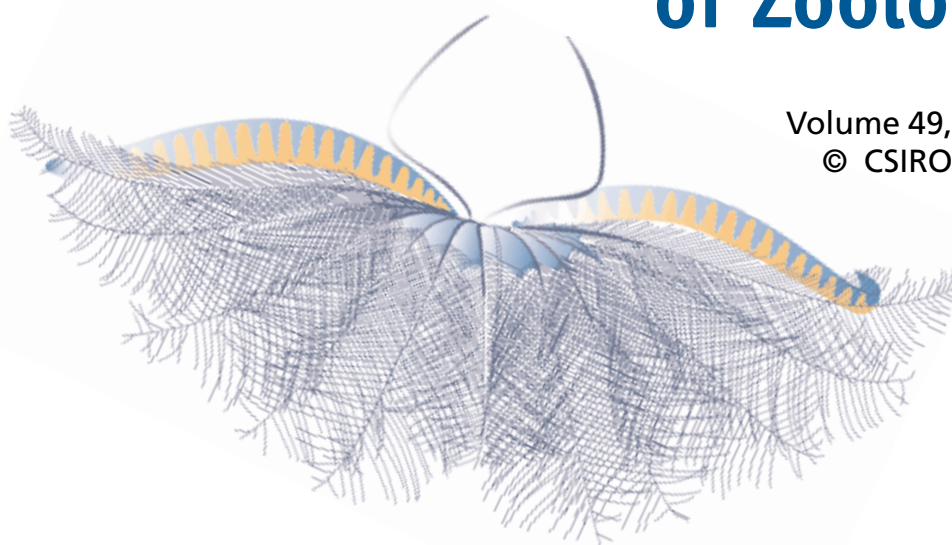


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## Metabolic response to feeding and fasting in the water python (*Liasis fuscus*)

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### Abstract

Compared with other reptiles, pythons have a relatively low standard metabolic rate (SMR) when post-absorptive, but metabolism increases substantially after feeding. This study examined the effects of feeding and fasting on adult and hatchling water pythons (*Liasis fuscus*). We compared ratios of peak digestive metabolic rate (PDMR) after feeding with the metabolic rate of both post-absorptive (SMR) and fasted water pythons. If metabolic rate of a fasting snake is taken as 'SMR', then the ratio PDMR/SMR becomes increasingly exaggerated as fasting continues. After 56 days of fasting in adults, or after 45 days in hatchlings, the metabolic rate of water pythons was significantly lower than that of post-absorptive animals. Peak digestive metabolic rate of post-absorptive adult water pythons was only 6.3–12.0 times SMR, but the ratio was twice that if fasted (metabolically depressed) animals were used to determine the 'SMR' denominator. Thus, this ratio should be used with caution. Peak digestive metabolic rate after feeding increased with increasing meal size for meals less than 20% of body mass, but PDMR did not increase for meals between 20% and 39% of body mass for adult water pythons. Similarly, the PDMR did not increase significantly between 25% and 50% meal sizes for hatchlings. The digestive physiology of water pythons is apparently better suited to frequent meals of relatively small prey compared with the digestive physiology of some other pythons.

### Introduction

Standard metabolic rate (SMR) has been a useful benchmark in the study of ectotherms because it represents a repeatable minimum measure of the energy needed for life maintenance in reptiles (Bennett and Dawson 1976). Conventionally, SMR is measured from an ectotherm that is inactive and in a post-absorptive state (Kleiber 1975; Bennett and Dawson 1976; Niewiarowski and Waldschmidt 1992).

Pythons have both a very low SMR (Bennett and Dawson 1976; Andrews and Pough 1985; Chappell and Ellis 1987), and, under at least two circumstances, the capacity to raise their metabolic rate many times above SMR. Metabolic rate is substantially elevated up to 22 times SMR during the brooding of eggs (Harlow and Grigg 1987; Slip and Shine 1988a) and up to 45 times SMR after feeding (Benedict 1932; Secor 1995; Secor and Diamond 1995, 1997, 2000; Thompson and Withers 1999). In the Burmese python (*Python molurus bivittatus*), the peak digestive metabolic rate (PDMR) is positively correlated with the amount of food eaten (Secor and Diamond 1997).

