Effects of meal size, clutch, and metabolism on the energy efficiencies of juvenile Burmese pythons, *Python molurus*

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Abstract

We explored meal size and clutch (*i.e.*, genetic) effects on the relative proportion of ingested energy that is absorbed by the gut (apparent digestive efficiency), becomes available for metabolism and growth (apparent assimilation efficiency), and is used for growth (production efficiency) for juvenile Burmese pythons (*Python molurus*). Sibling pythons were fed rodent meals equaling 15%, 25%, and 35% of their body mass and individuals from five different clutches were fed rodent meals equaling 25% of their body mass. For each of 11–12 consecutive feeding trials, python body mass was recorded and feces and urate of each snake was collected, dried, and weighed. Energy contents of meals (mice and rats), feces, urate, and pythons were determined using bomb calorimetry. For siblings fed three different meal sizes, growth rate increased with larger meals, but there was no significant variation among the meal sizes for any of the calculated energy efficiencies. Among the three meal sizes, apparent digestive efficiency, apparent assimilation efficiency, and production efficiency averaged 91.0%, 84.7%, and 40.7%, respectively. In contrast, each of these energy efficiencies varied significantly among the five different clutches. Among these clutches production efficiency was negatively correlated with standard metabolic rate (SMR). Clutches containing individuals with low SMR were therefore able to allocate more of ingested energy into growth.
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1. Introduction

Each living organism possesses the capacity to extract energy from its environment, process that energy, and allocate it to metabolism (for maintenance and activity) and growth (somatic and reproductive). For multicellular animals, ingested food energy is broken down by mechanical and chemical processes into components which are transported across the gut wall into circulation. Once absorbed, meal nutrients are either channeled into metabolic pathways, used to build structures (*i.e.*, tissue growth, gametes, embryos), or are stored (*i.e.*, glycogen and fat bodies). Thus the capacity and efficiency by which an animal can extract and utilize meal nutrients is crucial for its survival, growth, and reproductive fitness, and hence is under strong selective pressure. Analysis of energy flux has historically relied upon three calculated indices of energy efficiencies (Brody, 1945). Digestive efficiency represents the percentage of ingested food energy that is absorbed across the gut wall. Assimilation efficiency is the percentage of ingested energy that is absorbed and is available for metabolism and growth. Finally, production efficiency is the percentage of ingested energy that is channeled into growth.

While natural selection would predictably favor traits that maximize these energy efficiencies, significant variation of each efficiency that reflects differences in the meal (*i.e.*, composition and size), the environment (*i.e.*, temperature), and features of the organism (*i.e.*, size, genetics, and metabolism) exists both within and among species (Xu and Ji, 2006; Woods, 1982). For example, digestive and assimilation efficiencies decrease with meal size for the phantom midge larvae, *Chaoborus trivittatus* and the perch, *Perca fluviatilis* (Solomon and Brafield, 1972; Guigere, 1981). An increase in dietary protein and cellulose is characterized by respective increases and decreases in digestive and assimilation efficiencies for reptiles (Zimmerman and

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Tracy, 1989; Spencer et al., 1998) and mammals (Pritchard and Robbins, 1990).

Whereas body temperature has a predicted influence on the rates of digestion for ectotherms (increasing with body temperature), its effects on the digestive and assimilation efficiencies has been found to be variable. Digestive efficiencies were found to be higher at lower body temperatures for the yellow bellied slider, Trachemys scripta, and the alligator lizard, Gerrhonotus carinatus, higher at intermediate body temperatures for the grass lizard, Takydromus septentrionalis, and higher at higher body temperatures for the desert iguana, Dipsosaurus dorsalis, the lacertid, Eremias brenchleyi, and the whiptail, Cnemidophorus tigris, (Harlow et al., 1976; Harwood, 1979; Avery et al., 1993; Xiang et al., 1996; Xu and Ji, 2006). In contrast, digestive efficiency does not vary with body temperature for either the corn snake, Elaphe guttata, or the crag lizard, Cordylus melanotus (Greenwald and Kanter, 1979; McConnachie and Alexander, 2004).

