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Digestive Response to the First Meal in Hatchling Burmese Pythons (*Python molurus*)

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Juvenile Burmese pythons (*Python molurus*) undergo dramatic increases in intestinal nutrient transport, hypertrophy of intestinal mucosa, and very large increases in metabolic rate in response to feeding. This study investigates whether hatchling *P. molurus*, after their very first meal, experience magnitudes of digestive responses greater than or equal to those occurring for juveniles that have consumed many previous meals. After consuming their first meal, hatchling *P. molurus* increased oxygen consumption rates 12-fold, up-regulated intestinal nutrient transport three- to fourfold, and experienced a twofold increase in small intestinal wet mass. One day after feeding, their stomachs and livers significantly increased in mass, whereas the mass of their gallbladders significantly decreased. These postfeeding responses of hatchlings are similar in magnitude and mass-specific values to those of juvenile *P. molurus*. Thus, young *P. molurus* up-regulate intestinal nutrient transport and undergo intestinal hypertrophy to the same magnitudes after their first meal as they do following future meals. The significance of this phenomenon is that, at the completion of digestion, the small intestine of juvenile pythons atrophies and down-regulates its functions to values comparable to those of the naive gut of hatchlings. This study demonstrates that, regardless of previous digestive history, the intestine of young *P. molurus* exhibits conserved magnitudes of postfeeding responses and that, during digestive quiescence, the energetic cost of maintaining the intestine is minimized.

HYPOTHESIZED as adaptations to feeding on relatively large prey at long intervals, sit-and-wait foraging snakes possess an unprecedented gastrointestinal response to the initiation and completion of digestion (Secor et al., 1994; Secor and Diamond, 1995). Following feeding, sit-and-wait foraging sidewinders (*Crotalus cerastes*) and Burmese pythons (*Python molurus*) dramatically up-regulate intestinal nutrient transport by a factor of 5–26, more than double small intestinal mass, and experience as much as a 45-fold increase in metabolic rate (Secor et al., 1994; Secor and Diamond, 1995). With the completion of digestion, their intestine down-regulates nutrient transport and atrophies, and their metabolic rates return to prefeeding levels. The adaptive significance of down-regulating gut function and the associated tissue atrophy after digestion is to reduce the energy allocated to the energetically expensive digestive system during the long intervals of digestive quiescence between feeding bouts (Secor et al., 1994). Thus, the postfeeding up-regulation of intestinal nutrient transport coupled with hypertrophy of the small intestine are necessary to effectively digest the potentially huge meal.

Sit-and-wait foraging pythonids and viperids are known to feed in the wild at 1–2 month intervals and fast for as long as one year (Slip and Shine, 1988; Martin, 1992; Secor and Nagy, 1994). Additionally, they can consume relatively large prey equivalent to 50–160% of their body mass (Slip and Shine, 1988; Greene, 1992). For these snakes, the energetic cost of digesting these meals is relatively large (as much as 40% of the ingested metabolizable energy), due to the added costs of transporter and enzyme up-regulation and growth of the intestine and other organs (Secor et al., 1994; Secor and Diamond, 1995). Because the elevated cost of digestion is offset by long periods of low postabsorptive metabolism (reduced by minimizing the expenditure of the gastrointestinal tract), sit-and-wait foraging snakes theoretically expend less energy than if they continuously maintained a fully functional gut between bouts of digestion, even when assuming that the relative cost of digestion would be less (no additional costs for up-regulation and tissue growth). In contrast, several species of widely foraging snakes do not regulate gut function or morphology with the initiation or completion of digestion (Secor and Diamond, 1994b). For these snakes, which feed more frequently in the wild, maintaining gut function between feeding bouts (resulting in higher standard metabolism) and thus experiencing relatively lower cost of digestion appears to be the more economical strategy energy-wise.

I previously documented the postfeeding responses of *P. molurus* which were approximately one year old (Secor and Diamond, 1995). The snakes of that study had been maintained on biweekly meals of laboratory rodents that weighed 25% of the snakes' body mass. Following a 30-day fast, this size meal resulted in six- to 26-fold increases in intestinal nutrient transport rates, a doubling of small intestinal mass, and a 17-fold increase in oxygen consumption rates (Secor and Diamond, 1995). Upon observing these dramatic responses to feeding in juvenile *P. molurus*, I asked whether the magnitudes of those responses were fixed or shifted with respect to age and/or previous feeding history. My separate finding that the cost of digestion (specific dynamic action) for *P. molurus*, normalized to body mass, does not vary with body size (S. M. Secor and J. M. Diamond, unpubl. data) suggests that the magnitudes of other digestive responses are stable with respect to age. Alternatively, if the gut has had no prior digestive experience, as for hatchlings, it might have minimal functional capabilities. Thus, the first meal would produce a much greater digestive response than those occurring after subsequent meals.

