

Short and chubby or long and slim? Food intake, growth and body condition in free-ranging pythons

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Abstract An animal's sex and body size can influence not only its rate of food consumption, but also the way in which it allocates the resultant energy among the competing demands of maintenance, growth, reproduction and storage. A 13-year mark–recapture study of pythons (*Liasis fuscus*) in tropical Australia provides extensive data on these topics. Rates of food intake and growth were highest in small pythons, and decreased more rapidly with body size in males than in females. Allocation to storage (as measured by the snake's mass relative to its body length) showed a more complex pattern. Body condition was high at hatching, but dropped rapidly as energy was allocated to growth rather than storage. Condition then increased through juvenile life, was at a maximum close to maturation, and was higher in females than in conspecific males. Body condition thereafter decreased with increasing body length. These allocation 'decisions' reflect the relative advantages of growth versus energy storage at different body sizes. Hatchling snakes grow rapidly (and hence become thin) because greater body size enables the snake to ingest larger prey items. Adult females amass larger energy reserves than males, because they need reserves to produce the clutch. Large snakes become thinner because their feeding rates are low, and they cannot compensate with increased prey size because large-bodied mammalian prey are rare in our study area.

Key words: energy allocation, *Liasis fuscus*, life-history, Pythonidae, snake.

INTRODUCTION

Life-history tactics can be visualized as a set of 'rules' that determine the rate at which resources (such as food) are gathered, and the subsequent division of those resources among four competing demands: maintenance costs, growth, reproduction and storage. Studies of allocation rules have been a major theme of research into life-history evolution (Roff 1992). In both theoretical and empirical studies, the classical emphasis has been on the 'decision' about allocation to growth versus reproduction (e.g. Fisher 1958), but recent years have seen an increasing appreciation of the crucial role of energy storage in the life-history (Bonnet & Naulleau 1996; Naulleau & Bonnet 1996; Doughty & Shine 1998).

Although many studies on allocation strategies have been based on 'model organisms' such as birds and lizards (Derickson 1976; Sinervo 1994; Gustafsson *et al.* 1995), snakes may offer particular advantages for research on this topic. Their simple morphology facilitates the use of straightforward body-condition indices (mass relative to length) as measures of energy storage. As ectotherms, they do not display massive seasonal shifts in fat storage levels associated with thermoregulatory challenges or migration (Bonnet *et al.* 1998b). Also, all of these energy-flow pathways depend

on body size, because a snake's size determines its maximal ingestible prey size, its growth rate, its maintenance costs and its reproductive output (Fitch 1970; Ellis & Chappell 1987; Arnold 1993). Body sizes in snakes are highly variable both within and among populations. A single population contains ecologically independent individuals that span a very wide range of body sizes, and geographically adjacent populations may differ substantially in mean adult body sizes (Schwaner & Sarre 1988; Madsen & Shine 1993), which facilitates the analysis of size-related shifts in allocation rules. In contrast, endotherms generally display far less intraspecific variation in body size (Pough 1980; Bonnet *et al.* 1998b).

In the course of a long-term field study of pythons in tropical Australia, we have gathered extensive data on the snakes' rates of food intake and growth, and on their body condition. We have analysed these data to investigate the ways in which a snake's sex and body size influence its rate of feeding, and its subsequent allocation of resources between growth and energy storage.

MATERIALS AND METHODS

Study area and species

The study was conducted in the Fogg Dam conservation reserve, in the lower reaches of the Adelaide

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River floodplain 60 km south-east of Darwin in the Northern Territory, Australia. Our previous papers on this system have described the climate, topography and environment (e.g. Madsen & Shine 1999a). The area is in the wet-dry tropics; it is hot year-round but rainfall is concentrated in a 4-month wet season (December–March), with resultant seasonal flooding.

Water pythons (*Liasis fuscus*) are large (to 3 m, 5 kg) non-venomous snakes that occur over a wide area of tropical Australia (Cogger 1992). The species is very abundant in our study area. The reproductive rates of the pythons vary considerably among years, with prey abundance determining python feeding rates, body condition, and the proportion of adult-size female snakes that reproduce each year (Shine & Madsen 1997). Male pythons mature at a snout–vent length (SVL) of approximately 140 cm. Some females begin reproducing at this size also, but most delay maturation until they attain a SVL of 160 cm. Reproduction is highly seasonal. Mating occurs in the middle of the dry season (July–mid-August), and the eggs are laid approximately one month later (Madsen & Shine 1996a, 1999b). Females reproduce, on average, approximately once every second year, but with substantial variation due to body size, local food availability and nest-site location (Shine & Madsen 1997; Madsen & Shine 1999b). Reproductive females are easily recognizable by their body shape in July, August and September (Madsen & Shine 1999c).