Less explored are the intrinsic effects of genetics and metabolism on energy efficiencies. Whereas digestive efficiencies were found not to differ among different genetic strains of dairy cattle, Bos taurus, and chickens, Gallus gallus, strains do vary in production efficiencies (Veerkamp and Emmans, 1995; Jackson and Diamond, 1996; Scholz et al., 1998; Johnson et al., 2003). Conceivable for any organism, a tradeoff exists between the energy expended on metabolism and the energy allocated to growth (Calow and Townsend, 1981; Angiletta, 2001). For the hispid cotton rat, Sigmodon hispidus, it is suggested that digestive and assimilation efficiencies decreased with an increase in basal metabolic rate (Derting, 1989). Although the different indices of energy efficiency have been examined for a variety of taxa, the impact of genetics, meal size, and basal metabolism has not been well defined.

We undertook this study to examine the effects of meal size and clutch on the digestive, assimilation, and productive efficiencies for juvenile Burmese pythons, Python molurus. Burmese pythons are very tractable for such a study of energy efficiencies for the following reasons. They produce large clutches allowing multiple sets of siblings to be exposed to different treatments (Pope, 1961). They can consume a wide range of meal sizes thereby easily assessing meal size effects (Secor and Diamond, 1997). Whereas other reptiles excrete their feces and urate mixed together, pythons excrete them separately thereby facilitating their collection and measurement. Pythons are relatively inactive in captivity, thus much of their assimilated energy is therefore allocated to specific dynamic actions (the metabolic cost of meal digestion and assimilation) and resting metabolism (Secor and Diamond, 1995).

The objectives of our study were to: 1) evaluate the effects of meal size on energy efficiencies by comparing digestive, assimilation, and digestive efficiencies of sibling Burmese pythons that consumed rodent meals equaling 15%, 25%, or 35% of snake body mass; 2) assess clutch (genetic) effects on energy efficiencies by comparing each efficiency among individuals originating from five different clutches, each maintained on rodent meals equaling in mass to 25% of snake body mass; and 3) determine whether a tradeoff exists between the

energy expended on metabolism and the energy allocated to growth. In this study, we will demonstrate for juvenile Burmese pythons the lack of a meal-size effect and the presence of a clutch effect on energy efficiencies, and show that a tradeoff exists between the energy allocated to metabolism and to growth.

2. Materials and methods

2.1. Pythons and their maintenance

We used 103 juvenile Burmese pythons (P. molurus) that were purchased commercially (Captive Bred Reptiles, Oklahoma City, OK, USA) as hatchlings and had originated from five different unrelated clutches (designated as clutches A, B, C, F, and G). Upon arrival, pythons were maintained individually in 20 L plastic boxes at 27–29 °C under a 14 L:10D photoperiod. For several months prior to the study, snakes were feed biweekly with a diet of rodents with water available ad libitum. Before the start of the study, pythons were fasted for one month to ensure that they were postdigestive. Any feces detected in the large intestine at this time were palpated out through the cloaca.

2.2. Experimental procedure

To assess meal-size effects, 24 individuals from clutch B were equally divided into three meal-size treatments, meals equaling 15% (actual $15.5 \pm 0.3\%$), 25% (actual $25.0 \pm 0.4\%$), and 35% (actual $33.8 \pm 0.4\%$) of the snake's body mass. For each meal-size group, individuals were weighed the day prior to feeding in order to determine their target meal mass. The next day pythons were each fed meals of adult mice and or juvenile rats such that the mass of the meal matched the target meal mass. Following feeding, cages were checked daily and any urate or feces found was collected, weighed, dried for two weeks at 60 °C, and reweighed. This cycle of weighing, feeding, and feces and urate collecting continued at 10-day intervals for 12 consecutive feeding trials.

To access clutch effects on energy efficiencies, we used eight individuals from each of the five different clutches. Pythons were similarly weighed, fed rodent meals equaling 25% of snake body mass (Clutch A $= 23.7 \pm 0.1\%$, Clutch B $= 25.0 \pm 0.4\%$, Clutch C $= 27.6 \pm 0.9\%$, Clutch F $= 24.3 \pm 0.5\%$, Clutch G $= 25.1 \pm 0.2\%$) and feces and urate collected, weighed, dried, and reweighed. Snakes were fed at 10-day intervals for 11 (clutches F and G) or 12 (clutches A, B, and C) consecutive feeding trials. Following the completion of feeding trials, the total amount of rodents consumed, feces and urate excreted, and the increase in body mass was tabulated for each python. We calculated the energy of food, feces, urate, and growth as a product of their mass (wet or dry) times mass-specific values of energy (kJ g^{-1}) determined by bomb calorimetry (see below). We evaluated for the five clutches the relationship between each energy efficiency and standard metabolic rate (SMR).

