Comparative Biochemistry and Physiology, Part A 169 (2014) 60–69

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Determinants and repeatability of the specific dynamic response of the corn snake, *Pantherophis guttatus*

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ARTICLE INFO

Article history:
Received 5 October 2013
Received in revised form 1 December 2013
Accepted 10 December 2013
Available online 17 December 2013

Keywords:
Digestion
Metabolic rate
Pantherophis
Snake
Specific dynamic action

ABSTRACT

Ingesting, digesting, absorbing, and assimilating a meal are all energy consuming processes that accumulate to form the specific dynamic action (SDA) of the meal. Sensitive to digestive demand, SDA is theoretically fixed to a given meal size and type. In this study, we altered relative meal size to explore the effects of digestive demand on the postprandial metabolic profile and SDA of the corn snake, *Pantherophis guttatus*. We also examined the effects of body temperature on the SDA response while controlling for meal size and type and assessed whether these responses are highly repeatable under the same conditions. Additionally, the effects of body mass on SDA were investigated by feeding snakes the same relative and absolute meal size. With increases in digestive demand (meals from 5% to 45% of body mass), *P. guttatus* responded with incremental increases in the postprandial peak in oxygen consumption ($\dot{V}O_2$), the duration of the significantly elevated $\dot{V}O_2$, and SDA. Body temperature had an observable impact on the postprandial metabolic profile, decreasing the duration and increasing the peak $\dot{V}O_2$, however, body temperature did not significantly alter SDA. Regardless of temperature, and hence duration, snakes expended the same amount of energy in digesting a given meal. This was additionally borne out when testing the individual repeatability of the SDA response, individual *P. guttatus* exhibited nearly identical postprandial responses to the same meal. Over a 90-fold range in body mass, and fed meals equaling 25% of body mass, *P. guttatus* exhibited an isometric relationship between SDA and body mass. When fed a set 10-gram meal, snakes regardless of body size expended the same amount of energy on digestion and assimilation. Characteristically, *P. guttatus* experience a rapid postprandial increase in metabolic rate that peaks and gradually descends to prefeeding levels. The magnitude of that response (quantified as SDA) varies as a function of digestive demand (i.e., meal size); however, when demand is fixed, SDA is constant regardless of body temperature and body size.

1. Introduction

There is no such thing as a free meal. Each step of chewing, swallowing, digesting, absorbing, and assimilating a meal requires the expenditure of energy (Tandler and Beamish, 1979; Secor, 2009). The cumulative energy expended on these activities is termed specific dynamic action (SDA), and is observed as a postprandial increase in heat production and metabolic rate (Secor, 2009). The individual processes contributing to SDA include gut peristalsis, gastric acid production, pancreatic enzyme and bicarbonate secretion, intestinal transport, and the postabsorptive synthesis of macromolecules (e.g., glycogen and protein) (reviewed in Secor, 2009). Equivalent to 10–30% of the gross ingested energy, SDA is a potentially significant component of an animals' daily energy expenditure, and is known to contribute to 16–43% of a free-ranging snake's daily energy budget (Secor and Nagy, 1994; Peterson et al., 1998; Christian et al., 2007; Bessler et al., 2010). Variations in SDA are attributed to differences in meal size, meal type, body temperature, body size, and feeding habits (Secor and Diamond, 2000; Secor and Faulkner, 2002; Fu et al., 2005; Secor et al., 2007; Bessler et al., 2010).

It is well described that any change in a meal that increases the workload of digestion and assimilation results in a greater SDA (Secor, 2009). An increase in meal size and meal toughness will require more effort, and hence more energy expended, for meal break down and absorption (Secor and Boehm, 2006; Secor et al., 2007). Especially for ectotherms, any shift in environmental and thus body temperatures will impact metabolic rate and the rate of meal digestion and assimilation. A rise in body temperature will speed up digestion and shorten the duration of the postprandial metabolic response (Wang et al., 2003; Luo and Xie, 2008; Bessler et al., 2010). Mixed among studies is whether the SDA of a given meal varies or is held constant across a range of body temperatures (Jobling and Davies, 1980; Hailey and Davies, 1987; Secor et al., 2007; Luo and Xie, 2008). Temperature-dependent variation in SDA could indicate that there is an optimal range of temperatures that minimize the energy expended on digestion and assimilation. However, a constant SDA supports the hypothesis that regardless

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http://dx.doi.org/10.1016/j.cbpa.2013.12.008

of temperature and rate of digestion, the same amount of energy is expended on the digestion and absorption of a given meal (Secor et al., 2007).

If the digestion of a given meal entails the same set of energy-consuming events involved in the motility, breakdown, absorption, and assimilation of the meal, then expectedly the resulting postprandial metabolic response and SDA would be highly repeatable. An individual would invest the same amount of energy when meal size, meal type, and body temperature are held constant. Whereas, metabolic rates characteristically scale allometrically with body mass, SDA has been found to scale isometrically with body mass when relative meal size, meal type, and body temperature are held constant (Peters, 1983; Schmidt-Nielsen, 1984; Secor and Diamond, 1997; Secor and Faulkner, 2002). This suggests that regardless of body size, the same amount of energy is expended to digest and assimilate meals of the same type and size.

We undertook this study to address these predictions of SDA using the corn snake (*Pantherophis guttatus*). We quantified the postprandial metabolic response and SDA of corn snakes under different treatments to test whether: (1) an increase in digestive work load generates a larger SDA response; (2) altering body temperature impacts the profile of the postprandial metabolic response, but does not vary SDA; (3) SDA is highly repeatable when controlling for meal type, size, and body temperature; and (4) SDA is dictated by meal size and scales isometrically with body mass. Our predictions held in all cases: (1) an increase in meal size, and hence digestive demand, was matched by an increase in SDA; (2) SDA did not significantly vary across temperature treatments; (3) SDA was highly repeatable; and, (4) SDA scaled isometrically with body mass.

2. Materials and methods

2.1. Snakes and their maintenance

P. guttatus is a medium-sized colubrid snake that occupies terrestrial habitats of the southeastern United States, feeding mainly on small mammals and birds (Conant and Collins, 1998; Ernst and Ernst, 2003). The 15 individuals used in this study were captive bred and ranged in mass from 8.4 to 753 g. Snakes were housed individually in 14-L plastic containers, maintained at 25 °C, and exposed to a photoperiod of 14L:10D. They were fed rodents weekly and had access to water ad libitum. All individuals were fasted for one month prior to experimentation to ensure that all digestive and postabsorptive activities had concluded. Animal care and experimentation was conducted with the approval of the University of Alabama Institutional Animal Care and Use Committee.

2.2. Measurements of gas exchange

We measured rates of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) of fasted and fed snakes using closed-system respirometry as described by Vleck (1987) and Secor and Diamond (1997). Snakes were placed individually into respirometry chambers (0.7–4.5 L) fitted with incurrent and excurrent air ports, each connected to a three-way stopcock. Respirometry chambers were placed into an environmental chamber (model DS54SD; Powers Scientific, Pipersville, Pennsylvania, USA), set at a constant target temperature (±0.5 °C), with ambient air constantly pumped through the respirometry chambers. For each metabolic trial, an initial 45-mL air sample was pulled from the excurrent port and both incurrent and excurrent ports were closed. An hour later, the excurrent port was opened and a second 45-mL sample was drawn. Air samples were pumped (75 mL min^{-1}) through a column of water absorbent (Drierite) into a CO_2 analyzer (CD-3A, AEI Technologies, Pittsburg, Pa.) and through a column of Drierite and CO_2 absorbent (Ascarite) into an O_2 analyzer (S-3A/II, AEI Technologies). Oxygen and CO_2 content of chambers did not drop below 19% or rise above 2%, respectively. We calculated whole animal (mL h^{-1}) and mass specific (mL g^{-1} h^{-1}) rates of gas exchange ($\dot{V}O_2$ and $\dot{V}CO_2$) corrected for standard pressure and temperature using a modification of Eq. (9) of Vleck (1987).