METHODS

Pythons were collected by spotlighting at night from a slow-moving car. We recorded SVL, mass, sex and individually marked all snakes by clipping ventral scales. All pythons were palpated for the presence of faeces (an indication of recent feeding) before being released at their site of capture the following day. The field-captured snakes were divided into 12 size classes (hereafter, ‘cohorts’) based on their SVL. In order to achieve adequate sample sizes for statistical analyses, these size-based cohorts did not span identical SVL intervals. The two smallest cohorts of field-collected snakes consisted of: (i) pythons with SVL <80 cm; and (ii) snakes with SVL of 80–99 cm. Similarly, all snakes with SVL ≥ 190 cm were pooled into a single cohort. The remaining nine cohorts were based on 10-cm SVL intervals ranging from 100–109 cm to 180–189 cm. We also measured hatchling pythons that emerged from eggs laid in captivity by wild-caught females. To estimate growth rates over the first month of life, we re-measured the same animals 30 days after hatching. They were maintained in captivity without food during the intervening period (Shine *et al.* 1997).

The growth rates of field-collected snakes (mm SVL per day) were based on recaptures separated by inter-

vals of 6 months to 2 years. A snake was allocated to a particular SVL category based on its SVL at the time of initial capture. All analyses on growth and body condition were based on one record per snake, because data taken from successive captures would violate the assumption of independence. Our data on feeding rates were based on samples collected during the dry season only, because the snakes move out of the Fogg Dam reserve with the onset of wet season flooding in December–January (Madsen & Shine 1996b). Our estimates of feeding rates do not include reproductive females, or adult males collected during the mating season (July–August), because these groups of snakes do not feed (Madsen & Shine 2000). Because a snake’s status as fed or unfed should not influence its feeding status when recaptured several months later, our calculations of feeding frequency include all records, including repeated records from snakes that were recaptured during different years of the study.

Using the proportion of snakes containing food as an index of feeding rates assumes low variation in prey sizes and rates of digestion among snake size classes. The Fogg Dam pythons feed almost exclusively on a single prey species with a very small range in adult body sizes. Apart from very small juvenile snakes (which cannot physically ingest large adult rats), all snakes can eat rats of all sizes. Thus, snakes of different sizes generally take rats of similar sizes. Also, our studies on the thermal biology of these animals detected no strong differences among size cohorts in

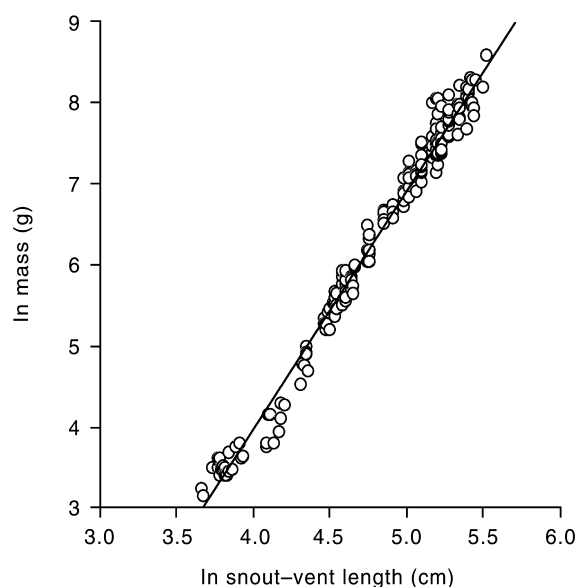


Fig. 1. Body mass relative to snout–vent length (SVL) in a sample of water pythons. Both axes are ln-transformed. The least-squares linear regression of best fit for the overall data set is shown by the line, and by the equation $\ln \text{ mass} = 2.905 \times \ln \text{ SVL} - 7.564$. Separate equations for each sex are as follows: males, $\ln \text{ mass} = 2.905 \times \text{SVL} - 7.569$; females, $\ln \text{ mass} = 2.903 \times \text{SVL} - 7.54$.

body temperatures or activity times (Shine & Madsen 1996). Body temperature is undoubtedly the strongest determinant of digestive rate. We thus conclude that these assumptions (low variation in prey size and rates of digestion) are likely to be met in our system.