2.3. Bomb calorimetry

Representative samples of mice (7.3–35.9 g, $n = 19$), rats (20–302 g, $n = 31$), feces ($n = 40$), urate ($n = 22$), and juvenile

pythons (106–373 g, $n = 5$) were weighed wet, dried to a constant mass at 60 °C, and reweighed (Table 1). Dried samples were ground to a homogenous fine powder and pressed into pellets. Three pellets from each sample were ignited in a bomb calorimeter (model 1266; Parr Instrument Co., Moline, IL, USA) to determine the energy content (kJ g^{-1} dry mass). For rodents and the python, wet mass energy equivalent was determined as the product of dry-mass energy content from bomb calorimetry and the rodents or the snakes' dry-mass percentage (Table 1). For feces and urate energy, we used the product of fecal or urate dry mass and their dry mass-specific energy content (Table 1).

2.4. Meal energy determination

Table 1 presents the mean energy content (kJ g^{-1}) of juvenile pythons and their feces and urate as determined from bomb calorimetry. Because of the respective 3 and 10-fold range in the mass of individual mice and rats fed to pythons, we developed the following regression equations to calculate each meal's energy content based on individual rodent mass (Fig. 1).

$$\text{Mice meal energy (kJ)} = (\text{mouse wet mass} \times 8.36) - 12.44 \, (r^2 = 0.996, P < 0.0001)$$

$$\text{Rat meal energy (kJ)} = (\text{rat wet mass} \times 7.06) - 9.81 \, (r^2 = 0.999, P < 0.0001)$$

2.5. Standard metabolic rates

For each clutch of pythons, we measured the SMR of 9–27 individuals (overall mass range: 113–975 g) as rates of O_2 consumption using a closed-system respirometry as described by Secor and Diamond (1997). Pythons were fasted for one month and placed within respirometry chambers (2–4 L) and maintained at 30 °C within an environmental chamber. Each respirometry chamber was fitted with an incurrent and excurrent
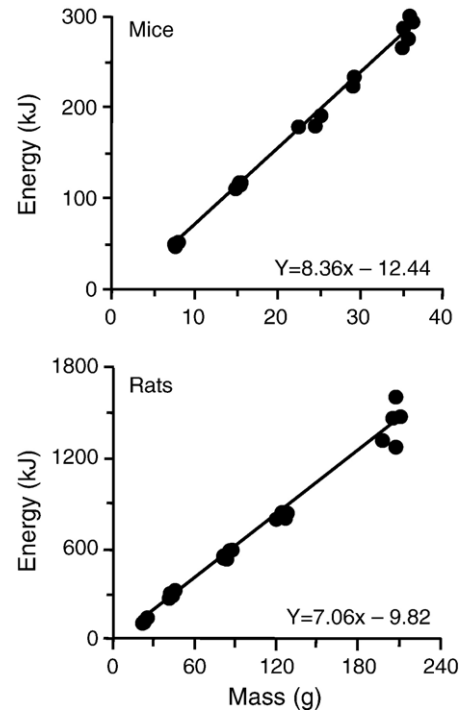

Fig. 1. Total energy content (kJ) of mice and rats, determined by bomb calorimetry, plotted against body mass. The resulting linear regressions were used to predict the energy content of each rodent meal.

air port, each attached to a three-way stopcock. Between measurements air was pumped into the chambers through the incurrent air port. For each metabolic measurement, a 50-mL air sample was withdrawn from the excurrent air port, and both incurrent and excurrent ports were then closed to seal the chamber. Thirty to sixty minutes later, the excurrent air port was opened and a second 50-mL air sample was withdrawn. The air sample was pumped (125 mL min^{-1}) through a column of water absorbent (Drierite; W. A. Hammond Drierite Co., Xenia, OH, USA) and CO_2 absorbent (Ascarite II; Thomas Scientific, Swedesboro, NJ, USA) into an O_2 analyzer (S-3A II; AEI Technologies, Pittsburgh, PA, USA). We calculated whole-animal (mL h^{-1}) $\dot{V}O_2$ corrected for standard pressure and temperature using a modification of equation 9 of Vleck (1987). We assigned each snake's SMR as the lowest calculated $\dot{V}O_2$ measured over a five-day period.

