

The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*

R. SHINE,* P. S. HARLOW,* J. S. KEOGH* and BOEADI†

*School of Biological Sciences A08, University of Sydney, NSW 2006, Australia and †Centre for Research in Biology, Museum of Zoology, LIPI, Bogor 16122, Indonesia

Summary

1. In many animal species, dietary habits shift with body size, and differ between the sexes. However, the intraspecific range of body sizes is usually low, making it difficult to quantify size-associated trophic shifts, or to determine the degree to which sex differences in diet are due to body-size differences. Large snakes are ideal for such a study, because they provide a vast range of body sizes within a single population.

2. More than 1000 Reticulated Pythons (*Python reticulatus*) from southern Sumatra were examined, with specimens from 1.5 to > 6 m in snout–vent length, and from 1 to 75 kg in mass. Females attained much larger body sizes than did conspecific males (maxima of 20 vs 75 kg, 5 vs 7 m), but had similar head lengths at the same body lengths.

3. Prey sizes, feeding frequencies and numbers of stomach parasites (ascarid nematodes) increased with body size in both sexes, and dietary composition changed ontogenetically. Small snakes fed mostly on rats, but shifted to larger mammalian taxa (e.g. pangolins, porcupines, monkeys, wild pigs, mouse deer) at 3–4-m body length.

4. Adult males and females showed strong ecological divergence. For some traits, this divergence was entirely caused by the strong allometry (combined with sexual size dimorphism), but in other cases (e.g. feeding frequency, dietary composition), the sexes followed different allometric trajectories. For example, females shifted from rats to larger mammals at a smaller body size than did conspecific males, and feeding frequencies increased more rapidly with body size in females than in males. These allometric divergences enhanced the degree of sex difference in trophic ecology induced by sexual size dimorphism.

Key-words: Allometry, dietary habits, python, reptile, trophic ecology

Functional Ecology (1998) **12**, 248–258

Introduction

In many animal species, the sexes differ not only in mean adult body sizes, but also in dietary habits. For example, one sex may feed more frequently than the other, or take different kinds of prey (e.g. Selander 1966, 1972; Shine 1989; Forsman 1991a). The phenomenon has attracted considerable interest from evolutionary biologists, who have attempted to interpret the causes of this kind of intraspecific niche partitioning (e.g. Slatkin 1984; Shine 1989). Unfortunately, it is very difficult to disentangle cause and effect in such a situation. For example, sexual size dimorphism can be interpreted as a result of selection for intra-sexual dietary divergence, or as a consequence of sexual selection (in which case, the dietary divergence may be an epiphenomenon). One way to illuminate the processes at work in intersexual niche divergence in a sexually dimorphic predator is to look in detail at the

allometry of diet-related traits in both sexes. Figure 1 depicts three possible scenarios in this respect. First, the sex divergence in diets might arise as a direct consequence of sexual size dimorphism (i.e. the sexes fall on the same allometric line linking the dietary trait to body size: see graph a). A second possibility is that the traits show no allometry, such that the sex divergence is caused by an ecological shift between the sexes that is independent of body size (b). Thirdly, the trait may show allometry, but the degree of sex divergence in the trait may be increased (or reduced) by sex differences in the allometric slope or intercept (c).

These three possibilities will be difficult to tease apart in organisms that display a small range of adult body sizes. This situation can be clearly seen in birds, the 'model organisms' used for most previous analyses of intersexual divergence in diets (e.g. Selander 1966, 1972). A bird's body size (at least in terms of linear dimensions) is essentially constant throughout

the animal's postfledging life, and the range of individual variation in adult body sizes within a single population is usually quite small. Clearly, the solution to this problem is to examine ecological traits within a species displaying wide variation in body size within a single population. Most such variation is likely to be ontogenetic rather than among-individuals. Snakes offer ideal model systems for such an analysis, for the following reasons:

1. Unlike lizards, which typically show determinate growth and thus a limited size range of adults within a population, many snakes continue growing throughout their lives (Andrews 1982).
2. The absence of post-hatching parental care (Shine 1988) means that snakes of all body sizes must interact with their environment as independent entities, rather than receiving nutrients from larger, parental organisms (as occurs in most endothermic vertebrates). This trophic independence of offspring maximizes the body-size range over which one can meaningfully examine feeding habits.
3. Snakes are gape-limited predators that consume their prey whole, so that the head size of a snake sets an upper limit to its maximum ingestible prey size (e.g. Forsman 1991a,b). Gape-limitation increases the likelihood of significant shifts in prey size with the body size of the predator (Arnold 1993).
4. Sexual dimorphism in body size, and intrasexual dietary divergence, are both common in snakes (Shine 1991, 1993).

Ideally, then, one might illuminate the dietary consequences of body-size dimorphism by studying a snake species with a very high intraspecific range of body sizes. Species with large body sizes offer the

greatest opportunity in this respect: not only do they show the largest *range* of body sizes in absolute terms, but they also tend to mature at a smaller proportion of maximum body size (Andrews 1982; Shine & Charnov 1992). Thus, the size range of adult organisms within such a population may be considerable.

Unfortunately, large snakes have attracted relatively little scientific attention. Very large snakes are almost entirely tropical, probably because of thermal constraints in temperate-zone climates (Shine & Madsen 1996). Given the paucity of detailed ecological information from tropical areas world-wide, the lack of study of giant snakes is not surprising. Giant reptiles of several taxa, however, are exploited in huge numbers for the commercial leather industry, and it is thus possible to gather data on animals brought in to be killed and skinned as part of this operation (e.g. Fitzgerald, Cruz & Perroti 1993; Shine *et al.* 1995, 1996). We took advantage of this commercial trade to obtain the first detailed ecological information on Reticulated Pythons (*Python reticulatus*), a giant snake that most authorities rate as the longest and second-heaviest snake species in the world (e.g. Pope 1975). The data were gathered in the course of our studies to evaluate ecological sustainability of the commercial trade in pythons.