In this study, I address these competing hypotheses by measuring the following set of postfeeding responses in hatchling *P. molurus* after their first meal: (1) metabolic response, as the change in oxygen consumption during digestion; (2) functional response, as the regulation of nutrient transport across the intestinal brush-border membrane; and, (3) morphological response, as hypertrophy of gut tissues and other organs. My prime objective was to determine whether the magnitudes of these responses for hatchling *P. molurus*, after their first meal, were equivalent to or differed from those of older snakes with previous digestive experiences.

Materials and Methods

Python molurus inhabits the Indo-China subregion and are one of the largest species of snakes, reaching lengths of > 6 m and mass of > 100 kg (de Vosjoli, 1991). All 13 individuals of this study were siblings and had hatched 10 July 1993. They were maintained individually in plastic shoe boxes (30 × 16 × 8 cm) at 26–29 C, with water available ad libitum. Methods for measuring the responses to digestion are detailed in Secor et al. (1994) and Secor and Diamond (1995).

I measured the metabolic response to digestion using closed-system respirometry as described by Vleck (1987). Seven, unfed, five-week-old hatchlings (mean mass ± 1 SE = 113 ± 1 g) were placed in opaque respirometry chambers (1.5 or 3 liters) in a temperature-controlled environmental cabinet maintained at 30 C. For each measurement, I drew a 50-cc gas sample from each chamber, sealed the chambers, and 0.25–1 hr later took a second gas sample. During the sampling intervals, chamber O_2 never dropped below 18% (typically > 19.5%). Gas samples were scrubbed of water (Drierite) and CO_2 (Ascarite) prior to being injected into an Applied Electrochemistry (model S-3A) oxygen analyzer. I measured oxygen consumption rates ($\dot{V}O_2$, corrected for standard temperature and pressure) daily for three days prior to and 10 days after each snake had consumed its first meal of two small laboratory mice whose combined mass equaled 25.2 ± 0.1% of each snake's body mass.

I used an additional six six-week-old hatchlings (101 ± 6 g) to document the magnitude of the functional and morphological responses to the first meal. I divided these six snakes into two groups; three snakes were sacrificed (by severing their spinal cord just posterior to the head) before they ever had a meal and three sacrificed 24 hr after consuming their first meal of two small mice whose combined weight averaged 25.2 ± 0.2% of each snake's body mass. I sacrificed snakes 24 hr after their first meal because it coincided with the peak in postfeeding $\dot{V}O_2$. My previous studies found that indices of intestinal function and morphology peaked concurrently with maximum post-feeding $\dot{V}O_2$ (Secor et al., 1994; Secor and Diamond, 1995).

I measured nutrient uptake by the brush-border membrane of intestinal epithelial cells as described by Karasov and Diamond (1983) and Secor and Diamond (1995). Briefly, the intestine was quickly removed after the snake was sacrificed, washed with ice-cold Ringer solution, everted, and cut into 1-cm sleeves. Intestinal sleeves, mounted on glass rods, were first preincubated for 5 min in Ringer solution at 30 C and then incubated for 2 min at 30 C in a Ringer solution containing a radiolabeled nutrient that was transported across the brush-border membrane and a radiolabeled adherent fluid maker. I measured uptake rates of the amino acids L-leucine and L-proline (both labeled with ^3H) and the sugar D-glucose (labeled with ^{14}C). I selected these three solutes because they were similarly measured in juvenile *P. molurus* (Secor and Diamond, 1995), thus allowing a direct ontogenetic comparison, and because L-leucine and L-proline are transported predominantly by a different amino acid carrier—the neutral and imino acid transporters, respectively (Ste-

vens et al., 1982). To correct for the amount of these nutrients in the adherent fluid, I used ^{14}C-polyethylene glycol for the amino acids and ^{3}H-L-glucose for D-glucose. Additionally, L-glucose which is not actively absorbed, corrects for passive D-glucose transport, thus providing a measure of carrier-mediated uptake of D-glucose.