The increased metabolism during digestion is commonly referred to as specific dynamic action (SDA), and is characteristic of most animals. Generally, metabolism increases by 25–50% above SMR in mammals (Brody 1945), 60–160% in fish (Jobling 1981) and 200% in *Alligator mississippiensis* (Coulson and Hernandez 1979). Much larger increases in metabolism after feeding were reported for pythons over half a century ago (Benedict 1932). Recently, the peak digestive metabolic rate in pythons has been reported as being between 7 and 45 times SMR (Secor and Diamond 1995, 1997).

The relatively large increase in oxygen consumption during digestion in pythons compared with mammals is attributable to three factors: (1) the relatively large meal size consumed by pythons, which can be more than 100% of their body mass (Pope 1961;

Mavromichalis and Bloem 1994); (2) the low SMR of pythons (Andrews and Pough 1985; Chappell and Ellis 1987); and (3) the ability of pythons to atrophy the gut and other organs during periods of fasting (Secor and Diamond 1995, 2000). It is possible that considerable energy is needed to maintain the gut in an active mode. Presumably as a mechanism to conserve energy, pythons have refined the ability to atrophy the gut and other organs after digestion (Secor and Diamond 1995, 2000). Some large pythons have fasted for more than two years without obvious detrimental effects (Benedict 1932; Slip and Shine 1988b).

This study reports post-absorptive SMR, PDMR after feeding, and metabolic rate as a function of fasting duration for hatchling and adult water pythons (*Liasis fuscus*). We also examine the extent to which PDMR is affected by relative meal size, evaluate the index of metabolic increase, as expressed by PDMR/SMR, and discuss how the conditions under which SMR is measured can influence this index.

## Materials and Methods

### *Animals, maintenance and sampling*

Water pythons (*Liasis fuscus*) are medium-sized pythons reaching a maximum length of 3 m (Barker and Barker 1994). They are endemic to areas of high annual rainfall in the tropical northern part of the Australian mainland (Shine 1991; Cogger 2000). Water pythons, like most pythons, are nocturnal hunters, feeding on birds and mammals (Barker and Barker 1994). This species is considered to be a sit-and-wait ambush predator, but may also actively forage when food is abundant (Madsen and Shine 1996).

Five adult *L. fuscus* were caught from the Fogg Dam area, 75 km east of Darwin, Northern Territory. All animals were at least 1 m long, with masses of 314–2200 g, and were considered to be adult (Shine 1991). They were housed in individual plastic cages at the Northern Territory University. These cages were maintained in an outside animal house, and exposed to ambient shaded conditions for Darwin in the wet season (Christian and Bedford 1995). All animals were offered food once per week and were eating consistently before experiments commenced.

Twelve captive-hatched water pythons were housed in 4-L plastic containers and maintained at a temperature of 30°C in a constant-temperature room for the duration of experiments. These animals were randomly selected from six clutches hatched from wild-caught females in August. These hatchling water pythons had masses of 25.0–60.5 g. Metabolic rate was determined at hatching. They were then fasted for six weeks before being fed dead laboratory mice equalling 10% of their mass, from which point feeding and fasting experiments commenced.

### *Metabolic response to feeding*

Adult animals were fed meals consisting of 5%, 10%, 20% and 25% ( $\pm 1\%$ ) of body mass and also fed more than 30% (range: 30–39%) of their body mass. Hatchlings were fed mice equalling  $25 \pm 2\%$ ,  $35 \pm 3\%$  and  $50 \pm 4\%$  of their body mass. Attempts were also made to feed hatchling animals meals of small mice totalling 75% of their body mass. The timing of each feeding event was at least 2-month intervals. Animals were fed the relative meal masses in no particular order. When feeding experiments were complete, fasting experiments began immediately.

During feeding and fasting experiments, each animal was placed in a perspex chamber inside a constant-temperature cabinet (Forma Scientific) at 30°C. Open-system respirometry was used to measure the metabolic response to digestion. Three animals were placed in individual chambers with air samples drawn consecutively from each of the animal chambers for a period of 2 h. Samples were drawn on a rotating basis over a 12-h period during daylight hours, therefore each animal was monitored for a total of 4 h over the 12-h period during the period when pythons are inactive. Metabolism was taken as the lowest stable measurements of oxygen consumption over a period of at least 40 min. Oxygen concentrations were measured with an Applied Electrochemistry S-3A oxygen analyser with rates of oxygen consumption calculated by the methods of Withers (1977).

