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MEAL SIZE AND SPECIFIC DYNAMIC ACTION IN THE RATTLESNAKE *CROTALUS DURISSUS* (SERPENTES: VIPERIDAE)

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ABSTRACT: We studied the effect of meal size on specific dynamic action (SDA) in the South American rattlesnake *Crotalus durissus*, by measuring oxygen consumption rates ($\dot{V}O_2$) prior to and after the ingestion of meals ranging from 10–50% of snake's body mass. Regardless of meal size, variation in $\dot{V}O_2$ with time during digestion demonstrated the same general pattern. Oxygen consumption rates peaked between 15 and 33 h post-feeding, at values 3.7–7.3 times those prior to feeding. Snakes, while digesting meals of 30% and 50% of their body mass, experienced $\dot{V}O_2$ that exceeded rates measured during forced activity. Following peaks in $\dot{V}O_2$, rates returned to pre-feeding values within 62–170 h post-feeding. Post-prandial peak in $\dot{V}O_2$ and the duration of the metabolic response to feeding increased with meal size. Digestion is an energetically demanding activity for *C. durissus*, with an estimated cost equaling 12–18% of the ingested assimilated energy.

Key words: SDA; Oxygen uptake; Digestion; Energetics; Metabolism; Feeding

SNAKES have engaged in an impressive adaptive radiation since their origin during the Cretaceous Period (Pough, 1983). Pivotal to their occupation of different ecological niches was the evolution of their diverse adaptations to feeding (Gans, 1961; Greene, 1983, 1992). The ability of snakes to consume large prey without mastication has attracted the attention of numerous scientists (e.g., Gans, 1983; Pough, 1983). Investigations on predator-prey relationship, kinematics of jaw apparatus during prey handling and ingestion, and dietary correlates, among others, have proposed the morphological, behavioral, and evolutionary basis of such specializations (Arnold, 1983, 1993; Cundall, 1983; Greene, 1992; Rochelle and Kardong, 1993).

From a functional point of view, the feeding biology of snakes still deserves attention. In this regard, studies on the physiological and ecological consequences of digesting large prey lag behind those studies concerned with prey acquisition and swallowing (Lillywhite, 1989; Mushinsky, 1987). The sparse studies on the digestive process in snakes have included those on gut retention time (Greenwald and Kanter, 1974; Stevenson et al., 1985), effects of venom injection on the speed of digestion (Thomas and Pough, 1979), functional and morphological regulation of the intestine (Secor and Diamond, 1995; Secor et al., 1994), and the impairment on fitness associated with the presence of a bulky food item in the stomach (Garland and Arnold, 1983).

An aspect of digestion that has been widely investigated among vertebrates is the post-prandial increase in metabolic rate, commonly referred to as specific dynamic action (SDA: Kleiber, 1961). For snakes, early reports of SDA included those by Benedict (1932) on *Python, Boa,* and *Pituophis* and by Hailey and Davies (1987) on *Natrix maura.* Recently, Secor and coworkers (Secor and Diamond, 1995; Secor and Nagy, 1994; Secor et al., 1994) have undertaken investigations on the morphological and physiological aspects, as well as the energetic and ecological implications, of SDA in *Crotalus cerastes, Masticophis flagellum,* and *Python molurus.* These studies have filled some gaps in our understanding of digestive processes in snakes, but many basic questions still deserve investigation. For example, meal size is know to affect the magnitude and duration of SDA in a variety of organisms (e.g., mammals Gallivan and Ronald, 1981; fish Jobling, 1981; birds Janes and Chappell, 1995), but this issue has not been addressed for snakes. Sit-and-wait foraging

snakes are characterized by the infrequent ingestion of meals with a wide size range, which are always swallowed whole (Greene, 1992). Therefore, in this context, these snakes may be considered as model organisms to study the effect of meal size on the parameters associated with SDA.

Based on these considerations, we studied the effects of meal size on SDA for the sit-and-wait foraging South American rattlesnake, *Crotalus durissus*. Specifically, we investigated whether post-prandial $\dot{V}O_2$ of *C. durissus* has an upper limit, or if $\dot{V}O_2$ increases concurrently with meal size (no plateau). We also measured maximum $\dot{V}O_2$ during activity to compare with the peak rates measured during digestion. Finally, we determined if snakes are rewarded with a large energetic return when feeding on larger meals.

