# Determinants of the Postfeeding Metabolic Response of Burmese Pythons, *Python molurus*

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Accepted by C.P.M. 8/30/96

## ABSTRACT

The relatively large meal sizes consumed by sit-and-wait-foraging snake species make them favorable for investigating specific dynamic action, the rise in metabolic rate associated with digestion. Hence, we measured $O_2$ consumption rates ($\dot{V}O_2$) before and up to 20 d after Burmese pythons (*Python molurus*) either had only constricted and killed rodent meals or had also been allowed to consume meals ranging in size from 5% to 111% of their body mass. Postprandial $\dot{V}O_2$ peaked within 2 d at a value that increased with meal size, up to 44 times standard metabolic rate for the largest meals. In addition to being the largest known magnitude of postprandial metabolic response, this also exceeds the factorial increase in $\dot{V}O_2$ during peak physical activity for all studied animals except perhaps racehorses. Specific dynamic action, calculated from the extra $\dot{V}O_2$ above standard metabolic rate over the duration of digestion, increased with meal size and equaled 32% of ingested meal energy. The allometric exponent for body mass was 0.68 for standard metabolic rate, 0.90 for peak postprandial $\dot{V}O_2$, and 1.01 for specific dynamic action. Specific dynamic action is higher, and standard metabolic rate is lower, in sit-and-wait-foraging snake species than in actively foraging snake species. This suggests that sit-and-wait-foraging snakes, which consume large meals at long and unpredictable intervals, reduce standard metabolic rate by allowing the energetically expensive small intestine and other associated organs to atrophy between meals but thereby incur a large specific dynamic action while rebuilding those organs upon feeding.

*Physiological Zoology* 70(2):202–212. 1997.  0031-935X/97/7001-95137$02.00

## Introduction

The heat expenditure or increased metabolic rate associated with digestion, assimilation, and biosynthesis is termed "specific dynamic action" (SDA: Brody 1945; Kleiber 1975; Jobling 1981). This postfeeding response involves increases in metabolic rate by up to 50% for humans, up to 320% for most other animals, and up to 1,600% for sit-and-wait-foraging snakes (Brody 1945; Jobling 1981; Hailey and Davies 1987; Westerterp-Plantenga et al. 1992; Kalarani and Davies 1994; Janes and Chappell 1995; Secor and Diamond 1995). Many different underlying energy expenditures have been proposed as contributing to SDA, including swallowing, acid and enzyme secretion, nutrient transport, and protein synthesis (Webster 1983; Blaxter 1989; Lyndon et al. 1992).

The magnitude and duration of SDA increase intraspecifically with meal size relative to body size (Gallivan and Ronald 1981; Jobling 1981; Janes and Chappell 1995). One might therefore expect species consuming relatively large meals to experience long-maintained high levels of postprandial metabolism. Sit-and-wait-foraging snakes do consume relatively large meals, at times exceeding their own body mass in weight (Slip and Shine 1988; Greene 1992). Hence, such snakes would be good candidates for testing this prediction.

Although body mass influences SDA's magnitude (Jobling 1981), little attention has been given to its precise allometric scaling (see Tandler and Beamish 1981). Whole-animal rates of metabolism (whether basal, standard, resting, field, or maximum) scale logarithmically with body mass, with mass exponents generally in the range 0.67 to 1.00 (Peters 1983; Schmidt-Nielsen 1984; Nagy 1987). But it remains unknown whether total SDA and peak metabolic rates during digestion scale with exponents in the same range.

We used Burmese pythons to study SDA because they consume a wide range of meal sizes (up to 111% of body mass in this study), experience large increases in $\dot{V}O_2$ after feeding, remain virtually motionless during digestion (hence, postprandial metabolism involves no cost of locomotor activity), and span a 1,000-fold range in body mass (thus, they are attractive for investigating allometric relationships). Our study had four objectives: to document the time course of postprandial $\dot{V}O_2$, to determine whether pythons respond to increasing meal size by increasing $\dot{V}O_2$ and total SDA without reaching a plateau, to assess whether SDA

as a percentage of the ingested energy of the meal varies with meal size, and to determine whether standard metabolic rate (SMR), peak $\dot{V}O_2$ during digestion, and SDA scale as the same exponent of body mass.