To be certain that animals had completed the metabolic response to feeding, the period of 10–14 days after a moderate-sized meal (30% or less of body mass) was selected to represent post-absorptive SMR (Bedford 1996; Thompson and Withers 1999).

Oxygen consumption was measured continuously over the first 3 days after feeding to obtain the peak level of consumption. However, in this and other unpublished studies of pythons, Day 2 after feeding was

consistently the time when oxygen consumption peaked at 30°C, thus measurements of PDMR were obtained from Day 2 data.

#### *Metabolic response to fasting*

To determine the effect of fasting on metabolism, adult and hatchling *L. fuscus* were fasted for 98 and 114 days respectively. They were given water once a week, but no food. Metabolic rate was measured at various intervals during fasting. Hatchling animals were placed in a constant-temperature room at 30°C and given water once a week throughout the 114 days of their fast. No animal was measured during an ecdysis cycle.

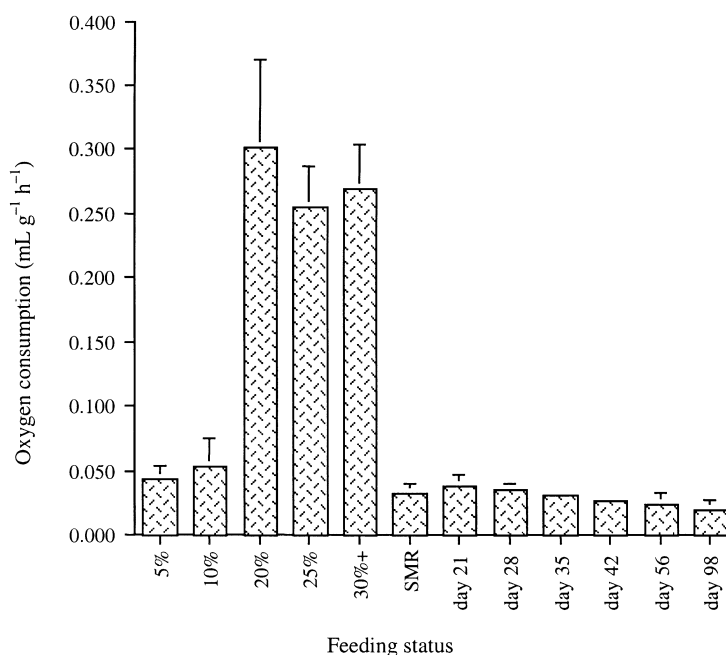
#### *Statistical analyses*

Measurements of metabolic rate immediately post-absorptive, after feeding, and after having fasted for some length of time were analysed statistically using analysis of covariance (ANCOVA) for adult water pythons, and repeated-measures ANCOVA was used to analyse data obtained from hatchling water pythons. All data were log-transformed, with  $\log(\text{mass})$  as a covariate. SYSTAT statistics package (Version 5.2 1992) was used for the repeated-measures ANCOVA. All other data were analysed using Statview and SuperAnova statistics packages.

## Results

### *Adult water pythons*

There was no significant difference between post-absorptive SMR (measured between Days 10 and 14 after feeding) and PDMR in pythons fed meals that were 5% or 10% of body mass (ANCOVA,  $P > 0.05$ ). However, PDMR was significantly higher than post-absorptive SMR when animals were fed 20%, 25% or more than 30% of their body mass in



**Fig. 1.** Metabolism after feeding (% values refer to size of meal relative to body size) and during a fasting period in adult water pythons (*Liasis fuscus*). Value of SMR was measured 10–14 days after a small meal (<10% body mass). Days 2–98 are days after a meal. Error bars indicate standard errors.