For each target temperature, we determined each snake's standard metabolic rate (SMR) from measurements of gas exchange prior to feeding. For SMR trials, gas exchange was measured in the morning (~0700) and evening (~1900) for four consecutive days. For each individual, SMR was assigned as the mean of the two lowest measured $\dot{V}O_2$ (Bessler et al., 2010). Following SMR trials, snakes were fed rodent meals equaling a target percentage of their body mass. Snakes were then returned to the respirometry chambers and measurements of gas exchange were continued at 12-h intervals for 3 days and thereafter at 24-h intervals for the following 4–10 days.

2.3. Experimental procedure

We determined individual effects of meal size and body temperature on the postprandial metabolic response and SDA of *P. guttatus* using the following procedures. Meal size effects were investigated at 30 °C by feeding snakes rodent meals (neonatal mice to small rats) equaling in mass to targeted percentages (5%, 15%, 25%, 35%, and 45%) of snake body mass. Temperature effects were assessed at 20, 25, 30, and 35 °C for snakes that had consumed rodent meals equaling in mass to 25% of their body mass. To examine the repeatability of individual postprandial metabolic responses and SDA, we measured gas exchange rates for three trials where the same set of nine snakes were fed 25%-size meals and maintained at 30 °C. We employed two methods to explore body size effects on postprandial metabolism and SDA. First, snakes were fed rodent meals equaling in mass to 25% of their body mass, thereby holding constant relative meal size (Secor and Diamond, 1997). Second, snakes were fed juvenile mice each weighing 10 g, thereby holding constant absolute meal size.

2.4. Quantifying the SDA response

For each metabolic trial, we quantified the following seven variables as described by Secor (2009): SMR (mean of the two lowest $\dot{V}O_2$ prior to feeding), peak $\dot{V}O_2$ (highest recorded $\dot{V}O_2$ after feeding), factorial scope of peak $\dot{V}O_2$ (calculated as peak $\dot{V}O_2$ divided by SMR), respiratory exchange ratio (RER; quantified as $\dot{V}CO_2/\dot{V}O_2$ at peak $\dot{V}O_2$), duration (time from feeding until $\dot{V}O_2$ was no longer significantly greater than SMR), SDA (total energy expended about SMR over the duration of elevated $\dot{V}O_2$), and SDA coefficient (SDA as a percentage of meal energy). SDA (kJ and kJ kg^{-1}) was quantified as the product of the summed extra O_2 consumed (mL) above SMR during the duration of the significantly elevated $\dot{V}O_2$ and 19.8 J, assuming 19.8 J is expended per mL of O_2 consumed given that the dry matter of the meal is 70% protein, 25% fat, and 5% carbohydrate and generates a respiratory quotient of 0.73 (Gessman and Nagy, 1988).

Energy content of each meal type was determined by bomb calorimetry. Five samples of each meal type (particular size mouse or rat) were weighed (wet mass), dried to a constant mass at 60 °C, reweighed (dry mass), ground to a fine powder, and pressed into pellets. Three pellets of each sample were ignited in a bomb calorimeter (model 1266; Parr Instruments, Moline, IL, USA) to determine energy content. For each meal type, we determined wet mass energy equivalent (kJ g^{-1}) as the product of dry mass energy content and the meal's dry mass percentage (Table 1). Each meal's energy content was calculated as the product of meal mass and wet mass energy equivalent.

2.5. Statistical analysis

For each metabolic trial, we used repeated measures design analysis of variance (ANOVA) to test for significant effects of time (before and after feeding) on $\dot{V}O_2$, $\dot{V}CO_2$, and RER. Each ANOVA was accompanied

Table 1
Wet mass, dry mass, percent dry mass, and energy content of 12 different meal sizes fed to corn snakes (*Pantherophis guttatus*) to characterize their postprandial metabolic response and quantify their specific dynamic action.

Meal type	n	Mass			Energy	
		Wet (g)	Dry (g)	Dry (%)	Dry mass (kJ g^{-1})	Wet mass (kJ g^{-1})
Extra small pinky mouse	5(15)	1.66 ± 0.03	0.31 ± 0.01	18.7 ± 0.2	22.7 ± 0.4	4.25 ± 0.07
Small pinky mouse	5(15)	2.04 ± 0.05	0.44 ± 0.02	21.4 ± 0.4	22.7 ± 0.4	4.86 ± 0.16
Large pinky mouse	5(15)	2.64 ± 0.07	0.72 ± 0.09	27.0 ± 2.5	24.2 ± 0.2	6.54 ± 0.62
Peach fuzzy mouse	5(10)	3.56 ± 0.19	0.98 ± 0.06	27.5 ± 0.3	24.0 ± 0.2	6.61 ± 0.12
Fuzzy mouse	5(10)	5.66 ± 0.15	1.83 ± 0.08	32.2 ± 0.6	27.9 ± 0.4	8.98 ± 0.30
Hopper mouse	5(10)	10.3 ± 0.7	2.74 ± 0.16	26.6 ± 0.3	23.7 ± 0.3	6.30 ± 0.13
Weanling mouse	5	16.7 ± 0.4	4.81 ± 0.09	28.9 ± 0.5	24.3 ± 0.3	7.00 ± 0.15
Large adult mouse	5	22.5 ± 0.8	6.46 ± 0.22	28.8 ± 0.4	23.7 ± 0.2	6.82 ± 0.13
Extra-large adult mouse	5	35.5 ± 0.2	11.6 ± 0.8	32.7 ± 2.3	25.3 ± 0.8	8.35 ± 0.84
Pinky rat	5	6.87 ± 0.33	2.31 ± 0.20	16.8 ± 0.5	23.0 ± 0.7	3.86 ± 0.16
Fuzzy rat	5	11.5 ± 0.1	2.35 ± 0.05	20.5 ± 0.3	24.5 ± 0.1	5.01 ± 0.08
Small rat	5	66.3 ± 5.2	19.7 ± 1.7	29.7 ± 1.0	23.6 ± 0.7	7.02 ± 0.41

Note: For the smaller mice, numbers in parentheses represent the number of individuals that were equally divided (two or three individuals) into five samples for the determination of wet and dry mass and energy content. Values are means ± 1 SE.

by a post hoc pairwise mean comparison (Tukey–Kramer) to identify significant differences in $\dot{V}O_2$, $\dot{V}CO_2$, and RER between sampling time points and when $\dot{V}O_2$ did not differ significantly from SMR. To investigate the effects of meal size and body temperature on metabolic measures, we used ANOVA for measures of body mass, target meal mass percentage, SMR (mL O_2 g^{-1} h^{-1}, mL CO_2 g^{-1} h^{-1}), peak $\dot{V}O_2$ (mL g^{-1} h^{-1}), scope of peak $\dot{V}O_2$, RER at peak $\dot{V}O_2$, SDA (kJ kg^{-1}), and SDA coefficient. We used ANCOVA (body mass as a covariate) to examine treatment effects for whole-animal measures of SMR (mL O_2 h^{-1}, mL CO_2 h^{-1}), peak (mL h^{-1}), and SDA (kJ). In the following Results, we report the findings from analyses of whole-animal measurements of SMR and peak $\dot{V}O_2$ and present in the tables mass-specific and whole-animal values and analyses. The ANOVA and ANCOVA analyses were followed by pairwise mean comparison to identify differences between treatments. We report the results of the ANOVA and ANCOVA tests in terms of their *F* and *P* values and note the *P* values of significant pairwise mean comparisons. We used least square regression analysis to examine the scaling relationship between body mass and SMR, peak $\dot{V}O_2$, and SDA. Prior to regression analysis, we logged transformed body mass and metabolic data. The level of statistical significance for this study was set at $P < 0.05$ and results are reported as means ± 1 SE.