Materials and methods

Data were gathered during three trips to the city of Palembang in southern Sumatra, Indonesia: from 29 July to 6 August 1993, 6–20 October 1994 and 3–19 April 1995. Live pythons (as well as acrochordid snakes and varanid lizards: see Shine *et al.* 1995, 1996) are brought to commercial premises in Palembang to be killed and skinned. The pythons are collected over a wide area, and the origin of individual snakes was not determined. At the skinning factory, snakes were weighed and measured as soon as they were killed, and their carcasses were counted after skinning. The snout–vent length (SVL) and head length (along the lower jaw, from the tip of the snout to the posterior edge of the quadrate-articular projection) of each individual were measured.

Any prey in the alimentary tract were recorded, and removed for later analysis if they could not be identified at the time. Most such prey consisted of highly digested material in the hindgut. These prey were identified by microscopic analysis, via comparison with a reference collection of fur from mammals in the Bogor Museum. Approximate prey masses were estimated from mean adult masses of each prey species, from published compendia. The total number of parasitic worms (ascarid nematodes) penetrating the stomach walls of the dissected pythons were also counted. The gonads were examined to determine sex and reproductive condition.

It is emphasized that no animals were killed for our project; all were part of the existing commercial trade.

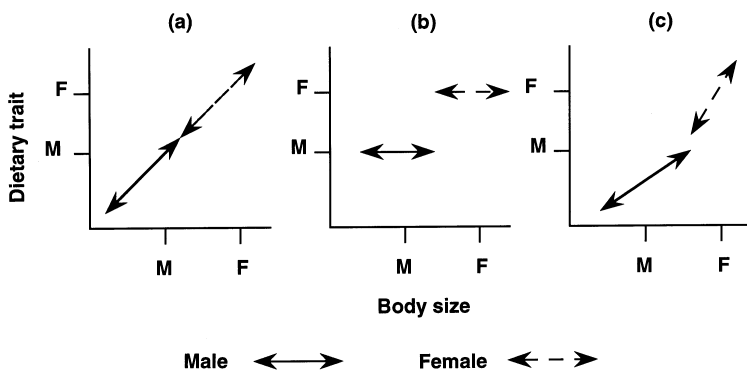


Fig. 1. Theoretical scenarios to explain the underlying causes for sex divergence in dietary traits in a sexually dimorphic predator. The graphs show a dietary trait (e.g. prey size) plotted against body size (e.g. SVL) for males (M) and females (F) within a species. In all three graphs, the mean values (for body size as well as for the dietary trait) are the same within each sex but in each case, females are the larger sex and average a larger value for the dietary trait. However, this dietary divergence has arisen in three different ways: (a) the dietary divergence results purely from the body-size difference, with both sexes following the same allometric relationship between body size and diet; (b) the dietary divergence is unrelated to body size, with no allometry of the trait in either sex; or (c) the dietary divergence results from the size dimorphism *as well as* sex differences in the allometric relationship between body size and the dietary trait.

Results

Data were obtained from 1070 Reticulated Pythons. Our data show strong correlations between body size and dietary traits, and significant differences between the sexes for many characteristics. Data are provided below on morphology (sex differences in size and proportions), and on the effects of sex and body size on several variables related to the trophic ecology of these animals.

MORPHOLOGY

Sexual dimorphism

Female Reticulated Pythons grow much larger than males, and mature at a larger body size (Fig. 2). Thus, our sample consisted primarily of adult males and juvenile females (Fig. 2). In terms of feeding habits, head size may be more important than body

size, and in some snake species the sexes diverge in head sizes relative to body length (Shine 1991). To check this possibility, single-factor analysis of covariance was used, with sex as the factor. Male and female pythons did not differ in head length relative to SVL (slopes $F_{1,353}=0.34, P=0.56$; intercepts $F_{1,354}=0.28, P=0.60$). Body shape might also influence a snake's ability to overpower large prey, so mass relative to length was examined in the same way. Male pythons were heavier than females at the same body length (using \ln mass to overcome variance heterogeneity: slopes $F_{1,716}=29.36, P<0.0001$). However, further analysis showed that sex differences in body shape (mass relative to SVL) varied between trips, perhaps in relation to reproductive state. Both sexes were in better body condition (i.e. were heavier relative to length) in April 1995 than in October 1994, and this difference was greater in males than in females.

