# The Benefits of a Hot Meal:

# Identifying the Advantages of Postprandial Thermophily in Snakes

MS Thesis Proposal

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**Abstract**

Temperature profoundly affects the biology of most organisms, but particularly reptiles, which regulate their body temperature ($T_b$) behaviorally by shuttling between heat sources and sinks. Some reptiles select higher $T_b$s after feeding, a behavior termed postprandial thermophily (PPT). Although rarely tested, this increase in $T_b$ is assumed to increase nutrient and energy assimilation and reduce meal retention time. Yet if PPT is beneficial to digestion, than why isn't it ubiquitous in reptiles? My study tests the presumed benefits of PPT and the underlying mechanistic basis of these benefits in closely related species of watersnakes (*Nerodia* spp.). My objectives are to determine (1) the correlation between meal size and PPT, (2) the effects of PPT on passage rate (PR) and digestive efficiency (assimilable digestive coefficient, ADC), and (3) the temperature sensitivity of digestive enzymes, which addresses a likely mechanism underlying the digestive benefits of PPT. My experiments will be conducted on three species of watersnakes that have or lack PPT. To determine if PPT is elicited in proportion to meal size, snakes implanted with temperature-sensitive transmitters will be fed meals (goldfish) 10, 20, and 50% of their body mass and body temperatures selected ($T_{sel}$) in a thermal gradient will be recorded. To determine the effects of PPT on PR and ADC, snakes will be held in environmental chambers set at the $T_{sel}$ recorded for fasted and fed individuals of each species. Meals will be marked prior to feeding to determine the evacuation time and feces and urates will be recovered for bomb calorimetry to compare PR and ADC between snakes with and without PPT. To identify the mechanism behind PPT, the *in vitro* activity of three ecologically relevant digestive enzymes will be measured at each of four temperatures to compare the temperature sensitivity of enzyme activity between species with and without PPT. In most analyses, individuals will be compared to themselves ($T_b$

unfed vs. fed) and species means will be used to test for differences between species with and without PPT. My study is the first to adopt a mechanistic approach to investigating the evolution and distribution of PPT. If supported, my hypotheses would call for additional experiments on other closely related species among which PPT is also not ubiquitous. If not supported, biotic and/or abiotic pressures may explain why species that would digestively benefit from increasing $T_b$ following feeding do not exhibit PPT and alternative mechanisms should be explored.

## Background

Many reptiles rely on external sources of heat energy (e.g., solar radiation and sun-warmed rocks) to maintain body temperatures ($T_b$s) different from their surroundings. Despite a lack of endogenous thermal control, thermoregulating reptiles can maintain relatively constant $T_b$s when active by shuttling between heat sources and sinks in their environment. In fact, many reptiles maintain ($\pm$ 2–4 °C) high 'preferred' body temperatures ($T_{pref}$) when active, which generally optimizes physiological performance (Espinoza and Tracy 1997). For example, at higher $T_b$s many reptiles achieve greater digestive efficiency and a shorter retention time of the meal (Lillywhite 1987; Espinoza and Tracy 1997). Furthermore, higher $T_b$s reduce the net metabolic cost of digestion or specific dynamic action (SDA) (Toledo et al. 2003). Given the apparent digestive advantages, it is not surprising many reptiles raise their $T_b$ above prefed levels within a few hours after ingesting a meal, a phenomenon know as postprandial thermophily (PPT). Ectothermic vertebrates exhibiting PPT actively search for thermally favorable microhabitats (Tsai and Tu, 2005). PPT has been widely reported in reptiles (Lang 1979; Brown and Brooks 1991), but is particularly well known in snakes (Table 1). Curiously however, PPT is not

ubiquitous in reptiles (Kitchell 1969; Lysenko and Gillis 1980; Sievert 1989; Tu and Hutchison 1995; see Touzeau and Sievert 1993 for review; Table 1) and even one subspecies may exhibit PPT, whereas another may not (e.g., Lysenko and Gillis 1980).

Cowles and Bogert (1944) were the first to note the selection of high $T_b$s in a reptile following feeding in their lab observations of a desert spiny lizard (*Sceloporus magister*). Later, Regal (1966) described how a large snake (*Boa constrictor*) placed the region of its body containing a recently ingested meal directly under a heat source, thereby warming that region of its body. In the subsequent 40 years PPT has been widely cited as providing an energy-extraction benefit.