I measured uptake rates from equal length thirds (proximal, middle, and distal) of the small intestine and from the proximal half of the large intestine. I normalized uptake rates to tissue wet mass, expressed as nmoles·min^{-1}·mg^{-1}. I calculated total uptake capacity (μmoles/min) of the complete small intestine by summing each region's uptake capacities, calculated as the product of a region's uptake rate (J) times its wet mass (M) as described in the following equation: total uptake capacity $= J_{\text{proximal}} \cdot M_{\text{proximal}} + J_{\text{middle}} \cdot M_{\text{middle}} + J_{\text{distal}} \cdot M_{\text{distal}}$.

I quantified the morphological response of the small intestine to the first meal by measuring the wet mass of the total small intestine (emptied of its contents) and wet and dry (dried to constant mass at 60 C) masses of scrapable mucosa and residual serosa from 1-cm sleeves from each region of the small intestine (Diamond and Karasov, 1984). These measures were used to estimate the dry mass of the total small intestine and the wet and dry masses of the anterior and distal mucosa and serosa. Since postfeeding changes in mass of other organs occur for juvenile *P. molurus* (Secor and Diamond, 1995), I also measured, from hatchlings, the wet and dry masses of the heart, paired lungs, liver, empty stomach, full gallbladder, pancreas, spleen, empty large intestine, paired fat bodies, and paired kidneys.

I conducted all statistical analyses using the microcomputer version of Statistical Analysis Systems (PC-SAS; SAS Institute, Inc., 1988). I employed a repeated-measures ANOVA to test the effects of sampling day on $\dot{V}O_2$ and intestinal position on nutrient uptake rates (Zar, 1974). I used a one-way ANOVA to test the effects of digestive state on intestinal uptake rates, total uptake capacities, regional mucosa and serosa masses, and organ masses. An ANCOVA analysis detected no significant covaried effect of body mass for any variables. The absence of a body mass covariate on several variables (uptake capacities and organ masses) results from the narrow range of body masses (83.9–117.5 g) among snakes. I used a pairwise planned comparison to determine whether $\dot{V}O_2$ differed significantly between sampling days and whether uptake rates differed significantly between intestinal regions and between hatchling and juvenile pythons. I designated statistical significance at $P \leq 0.05$ and present results as mean ± 1 SE.

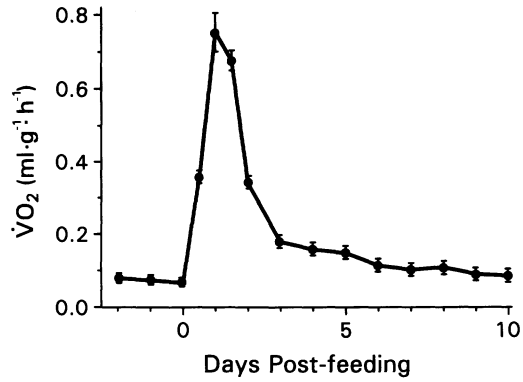

Fig. 1. Oxygen consumption rates ($\dot{V}O_2$ as ml·g^{-1}·h^{-1}) of five-week-old hatchling *Python molurus* (n = 7) for three days prior to and 10 days after consuming their first meal (25% of snake's body mass). Values are presented as means (solid circle) ± 1 SE (bars). Note that $\dot{V}O_2$ peaks at 24 hr after feeding, at a value 11.5-fold prefeeding rates.

Results

Metabolic response.—I found that oxygen consumption rates ($\dot{V}O_2$) of hatchling *P. molurus* differ significantly ($F_{14,84} = 51.8$, $P \leq 0.0001$) among days prior to and after consuming their first meal (Fig. 1). Minimum $\dot{V}O_2$, prior to the first meal, averaged 0.065 ± 0.002 ml O_2·g^{-1}·h^{-1}. Within 12 hr after this meal, $\dot{V}O_2$ had increased significantly ($P \leq 0.0001$) to 0.36 ± 0.01 ml O_2·g^{-1}·h^{-1}; a 5.5-fold increase. By 24 hr, $\dot{V}O_2$ had again increased significantly ($P \leq 0.0001$) to peak at 0.75 ± 0.06 ml O_2·g^{-1}·h^{-1}; 11.5 times minimum prefeeding $\dot{V}O_2$. $\dot{V}O_2$ then declined significantly (*P*s ≤ 0.0001) by day 2 and again by day 3. By day 6 and thereafter, $\dot{V}O_2$ of these young pythons declined to values not significantly (*P*s > 0.095) greater than prefeeding rates.