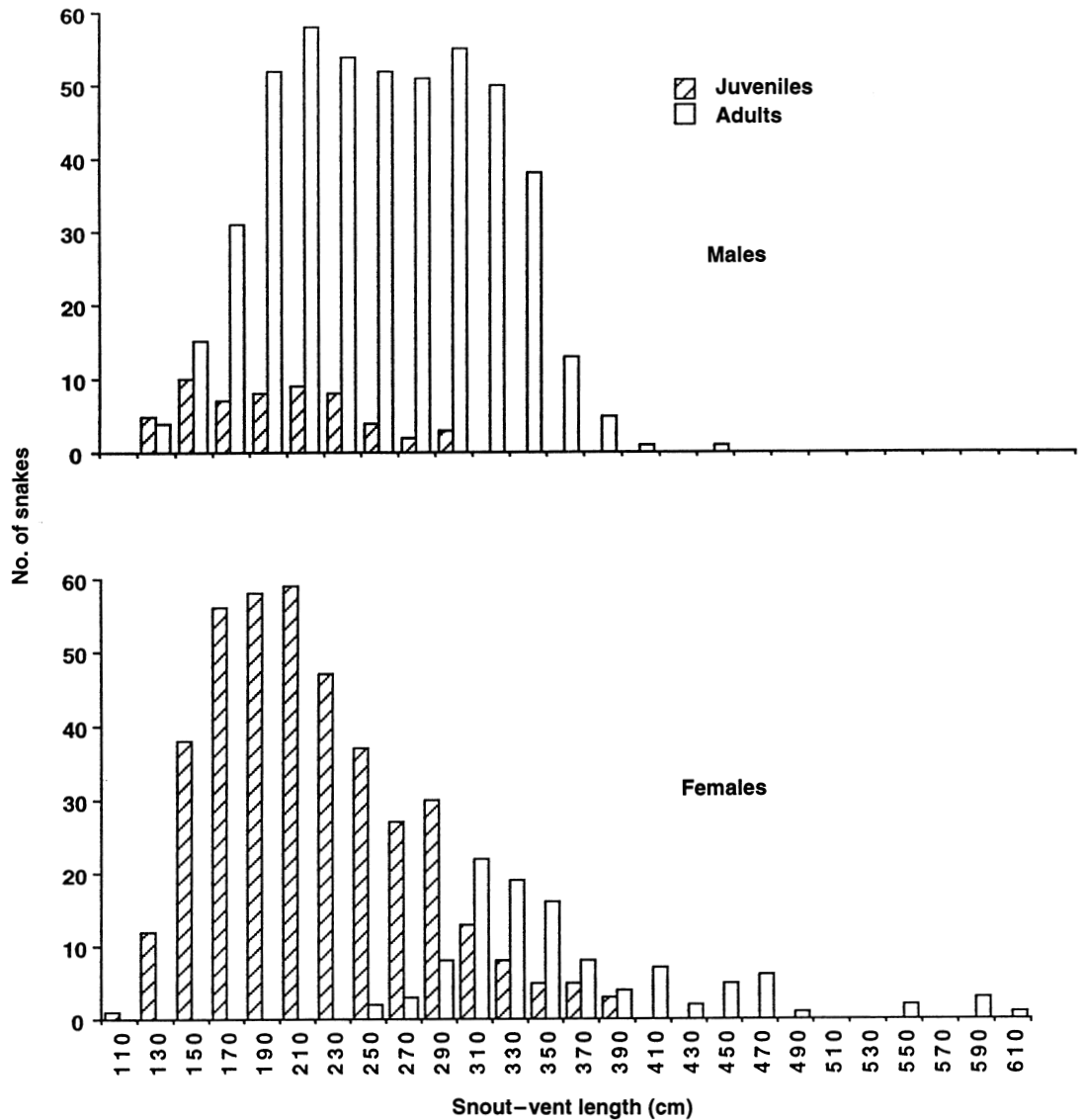


Fig. 2. Body sizes and sexual size dimorphism in Reticulated Pythons from southern Sumatra. Stippled columns show juvenile snakes, whereas open columns show adults.

Our data paint a complex picture in terms of the factors that influence feeding frequency and overall composition of the diet in Reticulated Pythons. Both factors change only slightly with season, but depend upon the sex and body size of the snakes. Because of the significant sexual size dimorphism in Reticulated Pythons, effects of sex and size are not independent, and must be disentangled.

Frequency of feeding

The frequency of feeding can only be judged from the proportion of snakes containing food. There are at least four potential problems with this index. First, snakes may move about more when they are hungry, and so they are more likely to encounter humans, and be captured. Second, some snakes may have been held in captivity for a long time prior to slaughter, and so may have emptied their alimentary tracts during this period. On the other hand, snakes may retain rectal contents for very long periods after feeding, and so some of the prey remains that we recorded may have been held in the hindgut for a long time. And fourth, larger prey (which are more likely to be eaten by larger snakes) may be more likely to leave identifiable remains than smaller prey. For all of these reasons, absolute values cannot be calculated for feeding frequency. Nonetheless, under the assumption that these factors should apply equally to snakes of different sizes, collected at different seasons, the proportion of snakes with prey can be used as an approximate index of feeding frequency.

Effect of season: The proportion of adult male snakes containing food varied among the three trips ($\chi^2 = 24.64$, 2 df, $P < 0.0001$) but no significant variation was detected for juvenile males, or for adult or juvenile females (χ^2 with 2 df, $P > 0.10$ for each of these groups). Hence, our most important result is that feeding continues throughout the year (as is evident from freshly ingested prey seen during all three trips), rather than minor seasonal differences in feeding rates.

Effect of body size and sex: The proportion of specimens containing prey was higher in females (49 of 109, 45%) than in males (176 of 476, 37%), but the reasons for this difference are complex. The proportion of snakes containing prey in their guts increased with body size in both sexes, but did so at a faster rate in females than in males. Comparing 200-mm SVL intervals, and restricting analysis to the size range common to both sexes, a single-factor heterogeneity of slopes test with sex as the factor yielded a significant interaction term between sex and SVL category ($F_{1,24} = 6.65$, $P < 0.017$). Thus, there are two reasons why females contained food more frequently than did males: (i) larger snakes (in both sexes) were more likely to contain food, and females grow larger than males, and (ii) feeding rate increased more rapidly

with body size in females than in males. These results mean that the sex difference in feeding rate is partly, but not entirely, an epiphenomenon of sexual size dimorphism. The same result holds true for dietary composition (see below).

Dietary composition

Table 1 lists the prey species that were identified from the alimentary tracts of Reticulated Pythons. The pythons consumed a wide variety of prey, with the 15 identified prey species representing a diverse array both taxonomically and ecologically (Table 1). Mammals were the most frequent prey, with murids (rats) the main prey of small pythons. The prevalence of commensal rats and domestic chickens suggests that many prey items were taken from disturbed habitats close to villages, but other prey may have come from more pristine forest environments. Some of the prey consumed were relatively large and formidable creatures (e.g. wild pigs, porcupines), as might be expected from the massive body sizes of the predators. Although general dietary composition was consistent across all of our samples, detailed analysis revealed several significant patterns:

Effect of season: for statistical analysis, the prey were divided into three categories: murids (rats), birds (mostly domestic chickens) and 'other prey' (a taxonomically diverse array). The proportions of the diet composed of each of these prey categories remained relatively consistent among the three trips, varying significantly among trips only in juvenile females ($\chi^2 = 13.81$, 2 df, $P < 0.01$; for the other three snake groups, $P > 0.40$). Inspection of the raw data indicates that the seasonal shift in dietary composition in juvenile female pythons reflected a higher proportion of birds taken in April 1995 (i.e. trip 3) than on the other two trips.

Effect of body size and sex: body size strongly affected dietary composition in both male and female pythons, with a consistent ontogenetic shift from rats to larger mammals in both sexes. Rats were virtually the only prey recorded in the guts of small pythons, but were rarely found in snakes > 4 m long (Tables 1 and 2). The proportion of the diet composed of birds was low in all size groups, and showed no consistent shifts with snake body size in either sex. Although the shift from rats to other mammals was evident in both sexes, males and females differed in the rate at which this dietary shift occurred with increasing body size. Females began switching away from rats at a smaller body size than did males (Fig. 3: with analysis restricted to the size range common to both sexes, heterogeneity of slopes $F_{1,24} = 4.30$, $P < 0.05$).

