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Comparative Energetics and Responses to Feeding of  
Copperhead and Cottonmouth Snakes (*Agkistrodon*)

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Comparative Energetics and Responses to Feeding of Copperhead and Cottonmouth

Snakes (*Agkistrodon*)

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Presented to

The College of Graduate Studies

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In Partial Fulfillment

Of the Requirements for the Degree

M.S. Biology

McKayla M. Spencer

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To the College of Graduate Studies:

We are submitting a thesis written by McKayla M. Spencer entitled “Comparative Energetics and Responses to Feeding of Copperhead and Cottonmouth Snakes (*Agkistrodon*).” We have examined the final copy of this thesis for form and content. We recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science in Biology.

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## **DEDICATION**

I dedicate this work to my family and friends. My mother, father, and brother who have always supported my eccentric nature. Also my Grandma Anna, whose love of nature has been an inspiration.

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## ABSTRACT

McKayla M. Spencer. Comparative Energetics and Responses to Feeding of Copperhead and Cottonmouth Snakes (*Agkistrodon*).

(Under the direction of Dr. C. M. Gienger).

The breakdown of food and absorption of nutrients are essential physiological processes in animals. Differences in response to feeding have been attributed to a variety of ecological factors such as foraging mode and body shape, but other ecological attributes could lead to differences in important behaviors and physiological ecological interactions as well. We compare responses to feeding between two similar species with differing use of habitat; copperheads (*Agkistrodon contortrix*; a terrestrial species) and cottonmouths (*Agkistrodon piscivorus*; a semi-aquatic species). To make these comparisons we measured pre- and post-feeding metabolic rates (at 20, 25, and 30°C) and body temperature ( $T_b$ ) selection by digesting snakes. Following the consumption of rodent meals, specific dynamic action (SDA) was significantly affected by temperature and species. SDA was approximately 1.5 to 2 times higher in *A. piscivorus* than *A. contortrix*. Post-feeding, *A. contortrix* did not select different temperatures but *A. piscivorus* selected 5-6°C warmer temperatures. After feeding, *A. contortrix* selected a mean post-feeding temperature of 26°C and *A. piscivorus* selected a mean post-feeding temperature of 29°C. Differences in post-feeding temperature selection may differentially maximize net energy intake for each species.



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**Table 1:** Comparison of metabolic rates among species (*Agkistrodon contortrix* and *A. piscivorus*), temperatures (20, 25, and 30°C), and feeding treatment (pre and post-feeding). Post- 20°C results were not included in analysis because only two snakes ate at that temperature. Variables are defined in the text. Values are means  $\pm$  s.e.m. .... 22





# CHAPTER I

## INTRODUCTION

Digestion is an essential physiological process in animals that provides energy for survival, growth, and reproduction. Before energy is available for use, energy is required to breakdown food and assimilate nutrients, a process known as Specific Dynamic Action (SDA) (Secor and Diamond 1995, Starck et al. 2004). Increases in metabolic rate (i.e. energy expenditure per unit time) after feeding range from 25% in humans up to 687% in snakes (Secor 2009). Several ecological factors have been found to influence metabolism including species occupying different habitats (mammals; Elgar and Harvey 1987, fishes; Killen et al. 2010, 2016), swimming mode (fishes; Killen et al. 2010), flying versus non-flying locomotion (insects; Reinhold 1999), foraging mode (squamates; Andrews and Pough 1985, Secor and Nagy 1994), and dietary habits (squamates; McCue et al. 2005, Britt 2006). Differences in ecological attributes could lead to differences in important behaviors and physio-ecological interactions. Different environments, such as aquatic and terrestrial, are associated with different dietary habits (Tucker et al. 2014). Dietary habits consist of variables such as how often an animal feeds, type of prey, and nutritional composition of prey; all variables that have an affect on SDA (Secor 2009). Dietary habits and habitat use are considered adaptive responses to different predator and competitive pressures (Kenagy 1973, Henderson 1982) and since similar pressures influence dietary habits and habitat use, both likely affect SDA.

One way that species interact both behaviorally and physiologically with their environment is in response to feeding. After feeding, ectotherms may select warmer temperatures in their environment (winchuka bugs; Lazzari 1991, chelonians; Gatten Jr. 1974, and snakes; Touzeau and Sievert 1993, Sievert and Andreadis 1999, Sievert et al. 2013, Regal 1966). The selection of warmer temperature is presumably to optimize digestive efficiency and to decrease food passage time (Wang et al. 2003). Since environmental temperature has an significant effect on behavioral thermoregulation and metabolic rate, it is expected that the two are linked (Sievert and Andreadis 1999).

With the ability to eat large meals, sometimes up to 100% of their body mass, snakes are a unique group in that many species have a dramatic physiological response to feeding (Slip and Shine 1988, Secor and Diamond 1995, Ott and Secor 2007). We examined whether differences in digestive response (thermal and metabolic responses to feeding) can be related to differences in habitat use between two similar snake species; copperheads (*Agkistrodon contortrix*) and cottonmouths (*Agkistrodon piscivorus*). These species share a close evolutionary history as well as a similar foraging mode (ambush predators; Greenbaum et al. 2003, Lillywhite and McCleary 2008), reproductive strategy (ovoviviparous; Lynch 2009), and body shape. However, the species vary considerably in habitat use: Copperheads are almost exclusively terrestrial (Reinert 1984), typically occupying mesic mixed-hardwood forests, while cottonmouths are primarily semi-aquatic and inhabit shallow slow-moving water bodies such as swamps and sloughs (Blem and Blem 1990, Willson et al. 2006, Eskew et al. 2009). Since dietary habits affects the post-feeding response in snakes (Secor and Diamond 1997, McCue et al. 2005) and similar

adaptive pressures affect habitat use, we expected differences in SDA and postprandial thermoregulation between these species.

## CHAPTER II

### METHODS

#### *Study Animals*

Cottonmouths (*Agkistrodon piscivorus*) were opportunistically collected from the Cumberland River Bicentennial Trail, Tennessee and copperheads (*Agkistrodon contortrix*) were collected from Land Between the Lakes NRA, Kentucky (sites are approximately 89 km SLD apart). Snakes were collected from April to September 2016 and housed in individual cages at 25°C with a 12L : 12D photoperiod. Each cage had an appropriate sized hide box (based on size of snake), undertank heating pad, and water provided *ad libitum*. To ensure a post-absorptive digestive state, snakes were kept for a minimum of seven days before beginning experimental trials.

#### *Respirometry*

We measured rates of oxygen consumption ( $VO_2$ ) using open-flow respirometry (Withers 1977, Lighton 2008). We used a Sable Systems FC-10 oxygen analyzer and Sable Systems MUX flow multiplexer to alternately measure five animals and one reference baseline chamber ( $N=53$ ). An Ametek R-1 flow controller pumped room air through a Drierite drying column, then through a manifold that split the air stream to separate mass flow controllers (Sierra Mass Trak). The mass flow controllers maintained chamber airflow rates between 15 to 100 mL/min, depending on the trial temperature and size of the snake. Respirometry chambers were constructed from translucent plexiglass cylinders ranging from 1.2 L to 4.3 L in volume to accommodate different sized snakes.