Functional response.—The three fed hatchlings, while maintained at 30 C, had within 24 hr reduced the mass of the ingested meal within the stomach to 40 ± 7% of the meal's original mass. By this time, the anterior two-thirds of the first mouse and the anterior third of the second mouse had been broken down within the stomachs and passed into the small intestines. The small intestinal contents averaged 2.2 ± 0.6% of the mass of the ingested meal. The large intestine contained some fecal matter from the meal and urate from metabolism.

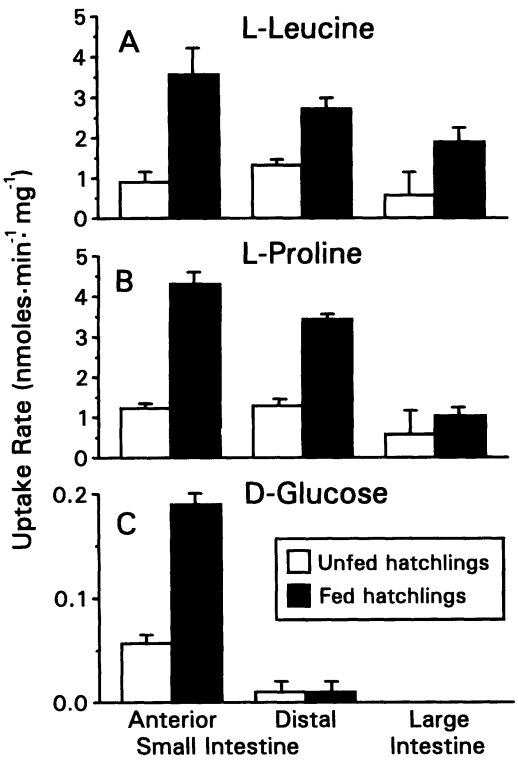

Fig. 2. Mean (bars = SE) uptake rates (nmoles·min^{-1}·mg^{-1}) of L-leucine (A), L-proline (B), and D-glucose (C) by anterior and distal small intestine and anterior large intestine of unfed (n = 3) and fed (n = 3) six-week-old hatchling *Python molurus*. Measurements from fed snakes were made at one day postfeeding. Uptake rates were significantly up-regulated one day after the first meal for all three nutrients in the anterior small intestine and for L-leucine and L-proline in the distal small intestine. No measurable uptake of D-glucose by the large intestine was detected. Note that uptake rates for D-glucose are an order of magnitude less than uptake rates for the two amino acids.

At one day postfeeding, uptake rates of hatchlings differed significantly ($Ps < 0.003$) among the four intestinal regions for each nutrient; uptake rates of L-leucine and L-proline by the proximal and middle regions were similar and significantly greater than those by the distal region. For unfed snakes, only D-glucose uptake differed among intestinal positions. Therefore, I averaged uptake values for the proximal and middle regions and hereafter refer to this combined region of the small intestine as the anterior region. Uptake rates by the large intestine for L-leucine and L-proline were less than uptake rates by each region of the small intestine, averaging 51 ± 2% and 34 ± 2%, respectively, of uptake rates by the anterior small intestine. I detected no measurable uptake of D-glucose by the large intestine of fed or unfed hatchling *P. molurus*.

Within 24 hr after ingesting their first meal, hatchlings' small intestinal uptake of L-leucine ($F_{1,4} = 18.9$, $P < 0.05$), L-proline ($F_{1,4} = 85.0$, $P < 0.001$), and D-glucose ($F_{1,4} = 76.1$, $P < 0.001$) had increased to values 4, 3.5, and 3.3 times, respectively, of those of unfed hatchlings (Fig. 2). At this time, the uptake of L-leucine ($F_{1,4} = 27.3$, $P < 0.01$) and L-proline ($F_{1,4} = 129$, $P < 0.001$), but not D-glucose ($F_{1,4} = 0.0$, $P = 1.0$), by the distal small intestine had also increased (Fig. 2). I observed no significant change within 24 hr after the first meal in the uptake of L-leucine ($F_{1,4} = 3.88$, $P = 0.120$) and L-proline ($F_{1,4} = 0.55$, $P = 0.501$) by the large intestine (Fig. 2).