To quantify variation in body condition, we calculated residual scores from the general linear regression of ln-transformed mass versus ln-transformed SVL (Fig. 1; see Figure caption for equation). This measure compares a snake's mass to that expected for a snake of that body length within the population. In effect, our body-condition scores thus express the extent to which any given snake deviates from a null model whereby mass is proportional to body length raised to an exponent of 2.905.

RESULTS

Over the period 1987–1999, we captured and marked 3942 pythons (2171 males and 1771 females). Table 1 shows the number of male and female pythons in each of the 13 SVL cohorts defined previously.

Feeding rates

In the field-collected pythons, the proportion of snakes that were recorded as having recently fed varied significantly among the 12 cohorts in both males and females ($\chi^2 = 126.4$, d.f. = 11, $P = 0.0001$; $\chi^2 = 182.2$, d.f. = 11, $P = 0.0001$, respectively). The feeding rate of female pythons was higher than that of the males in 10 of the 12 cohorts (Fig. 2a; Wilcoxon signed-rank test $Z = 2.82$, $P = 0.005$). Feeding rates of both male and female pythons were very low in the smallest cohort (≤ 79 cm), but increased dramatically at larger body

sizes (Fig. 2a). Feeding rates of both male and female water pythons were highest in the 100–109 cm cohort (Fig. 2a). Males continued to feed frequently until they reached a body size of 130–139 cm (Fig. 2a) but feeding rates declined at maturity (140–149 cm) and continued to fall thereafter, reaching a minimum in the largest body size cohort (Fig. 2a). In contrast to males, female pythons in the 140–149 cm cohort continued to feed frequently (Fig. 2a). However, as for the males, the feeding rates of female pythons declined considerably at larger body sizes. The lowest feeding rates were recorded in the largest snakes (≥ 190 cm; Fig. 2a).

Food supply for the pythons, and thus their feeding rates, varied substantially among the years of our study (Shine & Madsen 1997). Did this annual variation in food supply affect the feeding rates of subadult and adult snakes in similar ways? To answer this question, we calculated mean annual feeding rates for subadult and adult snakes of both sexes. These analyses excluded data from the breeding season, as explained previously. Our analyses showed that in years when subadults had high feeding rates, adults also had high feeding rates, but that adult feeding rates increased at a lower rate than did those of subadult snakes. This result can most easily be seen by plotting the proportion of adults with food against the proportion of subadults with food (Fig. 3). The regressions are significant for both sexes (males: $r = 0.92$, d.f. = 10, $P = 0.0001$; females: $r = 0.68$, d.f. = 10, $P = 0.02$). In both cases, the slope of the calculated regression line is less than 1.0 (forcing the line through the origin: males, slope = 0.54, with 95% confidence limits (CL) 0.49–0.59; for females, slope = 0.55, 95% CL = 0.39–0.70). That is, feeding rates of both size classes increased in similar ways in years with higher food supply, but juveniles exploited this opportunity to a greater degree than did adult conspecifics.

Table 1. Numbers of female and male pythons in each of the 13 body-size cohorts

Snout–vent length (cm)	Total no. males	Total no. females	No. gravid females	Percentage gravid females
Hatchlings	60	66	0	0
≤ 79	26	16	0	0
80–99	80	78	0	0
100–109	112	103	0	0
110–119	149	99	0	0
120–129	259	129	0	0
130–139	313	215	0	0
140–149	325	254	11	4.3
150–159	289	193	13	6.7
160–169	306	198	36	18.2
170–179	201	200	32	16.0
180–189	89	123	92	25.2
≥ 190	22	163	15	9.2

Hatchlings were obtained from eggs laid in captivity, but numbers in all other size classes are based on snakes captured in the field. The number and proportion of reproductive (gravid) females in each size class are also shown.

Growth rates

Although the captive-hatched snakes were not fed during their first month of life, they increased substantially in SVL, from a mean of 43.0 cm to 50.3 cm. Indeed, they grew more rapidly over this period than at any other time in their lives (Fig. 2b). After

