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# The Effects of Fasting Duration on the Metabolic Response to Feeding in *Python molurus*: An Evaluation of the Energetic Costs Associated with Gastrointestinal Growth and Upregulation

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## ABSTRACT

The oxygen uptake of *Python molurus* increases enormously following feeding, and the elevated metabolism coincides with rapid growth of the gastrointestinal organs. There are opposing views regarding the energetic costs of the gastrointestinal hypertrophy, and this study concerns the metabolic response to feeding after fasting periods of different duration. Since mass and function of the gastrointestinal organs remain elevated for several days after feeding, the metabolic increment following a second meal given soon after the first can reveal whether the metabolic costs relate to the upregulation of gastrointestinal organs or merely the metabolic cost of processing a meal. Eight juvenile pythons were kept on a regular feeding regime for 6 mo after hatching. At the beginning of the metabolic measurements, they were fed mice (20% of body mass), and the metabolic response to similarly sized meals was determined following 3, 5, 7, 14, 21, 30, and 60 d of fasting. Our data show that the metabolic response following feeding was large, ranging from 21% to 35% of ingested energy (mean = 27%), but the metabolic response seems independent of fasting duration. Hence, the extraordinarily large cost of digestion in *P. molurus* does not appear to correlate with increased function and growth of gastrointestinal organs but must be associated with other physiological processes.

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## Introduction

Animals continuously respond to environmental or behavioral demands by physiological responses or structural adjustments

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that ensure appropriate function. The morphological responses, often referred to as “adaptive phenotypic flexibility,” are generally believed to match maintenance costs of a structure with functional demands (e.g., Piersma and Lindstrom 1997). The gastrointestinal organs of snakes appear to provide an exceptional example of phenotypic flexibility. For example, for the Burmese python (*Python molurus*), one large meal (25%–50% of body mass), following a fasting period of 30 d, evokes a doubling of intestinal mass and large increases in intestinal brush-border transport capacities within 24–48 h (Secor and Diamond 1998). It has also been reported that the mass of other organs increases following feeding (Secor and Diamond 1997b, 1998). The extensive postprandial growth and upregulated function of the gastrointestinal tract of pythons is concurrent with a large metabolic increment (specific dynamic action [SDA]) where oxygen consumption increases several-fold above resting values. Among snakes, it has been reported that the cost of digestion (energy used relative to energy uptake) is larger in species that naturally undergo prolonged fasting periods and ingest very large meals, compared with species that feed more frequently (Secor 2001). The considerably higher cost of digestion correlates with larger changes in intestinal mass and function of species that feed infrequently (Secor and Diamond 2000). On this basis, Secor and Diamond (1998, 2000) suggested that infrequently feeding species downregulate function and mass of their guts following feeding as a mechanism to reduce the maintenance cost of their digestive organs during fasting. In contrast, it was suggested that species that feed frequently maintain gastrointestinal performance during fasting at the expense of a higher standard metabolism (Secor and Diamond 1998, 2000; cf. Hailey 1998).

The apparent specific dynamic action of food incorporates the cost of digestion, absorption, and assimilation of food as well as prey handling and gastrointestinal growth. It has been assumed that the rapid and extensive increase in gastrointestinal mass and function following ingestion is energetically expensive for infrequently feeding snakes and that this upregulation, therefore, constitutes a major contributor to the SDA response. Furthermore, because most of the SDA response occurs before nutrients of the meal can be absorbed, the costs of initiating digestion and gastrointestinal growth appear to be covered by endogenous energy stores. Working on *P. molurus*, Secor and Diamond (1995) referred to this phenomenon as “pay before pumping.” However, the energetic consequences of the phe-

notypic flexibility of the intestine, and thereby the energetic model proposing a correlation between organ flexibility and feeding regime, have recently been challenged. For several species of snakes, intestinal growth is primarily caused by an increase in the size of the enterocytes (hypertrophy), while cell proliferation (hyperplasia) increases only modestly (Secor et al. 1994, 2000b; Jackson and Perry 2000; Starck and Beese 2001, 2002). Based on morphological changes of the small intestine in *P. molurus* after feeding, Starck and Beese (2001) suggested that intestinal growth is energetically inexpensive and that intestinal hypertrophy does not contribute significantly to the SDA response of *Python*.

To investigate the opposing views regarding the energetic cost of increased intestinal mass in infrequently feeding snakes, we compared the metabolic response to voluntary feeding following fasting periods of 3–60 d in the Burmese python (*P. molurus*). Gastrointestinal mass and intestinal nutrient uptake rates of Burmese pythons remain elevated at least 6 d following the ingestion of a meal equaling 25% of their body mass (Secor and Diamond 1995). Therefore, the metabolic increment following a second meal taken soon after the first meal, and before the downregulation of the gut, will reveal to what extent the metabolic increment following a meal relates to the reformation of digestive organs or merely to the metabolic cost of handling a meal. Thus, if growth of the stomach and intestines constitutes a significant proportion of the SDA response, the magnitude of the SDA response would be smaller in the second, closely spaced meal and increase progressively with the fasting duration between meals.