3. Results

3.1. Effects of meal size

Mean body mass and SMR of *P. guttatus* did not vary significantly among the five meal-size treatments (Table 2). For each meal size, snakes experienced significant variation in $\dot{V}O_2$ and $\dot{V}CO_2$ among pre- and postfeeding time periods, but no variation in RER. After feeding, rates of gas exchange of *P. guttatus* increased quickly and peaked between 1 and 2 days postfeeding (Fig. 1). Peak $\dot{V}O_2$ varied ($P < 0.0001$) among the meal sizes, increasing from a factorial scope of 2.90 ± 0.12 for 5% meals to 7.58 ± 0.49 for 45% meals (Table 2). At peak $\dot{V}O_2$, RER did not significantly differ among meal sizes, averaging 0.687 ± 0.013 (Table 2). Following the peaks, rates of gas exchange declined more slowly and returned to values not significantly greater than SMR at 2.5, 4, 5, 6, and 7 days postfeeding for the 5%, 15%, 25%, 35%, and 45% meals, respectively (Fig. 1). Specific dynamic action (as kJ and kJ kg^{-1}) varied significantly (*P*'s < 0.0001) among meal sizes, ranging from 2.4 ± 0.8 kJ for the 5% meals to 27.4 ± 8.0 kJ for the 45% meals (Table 2). Meal size also impacted the SDA coefficient; significantly less for 5% meals compared to the 25% meals (Table 2). Plotted against meal energy, SDA

Table 2
Body mass, meal size, standard metabolic rate (SMR), and six experimental variables of the postprandial metabolic response of the corn snake (*Pantherophis guttatus*) to rodent meals equaling in mass to 5%–45% of snake's body mass. Metabolic measurements were conducted at a body temperature of 30 °C.

Variable	Meal size (% of body mass)						
	5%	15%	25%	35%	45%	*F*	*P*
n	9	9	9	9	9		
Body mass (g)	53.6 ± 17.2	47.4 ± 15.3	44.9 ± 14.7	49.6 ± 16.6	52.4 ± 17.0	0.048	0.995
Meal mass (g)	2.67 ± 0.86^{a}	7.12 ± 2.30^{a}	11.2 ± 3.7^{ab}	17.3 ± 5.8^{bc}	23.6 ± 7.6^{c}	11.7	<0.0001
Meal mass (% of body mass)	4.98 ± 0.01^{a}	15.0 ± 0.1^{b}	24.9 ± 0.1^{c}	34.8 ± 0.2^{d}	45.1 ± 0.1^{e}	26,124	<0.0001
SMR (mL O_2 h^{-1})	2.40 ± 0.65	2.23 ± 0.64	2.11 ± 0.61	2.33 ± 0.70	2.52 ± 0.64	0.331	0.856
SMR (mL O_2 g^{-1} h^{-1})	0.049 ± 0.002	0.051 ± 0.002	0.051 ± 0.002	0.051 ± 0.002	0.050 ± 0.002	0.093	0.984
SMR (mL CO_2 h^{-1})	1.72 ± 0.47	1.53 ± 0.42	1.44 ± 0.40	1.59 ± 0.46	1.69 ± 0.47	0.338	0.850
SMR (mL CO_2 g^{-1} h^{-1})	0.035 ± 0.002	0.035 ± 0.002	0.035 ± 0.002	0.035 ± 0.002	0.035 ± 0.002	0.020	0.989
Peak $\dot{V}O_2$ (mL h^{-1})	7.11 ± 2.05^{a}	11.0 ± 3.6^{ab}	15.3 ± 5.7^{bc}	17.4 ± 5.4^{bc}	19.4 ± 5.6^{c}	10.1	<0.0001
Peak $\dot{V}O_2$ (mL g h^{-1})	0.142 ± 0.008^{a}	0.242 ± 0.11^{b}	0.332 ± 0.12^{c}	0.363 ± 0.008^{c}	0.374 ± 0.018^{c}	66.8	<0.0001
Scope	2.90 ± 0.12^{a}	4.79 ± 0.20^{b}	6.64 ± 0.39^{c}	7.25 ± 0.31^{c}	7.58 ± 0.49^{c}	36.5	<0.0001
RER	0.697 ± 0.012	0.691 ± 0.011	0.654 ± 0.021	0.706 ± 0.014	0.685 ± 0.011	2.05	0.106
Duration (days)	2	3	5	6	8		
SDA (kJ)	2.40 ± 0.82^{a}	7.05 ± 2.45^{ab}	14.6 ± 5.3^{bc}	23.5 ± 8.0^{cd}	27.4 ± 8.0^{d}	12.8	<0.0001
SDA (kJ kg^{-1})	43.9 ± 2.6^{a}	151 ± 10^{b}	323 ± 13^{c}	460 ± 19^{d}	542.5 ± 15^{e}	245	<0.0001
SDA coefficient (%)	15.8 ± 1.6^{a}	16.5 ± 1.1^{ab}	20.8 ± 0.5^{b}	18.3 ± 1.0^{ab}	20.3 ± 1.9^{ab}	2.80	0.038

Note: Variables are defined in the text. Values are presented as means ± 1 SE. Values of *F* and *P* are from ANOVA for body mass (g), meal mass (% of body mass), SMR (mL O_2 g^{-1} h^{-1}), SMR (mL CO_2 g^{-1} h^{-1}), peak oxygen consumption (mL O_2 g^{-1} h^{-1}), scope, respiratory exchange ratio (RER), specific dynamic action (SDA as kJ kg^{-1}), and SDA coefficient, whereas values of *F* and *P* are from ANCOVA (body mass as a covariate) for meal mass (g), SMR (mL O_2 h^{-1}), SMR (mL CO_2 h^{-1}), peak oxygen consumption (mL O_2 h^{-1}), and SDA (kJ). RER values in this table represent individual RER mean values calculated at peak oxygen consumption. Differing letters indicate significant differences (P < 0.05) between meal-size treatments as determined with a post hoc pairwise mean comparison test (Tukey HSD).

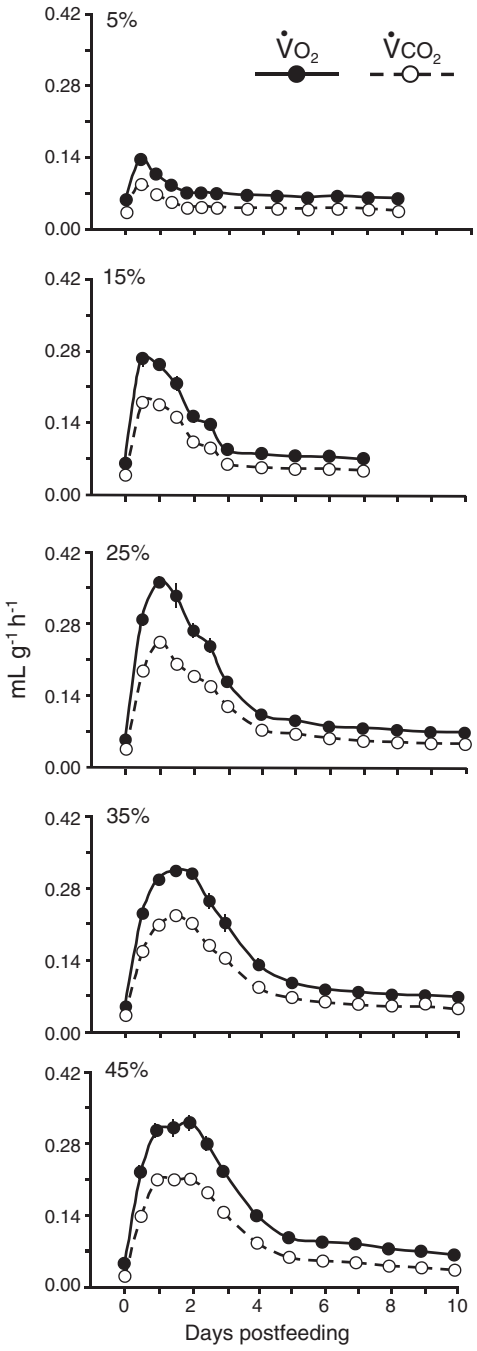

Fig. 1. Mean oxygen consumption and carbon dioxide production (mL g^{-1} h^{-1}) for the corn snake (*Pantherophis guttatus*) at 30 °C prior to (day 0) and following the ingestion of a rodent meal equaling in mass to 5%, 15%, 25%, 35%, and 45% of snake's body mass. For each trial, n = 9. Error bars represent SE and are omitted if the SE is smaller than the symbol for the mean.