## Material and Methods

### *Study Animals and Their Maintenance*

Burmese pythons, native to subtropical regions of Southeast Asia, are one of the largest snake species (length up to 6 m, mass up to 100 kg; Pope 1961). The 71 pythons used in this study originated from eight different clutches and were either purchased from a commercial breeder or hatched in the home of the first author. They ranged in mass from 0.1 to 12.0 kg (0.96 ± 0.14 kg [$\bar{X}$ ± SE]) and in age from 2 mo to 8 yr. Of these snakes, 64 weighed less than 2 kg and were less than 2 yr old. We housed pythons individually at 27°–30°C under a photoperiod of 14L : 10D. Snakes were fed laboratory mice and rats every other week and provided with water ad lib. Prior to metabolic measurements, we withheld food from snakes for at least 1 mo to ensure that they had become postabsorptive. We showed previously by x-ray studies, dissections, and observations that pythons at 30°C complete digestion 10–14 d after feeding and usually defecate within the following week (Secor and Diamond 1995).

### *Measurement of $\dot{V}O_2$*

We measured $\dot{V}O_2$ of pythons by closed-system respirometry as described by Vleck (1987) and Secor et al. (1994). In brief, individual respirometry chambers (3–91 L) were maintained within a temperature-controlled environmental cabinet adjusted such that chamber temperatures (and snake body temperatures) varied from 30°C by no more than 1.0°. For each sampling period, a 50-mL gas sample was first drawn from each chamber, chambers were sealed, and a second gas sample was drawn 0.2–1 h later (depending on the expected $\dot{V}O_2$). Gas samples were injected (150 mL $min^{-1}$) into an $O_2$ analyzer (Electrochemistry, model S-3A) after first passing through columns of water absorbent (Drierite) and $CO_2$ absorbent (Ascarite). We calculated $\dot{V}O_2$ (mL $g^{-1}$ $h^{-1}$), corrected for standard pressure and temperature, by equation (9) of Vleck (1987).

After the 1-mo fast, pythons were acclimated for 2–3 d in the chambers prior to metabolic measurements. We then measured each snake's $\dot{V}O_2$ daily between 0600 and 0900 hours for 3 d. The lowest measured $\dot{V}O_2$ (usually occurring on the third day) was recorded as that snake's SMR. On the morning after SMR measurements, we fed each snake one or several laboratory mice or rats such that the mass, or combined mass, of the rodent(s) equaled (within ± 2%) a selected target meal mass between 5% and 100% of the snake's body mass. Meals ranged from a single mouse (5% meals) to five subadult rats (100% meals), with the exception that the two largest pythons (11.8 and 12.0 kg) each consumed two young rabbits.

Following feeding, we measured $\dot{V}O_2$ at 12-h intervals (at 0700–0900 and 1900–2100 hours) until $\dot{V}O_2$ had begun to decline (generally within 72 h). Thereafter, we made measurements daily between 0700 and 0900 hours; these measurements were continued until $\dot{V}O_2$ returned to a value not significantly greater than its value before feeding. At 5-d intervals, snakes were removed from the respirometry chambers, weighed, provided with water, and returned to the chambers until completion of metabolic measurements. Because of changes in snake mass (increasing) and volume (decreasing) during digestion, we reestimated individual mass and volume daily in order to calculate $\dot{V}O_2$. In brief, we used snake mass prior to feeding and after digestion (increased by 40% of ingested meal mass) to interpolate (assuming linear change) daily mass values. Snake volume (estimated from combined weight of snake and meal) immediately following ingestion, during digestion, and following $\dot{V}O_2$ measurements was used to interpolate daily snake volume.

### *Effects of Meal Size*

We investigated the effect of meal size on postfeeding metabolic response of pythons (body mass = 198–1,393 g, $\bar{X}$ = 621 ± 33 g) that consumed meals equaling 5%, 15%, 25%, 35%, 45%, 55%, 65%, 75%, or 100% of their body mass. For each meal size ranging from 0% to 65% of body mass, we measured the metabolic response of eight snakes; for 75% and 100% meal sizes, we measured the response of four snakes. In addition, eight pythons (670 ± 70 g) were each given a juvenile rat (80–100 g) that it was allowed to constrict and kill, but which was removed from the snake before it could be swallowed. We thereby sought to evaluate the metabolic response following constriction alone (hereafter referred to as the "0% meal size") and to detect any metabolic changes resulting from cephalic stimulation of the digestive system, a phenomenon present among mammals (Diamond and LeBlanc 1987).

