

The allometry of life-history traits: insights from a study of giant snakes (*Python reticulatus*)

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Abstract

Many life-history traits are allometrically tied to body size, in snakes as well as in other animals. Two problems with previous analyses on this topic for snakes are that: (i) the range of body sizes within species is generally small, so that most analyses have relied on interspecific comparisons; and (ii) available data have been heavily biased towards small, temperate-zone colubroid species. We test the generality of results from previous work with data on a species of giant tropical snake that is phylogenetically and ecologically distinctive, and encompasses such a massive size range that we can examine intraspecific allometries. We use data from >1,000 field-collected reticulated pythons from southern Sumatra to ask two questions: (i) do life-history traits show intraspecific allometries similar to those revealed by interspecific comparisons?; and (ii) are mean values for life-history traits in a giant snake consistent with allometric trends in smaller species? As predicted, strong intraspecific allometry was evident for most of the life-history traits we measured, including reproductive output (e.g. clutch size, frequency of reproduction in females, testis volume relative to body mass) and energy stores (relative size of the abdominal fat bodies). For many traits (e.g. the means and variances of clutch sizes and maternal body sizes, relative offspring size, body size at maturation relative to size at hatching and maximum adult size), these giant pythons were near or beyond the extremes reported for smaller species of snakes, supporting the importance of allometry. None the less, reticulated pythons deviate from many of these previously-documented allometries in significant ways, suggesting that current generalizations about life-history allometry in snakes may be premature.

Key words: life-history, reproduction, reptile, snake, tropical

INTRODUCTION

The body size of an organism is its most obvious characteristic, and has enormous life-history implications. Comparative analyses have revealed very strong associations between body size and life-history traits, such as age at maturity, reproductive output, and the direction and degree of sexual size dimorphism (e.g. Calder, 1984; Harvey & Pagel, 1991; Shine, 1994a). Studies of this topic, however, often involve two fundamental problems: (i) most published analyses of allometric effects on ecological traits have relied on interspecific comparisons, because the range of body sizes within a single taxon is usually too small to engender enough variation in reproductive biology for quantitative analysis. Even if size-associated shifts occur intraspecifically, they are likely to be so subtle that they are difficult to quantify without detailed study; (ii) the

taxa studied constitute only a subset of all that exist, with strong biases in terms of phylogenetic affinities, ecological traits, and geographic distributions. These biases usually result from logistical constraints (e.g. some taxa are difficult to study) or from the accidents of academic history (e.g. location of particular research centres).

These shortcomings have significant implications for the conclusions that can be drawn from allometric studies. For example, the reliance upon interspecific comparisons inevitably introduces confounding factors. In many cases, interspecific and intraspecific patterns may be very different (e.g. Leamy & Atchley, 1984; see Harvey & Pagel, 1991 for a detailed analysis of this issue). Similarly, the lack of data on important lineages within a major group introduces obvious problems in terms of the lack of generality of any patterns that are discerned. Clearly, one solution to these problems is to examine reproductive traits within a species that: (i) displays a wide variation in body size within a single population, so that intraspecific allometries can be

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described; and (ii) differs in important respects (e.g. size, ecology, phylogeny, distribution) from the taxa that have formed the basis for previous studies. For example, unusually large or small animals offer a powerful test of the generality of allometric patterns described from a more restricted size range of organisms.

Large snakes offer an ideal model system for such an analysis. Previous interspecific analyses have identified body size as a primary axis of ecological variation in life-history traits within snakes (e.g. Shine, 1994a, 1996). Ideally, then, one might illuminate the reproductive consequences of body size by studying a species of large snake. Unfortunately, very large snakes have attracted relatively little scientific attention, for several reasons: (i) their tropical distributions, compared to the primarily temperate-zone distribution of universities; (ii) the scarcity and crypticity of most of these species; (iii) the difficulty of capturing and restraining giant snakes in densely vegetated tropical habitats; (iv) the logistical problems of preserving and storing large specimens in museum collections; and (v) ecological and ethical problems with killing large numbers of top predators. None the less, an alternative technique is feasible. Giant pythons are killed in huge numbers for their skins, and it is thus possible to gather data on animals collected and killed for the commercial trade (e.g. Fitzgerald, Cruz & Perotti, 1993; Shine *et al.*, 1995, 1996, In press). We used this method to obtain the first detailed ecological information on reticulated pythons (*Python reticulatus*), a giant snake that most authorities consider as either the largest or second largest snake species in the world (e.g. Pope, 1975).

METHODS

We gathered data during 3 trips to the city of Palembang in southern Sumatra: from 29 July–6 August 1993, 6–20 October 1994 and 3–19 April 1995. Each day, we went to the commercial premises of P. D. Budiman Co., where live pythons (as well as acrochordid snakes and varanid lizards: see Shine *et al.*, 1995, 1996, In press) were brought to be killed and skinned. The pythons were collected over a wide area and the origin of individual snakes was not determined. As well as examining specimens at the Budiman skinning factory, we visited other skinners in Palembang and arranged for skinned carcasses from other premises to be brought to the Budiman factory so that we could examine those animals also. At the skinning factory, we weighed and measured snakes as soon as they were killed, and then examined their bodies after skinning. We did not weigh snakes that had already been skinned, or that had their alimentary tracts pumped full of water prior to skinning. We measured snout-vent length (= SVL hereafter), tail length, head length (along the lower jaw, from the tip of the snout to the posterior edge of the quadrate-articular projection) and the length of the cloacal spurs. We recorded and identified any prey items in the alimentary tract (see Shine *et al.*, 1996, In

press). Males were scored as mature if they had enlarged turgid testes and/or thickened opaque efferent ducts (indicating the presence of sperm). Lengths and widths of testes were measured. Females were scored as mature if they had enlarged vitellogenic follicles (arbitrarily defined as > 8 mm diameter), oviducal eggs, or thickened muscular oviducts. Oviducal eggs were removed and weighed. We scored relative size of the abdominal fat bodies on a 4-point scale, from no discernible fat (0), minor reserves (1 = <10% of body mass), moderate reserves (2 = 10–20%), to massive stores that filled much of the posterior part of the body (3 = >20% of body mass; maximum recorded = 28%). We emphasize that no animals were killed specifically for our project; we simply took advantage of the existing commercial trade.