Although higher $T_b$s generally enhance digestive efficiency and accelerates passage rate in reptiles (Phillips 1986; Espinoza and Tracy 1997), the mechanisms underlying these physiological changes have not been investigated. Given the apparent digestive advantages of PPT, and the fact that such benefits should boost fitness by enhancing growth rate and fat storage (Lillywhite 1987; Sievert et al. 2005), it is surprising that this phenomenon is not ubiquitous in reptiles. Even more puzzling is the fact that some species with PPT share habitat and food preferences with other closely related species that lack PPT (e.g., subspecies of *Thamnophis sirtalis*; Lysenko and Gillis 1980).

Small meals may not elicit a thermophilic response, thereby misleading researchers seeking evidence of PPT. Tsai and Tu (2005) detected PPT in Chinese green tree vipers (*Trimeresurus stejnegeri*) fed meals ranging 20–25% of snake body mass, but meal sizes in other studies were considerably smaller (10–15% of body mass; Naulleau 1983; Lutterschmidt and Reinert 1990; Dorcas et al. 1997; Sievert and Andreadis 1999; Sievert et al. 2005), leaving open the possibility of false negatives.

## Objectives and Hypothesis

My study examines the occurrence and significance of PPT in three species of water snakes: two species previously tested for PPT—one that exhibits the behavior and another that does not—and another whose post-feeding thermal preference is unknown. I seek to identify the mechanism(s) underlying the digestive benefits of PPT and, by comparing the temperature dependence of digestive processes (passage rate, digestive efficiency, and digestive enzyme kinematics) in snake species exhibiting and lacking this behavior, its adaptive significance. I have chosen to study North American water snakes (*Nerodia* spp.) because PPT is present but not ubiquitous in this lineage, which will allow me to test the adaptive significance of my findings (sensu Garland and Adolph 1994). My study will include three widely foraging species from the temperate region of the southeastern United States: (1) northern water snakes (*Nerodia sipedon*), which exhibit PPT (Sievert and Andreadis 1999), (2) diamondback water snakes (*Nerodia rhombifer*), which are considered not to exhibit PPT (Tu and Hutchison 1995), and (3) either the banded water snake (*Nerodia fasciata*) or the plain-bellied water snake (*Nerodia erythrogaster*), for which the thermoregulatory responses following feeding have not been investigated.

Based on the findings of previous studies, I expect to confirm that *Nerodia sipedon* exhibits PPT, but that *N. rhombifer* does not. Although *N. fasciata* and *N. erythrogaster* are closely related to *N. sipedon* (Lawson 1987; Gibbons and Dorcas 2004), I hypothesize that neither will exhibit PPT because I suspect that PPT is more dependent on habitat and feeding behavior. Because water snakes are primarily aquatic, they experience high rates of evaporative cooling, even when basking out of water. Additionally, these actively foraging snakes feed frequently. Consequently, I expect them to maintain their gut morphology and physiology in a

constant state of readiness (Secor 2005). However, if higher temperature selection results in greater physiological performance, higher enzyme activity is expected in *N. sipedon* following feeding, relative to *N. rhombifer* and *N. fasciata* or *N. erythrogaster* (assuming that *N. fasciata* or *N. erythrogaster* do not exhibit PPT). The fact that *N. sipedon* exhibits PPT is most likely an anomaly for water snakes. Accordingly, I expect to find strong temperature-dependent responses in digestion (passage rate, digestive efficiency, and enzyme kinematics) following feeding in *N. sipedon*, but no such responses in *N. rhombifer*. Whether *N. fasciata* or *N. erythrogaster* exhibit the noted temperature-dependent digestive responses will depend on whether each has PPT. These predictions are summarized in Table 2.

**Materials and Methods**

*Animals*.—Ten to fifteen juveniles (~100 g) of each of three species of water snakes (*Nerodia sipedon*, *N. rhombifer*, and *N. fasciata* or *N. erythrogaster*) have been captured in the field. Snakes are housed in cages (58 Õ 53 Õ 33 cm) in small groups (2–3 individuals) in the CSUN Vivarium. Fluorescent UV lights provide a 12:12 photocycle and heating pads placed under half of each cage provide opportunities for thermoregulation. The floors of the cages are lined with ground coconut husks and plastic pipes are provided for refugia. Water is provided ad libitum from a dish large enough for the snakes to submerge their entire bodies. These snakes are aquatic and eat primarily fish and amphibians (Gibbons and Dorcas 2004). In captivity the snakes will be fed juvenile goldfish (*Carassius auratus*) biweekly up to 15% of their body mass. Body size (mass and snout-vent-length) will be recorded twice monthly to monitor growth and changes in body condition.