We evaluated meal-size effects on postfeeding metabolic response by quantifying the following five parameters of SDA (Fig. 1) as partly described by Jobling (1981): peak $\dot{V}O_2$, scope of peak $\dot{V}O_2$ (peak $\dot{V}O_2$/SMR), duration of significantly elevated $\dot{V}O_2$, mean $\dot{V}O_2$ (averaged $\dot{V}O_2$ during the period of significantly elevated $\dot{V}O_2$), and total magnitude of SDA (calculated as the extra $O_2$ consumed beyond SMR during the duration of significantly elevated $\dot{V}O_2$; the shaded area of Fig. 1). We converted the value of this extra $O_2$ consumed to kilojoules, assuming 19.8 J of energy expended per milliliter of $O_2$ consumed (Gessaman and Nagy 1988). We also expressed the extra $O_2$ consumed as a percentage of the energy content of the meal

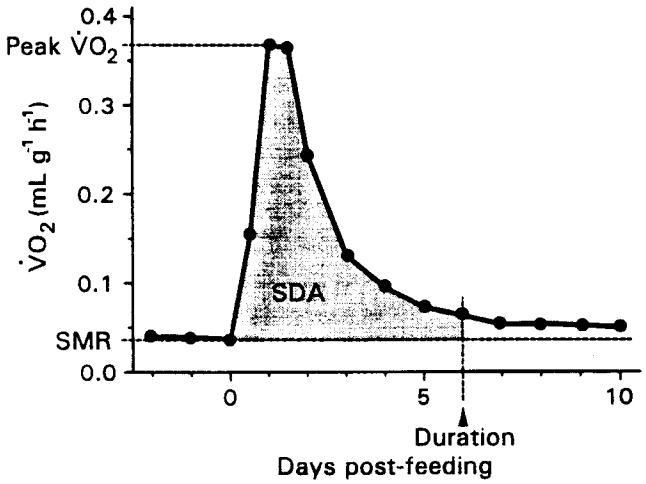


Figure 1. Pre- and postfeeding $\dot{V}O_2$ of a *Python molurus* that consumed a meal 15% of body mass to illustrate parameters measured for the postprandial metabolic response of pythons. SMR was calculated as the lowest recorded $\dot{V}O_2$ before feeding; peak $\dot{V}O_2$, as the highest recorded $\dot{V}O_2$ after feeding; duration of metabolic response, as the number of days that postfeeding $\dot{V}O_2$ values were significantly greater than prefeeding $\dot{V}O_2$ values; and SDA, as the extra $O_2$ consumed above SMR during the duration of significantly elevated $\dot{V}O_2$ (*shaded area*).

(Kleiber 1975), assuming an energy equivalent of 8 kJ $g^{-1}$ of rodent wet mass (Secor and Diamond 1995).

Snake age (ANOVA; $F_{9,62} = 1.41$, $P = 0.204$) and body mass (ANOVA, $F_{9,62} = 0.11$, $P = 0.999$) did not differ significantly among the 10 meal-size treatments. Sex and clutch of origin also did not significantly affect the measured variables or interact significantly with effects of meal size.

### *Allometry of Metabolic Response*

We used 60 pythons (mass 0.1–12.0 kg, $\bar{X} = 1.3 \pm 0.3$ kg) to assess how SMR, peak $\dot{V}O_2$ during digestion, and SDA scaled with body mass. Following measurements of SMR, each snake consumed a meal equaling 25.1% ± 0.1% of its body mass. We selected this meal size because we were confident that all snakes would easily consume it and that it would produce a substantial metabolic response (Secor and Diamond 1995). We monitored postfeeding metabolic rates of these snakes for a minimum of 2 wk, as previously described.

### *Statistical Analysis*

For each meal-size treatment, we employed a repeated-measures ANOVA (GLM procedure of SAS [SAS Institute 1988]) to test whether time (days prior to and after feeding) significantly affected $\dot{V}O_2$ (mL $g^{-1}$ $h^{-1}$). Because of the variation in snake body mass, we tested by ANCOVA whether body mass was a significant covariate and whether body mass significantly interacted with time (Zar 1974). Body mass proved not to be a significant covariate ($P > 0.08$) for the 25%, 45%, 55%, 75%, and 100% meal-size treatments. For the remaining meal-size treatments, body mass was a significant covariate ($P < 0.016$), although it significantly interacted with time for the 5% meal-size treatment ($P \leq 0.0001$). We report the results of the repeated-measures ANOVAs and note that these results are equivalent in significance to ANCOVA (body mass as covariate) results. For each meal-size treatment, we made pairwise mean comparisons in order to identify when differences in $\dot{V}O_2$ occurred between sampling times.

