why *C. bottae* thermoregulate during digestion at temperatures higher than those that optimize gastric digestive rate. These studies have shown that some snakes rapidly upregulate their intestine to prepare for digestion and absorption immediately after ingestion. This process includes substantially increasing

Figure 4. Simulated  $T_b$ 's, gastric digestive rates, and passage rates for snakes behaving as digesting and nondigesting snakes on a typical spring day (May 25, 1991). A, Simulated  $T_b$ 's of "digesting" and "nondigesting" snakes (see text for a description of how the modeled  $T_b$ 's were generated) when constrained by the minimal and maximal operative temperatures ( $T_e$ ) on a typical spring day. Note that neither "digesting" nor "nondigesting" snakes would be able to reach preferred  $T_b$ 's at night. B, Predicted gastric digestive rates calculated from the simulated  $T_b$ 's in A. The lightly shaded region represents the difference between the calculated gastric digestive rates for "digesting" and "nondigesting" snakes. C, Predicted passage rates calculated from the simulated  $T_b$ 's in A. The darkly shaded region represents the difference between the calculated passage rates for "digesting" and "nondigesting" snakes. Note that there would be little difference in either predicted gastric digestive rates or predicted passage rates between "digesting" or "nondigesting" snakes.

the number of amino acid transporters and more than doubling intestinal mass (Secor et al. 1994). Higher temperatures, above the optimal temperature for gastric digestion, might be critical for this upregulation, and thus snakes may accept slightly slower gastric digestion to accomplish this.

The concept of multiple optima leads to an interesting question: Why have the optimal temperatures for different components of the digestive process evolved differently? Constraints (e.g., genetic) may limit the evolution of the thermal optima of different processes. Alternatively, as long as thermal optima

are relatively close and performance of one function is not substantially reduced at the optimal temperature of another, selection to evolve matching optima may be weak. This may be the case when we consider that gastric digestive rate is still 90% at the optimal temperature for passage rate and that *C. bottae* apparently forage only about once every 8 d, and presumably feed even less frequently, thus reducing the need to digest food quickly (Dorcas 1995).

#### Simulation of Free-Ranging Snakes

The results of simulating the  $T_b$ 's of free-ranging snakes showed that there were substantial differences between the simulated  $T_b$ 's of snakes in the spring and summer. As expected, in the spring, low nighttime temperatures would prevent snakes from maintaining  $T_b$ 's even close to their preferred temperatures (Fig. 4A). Consequently, the passage rates and gastric digestive rates of snakes would be reduced (sometimes to 0%) at night. However, during a typical spring day snakes would be able to reach preferred  $T_b$ 's at least some of the time and would thus be able to maximize gastric digestive rate and passage rate during those times. Results showed that the daily mean for both functions would be between 42% and 46% of maximum (Fig. 4B, C). Because of the constraints on  $T_b$ 's during the spring, differences in passage rates and gastric digestive rates were minimal. Consequently, and surprisingly, there seemed to be no significant advantage to precise thermoregulation as a "digesting" snake in the spring.

During the summer, "nondigesting" snakes were able to maintain preferred  $T_b$ 's for the entire day (Fig. 5A). In contrast, "digesting" snakes were usually constrained from reaching preferred  $T_b$ 's at night (Fig. 5A). However, the reduction in  $T_b$  due to environmental constraint was typically only 2°–3°C below the preferred temperature. Interestingly, there were no substantial differences (only 3.4%) in gastric digestive rate between "digesting" and "nondigesting" snakes (Fig. 5B). How-