2.6. Calculations of energy efficiencies

While theoretically simple, empirically quantifying these energy efficiencies is problematic. Feces, while largely composed of unabsorbed food, also includes sloughed intestinal cells, intestinal microbes, and digestive enzymes and secretions. Therefore, in subtracting fecal energy from food energy the amount of excreted energy is overestimated, therefore resulting in the underestimation of digestive and assimilation efficiencies. In acknowledging these inherent errors, we, as others, will refer to these indices as 'apparent digestive efficiency' and 'apparent assimilation efficiency' (McKinnon and Alexander, 1999). We quantify apparent digestive efficiency (ADE), the relative

Table 1
Wet mass, dry mass, and dry and wet energy densities (kJ g^{-1}) of mice, rats, pythons and python feces and urates

Item	n	Wet mass (g)	Dry mass (g)	Energy dry (kJ g^{-1})	Energy wet (kJ g^{-1})
Mice					
Weanlings	5	7.33±0.08	2.02±0.03	24.1±0.1	6.64±0.08
Juveniles	5	15.0±0.1	4.49±0.11	25.5±0.1	7.62±0.04
Subadults	5	25.7±1.3	8.37±0.46	23.9±0.3	7.77±0.12
Adults	5	35.2±0.2	11.6±0.3	24.4±0.2	8.04±0.15
Rats					
Pups	5	20.4±0.6	4.98±0.20	24.4±0.2	5.98±0.12
Weanlings	5	40.3±0.8	11.7±0.4	25.4±0.1	7.41±0.13
Smalls	5	81.5±1.3	23.8±0.5	24.1±0.1	7.11±0.09
Mediums	5	137±7	42.6±2.4	23.5±0.4	7.29±0.14
Adults	5	196±8	61.6±1.5	23.7±0.3	7.48±0.28
Pythons	5	240±51	66.4±14.1	22.2±0.4	6.30±0.06
Feces	40			16.0±0.4	
Urates	22			11.4±0.2	

amount of ingested meal energy absorbed by the gastrointestinal tract as:

$$ADE = (\text{meal energy} - \text{feces energy})/\text{meal energy}$$

Apparent assimilation efficiency (AAE), the relative amount of ingested meal energy available for metabolism and growth, was quantified as:

$$AAE = (\text{meal energy} - \text{feces and urate energy})/\text{meal energy}$$

Production efficiency (PE), the relative amount of meal energy that is invested in growth, was quantified as:

$$PE = \text{energy of body mass increase}/\text{meal energy}$$

2.7. Statistical methods

Effects of meal size and clutch on growth rates and energy efficiencies were tested using an ANCOVA, using body mass as the covariate. *Post-hoc* pairwise comparisons (Tukey test) were undertaken when ANCOVA showed significant differences among groups ($P<0.05$). ANCOVA results and significant pairwise comparisons are reported as P values. For each clutch we plotted (log–log) SMR against body mass and calculated an allometric equation. We used the clutch-specific regression equation and each snake's SMR to predict their SMR to a common body mass of 450 g (approximate mean body mass of the 76 snakes used to measure SMR). For all statistical comparisons we set the level of significance to $P<0.05$ and report values as mean±1 SE.

3. Results

3.1. Effects of meal size

Body mass of pythons at the beginning of this experiment varied significantly ($P<0.0001$) among the three meal-size treatments, with the 35% meal-size snakes averaging 22% and

Fig. 3. Mean body mass of juvenile Burmese pythons for each meal-size treatment over the course of the study (top panel), and individual pythons from each meal-size treatment (bottom panel). Note that animals fed 35% of body mass grew twice as large as the 15% meal-size group. In this and similar figures, error bars indicate±1 SE. and are omitted if the SE is smaller than the width of the symbol used for the mean value.