We tested by ANOVA and ANCOVA (body mass and age as covariate) the effects of meal-size treatments on the following parameters: SMR, peak $\dot{V}O_2$ during digestion, scope of peak $\dot{V}O_2$, mean $\dot{V}O_2$ during digestion, and SDA, alternatively expressed as kilojoules, kilojoules per kilogram per day, and percentage of ingested energy. For each variable, body mass and age proved not to be significant covariates ($P > 0.063$), with the exception of SDA expressed as kilojoules. Differences between treatment groups were assessed by pairwise mean comparisons. We used least-square regression analysis (REG procedure of SAS [SAS Institute 1988]) to test for relationships between variables and meal size (percentage of body mass consumed).

For the allometric study, we similarly used least-square regression analysis to determine how SMR, peak $\dot{V}O_2$, scope of peak $\dot{V}O_2$, and SDA scaled with body mass. Body mass and metabolic data (except for scope of peak $\dot{V}O_2$) were $\log_{10}$ transformed prior to analyses in order to linearize relationships and meet the assumptions of variance homoscedasticity (Zar 1974). We found age and sex not to contribute significantly to scaling relationships. Throughout the text, we report the results of ANOVAs in terms of their $F$ and $P$ values, and we state the $P$ values of pairwise comparisons. We take $P \leq 0.05$ as the level of statistical significance, and we present our results as mean ± 1 SE.

## Results

### *$\dot{V}O_2$ Response during Digestion*

Figure 2 depicts $\dot{V}O_2$ as a function of time for pythons digesting meals ranging in mass from 0% to 100% of body mass. For all meal sizes, $\dot{V}O_2$ proved to differ significantly ($P < 0.012$) among sampling periods (days pre- and postfeeding). Prior to feeding, $\dot{V}O_2$'s of fasting snakes were relatively stable, exhibiting a coefficient of variation of only 7.7% ± 0.6%. Within 12 h of consuming any size meal, including even noningested meals (0% meal size), pythons had significantly ($P < 0.003$) increased their $\dot{V}O_2$ over SMR, by a percentage ranging from 23% (0% meal size) to 1,170% (100% meal size). Peak $\dot{V}O_2$ occurred at 24 h (0%, 5%, 15%, and 25% meals), 36 h (35%, 45%, 65%,