Materials and Methods

Experimental Animals and Maintenance

For the measurement of SDA, we used a group of juvenile *Crotalus durissus* (mean mass = 59 g, SD = 24, range 26–111 g, n = 20). Another group (mean mass = 140 g, SD = 22, range 104–172 g, n = 8) was used to measure the aerobic scope. All animals were born in captivity from gravid females collected at Rio Claro, São Paulo State, southeastern Brazil. Rattlesnakes were individually housed in 17 × 24 × 35 cm boxes within a temperature-controlled room maintained at 30 ± 1 C. Water was provided ad libitum and snakes were fed mice (15–30% of their body mass) every other week. Snakes were fasted for at least 10 days prior to metabolic measurements. We have observed that such time is sufficient for *C. durissus* to complete digestion. Therefore, we were confident that snakes were post-absorptive prior to measurements. We used only healthy snakes that were not involved with ecdysis.

Experimental Protocol

We quantified specific dynamic action (SDA) from measurements of oxygen consumption rates ($\dot{V}O_2$ = ml $O_2 \cdot g^{-1} \cdot h^{-1}$) of snakes prior to (fasting) and after they had consumed meals of different sizes. We conducted all experiments at 30 C, which is within the body temperature range of active *C. durissus* (Abe and Cruppi, 1993). We measured $\dot{V}O_2$ using an automated respirometer similar to that described by Cruz-Neto and Abe (1994). Briefly, a computer operated system was programmed for cycles of 9 min to flush the respirometric chamber (vol. = 1.3–2.3 l) with fresh air, followed by 10 min of $\dot{V}O_2$ measurements. Oxygen content inside the respirometric chambers was monitored with an O_2 analyzer (Servomex 570A), and $\dot{V}O_2$ was automatically calculated from the decline in chamber O_2 for each 10-min cycle. Oxygen content inside respirometric chambers never fell below 20%.

For each measurement, a snake was first weighed and then placed into the respirometric chamber where its $\dot{V}O_2$ (pre-feeding) was measured for 24 h. Afterward, the snake was removed and fed a mouse weighing either 10%, 20%, 30%, or 50% (±1% for all cases) of its body mass. Mice were offered alive, and all of them were killed by the snakes by envenomation. After consuming a mouse, we returned the snake to the respirometric chamber and continued $\dot{V}O_2$ measurements until values approached pre-feeding values (see below).

We measured aerobic scope from juvenile *C. durissus* using closed-system respirometry. A snake was placed in a 1.5 l plastic chamber vented to room air and was allowed to rest for at least 2 h. Thereafter, we sealed the chamber and drew a 10-ml air sample to measure initial O_2 concentration. We took a second air sample 30 min later. Following the second air sample, the snake was mechanically stimulated by manually rotating the chamber for 5 min (Miller and Hutchison, 1980), after which another 10-ml air sample was taken. During the 5-min period of stimulation, we could observe, through the transparent lid of the respirometer, that the snakes tried to right their bodies when turned on their backs, to strike, and to escape from the chamber, and that they were actively moving throughout the 5-min period of mechanical stimulation. The animals' responses to disturbance were in-

tense and were assumed to represent maximal levels of activity. We injected air samples through a column containing water + CO_2 absorbent into an oxygen analyzer (Applied Electrochemistry S3A) at a flow rate of 150 ml/min. Oxygen fractional concentrations were read directly from the digital output of the analyzer. We calculated $\dot{V}O_2$, normalized to standard temperature and pressure, using equations provided by Vleck (1987).

Data Handling and Analysis

In measuring post-prandial metabolism, snakes were used only once and were equally divided among the four meal sizes ($n = 5$ for each). Thus, for each meal size, we measured the metabolic response of five individuals. Hereafter, we refer to these groups, that consumed meals equaling 10%, 20%, 30%, or 50% of snake body mass, as G10%, G20%, G30%, and G50%, respectively.