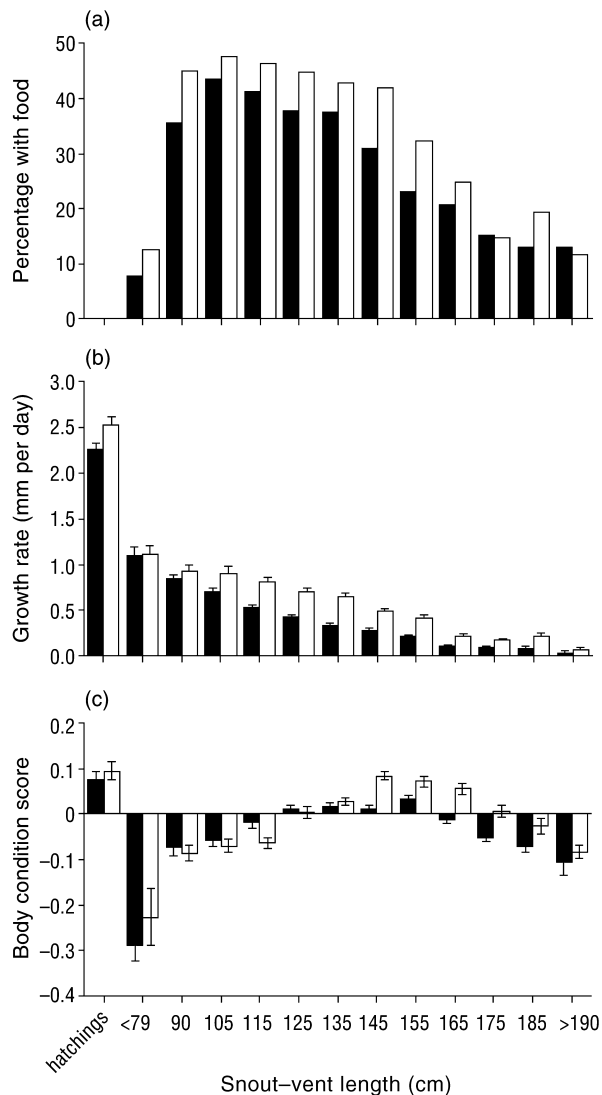


Fig. 2. (a) Mean proportion of male and female water pythons recorded as having recently fed (as indicated by faeces) in the 12 cohorts of field-collected snakes. The mid-point of snout-vent length (SVL) is shown for each cohort. Sample sizes for males = 26, 84, 115, 167, 290, 394, 487, 481, 629, 485, 262, 62; females = 16, 80, 105, 110, 143, 240, 300, 247, 304, 345, 236, 309. (b) Mean growth rates (mm per day) and associated standard errors (SE) of male and female water pythons for each size-based cohort. (c) Mean body condition scores and associated standard errors (SE) of male and female water pythons of each size-based cohort. The condition scores were calculated from residual scores of the general linear regression of ln-transformed mass to ln SVL. (■), Males; (□), females.

this period, growth rates of both male and female pythons (mm SVL per day) declined with increasing body size (Fig. 2b; Spearman rank correlation coefficient $r_s = -1.00$, d.f. = 11, $P = 0.0005$; $r_s = -0.995$, d.f. = 12, $P = 0.0006$). ANCOVA on these data after ln-transformation revealed that the overall growth rate of females was significantly faster than that of males (slopes $F_{1,22} = 0.02$, $P = 0.90$; intercepts $F_{1,23} = 5.31$, $P = 0.03$). However, closer inspection shows that this sex difference was restricted to the mid-range of body sizes. The sexes did not differ significantly in growth rates at the smallest or largest body sizes (Table 2).

Body condition

The body condition scores of pythons (mass relative to SVL) changed in a complex way with body size and sex. Neonates hatched in the laboratory were very heavy-bodied, more so than at any other time in their lives (Fig. 2c). However, they rapidly dropped in condition. Hatchlings collected in the field during their first month of life exhibited the lowest condition scores of all of the 13 cohorts (Fig. 2c). The relationship between body size and body condition in field-collected snakes was strongly curvilinear, with both sexes being more heavy-bodied at intermediate body sizes (Fig. 2c). ANOVA revealed a highly significant variation in condition among size cohorts in both sexes (Fig. 2c; males: $F_{12,2230} = 20.86$, $P = 0.0001$; females: $F_{12,1836} = 23.39$, $P = 0.0001$). Females were more heavy-bodied than