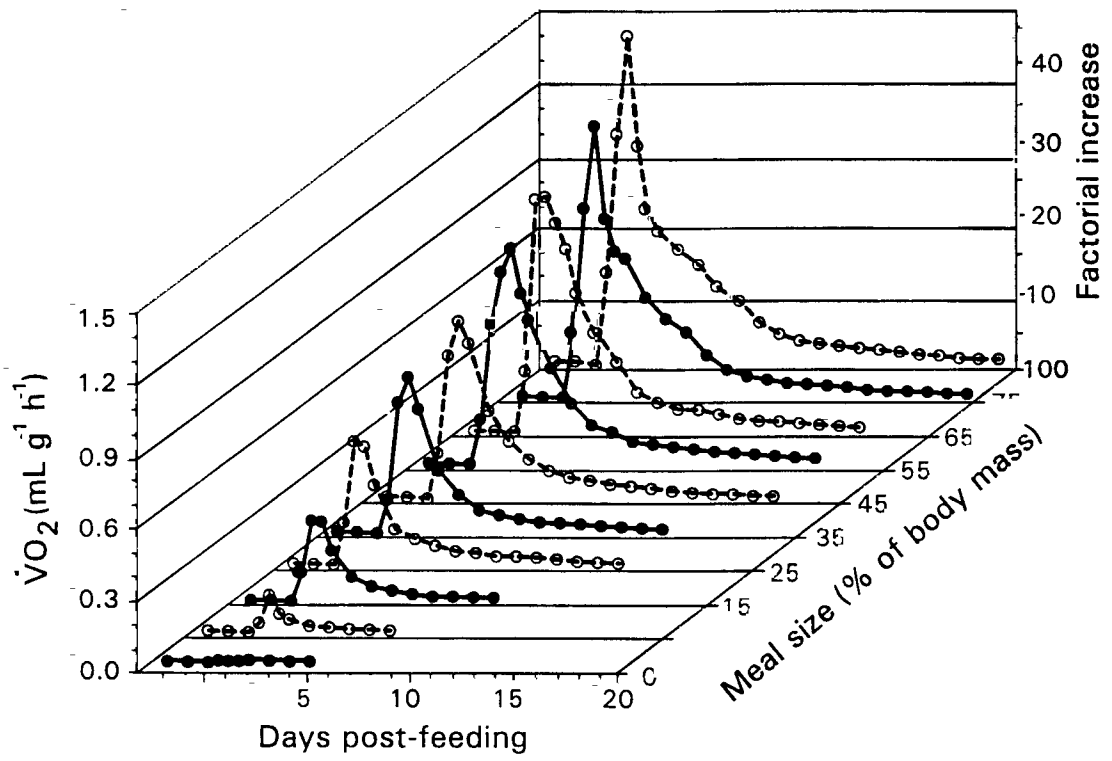


Figure 2. Mean $\dot{V}O_2$ of pythons prior to feeding and daily $\dot{V}O_2$ values for 5–20 d after feeding, for ingestion of meals varying in mass between 0% and 100% of snake body mass. $n$ = 8 for meal sizes ranging up to 65% of body mass; $n$ = 4 for 75% and 100% meal sizes. The right ordinate scale is the factorial increase of postfeeding $\dot{V}O_2$ over prefeeding values.

75%, and 100% meals), or 48 h (55% meals) postfeeding. Thereafter, $\dot{V}O_2$ declined significantly at intervals of 1–3 d depending on meal size. Eventually (at 2–16 d postfeeding), $\dot{V}O_2$ declined to values not significantly greater than those prior to feeding (Table 1).

### *Effects of Meal Size*

*SMR.* For the 10 meal-size treatments, SMR averaged 0.032 ± 0.002 to 0.038 ± 0.002 mL $O_2$ g$^{-1}$ h$^{-1}$ (Table 1). We found no significant difference in SMR among ($F_{9,62}$ = 0.81, $P$ = 0.612) or between ($P > 0.088$) meal-size treatments, undoubtedly a result of the similarity of body masses among treatments.

*Peak $\dot{V}O_2$ during Digestion.* Peak $\dot{V}O_2$ (mL g$^{-1}$ h$^{-1}$) during digestion differed significantly ($F_{9,62}$ = 93.7, $P \leq 0.0001$) among meal-size treatments. Peak rates also differed significantly ($P < 0.039$) between pairs of meal sizes (except between 55% and 65% meals and between 65% and 75% meals). With each increase in meal size, pythons responded with higher levels of peak $\dot{V}O_2$ (Table 1). Over the range of meal sizes (0%–111% of body mass), peak $\dot{V}O_2$ increased curvilinearly with meal size (expressed as actual percentage of snake body mass) according to the following quadratic equation: peak $\dot{V}O_2$ = 0.09 + 0.02 (meal size) − 0.0001 (meal size)$^2$ ($F_{2,69}$ = 500, $P \leq 0.0001$, $r^2$ = 0.936). Although this relationship is significantly curvilinear, peak $\dot{V}O_2$ did not plateau at even the largest meal size studied (Fig. 3*A*).

*Scope of Peak $\dot{V}O_2$.* The ratio of peak $\dot{V}O_2$ to SMR increased significantly ($F_{2,69}$ = 385, $P \leq 0.0001$, $r^2$ = 0.918) with meal size according to the following quadratic equation: scope = 2.4 + 0.5 (meal size) − 0.001 (meal size)$^2$ (Fig. 3*B*).

*Duration of Elevated $\dot{V}O_2$.* The duration of the postfeeding metabolic response, measured as the time between ingestion and the time when $\dot{V}O_2$ was no longer significantly greater than SMR, increased with meal size (Table 1), from 4 d for 5% meals to 16 d for 100% meals.

*Mean $\dot{V}O_2$.* $\dot{V}O_2$ averaged over the duration of significantly elevated rates differed significantly ($F_{9,62}$ = 137, $P \leq 0.0001$) among all and between most meal-size treatments. Mean $\dot{V}O_2$ increased with meal size (Fig. 3*C*) from 0.11 ± 0.01 mL g$^{-1}$ h$^{-1}$ for 5% meals to 0.33 ± 0.02 mL g$^{-1}$ h$^{-1}$ for 100% meals.