Because we were interested in comparing reticulated pythons to other snake species, we assembled published data on relevant topics, relying heavily on recent reviews of snake growth patterns (Parker & Plummer, 1987; Shine, 1994a), variances in clutch size (Shine & Seigel, 1996), and sexual size dimorphism (Shine, 1994b).

RESULTS

Our data are of interest in two respects: what they tell us about a very poorly-known component of the world's reptilian fauna (giant tropical snakes); and what they can reveal about allometric relationships between body size and life-history traits.

Seasonal shifts

First, we examine the degree of seasonal variation in traits that we measured. This information provides an essential background to any comparisons between tropical and temperate-zone snakes. For example, if the Sumatran reticulated pythons show no reproductive seasonality, estimates of reproductive frequency based on the proportion of females reproductive in any one sample would be difficult to compare with data on seasonally-reproducing species. We detected significant seasonal shifts in a number of traits, as follows:

(i) Seasonal shifts in body-size distributions

We noted a consistent difference in body-size distributions of juvenile pythons between the two trips for which we had large enough sample sizes to investigate this question. Small snakes (i.e. <2 m SVL) were well represented in the October 1994 sample, but scarce in the April 1995 sample (Fig. 1). A contingency-table analysis confirmed that the proportion of snakes <2 m in length decreased significantly between the two trips, for both males ($\chi^2 = 20.14$, 1 *d.f.*, $P < 0.0001$) and females ($\chi^2 = 41.29$, 1 *d.f.*, $P < 0.0001$).

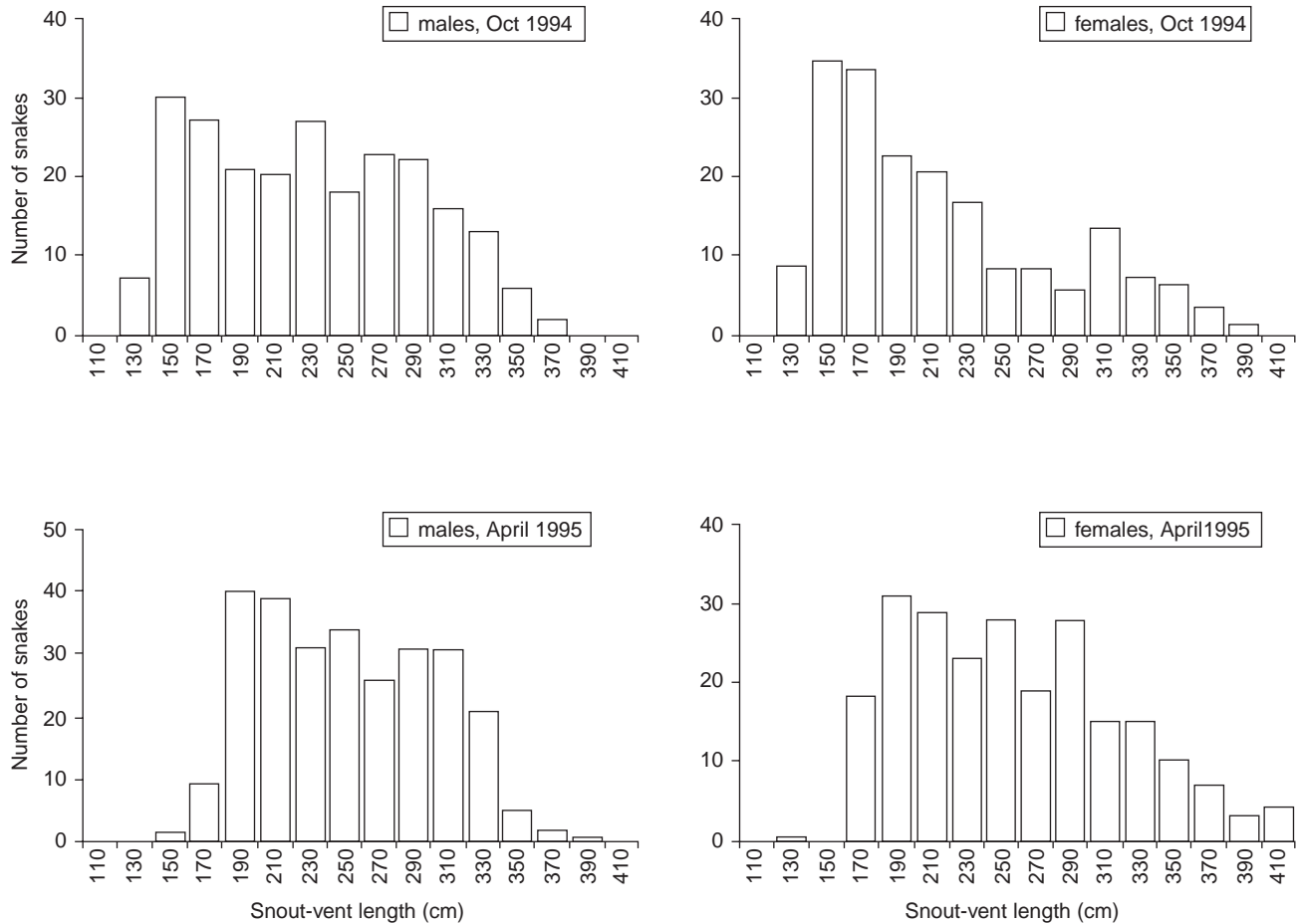


Fig. 1. Comparisons of body-size distributions of male and female pythons collected in October 1994 and April 1995. Note that the October samples included many small (<2 m) animals of both sexes, but animals of this size were scarce in the April samples.