64% heavier than the 25% and 15% meal-size snakes, respectively. However, there was no significant relationship between body mass and any of the energy efficiencies among meal sizes. Independent of starting body mass, growth rates (g d^{-1}) varied significantly (P values <0.001, Fig. 2) among and between meal-size treatments, such that by the end of the experiment 35% meal-size snakes averaged 71% and 200% heavier than 25% and 15% meal-size snakes, respectively (Fig. 3). In contrast, meal size had no significant (P values >0.18) effects
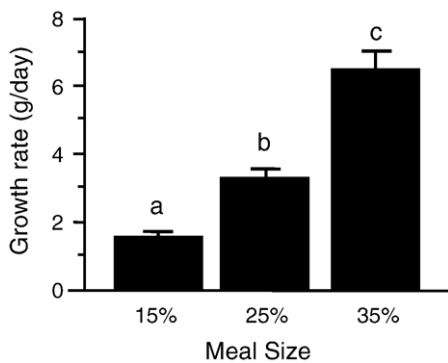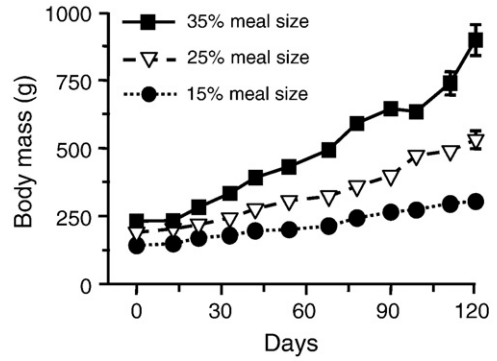

Fig. 2. Mean growth rates for juvenile Burmese pythons for the three different relative meal sizes. Growth rates were greatest for the largest meal size (35%), and least for the smallest meal size (15%). In this and the following histograms, error bars indicate±1 SE. and letters above bars that are different denote significant ($P<0.05$) differences between means as determined from *post hoc* pairwise comparisons.
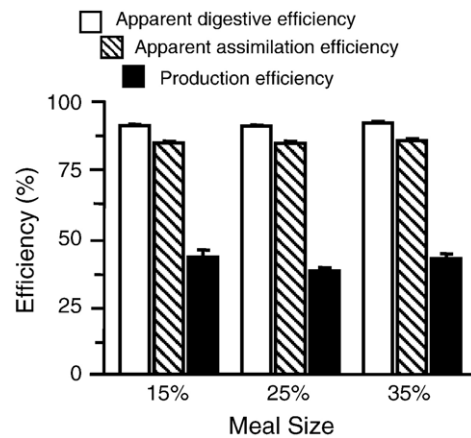

Fig. 4. Apparent digestive efficiency, apparent assimilation efficiency, and production efficiencies of juvenile Burmese pythons maintained on three different size diets (15%, 25%, and 35% of body mass). Note that none of the energy efficiencies statistically differed among the relative meal-size treatments.

on ADE, AAE, or PE for snakes of clutch B (Fig. 4). Pooled for the three meal-size treatments, ADE, AAE, and PE averaged 91.0±0.3%, 84.7±0.4%, and 40.7±1.1%, respectively.

3.2. Effects of clutch

Starting body mass varied significantly ($P<0.0001$) among the five clutches of snakes, as snakes of clutch A averaged twice as heavy as those of clutch C. However, there was no significant relationship between body mass and any of the energy efficiencies among clutches. Following the 11 or 12 feedings, clutches varied significantly (P values<0.001) in both ADE and AAE (Fig. 5). For both indices of efficiency, snakes of clutches A, B, and C, possess significantly (P values<0.001) greater efficiencies than snakes of clutches F and G (Fig. 5). Likewise, PE varied significantly ($P<0.001$) among the five clutches, but with a pattern different from that of ADE and AAE (Fig. 5). Snakes of clutch F, G, and B, possessed significantly (P values<0.01) greater PE than snakes of clutch C.
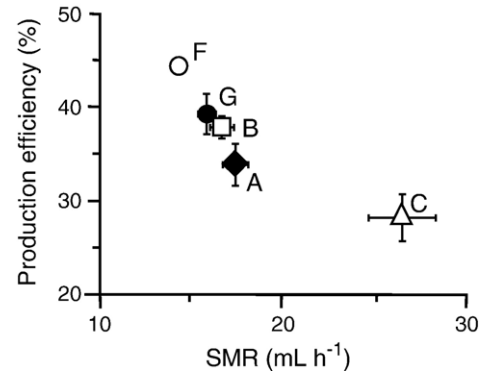
Fig. 6. Mean clutch standard metabolic rate (SMR) plotted against mean clutch production efficiency. We used a regression equation of standard metabolic rate against body mass to predict individual SMR at a common body mass of 450 g. Among python clutches there was a negative relationship between SMR and clutch production efficiency.