In this study, we report on measurements of oxygen uptake ( $\dot{V}O_2$ ) and carbon dioxide excretion ( $\dot{V}CO_2$ ) in *P. molurus* over a continuous period of 6 mo where the snakes were fed similar meal sizes following various fasting times. On the basis of these measurements, we calculate the cost of digestion (SDA) to evaluate the energetic costs of digestion with specific attention to the costs of intestinal upregulation.

## Material and Methods

### Experimental Animals

Eight juvenile Burmese pythons (*Python molurus*) were purchased from a commercial supplier and kept for 6 mo at Aarhus University before experiments. The snakes were housed in a 1.5 × 0.8 × 1.0-m container at a 12L : 12D cycle until use. All snakes fed voluntarily on a diet of mice and gained weight during this period. The average body mass was 154 ± 10 g at the start of the experiment and 447 ± 27 g when the experiments ended.

Sixty days before the first measurements of gas exchange, the snakes were allowed to consume approximately 30% of their body mass and were then placed in individual plastic respirometry chambers (2.6–2.9 L) situated in a climatic chamber maintained at 30°C. The plastic respirometry chambers were

airtight with two small holes for continuous ventilation supplied by mechanical pumps. The snakes always had access to water ad lib., and feces, urine, and shed skin were collected daily throughout the experimental period.

### Measurements of $\dot{V}O_2$ and $\dot{V}CO_2$

Rates of  $\dot{V}O_2$  and  $\dot{V}CO_2$  were measured using closed-system respirometry. At the start of each measurement, a 30-mL gas sample was withdrawn from each chamber with a syringe and injected into serially connected  $O_2$  (S-3A/I) and  $CO_2$  (CD-3A) analyzers (Applied Electrochemistry, Sunnyvale, Calif.) for measurement of fractional content of  $O_2$  and  $CO_2$  ( $F_{O_2}$  and  $F_{CO_2}$ , respectively). The chambers were then sealed for 20–60 min, depending on the digestive state of the snake, after which a second gas sample was withdrawn for  $O_2$  and  $CO_2$  analysis. The gas samples taken from the respirometers were fully saturated with water by adding small water droplets to the syringe, and the gas analyzers were calibrated using saturated gas mixtures. Throughout the study,  $F_{CO_2}$  never exceeded 2.5%, and  $F_{O_2}$  was never below 18% (Secor and Diamond [1997b] reported that pythons were unaffected by  $CO_2$  and  $O_2$  fractions within these limits).

The respiratory gas exchange ratio (RE) was calculated as

$$RE = \frac{F_{end}CO_2 - F_{start}CO_2}{F_{start}O_2 - F_{end}O_2},$$

where  $F_{start}$  and  $F_{end}$  denote the fractions of  $CO_2$  or  $O_2$  determined at the start and end of the measurement.  $\dot{V}O_2$  and  $\dot{V}CO_2$  were calculated as described by Vleck (1987):

$$\dot{V}O_2 = \frac{V_{chamber} \times (F_{start}O_2 - F_{end}O_2)}{1 - (1 - RE) \times F_{start}O_2} / t$$

and

$$\dot{V}CO_2 = RE \times \dot{V}O_2.$$

$V_{chamber}$  is the volume of the respirometer chamber minus the volume of the water container and the experimental animal (assuming a density of 1 mL g<sup>-1</sup>), and  $t$  is the period during which the chamber was sealed. We corrected  $\dot{V}O_2$  and  $\dot{V}CO_2$  to STPD and calculated mass-specific rates of gas exchange using daily calculated body mass as described below.

### Experimental Protocol and Calculation of Meal Size

The eight snakes were divided into two groups of four individuals each. Both groups were exposed to the same fasting periods but differed in the order of fasting durations. Group 1 was fed after fasting periods of 60, 3, 30, 5, 21, 7, and 14 d, whereas group 2 was fed after 60, 5, 30, 3, 21, 14, and 7 d of

fasting. After these experiments, additional measurements of gas exchange were performed after 30 and 60 d of fasting for group 1 and 2, respectively. These measurements were made to investigate whether the SDA response changed over the experimental period and to measure an entire SDA response (following 30 and 60 d of fasting) without a temporally overlapping meal commencing soon after.