(ii) Seasonal shifts in fat-body scores

For simplicity, our analysis treated fat-body scores as a continuous variable. Two-factor ANOVA (factors = sex and trip#) showed no effect of sex ($F_{1,1036} = 0.05$, $P=0.83$) on overall fat-body score, and no significant interaction between sex and trip # ($F_{2,1036}=0.54$, $P=0.59$), but a highly significant difference in the size of fat bodies among trips ($F_{2,1036}=58.65$, $P<0.0001$). Post-hoc tests showed that fat scores were lower during October (just after reproduction: see below) than during either of the other trips.

(iii) Seasonal shifts in male reproduction

We calculated testis volumes of adult males from data on the linear dimensions of the testes (using the formula for volume of a cylinder). A homogeneity of slopes test showed that testis volumes increased more rapidly with SVL in specimens examined during October 1994 than in those examined during April 1995 ($F_{1,346} = 14.58$, $P<0.0002$). Thus, testes of adult male pythons were consistently larger (relative to body size) in October 1994 than in April 1995 (Fig. 2).

(iv) Seasonal shifts in female reproduction

For analysis, we divided all adult-size females into two categories: non-reproductive or reproductive. The latter category included females that contained oviducal eggs, vitellogenic ovarian follicles >15 mm in diameter, or oviducal 'pockets' and large (>5 mm) corpora lutea, indicating recent oviposition. Contingency-table analysis revealed significant differences among trips in the proportions of adult females that were in reproductive condition (15 of 40, 6 of 15, 1 of 41 females; $\chi^2 = 17.03$, 2 *d.f.*, $P<0.0002$). The virtual lack of reproductive activity during the third trip (April 1995; only one of 41 adult females contained vitellogenic follicles) contributed to this significant result, but inspection of the data for the first two trips shows a difference between these two trips also. Most (5/6) of the reproductive females we examined in July 1993 were pre-ovulatory; the remaining reproductive female contained oviducal eggs. In contrast, most of those examined in October 1994 (13/15) were post-ovulatory (6 gravid, plus 7 recently oviposited). Again, the difference is statistically significant ($\chi^2 = 6.56$, 2 *d.f.*, $P<0.011$). These results suggest that female reproductive cycles are highly synchronized, with most oviposition occurring in September–October.

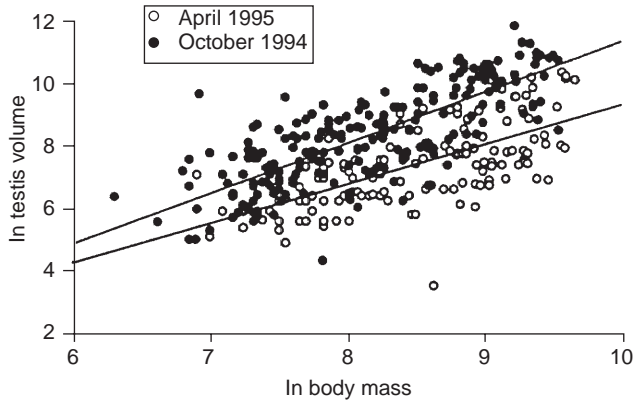


Fig. 2. A comparison of testis volume (mm^3) relative to body mass (g) in adult male reticulated pythons collected in October 1994 and April 1995. Relative testis mass declined over the intervening period, but increased with body mass in each trip; see text for statistical analyses.

Life-history traits in relation to body size

We now examine life-history traits, with special emphasis on their relationship to body size — both intraspecifically (within *Python reticulatus*) and in comparison with interspecific patterns documented by published studies on other species of snake.

(i) Sexual dimorphism

Female reticulated pythons grow much larger than males; adult females averaged significantly larger than adult males for most of the morphological traits that we measured (SVL, tail length, head length, mass: Table 1). Thus, reticulated pythons display more extreme female-biased sexual size dimorphism than do most other snakes (Fig. 3). However, pelvic spurs were consistently larger in males than in females. Some of these morphological differences reflect sexual dimorphism in overall body size, but others are affected by sex differences in body proportions. Single-factor analysis of covariance, with sex as the factor, showed that male and female pythons did not differ in head length relative to SVL

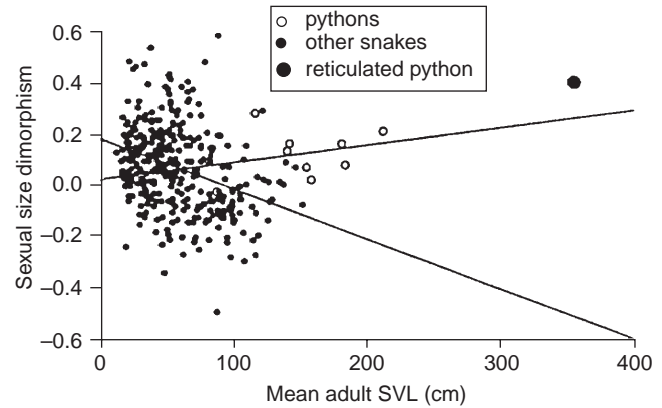


Fig. 3. Sexual size dimorphism in snakes, as a function of mean adult body size. Using the index of Lovich & Gibbons, 1992 to quantify sexual dimorphism, snakes with a larger mean adult body size tend to have a lower dimorphism index (i.e. males are larger, relative to females). However, among pythons (circles, and upper regression line), the index increases with absolute body size, and reticulated pythons fit this trend. Small dots show species means for non-pythonid snakes, and lower regression line fits these data.

(slopes $F_{1,353} = 0.34$, $P = 0.56$; intercepts $F_{1,354} = 0.28$, $P = 0.60$). However, males had longer tails relative to SVL (slopes $F_{1,353} = 4.60$, $P < 0.033$), longer spurs relative to SVL (slopes $F_{1,80} = 6.06$, $P < 0.018$), and, on average, were heavier than females at the same body length (using \ln mass to overcome variance heterogeneity: slopes $F_{1,716} = 29.36$, $P < 0.0001$; see Fig. 4). 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.