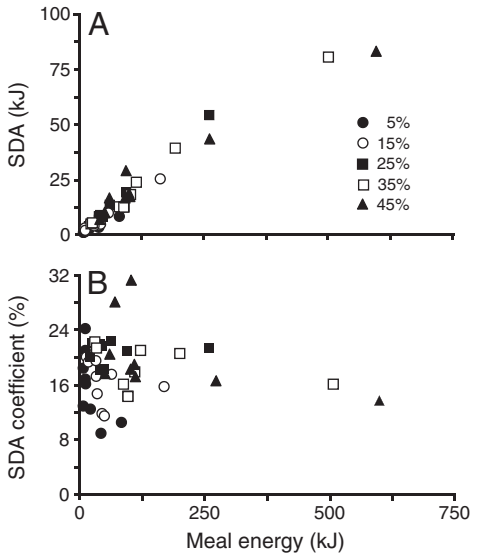

Fig. 2. (A) Specific dynamic action (SDA) and (B) SDA coefficients of corn snakes (*Pantherophis guttatus*) plotted against the energy of rodent meals that were equal in mass to 5%, 15%, 25%, 35%, and 45% of snake body mass. Note the increase in SDA with increase in meal energy and that SDA coefficients are not affected by meal energy.

increased linearly with a generalized slope of 0.156 while the SDA coefficient did not vary with respect to meal size (Fig. 2A & B).

3.2. Effects of body temperature

Mean body mass did not vary significantly among the four temperature trials. Body temperature significantly ($P < 0.0001$) impacted SMR, which increased with each 5 °C increase in treatment temperature (Table 3). For each trial, $\dot{V}O_2$ and $\dot{V}CO_2$, but not RER, varied significantly (P values < 0.0001) among sampling periods. The shape of the postprandial metabolic profile shifted from being shallow and elongated at 20 °C to becoming increasingly more narrow, taller, and shorter in duration with each increase in temperature (Fig. 3). The postprandial peak in $\dot{V}O_2$ varied significantly ($P < 0.0001$) among temperature treatments with each 5 °C increase in body temperature (Table 3). Factorial scopes of peak $\dot{V}O_2$ also varied significantly ($P < 0.0001$) among temperatures, due to the lower scopes (5.52–6.35) at 20, 30, and 35 °C compared with that at 25 °C (7.55; Table 3). With an increase in body temperature, the duration of elevated metabolism decreased from 10 days at 20 °C to 4 days at 35 °C (Table 3). As predicted, SDA as kJ or kJ kg^{-1} did not vary among temperature treatments. Likewise, we observed no significant variation among temperature trials for the SDA coefficients (Table 3).

3.3. Repeatability of postprandial metabolism and SDA

Mean body mass and SMR did not differ significantly among these three trials (Table 4). Among trials, snakes experienced no significant variation in $\dot{V}O_2$ and $\dot{V}CO_2$ for each pre- and postfeeding time period. After feeding, rates of gas exchange of *P. guttatus* increased similarly for each trial, peaking at 1 day postfeeding (Fig. 4). Peak $\dot{V}O_2$ did not vary significantly among the three trials and there was no significant variation in scope of peak $\dot{V}O_2$ and RER at peak $\dot{V}O_2$ (Table 4). Likewise, SDA (as kJ or kJ kg^{-1}) and the SDA coefficient did not vary significantly among trials (Table 4). When ranked lowest to highest in SDA (kJ kg^{-1}) for each of the three trials, snakes tended to maintain their position in the ranking (individual mean variation in rankings = 6.1) more so than expected by random assortment of rankings (mean variation = 13.5).

3.4. Effects of body size

We assessed the scaling relationships of SMR, peak $\dot{V}O_2$, scope, and SDA over a 90-fold range in body mass (8.4–753.2 g) of *P. guttatus* that had consumed a rodent meal equaling 25% of snake body mass at 30 °C. Mass exponents of SMR (0.765 ± 0.030) and peak $\dot{V}O_2$ (0.930 ± 0.025) were significantly different, as peak $\dot{V}O_2$ increased at a greater rate than SMR with body mass (Fig. 5A). Hence, larger snakes experienced a greater scope of peak $\dot{V}O_2$ than smaller snakes (Fig. 5B). For these snakes, SDA scaled with body mass with a mass exponent of 0.999 ± 0.035, essentially an isometric relationship (Fig. 5C). For 12 snakes weighing 17.1–732.2 g that had consumed a 10-gram hopper mouse (1.4–53.4% of snake body mass), SMR and peak $\dot{V}O_2$ scaled with mass exponents of 0.788 ± 0.024 and 0.442 ± 0.024, respectively

Table 3
Body mass, meal size, standard metabolic rate (SMR), and five experimental variables of the postprandial metabolic response of corn snakes (*Pantherophis guttatus*) to the digestion of rodent meals equaling in mass to ~25% of snake's body mass at body temperatures of 20, 25, 30, and 35 °C.

Variable	Body temperature (°C)					
	20	25	30	35	*F*	*P*
n	8	8	8	8		
Body mass (g)	43.8 ± 8.6	38.1 ± 7.1	31.7 ± 7.3	44.4 ± 8.5	0.567	0.641
Meal mass (g)	10.9 ± 2.1	9.5 ± 1.8	7.9 ± 1.8	11.1 ± 2.1	1.44	0.252
Meal mass (% of body mass)	24.9 ± 0.1	25.0 ± 0.0	24.9 ± 0.1	25.1 ± 0.1	2.19	0.111
SMR (mL O_2 g^{-1} h^{-1})	0.023 ± 0.001[a]	0.028 ± 0.001[a]	0.052 ± 0.002[b]	0.080 ± 0.003[c]	149	<0.0001
SMR (mL O_2 h^{-1})	0.99 ± 0.15[a]	1.03 ± 0.17[ab]	1.55 ± 0.27[b]	3.41 ± 0.51[c]	48.1	<0.0001
SMR (mL CO_2 g^{-1} h^{-1})	0.017 ± 0.001[a]	0.021 ± 0.001[a]	0.036 ± 0.002[b]	0.059 ± 0.003[c]	126	<0.0001
SMR (mL CO_2 h^{-1})	0.72 ± 0.11[a]	0.78 ± 0.15[a]	1.08 ± 0.20[a]	2.50 ± 0.37[b]	50.2	<0.0001
Peak $\dot{V}O_2$ (mL g h^{-1})	0.127 ± 0.009[a]	0.208 ± 0.004[b]	0.324 ± 0.011[c]	0.435 ± 0.018[d]	134	<0.0001
Peak $\dot{V}O_2$ (mL h^{-1})	5.77 ± 1.31[a]	7.89 ± 1.46[ab]	9.86 ± 1.93[b]	19.8 ± 5.5[c]	25.5	<0.0001
Scope	5.52 ± 0.47[a]	7.55 ± 0.22[b]	6.35 ± 0.29[a]	5.53 ± 0.35[a]	7.83	0.0006
RER	0.695 ± 0.025	0.714 ± 0.016	0.668 ± 0.016	0.696 ± 0.009	1.15	0.334
Duration (days)	10	8	5	4		
SDA (kJ)	14.5 ± 3.4	11.9 ± 2.0	9.5 ± 1.8	13.5 ± 2.9	0.400	0.754
SDA (kJ kg^{-1})	320 ± 23	315 ± 11	318 ± 14	290 ± 17	0.607	0.616
SDA coefficient (%)	25.9 ± 3.7	22.7 ± 1.4	20.7 ± 0.6	23.9 ± 1.2	1.18	0.335

Note: Variables are defined in the text. Values are presented as means ± 1 SE. Values of *F* and *P* are from ANOVA for body mass (g), meal mass (% of body mass), SMR (mL O_2 g^{-1} h^{-1}), SMR (mL CO_2 g^{-1} h^{-1}), peak oxygen consumption (mL O_2 g^{-1} h^{-1}), scope, respiratory exchange ratio (RER), specific dynamic action (SDA as kJ kg^{-1}), and SDA coefficient, whereas values of *F* and *P* are from ANCOVA (body mass as a covariate) for meal mass (g), SMR (mL O_2 h^{-1}), SMR (mL CO_2 h^{-1}), peak oxygen consumption (mL O_2 h^{-1}), and SDA (kJ). RER values in this table represent individual RER mean values calculated at peak oxygen consumption. Differing letters indicate significant differences ($P < 0.05$) between body temperature treatments as determined with a post hoc pairwise mean comparison test (Tukey HSD).