*Postprandial Thermophily.*—I will use a thermal gradient (2.4 Õ 0.6 Õ 0.7 m) to examine body temperatures selected ($T_{sel}$) by snakes before and after feeding. One end of the gradient is heated by thermostatically controlled heat tape (Thermolyne BSAT 101-100, Dubuque, IA) and the other end is cooled by cycling chilled water (ThermoNESLAB RTE 7, Newington, NH) through a copper coil on the underside of the gradient. This creates a temperature range from 20–40 °C, which exceeds the range of temperatures selected by water snakes in the lab and in nature (24–28 °C; Lutterschmidt and Reinert 1990; Ming-Chung and Hutchison 1995). The gradient is illuminated by fluorescent UV lighting suspended 1 m overhead. The gradient floor is lined with 2–3 cm of silica sand.

To monitor $T_{sel}$ while in the gradient, snakes will be surgically implanted with temperature-sensitive radio transmitters (9-g SI-2T, Holohil Systems, Ontario, Canada). Transmitters will not exceed 10% of a snake's mass. I will anesthetize snakes by placing them into a transparent tube (ca. twice the snake's diameter) and dosing a cotton ball with 1 ml of isofluorane. Once anesthetized, snakes will be positioned with a funnel mask with isofluorane on a cotton ball and their heart rate will be monitored via visual inspection. A small ventral incision (<2 cm) will be made into the distal peritoneal cavity using sterilized instruments. A sterilized transmitter, which will be dipped in wax to prevent abrasion, will be inserted and the incision will be sutured with surgical silk. Following recovery from surgery (3 d), snakes will be subjected to behavioral studies to determine $T_{sel}$ in the thermal gradient following a fast or recent feeding (see below). Alternative methods of monitoring $T_b$ were considered, such as periodic measures via cloacal probing or using implanted cloacal thermocouples, but these pose several problems or are prone to errors (Tsai and Tu 2005).

Snakes will be randomly assigned to one of two treatment groups: fed or fasted. Snakes will be fed juvenile goldfish (*Carassius auratus*) with a total wet mass of 10, 20, or 50% of the snake's body mass. Following 24 h of acclimation to the gradient (following Harwood 1979), $T_{sel}$ will be recorded every 10 min for 6 d to determine the magnitude (if any) of PPT (Tu and Hutchison 1995). Fasted individuals will not be fed for approximately 2 wk to ensure their guts are in a post-absorptive state (Tu and Hutchison 1995; Tsai and Tu 2005), but otherwise treated as for the fed group. After their first trial in the gradient, snakes will be returned to their cages for 2 wk and provided water as described above. Thereafter, each snake will be subjected to the treatments (fed a different meal size or fasted) that it did not receive in the previous trial, so each animal will be subjected to all treatments and serve as its own control.

*Digestive Physiology.*—To determine the temperature dependence of digestive responses following feeding, I will take two whole-animal measures of digestive performance (passage rate and digestive efficiency) and also measure the temperature dependence of enzyme activity for three ecologically relevant digestive enzymes. The temperature dependence of these enzymes (Hochachka and Somero 2002) may explain the whole-animal digestive benefits of PPT. Passage rate (PR, the time it takes a meal to pass through the digestive tract) and assimilable digestive coefficient (ADC, how well the meal is assimilated, sensu Levey and Karasov 1989) will be measured at the mean fed and fasted $T_{sel}$ (if different) for each species (as determined from the gradient study). To estimate PR, snakes will be fed freshly killed juvenile goldfish (~25% of the snake's body mass), the first and last of which will be gut loaded with distinctly colored indigestible markers (20, 2 Õ 0.5 mm strips of flagging tape). Snakes will be housed individually in ventilated plastic tubs (30.0 Õ 16.5 Õ 9.0 cm) with a plastic grate on the floor to reduce

contact between the animal and its feces. The tubs will be placed in environmental chambers

(CMP 4030 Equipped Chamber, Conviron, Winnipeg, Manitoba, Canada) with each tub's

position in and among chambers assigned randomly each day to mitigate chamber effects.