Prey size

Approximate masses of prey were estimated from mean adult masses of each prey species (Table 1).

Given the enormous size range of Reticulated Pythons in our sample, and the ontogenetic shift among prey categories (see above), it is not surprising to find that larger snakes consume larger prey. However, the pattern is of interest because it suggests a threshold effect rather than a gradual increase in prey size with increasing snake size (Fig. 4). Small snakes ate very small prey (primarily rats), but mean prey size shifted suddenly at intermediate body sizes (SVLs around 3 m). Snakes between 3 and 4 m took a wide range of prey sizes (i.e. rats as well as other mammals) but snakes > 4 m in size (almost entirely females) stopped taking small prey (Fig. 4).

This abrupt shift to larger prey, and the apparent lack of any increase in prey size in very large snakes, means that relative prey mass (prey/predator mass) was maximized for snakes at intermediate body sizes (Fig. 4). However, it remains possible that the individual prey taken by very large pythons were larger than conspecific prey consumed by intermediate-sized snakes. For example, wild pigs attain body masses several times larger than the mean estimate we have used for records of this taxon (Table 1, Fig. 4), and one snake-skinner told us that he had found a 60-kg wild pig in the stomach of a large python. Although overall mean prey mass was higher for females (1.35 kg, SD = 2.70, $n = 158$ prey items) than for males (0.75 kg, SD = 1.71, $n = 163$ items: unpaired $t = 2.38$, $P < 0.02$), this difference is entirely attributable to the sexual size dimorphism of Reticulated Pythons. When predator mass is taken into account, relative prey mass did not differ significantly between the sexes (mean for females = 0.17, for males = 0.14, unpaired $t = 1.47$, $P = 0.14$). Single-factor ANCOVA (with sex as the factor, SVL as the covariate, and prey mass as the dependent variable) confirmed that prey mass increased with predator size ($F_{1,292} = 53.12$, $P < 0.0001$), and that this relationship was similar in the two sexes (restricting analysis to the size range common to both sexes: slopes $F_{1,292} = 0.06$, $P = 0.81$; intercepts $F_{1,293} = 0.78$, $P = 0.38$).

PARASITE NUMBERS

Levels of parasite infestation may be biologically important, and presumably reflect the feeding history of the predator. The proportion of pythons containing macroscopically visible gut nematodes was higher in males (127 of 353, 36%) than in females (91 of 316, 29%), although this difference fell just short of statistical significance ($\chi^2 = 3.59$, 1 df, $P = 0.058$). The mean number of parasites per individual was similar in males (mean = 5.65, SD = 23.2, $n = 353$ snakes) and females (mean = 4.97, SD = 20.93, $n = 316$ snakes; unpaired $t = 0.40$, 669 df, $P = 0.69$). Single-factor ANCOVA with sex as the factor showed that parasite numbers increased with body size ($F_{1,667} = 13.96$, $P < 0.001$) and that males and females did not differ in the relationship between

SVL and parasite burden (slopes $F_{1,667} = 0.82$, $P = 0.37$; intercepts $F_{1,668} = 0.41$, $P = 0.52$).

Discussion

Our study provides the first quantitative ecological information on giant tropical snakes, and shows that Reticulated Pythons offer an excellent system in which to examine the ways in which body size and sex interact to affect the trophic ecology of a predator. The tropical environment inhabited by these snakes also facilitates our analysis, for two reasons. First, we did not see any major seasonal changes in feeding rates or prey types (see above analyses), presumably because of the relative aseasonality of the area. Second, the high species diversity of potential prey in Sumatra means that the snakes are exposed to prey of a wide range of body sizes (e.g. see Table 1). In temperate-zone habitats, snakes encounter a prey species diversity considerably lower than that available in Sumatra (Arnold 1972; Vitt 1987). If only two or three prey taxa are available, the snakes may thus encounter a limited size range of prey, or highly discontinuous prey-size distributions. Allometric relationships between predator size and prey size may be obscured by such complications (e.g. Mushinsky, Hebrard & Vodopich 1982).

The enormous body-size range of Reticulated Pythons is accompanied by major size-associated shifts in all of the dietary traits measured. Feeding rates, the size and species of prey taken, and levels of parasite infestation in the alimentary tract, all shifted with body size, and differed between the sexes. However, the mechanisms responsible for this ecological divergence between the sexes differed among traits, as follows:

1. The sex divergence in prey sizes was caused by strong allometry combined with sexual size dimorphism: that is, the first of the hypothetical patterns depicted in Fig. 1. Our data suggest that there is no sex effect *per se* on these traits, so that the significant divergence in mean values between adult male and female pythons was caused by body-size differences. Thus, even major sex differences (approximately twofold for mean prey mass) can be induced by sexual size dimorphism alone.
2. The sex divergence in feeding rates and the kinds of prey taken is a consequence of two processes. The first of these is sexual size dimorphism: both traits showed strong allometry, so that the sexes would have differed strongly even if they had followed the same allometric relationship between body-size and the dietary trait in question. In both cases, however, the sexes displayed significantly different allometries, so that the overall divergence between males and females was greater than would have been produced from sexual size dimorphism alone. Thus, these traits displayed the third of the hypothetical patterns shown in Fig. 1.