3.3. Relationship between SMR and PE

We evaluated the relationship between SMR and PE in two fashions. First, we plotted for 28 snakes for which we had both sets of data, PE against SMR (not shown). For this set of snakes, we found a significant negative relationship between individual PE and SMR ($P=0.032$). Second, we plotted clutch averages of SMR (individual SMR was adjusted to a common body mass of 450 g) against clutch averages of PE and likewise found a negative relationship between PE and SMR (Fig. 6). Individual snakes, as well as clutches that have a lower SMR tend to have a higher PE.

4. Discussion

For the Burmese python, while energy efficiencies do not vary with meal size, both clutch and metabolism impact energy efficiencies. In the ensuing discussion we will comment on the energy efficiencies of snakes, the effects of meal size on growth and efficiencies, clutch effects on energy efficiencies, the relationship between SMR and production efficiency, and the application of this data for constructing an energy budget.

Valid calculations of energy efficiencies are dependent upon the accurate determination of energy input, the energy lost to feces and urate, and the allocation of energy to growth. Because of the age-related variation in mass-specific energy content of rodents, we employed regression equations to calculate the energy content of individual mice and rats fed to snakes during this study. Over a 5 and 15-fold increase in body mass, mass-specific energy content of mice and rats increased by 21% and 64%, respectively. This increase in mass-specific energy reflects an increase in body fat and a corresponding increase in dry-mass content. Two previous studies using bomb calorimetry calculate the energy content of mice as 6.81 kJ g^{-1} wet mass (mouse mass=27.4 g; Greenwald and Kanter, 1979), and 8.95 kJ g^{-1} wet mass (mouse mass ranging from 7 to 35 g; Brisbin, 1970). Our values for mice reside within these previous estimates. Bomb calorimetry has likewise been used to determine the energy content of snake feces and urate. For the corn snake, *E. guttata*, energy content of feces and
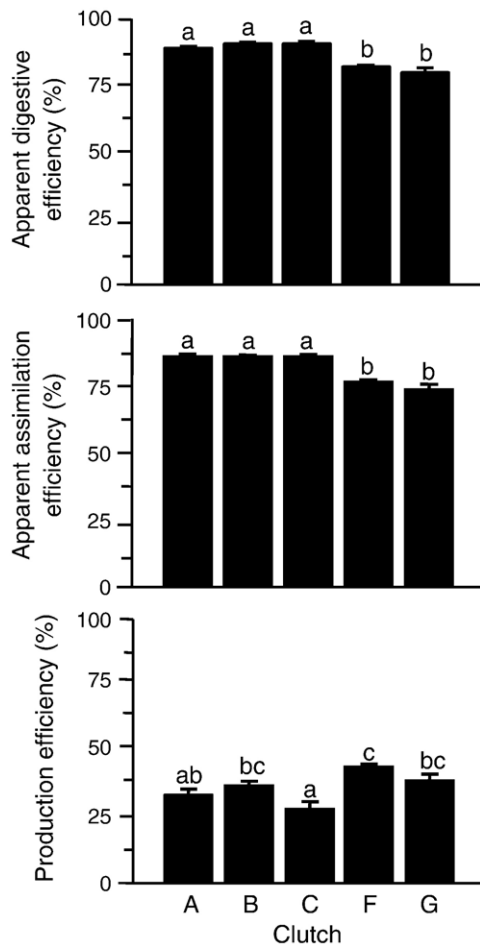

Fig. 5. Apparent digestive efficiency, apparent assimilation efficiency, and production efficiencies of juvenile Burmese pythons from five different clutches. Each of the energy efficiencies varied significantly among clutches (P values<0.05).
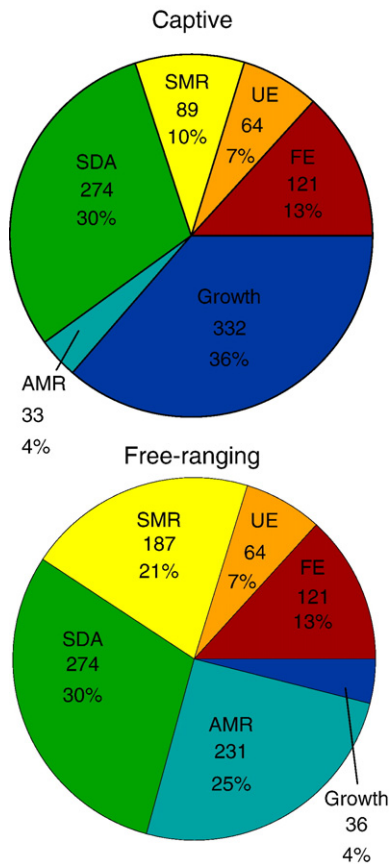
Fig. 7. Energy budgets (in kJ) for 500 g captive (duration of 10 days) and free-ranging Burmese pythons (duration of 21 days). Fecal energy (FE), urate energy (UE), standard metabolic rate (SMR), specific dynamic action (SDA), activity metabolic rate (AMR), and growth are presented both as energy (kJ) and as a percentage of ingested energy (EI; 913 kJ). Note for the captive pythons, a large proportion of EI is allocated to growth, whereas for a free-ranging python, more of the ingested energy is channeled into metabolism.