$\dot{V}O_2$  and  $\dot{V}CO_2$  were measured twice a day (at approximately 8:00 A.M. and 8:00 P.M.) during the first 3 d following a meal. Subsequently,  $\dot{V}O_2$  and  $\dot{V}CO_2$  were measured once a day (8:00 A.M.) until 14 d after feeding, after which gas exchange rates were measured at least twice a week. Measurements were discarded if animals were visibly active. The respiratory chambers were examined daily for feces and uric acid pellets to determine the time of defecation and excretion of nitrogenous waste.

Each snake for each feeding trail was fed mice (15–35 g per mouse) such that the total meal mass was equivalent to 20% (range = 19%–21%) of the snake's body mass. Because part of the ingested food remains undigested within the gastrointestinal organs or is retained as feces within the large intestine, we calculated actual snake body mass daily during the 3 wk following a meal. We used the calculated snake body mass to determine appropriate meal sizes for closely spaced meals and to calculate mass-specific rates of gas exchange. Body mass was calculated by assuming a constant rate of mass gain of 5% of the consumed meal per day for 10 d following feeding (i.e., a total assimilation of 50% of ingested mass). The implications of these assumptions are discussed below in "Critique of Assumptions." Since the snakes did not always defecate within the first 10 d, we continued to use the calculated body mass until 3 wk after feeding, when most snakes had defecated. Hence, body mass was assumed to be constant from day 10 until day 21 following a meal. After day 21, we assumed that body mass equaled the measured values.

#### Calculation of Specific Dynamic Action (SDA)

The standard metabolic rate (dark gray area in Fig. 1A) was calculated as the mean of all measurements where the animal had fasted longer than 14 d. SDA (light gray area in Fig. 1A) was calculated as the energy consumption exceeding that of the standard metabolic rate. SDA was calculated from the time of feeding until 14 d after feeding, after which  $\dot{V}O_2$  had returned to resting values.  $\dot{V}O_2$  was converted to Joules using a conversion factor of 19.67 J mL<sup>-1</sup> O<sub>2</sub> (Gessaman and Nagy 1988), and SDA was reported as the SDA coefficient (Jobling and Davies 1980), that is, energy expended divided by energy ingested, assuming an energy content of 8 kJ g<sup>-1</sup> rodent (Secor and Diamond 1995).

When fasting periods are short (3, 5, and 7 d), the metabolic increments associated with the two meals overlap temporally as depicted in Figure 1B. The cost of the first meal equals areas A + B, whereas the cost of the second meal equals area C. It

is, however, only possible to measure area A and the sum of areas B and C. To estimate B, we used data from all SDA responses after at least 2 wk of fasting and without subsequent meals in the following 2 wk. These data are shown as the fraction of the entire SDA response versus time in Figure 1C and allow for an estimation of the relationship between the size of areas A and B at any given time (days 1–14) following feeding. Accordingly, the SDA response of the first meal was calculated as area A (measured) + area B, where area B equals a known percentage of area A (Fig. 1C). Likewise, the second meal was calculated as area B + C (measured) – area B (percentage of area A). This procedure relies on the assumption that the SDA response of all meals in our study follows the same temporal pattern.

#### Statistical Analysis

The SDA response was tested for differences in relation to the two factors (1) fasting duration and (2) experimental group using a two-way ANOVA for repeated measures. A post hoc Student-Newman-Keuls test was used to identify possible significant differences between groups and fasting periods. As no differences were found between experimental groups, the groups were pooled, and the test was reduced to a one-way ANOVA testing for differences between fasting times. A paired *t*-test was used to compare the results from the additional fasting periods occurring at the end of the experimental period with those measured earlier (30 d [group 1] and 60 d [group 2]). Statistical analysis was made using Sigma Stat for Windows, version 2.03, and a *P* < 0.05 level of significance as an indication of significant differences. Data are presented as means ± 1 SEM.

#### Results

$\dot{V}O_2$  of both experimental groups are presented for the entire duration of the study in Figure 2A.  $\dot{V}O_2$  of fasting snakes (minimum of 14 d since previous meal) was  $0.59 \pm 0.02$  and  $0.57 \pm 0.01$  mL O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> for groups 1 and 2, respectively, and remained constant throughout the entire study (Fig. 2A).  $\dot{V}CO_2$  values of resting snakes were  $0.44 \pm 0.02$  mL CO<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> for both groups, resulting in respiratory exchange ratios of  $0.75 \pm 0.01$  and  $0.76 \pm 0.01$  for groups 1 and 2, respectively. Following the ingestion of each meal, the SDA response was characterized by a rapid increase in gas exchange during the first 12 h, with  $\dot{V}O_2$  peaking at approximately 5–6 mL O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> 1.5–2 d after feeding. The highest recorded  $\dot{V}O_2$  occurred following a second meal given shortly after the first meal, indicating an additive effect of the SDA responses. RE ranged between 0.65 and 0.85 in 90% of the measurements, with no obvious trends associated with feeding (Fig. 2B).