(ii) Body size and age at maturation

Adult reticulated pythons span an enormous range of body sizes, from <1.5 m (<1 kg) to >6 m (>70 kg; Table 1). Thus, maturation occurs at a low proportion of

Table 1. Sample sizes, body sizes and sexual size dimorphism in adult reticulated pythons from southern Sumatra. The table shows mean values for each trait, with standard deviation in brackets. The last two columns show the results of unpaired two-tailed t -tests for statistical significance of the differences between the sexes. 'SVL' = snout-vent length

Trait	Males	Females	t (558 d.f.)	P
Sample size	463	97		
Snout-vent length (mm)	2525.3 (531.6)	3597.4 (752.2)	16.31	<0.0001
Range of SVLs (mm)	1370–4250	2100–6080		
Tail length (mm)	388.75 (87.25)	533.60 (104.53)	11.83	<0.0001
Range of tail lengths (mm)	50–625	300–830		
Head length (mm)	86.61 (14.38)	114.59 (19.50)	9.89	<0.0001
Range of head lengths (mm)	62–135	89–168		
Mass (g)	5899.7 (3671.7)	17639 (18040.5)	10.88	<0.0001
Range in mass (g)	950–19300	2500–75000		
Spur length (mm)	4.37 (2.21)	0.73 (1.62)	5.56	<0.0001
Range in spur lengths (mm)	0–10	0–6		

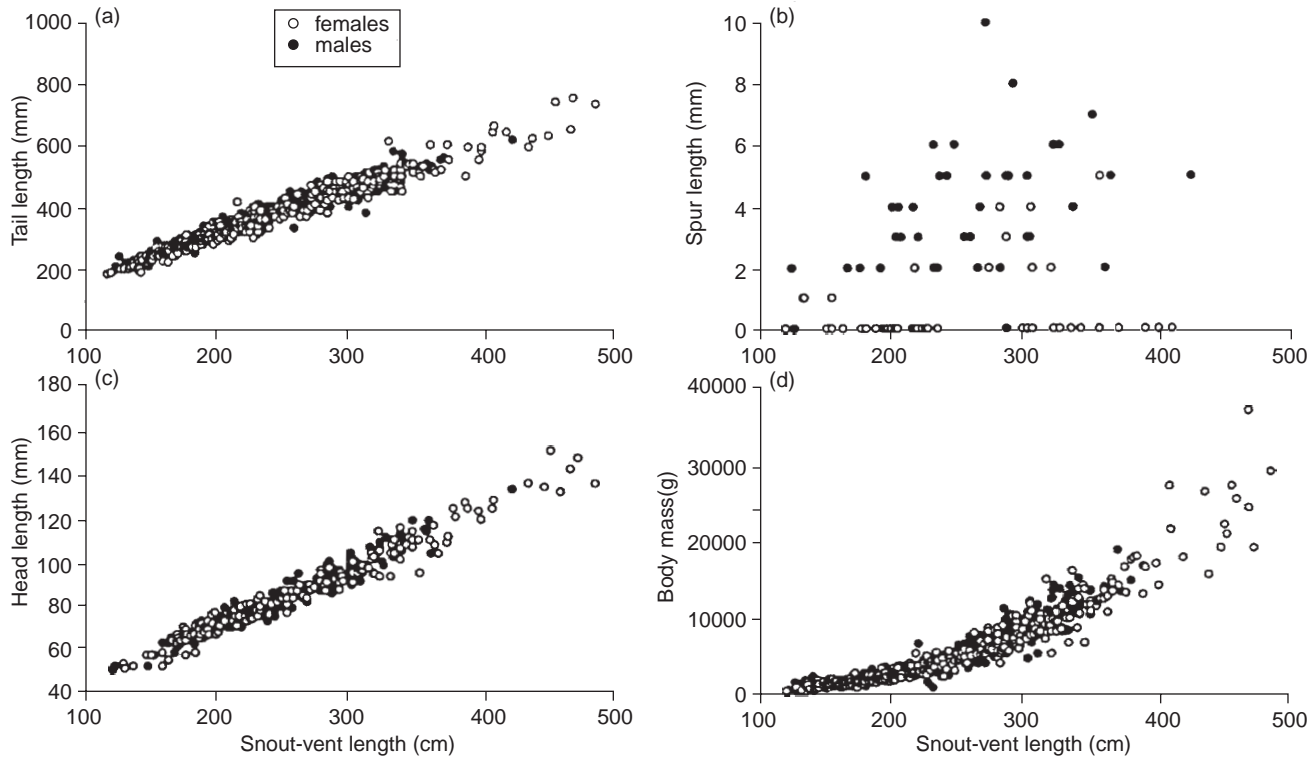


Fig. 4. Body proportions of reticulated pythons from southern Sumatra. Compared to females of the same body lengths, male pythons have longer tails (a) and cloacal spurs (b), and are heavier than females at the same body length (c). See text for statistical analyses of these data (d). However, head sizes relative to body length do not differ between the sexes.

maximum body length (from Table 1, 34% of maximum SVL in females, 32% in males). In terms of mass, the proportional size at maturation is much lower: for example, newly-matured females weigh <4% of maximum female mass (<5% in males). Thus, *P. reticulatus* mature at a lower proportion of maximum SVL, and grow proportionally less between hatching and maturation, than do most other large snake species (Fig. 5).

We do not have any direct evidence on age at maturation in reticulated pythons, but strong seasonal shifts in size distributions suggest that growth is very rapid (Fig. 1). Snakes <1.3 m in length are not used in the commercial leather industry, and so are not represented in our data. In combination with extensive data from captive snakes (e.g. Williamson, 1967; Ross, 1978; de Vosjoli, 1989), these seasonal shifts suggest that male *P. reticulatus* mature at about two years of age, and females at about three years (Shine *et al.*, unpubl. analyses). The age at maturation in *P. reticulatus* is thus similar to that seen in much smaller snakes from the temperate-zone (Fig. 5).