The respirometry setup provided a large number of oxygen consumption measurements (one every 20 min) that were used to calculate mean $\dot{V}O_2$ values. Before $\dot{V}O_2$ calculations, however, we discarded the readings whenever activity was detected during the experiments, indicated by a sudden increase in the oxygen uptake values (Wang and Abe, 1994). Moreover, we also eliminated very low $\dot{V}O_2$ values that indicate long apneic periods (personal observation). After that, $\dot{V}O_2$ measured during the 24-h period prior to feeding was used to calculate each snake's standard metabolic rate (SMR). Values measured after feeding, and above SMR, were assumed to be due to the SDA. During SDA, the unsuitable readings were not eliminated, because such a procedure would affect the analysis of time and energetic variables. In such cases, the unsuitable values were normalized in relation to the mean values of proximate readings. Afterward, $\dot{V}O_2$ measurements made post-feeding were hourly averaged for each individual and subjected to a statistical and graphical program (Jandel Scientific) that generated the best curve (and related equation) describing the variation of $\dot{V}O_2$ as a function of time post-feeding. Each generated equation allowed us to identify the post-prandial maximum oxygen consumption rate ($\dot{V}O_{2peak}$), and the time to reach $\dot{V}O_{2peak}$ (T_{peak}). We integrated the area under each curve to quantify the total amount of oxygen consumed during digestion (Jobling, 1981). In all experiments, after meal ingestion, post-prandial $\dot{V}O_2$ eventually stabilized above pre-feeding values. We judge the duration of significant post-prandial response as the time it took for the lower confidence limit of the SDA curve to overlap the upper confidence limit of pre-feeding values (Bushnell et al., 1994). We observed that this occurs when $\dot{V}O_2$ readings have stabilized with respect to time. Calculations were done by using a sub-routine available on the Jandel Scientific software.

To calculate the digestive energetics of *C. durissus*, we assumed the energy yield of the mouse meal as 8.95 kJ/g wet mass (Smith, 1976), the assimilation efficiency of *C. durissus* as 80% (Greenwald and Kanter, 1974), and that each 1 ml of oxygen consumed results in the expenditure of 19.8 J (Gessman and Nagy, 1988). The product of total meal energy (8.95 times mouse mass) and assimilation efficiency provides an estimate of assimilated energy (kJ) gained. The total oxygen consumed (area under the curve) minus that used for standard metabolism is the SDA, which we equate as the cost of digestion. Subtracting the cost of digestion from the assimilated energy intake results in the energy profit from the meal. We also calculated the percentage of ingested assimilated energy that was equivalent to SDA. To calculate activity $\dot{V}O_2$ ($\dot{V}O_{2max}$), we assumed that the O_2 consumed during each snake's stimulation represented the maximum rate of oxygen consumption.

We used one-way analysis of variance (ANOVA) to test the overall effect of meal size on metabolic variables (Sokal and Rohlf, 1986). ANOVA's were followed with a post-hoc Tukey test to identify significant differences between pairs of meal sizes. To assure normality and homogeneity of variance, we log-transformed (base 10) all metabolic values prior to analyses. We present our results as $\bar{x} \pm 1$ SD and des-

TABLE 1.—Meal size and SDA in juveniles of *Crotalus durissus*. BM = snake body mass (g); SMR = "Standard Metabolic Rate" (ml $O_2 \cdot g^{-1} \cdot h^{-1}$); $\dot{V}O_{2peak}$ = maximum oxygen uptake measured during SDA (ml $O_2 \cdot g^{-1} \cdot h^{-1}$); T_{peak} = time to reach the $\dot{V}O_{2peak}$ (hours); Ts = time for $\dot{V}O_2$ return to levels approaching SMR (hours). All values presented as $\bar{x} \pm 1$ SD. Values in parentheses denote range of observations ($n = 5$ for each group).