The SDA coefficient ranged between 21% and 35% (mean = 27% ± 1%) (Fig. 3), and the values of the two ex-

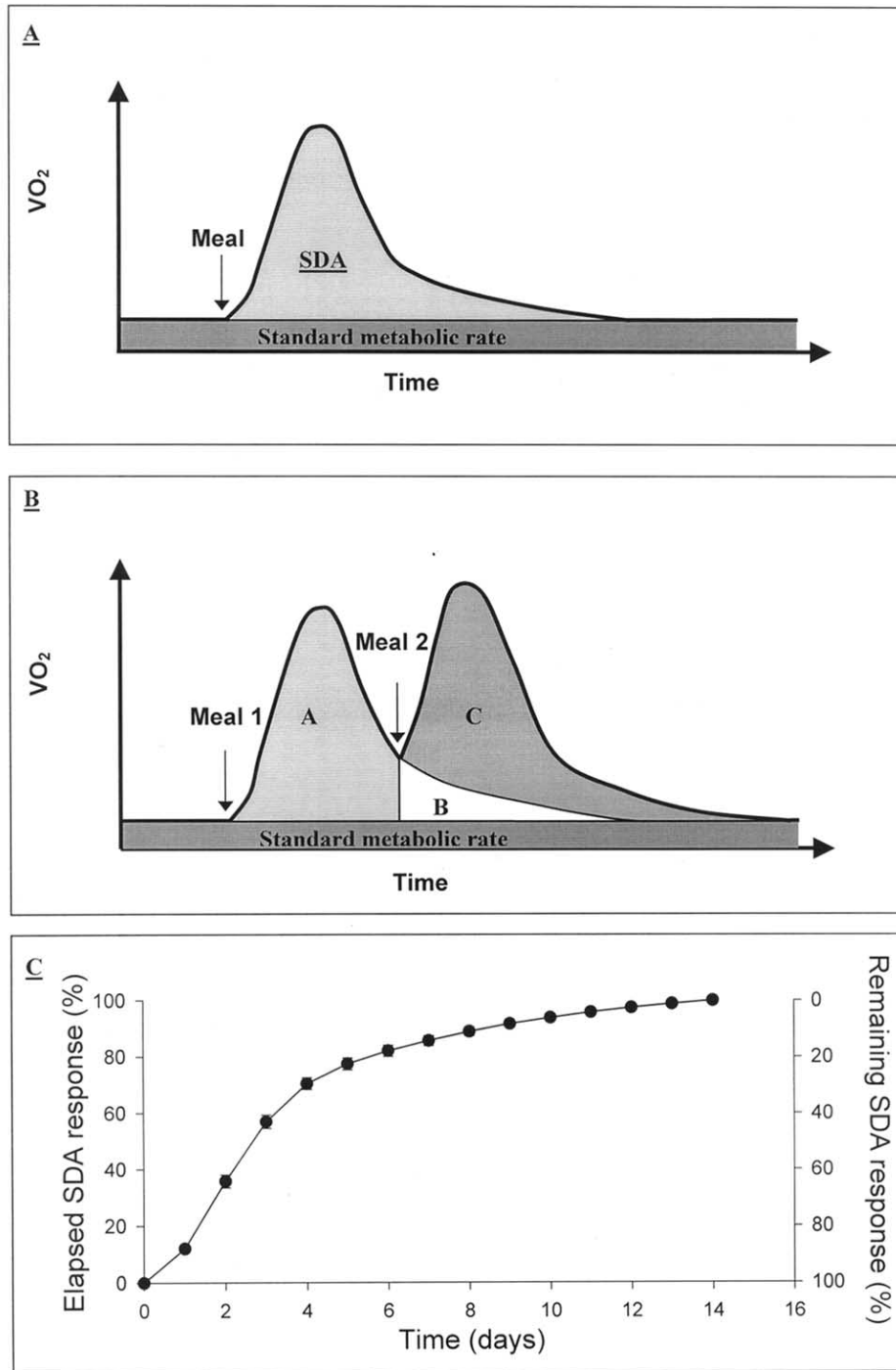


Figure 1. Temporal development of SDA response. *A*, Schematic presentation of the metabolic response to feeding. The bottom dark gray area is the oxygen used for standard metabolic rate, and the light gray area is the  $\dot{V}\text{O}_2$  associated with digestion. *B*, Schematic presentation of the metabolic response to feeding following two temporally overlapping meals. The bottom dark gray area is the  $\dot{V}\text{O}_2$  associated with standard metabolic rate. Areas *A* and *B* represent the specific dynamic action (SDA) associated with the first meal, and area *C* represents the SDA associated with the second meal. *C*, Temporal development of the SDA response following feeding. The total costs associated with digestion (100%) have, per definition, taken place 14 d after feeding. (See text for further explanation.)