Table 1. Prey species identified from the alimentary tracts of Sumatran Reticulated Pythons, with information on the numbers of each prey type in adult and juvenile pythons of each sex. Adult body sizes and habits of the prey species are also summarized, based on published records. Superscripts refer to sources of information on body sizes and habits of prey species: 1, Nowak & Paradiso (1983); 2, Parker (1990); 3, Corbet & Hill (1992); 4, Shine *et al.* (1996)

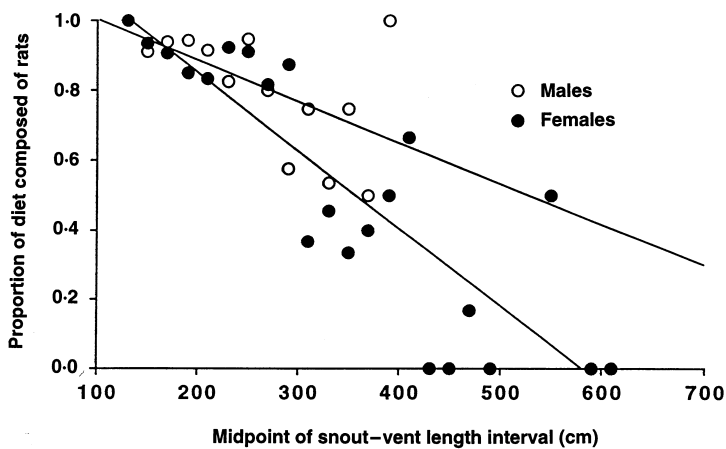
Family	Species and common name	Adult mass	Adult body length	Habit	No. in male pythons		No. in female pythons	
					Juvenile	Adult	Juvenile	Adult
Muridae	<i>Leopoldamys sabanus</i> (Long-tailed Giant Rat)	200–495 g ¹	180–275 mm ³	Found in evergreen forest, generally below 750 m; arboreal but mainly in lower strata, and also active on the ground ^{1,3}	3	12	14	2
	<i>Maxomys rajah</i> (Rajah Rat; Spiny Rat)	35–284 g ¹	100–235 mm ^{1,3}	Cursorial; adapted for life on the floor of evergreen or semi-evergreen forests in tropical lowlands and mountains ¹	0	1	4	1
	<i>Rattus argentiventer</i> (Rice Field Rat)	200–300 g	150–210 mm ³	A terrestrial synanthropic species, found mainly in ricefields, grassland and shrub, and also plantations ³	12	63	63	10
Tragulidae	<i>Tragulus javanicus</i> (Lesser Malay Mouse Deer)	1.5–2.5 kg ²	195–550 mm ^{2,3}	Terrestrial; found in thickly overgrown primary and secondary forests, and bush zones in cultivated areas; often near water ²	0	0	2	1
	<i>Tragulus napu</i> (Greater Malay Mouse Deer)	5.0–8.0 kg ²	500–750 mm ^{2,3}	As above	0	0	1	0
Viverridae	<i>Arctogalidia trivirgata</i> (Small-toothed Palm Civet; Three-striped Palm Civet)	2.0–2.5 kg ²	up to 530 mm ²	Predominantly arboreal; prefers primary forests and avoids human settlements ²	0	1	0	0
Hystriidae	<i>Hystrix brachyura</i> (Short-tailed Porcupine)	8.0–27.0 kg ²	450–930 mm ^{2,3}	Terrestrial, prefers dry, rocky areas from sea level to elevations of 3500 m ²	0	0	0	2
Cercopithecidae	<i>Macaca fascicularis</i> (Crab-eating Monkey; Long-tailed Macaque; Java Monkey)	male: 5.0–9.0 kg ² male: 400–650 mm ^{2,3}	female: 3.0–6.0 kg ² female: 380–510 mm ^{2,3}	Arboreal in dense forest, often along rivers; also in secondary or mangrove forests; readily descends to ground; swims well ² Characteristic of forest edge and occur extensively in plantations and other disturbed habitats ³	0	2	0	0

Table 1. Continued.

Family	Species and common name	Adult mass	Adult body length	Habit	No. in male pythons		No. in female pythons	
					Juvenile	Adult	Juvenile	Adult
	<i>Presbytis melalophos</i> (Banded Leaf Monkey; Mitre Leaf Monkey)	6.6–7.0 kg ²	435–590 mm ²	Predominantly arboreal, but will descend to the ground; found in tropical rain and swamp forests, at elevations up to 2000 m; often found near human settlements ²	0	0	0	1
	<i>Semnopithecus cristatus</i> (Silvered Leaf Monkey)	5.2–8.6 kg ²	male: 525–560 mm ² female: 465–495 mm ²	Predominantly arboreal, occasionally on ground; found in coastal and mountain forests and near human settlements ²	0	5	5	1
Suidae	<i>Sus scrofa</i> (Wild Boar)	male: 54–320 kg ² female: 44–123 kg ²	900–2000 mm ^{2,3}	Found in brush, jungles, and rainforests, at elevations up to 4000 m ²	0	2	0	4
Manidae	<i>Manis javanica</i> (Sunda Pangolin)	5–15 kg	400–650 mm ³	Found mainly in forests, living in burrows in the ground but foraging to some extent by climbing ³	0	1	0	5
Varanidae	<i>Varanus salvator</i> (Asian Water Monitor)	male: 1–11 kg ⁴ female: 2–8 kg ⁴	male: 390–910 mm ⁴ female: 470–770 mm ⁴	Occur in a wide variety of habitats ranging from mangrove swamps to the vicinity of large towns and cities ⁴	0	2	0	0
Erinaceidae	<i>Echinorex gymnorus</i> (Moonrat; Gymnure)	500–1200 g ²	260–460 mm ²	Nocturnal; found in wet forests, mangrove swamps, on rubber plantations and farmland; usually near rivers ²	0	1	0	0
Gallinae	<i>Gallus sp.</i> (Domestic Chicken)	500–1000 g	250–350 mm	Near human settlements	0	0	7	1
Unidentified	Rat				9	50	38	9
	Non-murid mammal				0	20	15	13
	Bird				4	19	10	1

Table 2. Numbers of the three main prey types identified from Sumatran Reticulated Pythons as a function of the sex and body size (snout–vent length) of the snake. The table also provides information on the relative numbers of snakes in each category that contained identifiable prey remains in their alimentary tracts. See text for statistical analyses of these data