Mean size	BM	SMR	$\dot{V}O_{2peak}$	T_{peak}	Ts
10%	57 ± 21	0.046 ± 0.017	0.17 ± 0.02	15.4 ± 4.4	62 ± 12
	(38–93)	(0.033–0.067)	(0.14–0.19)	(11–22)	(50–80)
20%	42 ± 13	0.059 ± 0.017	0.22 ± 0.04	22.2 ± 5.8	85 ± 22
	(26–61)	(0.042–0.087)	(0.19–0.28)	(17–31)	(60–110)
30%	43 ± 8	0.056 ± 0.019	0.29 ± 0.04	22.4 ± 7.3	102 ± 16
	(31–51)	(0.038–0.086)	(0.25–0.36)	(17–35)	(90–120)
50%	93 ± 11	0.049 ± 0.06	0.36 ± 0.027	33.4 ± 6.3	170 ± 12
	(83–111)	(0.04–0.055)	(0.33–0.41)	(23–40)	(150–180)

ignate the level of statistical significance as $P \leq 0.05$.

RESULTS

Variations in $\dot{V}O_2$ before and during digestion for all meal-size groups are illustrated in Fig. 1. We observed no difference in SMR among meal size treatments ($F_{3,16} = 2.09$, $P = 0.14$: Table 1) Regardless of meal size, post-prandial $\dot{V}O_2$ increased rapidly after feeding, and after reaching $\dot{V}O_{2peak}$ declined at a slower pace. We characterized the post-prandial $\dot{V}O_2$ of juvenile *C. durissus* using the following fourth-order exponential equation:

$$\dot{V}O_2 = a + b^{-0.5(\ln(x/c)/d)^2}$$

where x = time post-feeding in hours and a, b, c, and d are constants that describe the rate of change of $\dot{V}O_2$ with respect to time for each meal size (see Table 2 for constant values and accuracy of statistical prediction).

During digestion, $\dot{V}O_2$ peaked at rates 3.7–7.3 times the pre-feeding values (Table 1, Fig. 1). We found $\dot{V}O_{2peak}$ to be dependent upon meal size ($F_{3,16} = 35.3$, $P < 0.00001$), as $\dot{V}O_{2peak}$ was significantly greater in G50% and G30% compared to G10% and G20% snakes (Tukey pairwise comparisons, $P < 0.01$ in all cases), and greater in G20% than G10% snakes ($P = 0.012$). In addition, $\dot{V}O_{2peak}$ of G30% and G50% snakes were significantly greater ($P = 0.017$) than $\dot{V}O_{2max}$ resulting from forced activity ($\bar{x} = 0.23 \pm 0.05$ ml $O \cdot g^{-1} \cdot h^{-1}$, range = 0.12–0.30: Fig. 2).

The time to reach $\dot{V}O_{2peak}$ differed among meal sizes ($F_{3,16} = 7.59$, $P = 0.002$: Table 1) and was significantly greater ($P < 0.044$ in all cases) in G50% than in all other meal size groups. Following $\dot{V}O_{2peak}$, oxygen consumption gradually decreased, returning to values not significantly different than pre-feeding values within 62–170 h following ingestion (Fig. 1). The duration of elevated $\dot{V}O_2$ differed among meal sizes ($F_{3,16} = 41.1$, $P < 0.0001$: Table 1) and was significantly greater for G50% snakes compared with each other group ($P < 0.0001$ for all pairwise comparisons), and greater for G30% than for G10% snakes ($P = 0.007$).

The amount of energy assimilated increased with meal size ($F_{3,16} = 159$, $P < 0.0001$: Table 3), with significant differ-

TABLE 2.—Summary statistic and constant values of the fourth order equations (provided in text) that describe time-dependent variation in VO_2 of *Crotalus durissus* digesting meals ranging from 10–50% of its body mass. Goodness of fit for all equations was determined by the fit standard error (FSE, %). All *F*-values are significant. $P < 0.0001$ in all cases ($n = 5$ for each group).