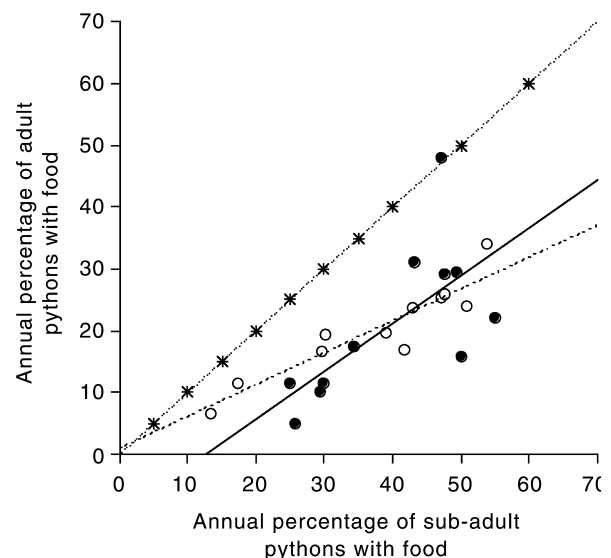


Fig. 3. Annual percentage of adult pythons containing prey when captured, compared with the percentage of subadult pythons with food in the same year. Each data point shows data for one year for one sex. A regression line with a slope of 1.0 is provided for comparison. Dashed line shows regression fitted to data for males. (●), Females; (○), males.

males over the middle range of body sizes (140–149 to 170–179 cm), but not at smaller or larger sizes (see Table 3).

Reproduction

Based on the presence of sperm, we conclude that all adult-size (>140 cm SVL) male water pythons reproduce every year (T. Madsen & R. Shine, unpubl. data). However, most females reproduce less frequently than on an annual schedule. The proportion of females that were reproductive was very low in pythons <160 cm SVL, peaked in the 180–189 cm size class, and fell again in very large snakes (Table 1; see also Madsen & Shine 1996a).

Feeding rates, growth and condition

We might expect to see strong relationships between size-associated shifts in food intake, growth and energy storage (body condition). That is, snakes should be in better condition (heavier relative to SVL) in size classes where they eat more often, or allocate less energy to growth. Multiple regression analysis supports this prediction, using body condition as the dependent variable and rates of feeding and growth as the regressors. For both male and female pythons, the resulting regressions were highly significant (males: $r = 0.94$, d.f. = 11, $P = 0.0001$; females: $r = 0.88$, d.f. = 11, $P = 0.001$; $r^2 = 0.86$ and 0.78 , respectively). Thus, size-associated shifts in rates of feeding and

Table 2. Comparison of growth rates (mm snout-vent length increment per day) for male and female water pythons of various size classes

Snout-vent length (cm)	<i>t</i>	<i>P</i>	d.f.
Hatchlings	2.28	0.025	124
Field, ≤79	0.10	0.92	17
80–99	1.06	0.30	46
100–109	2.27	0.03	54
110–119	4.77	0.0001*	74
120–129	7.15	0.0001*	95
130–139	7.06	0.0001*	103
140–149	5.62	0.0001*	109
150–159	6.45	0.0001*	90
160–169	4.92	0.0001*	78
170–179	3.32	0.0016*	57
180–189	2.95	0.007*	25
≥190	0.49	0.63	21

Growth data for the first size class are derived from captive hatchlings, whereas all other growth rates are derived from recaptures of free-living snakes. Numbers represent results from two-tailed *t*-tests comparing males and females within each size class. See Fig. 2b for raw data. * $P < 0.05$ after Bonferroni correction.

growth could explain 86% of the size-associated variation in body condition scores of male pythons, and 78% of the variation in body condition scores of females.

Seasonal effects on feeding rates and condition in large pythons

Our analyses (discussed later) suggested that an inability to penetrate soil cracks might limit feeding opportunities for large pythons in the dry season but not the wet season. To test this prediction, we can use data on large pythons (mean SVL of 185.4 cm, SD = 11.1, range 170–210 cm, $n = 14$) captured on the floodplain up to 10 km from Fogg Dam (and thus not included in our previous analyses). Comparing same-sized cohorts, the proportion of snakes with food in the wet season was 50%, versus 14.6% in the dry season ($\chi^2 = 19.2$, d.f. = 1, $P = 0.0001$). Also, the body condition scores of large pythons increased rapidly during the wet season and became significantly higher than during the dry season ($t_{816} = 4.94$, $P = 0.0001$).