(iii) Energy stores

Comparisons of SVL distributions of snakes with different fat-body scores showed a consistent allometric trend: fat-body scores were higher in larger snakes (Fig. 6; effect of 20-cm SVL category on fat-body score, $F_{12,984} = 15.81$, $P < 0.0001$). The relationship between fat-

body scores and snout-vent length was similar in the two sexes, but the overall average fat-body score was higher for females than for males because of the larger average body size of females than of males (Fig. 6).

(iv) Reproductive output in females

Oviducal eggs averaged 123.81 g (S.D. = 31.66, based on 7 clutches; range = 67.7–166.7 g). Mean egg mass per clutch was not correlated to female body length ($n = 7$, $r = 0.04$, $P = 0.93$), but this is a very weak test (because of small sample size, and the probability that egg size changes markedly at oviposition owing to water uptake). However, clutch sizes increased with maternal body length ($n = 17$ clutches, $r = 0.66$, $P < 0.005$; see Fig. 7). Relative clutch mass (= clutch mass divided by maternal post-oviposition mass) averaged 0.40 (S.D. = 0.16, $n = 5$, range = 0.13–0.55). The mean clutch size we recorded (23.82, range = 11–46, S.D. = 10.36, $n = 17$) is larger than for most previously-studied snake species, consistent with the general allometry of this trait in snakes (Fig. 7). At around 60 to 70 cm SVL (Ross, 1978; de Vosjoli, 1989), hatchlings of *P. reticulatus* are much larger than those of most other snakes. None the less, the ratio of individual egg mass to maternal body mass (“expenditure per progeny”) is very low (mean = 0.013, S.D. = 0.006, based on 7 clutches) in reticulated pythons.

Trips 1 and 2 occurred close enough to median

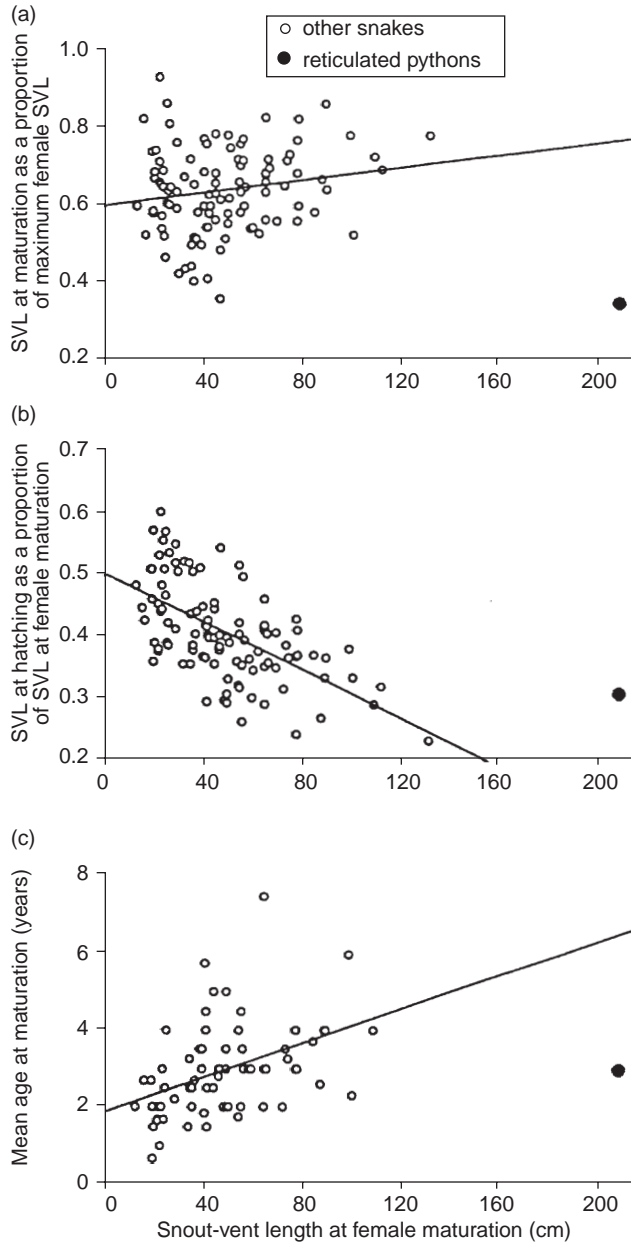


Fig. 5. Body length (snout-vent length) at maturation in female snakes, in relation to other life-history variables. Relative SVL at maturation (as a proportion of maximum SVL) does not change with absolute body size (a; but see text), but larger species of snakes tend to have smaller hatchlings relative to maturation SVL (b). Larger species also tend to mature at later ages (c). See text for statistical tests and further explanation.

ovulation time that we could confidently rank all adult females as either reproductive or non-reproductive for that year. Thus, these trips provided useful data on the frequency of reproduction in adult female pythons. We estimated the proportion of reproductive females to be 6 of 15 (40%) in the first trip, and 15 of 40 (38%) in the second. These results suggest that female reticulated pythons reproduce about once every two or three years (on average). More detailed analysis shows that the

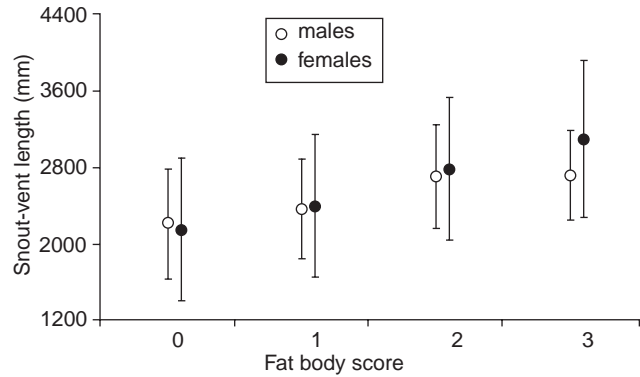


Fig. 6. Fat-body scores (an index of relative size) increase with body length in reticulated pythons; higher scores are found mostly in larger snakes. Symbols show mean values \pm S.D. See text for analysis.

proportion of reproductive females shifted consistently with body size (Fig. 7: proportion of reproductive females vs. body size: $n = 12$ SVL intervals, $r = 0.76$, $P < 0.004$). Thus, small females appear to reproduce more frequently than larger conspecifics. This result fits well with the allometric trend in reproductive frequency evident from studies of other species of snake (Fig. 7).