Before pushing air through the oxygen analyzer, excurrent chamber air was scrubbed of CO<sub>2</sub> and water vapor using drying columns packed with Ascarite II and Drierite. A Percival Scientific incubator was used to house the respirometry chambers during trials and control temperature and light cycle in the chambers.

Individual snakes were measured for 30-minute intervals with a 15-minute baseline (room air) between samples and O<sub>2</sub> concentration was recorded every three seconds. Chamber O<sub>2</sub> concentrations were measured 8 times per day (every 3 hours in a 24 hour period) and we used the most level 15-minute period from each 30-minute sample to calculate the rate of gas exchange. Individuals were randomly assigned to one of three temperatures (20°C, 25°C, and 30°C). At each temperature snakes were measured for 72 hours and the mean of the three lowest 15-minute measurements (out of 24 measurements) was considered the Standard Metabolic Rate (SMR). The mean of the three lowest measurements was used in place of the lowest measure to help eliminate artificially low estimates due to routine periods of apnea (Heatwole 1977).

After the three day SMR measurement period, snakes were removed from respirometry chambers and placed into separate cages where they were fed 1-2 thawed rodents (lab mice or rats) equivalent to 20% of their body mass (mean±SE= 0.05±0.005 kg for all trials). Not all snakes were willing to feed (25 of 53 individuals ate), and those that ate were returned to the metabolic chambers within an hour after feeding. If a snake refused to eat it was removed from the post-feeding study group (SMR was still used). When snakes were being fed they were provided water *ad libitum* (snakes went no more than 7 days without water). VO<sub>2</sub> was measured for seven consecutive days after feeding.



Snakes were only used in a single feeding experiment and after data was collected they were released at their site of capture in the field.

VO<sub>2</sub> was calculated using Warthog Systems LabAnalyst implementing the equations of Withers (1977) and converted to energy equivalent units using 19.5 J mL<sup>-1</sup> O<sub>2</sub> consumed (Gessaman and Nagy 1988). Meal energetic values were calculated by multiplying the total meal mass by the mass-specific nutritional value of the meal following Cox and Secor (2007; subadult mice= 7.77±0.12 kJ g<sup>-1</sup> wet mass; adult mice= 8.04±0.15 kJ g<sup>-1</sup> wet mass; weanling rats= 7.41±0.13 kJ g<sup>-1</sup> wet mass; medium rats= 7.29±0.14 kJ g<sup>-1</sup> wet mass).

For each individual we calculated several metrics that describe the energetic response to feeding. We calculated the highest recorded VO<sub>2</sub> after feeding (peak VO<sub>2</sub>), the peak VO<sub>2</sub> divided by SMR (factorial scope of peak VO<sub>2</sub>), time to peak VO<sub>2</sub>, and time from feeding to time when VO<sub>2</sub> was no longer significantly different from SMR (determined from Tukey-Kramer *post hoc* analysis; duration of elevated metabolic rate). We also calculated the total energy expended above SMR during the period of significantly elevated VO<sub>2</sub> (SDA), and SDA divided by meal energy (SDA coefficient; see variable explanations in McCue 2006, Secor 2009). We grouped post-feeding measurements into 6-hour increments after feeding for a total of 28 post-feeding time increments per individual.

### ***Thermal Response to Feeding***

A laboratory thermal gradient was used to determine snake thermal preference for three days pre-feeding and then again for seven days post-feeding. The thermal gradient was comprised of a V632 Vision Cage (183 cm W x 91 cm D x 46 cm H) with cool water

circulated through copper tubing placed under 46 cm W at one end and eight heat pads of increasing temperature placed sequentially across the length of the gradient. This provided a 16°C to 34°C available temperature range (0.09 degrees increase per linear cm). Water was provided *ad libitum* in three bowls placed along the length of the gradient and a 5 cm deep layer of dried leaf litter was used as substrate. The leaf litter allowed snakes to camouflage and shelter themselves in a similar manner as their natural environment.

Thermochron ibutton dataloggers (DS1922L) were surgically implanted (Reinert and Cundall 1982) and programmed to record internal body temperature ( $T_b$ ) every 10 minutes. Snakes were given a minimum of 24 hours to recover after surgery. To allow snakes to acclimate inside the gradient, individuals were placed on the gradient 24 hours before initiation of datalogging (Hertz et al. 1993). Pre-feeding  $T_b$  was recorded for three days and snakes were then fed one to two rodents totaling approximately 20% of the snake's body mass (mean $\pm$ SE= 0.081 $\pm$ 0.022 kg for all trials). Post-feeding temperatures were recorded for seven days after feeding. Not all snakes were willing to feed (11 of 28 individuals ate) and those that did not feed were removed from the study. After measuring postprandial  $T_b$  for seven-days, the dataloggers were removed and the snakes were released at their capture location after 24-48 h of recovery from surgery.

We calculated individual pre-feeding preferred body temperature range ( $T_{set}$ ) using the bounds of the central 50 percent of temperatures for the three days prior to feeding (25 and 75 quartiles; Hertz et al. 1993). Mean pre-feeding  $T_b$  was calculated using the mean  $T_b$  for the three days prior to feeding. We compared post-feeding mean  $T_b$

in 6-hour increments following feeding for a total of 28 post-feeding time increments per individual.

### ***Statistical Analysis***

We used JMP statistical software for all analysis (SAS Institute, Cary, North Carolina). Allometric relationships of body mass and  $VO_2$  were compared within and between species at the three test temperatures (20°C, 25°C, 30°C) using repeated measured ANCOVA with  $VO_2$  being predicted by body mass, temperature, species, and individual (random variable). We used repeated measures ANCOVA to determine whether digestive state (pre- or post-feeding) had a significant effect on  $VO_2$  and followed overall comparisons with pairwise Tukey-Kramer HSD post hoc comparisons to determine whether  $VO_2$  varied significantly across the seven day post-digestive period. We used ANCOVA to determine whether the response variables of peak  $VO_2$ , time to peak  $VO_2$ , factorial scope, duration of elevated oxygen consumption above SMR, SDA, and the SDA coefficient were each significantly effected by predictor variables species, temperature, or body mass. We used ordinary least squares linear regression to calculate mass-adjusted scaling exponents ( $b$ ) between  $\log_{10}$  transformed body mass and  $\log_{10}$  transformed SMR, peak  $VO_2$ , and SDA. Allometric scaling exponents were calculated for both species at each of the three test temperatures. To calculate the mass adjusted value for SMR, peak  $VO_2$ , and SDA we divided the non-mass adjusted value by the body mass of each individual raised to its temperature-species-specific scaling exponent (mass adjusted value= non-mass adjusted value/ $M^b$ , where  $M$  is body mass and  $b$  is the scaling exponent). In order to meet assumptions for parametric testing, data were log-

transformed before analysis. The level of statistical significance was  $P < 0.05$  and mean values were reported as mean  $\pm$  standard error (SE).