Table 1: Body mass, SMR, and five parameters of the metabolic response to feeding as a function of meal size for juvenile *Python molurus* at 30°C

| Meal Size (% body mass) | *n* | Body Mass (g) | SMR ($mL\ g^{-1}\ h^{-1}$) | Peak $\dot{V}O_2$ ($mL\ g^{-1}\ h^{-1}$) | Scope (peak $\dot{V}O_2$/SMR) | Duration (d) | Mean $\dot{V}O_2$ ($mL\ g^{-1}\ h^{-1}$) | SDA | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | mL $O_2$ | kJ | $kJ\ kg^{-1}\ d^{-1}$ | % Ingested Energy |
| 0 | 8 | 670 ± 70 | .036 ± .002 | .051 ± .002 | 1.4 ± .1 | 2 | .044 ± .002 | 270 ± 80 | 5 ± 2 | 4 ± 1 | . . . |
| 5 | 8 | 680 ± 130 | .038 ± .002 | .19 ± .02 | 5.1 ± .3 | 4 | .11 ± .01 | 3,800 ± 500 | 80 ± 11 | 30 ± 2 | 29 ± 2 |
| 15 | 8 | 680 ± 120 | .038 ± .002 | .40 ± .03 | 11 ± 1 | 6 | .16 ± .01 | 12,000 ± 2,100 | 240 ± 40 | 59 ± 4 | 29 ± 2 |
| 25 | 8 | 690 ± 140 | .036 ± .002 | .55 ± .04 | 16 ± 1 | 8 | .20 ± .01 | 21,000 ± 4,200 | 420 ± 80 | 75 ± 3 | 30 ± 1 |
| 35 | 8 | 690 ± 70 | .038 ± .002 | .69 ± .03 | 19 ± 1 | 10 | .23 ± .01 | 30,000 ± 2,900 | 600 ± 60 | 88 ± 5 | 31 ± 1 |
| 45 | 8 | 640 ± 60 | .037 ± .002 | .81 ± .03 | 22 ± 2 | 12 | .25 ± .01 | 38,000 ± 3,700 | 760 ± 70 | 100 ± 3 | 33 ± 1 |
| 55 | 8 | 670 ± 60 | .034 ± .001 | .96 ± .04 | 28 ± 2 | 13 | .30 ± .01 | 56,000 ± 6,100 | 1,110 ± 120 | 126 ± 4 | 37 ± 1 |
| 65 | 8 | 680 ± 60 | .034 ± .001 | 1.05 ± .06 | 32 ± 2 | 14 | .32 ± .01 | 65,000 ± 6,500 | 1,280 ± 130 | 134 ± 5 | 36 ± 1 |
| 75 | 4 | 680 ± 110 | .035 ± .002 | 1.17 ± .09 | 33 ± 3 | 14 | .33 ± .01 | 65,000 ± 12,000 | 1,290 ± 240 | 134 ± 5 | 31 ± 1 |
| 100 | 4 | 790 ± 220 | .032 ± .002 | 1.39 ± .11 | 44 ± 2 | 16 | .33 ± .02 | 90,000 ± 25,000 | 1,790 ± 500 | 140 ± 8 | 28 ± 2 |

Note. Duration refers to the duration of metabolic response (the number of days that postfeeding $\dot{V}O_2$ values were significantly greater than prefeeding $\dot{V}O_2$s. SDA is expressed alternatively in mL $O_2$, the energy equivalent (kJ), mean daily energy expenditure ($kJ\ kg^{-1}\ d^{-1}$), and percentage of ingested energy. *n* = sample size. Values are presented as means ± 1 SE.