(v) Testicular size in males

Testicular volumes increased in larger males: not only in absolute terms, but also relative to body mass (regressions of testis volume divided by body mass vs. adult male SVL: for trip 2, $n = 157$, $r = 0.20$, $P < 0.015$; for trip 3, $n = 211$, $r = 0.45$, $P < 0.0001$). This allometry is also evident from the high (>1.0) slopes of the regression lines in Fig. 2.

DISCUSSION

First, we evaluate the seasonality of traits that we measured in reticulated pythons from southern Sumatra, before we explore allometry in ecological traits. Our among-trip comparisons suggest that the pythons show strong seasonality in their reproductive cycles (in both sexes), in their fat-body stores, and in seasonal size distributions. At first sight, this result is a surprising one, given the high temperatures year-round in southern Sumatra. However, rainfall patterns are highly seasonal in this area (Erdelen, 1991), and many other reptile species have been found to display seasonal cycles in tropical environments (e.g. Vitt & Vangilder, 1983; James & Shine, 1985). For example, studies on pythons in the Australian tropics suggest that all species show highly seasonal reproductive cycles (e.g. Shine & Slip, 1990; Madsen & Shine, 1996). Data for two other commercially-harvested Sumatran reptiles provide an interesting comparison. Females of one of these taxa (the water monitor *Varanus salvator*) reproduce during

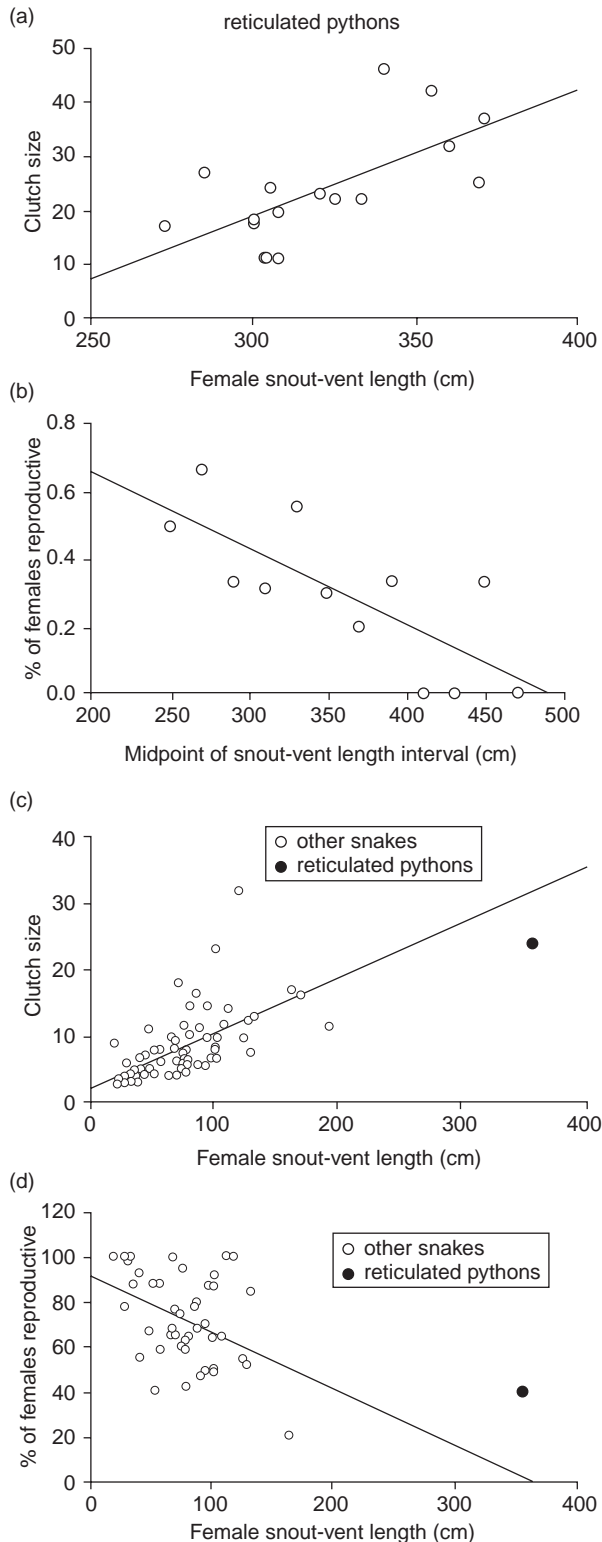


Fig. 7. The allometry of reproductive traits in reticulated pythons, compared to other snakes: (a, b) data for reticulated pythons: larger females produced larger clutches (a) but reproduced less frequently (as judged by the proportion of reproductive females in each size category: b); (c, d) compare mean values of these traits between reticulated pythons and other snake species; from published literature, see text for references), with the linear regression of best fit for these points. See text for statistical analyses.

most of the year, but reproduction in the other (the filesnake *Acrochordus javanicus*) is highly seasonal (Shine *et al.*, 1995, 1996).

Given the seasonality of reproduction, seasonal shifts in other traits might be expected also. For example, energy costs of reproduction may be responsible for seasonal changes in body condition and energy stores. Reproduction may affect energy stores not only via direct allocation of energy to eggs or mating behaviours, but also by constraining feeding rates. Reproducing adults cease feeding in at least one other python species (*Liasis fuscus*: Madsen & Shine, unpubl. data). The seasonal shift in body-size distributions almost certainly reflects the synchronized hatching, combined with the extraordinarily rapid growth rates of juvenile reticulated pythons. Well-fed captive specimens have been reported to attain lengths of >4 m less than 12 months after hatching (Williamson, 1967; Ross, 1978; de Vosjoli, 1989). Thus, the disappearance of snakes <2 m in size over the period from October to April (Fig. 1) almost certainly reflects growth rather than high mortality of young snakes.