## RESULTS

*Effect of Temperature on the Post-feeding Metabolic Response*

As body mass and temperature increased there was a significant increase in SMR for both species (Fig.1). SMR was approximately 2.8 times greater at 25°C than 20°C and 1.1 times greater at 30°C than 25°C. Snakes fed less after a 20°C trial (33% successful feeding rate) than at a 25°C trial (65% successful feeding rate) or a 30°C trial (44% successful feeding rate;  $\text{ChiSquare}_2=4.31$ ,  $P=0.12$ ). After feeding, temperature affected peak  $\text{VO}_2$ ; as temperature increased so did peak  $\text{VO}_2$  (Table 1). Prior to adjusting for body mass in *A. contortrix*, peak  $\text{VO}_2$  was 1.5 times greater at 30°C than at 25°C compared to 1.08 times greater at 25°C than at 30°C after adjusting for body mass.

Total SDA and SDA coefficient were also affected by temperature. As temperature increased so did SDA and the SDA coefficient. After mass-adjusting SDA, this trend changed in both species, with SDA being 1.3 times higher for *A. contortrix* and 1.15 times higher for *A. piscivorus* at 25°C than 30°C. The SDA coefficient increased 2% to 4% from 25°C to 30°C. Factorial scope was positively affected by temperature, ranging from 5.65 at 25°C to 7.85 at 30°C. Time to peak  $\text{VO}_2$  was not affected by temperature. In all post-feeding analysis prey type (mouse vs. rat) was not significant ( $P<0.51$ ), therefore, we removed prey-type from our analysis and it was not included in our reported results.

*Species Comparisons; Post-feeding Metabolic Response*

There were no significant differences in SMR between species at 20, 25, or 30°C; whole-animal SMR ranged from 2.75-7.23 mL/h in *A. contortrix* and 3.39-8.54 mL/h in *A. piscivorus* (Fig. 1). *Agkistrodon contortrix* were more likely to eat at 25°C (100% successful feeding rate) than *A. piscivorus* (47% successful feeding rate), but *A. piscivorus* were more likely to eat at 30°C (55% successful feeding rate) than *A. contortrix* (45% successful feeding rate; ChiSquare<sub>2</sub>=0.182, P=0.0060). At 20°C only two *A. contortrix* ate and we report the basic statistics for those two individuals in Table 1, but they were not included in any postprandial analysis.

*Agkistrodon contortrix* and *A. piscivorus* had similar postprandial time to peak VO<sub>2</sub> and factorial scope of peak VO<sub>2</sub> between 25 and 30°C (Table 1). The SDA coefficient was different between species, with *A. piscivorus* having approximately a 1.2 times greater SDA coefficient than *A. contortrix*. After adjusting peak VO<sub>2</sub> for body mass there was a significant difference between species with *A. piscivorus* mean peak VO<sub>2</sub> (mL h<sup>-1</sup> (kg<sup>b</sup>)<sup>-1</sup>) greater at 25 and 30°C than *A. contortrix* (Fig. 2b). Duration of elevated metabolic rate after feeding was different between the species; at 25°C duration was 6 hours longer for *A. piscivorus* than *A. contortrix* (Table 1). At 30°C duration of elevated metabolic rates was 18 hours longer for *A. piscivorus* than *A. contortrix* (Table 1).

The ANCOVA for SDA response when including species, temperature, and body mass as predictor variables was significant (F<sub>4, 20</sub>=113.03, P<0.0001, r<sup>2</sup>=0.96). As body mass increased so did SDA in both species (Fig. 3a). SDA was not significantly different between the species before adjusting for body mass (Fig.3a). After adjusting SDA for body mass, species and temperature were significant (Fig.3b). SDA was 1.6 times greater at 25°C and 1.8 times greater at 30°C for *A. piscivorus* than for *A. contortrix* (Fig. 4).



### ***Species Comparisons; Post-feeding Behavioral Temperature Selection***

Pre-feeding mean  $T_b$  and  $T_{set}$  were not significantly different between the two species, with pre-feeding temperature being only 2-3°C greater in *A. contortrix* than *A. piscivorus* (Table 2). The RMANOVA for  $T_b$  response when including species, trial (pre- vs. post-feeding), and the interaction term (Species X Trial) as predictor variables was significant (Table 3). Post-feeding  $T_b$ 's were not different between the species (Fig.5), but trial period and the interaction term were significant (Table 3). After being fed, *A. piscivorus* selected temperatures that were approximately 5-6°C warmer than pre-feeding temperatures while *A. contortrix* did not select different post-feeding temperatures (Fig.6). *Agkistrodon contortrix* selected pre-feeding and post-feeding temperatures of approximately 26°C while *A. piscivorus* selected a pre-feeding temperature of 24°C and a post-feeding temperature of 29°C.

## CHAPTER IV

### DISCUSSION

*Agkistrodon contortrix* and *Agkistrodon piscivorus* standard metabolic rates positively correlated to increasing temperatures: as body temperature increases so does SMR (Andrade et al. 2005, Greene et al. 2013, Killen et al. 2016). Both species demonstrated metabolic responses to feeding that were similar to the characteristic response observed in other snakes (Secor 2009); approximately 40 to 80 hours after feeding there was a 5-8x peak increase in metabolism, which returned to pre-feeding rates within a week. The postprandial responses of the two species had similar values as other viper studies that fed a rodent 20% of the snake's body mass at either 25 or 30°C (McCue and Lillywhite 2002, Gavira and Andrade 2013). Overall, we found the two species were different in their metabolic response to feeding.

We also found that *A. contortrix* and *A. piscivorus* had differing postprandial behavioral responses in body temperature selection. The magnitude of postprandial thermophilic responses in different species and the factors that affect these responses are not well understood (Peterson et al. 1993, Dorcas et al. 1997, Andrade et al. 2005, Sievert et al. 2013). The relative differences of the postprandial thermophilic response across ectotherms are unclear because the species that have been studied do not appear to follow any patterns for post-feeding temperature selection.

#### *Temperature and Species Effects on Standard Metabolic Rate*

We found that SMR in two species of *Agkistrodon* had temperature dependent shifts, a trend reported in other studies of ectotherm metabolism (Toledo et al. 2003,

Bessler et al. 2010, Killen et al. 2010, Greene et al. 2013). As temperature increased there was approximately a 2-3 fold increase in metabolic rate for *A. piscivorus*. The magnitude of this response was similar to the 2-3 fold increase observed previously for *A. piscivorus* (McCue and Lillywhite 2002). These similar temperature dependent shifts in SMR of different populations suggest SMR is species dependent, not population dependent. In our study, for both species, as temperature increased from 20 to 25°C there was approximately a 2.1 times increase in SMR, compared to 25 to 30°C where there was only a 1.2 times increase in SMR. The magnitude of the response from 20 to 25°C partially explains some of the significant differences in SMR due to temperature. At lower temperatures ectotherms generally have decreased oxygen consumption, and this is thought to be a mechanism to conserve energy during colder periods when prey may not be as accessible (Zaidan 2003, Killen et al. 2016). At lower temperatures snakes can have an overall reduction in performance (Bessler et al. 2010) and this could explain why snakes were less willing to feed at 20°C. If performance is hindered at low temperatures, and digestion efficiency is considered a measurement of performance (Dorcas et al. 1997, Wang et al. 2003, Andrade et al. 2005), then hindered performance could be an explanation for low SMR at cooler temperatures.