Total uptake capacities of hatchlings' small intestine, a product of uptake rate times intestinal mass (described in Materials and Methods), increased significantly one day after feeding for L-leucine ($F_{1,4} = 107$, $P < 0.001$), L-proline ($F_{1,4} = 6102$, $P \leq 0.0001$), and D-glucose ($F_{1,4} = 1521$, $P \leq 0.0001$). Compared to unfed hatchlings, uptake capacities of fed hatchlings were 6.8, 6.9, and 7.8 times greater for L-leucine, L-proline, and D-glucose, respectively.

Morphological response.—Wet mass of the small intestine of fed hatchlings averaged 4.9 ± 0.4 g, nearly twice that from unfed individuals (Table 1). Much of this difference can be attributed to the 2.3-fold greater wet mass of the anterior mucosa ($F_{1,4} = 56.1$, $P = 0.002$) of fed compared to unfed hatchlings. Dry masses of the total small intestine (calculated as sum of dry mass of mucosa and serosa) and anterior mucosa were also significantly ($Ps < 0.009$) greater for fed compared to the unfed hatchlings (Table 1). The wet and dry masses of the anterior serosa layer did not differ ($Ps > 0.056$) between fed and unfed hatchlings and neither did ($Ps > 0.11$) the wet and dry masses of the distal mucosa and serosa.

In digesting hatchlings, the wet mass of the liver ($F_{1,4} = 23.3$, $P = 0.009$) and stomach ($F_{1,4} = 7.4$, $P = 0.049$) were 55% and 67% greater, respectively, whereas wet mass of the full gallbladder was 46% less ($F_{1,4} = 18.4$, $P = 0.023$) than in unfed hatchlings (Table 1). Dry mass of the liver ($F_{1,4} = 16.0$, $P = 0.016$) and stomach ($F_{1,4} = 7.83$, $P = 0.049$) were also greater (52% and 75%, respectively) in fed hatchlings compared to unfed hatchlings. I detected no sig-

TABLE 1. MEAN ± 1 SE AND STATISTICAL COMPARISON (ONE-WAY ANOVA) OF BODY MASS AND WET AND DRY MASSES (G) OF THE SMALL INTESTINE (TOTAL AND REGIONAL MUCOSA AND SEROSA) AND OTHER ORGANS BETWEEN UNFED AND FED SIX-WEEK-OLD *Python molurus*. For fed snakes, body mass (minus gut contents) and tissue and organ masses were measured one day after snakes consumed their first meal (25% of their body mass). Note the significantly greater wet and dry masses of the small intestine, mucosa of the anterior intestine, stomach, and liver, and significantly smaller wet mass of the full gallbladder of postfed hatchlings compared to unfed hatchlings.

	Wet mass			Dry mass		
	Unfed (n = 3)	Fed (n = 3)	ANOVA *P* values	Unfed (n = 3)	Fed (n = 3)	ANOVA *P* values
Body mass	94.1 ± 6.9	115.7 ± 9.4	0.139			
Small intestine						
Total	2.52 ± 0.11	4.90 ± 0.41	0.006	0.44 ± 0.04	0.84 ± 0.08	0.008
Anterior mucosa	1.25 ± 0.14	3.07 ± 0.19	0.002	0.24 ± 0.02	0.58 ± 0.05	0.003
Anterior serosa	0.68 ± 0.07	0.88 ± 0.03	0.056	0.11 ± 0.01	0.13 ± 0.01	0.330
Distal mucosa	0.34 ± 0.02	0.61 ± 0.13	0.112	0.05 ± 0.01	0.08 ± 0.02	0.123
Distal serosa	0.25 ± 0.02	0.34 ± 0.09	0.398	0.04 ± 0.01	0.05 ± 0.01	0.369
Other organs						
Heart	0.62 ± 0.01	0.89 ± 0.16	0.182	0.11 ± 0.01	0.14 ± 0.03	0.253
Lungs	0.87 ± 0.05	1.08 ± 0.11	0.147	0.17 ± 0.01	0.21 ± 0.02	0.157
Liver	2.76 ± 0.29	4.28 ± 0.13	0.009	0.83 ± 0.08	1.26 ± 0.07	0.016
Stomach	2.05 ± 0.30	3.43 ± 0.41	0.049	0.40 ± 0.05	0.70 ± 0.09	0.049
Gall bladder	0.19 ± 0.01	0.10 ± 0.01	0.023	0.03 ± 0.01	0.02 ± 0.01	0.196
Spleen	0.03 ± 0.01	0.04 ± 0.01	0.153	0.005 ± 0.001	0.01 ± 0.00	0.696
Pancreas	0.12 ± 0.01	0.19 ± 0.03	0.090	0.03 ± 0.01	0.05 ± 0.01	0.058
Large intestine	1.31 ± 0.14	3.85 ± 1.33	0.131	0.22 ± 0.02	0.59 ± 0.28	0.252
Kidneys	0.97 ± 0.06	1.32 ± 0.24	0.234	0.20 ± 0.01	0.24 ± 0.03	0.247
Fat	4.50 ± 0.69	3.82 ± 0.09	0.379	2.62 ± 0.46	2.31 ± 0.13	0.544