We turn now to the question of allometry. The clear overall result from our analyses was that reticulated pythons display significant effects of body size on virtually every trait that we examined. Such allometries are probably very widespread, but are difficult to detect in most species because of their limited range of variation in body sizes.

Sexual dimorphism – reticulated pythons show more extreme sexual size dimorphism (SSD) than do most other snakes. As in other snake species, this dimorphism reflects differential size at maturation rather than large sex differences in post-maturation mortality rates (e.g. Shine, 1994a). Adult female reticulated pythons are 42% longer than adult males, on average, and weigh approximately three times as much (Table 1). The length-based index of SSD (calculated as per Lovich & Gibbons, 1992) for this species (0.42) is higher than in 365 of the 374 snake species reviewed by Shine (1994a). The magnitude of the dimorphism in absolute terms may be higher than in any other snake, although the anaconda (*Eunectes murinus*) may be even more extreme in this respect (e.g. Henderson, 1994). Regardless of which of these two massive species shows the more extreme dimorphism, it seems clear that the largest living snake in the world is a female.

Comparison with SSD in other species of snakes indicates that *P. reticulatus* fits well with trends within the Pythonidae, but that this group offers a strong contrast to other snakes (Fig. 3). We do not know why interspecific allometries should vary among familial lineages in this way. However, such variation may be widespread. For example, sex differences in body size show strong allometry in kinosternid turtles, but not in turtles as a whole (Berry & Shine, 1980; note that Gibbons & Lovich, 1990 disputed this claim, but analysis of their data shows highly significant allometry within the kinosternids: Shine, unpubl.).

The massive disparity in body sizes of male and

female reticulated pythons is accompanied by only modest sexual divergence in body proportions. Males have longer tails, in keeping with a general trend for tail-length dimorphism to be most pronounced in snake species with a high degree of body-size dimorphism (King, 1989; Shine, 1993). Males also have larger pre-cloacal spurs, presumably related to their function in courtship and mating (e.g. Ross & Marzec, 1990). Sexual divergence in spur length is probably widespread in pythons, but is difficult to detect in smaller species because of measurement error (see Shine & Slip, 1990). As with so many other traits, the large size of reticulated pythons allows us to detect patterns that would be difficult to quantify in smaller snakes.

In contrast, we found no evidence of significant sex divergence in head size relative to body size, despite the widespread occurrence of such divergence even in small species of snakes (e.g. Shine, 1994b). This divergence probably relates to sex differences in dietary composition, especially in prey size relative to predator size (Shine, 1991). Given the general similarity between male and female *P. reticulatus* in relative prey mass (Shine *et al.*, In press), however, we would not expect the sexes to experience different selection pressures on feeding structures in this species.

The growth trajectories of reticulated pythons may differ in important ways from those expected from general allometric relationships among snakes. Compared to these 'expected' values, *P. reticulatus* matures surprisingly early (and hence, at a small body size, and having grown relatively little since hatching: Fig. 5). These traits are clearly linked, and reticulated pythons are an extreme case among snakes. For example, the mean ratio of length at maturation to maximum length in snakes is approximately 0.68 (Shine & Charnov, 1992), whereas in *P. reticulatus* this value is 0.35 (from Table 1). Why do reticulated pythons mature at such a small size and such an early age? Part of the answer probably lies with general allometric trends, in that large species of reptiles tend to mature at a small proportion of maximum body size (Andrews, 1982; Shine & Charnov, 1992). This trend is not evident in Fig. 5, because we have used minimum SVL at maturation as the independent variable. Much of the interspecific variation involves the magnitude of growth from maturation to maximum size, and plotting this proportion against maximum size (rather than SVL at maturation) shows a much stronger allometric trend (Andrews, 1982; Shine & Charnov, 1992).

The tendency for large snake species to mature at a relatively small size, combined with their generally tropical habitats (and thus, year-round growth), will tend to minimize any variation in age at maturity in snakes of different body sizes. This phenomenon may have significant implications for the ecology and mating systems of large snakes. For example, it means that adults within a population span an enormous range of body sizes. This size range may engender variation in reproductive output in females, if clutch sizes, egg sizes or reproductive frequencies are linked to body size (see

below). Equally, male mating 'tactics' may be modified. In a species with vigorous male-male combat that can involve serious injury to unsuccessful males (as in *P. reticulatus*: Anon., 1990), combat against much larger rivals is clearly not a viable option for newly-matured males (i.e. with masses of 1 kg vs. 20 kg in the largest males).

Other traits also changed with body size within *P. reticulatus*. The consistent increase in relative size of the fat bodies with increasing body length, in both sexes (Fig. 6), may reflect allometric shifts in energy acquisition (larger pythons feed more often, and take larger prey: Shine *et al.*, 1996, In press) and expenditure (larger pythons have lower mass-specific metabolic rates [Ellis & Chappell, 1987] and may modify size-specific reproductive rates: see below). Energy stores reflect a balance between these two processes.

The consistent intraspecific increase in clutch size with increased female body size is a common phenomenon in snakes (e.g. Seigel & Ford, 1987), and the clutch sizes that we recorded for *P. reticulatus* are about what one might expect from their body sizes (Fig. 7). Interestingly, most published records for fecundity of reticulated pythons cite much higher values (e.g. Fitch, 1970; Pope, 1975; Ross & Marzec, 1990), probably because these records are based on unusually large, well-fed captive snakes. Similar biases have been noted in other studies of reproduction in free-ranging snakes (e.g. Fitch, 1970).

Although the eggs and hatchlings of reticulated pythons are massive in absolute terms, they comprise a very small proportion of maternal mass (i.e. 'expenditure per progeny' is low). In this respect, reticulated pythons conform to a general feature of reptilian reproduction (e.g. Shine, 1978). In many small snake species, females produce only two or three offspring, each of them a high proportion of maternal body mass — but in larger species, clutches consist of larger numbers of (relatively) smaller offspring. The adaptive significance of this pattern remains unclear, but may involve 'diminishing returns' from maternal investment in extremely large offspring (Shine, 1978).