After accounting for differences in body mass, *A. contortrix* had higher SMR than *A. piscivorus* at 20, 25, and 30°C. The observed differences could be related to the species-specific activity levels when foraging for prey. Actively foraging snakes tend to have higher metabolic rates than less actively foraging snakes (Secor and Diamond 2000). This may be due, in part, to actively foraging snakes eating smaller meals more often, while less actively foraging snakes (ambush/ sit and wait snakes) eat larger meals



less often (Secor and Diamond 2000). Both *Agkistrodon* species are considered sit and wait predators (in contrast to actively foraging predators) but *A. contortrix* are more active than other sit and wait viper species (Beaupre and Montgomery 2007).

Studies have started taking into account ecological variables that affect metabolism. For example, Thompson and Withers (1997) measured nine goanna species that were either arboreal or terrestrial and concluded that arboreal goannas had higher metabolic rates than similar-sized terrestrial goannas. They speculated that higher rates of metabolism in arboreal species might be due to more rapid movement vertically than experienced by species in terrestrial habitats. Killen et al. (2016) found pelagic teleost fishes had higher metabolic rates than benthic or benthopelagic fishes due to their increased locomotor performance relative to more benthic species. We found that a terrestrial species, *A. contortrix*, had a slightly higher SMR at three temperatures than a semi-aquatic species, *A. piscivorus*. A higher metabolism may support higher activity levels (Burton et al. 2011). Given that terrestrial *A. contortrix* are more active than semi-aquatic *A. piscivorus* (Beaupre and Montgomery 2007), this difference in activity may account for the subtle differences in the species-specific metabolic rates observed. Our study on *Agkistrodon*, the study on goannas, and the study on teleost fishes support metabolic differences between species with different habitat use. None of these studies test what specifically in habitats causes differences in metabolism. The studies only offered possible explanations to differences related to their habitat that may be causing metabolic differences. Further studies concerning differences in species because of their occupation of different habitats (such as a semi-aquatic species hunting in water versus a

terrestrial species hunting on land), could help elucidate specific ecological effects on metabolism.

### ***Species Effects on Post-feeding Metabolism and SDA***

The postprandial profiles between *A. contortrix* and *A. piscivorus* were different. Temperature had an effect on all postprandial variables except time to peak  $\text{VO}_2$  and mass adjusted peak  $\text{VO}_2$ . When we compared these *Agkistrodon* species to other vipers such as *Bothrops alternatus*, fed rodents 20% of their body mass at 30°C (scope= 6.25, duration= 107 hours, and SDA coefficient= 20.93%) (Gavira and Andrade 2013), and *Crotalus horridus*, fed rodents 30% of their body mass at 30°C (scope= 6.46, duration= 130 hours) (Zaidan and Beaupre 2003), there were similar postprandial patterns. At higher temperatures peak  $\text{VO}_2$  increased; a similar trend seen in other reptiles (Andrade et al. 2005), amphibians (Secor and Faulkner 2002, Secor and Boehm 2006), and fishes (Luo and Xie 2008).

After feeding there was a difference between *A. contortrix* and *A. piscivorus* mass-adjusted peak  $\text{VO}_2$ , SDA, and SDA coefficient at 25 and 30°C but no differences in duration of elevated metabolism. Generally in amphibian and snake species, as  $T_b$  increases the duration of elevated metabolism decreases and the peak  $\text{VO}_2$  increases (Wang et al. 2003, Zaidan and Beaupre 2003, Ott and Secor 2007, Tsai et al. 2009, Greene et al. 2013). The increase in peak  $\text{VO}_2$  is balanced by a shorter duration of elevated metabolism (Wang et al. 2003). *Agkistrodon contortrix* and *A. piscivorus* had an increase in peak  $\text{VO}_2$  balanced by a shorter duration of elevated metabolism at higher temperatures. *Agkistrodon contortrix* had a 30% decrease in duration of elevated metabolism from 25 to 30°C and *A. piscivorus* had a 22% decrease. Comparable to both

focal *Agkistrodon* species, *Crotalus horridus* exhibited a 22% decrease in duration from 25°C to 30°C (Zaidan and Beaupre 2003). There have also been recorded decreases in postprandial duration of elevated metabolism at higher temperatures in amphibians (Secor and Faulkner 2002, Secor and Boehm 2006), fishes (Jobling and Spencer Davies 1980), and crustaceans (Whiteley et al. 2001). South-central Florida *A. piscivorus* fed a meal at 25°C had a duration of elevated postprandial metabolism at 221 hours (McCue and Lillywhite 2002). This is longer than our study's duration of elevated postprandial metabolism at the same temperature. A possible explanation is that oxygen consumption increases with decreasing latitude (Zaidan III 2001). Thus, our study's *A. piscivorus* duration of elevated postprandial metabolism from Northern Tennessee were moderate in comparison to South-central Florida *A. piscivorus*. These temperature-dependent shifts in duration of elevated postprandial metabolism may be indicative of a behavioral postprandial thermophilic response that reduces or increases the speed of digestion (Wang et al. 2003).

The SDA coefficient (energy expended towards SDA) was 19-22% of energy that *A. contortrix* could gain from a meal and 22-26% in *A. piscivorus*. This difference between species was significant and is different when compared to other reptiles fed flesh meals: 32% in *Python molurus* (Secor and Diamond 1995), 30% in *Kinixys spekii* (Hailey 1998), and 21% in *Varanus exanthematicus* (Hartzler et al. 2006). This suggest that species and other factors such as food type (McCue et al. 2005), meal size (Secor and Faulkner 2002), and temperature are significant when calculating the SDA coefficient. In this study, as temperature increased SDA decreased and the SDA coefficient increased, comparable with other snakes (Hailey and Davies 1987, Tsai et al. 2009) and amphibians



(Powell et al. 1999, Secor and Boehm 2006). This means as temperature increased there was less energy being used to breakdown and assimilate the meal (SDA) counterbalanced by less energy being gained from the meal (SDA coefficient). The magnitude of this trade-off may be related to different temperature related postprandial behavioral strategies.

We found that after adjusting for body mass, both species had a greater SDA at 25°C than 30°C, a trend recorded in *Python molurus* (Toledo et al. 2003) and *Bufo marinus* (Secor and Faulkner 2002). Mass adjusted SDA was different between the species, with *A. piscivorus* having higher SDA at 25°C and 30°C than *A. contortrix*. This could reflect adaptations to different habitats. Differing SDA responses are mechanically affected by differences in the physical shape of the digestive tract of an animal (Secor and Diamond 1995, Secor 2008). The shape and function of the digestive tract is adapted to species-specific food and feeding habits (Secor 2005).