SVL (mm)	Males				Females			
	Bird	Rat	Other prey	No food	Bird	Rat	Other prey	No food
1000–1200	0	0	0	0	0	0	0	1
1200–1400	0	2	0	7	0	9	0	3
1400–1600	1	10	1	19	1	14	1	22
1600–1800	0	16	1	24	0	19	2	36
1800–2000	2	17	1	44	2	17	3	37
2000–2200	2	21	2	41	4	15	3	38
2200–2400	3	19	4	38	3	12	1	31
2400–2600	5	18	1	32	1	10	1	27
2600–2800	3	12	3	36	2	9	2	17
2800–3000	4	11	8	35	2	14	2	20
3000–3200	3	12	4	31	2	4	7	22
3200–3400	1	7	6	24	1	5	6	15
3400–3600	0	3	1	9	0	3	6	12
3600–3800	1	1	1	2	0	2	3	8
3800–4000	0	1	0	0	1	1	1	4
4000–4200	0	0	0	0	0	2	1	4
4200–4400	0	0	0	1	0	0	1	1
4400–4600	0	0	0	0	0	0	3	2
4600–4800	0	0	0	0	0	1	5	0
4800–5000	0	0	0	0	0	0	1	0
5000–5200	0	0	0	0	0	0	0	0
5200–5400	0	0	0	0	0	0	0	0
5400–5600	0	0	0	0	0	0	1	0
5600–5800	0	0	0	0	0	0	0	0
5800–6000	0	0	0	0	0	0	1	2
6000+	0	0	0	0	0	0	1	0

**Fig. 3.** Size-related shifts in dietary composition in male and female Reticulated Pythons from southern Sumatra. The proportion of the diet composed of rats declines with the body size of the snakes, but this decline occurs more rapidly in males than in females. See text for statistical analysis.

None of the traits we measured showed the second pattern in Fig. 2 (i.e. sex divergence without allometry), but it seems likely that this pattern will also occur in nature. The huge size range of Reticulated Pythons undoubtedly made it easier for us to detect size-associated ecological shifts, and it is difficult to envisage any dietary trait that would *not* change with body size over such a vast range. Nonetheless, many traits remained

relatively invariant over significant subsets of the size range of our Reticulated Pythons. For example, prey size showed little change over the python body-size range from 1 to 2.5 m, or from 3.5 to 6 m SVL (Fig. 4). If males ceased growing at 2.5 m, and females delayed maturation until 3.5 m, we would have concluded that prey size in adult males and females conformed to this second pattern. More generally, species that cover a smaller size range are likely to show less marked size-related shifts in dietary traits, and thus may be more likely to exhibit this kind of 'non-allometric' sexual divergence in food habits.

Despite the profound difference in dietary composition and mean prey size between male and female Reticulated Pythons, no indication of any sex divergence in trophic morphology (i.e. head size relative to body length) was detected. This result is consistent with the observation that *relative* prey mass (i.e. prey mass as a proportion of snake mass) did not differ between the sexes. Disproportionate enlargement of feeding structures would be expected to evolve only if one sex consumed prey that were larger relative to their own body size (Slatkin 1984; Shine 1989; Forsman 1991b). Nonetheless, it is interesting to note that the sexes diverged in prey species, but not in prey size, over an intermediate range of python body sizes (note the analyses showing a similarity between sexes in prey mass relative to body size, but a divergence in

prey species). This result suggests that females shifted to some alternative habitat, or some alternative foraging tactic, at a smaller body size than males. One obvious possibility is that females moved from disturbed habitats to more pristine forest, with a consequent decrease in rat abundance and an increased availability of larger mammals. Behavioural ecology studies to evaluate this hypothesis would be of value. Regardless, this putative shift was not accompanied by any increase in absolute prey size, perhaps because of gape-limitation. Relative prey mass was highest at this 'transitional' SVL (Fig. 4), and the snakes may not be physically capable of swallowing even larger prey.

Some of the dietary allometries detected in Reticulated Pythons are relatively easy to interpret, but others remain obscure. For example, the apparent increase in feeding frequency with larger body size (especially in females) may reflect greater energy needs of reproductive animals than their juvenile conspecifics. The ontogenetic shift from rats to larger mammals is presumably related to prey size. Inevitably, this increase in prey size requires a shift in prey species, because the size range of Reticulated Pythons is so massive compared with the size range

within any one prey species. In smaller snake species, by contrast, the full size range of animals may be small enough (in absolute terms) that a single prey species spans the entire size range of appropriate prey (e.g. Forsman 1991a,b). Thus, such species can 'afford' to be highly specialized. Specialization on one (or, at most, a few) prey species has been identified as a distinctive ecological feature of snakes as a whole (e.g. Toft 1985; Mushinsky 1987). It would be interesting to know how much of this putative dietary specialization reflects a bias of studies towards temperate-zone snake species. Compared with tropical species, temperate-zone snakes tend to be smaller, with a relatively small range in adult body sizes, and they live in an environment with fewer potential prey species. Information on Australian snakes indicates a greater dietary diversity (and stronger ontogenetic shifts in prey type) among large species (mostly pythons) than among smaller taxa (mostly elapids and typhlopids; see Shine & Slip 1990; Shine 1994). Additional data on large tropical snakes are needed before we can accept the generalization that dietary specialization is a consistent feature of the ecology of snakes.

Our data on the abundance of parasitic nematodes in python stomachs provide the first quantitative information on this topic. Presumably, the level of parasite abundance is related to an animal's previous feeding history, as well as to its defence mechanisms against parasite attachment. A general increase in parasite numbers with python body size may simply reflect the age of the snake (and, hence, the cumulative opportunity for infestation), or the physical size of the stomach (and, hence, of the available habitat for the nematodes). More detailed studies might well find species-level differences in the nematode faunas of Reticulated Pythons of different body sizes or sexes (owing to differences in dietary composition; see Table 2), but this issue was outside the scope of our study. Our data do, however, demonstrate an allometric increase in parasite abundance with body size of the predator, and suggest a sex difference in the frequency of infestation. As we learn more about the potential importance of parasites in natural populations, such information may prove to be extremely valuable.