Meal size	r^2	FSE	F_{stat}	a ± 1 SE	b ± 1 SE	c ± 1 SE	d ± 1 SE
10%	0.91	0.014	506	0.05 ± 0.003	0.15 ± 0.004	16.8 ± 0.5	0.89 ± 0.03
20%	0.96	0.011	1508	0.06 ± 0.002	0.17 ± 0.003	18.4 ± 0.3	0.91 ± 0.02
30%	0.96	0.001	1791	0.05 ± 0.003	0.26 ± 0.004	24.1 ± 0.3	0.84 ± 0.02
50%	0.98	0.01	8053	0.05 ± 0.001	0.31 ± 0.002	34.9 ± 0.2	0.93 ± 0.01

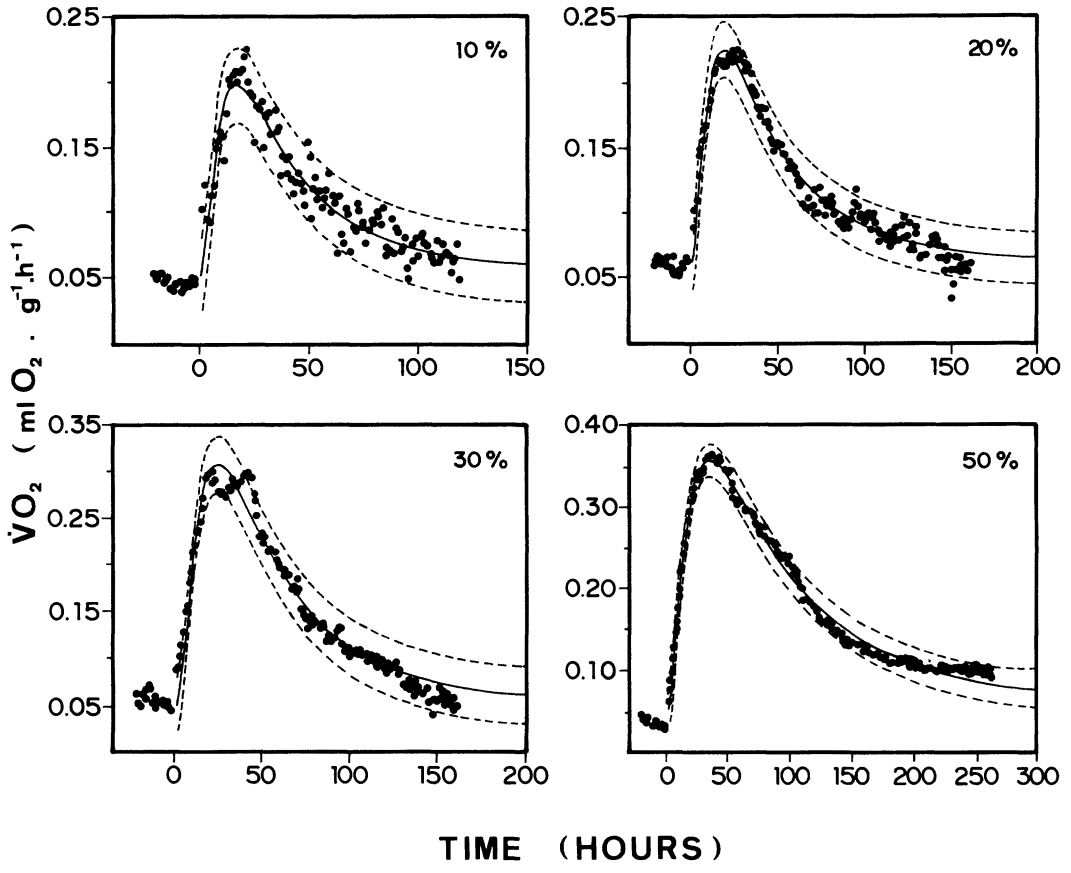

FIG. 1.—Relationship between time course variation in oxygen consumption rates ($\dot{V}O_2$) and meal size for *Crotalus durissus*. Percentages on graphs denote relative meal size (% of snake body mass). Each point represents a 1 h average of five individual measurements. Solid lines around points denote, respectively, best-equation fit and 95% confidence intervals.

ences found between G50% and the remaining groups ($P < 0.0001$ in all cases) and between G30% and G10% group ($P = 0.02$). The total energy spent on digestion (SDA) was highly dependent upon meal size ($F_{3,16} = 162$, $P < 0.0001$) and was higher in G50% snakes compared to the other meal sizes ($P < 0.0001$ in all cases), and higher in G30% snakes than for G10% snakes ($P = 0.05$). The net gain of energy (ingested assimilated energy minus SDA) also differed among meal sizes ($F_{3,16} = 111$, $P < 0.0001$: Table 3), and was significantly greater for G50% snakes than for the other three groups ($P < 0.001$ in all cases), and for G30% than G10% snakes ($P = 0.03$). The energy expended on digestion equaled 12–18% of the energy assimilated from meals and did not differ significantly among meal sizes ($F_{3,16} = 2.87$, $P = 0.07$).