Secor and Diamond (2000) found that feeding habits, specifically feeding frequency and size of the meal, are relevant predictors of SDA and other postprandial responses. They found that infrequent feeding snakes (snakes that feed on large meals less often), digest meals more slowly, have lower metabolic rates, have higher absolute energy expenditure during digestion, and have higher postprandial increases in metabolic rate compared to frequently feeding snakes (snakes that feed on small meals more often). In our study, *A. piscivorus* followed all four of the infrequent feeder criteria when compared to *A. contortrix*. Both of these species are vipers and are considered infrequent feeding snakes when compared to other snake families. When comparing these two *Agkistrodon* species to each other, our results suggest that *A. contortrix* feed more

frequently on smaller prey than *A. piscivorus*. Feeding frequency differences are possible when comparing *A. contortrix* which feed in a terrestrial habitat on predominantly mice (Garton and Dimmick 1969, Ernst and Ernst 2003) to *A. piscivorus* which feed in an aquatic habitat on approximately 60% fish (Ernst and Ernst 2003, Gibbons and Dorcas 2005). When striking in a water medium at a fish *Agkistrodon* have a 13% catch success rate versus a 95% catch success rate when striking terrestrially at a mouse (Vincent et al. 2005). Movement uses energy (Ruben 1976, Walton et al. 1990, Secor et al. 1992), so *A. piscivorus* might be compensating for the energy used towards failed strikes by catching larger fish during successful strikes. *Agkistrodon contortrix* would not need to compensate for many failed strikes, so energetically they could afford to eat smaller meals more often than *A. piscivorus*. The results from our study support feeding frequency differences between *A. contortrix* and *A. piscivorus* likely as a result of hunting in different mediums related to habitat (aquatic versus terrestrial).

### ***Species Effects on Post-feeding Temperature Selection***

Snakes often control their  $T_b$  by selecting different temperatures within their environment. In this study we found that feeding also influences the behavioral temperature selection response in snake species. Within three days after being fed, *A. piscivorus* selected 5-6°C higher temperatures than before feeding. In contrast, *A. contortrix* did not select significantly higher temperatures after feeding. Touzeau and Sievert (1993) discussed multiple studies on snakes and their postprandial thermophily, concluding that snakes that have pre-feeding body temperatures less than 28°C tend to select warmer post-feeding temperatures. Presumably, the benefits of increasing postprandial  $T_b$  are to reduce the time required for digestion, which in turn may reduce

predation risk (Wang et al. 2003, Tsai and Tu 2005). However, *A. contortrix*, in this study, *Nerodia sipedon* (Brown and Weatherhead 2013), *Nerodia rhombifera* (Ming-chung and Hutchison 1995), and *Thamnophis sirtalis* (Kitchell 1969) did not select warmer post-feeding temperatures when tested in a laboratory thermal gradient. These species may choose to remain more cryptic because movement increases the risk of being seen by a predator (Steinberg et al. 2014) especially if they have a stomach full of food. *Agkistrodon piscivorus* in our study, *Opheodrys aestivus* (Touzeau and Sievert 1993), *Heloderma suspectum* (Gienger et al. 2013), and *Trimeresurus stejnegeri* (Tsai and Tu 2005) are all arguably cryptic as well, but they selected warmer postprandial temperatures in a gradient. There does not appear to be any obvious patterns between ectotherms that select or do not select warmer post-feeding temperatures. Further studies on postprandial thermal responses to feeding between species are needed to clarify adapted ecologically related patterns in postprandial thermal behavior.

### ***Post-feeding Temperature Selection and Duration of the Metabolic Response***

Overall there were differences in postprandial metabolism and postprandial temperature selection between the two focal *Agkistrodon* species. However, there was no observable pattern between postprandial physiology and behavior. *Agkistrodon piscivorus* selected post-feeding temperatures of 29°C; physiologically they had a shorter duration of elevated metabolism after feeding at 30°C than 25°C. *Agkistrodon contortrix* selected post-feeding temperatures of 26°C; physiologically they had a longer duration of elevated metabolism after feeding at 25°C than at 30°C. In past studies it was suspected that snakes selected higher post-feeding temperatures to shorten digestive duration time which could provide decreased risk of predation (Wang et al. 2003, Andrade et al. 2005)



and/or may provide enhanced efficiency of digestion (Hailey and Davies 1987, Sievert and Andreadis 1999).

Our study suggests that not all species select warmer post-feeding temperatures even when physiologically there is a shorter duration of elevated postprandial metabolism, as observed in *A. contortrix*. Tsai et al. (2009) used a bioenergetic model to predict maximum net energy gain through postprandial body temperature selection in *Trimeresurus stejnegeri* (Chinese green tree viper) and concluded that this species selects increased postprandial temperatures to maximize net energy intake from a meal. If this trend carries across to the two viper species in our study, then our results suggest that *Agkistrodon* species have different post-feeding temperatures that provide maximal net energy assimilation. Future studies that further examine postprandial temperature patterns between species and how it affects efficiency of digestion will elucidate whether a snake's environment affects its ability to maximize net energy gained from meals.

Variable	20°C		25°C		30°C		Species		Temp.	
	<i>A. contortrix</i>	<i>A. piscivorus</i>	<i>A. contortrix</i>	<i>A. piscivorus</i>	<i>A. contortrix</i>	<i>A. piscivorus</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<u>Pre-feeding</u>										
<i>N</i>	12	10	17	23	18	19	-	-	-	-
Body mass (kg)	0.25 ± 0.05	0.30 ± 0.04	0.24 ± 0.03	0.29 ± 0.03	0.22 ± 0.02	0.27 ± 0.02	-	-	-	-
SMR (mL O <sub>2</sub> h <sup>-1</sup> )	2.75 ± 0.34	3.39 ± 0.44	6.58 ± 0.95	6.20 ± 0.71	7.23 ± 0.60	8.54 ± 0.74	0.76	0.39	87.31	<0.0001
SMR (mL O <sub>2</sub> h <sup>-1</sup> (kg <sup>b</sup> ) <sup>-1</sup> )	7.14 ± 0.51	6.98 ± 0.52	22.09 ± 2.62	17.18 ± 1.26	21.81 ± 1.05	20.68 ± 1.42	2.79	0.10	120.36	<0.0001
<u>Post-feeding</u>										
<i>N</i>	2	0	6	6	5	6	-	-	-	-
Body mass (kg)	0.35 ± 0.22	N/A	0.23 ± 0.05	0.23 ± 0.05	0.20 ± 0.03	0.32 ± 0.05	0.84	0.37	0.53	0.47
Peak VO <sub>2</sub> (mL O <sub>2</sub> h <sup>-1</sup> )	23.64 ± 11.50	N/A	30.82 ± 5.80	33.07 ± 9.06	46.71 ± 4.27	71.69 ± 12.52	0.01	0.91	66.26	<0.0001
Peak VO <sub>2</sub> (mL O <sub>2</sub> h <sup>-1</sup> (kg <sup>b</sup> ) <sup>-1</sup> )	53.35 ± 0.08	N/A	116.64 ± 5.58	157.8 ± 10.1	108.4 ± 7.30	212.78 ± 10.2	45.76	<0.0001	3.05	0.10
Time to Peak VO <sub>2</sub> (hrs)	77.38 ± 18.95	N/A	67.19 ± 17.07	41.20 ± 2.72	31.09 ± 2.07	53.95 ± 9.18	0.0001	0.99	1.70	0.21
Scope (peak VO <sub>2</sub> /SMR)	6.81 ± 0.34	N/A	5.65 ± 0.85	6.14 ± 0.55	6.97 ± 0.49	7.85 ± 0.57	0.80	0.38	5.54	0.03
Duration (hrs)	108	N/A	162	168	114	132	-	-	-	-
SDA (kJ)	38.49 ± 18.38	N/A	65.74 ± 13.39	80.48 ± 21.6	70.50 ± 6.58	124.31 ± 21.0	1.76	0.20	8.93	0.0076
SDA (kJ (kg <sup>b</sup> ) <sup>-1</sup> )	85.13 ± 0.12	N/A	282.02 ± 10.9	449.21 ± 22.9	218.2 ± 3.00	390.36 ± 10.9	186.54	<0.0001	25.52	<0.0001
SDA coeffi. (%)	8.63 ± 1.79	N/A	19.25 ± 0.57	22.56 ± 1.42	22.44 ± 0.64	26.43 ± 0.87	4.79	0.04	6.02	0.02

**Table 1:** Comparison of metabolic rates among species (*Agkistrodon contortrix* and *A. piscivorus*), temperatures (20, 25, and 30°C), and feeding treatment (pre and post-feeding). Post- 20°C results were not included in analysis because only two snakes ate at that temperature. Variables are defined in the text. Values are means ± s.e.m.