(Fig. 6A). Therefore in this trial, the scope of peak $\dot{V}O_2$, decreased with body mass, ranging from 9.0 for a 19.5 g snake to 2.3 for a 732 g snake (Fig. 6B). Duration of elevated $\dot{V}O_2$ ranged from two to ten days, increasing with a decrease in body mass and an increase in relative meal size. Among this range of individuals, SDA varied little; the mass exponent of −0.091 ± 0.039 did not differ significantly from zero (Fig. 6C). As demonstrated in these two studies, absolute meal size dictates the magnitude of SDA independent of body mass.

4. Discussion

Feeding induces for *P. guttatus* a postprandial metabolic profile that is very characteristic of other organisms (Secor, 2009). Ingestion triggers a rapid increase in metabolic rate that peaks a day or two into digestion and is followed by a slower decline to prefeeding values. Very similar metabolic profiles have been documented for other snakes, reptiles, amphibians, fishes, and invertebrates (Secor, 2009). While birds and mammals exhibit similar profiles in shape, their duration is much shorter due to more rapid processing of meals. Likewise, meal size and hence digestive demand significantly impacts the postprandial metabolic profile and SDA, as previously documented (McCue, 2006; Secor, 2009). The effect of body temperature is noted in the changing shape of the metabolic profile with an increase in body temperature; however across temperatures, SDA did not significantly vary. We found individual snakes to respond metabolically in near identical fashion to the digestion and assimilation of meals of the same relative size. Corn snakes exhibited allometric scaling with body mass of SMR and peak $\dot{V}O_2$, whereas SDA scaled isometrically with body mass. In the following we shall discuss each of these determinants of *P. guttatus* postprandial metabolic response and SDA with attention to the underlying mechanisms of the SDA response and how these responses compare with those of other colubrid snakes.

4.1. Effects of demand

An established tenet of SDA is that any change in a meal that increases or decreases the workload of digestion and assimilation will similarly affect SDA (Secor, 2009). Reducing the structural integrity of a meal prior to ingestion lessens the efforts of the stomach for mechanical and chemical breakdown before its passage into the small intestine. Foods that have been fragmented or ground generate a lower SDA than foods consumed intact and whole (Secor, 2003; Boback et al., 2007). Likewise, meals that are harder in structure take more energy to process than softer meals (Christel et al., 2007). Observed is that meals composed of insects with hard exoskeletons results in SDA's that are 80% greater than similar-size meals of soft-bodied organisms (Secor and Faulkner, 2002; Secor and Boehm, 2006; Secor et al., 2007).

The causal relationship between digestive effort and postprandial metabolic responses and SDA are best demonstrated by manipulating meal size (Secor and Diamond, 1997; Tsai et al., 2008; Bessler et al., 2010). Understandably, by increasing the size of the meal, more time and effort will be needed for gastric breakdown, intestinal passage and absorption, and cellular assimilation. This is reflected in postprandial metabolic profiles with higher peaks and longer durations for larger meals. The combined increase in these parameters results in a greater calculated SDA. The extent that SDA increases tends to match the increase in workload. For 43 species of animals, whose SDA were quantified across multiple meal sizes, a doubling of meal size generated on average a 2.06-fold increase in SDA, that was contributed to nearly equally by increases in peak $\dot{V}O_2$ and the duration of elevated metabolism (Secor, 2009). Quantified as a response coefficient (Q_{2x}, the factorial increase in a parameter with a doubling of demand) a doubling of meal size for *P. guttatus* generated on average a Q_{2x} of 1.28 for peak $\dot{V}O_2$, 1.43 for duration, and 2.42 for SDA. Snakes tend to have a Q_{2x} of SDA greater than two when doubling meal size, as similar Q_{2x}'s of SDA have been observed for *Bothrops alternatus* (2.50), *Crotalus durissus* (2.35), *Python molurus* (2.35), and *Python sebae* (2.65) (Andrade et al., 1997; Ott and Secor, 2007; Secor, 2009; Gavira and Andrade, 2013). With an increase in meal size, corn snakes, like other snakes, invest a proportionately greater amount of energy into digestion and assimilation.

4.2. Influence of temperature

The effects of ambient temperature on pre and postprandial metabolic rates are showcased when comparing metabolic profiles across temperatures (Fig. 3). Prefeeding standard metabolic rates (SMR) increase in clear stepwise fashion with each 5 °C increase in experimental temperature. Likewise, the postprandial peak in $\dot{V}O_2$ increased at a near identical pace. From 20 °C to 35 °C, the Q_{10} of SMR and peak $\dot{V}O_2$ of

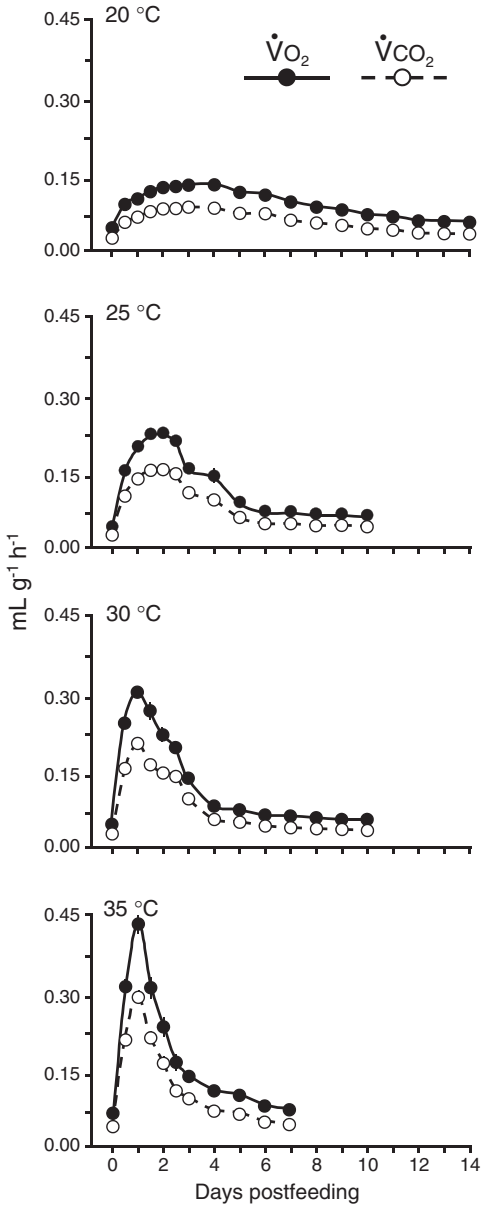

Fig. 3. Mean oxygen consumption and carbon dioxide production (mL g^{-1} h^{-1}) for the corn snake (*Pantherophis guttatus*) prior to (day 0) and following ingestion of a rodent meal equaling in mass to 25% of snake's body mass at body temperatures of 20, 25, 30, and 35 °C. For each trial, n = 8. Note that as body temperatures increases, the postprandial metabolic profile becomes more elevated and shorter.

P. guttatus were 2.29 and 2.27, respectively. Over the same span of temperatures, Q_{10} of SMR and peak $\dot{V}O_2$ of the colubrid snakes *Thamnophis sirtalis* were the same; 2.29 and 2.27, respectively (Bessler et al., 2010).