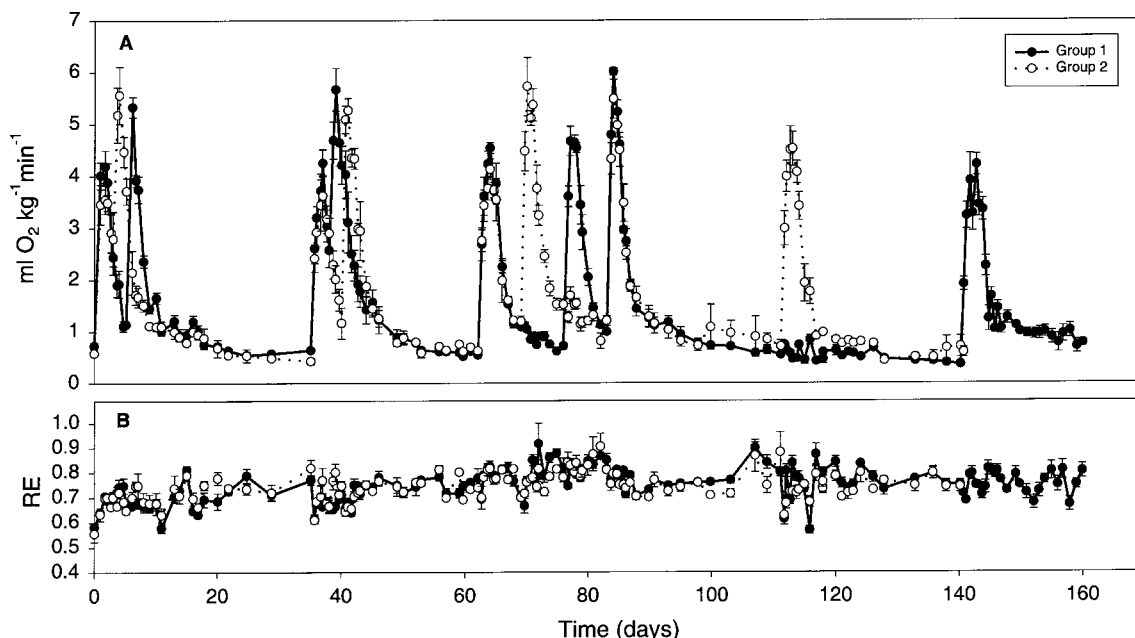


Figure 2. Gas exchange of digesting *Python molurus* following various fasting periods. (A)  $\dot{V}\text{O}_2$  and (B) respiratory exchange ratio (RE) of pythons during the experimental period. The snakes were divided into two groups of four individuals that differed in the order of fasting periods. The snakes were maintained at 30°C and were repeatedly fed meals of 20% of body mass. Data are presented as mean  $\pm$  SEM.

perimental groups were not statistically different, after which the groups were pooled. The one-way ANOVA revealed that the SDA coefficient after the 7-d fast differed from the responses following 30- or 60-d fasting periods (Fig. 3).

The SDA responses following 30 and 60 d of fasting measured at the start and the end of the experimental period were not different following 30 d of fasting for group 1 ( $23\% \pm 1\%$  and  $27\% \pm 2\%$  at the start and end, respectively). However, for group 2, the SDA coefficient after 60 d was significantly larger ( $29\% \pm 1\%$ ) at the end of the experimental period, where the entire SDA response was measured, compared with the initial value ( $25\% \pm 1\%$ ), which was calculated according to the principle in Figure 1B.

Growth efficiency (assimilation), which was estimated as total mass gained divided by mass ingested, was  $66\% \pm 2\%$  over the entire experimental period. The time at which uric acid pellets and feces were excreted are presented in Figure 4. Out of the 79 recorded events of defecation or uric acid excretion, 78 occurred within the first 3 wk following a meal (or group of closely occurring meals). All snakes excreted uric acid following a meal (typically within the first 3–4 d), but not all individuals defecated after each meal. A more regular excretion of nitrogenous waste was also seen through the number of events. Thus, on average, snakes excreted uric acid pellets twice as often as they defecated.