Variable	Gradient		Species	
	<i>A. contortrix</i>	<i>A. piscivorus</i>	<i>F</i>	<i>P</i>
<u>Pre-feeding</u>				
<i>N</i>	7	4	-	-
Body mass (kg)	0.27 ± 0.05	0.67 ± 0.26	3.63	0.09
Mean <i>T<sub>b</sub></i> (°C)	26.9 ± 0.6	23.7 ± 1.5	3.32	0.11
<i>T<sub>set</sub></i> (°C), 25%	25.2 ± 0.6	22.9 ± 1.8	2.79	0.13
<i>T<sub>set</sub></i> (°C), 75%	26.6 ± 0.8	24.1 ± 1.6	2.75	0.13
<u>Post-feeding</u>				
Mean <i>T<sub>b</sub></i> (°C)	26.4 ± 0.7	28.6 ± 0.6	5.23	<b>0.05</b>
<i>T<sub>set</sub></i> (°C), 25%	26.4 ± 0.8	28.9 ± 0.6	6.01	<b>0.04</b>
<i>T<sub>set</sub></i> (°C), 75%	26.8 ± 0.8	29.9 ± 0.8	5.44	<b>0.05</b>
Peak <i>T<sub>b</sub></i> (°C)	30.3 ± 1.0	31.0 ± 1.0	0.25	0.63
Time to Peak, <i>T<sub>b</sub></i> (hrs)	72.57 ± 18.82	43.96 ± 9.56	0.23	0.63
Scope (peak <i>T<sub>b</sub></i> /Pre- Mean)	1.2 ± 0.1	1.3 ± 0.1	3.39	0.09

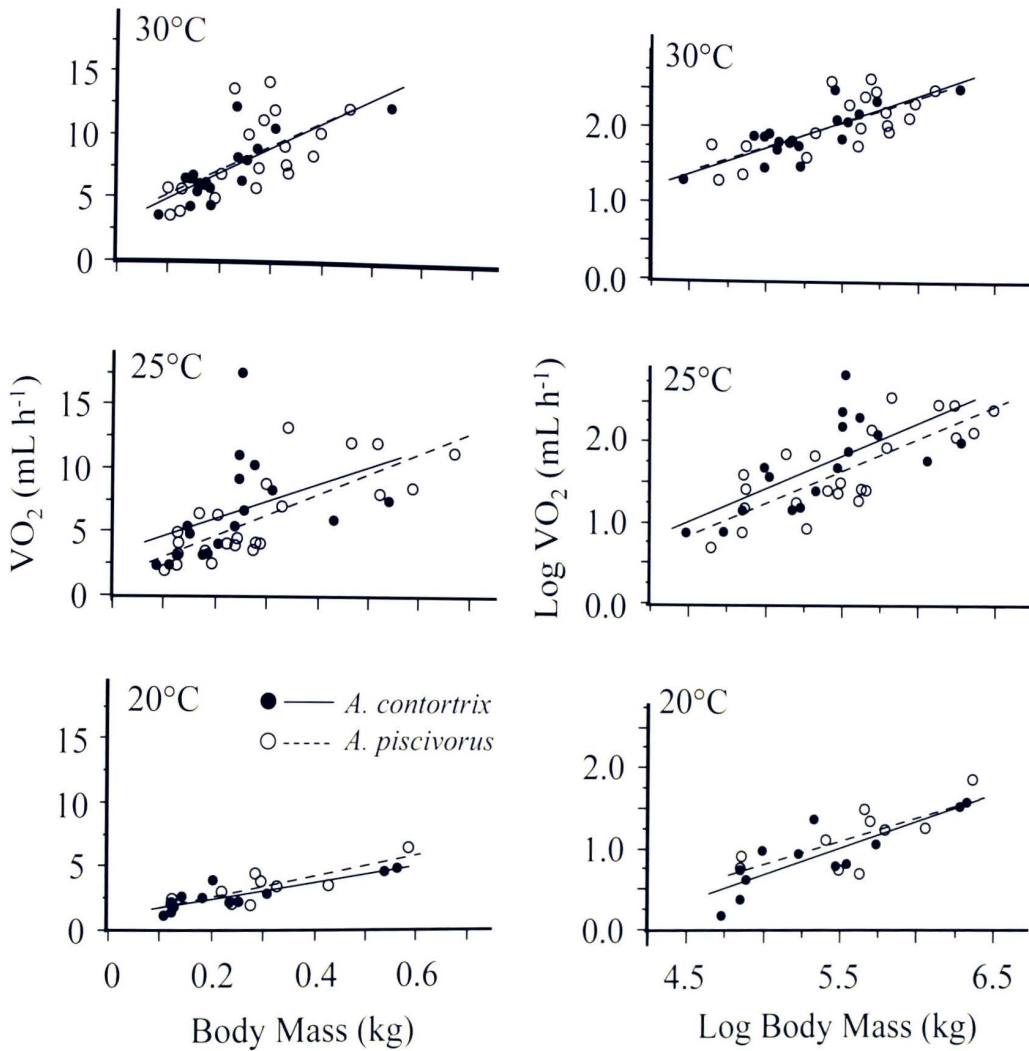
**Table 2:** Comparison of body temperature selection in response to feeding between *Agkistrodon contortrix* and *A. piscivorus*. Pre-feeding represents calculations for the 3 days before feeding and Post-feeding represents calculations for the first 3 days after feeding. Values are mean ± s.e.m.

Variable	Species		Trial		Species X Trial		RMANOVA		
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>r</i> <sup>2</sup>	<i>t</i>	<i>P</i>
Pre- vs Post-									
Mean <i>T<sub>b</sub></i> (°C)	0.0008	0.98	20.29	<b>0.0015</b>	15.76	<b>0.0033</b>	0.82	51.12	<b>&lt;0.0001</b>
<i>T<sub>set</sub></i> (°C), 25%	0.0004	0.99	20.24	<b>0.0015</b>	13.02	<b>0.006</b>	0.79	48.23	<b>&lt;0.0001</b>
<i>T<sub>set</sub></i> (°C), 75%	0.06	0.81	19.89	<b>0.0016</b>	16.26	<b>0.003</b>	0.83	43.64	<b>&lt;0.0001</b>