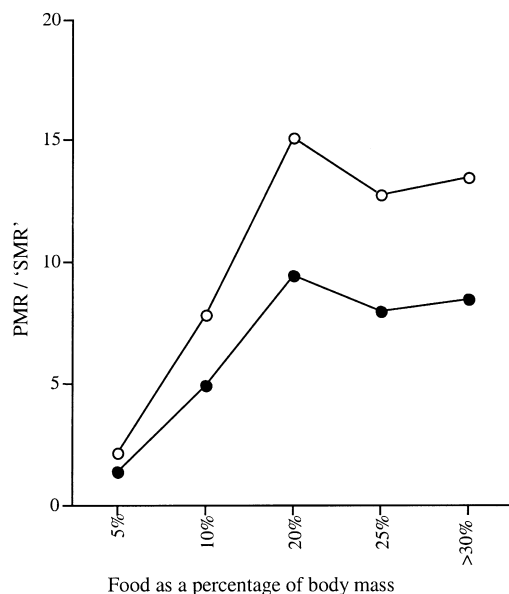
food (ANCOVA,  $F_{4,26} = 3.12$ ,  $P = 0.03$ ). The PDMR of oxygen consumption of pythons fed meals 20%, 25% or >30% of their body mass were not different from each other (ANCOVA,  $P > 0.05$ ). Thus, it appears that oxygen consumption reaches a plateau with meal sizes between 20% and 39% of body mass (Fig. 1).

Animals were fasted for 98 days, and oxygen consumption measurements were taken on the same day of the week at weekly intervals. Day 56 (six weeks after SMR measurements were taken) is the first measurement for which oxygen consumption had declined to a value that was significantly lower than SMR ( $F_{8,25} = 10.87$ ,  $P = 0.0001$ ; SMR =  $0.036 \text{ mL} \pm 0.017$  (s.d.)  $\text{g}^{-1} \text{ h}^{-1}$ ; mean ( $\pm$ s.d.) after 56 days =  $0.027 \pm 0.017 \text{ mL g}^{-1} \text{ h}^{-1}$ ). A *post hoc* Fisher's test showed that oxygen consumption on all days examined thereafter was significantly lower than SMR (Fig. 1).

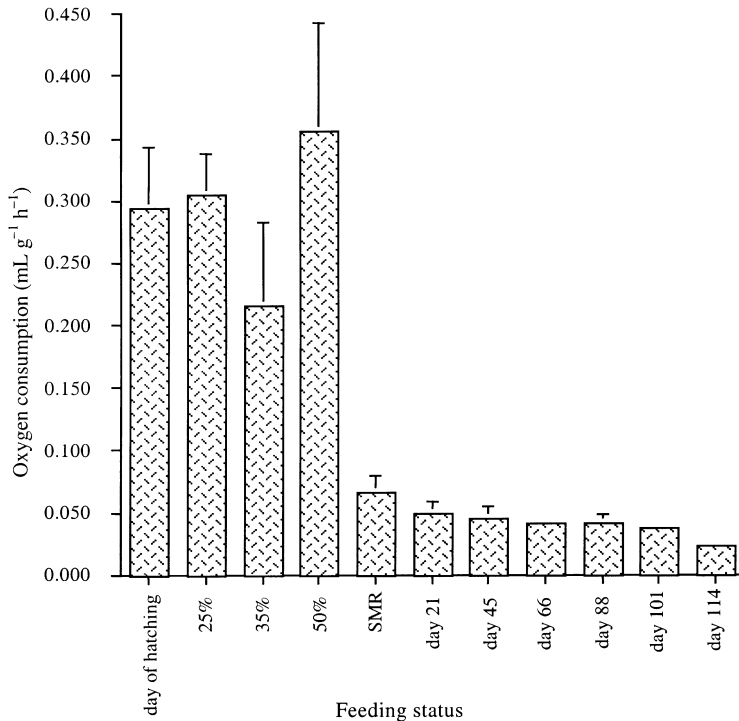
The mean ratios determined by dividing PDMR by post-absorptive SMR are shown by the solid circles in Fig. 2. These ratios varied from no appreciable difference from SMR for animals that had consumed a meal equalling 5% of their body mass to a maximum of 8.3 for an animal that had consumed food equalling 20% of its body mass. The open circles in Fig. 2 are mean ratios calculated using PDMR divided by the metabolism of pythons fasted for 98 days. Although both ratios reach a plateau with meal mass greater than 20% of body mass, the values calculated using the metabolic values of fasted animals as the denominator are almost twice that of data using the SMR in the denominator.

#### *Hatchling water pythons*

Peak digestive metabolic rate was significantly higher than post-absorptive SMR for hatchlings fed 25%, 35% and 50% of their body mass in food (ANCOVA,  $F_{3,13} = 6.9$ ,  $P = 0.005$ ). The rates of oxygen consumption of hatchlings fed 25%, 35% and 50% of their body mass were not significantly different from each other (ANCOVA,  $P > 0.05$ ) (Fig. 3). Metabolic rate within three days of hatching was high ( $0.285 \pm 0.150 \text{ mL g}^{-1} \text{ h}^{-1}$ ,  $n = 8$ ) but not significantly different from that of the three feeding categories (ANCOVA,  $P > 0.05$ ).