DISCUSSION

Crotalus durissus experiences 3.7–7.3-fold increases in oxygen consumption 15–33 h after feeding. These values are comparable to the 7.8-fold increase reported for *Crotalus cerastes* after consuming meals weighing 26.4% of their body mass (Secor et al., 1994). The factorial scope of the post-prandial $\dot{V}O_2$ of these two rattlesnake species, however, is far below those reported for *Python molurus*, which experience 17-fold increases in $\dot{V}O_2$ after ingesting meals equaling 25% of their body mass (Secor and Diamond, 1995). Differences in the factorial scope of post-pran-

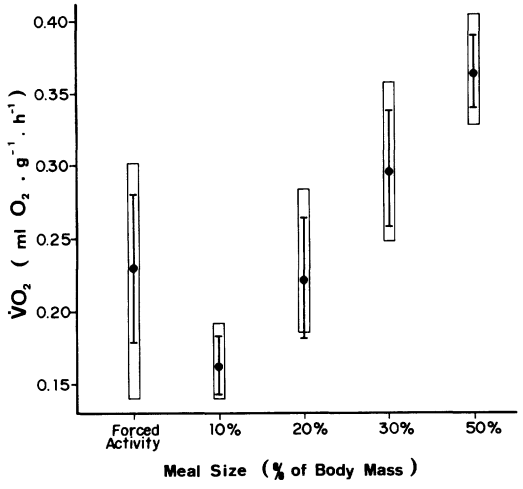

FIG. 2.—Maximum oxygen consumption rates ($\dot{V}O_2$) for *Crotalus durissus* during the digestion of meals ranging from 10–50% of the snake's mass and during mechanical stimulation (forced activity). Dots, vertical lines, and bars denote, respectively, $\bar{x}$, ± 1 SD, and range of observations.

dial metabolism can be related to the value of SMR of the animals under examination (Coulson and Hernandez, 1980; Hailey and Davies, 1987). For a given magnitude of increase in metabolic rate, the factorial scope will be higher in animals with lower SMR. However, the SMR of *P. molurus* ($\bar{x}$ = 0.034 ± 0.003 ml $O_2 \cdot g^{-1} \cdot h^{-1}$: Secor and Diamond, 1995) is in fact slightly higher than the SMR of *C. cerastes* ($\bar{x}$ = 0.030 ± 0.007 ml $O_2 \cdot g^{-1} \cdot h^{-1}$: Secor et al., 1994), but 32% less than the SMR of *C. durissus*. Therefore, characteristics other than SMR may be responsible for the greater than two-fold difference in peak factorial scopes between *Crotalus* and *Python* when digesting same size meals. First, it is possible that $\dot{V}O_{2peak}$ shows a different allometric scaling with respect to body mass than SMR. In fact, for *P. molurus* the $\dot{V}O_{2peak}$ increases with a higher slope than SMR as body mass increases (Secor and Diamond, 1997). At present, however, it is uncertain if such a pattern will hold true for snakes other than for pythons. Second, rattlesnakes could have a lower SDA factorial scope because they rely on a parenteral injection of venom to kill their prey (Gans and Elliot, 1968; Meier and Stocker, 1991), and because proteolytic enzymes present in snake venoms have been demonstrated to improve prey digestion (Thomas and Pough, 1979), it is plausible that venom injection attenuates $\dot{V}O_{2peak}$. Gathering quantitative data from a diversity of snake species, as well as examining the effects of other variables on SDA (venom injection and body mass, for example), will further our understanding of the energetics of snake digestion.