Previous analyses of the relationship between predator size and prey size in snakes have identified a trend for larger snakes to consume larger prey, and a wider range of prey sizes, than do smaller conspecifics (see review by Arnold 1993). There has been considerable interest in the question of whether larger snakes actively select larger prey (i.e. ignore smaller prey items), or continue to take small as well as large prey. Our data set on Reticulated Pythons clearly shows the former situation: large pythons cease feeding on rats, and take only very large prey (Fig. 4). However, our data also show that this result reflects the huge range of body sizes in this species. If analysis

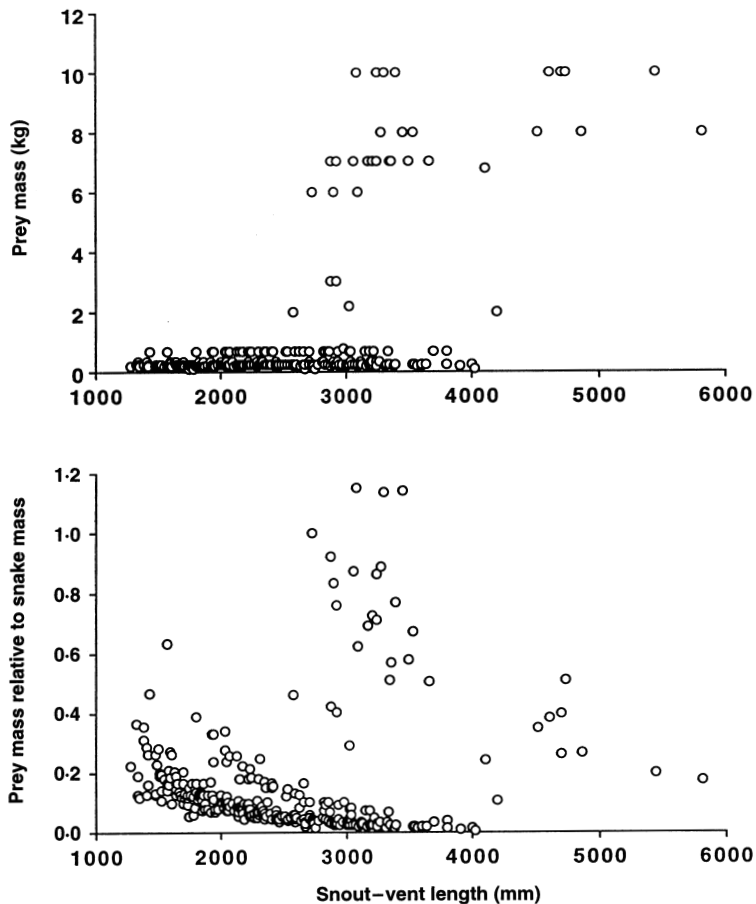


Fig. 4. Prey size compared with predator size in Reticulated Pythons. Larger snakes take larger prey items (upper graph), but relative prey mass (i.e. prey mass divided by snake mass) is highest for intermediate-sized snakes (lower graph). See text for statistical analysis.

was restricted to pythons < 4-m SVL, the strong conclusion would be that larger snakes simply expand the range of prey sizes they consume (i.e. they continue to take small as well as large prey; see Fig. 4). Thus, the size range of snakes within a population determines the degree to which the largest individuals continue to take small prey. Earlier studies on a range of snake species have revealed several cases where larger specimens cease to feed on small prey (e.g. *Tantilla gracilis*, Cobb 1989; *Enhydrina schistosa*, Voris & Moffett 1981; *Nerodia rhombifera*, Plummer & Goy 1984; *Cerberus rynchops*, Jayne, Voris & Heang 1988), but other cases in which larger specimens continue to take small as well as large prey (e.g. *Austrelaps ramsayi*, *Notechis scutatus*, *Pseudechis porphyriacus*, Shine 1977; *Regina grahamii* and *R. septemvittata*, Godley, McDiarmid & Rojas 1984). Arnold (1993) has suggested a number of reasons for this diversity in allometric relationships between predator and prey. One additional factor may simply be the absolute range of body sizes of the species under study, rather than any other biological differences between these systems.

Although most previous work on the allometry of snake diets has not investigated sex differences, there have been detailed analyses of the interplay between body size, sexual dimorphism and prey attributes in four North American watersnake species (*Nerodia*, Mushinsky *et al.* 1982) and one Australian filesnake (*Acrochordus*, Houston & Shine 1993). There are a number of significant differences between these species and our Reticulated Pythons. For example, feeding frequency tended to decrease rather than increase with body size, and males showed less dietary shift with body size than did conspecific females. Also, the two sexes show strong morphological divergence in all of these taxa (males have smaller heads than females, at the same body length: Shine 1991). Such head-size differences between the sexes are likely to be accompanied by dietary divergence between males and females at the same body length, rather than sex differences in diet resulting entirely from sexual size dimorphism (as in Fig. 1a). Such interspecific differences in the details of trophic allometry are likely to be widespread. Nonetheless, these studies also detected some of the same patterns that we found in Reticulated Pythons; for example, females grow larger than males in all five species, and tend to eat larger prey in three of these five taxa. The two exceptions involved anuran-eating species, in which the restricted size range of available prey means that males and females eat similar-sized prey, despite the significantly larger body sizes of females (Mushinsky *et al.* 1982).

Another generality concerns the interplay between habitat selection and ontogenetic and sexual shifts in diet. Our data on Reticulated Pythons suggest that some of the significant shifts in dietary composition (prey type and prey size) in this species reflect the fact

that different-sized prey are likely to occur in different habitats. The same kinds of spatial separation of prey of different sizes may drive ontogenetic dietary shifts in a diverse array of snake species, ranging from Gartersnakes feeding on Minnows in North American lakes (Arnold 1993) to acrochordids consuming fish in Australian billabongs (Houston & Shine 1993). Further studies would be valuable, particularly with other species of large snakes. The massive intraspecific range in body sizes provides an ideal opportunity to investigate allometries in ecological traits. Ideally, we also need detailed studies of the behavioural ecology of free-ranging specimens, to evaluate the possibility of size-related shifts in foraging tactics and habitats. Such shifts have been documented in several taxa of gape-limited predators (e.g. Cott 1961; Shine 1986) and our data on Reticulated Pythons suggest that the same phenomenon may also occur in these giant snakes.

Acknowledgements

We thank Mr Hasan and his helpful staff at Palembang; the Indonesian wildlife authorities (LIPI and PHPA), especially Dr Soetikno, for permits for the work; B. Yuwono and G. Saputra for logistical support; M. Elphick for bibliographic assistance; O. Crowe for identification of gut contents; and H. Jones for identification of gut parasites. The work was financially supported by the Australian Research Council and the Asian Conservation and Sustainable Use Group.