nificant (*P*s > 0.058) differences between unfed and fed hatchlings in wet and dry masses of the heart, lungs, pancreas, spleen, large intestine, fat bodies, and kidneys, together with dry mass of the gallbladder.

DISCUSSION

Metabolic response.—The metabolic response of hatchling *P. molurus* to their first meal resembles that of older snakes that have previously consumed numerous meals. I found that hatchlings attained a higher postfeeding peak of $\dot{V}O_2$ (0.75 ± 0.06 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) compared to yearold snakes (0.58 ± 0.06 ml $O_2 \cdot g^{-1} \cdot h^{-1}$; Secor and Diamond, 1995) that had also consumed meals equaling 25% of their body mass. Minimum prefeeding $\dot{V}O_2$ by hatchlings (0.065 ± 0.002 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) was nearly twice that of older pythons (0.034 ± 0.003 ml $O_2 \cdot g^{-1} \cdot h^{-1}$), hence their scope of maximum metabolic rate ($\dot{V}O_2max/\dot{V}O_2min$) was significantly ($F_{1,13}$ = 12.7, $P = 0.003$) less (11.5 for hatchlings vs 17.1 for juveniles).

The elevation of metabolism attributed to digestion is commonly referred to as specific dynamic action (SDA; Brody, 1945; Blaxter, 1989). For cows, horses, pigs, and sheep, SDA involves a 25–50% increase in metabolic rate (Brody, 1945). I have demonstrated that species of sit-and-wait foraging snakes undergo a seven- to 17-fold increase in metabolic rate following the ingestion of meals equaling 25% of their body mass (Secor et al., 1994; Secor and Diamond, 1995; this study). For *P. molurus*, larger meals will trigger even a greater metabolic response. For example, after ingesting a meal almost equal to their own body mass, *P. molurus* will experience a 45-fold increase in $\dot{V}O_2$ (Secor and Diamond, 1995). For these pythons, elevated rates of oxygen consumption are necessary for fueling the production and secretion of gastric acid and hydrolases, up-regulation of nutrient transport, and hypertrophy of the intestinal tract.

For adult *Crotalus cerastes* (Secor et al., 1994), juvenile *P. molurus* (Secor and Diamond, 1995), and hatchling *P. molurus* (this study), the energy equivalent of SDA [extra oxygen consumed during digestion times 18.3 J/ml O_2 Nagy, 1983)] after a snake digests a meal equaling one-quarter of its body mass is equivalent to 26 ± 1%, 32 ± 1%, and 37 ± 2%, respectively, of

the metabolizable energy of the ingested meal (assuming 8 kJ/g wet mass of meal and 85% assimilation efficiency of snakes; S. M. Secor and J. M. Diamond, unpubl. data). For hatchling *P. molurus*, this relative cost of digestion is significantly (Ps < 0.04) greater than that for juvenile *P. molurus* and adult *C. cerastes*. For pythons, digesting the first meal results in a greater energy cost, relative to the return, compared to later meals. The up-regulation of other digestive functions, not measured in this study, occurring after the first meal but not again after subsequent meals, could be responsible for the difference in cost.