We found that $\dot{V}O_{2peak}$ increased with meal size, although showing a less than proportional increase between 30% and 50%. Similarly, Secor and Diamond (1997) found *P. molurus* to continue to experience an increase in $\dot{V}O_{2peak}$ with increased meal size (up to 111% of body mass). Therefore, in contrast to some fishes (Jobling, 1981), the post-prandial metabolic response of sit-and-wait foraging snakes does not plateau with increasing meal size. This pattern of variation in $\dot{V}O_2$ could be related to the intestinal up-regulation of

TABLE 3.—Meal size differences in the energy ingested, assimilated, and used for digestion (SDA) for juveniles of *Crotalus durissus*. Ingested = energy content of the meal (kJ). Assimilated = net energy assimilated from the meal (kJ). SDA = energy used for digestion (kJ). Profit = energy assimilated − energy used for digestion (kJ). %SDA = percentage of the total energy assimilated that is used during the SDA. All values presented as $\bar{x}$ ± 1 SD. Values in parenthesis denote the range of observations (n = 5 for each group).

Meal size	Ingested	Assimilated	SDA	Profit	%SDA
10%	51 ± 19	41 ± 15	5.3 ± 3.1	35 ± 12	12.8 ± 3.5
	(33.8–82.8)	(27.1–66.2)	(2.9–10.7)	(22.8–55.5)	(7.4–16.3)
20%	75 ± 23	60 ± 18	7.3 ± 3.2	53 ± 17	12.2 ± 4.4
	(46.3–108.6)	(37.1–86.9)	(3.4–11.1)	(33.6–76.8)	(8.2–19.5)
30%	114 ± 22	91 ± 17	13.5 ± 5.1	78 ± 13	14.4 ± 3.4
	(82.8–136.2)	(66–108.9)	(7.4–19.8)	(58.8–92.1)	(11.2–19.7)
50%	414 ± 48	331 ± 38	59.8 ± 6.3	271 ± 40	18.2 ± 2.8
	(369.3–489)	(295.4–391.6)	(54.3–68.1)	(240–337.5)	(13.7–21.2)

sit-and-wait foraging snakes (discussed below), which requires a very high level of $\dot{V}O_2$ shortly after meal ingestion. After intestinal regeneration, this high level of O_2 consumption will be no longer necessary, and $\dot{V}O_2$ starts to fall (the descendent phase of the SDA curve), with no plateau formation.

$\dot{V}O_{2peak}$ of *C. durissus* digesting meals equaling 30% and 50% of its body mass exceeded $\dot{V}O_{2max}$ attained during physical activity. Similarly, *P. molurus* digesting meals equaling 25% of its body mass also experiences increases in $\dot{V}O_2$ that surpasses rates attained during locomotion (Secor and Diamond, 1995). Recently, Secor and Diamond (1997) found *P. molurus*, while digesting meals weighing 111% of their body mass, to experience a $\dot{V}O_{2peak}$ that averaged 44 times its SMR, whereas the snakes $\dot{V}O_{2max}$, during locomotion was only six times its SMR. This suggests that the determinants of the upper limit of $\dot{V}O_{2peak}$ during digestion are probably set by variables other than those involved with muscle exercise capacity. Thus, the long standing idea of equating aerobic scope from maximum $\dot{V}O_2$ values attained during forced activity needs to be reconsidered, particularly for ectotherms. For several species of anurans, maximum $\dot{V}O_2$ attained during calling exceeds maximum $\dot{V}O_2$ during forced activity (Taigen and Wells, 1985; Wells and Taigen, 1989). Moreover, the aerobic scope reached during locomotion depicts a metabolic response that is sustained only briefly, while snakes when digesting or frogs when calling must sustain higher metabolic levels for many hours or even days.