DISCUSSION

First, do our residual scores (mass relative to length) offer valid measures of body condition? Analyses of other snake species suggest that approximately half of the variance in such condition scores is attributable to variance in the mass of fat bodies as a proportion of

Table 3. Comparison of body condition indices (residual scores from the general linear regression of ln mass versus snout-vent length) for male and female water pythons at different ranges of body sizes

Snout-vent length (cm)	<i>t</i>	<i>P</i>	d.f.
Hatchling	0.79	0.43	124
Field, ≤79 cm	0.94	0.35	40
80–99	0.47	0.64	156
100–109	0.65	0.52	213
110–119	2.60	0.01	246
120–129	0.45	0.65	386
130–139	0.84	0.40	526
140–149	6.06	0.0001*	577
150–159	2.64	0.009*	480
160–169	4.71	0.0001*	502
170–179	3.71	0.002*	399
180–189	1.81	0.071	210
≥190 cm	0.58	0.57	183

Body-condition data for the first size class are derived from captive hatchlings, whereas all other data come from captures of free-living snakes. Numbers represent results from two-tailed *t*-tests comparing males and females within each size class. See Fig. 2c for raw data. * $P < 0.05$ after Bonferroni correction.

lean carcass mass (Weatherhead & Brown 1996 for *Nerodia sipedon*; our unpubl. analyses of data from Xavier Bonnet on carcass composition of *Vipera aspis*, *Coluber viridiflavus* and *Elaphe longissima*). Presumably, most of the remaining (unexplained) variance in mass relative to length is attributable to energy stored in places other than fat bodies (e.g. in liver or muscle). As Weatherhead and Brown (1996) point out, however, this method has the disadvantage that we cannot detect linear shifts (increases or declines) in 'absolute' condition with body size. For example, even if all snakes gradually become more slender-bodied as they grow longer, the residual scores will not decline consistently with absolute body size (because the regression will be fitted through the mean overall condition for each size class). Although this issue complicates the interpretation of shifts in body condition over a wide range of body sizes, it cannot generate curvilinear relationships between condition scores and body size (as observed in our analysis: see later). Thus, the broad size-associated shifts in condition scores revealed by our analysis are informative about relative amounts of energy storage in snakes of different sexes and body sizes.

Our data reveal that the rate at which a water python gathers energy, and the way in which it allocates that energy among competing demands (maintenance, growth, storage and reproduction) depend on the animal's body size. Perhaps surprisingly, differences between males and females were less extreme, with the two sexes generally following similar size-dependent trajectories in rates of energy acquisition and allocation (Fig. 2). In both sexes, feeding rates were higher at intermediate body sizes than at either very small or very large body sizes (Fig. 2a). Rates of body-length growth declined in larger snakes (Fig. 2b), whereas body condition scores (like food-intake rates) were maximized at intermediate body sizes for field-collected pythons of both sexes (Fig. 2c). Similarly, reproductive output (proportion reproductive) was highest for intermediate-sized females (Table 1). Following, we consider size classes separately to interpret the adaptive significance of these size-related shifts in rates of feeding, energy storage (condition), growth and reproduction.

Hatchling pythons (cohort ≤ 79 cm SVL)

Captive hatchlings do not commence feeding until they have resorbed the yolk in their alimentary tract (T. Madsen & R. Shine, unpubl. data). Although they did not eat, our captive hatchlings increased rapidly in body length during their first month of life (Fig. 2b). Hence, they rapidly dropped in body condition. Recaptures of hatchling snakes in the field show the same pattern. Growth rates were very high in both sexes (Table 2 and Fig. 2b), but the snakes exhibited low rates of feeding and very low body condition

(Fig. 2a,c; and note that these small pythons consumed smaller prey items than did the larger snakes, further reducing energy intake). Thus, hatchling water pythons rarely fed, and allocated their residual yolk to growth rather than energy storage.

Why do the young pythons grow so rapidly in length, at the expense of body condition? In our study area, water pythons of all body sizes feed almost exclusively on dusky rats (*Rattus colletti*), a native rodent that shows massive annual fluctuations in abundance depending upon local rainfall patterns (Redhead 1979; Madsen & Shine 1998, 1999a). Due to gape limitation, hatchling pythons cannot ingest rats larger than 30 g (Madsen & Shine 1998). The scarcity of alternative prey in our study area means that hatchling pythons rely on juvenile rats for their first few meals. However, dusky rats grow very rapidly, reaching >60 g at 8 weeks of age (Madsen & Shine 1999a). In order to track their fast-growing prey, neonatal pythons must therefore allocate most of their energy to rapid growth at the cost of extremely low fat deposits.

Because they depend upon small (young) rats, neonatal pythons are vulnerable to starvation in years when small rats are not available. The duration of the rat breeding season is determined by rainfall during the previous wet season. In dry years, the rats cease breeding before the hatchlings emerge (Madsen & Shine 1999a). Although adult rats may still be common, they are too large for the hatchlings to ingest. In such years, the scarcity of alternative prey results in widespread starvation of hatchling pythons (Madsen & Shine 1998).