**Fig. 2.** Mean PDMR / 'SMR' ratios for increasing meal size relative to body mass in adult water pythons. Solid circles are mean values calculated using post-absorptive SMR (10–14 days after feeding) as the denominator, and open circles are mean ratios calculated using the metabolism of pythons after 98 days of fasting as the denominator.



**Fig. 3.** Metabolism on day of hatching, post-feeding and days during a fasting period in hatchling water pythons (*Liasis fuscus*). The percentage values refer to size of meal relative to body mass. SMR was measured 11 days after a meal of 10% body mass. Error bars represent standard errors.

When metabolic rate was measured 45 days after the commencement of fasting, metabolic rate of hatchlings had declined to a level significantly lower than SMR (repeated-measures ANCOVA,  $F_{3,24} = 2.6$ ,  $P = 0.03$ ). By 114 days after feeding, metabolic rate was only 32.4% of post-absorptive SMR (Fig. 3).

## Discussion

It is important to have a general protocol or standard that can be repeated when measuring physiological processes such as metabolism, particularly when there is large variability relating to feeding status, as in pythons. SMR in ectotherms should be measured while the animal is recently post-absorptive (Kleiber 1975; Niewiarowski and Waldschmidt 1992; Thompson and Withers 1999). The magnitude of peak metabolism after feeding is dependent on the point at which 'standard' metabolic rate is determined; this has been noted in other studies on pythons (Bedford 1996; Thompson and Withers 1999). Results from this study indicate that at 30°C, after the peak, metabolism declines over time for adult and hatchling water pythons. Post-absorptive SMR for pythons should be measured after at least 10 days after a meal, but before metabolism drops in response to extended fasting at 56 days for adults and 45 days in hatchlings. It should be noted, however, that very large meals (>50% of body mass) may result in longer periods of elevated metabolism (Secor and Diamond 1997). With a meal mass of 100% of body mass, metabolic rate returned to a pre-fed level 16 days after feeding (Secor and Diamond 1997).

At hatching, water python metabolism was very high, similar to that of animals that had consumed a meal larger than 20% of their body mass. We suggest that this may be due to the absorption of yolk into the body. Because hatchlings have a higher mass-specific metabolic rate than adult animals and because they expend more energy on growth, it follows that hatchlings will expend their fat reserves at a faster rate than adult animals. It is therefore not surprising that the duration of stable post-absorptive SMR was shorter for hatchlings than for adult animals (45 days *v.* 56 days).

During periods of reduced activity and feeding, the metabolic rate of many ectothermic animals gradually declines, presumably as a mechanism to conserve energy and water (Hochachka and Guppy 1987; Storey and Storey 1990; Guppy and Withers 1999). Among vertebrates, metabolic depression occurs in lungfish (Smith 1930; Fishman *et al.* 1986), every estivating amphibian that has ever been measured (Pinder *et al.* 1992; Withers 1993), inactive turtles (Seidel 1978; Kennett and Christian 1994; Hailey and Loveridge 1997), some over-wintering lizards (Tsuji 1988; Christian and Conley 1994), and tropical lizards during the dry season when food and water are scarce (Christian *et al.* 1996a, 1996b, 1996c, 1999). There is evidence that the lack of food is the stimulus for metabolic depression in lungfish (Smith 1930; Fishman *et al.* 1986), and there is circumstantial evidence that the lack of food (and water) is the stimulus for metabolic depression in some reptiles (Christian *et al.* 1996a, 1996b, 1996c, 1999), but not in an aestivating turtle (Kennett and Christian 1994).

By 56 and 45 days after feeding, in adult and hatchling water pythons, respectively, the metabolic rate had dropped significantly below a level that would be considered a conventional post-absorptive SMR as determined within 10–14 days after feeding. Some ectothermic vertebrates for which metabolism has been monitored over time reach a state of metabolic depression in about a month after regular activity ceases (Fishman 1986; Withers 1993; Kennett and Christian 1994).