The other dominant effect that temperature has is on the shape and duration of the postprandial metabolic profile. Body temperature directly impacts the rate of biochemical activities. For digestion that would include the activities involved in the gastric breakdown and passage into the small intestine, pancreatic and intestinal enzyme activities, intestinal nutrient uptake and passage, and the assimilation of the nutrients. As body temperatures increase, all of these activities increase in rate, thereby shortening the time to digest and assimilate a meal. At the lowest body temperature studied (20 °C), the postprandial profile was elongated in a plateau fashion requiring 10 days before metabolic rates returned to SMR (Fig. 3). With each 5 °C increase in temperature, the duration of the response shortened and the profile became increasingly more narrow and taller. At 35 °C, the duration had been reduced to 4 days and the profile exhibited a very distinct narrow peak. Nearly identical postprandial metabolic profiles for each of these four experimental temperatures were exhibited by both *P. molurus* and *T. sirtalis* (Wang et al., 2003; Bessler et al., 2010). Similar temperature shifts in metabolic profiles have been documented for the other snakes that include *Dasypeltis inornata*, *Dasypeltis scabra*, and *Trimeresurus stejnegeri*, and as well as for fish and amphibians (Secor and Faulkner, 2002; Secor and Boehm, 2006; Luo and Xie, 2008; Tsai et al., 2008; Greene et al., 2013). Predictably, at an even lower body temperature (15 °C), the profile for *P. guttatus* would be even further extended, and at higher temperatures (>35 °C), would be even shorter and taller. We elected not to test at such temperatures in this study due to the concerns that snakes would not be able to digest at 15 °C and at 40 °C corn snakes would be within range of their thermal maximum, and therefore either or both temperature treatments could be lethal for these snakes.

Our hypothesis states that SDA would not vary among experimental temperatures if meal size and type were held constant. We assumed that for a given meal, the cumulative number of chemical reactions and metabolic processes is constant regardless of the speed that which they occur. Hence at any temperature, the same amount of HCl is produced, the same amount of pancreatic enzymes are secreted, the same number of small peptides and disaccharides are cleaved by brushborder hydrolases, the same number of amino acid and glucose molecules are transported across the epithelium, and the same amount of triglycerides, glucose, and amino acids are respectively repackaged as fat bodies, glycogen, and proteins. The statistical analyses of these data support this hypothesis; there was no significant variation among temperature treatments in SDA (whole animal or mass specific) or in the SDA coefficient. Regardless of the shape of the postprandial metabolic profile, the area under the curve for the duration of significantly elevated $\dot{V}O_2$, was statistically equivalent (Fig. 3). Thus, corn snakes expended the same amount of energy over a 10-day period digesting a rodent meal equaling in mass to 25% of their body mass at 20 °C as they did over a 4-day period at 35 °C. Consistent SDAs over experimental temperatures have also been documented for fishes, amphibians, and the snake *Python molurus* (Jobling and Davies, 1980; Peres and Oliva-Teles, 2001; Secor and Faulkner, 2002; Wang et al., 2003; Secor et al., 2007). However, across the same taxa of ectotherms, studies have also found SDA to vary among experimental temperatures (Hailey and Davies, 1987; Zaidan and Beaupre, 2003; Secor and Boehm, 2006; Secor et al., 2007; Luo and Xie, 2008). Typical among these studies is that SDA is significantly lower at the lowest treatment temperature compared to the higher temperatures (Hailey and Davies, 1987; Secor and Boehm, 2006; Bessler et al., 2010). In such cases, the reduced SDA may stem from a depressed assimilation efficiency at the lower temperature as has been noted for reptiles (Greenwald and Kanter, 1979; Angilletta, 2001).

4.3. Repeatability of the SDA response

Generated from the findings of the previous noted studies is the assumption that individual SDA is highly repeatable when holding meal type, meal size, and temperature constant. When tested with identical back-to-back trials, and a third trial five months later, individual corn snakes experienced very similar postprandial metabolic responses and SDA among the three trials. Individual variation from a mean (independent of body mass) of SDA for the three trials averaged only 10%. When ranked by SDA (kJ kg^{-1}), individuals tended to maintain their position in the ranking among the three trials. The repeatability of postprandial metabolism and SDA was also observed for the juvenile water snakes *Nerodia fasciata* that had consumed a fish meal equaling 20% of the snake's body mass (Hopkins et al., 2004). For two consecutive trials, these water snakes literally duplicated their factorial scope of peak $\dot{V}O_2$, SDA, and SDA coefficient.

Table 4
Comparison among three trials of the body mass, meal size, standard metabolic rate (SMR), and five experimental variables of the postprandial metabolic response of nine corn snakes (*Pantherophis guttatus*) to the digestion of rodent meals equaling in mass to ~25% of snake's body mass at a body temperature of 30 °C.

Variable	25% trials			*F*	*P*
	Trial 1	Trial 2	Trial 3		
n	9	9	9		
Body mass (g)	58.0 ± 18.9	44.9 ± 14.7	71.9 ± 22.1	0.120	0.888
Meal mass (g)	14.5 ± 4.7	11.2 ± 3.7	18.0 ± 5.5	1.073	0.357
Meal mass (% of body mass)	25.1 ± 0.2	24.9 ± 0.1	25.0 ± 0.0	0.344	0.712
SMR (mL $O_2.g^{-1}.h^{-1}$)	0.049 ± 0.002	0.051 ± 0.002	0.048 ± 0.003	0.031	0.969
SMR (mL $O_2.h^{-1}$)	2.44 ± 0.66	2.11 ± 0.61	3.00 ± 0.73	0.099	0.906
SMR (mL $CO_2.g^{-1}.h^{-1}$)	0.034 ± 0.002	0.035 ± 0.002	0.034 ± 0.002	0.012	0.987
SMR (mL $CO_2.h^{-1}$)	1.71 ± 0.47	1.44 ± 0.40	2.16 ± 0.55	0.783	0.467
Peak $\dot{V}O_2$ (mL.g.h^{-1})	0.308 ± 0.013	0.332 ± 0.12	0.296 ± 0.009	1.491	0.243
Peak $\dot{V}O_2$ (mL.h^{-1})	16.6 ± 5.2	15.3 ± 5.7	20.3 ± 5.9	1.182	0.323
Scope	6.40 ± 0.32	6.64 ± 0.39	6.27 ± 0.28	0.783	0.467
RER	0.657 ± 0.013	0.650 ± 0.021	0.678 ± 0.010	0.768	0.474
Duration (days)	5	5	5		
SDA (kJ)	18.3 ± 6.5	14.6 ± 5.3	25.1 ± 8.9	0.338	0.716
SDA (kJ.kg^{-1})	304 ± 11	323 ± 13	315 ± 26	0.225	0.800
SDA coefficient (%)	18.1 ± 0.4	20.8 ± 0.5	19.6 ± 1.9	0.492	0.616

Note: Variables are defined in the text. Values are presented as means ± 1 SE. Values of *F* and *P* are from ANOVA for body mass (g), meal mass (% of body mass), SMR (mL O_2 g^{-1} h^{-1}), SMR (mL CO_2 g^{-1} h^{-1}), peak oxygen consumption (mL O_2 g^{-1} h^{-1}), scope, respiratory exchange ratio (RER), specific dynamic action (SDA as kJ kg^{-1}), and SDA coefficient, whereas values of *F* and *P* are from ANCOVA (body mass as a covariate) for meal mass (g), SMR (mL O_2 h^{-1}), SMR (mL CO_2 h^{-1}), peak oxygen consumption (mL O_2 h^{-1}), and SDA (kJ). RER values in this table represent individual RER mean values calculated at peak oxygen consumption. Differing letters indicate significant differences ($P < 0.05$) between trials as determined with a post hoc pairwise mean comparison test (Tukey HSD).