Juvenile pythons (cohort 80–99 cm SVL)

The feeding rates of both male and female pythons increased dramatically when they reached a body size of >80 cm SVL (Fig. 2a). Pythons of this size are able to kill and ingest rats of up to 100 g (T. Madsen & R. Shine, pers. obs.). The mean body mass of dusky rats captured from 1990 to 1995 was 76 g (Madsen & Shine 1999a). Thus, juvenile pythons are physically capable of ingesting virtually any rat that they encounter. Compared with hatchlings, juvenile pythons could utilize a greater proportion of available prey and consequently fed more often. Body condition remained low for both male and female pythons in this size class, suggesting that most of the energy gained from their high feeding rate was allocated to growth in body length rather than energy storage (Fig. 2b,c).

Subadult pythons (cohorts 100–109 to 130–139 cm SVL)

The feeding rate of subadult pythons remained at the same high level as that recorded in the juvenile cohort

(Fig. 2a). However, in contrast to previous cohorts, the sexes differed in allocation patterns. Female pythons increased in body length faster than did conspecific males at the same initial body size (Table 2). As in all other cohorts, the feeding rates of female snakes were higher than those of males (Fig. 2a). However, the sexes did not differ in body condition (Table 3). This discrepancy suggests that most of the extra energy gained by the higher feeding rates of females was allocated to faster growth rather than energy storage.

Data on reproductive output of water pythons suggest reasons why females feed more often than males, and continue to invest heavily in growth rather than storage. A larger maternal body size results in a larger clutch size (Madsen & Shine 1996a). Females that grow more rapidly during juvenile life will be likely to mature at larger body sizes, thus enhancing their reproductive output. Although we do not have an equivalent data set on the relationship between body size and reproductive success in males, we have frequently observed courtship and mating in this population. Male–male combat has not been recorded, suggesting that larger body size may not substantially increase a male's reproductive success (unlike the situation in species exhibiting male combat: Madsen *et al.* 1993; Schuett 1997).

Small- to medium-sized adult pythons (cohorts 140–149 to 170–179 cm SVL)

All male water pythons, but only a small proportion of females, reach sexual maturity at approximately 140 cm SVL (Shine & Madsen 1997). Most female pythons delay maturation until they attain about 160 cm SVL (Shine & Madsen 1997). The feeding rate of males decreased dramatically at maturation, whereas the feeding rate of female pythons at the same body size remained high (similar to that of subadult snakes: Fig. 2a). However, the feeding rates of female pythons then fell rapidly with increasing body size (between the 140–149 and 150–159 cm cohorts: Fig. 2a). Beyond this size, the feeding rates of both male and female pythons continued to decline (Fig. 2a).

Although the dramatic decrease in feeding rates of male pythons coincided with size at maturation, the decrease cannot be attributed to reproductive activities. Male water pythons cease feeding during the mating season, but data from this period were excluded from our analyses. Likewise, the reduction in feeding rates among female cohorts of increasing body size cannot be caused by the anorexia of gravid female snakes (Madsen & Shine 2000), because these females were similarly excluded from our analyses.

Throughout this wide range of intermediate body sizes, female pythons were heavier bodied than males (Table 3, Fig. 2c). In fact, females were in higher body condition at 140–149 cm SVL than in any other size

class post-hatching (Fig. 2c). Females grew faster than males over these size ranges as well (Table 2). That is, medium-sized female pythons fed more frequently than males, and allocated more energy to both growth and storage than did their male counterparts. This result accords well with the idea that adult females in many snake species not only benefit more than males from larger body size (because of increased reproductive output), but also need to store substantial amounts of energy for reproduction (Bonnet *et al.* 1998a).

Large adult pythons (cohort 180–189 cm SVL)

Large female pythons fed approximately as frequently as smaller snakes (i.e. 170–179 cm SVL cohort), but their body condition declined (Fig. 2a,c). This decline presumably reflects their greater maintenance costs because of a larger body size. Because these larger females became progressively thinner, the difference in body condition between males and females disappeared within this group (Table 3). However, females continued to feed at a higher rate than males of the same body size (Fig. 2a) and as a consequence, continued to grow more rapidly than males (Table 2). Despite their relatively low body condition, there was a higher proportion of reproductive animals in this cohort (25.2%, 31 of 123) than in any other size class (Table 1). This result is an interesting one, because it indicates that even with these relatively low feeding rates and poor body condition, females can still amass enough energy to breed on a frequent basis.