urate was measured as 13.6 and 11.6 kJ g^{-1}, respectively (Greenwald and Kanter, 1979). Calculated feces and urate energy (16.0 and 11.1 kJ g^{-1} respectively) for the blood python, *Python brongersmai*, are nearly identical to those values determined in this study for Burmese pythons (Vinegar et al., 1970). The few published ADE and AAE values of snakes (all ingesting rodents) overlap the range of values for juvenile Burmese pythons. For six species of Australian pythons maintained at four different body temperatures, ADE and AAE ranged between 89.0–98.0% and 77.9–93.7%, respectively (Bedford and Christian, 2000). For two blood pythons, ADE and AAE averaged 93.3% and 88.9%, respectively (Vinegar et al., 1970). Calculated ADE and AAE for the corn snake at three temperatures (20, 25, and 31 °C) ranged between 84.8–89.0% and 75.5–81.6%, respectively (Smith, 1976; Greenwald and Kanter, 1979). Production efficiency has been estimated based on energy consumed and gained for the corn snake (34.5%), and based on mass consumed and gained for the blood python (40%), (Vinegar et al., 1970; Smith, 1976).

We found growth rates to be significantly impacted by meal size. Snakes fed the largest meals (35% of body mass) grew faster and attained twice the body mass after 12 feedings compared to their siblings fed the smallest meals (15% of body

mass). Although growth rates differed among the three meal-size treatments, growth was linear for all meal-size treatments over the course of the study. The increase in growth with larger meals is due to the larger proportion of ingested energy that can be allocated to growth given that assimilation efficiencies are equivalent, SMR may vary by no more than 2-fold, and SDA is equivalent to 31.5% of ingested energy (Secor and Diamond, 1997).

Over an eight month span, captive juvenile blood pythons grew an average rate of 2.6 g d^{-1} (Vinegar et al., 1970), a growth rate that is intermediate between that experienced by the Burmese pythons maintained at 15% (1.7 g d^{-1}) and 25% (3.4 g d^{-1}) meal sizes. Published growth rates for captive reticulated pythons, *P. reticulatus* (3.5–7.0 g d^{-1}), captive African rock pythons, *P. sebae*, (9.6 g d^{-1}), and a Burmese python (6.2 g d^{-1}) match growth rates of Burmese pythons maintained in captivity on the 35% relative meal size (Pope 1961; Minton and Minton, 1973). Estimated growth rates of free-ranging water pythons, *Liasis fuscus*, averaged 1.2 g d^{-1} (Madsen and Shine 2000, 2002). Relative to captive pythons, the lower growth rate of free-ranging water pythons could reflect less food consumed and more of the ingested energy being allocated to activity instead of growth.

In contrast to growth rates, apparent digestive, apparent assimilation, and production efficiencies of juvenile Burmese pythons did not differ among the three tested meal sizes. As Burmese pythons are able to consume meals up to 111% of their body mass (Secor and Diamond, 1997), it is uncertain whether these energy efficiencies remain stable over the full range of the potential meal sizes for the Burmese python. For other animals, the effects of meal size on energy efficiencies have been mixed. Meal size has no significant impact on either the digestive or assimilation efficiencies of the harp seal, *Phoca groenlandica* (Lawson et al., 1989). In contrast, the side-blotched lizard, *Uta stansburiana*, experience a 2.7% decrease in digestive efficiency when switched from a restricted to an unrestricted diet (Waldschmidt et al., 1986). Both the perch, *Perca fluviatilis*, and the phantom midge larvae, *Chaoborus trivirgatus*, experience decreased assimilation efficiency with 7 and 9-fold respective increases in meal size (Solomon and Brafield, 1972; Guigere, 1981).