Chambers will be maintained at the species-specific prefed or PPT $T_{sel}$ (if different) and

maintained on a 12L:12D photocycle. I will check the snakes hourly during photophase for the

appearance of feces and record the time it takes for 80% of flags to evacuate each animal's gut.

A mean PR will be recorded for each species for each digestive state (fed vs. fasted). Using the

feces and urates collected from the PR study, ADC will be estimated as:

$$ADC = (E_{in} - E_{out}) / E_{in},$$

where $E_{in}$ is the energy content of the meal and $E_{out}$ is the energy content of feces plus urates,

which will be determined via bomb calorimetry. The mean ADE will be recorded for each

species for each digestive state (fasted vs. fed).

Next, I will examine the activity of three digestive enzymes. Two weeks following the

PR/ADC experiments, five individuals of each species will be randomly assigned to one of two

groups: fed or fasted. Following feeding or fasting (2 d and 2 wk, respectively) snakes will be

killed via decapitation, their intestines removed, washed of their contents with phosphate-

buffered saline (PBS), homogenized in PBS (1 mg tissue to 30 ml PBS), and stored at –80 °C. I

will examine the temperature dependence of activity of trypsin, aminopeptidase, and lipase.

Polypeptides are needed for amino acid (AA) extraction and the formation of absorbable

peptides. These long peptide chains are produced as trypsin cleaves proteins. These products are

then used by aminopeptidase, which catalyzes the hydrolysis of the terminal peptide bond at the

amino end of the polypeptide, producing absorbable dipeptides and monopeptides (Daniel et al.

2003). Aminopeptidase exhibits high specificity, cleaving after alanine (a non-essential AA) and

leucine (an essential AA), which are important sources of energy for the brain, central nervous system, and muscles, and the production of essential biochemical components, respectively (Daniel et al. 2003). Thus, these two enzymes, working in concert, play an important role in protein digestion and assimilation in carnivorous vertebrates. Also, because the diet of water snakes is primarily fish and amphibians (Gibbons and Dorcas 2004), lipase activity is expected to be a critically important digestive enzyme as it converts triglycerides to monoglycerides and free fatty acids, which can be directly absorbed by the intestine. Enzyme activity will be determined using a modification (R. A. Hernandez, pers. comm.) of techniques developed by German et al. (2004) at five temperatures for each species: (1) the fasted $T_{sel}$, (2) an intermediate temperature (between fasted and fed $T_{sel}$), (3) PPT $T_{sel}$, (4) a temperature the sum of the PPT $T_{sel}$ and the intermediate temperature difference, and (5) a temperature the sum of PPT $T_{sel}$ and the fasted $T_{sel}$ difference.

*Data Analyses.*—Because the $T_{sel}$ of each snake will be measured after being fed and fasted, individuals can be compared to themselves using a paired *t*-test to statistically test for PPT. I will compare $T_{sel}$ over 4–6-h periods during mid photophase and scotophase to avoid times near changes in the light cycles. The effect of meal size will be tested with an analysis of covariance (ANCOVA) with the meal size as the covariate, with snakes again compared to themselves for $T_{sel}$. Differences in species-specific mean passage rates and assimilable digestive coefficients between fed and fasted $T_{sel}$ will be compared with paired *t*-tests. Mean enzyme activities will be compared between fed and fasted individuals for each enzyme and each species over the five temperature treatments (fixed factor) with an ANOVA. If meal sizes differ across treatments for

any of the experiments, this variable will be taken into account via ANCOVA, with meal size as the covariate.

## Predictions and Significance

*Postprandial Thermophily.*—If either *Nerodia erythrogaster* or *N. fasciata* exhibit PPT, than their fasted $T_{sel}$ may be below that which is optimal for nutrient and energy extraction from a meal. If PPT is observed in either of these species than this behavior is likely phylogenetically conserved, which would facilitate our understanding of the evolutionary history of PPT in this genus. Accordingly, I would expect the temperature dependence of digestion for these species to be similar to that predicted for *N. sipedon*. However, if PPT is not exhibited by either of these species, I expect the temperature dependence of digestion for these species to be similar to that predicted for *N. rhombifer* (Table 2).