Very large adult pythons (≥ 190 cm SVL)

Feeding rates declined with increasing body size, so that both the absolute rate and the magnitude of sex difference in this trait reached a minimum in very large snakes (Table 2). The same patterns were evident in body condition (Table 3). Growth was extremely slow, and virtually ceased in males. Reproduction was infrequent in females (Table 1). These results suggest that very large water pythons experience substantial difficulty in maintaining energy balance. Their maintenance requirements increase with body size, but there is no compensating increase in food intake (Fig. 2a). Although they allocate very little to growth or reproduction, they nonetheless fail to maintain body condition (Fig. 2c). The energetic disadvantages of large body size will be particularly intense in the Fogg Dam population, because of the snakes' reliance on a single prey species of small body size. In many other snake populations, larger snakes shift to larger prey types (e.g. Mushinsky *et al.* 1982; Arnold 1993). Hence, larger individuals may be able to maintain condition, and allocate energy to growth and reproduction. Water

pythons at Fogg Dam cannot do this, and we infer that many pythons in this size range are simply too large for their prey.

Overview

Our multiple regression analyses suggest that size-related shifts in energy allocation to growth and storage (body condition) are ultimately determined by size-related shifts in rates of food intake. Most of the patterns in energy allocation are readily explicable in light of the advantages of growth versus storage (discussed previously), leaving only one major issue to explain. Why does food intake decline in larger snakes? Adult pythons brought into captivity feed voraciously, except during the breeding season (T. Madsen & R. Shine, unpubl. data), so the decline in feeding rates cannot be attributed to an unwillingness to feed. Instead, it seems that larger snakes are unable to capture prey as frequently as smaller conspecifics. Why should a snake's body size affect its ability to capture prey?

The low feeding rates of very small pythons are easy to understand, because gape-limitation prevents these animals from ingesting most of the rodents living on the floodplain. It is the decline in feeding rates in larger snakes that poses a puzzle. The answer probably lies in the ability of smaller snakes to penetrate deep into the soil-cracks where dusky rats spend most of their time. Even when the rats are abundant, they rarely venture above ground (Redhead 1979; Madsen & Shine 1999a). Most soil cracks are too narrow for large pythons to enter, so the larger snakes must hunt by waiting in ambush for rats to emerge (T. Madsen & R. Shine, pers. obs.). In contrast, the smaller snakes can pursue their prey underground. In keeping with this putative mechanism to explain the decreased feeding rates of larger pythons, an increase in rat abundance had less effect on the feeding rates of large pythons than of smaller conspecifics (as seen in our comparison among years of differing rat numbers). A reduction in rat abundance will have a greater effect on rat availability above ground (as most feeding is conducted below ground, Madsen & Shine 1999a) rather than inside soil-crack crevices.

Other aspects of temporal variation in feeding rates also support our hypothesis. During the wet season, rainfall closes soil-cracks and forces the rats to a life above ground where they are potentially vulnerable to pythons of all body sizes (Madsen & Shine 1999a). As predicted, large snakes fed more often and were in better body condition during the wet season than the dry season. Last, years when rats were abundant during the wet season were followed by a high reproductive output in large pythons during the subsequent dry season (Shine & Madsen 1997). Each of these patterns

is consistent with the idea that feeding rates decline with python body size because larger snakes are unable to penetrate into the deep soil cracks where the rats live for most of the year.

Previous studies on snakes have revealed a considerable diversity in the way in which factors such as sex and body size affect prey types (e.g. Forsman 1991; Houston & Shine 1993; Shine *et al.* 1998). Presumably, the same kind of diversity exists for rates of food consumption as well. It seems likely that overall patterns of energy allocation to maintenance, growth, and reproduction will show many similarities among distantly related species of snakes. For example, we predict that most species will show shifts in body condition similar to that seen in water pythons (e.g. most heavy bodied at intermediate body sizes, and fatter in females than males: Fig. 2c), because of similarities in the relative priority accorded to growth versus energy storage at different life history stages. However, absolute rates of feeding will show vastly more variation not only among species, but also among populations of the same species, and even among years within a single population. There is immense spatial and temporal variation in the availability of prey of different body sizes, as well as in biophysical factors that influence a snake's ability to capture such prey. Hence, some species will increase feeding rates with increasing body size (e.g. Shine *et al.* 1998, 1999), whereas others (such as water pythons) show the reverse pattern. Such size-related shifts in trophic ecology may significantly modify life-history attributes (such as growth trajectories and reproductive frequencies) and, hence, warrant more detailed examination.

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