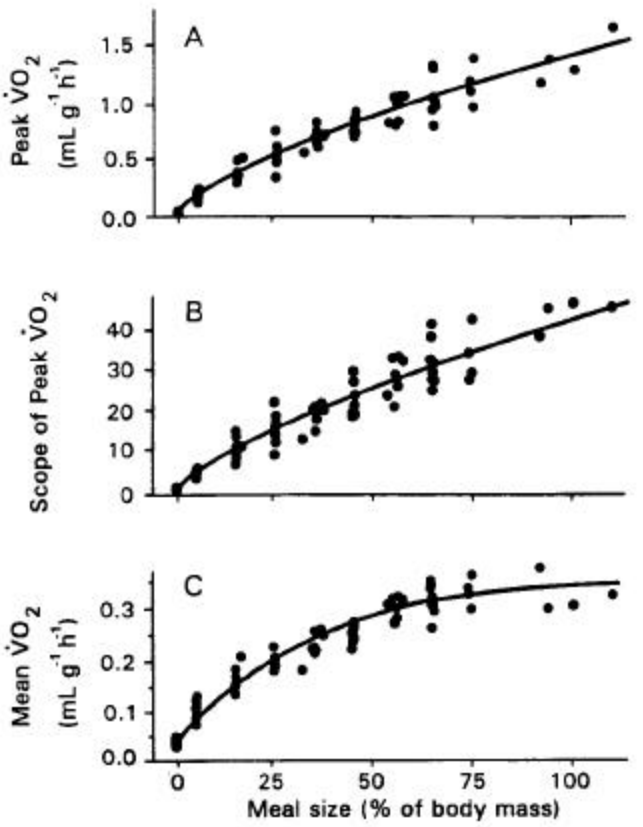


Figure 3. Peak $\dot{V}O_2$ (*A*), scope of peak $\dot{V}O_2$ (peak $\dot{V}O_2$/SMR) (*B*), and mean $\dot{V}O_2$ (averaged over the duration of significantly elevated $\dot{V}O_2$) (*C*), plotted against relative meal size (expressed as percentage of snake body mass). The lines are the best-fit curvilinear relationship between the ordinate variable and meal size. Note that all variables increase with meal size, but only mean $\dot{V}O_2$ appears to reach a plateau for large meals.

The relationship between mean $\dot{V}O_2$ and meal size fits the following quadratic equation: mean $\dot{V}O_2 = 0.062 + 0.006$ (meal size) $- 0.00003$ (meal size)$^2$ ($F_{2,69} = 565$, $P \leq 0.0001$, $r^2 = 0.942$). The shape of this relationship suggests a plateau of mean $\dot{V}O_2$ above meal sizes 55% of body mass (Fig. 3*C*).

*SDA.* Expressed as the total volume of $O_2$ consumed above SMR during digestion or as its energy equivalent (kJ), SDA differed significantly among ($F_{9,62} = 20.8$, $P \leq 0.0001$) and between ($P < 0.041$) meal-size treatments (except between consecutive pairs of meal sizes). A stepwise regression demonstrated that, together with meal size (as percentage of body mass consumed), body mass contributed significantly to determining SDA. Hence, the energy equivalent (kJ) of SDA can be explained by the following equation: SDA (kJ) = 18.0 (meal size) + 0.9 (body mass) − 577 ($F_{2,69} = 181$, $P \leq 0.0001$, $r^2 = 0.840$). In this multiple regression, meal size and body mass account for 71% and 13%, respectively, of the variance in SDA.

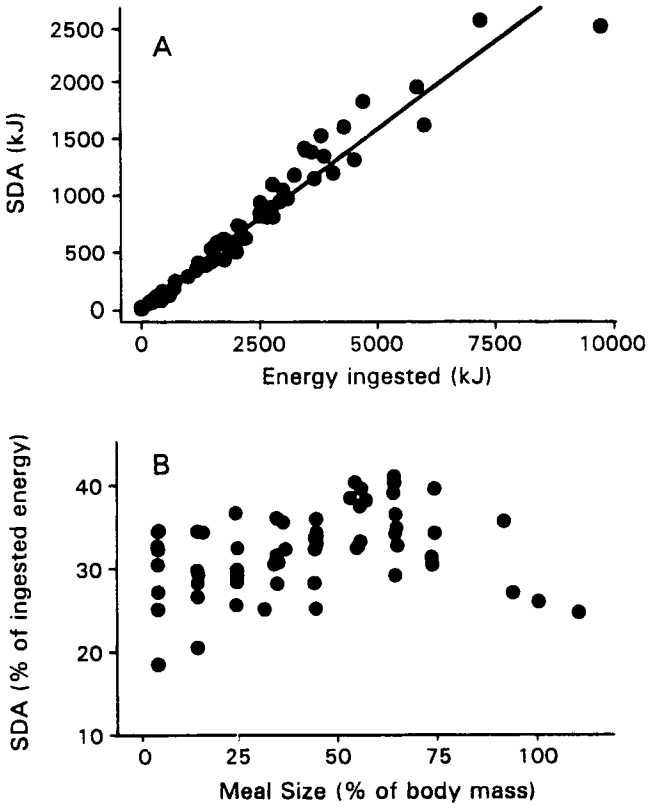


Figure 4. SDA, either expressed as kilojoules and plotted against ingested meal energy (*A*), or expressed as percentage of ingested meal energy and plotted against relative meal size (*B*). Note that SDA increases nearly linearly with energy ingested. SDA as a percentage of ingested energy reaches a maximum at meals 55% to 65% of body mass.

SDA (kJ) is also accurately predicted ($F_{1,70}$ = 1,380, $P \leq 0.0001$, $r^2 = 0.951$) by actual meal mass (g) or by the amount of energy ingested (kJ), according to the respective linear relationships: SDA (kJ) = 2.6 (meal mass [g]) + 19.0, or SDA (kJ) = 0.32 (kJ ingested) + 19.1 (Fig. 4*A*). The *y*-intercepts of both of these relationships (no meals consumed) did not differ significantly ($P = 0.42$) from zero.