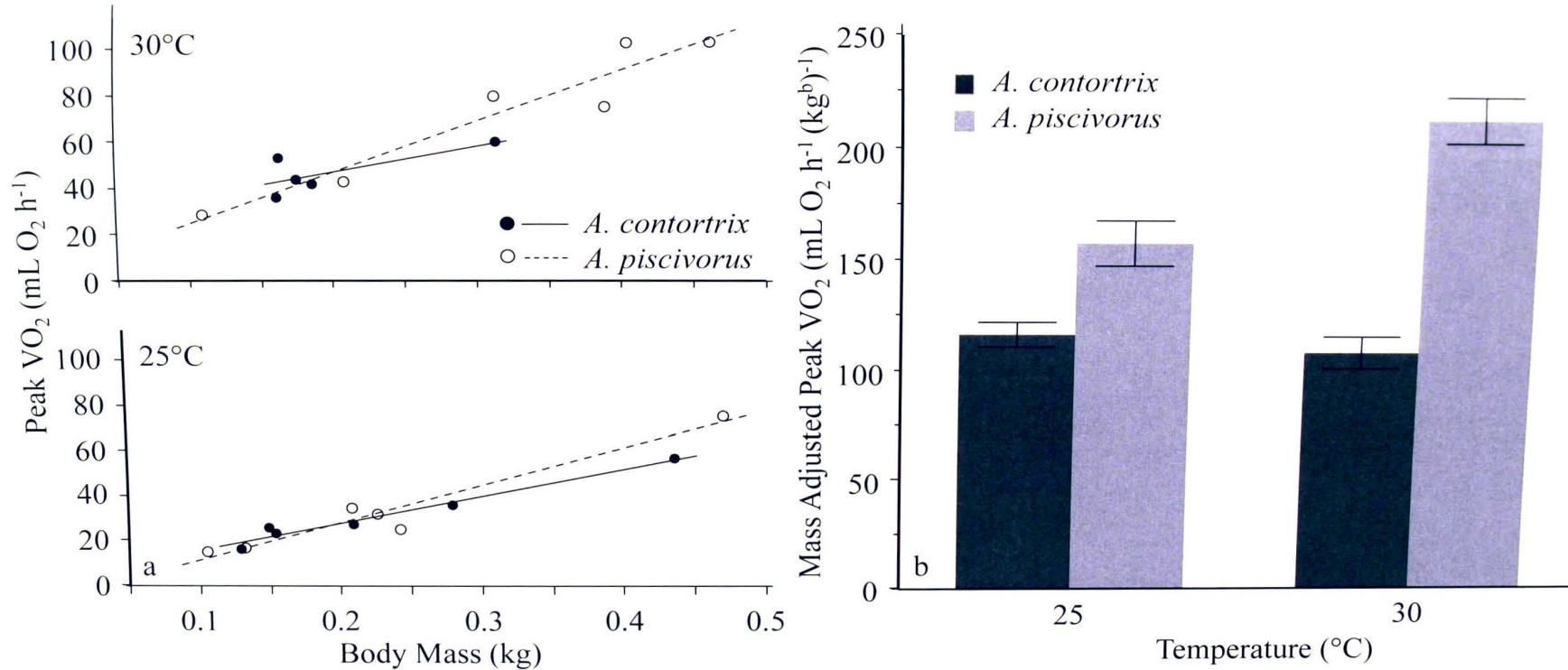
**Table 3:** Repeated measures ANOVA results comparing *Agkistrodon contortrix* and *A. piscivorus* pre- vs. post-feeding *T<sub>b</sub>*. The ‘Pre-’ represents calculations for the 3 days before feeding. The ‘Post-’ represents calculations for the first 3 days after feeding. The interaction term between species and trial was significant because *A. piscivorus* had a significantly higher post-feeding *T<sub>b</sub>* than pre-feeding *T<sub>b</sub>*.

## CHAPTER VI

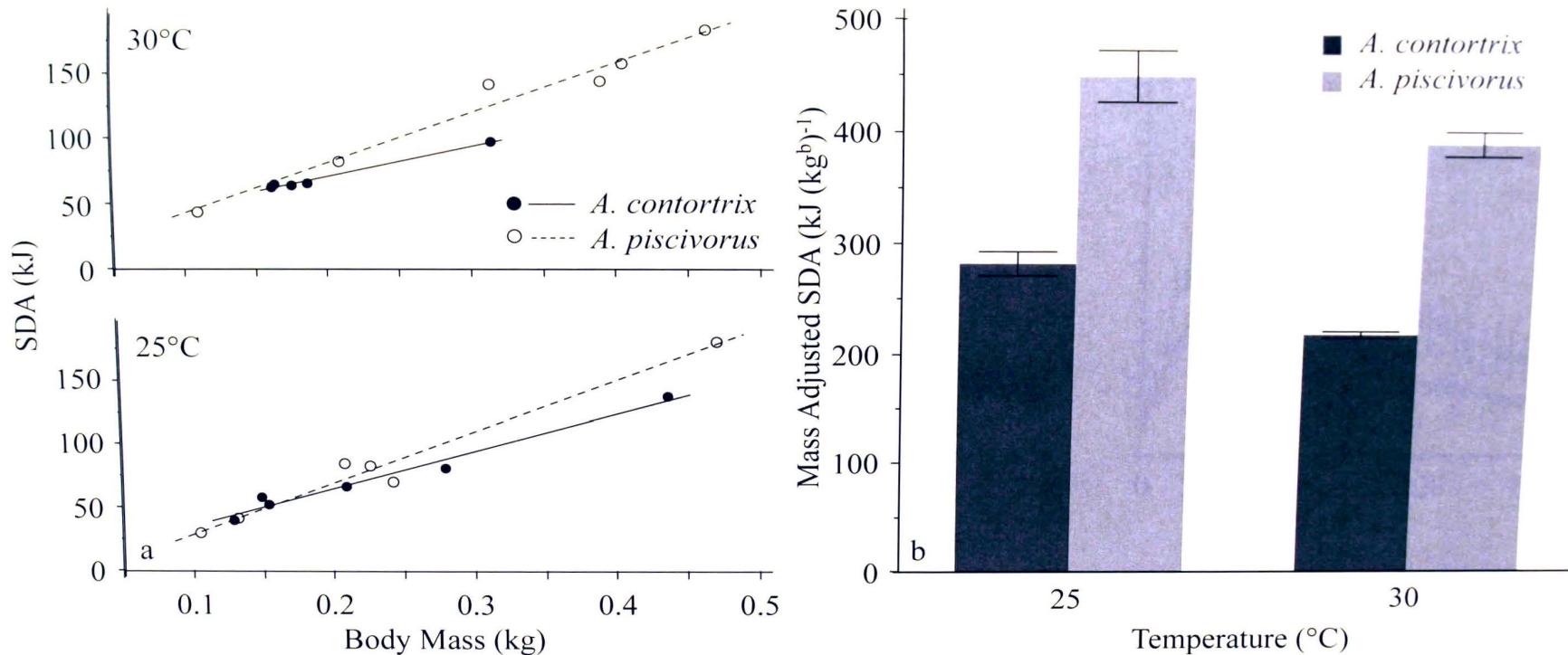
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**Fig. 1:** Standard metabolic rate (SMR) for *Agkistrodon contortrix* and *A. piscivorus*. As body mass and temperature increased there was a significant increase in SMR for both species. Species were not significantly different from each other at 20, 25, or 30°C.