There are numerous proposed causal mechanisms of SDA, including a well supported hypothesis that correlates SDA with the metabolic cost of growth (Ashworth, 1969; Brown and Cameron, 1991*a*,*b*; Coulson and Hernandez, 1979; Jobling, 1983; Vahl, 1984). Because growth rate is a function of post-absorptive and energetically expensive protein synthesis, the cost of protein synthesis may contribute substantially to SDA (Brown and Cameron, 1991*b*; Rosenlund et al., 1984). For sit-and-wait foraging snakes, pre-absorptive mechanisms additionally contribute to their post-prandial metabolic response. Sit-and-wait foraging snakes ingest large prey sporadically, and thus have evolved a mechanism of intestinal regulation that shuts down the gastrointestinal tract during fasting periods, in order to conserve energy (Secor and Diamond, 1994). Following feeding episodes, the unprecedented hypertrophy and functional up-regulation of the gut from a quiescent state occurs at a substantial energetic cost (Secor and Diamond, 1995; Secor et al., 1994). In a separate experiment, we forced individuals of *C. durissus* to disgorge their mouse meals (equaling 10–50% of their body mass) when the $\dot{V}O_{2peak}$ was reached (T_{peak}: from Table 1). We found the disgorged mice to be nearly intact, as only their head tissues (the mice were ingested head-first) were partially digested. Thus, the post-prandial $\dot{V}O_{2peak}$ of *C. durissus* occurs before much of the meal has been digested, indicating that the initial cost of digestion does not originate from the post-absorptive metabolic cost of growth. *Crotalus durissus*, as with other sit-and-wait foraging snakes, initially pays a high cost to prepare the gut for digestion before reaping the benefits of the ingested meal.

We calculated, for *C. durissus*, that the energy spent on digestion equals 12.2–18.2% of assimilated meal energy. The energetic return for *C. durissus* increased with meal size while the relative percent of the assimilated meal energy that equaled SDA did not differ significantly among meal sizes. However, it is possible that differences in the body composition of mice consumed by the different meal size groups may have affected our energetic estimations. Snakes fed with meals of 10%, 20%, and 30% of their mass consumed mainly neonate and juvenile mice that probably had a lower energy content than adult mice, but were assimilated with a higher efficiency. To assess these problems, detailed studies of snakes' assimilation efficiencies will be needed. In general, the estimated cost of digestion for *C. durissus* was lower than some previous estimations. For example, Hailey and Davies (1987) reported for *Natrix maura* that the

SDA resulting from the digestion of a goldfish meal weighing 10% of snake body mass was equivalent to 28% of the total meal energy. For *C. cerastes* and *P. molurus*, the SDA resulting from the digestion of rodent meals equaling approximately 25% of snake body mass equaled 28% and 32%, respectively, of assimilated meal energy (Secor and Diamond, 1995; Secor et al., 1994). Some of these differences in SDA cost may partly be attributed to differences in meal energy content and the methods to quantify SDA.

Data presently available demonstrate that digestion in snakes, especially for sit-and-wait foraging species, requires a substantial amount of energy. For example, during the active season, *C. cerastes* devotes 43% of daily energy expenditure to SDA (Secor and Nagy, 1994). On the other hand, searching, capturing, and ingesting prey are not thought to be energy demanding activities for viperids, because viperids forage by ambush and possess cranial specialization and venom that enhance prey capture (Andrews and Pough, 1985; Gans and Elliot, 1968; Meier and Stocker, 1991; Pough and Groves, 1983). For example, we have estimated for *C. durissus* that the cost of capturing and ingesting mice of 10–50% of body mass represents <1.5% of the assimilated meal energy (Abe et al., 1995; Cruz-Neto et al., unpublished data). Therefore, among the three phases of feeding in snakes [prey search, capture and ingestion, and digestion (Arnold, 1993)], the last phase is undoubtedly the most energy demanding for viperids. A feeding cost commonly neglected although directly related to prey capture by viperids is the metabolic cost of venom synthesis. Unfortunately, no attempt has been made in estimate such cost, and a cost-benefit analysis of venom synthesis will be a difficult task, because venoms have importance not just for prey capture but also for prey digestion and defense (Gans and Elliot, 1968; Meier and Stocker, 1991).

Finally, our observations on SDA and meal size in rattlesnakes depicte only a small view of a broad picture, with many questions remaining to be answered, especially regarding the mechanisms that mediate the digestive process in snakes. Further examination of other variables and other snake species would be fruitful in fulfilling this task.

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