Mean daily expenditure of SDA (kJ $kg^{-1}$ $d^{-1}$) differed among meal sizes ($F_{9,62}$ = 146, $P \leq 0.0001$), increased with meal size (actual percentage of body mass consumed), and plateaued at high meal sizes (Table 1). This curvilinear relationship is expressed by the following quadratic equation: SDA (kJ $kg^{-1}$ $d^{-1}$) = 11.2 + 2.9 (meal size) − 0.02 (meal size)$^2$ ($F_{2,69}$ = 596, $P \leq 0.0001$, $r^2 = 0.945$). During the time (14–16 d) that pythons were digesting the three largest meals (65%, 75%, and 100% of body mass), their daily energy expenditure of SDA averaged 8.6 times daily SMR (kJ $kg^{-1}$ $d^{-1}$).

Historically, SDA has also been quantified as a proportion of the ingested energy of the meal (Kleiber 1975; Jobling 1981). For pythons, this measure of SDA differed slightly but significantly ($F_{8,55}$ = 4.28, $P = 0.0005$) among meal-size treatments (Fig. 4*B*): 29% ± 2% for small meals (5%–15% of body mass), peaking at 37% ± 1% for 55% meals and then declining to 28% ± 2% for 100% meals (Table 1). For all meals consumed, the energy cost of SDA averaged 32 ± 1% of the energy ingested.

### *Allometric Relationships of Metabolic Response*

The SMR of the pythons (body mass = 0.1–12.0 kg, $n$ = 60) averaged 0.036 ± 0.002 mL $O_2$ $g^{-1}$ $h^{-1}$ (range = 0.016–0.070 mL $O_2$ $g^{-1}$ $h^{-1}$). Whole-animal SMR values (mL $O_2$ $h^{-1}$) scaled significantly with body mass (g) according to the following equation: log SMR = 0.68 (log body mass) − 0.58 (Table 2). Body mass accounted for 94.3% of the variance in SMR. Peak $\dot{V}O_2$ during digestion (mL $h^{-1}$) also scaled significantly with body mass (Table 2). We found a significant difference ($t_{116}$ = 6.2, $P < 0.001$) between the allometric mass exponents of SMR (0.68) and peak $\dot{V}O_2$ (0.90), determined on the same individuals just a few days apart. Individual pythons with higher-than-average SMR did not tend to possess higher-than-average peak $\dot{V}O_2$; that is, residuals of SMR and peak $\dot{V}O_2$, obtained from regressing $\dot{V}O_2$ (mL $h^{-1}$) on body mass, were not significantly correlated ($r = 0.23$, $P = 0.08$; Fig. 5*A*). The scope of peak $\dot{V}O_2$ increased linearly with body mass (Table 2), mainly because peak $\dot{V}O_2$ itself increased more steeply with body mass than did SMR.

SDA, calculated either as total extra $O_2$ consumed (mL) above SMR or as energy expended (kJ) during digestion, also scaled significantly with body mass (Table 2). The mass exponent of this scaling relationship (1.01 ± 0.02) did not differ from 1.0 and was significantly greater than the mass exponents of either SMR ($t_{116}$ = 10.3, $P < 0.001$) or peak $\dot{V}O_2$ ($t_{116}$ = 2.97, $P < 0.01$). Body mass (log transformed) accounted for 97.2% of the variance in SDA (log transformed). Whereas there was no significant correlation between the residuals of SMR and SDA, residuals of peak $\dot{V}O_2$ and SDA were significantly correlated ($r = 0.745$, $P \leq 0.0001$); that is, individuals with higher-than-predicted peak $\dot{V}O_2$ tended to have higher-than-predicted SDA (Fig. 5*B*). Body mass had no significant effect ($P = 0.67$) on daily expenditure of SDA normalized to body mass (kJ $kg^{-1}$ $d^{-1}$) or on the cost of SDA expressed as a percentage of ingested energy (Table 2). Among these 60 individuals consuming 25% meals, the calculated energy expended on SDA averaged 32% ± 1% of the energy ingested.

## Discussion

### *Time Dependence and Meal-Size Dependence of Postprandial $\dot{V}O_2$*

Postprandial metabolic response, characterized by a rapid increase in $\dot{V}O_2$ upon feeding and then a slower decline after