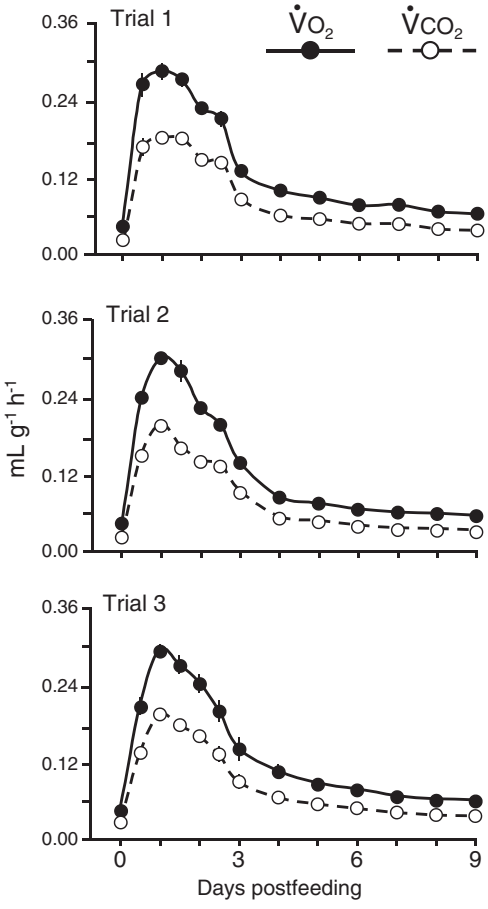

Fig. 4. Three replicated trials of mean oxygen consumption and carbon dioxide (mL g^{-1} h^{-1}) for the corn snake (*Pantherophis guttatus*) prior to (day 0) and following ingestion of a rodent meal equaling in mass to 25% of snake's body mass at 30 °C. Corn snakes responded metabolically in near identical fashion to the digestion of the same meal at the same temperature.

4.4. Digestion and metabolism

The postprandial metabolic profile illustrates the cumulative energy being expended at any one time on all the activities associated with the breakdown and absorption of the meal. To illustrate the interactions between metabolic response and digestive performance, we X-rayed four *P. guttatus* (mean mass = 217 g) that had consumed rodent meals (two mice) equaling in mass to 25% of the snake's body mass. Each snake was X-rayed daily until there were no observable skeletal

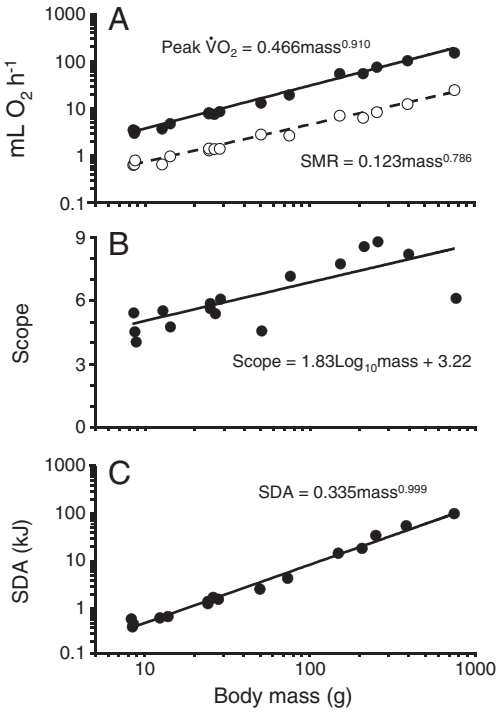

Fig. 5. (A) Standard metabolic rate (SMR), peak postprandial metabolic rate (Peak $\dot{V}O_2$), (B) Scope (Peak $\dot{V}O_2$/SMR), and (C) SDA plotted against body mass. The rodent meals in these trials were equivalent in mass to 25% of snake body mass and trials were conducted at 30 °C. Both SMR and Peak $\dot{V}O_2$ scale allometrically with body mass, however the higher scaling slope of Peak $\dot{V}O_2$ compared with SMR results in an increase in scope with body mass. In contrast, SDA scales isometrically with body mass.

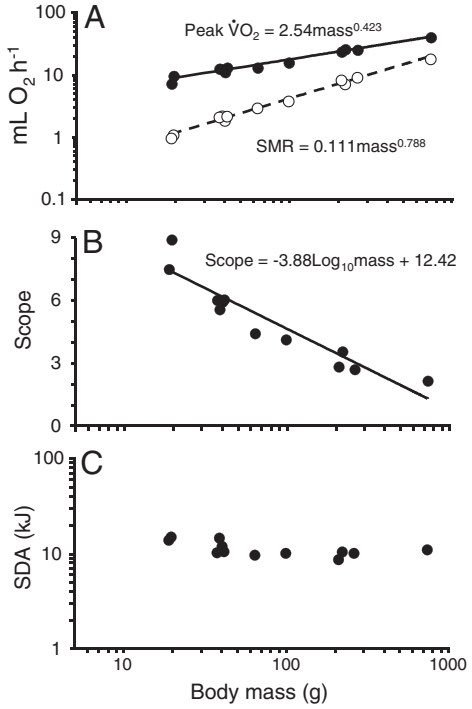

Fig. 6. (A) Standard metabolic rate (SMR), peak postprandial metabolic rate (Peak $\dot{V}O_2$), (B) Scope (Peak $\dot{V}O_2$/SMR), and (C) SDA plotted against body mass. The rodent meals in these trials all weighted 10 g and trials were conducted at 30 °C. Both SMR and Peak $\dot{V}O_2$ scale allometrically with body mass, however the lower scaling slope of Peak $\dot{V}O_2$ compared with SMR results in a decrease in scope with body mass. The SDA generated from a 10 g rodent meal did not vary with snake body size.

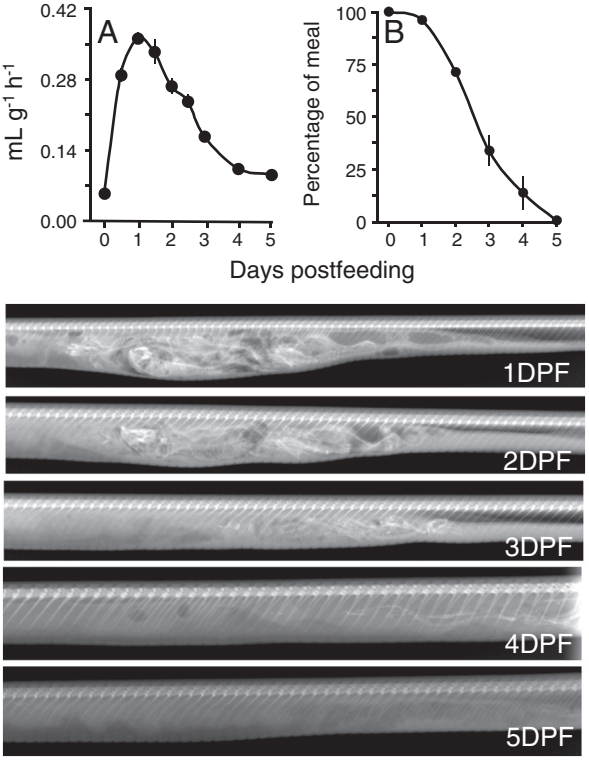

Fig. 7. (A) Mean oxygen consumption rates (mL g^{-1} h^{-1}) and (B) the relative percentage of the ingested meal remaining in the stomach (as determined by X-ray) during the first five days after feeding for the corn snake (*Pantherophis guttatus*). Meals were rodents equaling in mass to 25% of snake's body mass and snakes were maintained at 30 °C. Images of X-rays illustrate the daily rate (DPF = days postfeeding) of breakdown of the rodent meal (two mice) within the stomach of a corn snake.

components remaining within the stomach. One snake had cleared its stomach of rodent skeleton by day four of digestion, whereas the other three took five days to breakdown and pass the skeletons. From each X-ray we estimated the relative amount of mice skeletons remaining within the stomach (we X-rayed intact mice for reference). Within the first 24 h, little of the skeletons had been broken down and passed (Fig. 7). By day 2, roughly a quarter of the mouse meal (half a mouse) had been passed, and by day 3, two-thirds of the meal had been dissolved and passed into the small intestine (Fig. 7). Much of the rapid increase in metabolic rate within the first day following feeding stems from the upregulation in HCl production. Snakes literally shutdown HCl production between meals and therefore must rapidly restore an acidic gastric lumen after feeding (Secor, 2003; Bessler and Secor, 2012). The production of HCl is a relatively expensive endeavor, requiring the hydrolysis of one ATP per H^+ pumped into the lumen of the gastric pits (Reenstra and Forte, 1981). The observed elevated metabolic rate after day one would result largely in part from the continued production of HCl and pepsinogen which is converted to the protease pepsin. Previously identified is the substantial contribution of gastric performance to snake SDA. For the Burmese python, bypassing the stomach in the digestion of a rodent meal (homogenized) reduced SDA by nearly 50% (Secor, 2003) and the administration of omeprazole which blocks H^+ release from the oxyntopeptic cells and hence curtails HCl production, delayed the postprandial increase in metabolic rate until the omeprazole wore off (Andrade et al., 2004).