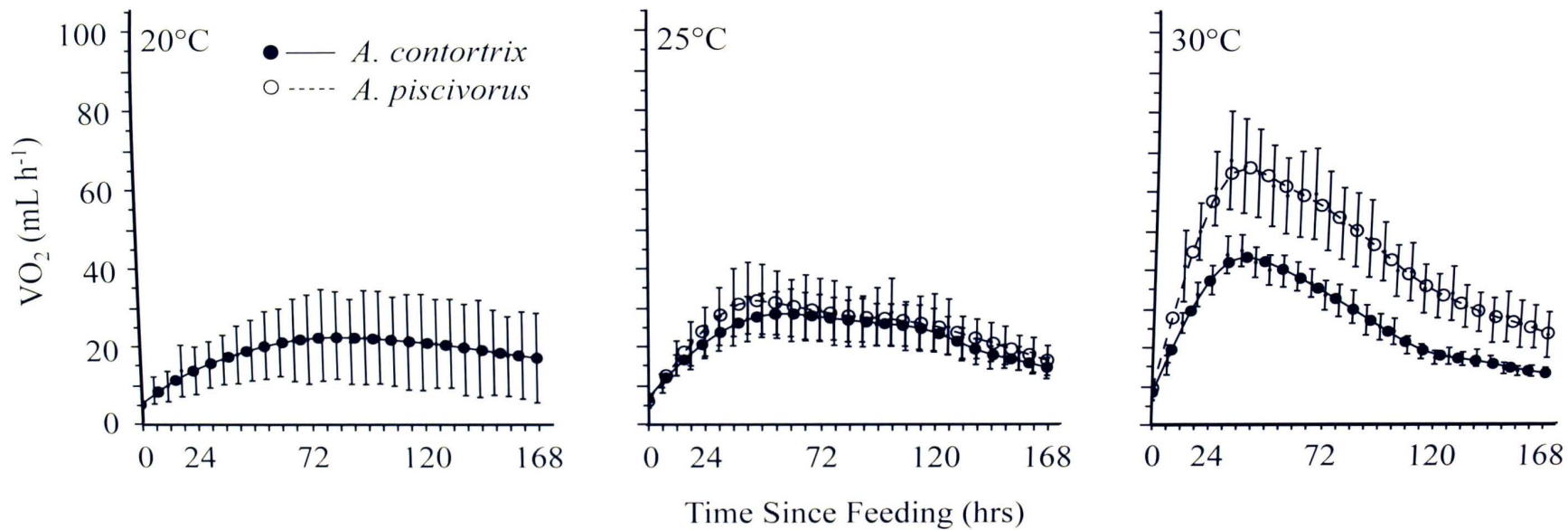


**Fig. 2:** a) Peak  $\text{VO}_2$  for *Agkistrodon contortrix* and *A. piscivorus* at 25 and 30°C after being fed a rodent meal approximately 20% of their body mass. Species were not significantly different from each other before b) adjusting for mass. After adjusting for body mass, species were significantly different from each other. Error bars are  $\pm 1$  SE.

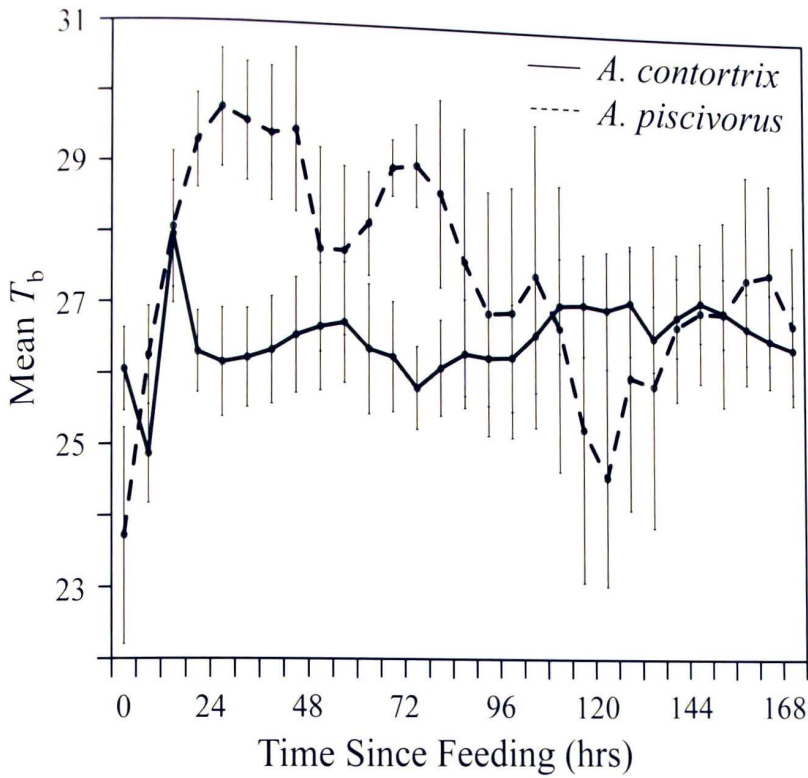


**Fig. 3:** a) Total SDA for *Agkistrodon contortrix* and *A. piscivorus* at 25 and 30°C after being fed a rodent approximately 20% of their body mass. Species were not significantly different from each other before b) adjusting for mass. After adjusting for body mass, species were significantly different from each other. Error bars are ±1 SE.

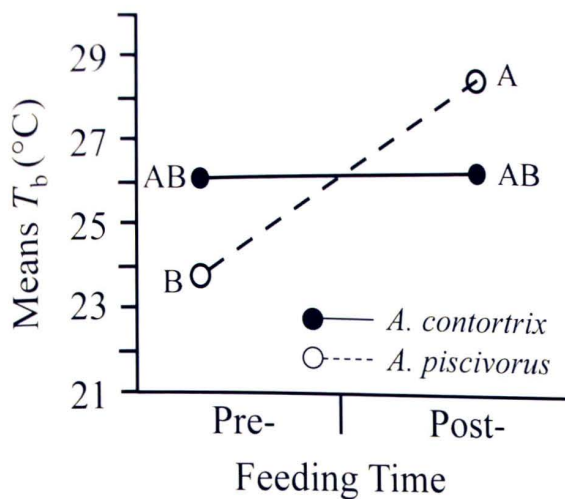




**Fig. 4:** SDA curves for *Agkistrodon contortrix* and *A. piscivorus* after being fed a rodent meal of approximately 20% of their body mass (20, 25, and 30°C). Error bars are  $\pm 1$  SE.



**Fig. 5:** Postprandial body temperatures ( $T_b$ ) for seven days after feeding of a rodent approximately 20% of the snakes body mass for *Agkistrodon contortrix* and *A. piscivorus*. Mean pre-feeding body temperature is represented at time 0. Pre-feeding  $T_b$  was not significantly different between species. *Agkistrodon contortrix* did not have a significant difference between pre- and post-feeding but *A. piscivorus* did have a significant increase in mean  $T_b$ . Analysis on post-feeding temperatures only included the first three days post-feeding. Error bars are  $\pm 1$  SE.



**Fig. 6:** Least squares mean body temperatures for *Agkistrodon contortrix* and *A. piscivorus* pre- and post-feeding. Analysis on post-feeding temperatures only included the first three days post-feeding. Points that do not share the same letter are significantly different (Tukey-Kramer HSD).

## CHAPTER VII

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