## Discussion

### *Metabolic Response to Feeding and Energy Budget*

Our determination of standard metabolic rate of *Python molurus* is similar to that found in previous studies (Secor and Diamond 1995, 1997a, 1997b; Secor et al. 2000a). However, maximal rates of  $\dot{V}\text{O}_2$  following feeding are lower than those reported by Secor and Diamond (1995, 1997a) on the same species after similar meal size but similar to values reported previously from our laboratory (Overgaard et al. 1999). As previously described,  $\dot{V}\text{O}_2$  increased rapidly after ingestion and peaked within 1–2 d, followed by a slow decline toward standard levels (Fig. 2A). RE was not affected by feeding (Fig. 2B). Earlier studies have reported postprandial increases in RE for *P. molurus* (Overgaard et al. 1999; Secor et al. 2000a) that may reflect a change from a lipid-based metabolism during fasting to a mixed protein/lipid/carbohydrate-based metabolism during digestion. Interpretations of RE during the postprandial period are, however, difficult because of the “alkaline tide,” where blood and tissue  $\text{CO}_2$  concentrations can change markedly (Overgaard et al. 1999; reviewed by Wang et al. 2001).

The SDA coefficient in our study ranged from 21% to 35% (mean = 27%), which is similar to the 30% reported by Secor and Diamond (1997a). Standard metabolic rate amounted to 18% of the energy ingested over the entire experimental period,

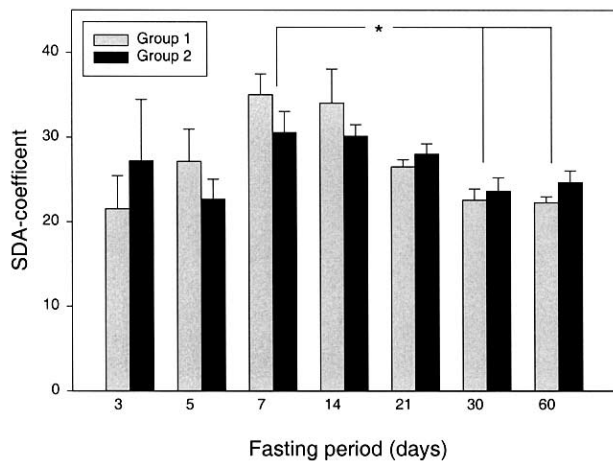


Figure 3. Metabolic response of digestion following different fasting periods. The specific dynamic action (SDA) response is presented relative to the ingested energy (SDA coefficient). The snakes were divided into two groups of four individuals that differed in the order of fasting periods. Data are presented as mean  $\pm$  SEM. Asterisk indicates significant difference between groups.

so total  $\dot{V}O_2$  (standard metabolic rate + SDA) amounts to  $45\% \pm 1\%$  of ingested energy, leaving the remaining 55% to growth or to be lost through feces and nitrogenous waste. Excretion of nitrogenous waste products has been estimated to approximately 4% of ingested energy in *Python curtus* (Vinegar et al. 1970). Digestive efficiency, defined as energy absorbed relative to energy ingested, in different species of *Python* ranges between 89% and 98% (Vinegar et al. 1970; Bedford and Christian 2000) and has been reported to be 90% in *P. molurus* (S. M. Secor, personal communication). With a digestive efficiency of 90%, we would estimate that 45% of the ingested energy was used for growth and loss excretion of renal waste products. Based on measurements of mass, we found a higher growth efficiency than the assumed value (66% vs. 40%–45%). Not all snakes defecated after all feeding events (Fig. 4), and long retention periods of feces have been reported for *Python* and other snakes (Lillywhite et al. 2002). Hence, the difference between the assumed and measured growth efficiency may be attributed to the possibility that the snakes had not defecated. Previous studies on *P. molurus* reported growth efficiency (assimilations) of 40% (Secor and Diamond 1997a), while Vinegar et al. (1970) found that growth efficiency ranged from 22% to 70% (mean = 49%) in *P. curtus*.

#### Critique of Assumptions

We relied on several assumptions to calculate SDA when feeding bouts overlapped temporally. Thus, our conclusion regarding the energetic costs of the gastrointestinal hypertrophy and func-

tional upregulation depend on the validity of these assumptions, and it seems appropriate to discuss possible pitfalls and magnitude of errors in some detail.

**Body Mass.** Estimated body mass during the first 3 wk after feeding was used to adjust meal size to 20% of body mass and also to calculate mass-specific  $\dot{V}O_2$ . Because body mass needed to be estimated, it is uncertain whether meals after short fasting periods were exactly 20% of body mass. The associated error is, however, relatively small since assumed growth efficiencies of either 0% or 100% changes the relative meal sizes to only 18% or 22% of body mass, and the SDA coefficient does not vary for meals between 15% and 25% of body mass (Secor and Diamond 1997a).

A 10-d assimilation time was applied since previous studies on *P. molurus* ingesting similarly sized meals show that 85% of the ingested food is processed within 6 d and that the stomach and small intestine are completely empty within 14 d (Secor and Diamond 2000). We did not measure the rate of digestion directly, but uric acid excretion and thus protein metabolism occur largely within the first 2 wk after feeding (Fig. 4). Body mass was estimated 3 wk after feeding to allow for defecation and uric acid excretion, and there was good agreement between estimated and measured values after 3 wk.