After 114 days, the metabolism of fasting water pythons was depressed to 32% of SMR, which puts it in the range of metabolic depression (5–40%) most commonly found (Guppy and Withers 1999). The pattern of metabolism we describe here suggests that fasting water pythons have metabolic depression that is analogous to that of many other ectothermic vertebrates during periods of low food availability (Christian *et al.* 1996a, 1996b, 1996c, 1999; reviewed by Guppy and Withers 1999). Thus, the lack of food (and/or water) represents an environmental stress that triggers metabolic depression (Guppy and Withers 1999). This response is similar to that of animals exhibiting metabolic depression due to decreased food availability within a season, but because pythons feed opportunistically and infrequently, the ability to decrease metabolism has evolved to compensate for the uncertainty of feeding events throughout the year, rather than during a certain period within a year.

Not only can the gut atrophy after a meal in infrequent feeders like pythons, but also other metabolically expensive organs such as the liver, kidneys and heart (Secor and Diamond 2000). These organs appear to use more energy per gram than other organs (Oikawa and Itazawa 1984; Secor and Diamond 2000). Atrophy of energetically expensive organs may occur in water pythons after digestion, and if this process is occurring in water pythons, it would presumably contribute to the generally continuous and gradual decline in metabolic rate with fasting. However, atrophy of the gut, as experienced by Burmese pythons, has not been demonstrated in Australian pythons, so the observed metabolic decline with fasting may be due to some other mechanism. As noted by Guppy and Withers (1999), despite the documentation of a number of inter-related biochemical changes, the

exact mechanism of metabolic depression is not known for any species. Determining the relative roles of morphological changes (atrophy of organs) and biochemical changes during metabolic depression is a formidable challenge for future python research.

When comparing data from *L. fuscus* with those from *P. molurus* (Secor and Diamond 1997) there is a large difference in relative PDMR. For example, when consuming meals of 25% of body mass, the increase in metabolism is close to seven times SMR for *L. fuscus*, whereas *P. molurus* has an increase of 16 times SMR (Secor and Diamond 1997). These two species have the same mass-specific SMR (*L. fuscus* and *P. molurus* SMR =  $0.036 \text{ mL g}^{-1} \text{ h}^{-1}$ ). Thus, the peak in metabolism after feeding in *L. fuscus*, and in Australian pythons in general (Bedford 1996; Thompson and Withers 1999), is moderate compared with that in *P. molurus*.

Peak digestive metabolic rate did not change for meal sizes between 20% and 39% of body mass in adult water pythons. Hatchling pythons that ate 25–50% of their body mass in food did not significantly increase PDMR with increasing meal sizes, although there was a slight trend in this direction. These results indicate a plateau in PDMR for at least part of the range of meal sizes offered, possibly encompassing the relative meal sizes most often encountered in the wild by water pythons (Madsen and Shine 1996). A plateau in PDMR exists in some fish (Jobling and Davies 1980), but PDMR in the Burmese python continues to increase with increasing meal mass even above 111% of body mass (Secor and Diamond 1997).

Why PDMR should reach a plateau with increasing meal size in some Australian pythons but continue to increase with increasing meal size in *P. molurus* is unknown. The Burmese python can grow to body sizes of 6 m and over 100 kg (Pope 1961). Adult water pythons are less than 10% of this mass, and most have a length of <3 m and a mass <3 kg. It is possible that the Burmese python has evolved an increasing digestive response to increasing meal size to exploit very large prey items. Water pythons, on the other hand, may have evolved in an environment where they feed on relatively small prey such as rats (Madsen and Shine 1996), and their body size may be an adaptation related to the available food resources (Shine and Slip 1990). Very rarely do water pythons have a full gut, and when they do it contains relatively small prey items (Shine and Slip 1990). Therefore, both the body size and the meal size relative to body size of water pythons may be related to the relative paucity of large prey items in water python environments.

Although adult water pythons were offered a larger mass of food during the experiments, none of the snakes ate more than 39% of their body mass. The 12 hatchling water pythons were offered a meal comprising 75% of body mass, but none were able to complete digestion. These observations may indicate that water pythons are unable to eat the relatively large meals that can be consumed by the gigantic Burmese python, at least under the experimental conditions of 30°C. A thermophilic response to a large meal is an important aid in python digestion (Regal 1966; Slip and Shine 1988c). Determining the effect of increasing temperature on increasing meal size would be a valuable contribution to our understanding of the digestive physiology of pythons.

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