Hatchling *P. molurus* expend a substantial amount of energy (15.9 ± 0.7 kJ), within the first 24 hr of digestion, before the meal has been transported across the gut wall. Because they have not eaten previously, they must rely upon natal energy stores to fuel at least the initial stages of digestion. I suggest that the start-up fuel for digestion originates in abdominal fat bodies, supported by an observed 60-fold increase in plasma triglycerides 24 hr after eating in juvenile *P. molurus* (Secor and Diamond, 1994a). For the three sacrificed unfed hatchlings, dry mass of abdominal fat bodies averaged 2.6 ± 0.5 g, which has an energy equivalent of 103 kJ (assuming 39.3 kJ/g dry mass; Schmidt-Nielsen, 1979). Thus, it appears that the abdominal fat bodies alone could easily meet the energetic demands of the first day of digestion. It is remarkable that the fat dry mass of fed hatchlings averaged 0.31 g less than that of unfed individuals, a difference with an energy equivalent of 12.3 kJ, similar to the cost of the first day of digestion. If none of the ingested energy was subsequently used to fuel the completion of digestion (total cost = 71 ± 3 kJ), the abdominal fat bodies should be able to do so but at the cost of a substantial depletion of itself and other possible energy stores (ex., liver and muscle).

Theoretically, abdominal fat bodies could fuel resting metabolism of a noneating hatchling *P. molurus* for approximately 52 days. This is assuming that daily maintenance expenditure of hatchlings is approximately 2 kJ/day (calculated from $\dot{V}O_2$ of unfed hatchlings). Three siblings of the snakes used in this study could never be enticed to eat and, thus, eventually died of starvation. Death of these snakes occurred 153–205 days (mean = 174 ± 16 days) after hatching, more than three times the duration predicted from the energy available from the depletion of abdominal fat bodies. From hatching to death, these snakes had lost an average of 41.2 ± 2.5 g, certainly more than could be accounted for from the complete use of abdominal fat bodies. At the time of their death, these snakes possessed no observable fat bodies, and the wet masses of their hearts, livers, small intestines, large intestines, kidneys, skin, and muscles were significantly (Ps < 0.03) less than those of their sacrificed unfed siblings. Wet masses of their esophagus, lungs, stomachs, and pancreas were not significantly (Ps > 0.35) different from those from sacrificed unfed hatchlings. These observations demonstrate that these snakes can use other energy stores besides fat bodies to meet metabolic requirements. Concurrent with and/or following the depletion of lipid stores, they catabolize other organs for available lipids, glycogen, and protein to fuel metabolism. Death occurs when all mobilizable energy sources are used up or when sufficient depletion causes organ failure.

Functional response.—Hatchling *P. molurus* had digested most of their ingested meal within 24 hr after feeding. Stomachs of sacrificed hatchlings contained 40% of meal mass, whereas stomachs of juvenile *P. molurus* at one-day postfeeding contained significantly (P = 0.0095) more (73%) of the ingested meal (Secor and Diamond, 1995). Higher standard metabolic rates and greater $\dot{V}O_2$ during digestion of hatchlings may be responsible for their faster rate of prey assimilation.

I found that regional uptake rates of L-leucine and L-proline were the same between unfed hatchling and 30-day fasted juvenile *P. molurus*, and between one-day postfeeding hatchlings and juveniles (Table 2). Uptake rates of D-glucose by the anterior small intestine were significantly (P = 0.016) greater for juveniles than hatchlings one day after feeding. These data demonstrate that the small intestine of hatchlings up-regulates amino acid transport in response to the very first meal to the same levels experienced by the small intestine of juveniles following many meals. Additionally, after a 30-day fast, the small intestine of juvenile *P. molurus* has down-regulated its nutrient uptake to levels experienced by the naive gut of unfed hatchlings.

To compare total uptake capacities among hatchling and juvenile *P. molurus*, I normalized values to body mass. Normalized total uptake capacities of L-leucine, L-proline, and D-glucose of one-day postfeeding hatchlings and juveniles were statistically indistinguishable from each other and significantly greater (Ps < 0.005) than normalized capacities of unfed hatchlings and fasted juveniles (Table 2).

Morphological response.—Changes in intestinal and organ masses, after the first meal for hatchlings, are similar in scope to those experienced by older snakes after one of many previous meals

TABLE 2. COMPARISON OF RELATIVE SMALL INTESTINAL MASS, NUTRIENT UPTAKE RATES, AND NORMALIZED UPTAKE CAPACITIES AMONG UNFED HATCHLING, ONE-DAY POSTFEEDING (FIRST MEAL) HATCHLING, 30-DAY FASTED JUVENILE, AND ONE-DAY POSTFEEDING JUVENILE *Python molurus*. Data for juvenile *P. molurus* are from Secor and Diamond (1995). Values are presented as means ± 1 SE. For each row of values, common superscript letters denote those values that do not differ significantly (*P*s > 0.05) from each other (planned pairwise comparison). Note that both hatchlings and juveniles, one day after feeding, experience similar degrees of intestinal hypertrophy and up-regulation of nutrient uptake.