To test the influence of the assumed growth efficiency (50%) and assimilation time (10 d), we recalculated the metabolic cost of a meal that otherwise resulted in an SDA coefficient of 28.3% using drastically altered assumptions. An assimilation period of 2 d and a growth efficiency of 10% resulted in an SDA coefficient of 27.8% of ingested energy, whereas an assimilation period of 14 d and a growth efficiency of 100% lead to an SDA coefficient of 29.4%. Clearly, these estimates do not differ substantially from the original value of 28.3%.

**Temporal Development of the SDA Response.** As shown in Figure 1C, 80% of the metabolic cost associated with feeding was expended within the first 5 d following feeding, with 45% of costs occurring on the second and third day. When the metabolic costs of two meals overlap temporally, we assume that the time course of the first SDA follows the pattern depicted in Figure 1C when we estimate the remaining cost of the first meal (i.e., area B in Fig. 1B). If area B were overestimated, the SDA response would be overestimated for the first meal and underestimated for the second meal. Conversely, if area B were underestimated, the SDA response would be underestimated for the first meal and overestimated for the second meal. Nevertheless, there do not appear to be any obvious indications that the “shape” of the SDA response differs according to the preceding fasting period. The potential errors of estimating area B are largest when the second feeding occurs after 3 or 5 d following the previous meal. To validate our assumptions, we performed an additional measurement of the SDA response after fasting periods of 30 and 60 d at the end of the experiment.

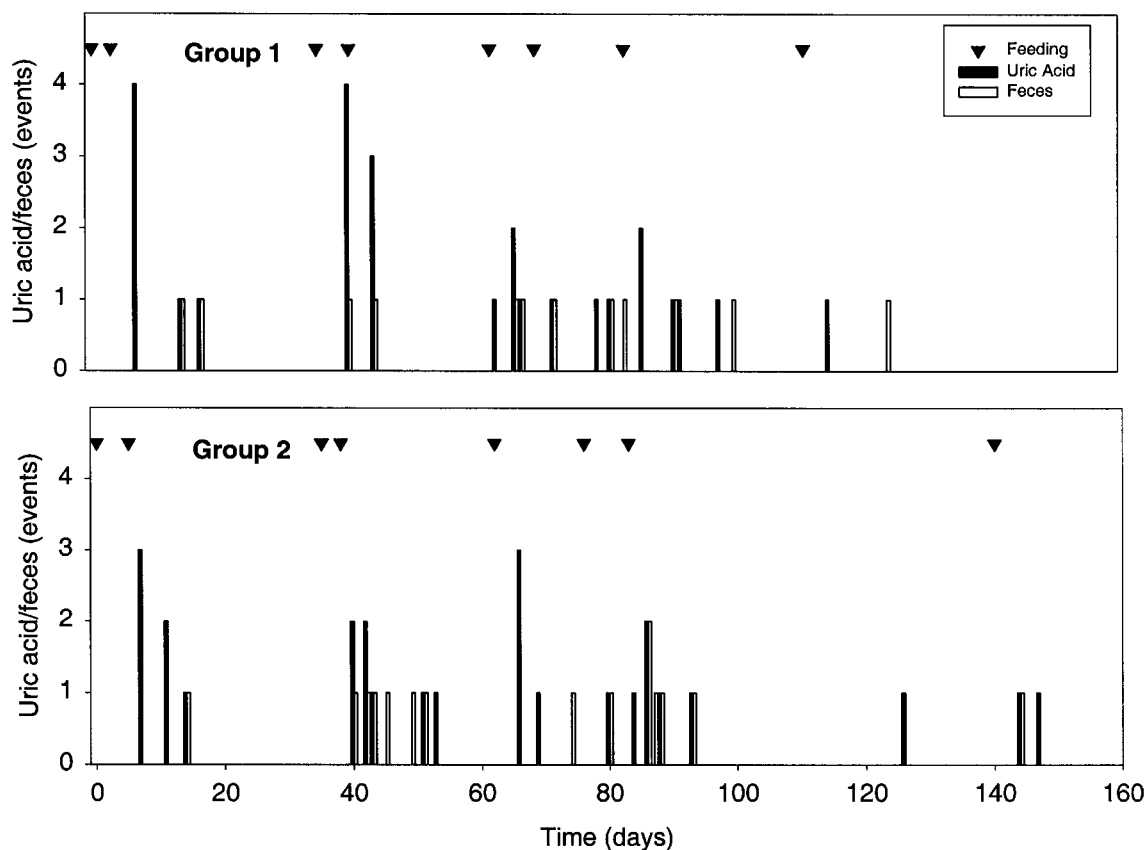


Figure 4. Events of defecation and excretion of uric acid following feeding during the experimental period. The snakes were divided into two groups of four individuals that differed in the order of fasting periods. A value of 1 corresponds to one event of either uric acid excretion (black bars) or defecation (white bars). A filled triangle indicates time of feeding.