Each index of energy efficiency varied significantly among the five clutches, suggestive of a genetic influence on the capacity to digest and assimilate a meal and on growth. We believe for this study the potential for environmental influences on interclutch variation in efficiencies is minor considering that each clutch of eggs was artificially incubated and all young snakes were maintained under similar temperatures and humidity. Whereas we found each index of energy efficiency to differ among clutches, variation in ADE and AAE has not been strongly linked to genetic relatedness for either cattle of poultry (Veerkamp and Emmans, 1995; Jackson and Diamond, 1996). Production efficiency, on the other hand, has been linked to genetics for strains of mice, *Mus musculus*, and for cattle (Schemmel et al., 1972; Johnson et al., 2003).

There are two physiological mechanisms for why production efficiencies may differ among clutches. One potential mechanism underlying clutch differences in PE is the clutch-based variation in digestive performance due to differences in enzyme

and transporter activities and densities, resulting in differences in the amount of ingested energy absorbed and hence allocated to growth (Jobling, 1995; Lemieux et al., 1999). If genetic based variation in digestive performance is the primary determinant of PE, then both ADE and AAE will be significantly correlated with PE. The lack of a significant relationship between ADE or AAE and PE among clutches dismisses this mechanism as a valid explanation for the observed differences among python clutches. A second potential mechanism responsible for differences in PE among clutches is the variation in metabolic expenditures. If more of the assimilated energy is expended on SMR and or activity metabolism, less energy is then available for growth, and hence production efficiency would decrease (Calow and Townsend, 1981; Angilletta, 2001). Therefore, clutch PE should be negatively correlated with clutch metabolic rate. We found in comparing clutch PE with clutch SMR that clutches with lower SMR (clutches B, F, and G) possessed higher PE, and clutches with higher SMR (clutches A and C) possessed the lowest PE. Thus for juvenile Burmese pythons, a genetic tendency to increase or decrease SMR is manifested in a respective decrease or increase in PE.

Calculated energy efficiencies are useful in the construction of energy budgets. An energy budget (1) quantitatively balances energy input from ingested food (EI) with the energy lost in feces (FE) and urates (UE), and the energy available for metabolism [(SMR, specific dynamic action (SDA), and activity metabolic rate (AMR)] and production (somatic growth, reproduction and fat stores; Congdon et al., 1982).

$$EI = FE + UE + SMR + SDA + AMR + growth + reproduction + fat \qquad (1)$$

We applied the results of this study and an earlier study on python SMR and SDA (Secor and Diamond, 1997) to develop a 10-day energy budget for a captive 500-g Burmese python, maintained at 30 °C, and fed a rat meal 25% of body mass (Fig. 7). Subtracting the energy lost as feces (13.3% of EI), and urate (7% of EI), the assimilated energy is allocated to SMR (9.7% of EI), SDA (30% of EI), and production (*i.e.*, somatic growth and fat gain; 36.4% of EI). The remaining assimilated energy (33.2 kJ) would represent the energy spent on activity. Although pythons are relatively inactive in their cages, they occasionally move about, especially after a week following feeding. This remaining energy, equivalent to 3.5 days of SMR, would fuel that activity. While we acknowledge that this captive energy budget is lacking in ecological relevance, these results can be used to model energy flux of free-ranging Burmese pythons. Applying laboratory results with field measurements, we constructed a hypothetical energy budget for a similar-size free-ranging Burmese python. We assumed equivalent energy intake, fecal and urate loss, daily SMR and meal SDA as the captive snake. We predicted that in the wild, pythons are eating less frequently and are more active (Goodyear, 1994). Therefore we extended the single meal budget to three weeks and calculate an AMR for the 13 days that the snake is not digesting, assuming that active field metabolic rates (sum of SMR and AMR) are 3 times SMR, based on Secor and Nagy (1994) for the sit-and-wait foraging sidewinder, *Crotalus cerastes*. With the

increase in energy allocated to SMR and AMR, the energy available for growth decreases to 36 kJ, 4% of EI (Fig. 7).

The accuracy of such an energy budget would be enhanced by field observations of feeding frequency, meal type, and meal size, and field measurements of body temperature and activity. The immediate utility of such an energy budget would be to model the energy intake, growth rates, and potential reproduction of the Burmese pythons that have colonized the Everglades National Park in Florida (Snow et al., 2007).

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