References

- Andrews, R.M. (1982) Patterns of growth in reptiles. *Biology of the Reptilia*, Vol. 13 (eds G. Gans & F. H. Pough), pp. 273–320. Academic Press, New York.
- Arnold, S.J. (1972) Species densities of predators and their prey. *American Naturalist* **106**, 220–236.
- Arnold, S.J. (1993) Foraging theory and prey-size–predator-size relations in snakes. *Snakes. Ecology and Behaviour* (eds R. A. Seigel & J. T. Collins), pp. 87–116. McGraw-Hill, New York.
- Cobb, V.A. (1989) *The foraging ecology and prey relationships of the flathead snake, Tantilla gracilis*. MSc thesis, University of Texas, Tyler, TX.
- Corbet, G.B. & Hill, J.E. (1992) *The Mammals of the Indomalayan Region*. Oxford University Press, New York.
- Cott, H.B. (1961) Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Transactions of the Zoological Society of London* **29**, 211–356.
- Fitzgerald, L.A., Cruz, F.B. & Perotti, G. (1993) The reproductive cycle and the size at maturity of *Tupinambis rufescens* (Sauria: Teiidae) in the dry Chaco of Argentina. *Journal of Herpetology* **27**, 70–78.
- Forsman, A. (1991a) Adaptive variation in head size in *Vipera berus* L. populations. *Biological Journal of the Linnean Society* **43**, 281–296.
- Forsman, A. (1991b) Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *Journal of Animal Ecology* **60**, 253–267.

- Godley, S.J., McDiarmid, R.W. & Rojas, N.N. (1984) Estimating prey size and number in crayfish-eating snakes, genus *Regina*. *Herpetologica* **40**, 82–88.
- Houston, D.L. & Shine, R. (1993) Sexual dimorphism and niche divergence: feeding habits of the arafura filesnake. *Journal of Animal Ecology* **62**, 737–749.
- Jayne, B.C., Voris, H.K. & Heang, K.B. (1988) Diet, feeding behaviour, growth, and numbers of a population of *Cerberus rynchops* (Serpentes: Homalopsinae) in Malaysia. *Fieldiana: Zoology* **50**, 1–15.
- Mushinsky, H.R. (1987) Foraging ecology. *Snakes: Ecology and Evolutionary Biology* (eds R. A. Seigel, N. B. Ford & S. S. Novak), pp. 302–334. Macmillan, New York.
- Mushinsky, H.R., Hebrard, J.J. & Vodopich, D.S. (1982) Ontogeny of water snake foraging ecology. *Ecology* **63**, 1624–1629.
- Nowak, R.M. & Paradiso, J.L. (1983) *Walker's Mammals of the World*, 4th edn. Johns Hopkins University Press, Baltimore.
- Parker, S.B. (1990) *Grzimek's Encyclopedia of Mammals*, Vol. 4. McGraw-Hill, New York.
- Plummer, M.V. & Goy, J.M. (1984) Ontogenetic dietary shift of water snakes (*Nerodia rhombifera*) in a fish hatchery. *Copeia* **1984**, 550–552.
- Pope, C.H. (1975) *The Giant Snakes*. Alfred A. Knopf, New York.
- Selander, R.K. (1966) Sexual dimorphism and differential niche utilization in birds. *Condor* **68**, 113–151.
- Selander, R.K. (1972) Sexual selection and dimorphism in birds. *Sexual Selection and the Descent of Man* (ed. B. Campbell), pp. 180–230. Heinemann, London.
- Shine, R. (1977) Habitats, diets and sympatry in snakes: a study from Australia. *Canadian Journal of Zoology* **55**, 1118–1128.
- Shine, R. (1986) Ecology of a low-energy specialist: food habits and reproductive biology of the arafura filesnake (Acrochordidae). *Copeia*, **1986**, 424–437.
- Shine, R. (1988) Parental care in reptiles. *Biology of the Reptilia*, Vol. 16 (eds C. Gans & R. B. Huey), pp. 275–330. Alan R. Liss, New York.
- Shine, R. (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* **64**, 419–461.
- Shine, R. (1991) Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* **138**, 103–122.
- Shine, R. (1993) Sexual dimorphism. *Snakes: Ecology and Behaviour* (eds R. A. Seigel & J. Collins), pp. 49–86. McGraw-Hill, New York.
- Shine, R. (1994) Allometric patterns in the ecology of Australian snakes. *Copeia* **1994**, 851–867.
- Shine, R. & Charnov, E.L. (1992) Patterns of survival, growth and maturation in snakes and lizards. *American Naturalist* **139**, 1257–1269.
- Shine, R. & Madsen, T. (1996) Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiological Zoology* **69**, 252–269.
- Shine, R. & Slip, D.J. (1990) Biological aspects of the adaptive radiation of Australasian pythons (Serpentes: Boidae). *Herpetologica* **46**, 283–290.
- Shine, R., Harlow, P., Keogh, J.S. & Boeadi (1995) Biology and commercial utilization of acrochordid snakes, with special reference to karung (*Acrochordus javanicus*). *Journal of Herpetology* **29**, 352–360.
- Shine, R., Harlow, P., Keogh, J.S. & Boeadi (1996) Commercial harvesting of giant lizards: the biology of water monitors, *Varanus salvator*, in southern Sumatra. *Biological Conservation* **77**, 125–134.
- Slatkin, M. (1984) Ecological causes of sexual dimorphism. *Evolution* **38**, 622–630.
- Toft, C.A. (1985) Resource partitioning in amphibians and reptiles. *Copeia* **1985**, 1–20.
- Vitt, L.J. (1987) Communities. *Snakes: Ecology and Evolutionary Biology* (eds R. A. Seigel, J. T. Collins and S. S. Novak), pp. 335–365. Macmillan, New York.
- Voris, H. & Moffett, M. (1981) Size and proportion relationship between the Beaked Sea Snake and its prey. *Biotropica* **13**, 15–19.

Received 4 November 1996; revised 23 June 1997; accepted 4 September 1997