Thus, we could measure the entire SDA response without assumptions concerning previous meals and compare this to the value calculated according to the principle of Figure 1B. There was no significant difference between calculated and measured SDA response after 30 d of fasting in group 1, but the measured SDA response after 60 d of fasting in group 2 at the end of the experiment was significantly larger (29% vs. 25%) than the value calculated after 60 d of fasting at the start of the experimental period. Hence, it is possible that the first SDA responses after 60 d are slightly underestimated. The possible errors are small, and both values were close to the overall mean of 27%. Thus, we believe that our assumptions are reasonable and that the magnitude of possible errors in the estimation of the SDA coefficient are so small that it does not affect the conclusions that can be drawn from our study.

#### *Effect of Fasting Duration on the SDA Response in Python*

Our study shows that the SDA response is similar after short (3–5 d) and long (14–60 d) periods of fasting. Studies on *P.*

*molurus* ingesting similar size meals have documented that gastrointestinal growth and the increase in intestinal nutrient uptake capacity occur within the first day after feeding and remain elevated for at least 6 d, whereupon gastrointestinal mass and function decrease (Secor and Diamond 1995, 1997b; Secor et al. 2000b; Starck and Beese 2001). Therefore, we can assume that the digestive organs remained upregulated when snakes were presented with a second meal following the short fasting periods (3, 5, and possibly 7 d). If gastrointestinal upregulation is energetically expensive, the energetic costs of meals following short fasting periods will be lower than those occurring after prolonged fasting periods (longer than 2 wk). Our results show that this is not the case, which leads to the conclusion that gastrointestinal upregulation must be energetically cheap compared to other costs associated with digestion. This conclusion supports the suggestion by Starck and Beese (2001) that postprandial hypertrophy of the small intestine by swelling of the individual enterocytes is energetically cheap in *P. molurus*. A low cost of upregulating digestive organs after fasting is con-

sistent with a study by Secor and Diamond (1997b) where the SDA responses as well as intestinal mass and nutrient-transport capacities were determined after ingestion of various meal sizes. This study showed that the SDA coefficient (energy used for digestion relative to ingested energy) after ingestion of 65% of body mass was three times higher than what was elicited by ingestion of 25% of body mass. The increased mass of gastrointestinal and other visceral organs was, however, similar for both meal sizes. In addition, although total brush border transport capacities were generally larger following ingestion of 65% compared to meals of 25% of body mass, the relative differences in uptake capacities were of much smaller magnitude than the differences in the absolute cost of digestion (Secor and Diamond 1997b). Thus, the relative increase in the SDA response was much higher than the concomitant upregulation of the gastrointestinal organs, which suggests that other digestive processes account for a large proportion of the SDA response and that the cost of gastrointestinal upregulation is relatively small compared to these other processes.

We found a significantly larger SDA response following 7 d of fasting compared with 30 and 60 d of fasting. The seemingly larger SDA response after 7 d of fasting may result from other factors (e.g., unnoticed activity/stress during measurements) because there were no significant differences between any other fasting periods.

The SDA coefficient is large in *P. molurus* compared with other species of reptiles (Secor and Diamond 2000; Secor 2001). Since gastrointestinal upregulation, including intestinal growth, does not appear to be a major contributor to the SDA response, it remains unclear why digestion is so costly in *Python*. A large proportion of the metabolic response occurs soon after ingestion and seemingly before the majority of absorption occurs (Secor and Diamond 1995; Fig. 1C), and the expense appears to be associated with physiological processes occurring early in digestion. In several studies on fish, it has been calculated that protein synthesis alone constitutes 20%–40% of SDA (Brown and Cameron 1991a, 1991b; Houlihan 1991). If this is the case for *Python*, it would imply that synthesis of digestive enzymes, transport proteins, and so forth, occur soon after ingestion and represent a larger cost than the protein synthesis following absorption and assimilation of amino acids from the meal. Clearly, the energy-consuming processes associated with digestion in *Python* need to be quantified in much greater detail.

In conclusion, the gastrointestinal organs, particularly the small intestine, of *Python* exhibit pronounced phenotypic flexibility where its mass and functions are rapidly adjusted to physiological demands. This response is common to most vertebrates, and *Python* seems to have adapted to infrequent feeding patterns by mechanisms that enable fast growth of the gastrointestinal organs at a low energetic cost.

## Acknowledgments

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