By day two and for the next few days, the efforts of the liver (bile production), pancreas (enzyme and bicarbonate production), and intestine (breakdown and absorption), together with the cost of nutrient assimilation (i.e., protein synthesis) also contribute to the SDA response. With the emptying of the stomach by day 5 (Fig. 7), metabolic rates approach baseline prefeeding levels as digestion is practically finished and all that remains is the assimilation of the last of the absorbed nutrients. Given that many of the corn snakes in this study were young (1–2 years old) and growing, the expense of repackaging absorbed biomolecules into body structures would constitute the "cost of growth" (Wieser and Medgyesy, 1990, 1991).

4.5. Colubrid SDA

Corn snakes experience with feeding a postprandial metabolic response that is characteristic of other colubrid snakes that includes a rapid increase in metabolic rate that peaks a day or two after feeding and returns to fasting levels within the next 2–4 days (Secor and Diamond, 2000; Roe et al., 2004; Bessler et al., 2010; Cox and Secor, 2010). As also observed for *T. sirtalis*, the magnitude of the response and duration of elevated metabolism are both a direct function of digestive demand (i.e., meal size and meal type) and body temperature (Bessler et al., 2010). The postprandial metabolic responses of *T. sirtalis* to meals equaling 5 to 45% of body mass and when exposed to temperatures of 20 to 35 °C practically mirror those of *P. guttatus* (Bessler et al., 2010). Bessler et al. (2010) in addition provided predicted models for estimating SDA of *T. sirtalis* based on body mass, meal mass, body temperature, and meal energy. Using a mixed meal model from that paper, the estimated SDA for a 45 g, *P. guttatus* consuming a meal 25% of body size at 30 °C is 15.7 kJ, similar to the average SDA of 14.6 kJ we report in Table 2.

The similarity of the postprandial metabolic response of corn snakes with other colubrids is not only with the metabolic profile, but also with SDA when controlling with relative meal size. We are aware of the published accounts of SDA for 15 species of colubrids (Table 6 in Secor, 2009; Bessler et al., 2010; Cox and Secor, 2010; Greene et al., 2013). However for only six species did snakes consume meals equaling 25% of body mass (Secor and Diamond, 2000; Zaidan and Beaupre, 2003; Bessler et al., 2010; Cox and Secor, 2010). To enhance a species comparison, we combined these published results with unpublished data from

our laboratory for three additional species. For ten species of colubrids that had consumed meals (rodent or fish) equaling 25% of body mass and maintained at 30 °C, the factorial scope of peak $\dot{V}O_2$ ranged from 5.4 to 8.0 and averaged 6.4 ± 0.3 (Table 5). Standardized, SDA averaged 295 ± 7 kJ kg^{-1} and 17.0 ± 1.2% of meal energy among these ten species. We took the opportunity with these ten species to examine the interspecific scaling of SDA given the 16-fold range in body mass. For these species, SDA scale isometrically with body mass, generating a mass exponent of 1.00 ± 0.03, nearly identical to the intraspecific scaling of body mass for *P. guttatus* (Fig. 8). Interspecific scaling of SDA has also been reported for ambystomatid salamanders and anurans, and in both cases the mass scaling exponent (1.05 and 1.08, respectively) did not did differ from 1.00 (Secor and Boehm, 2006; Secor et al., 2007). Regardless if the comparison is intra- or interspecific, SDA appears to scale isometrically with body mass. Concerns of the application of mass-specific values of SMR for intra and interspecific comparisons are justified given the well-established allometry of SMR (Beaupre, 2005). However, mass specific values of SDA would be applicable for comparisons since body mass effects are consistent. When controlling for relative meal size and in many cases body temperature, comparative analyses of mass-specific SDA are acceptable.

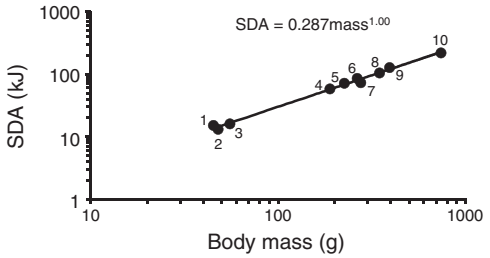

Fig. 8. Specific dynamic action (SDA) plotted against body mass for ten species of colubrid snakes that had consumed meals equaling in mass to 25% of snake body mass and maintained at 30 °C (see Table 2). Number signify the following species: 1 *Pantherophis guttatus*, 2 *Thamnophis sirtalis*, 3 *Thamnophis marcianus*, 4 *Lampropeltis getula*, 5 *Coluber constrictor*, 6 *Lamprophis fuliginosus*, 7 *Masticophis flagellum*, 8 *Nerodia rhombifer*, 9 *Elaphe obsoleta*, 10 *Pituophis melanoleucus*. Interspecifically among these ten colubrids, SDA scales isometrically (mass exponent = 1.00) with body mass.

Acknowledgments

We wish to thank Gretchen Anderson, Mimi Bach, Jonathan Belanich, Davis Diamond, Georgia Gamble, Evan Menzel, Schilling Nechtman, Scott White, and John Wyatt for their assistance in this project. This project was supported in part by the National Science Foundation (IOS-0466139 to S.M.S.) and the University of Alabama Department of Biological Sciences.

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Table 5
Tabulation of body mass, meal type, factorial scope of peak $\dot{V}O_2$, duration of elevated postprandial metabolism, SDA, and SDA coefficient for ten species of colubrid snakes. Sample size is noted in parentheses.

	Body mass (g)	Meal type	Scope	Duration (d)	SDA (kJ)	SDA (kJ kg^{-1})	SDA coefficient	Source
Coluber constrictor (6)	223	Rodent	5.4	4	68.9	309	15.0	Secor and Diamond (2000)
Elaphe obsoleta (1)	391	Rodent	6.2	6	122.2	313	13.7	Unpublished data
Lampropeltis getula (5)	188	Rodent	7.0	4	56.0	298	14.0	Secor and Diamond (2000)
Lamprophis fuliginosus (5)	261	Rodent	6.3	5	83.3	319	15.8	Unpublished data
Masticophis flagellum (6)	273	Rodent	5.9	5	70.4	258	13.0	Secor and Diamond (2000)
Nerodia rhombifer (12)	345	Fish	5.4	7	100.7	292	25.3	Cox and Secor (2010)
Pantherophis guttatus (9)	44.9	Rodent	6.6	5	14.6	325	20.8	This study
Pituophis melanoleucus (5)	732	Rodent	8.0	5	211.0	288	14.0	Secor and Diamond (2000)
Thamnophis marcianus (6)	55.0	Rodent	5.9	5	15.4	280	18.9	Unpublished data
Thamnophis sirtalis (7)	47.3	Fish	7.0	5	12.7	269	19.7	Bessler et al. (2010)

Note: Scope, duration, SDA, and SDA coefficient are defined in the text.

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