

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 fed 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±0.3%), 25% (actual 25.0±0.4%), and 35% (actual 33.8±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 assess 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±0.1%, Clutch B=25.0±0.4%, Clutch C=27.6±0.9%, Clutch F=24.3±0.5%, Clutch G=25.1±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

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