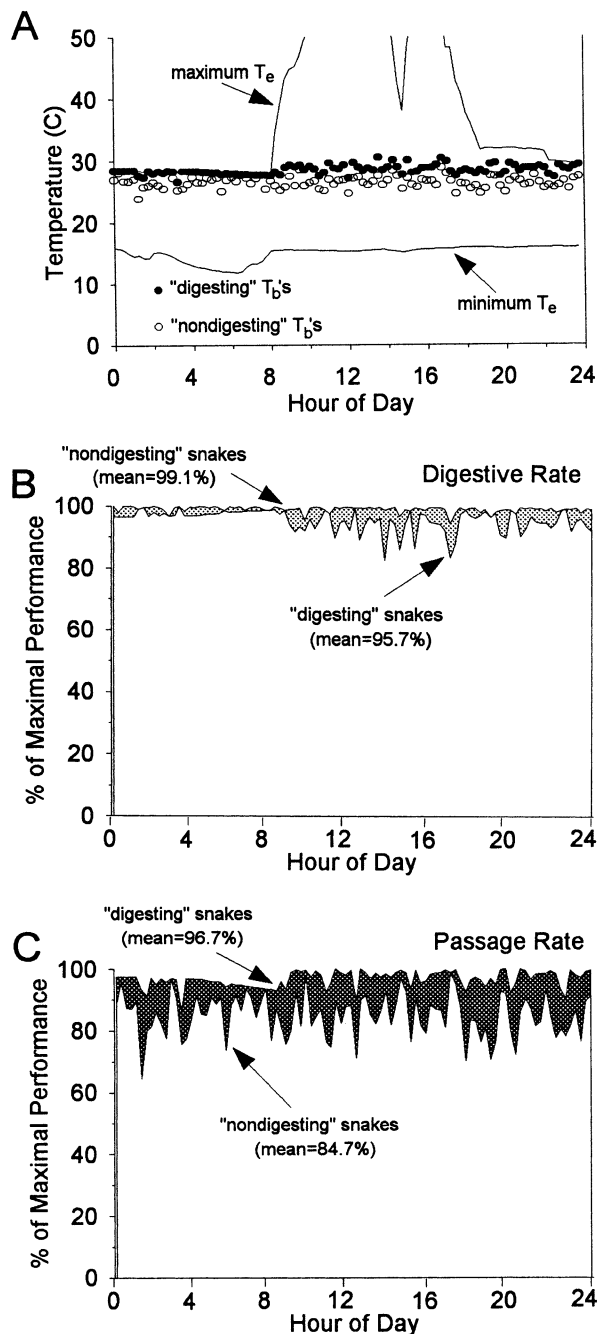


Figure 5. Simulated  $T_b$ 's, gastric digestive rates, and passage rates for snakes behaving as digesting and nondigesting snakes on a typical summer day (July 15, 1991). A, Simulated  $T_b$ 's of "digesting" and "nondigesting" snakes (see text for a description of how the modeled  $T_b$ 's were generated) when constrained by the minimal and maximal operative temperatures ( $T_e$ ) on a typical summer day. Note that while "nondigesting" snakes would be able to maintain preferred  $T_b$ 's all day, "digesting" snakes would be unable to reach preferred  $T_b$ 's at night. B, Predicted gastric digestive rates calculated from the simulated  $T_b$ 's in A. The lightly shaded region represents the difference between the calculated gastric digestive rates for "digesting" and "nondigesting" snakes. C, Predicted passage rates calculated from the modeled  $T_b$ 's in A. The darkly shaded region represents the difference between the calculated passage rates for "digesting" and "nondigesting" snakes. Note that there would be little difference in predicted gastric digestive rates between "digesting" and "nondigesting" snakes. However, "digesting" snakes would pass food 12% faster than "nondigesting" snakes.



ever, there were substantial differences in passage rate. "Digesting" snakes passed food 12% faster (nearly 6 h earlier) than "nondigesting" snakes (Fig. 5C). The biological significance of this difference is unclear, but these results raise the possibility that *C. bottae* are thermoregulating during digestion so as to optimize passage rate, or factors affecting it, rather than gastric digestive rate.

If we compare predicted gastric digestive rates and passage rates between spring and summer days, we find that during the summer, snakes could apparently process food more than twice as fast as during the spring (Figs. 4, 5). To interpret the fitness consequences of this phenomenon, we need to know more about the nutritional needs of *C. bottae* and how they vary with factors such as time, sex, age, and physiological condition.

### Conclusions

Two main conclusions arise from the results of this study. First, these results provide convincing evidence that when examining the match between physiology and behavior, one must compare the thermal dependence of physiological functions with a measure of thermoregulatory behavior made on animals with the physiological condition appropriate for the function being studied (Peterson et al. 1993). Second, the ecological interpretation of laboratory results can be greatly improved when combined with environmental measurements. This technique can be especially valuable when measurements and/or observations of free-ranging animals are difficult. The use of environmental measurements to interpret laboratory data may not only result in conclusions unrevealed by laboratory data alone but may also provide insights that contradict those generated outside an appropriate ecological context.

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