*Passage Rate and Digestive Efficiency.*—I expect PR to be faster and ADC to increase with each incremental increase in temperature because temperature affects PR and ADC proportionally in snakes (Dorcas et al. 1997; Sievert et al. 2005). Furthermore, if temperature and enzyme activity are closely linked, snakes with PPT should experience a reduction in ADC and a slower PR at lower temperatures compared to snakes without PPT (Table 2).

*Enzyme Kinetics.*—A likely underlying cause of PPT is that fasted $T_{sel}$ is below the $T_{b}$ that maximizes enzyme activity (Hochachka and Somero 2002). Consequently, enzyme activities will be lower at lower $T_{b}$s. If PPT facilitates ADC by lowering the activation energy of the enzymes, I

expect the digestive enzyme activities of snakes exhibiting PPT to be strongly temperature sensitive. Conversely, species lacking PPT should have enzyme activities that are less temperature sensitive.

If my hypotheses are supported, one selective force for PPT will be the strong temperature dependence of digestive enzyme activity. If species that exhibit PPT follow this prediction, but those without PPT do not, this relationship may explain the evolution and distribution of this phenomenon generally, and would call for additional experiments on other closely related species among which PPT is not ubiquitous (e.g., garter snakes, *Thamnophis* spp.). However, if my hypotheses are not supported, the temperature dependence of digestive enzyme activity may be ruled out as mechanism explaining the benefit of PPT and alternative mechanisms should be explored.

## Proposed Timeline

Animals were collected during summer–fall 2006 and were returned to CSUN for 14 d quarantine prior to moving them into the Vivarium. Snakes will be implanted with temperature-sensitive transmitters during in late fall 2006 and allowed to recuperate from the procedure before trials (3 d). Experiments to determine or confirm whether each species exhibits PPT will take place in late winter 2006, after which temperature-specific PR and ADC will be determined. Gut enzyme kinetics will be determined in spring 2006. Data analysis will begin in late spring 2007. I plan to defend my thesis in late summer/early fall 2007.

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Table 1. Snakes species studied for postprandial thermophily (PPT).

| Species | Exhibits PPT | $T_b$ Change (°C) | Source |
|---|---|---|---|
| *Boa constrictor* | Yes | 11.0 | Regal (1966) |
| *Charina bottae* | Yes | 2.3 | Dorcas et al. (1997) |
| *Coluber constrictor* | No | — | Hammerson (1987)* |
| *Heterodon platirhinos* | No | — | Kitchell (1969) |
| *Masticophis lateralis* | No | — | Hammerson (1979)* |
| *Morelia spilota* | Yes | 2.0–5.0 | Slip and Shine (1988) |
| *Nerodia rhombifer* | Yes | 1.9 | Tu and Hutchison (1995) |
| *Nerodia sipedon* | Yes | 8.3–8.7 | Lutterschmidt and Reinert (1990) |
| *Nerodia taxispilota* | No | — | Goodman (1971)* |
| *Opheodrys aestivus* | Yes | 3.5 | Touzeau and Sievert (1993) |
| *Pantherophis guttatus* | Yes | 6.0 | Sievert et al. (2005) |
| *Philodryas chamissonis* | Yes | ? | Bozinovic and Rosenmann (1988)* |
| *Thamnophis s. parietalis* | Yes | ? | Lysenko and Gillis (1980)* |
| *Thamnophis s. sirtalis* | No | — | Lysenko and Gillis (1980)* |
| *Trimeresurus s. stejnegeri* | Yes | ? | Tsai and Tu (2005)* |
| *Vipera aspis* | ? | — | Naulleau (1983) |

* PPT from results summarized by Touzeau and Sievert (1993)

Table 2. Known and predicted outcomes of postprandial thermophily (PPT) and potential thermal benefits for selected *Nerodia* species.

| Species | PPT studied | Exhibits PPT | $H_o$ for PPT | *T*-sensitivity of PR and ADC | *T*-sensitivity of enzyme activity | Closest relative |
|---|---|---|---|---|---|---|
| *erythrogaster* | No | ? | No | Low | Low | *sipedon* |
| *fasciata* | No | ? | No | Low | Low | *sipedon* |
| *rhombifer* | Yes | No | No | Low | Low | *taxispilota* |
| *sipedon* | Yes | Yes | Yes | High | High | *clarkii* |