	Hatchlings		Juveniles	
	Unfed (n = 3)	1-day postfeeding (n = 3)	Fasted (n = 3)	1-day postfeeding (n = 3)
Body mass (g)	94 ± 7	116 ± 9	703 ± 139	746 ± 73
Small intestine/body mass	0.026 ± 0.003^{a}	0.046 ± 0.002^{b}	0.023 ± 0.002^{a}	0.041 ± 0.002^{b}
Nutrient uptake rates (nmoles·min^{-1}·mg^{-1})				
Anterior small intestine				
L-leucine	0.90 ± 0.23^{a}	3.57 ± 0.57^{b}	0.55 ± 0.14^{a}	3.48 ± 0.36^{b}
L-proline	1.22 ± 0.20^{a}	4.30 ± 0.31^{b}	0.54 ± 0.03^{a}	3.94 ± 0.81^{b}
D-glucose	0.06 ± 0.01^{ab}	0.19 ± 0.01^{a}	0.03 ± 0.01^{b}	0.38 ± 0.09^{c}
Distal small intestine				
L-leucine	1.32 ± 0.10^{a}	2.73 ± 0.25^{b}	0.48 ± 0.24^{a}	2.39 ± 0.25^{b}
L-proline	1.29 ± 0.15^{a}	3.43 ± 0.12^{b}	0.80 ± 0.16^{a}	2.75 ± 0.27^{b}
D-glucose	0.01 ± 0.01^{a}	0.01 ± 0.01^{a}	0.04 ± 0.03^{a}	0.06 ± 0.06^{a}
Normalized total uptake capacity (μmoles·min^{-1}·body mass^{-1})				
L-leucine	0.026 ± 0.006^{a}	0.16 ± 0.03^{b}	0.013 ± 0.003^{a}	0.13 ± 0.01^{b}
L-proline	0.032 ± 0.004^{a}	0.19 ± 0.02^{b}	0.014 ± 0.001^{a}	0.15 ± 0.02^{b}
D-glucose	0.001 ± 0.000^{a}	0.007 ± 0.001^{b}	0.001 ± 0.000^{a}	0.013 ± 0.004^{b}

(Secor and Diamond, 1995). The twofold increase in small intestinal wet mass exhibited by hatchlings and juveniles 24 hr after feeding is largely a result of a ≈ 2.4-fold increase in wet mass of the anterior mucosa (Table 1). Hypertrophy of the intestinal mucosa, especially the epithelial layer which is responsible for the uptake of nutrients from the gut lumen, aids in increasing the intestine's total capacity to absorb nutrients. I suspect that hypertrophy of the mucosa results from an increase in enterocyte size and lengthening of microvillus; similar to that observed for adult *C. cerastes* (Secor et al., 1994) and juvenile *P. molurus* (unpubl. obs.).

Both hatchling and juvenile *P. molurus* demonstrated significant increases in stomach (75% vs 28%) and liver (52% vs 36%) dry masses and a significant decrease in wet mass of the full gallbladder (47% vs 59%) within 24 hr after eating. The arrival of food into the stomach triggers the increased production of gastric acid which is possibly correlated with hypertrophy of gastric parietal cells. The liver undergoes hypertrophy as its function is up-regulated to process the nutrients transported across the intestinal wall. The gallbladder responds to feeding by releasing its fluid contents (bile) into the proximal small intestine as digesta exits the stomach; thus, this response is not detected by a change in dry mass.

Hatchling *P. molurus* possess the remarkable trait of intestinal growth and functional up-regulation in response to their first meal. The significant findings of this study are as follows: first, the magnitude of postfeeding response is stable for at least the first year of life; and second, pythons continually respond to digestive quiescence by "shutting down" their small intestine to a minimal level of existence. The former conclusion is supported by my unpublished observations that for *P. molurus* there is no change in the mass-specific cost of digestion over a wide range of body sizes (100–10000 g). The latter phenomenon serves to minimize the energy expended on the quiescent gut. It remains to be seen whether pythons undergo ontogenetic changes in the magnitude of the functional and metabolic responses to feeding later in life. Such a change may occur if adult pythons feed on larger meals at longer intervals than juveniles and consequently experience greater extremes of digestive regulation.

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