Reproductive frequencies apparently decline with increased maternal body size in reticulated pythons, and the same correlation is evident at the interspecific level within other kinds of snakes (Fig. 7). Previous studies have documented a diversity of intraspecific relationships between body size and reproductive frequency in snakes. Most commonly, reproductive frequency appears to remain constant or to increase with body size (e.g. Glissmeyer, 1951; Blem, 1982; Shine, 1986). However, in the only other python species examined in detail (*Liasis fuscus*), reproductive frequencies were maximized at intermediate body sizes, with less frequent reproduction by animals either smaller or larger than this size (Madsen & Shine, 1996). Why should body size affect reproductive frequency? Theoretical models suggest that females of long-lived species should delay reproduction until they have gathered enough energy to produce a large clutch (e.g. Bull & Shine, 1979);

perhaps, enough to fill almost all available space within the body cavity (Shine, 1992). The absolute amount of energy required for such a clutch increases markedly with maternal body size. Also, dietary composition and feeding rates may shift (both occur in *P. reticulatus*: Shine *et al.*, 1996, In press) and maintenance requirements change also. Hence, it is not surprising to see a link between body size and reproductive frequency, and we expect that this relationship may prove to be a complex one that differs substantially among species, and may vary in time and space even within a single taxon. Indeed, the only generality may be that an organism's body size affects its energy balance and thus its reproductive output.

The finding that most adult-size female reticulated pythons are non-reproductive in most years, mirrors conclusions from field studies on other pythonid species (e.g. Slip & Shine, 1988; Shine & Slip, 1990). Even when exposed to an *ad libitum* food supply in captivity, female reticulated pythons may be unable to recoup their energy reserves fast enough to produce eggs every year (Pope, 1975; de Vosjoli, 1989). Lower reproductive frequencies in larger snake species (Fig. 7) may reflect not only the increased difficulty of finding enough food to produce a large clutch, but also higher survival rates of larger snakes (because of their lower vulnerability to predation, etc.). Life-history theory predicts that organisms with high survival rates should expend less reproductive effort, because their lifetime reproductive success is likely to be maximized by adopting a cautious approach to the risks associated with reproductive expenditure (e.g. Williams, 1966).

Our data on male reproduction are much more limited; all we can say with confidence is that testes of adult males vary in size seasonally, and show positive allometry with body size (i.e. testes comprise an increasing proportion of body mass as the snakes grow larger). In the absence of similar data on other species, the allometry is difficult to interpret. We suggest that large males experience higher mating success, perhaps because of their enhanced prowess in male-male combat, and that the positive allometry of testis size reflects this shift. An adaptive adjustment of testis size to mating opportunities has been documented in interspecific comparisons in other vertebrates (e.g. Harvey & Harcourt, 1984), and short-term responses of testis size to mating opportunities have been shown in humans (Baker & Bellis, 1995). Given the massive size disparities in body size among adult male *P. reticulatus*, it seems probable that small males obtain matings only if larger males are absent (cf. Madsen *et al.*, 1993).

The *variance* in reproductive output within a population may sometimes be as significant as the *mean* value, but has attracted much less scientific attention (Shine & Seigel, 1996). Because they mature at a relatively small proportion of mean adult body size, the coefficient of variation in body lengths of adult females is higher in *P. reticulatus* (19.5, from data in Table 1) than in most other snakes (e.g. this figure is higher than in 93 of 103 species of Australian snakes reviewed by Shine, 1994a).

Reptile species with highly variable maternal body sizes tend to have highly variable clutch sizes (Shine & Seigel, 1996), because of the functional relationship between these two traits (e.g. Fig. 7). From our data, the coefficient of variation in clutch size for *P. reticulatus* is 43.5. This value is higher than for 51 of 58 other snakes studied, and higher than for 140 of 148 other squamate reptiles in general (Shine & Seigel, 1996). Hence, unusually large reptile species may be distinctive in terms of the intrapopulation variances, as well as the means, of important life-history traits.

In summary, information on a very large snake species can illuminate life-history patterns in two ways. First, the very large intraspecific size range provides an opportunity to examine within-species effects of body size on life-history traits, and our analysis confirms that such effects are evident for most of the characteristics that we examined. Second, the large mean adult body size provides a strong test of the generality of allometric trajectories derived from studies on other, much smaller, snakes. In this respect, our results were mixed. Giant pythons display some traits (notably, aspects of growth trajectories and reproductive output) that differ considerably from the situation in smaller species, and accord with direct extrapolations from patterns in smaller taxa. In other respects, however, this agreement was much less impressive, suggesting that particular allometric 'rules' may be valid only over a limited range of body sizes, a limited set of phylogenetic lineages, or for species in a limited array of habitats. Additional data on giant tropical reptiles will be necessary before we can confidently accept any generalities about the allometric relationships of life-history traits in snakes as a whole.

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REFERENCES

- Andrews, R. M. (1982). Patterns of growth in reptiles. In *Biology of the Reptilia* 13: 273–320. Gans, G. & Pough, F. H. (Eds). New York: Academic Press.
- Anon. (1990). Snake bites snake. *Australasian Post*, September 15: 6.
- Baker, R. R. & Bellis, M. A. (1995). *Human sperm competition: copulation, masturbation and infidelity*. New York: Chapman & Hall.
- Berry, J. F. & Shine, R. (1980). Sexual size dimorphism and sexual selection in turtles (Order Chelonia). *Oecologia (Berl.)* 44: 185–191.

- Blem, C. R. (1982). Biennial reproduction in snakes: An alternative hypothesis. *Copeia* **1982**: 961–963.
- Bull, J. J. & Shine, R. (1979). Iteroparous animals that skip opportunities for reproduction. *Am. Nat.* **114**: 296–316.
- Calder, W. A. (1984). *Size, function and life history*. Boston: Harvard University Press.
- de Vosjoli, P. (1989). *The general care and maintenance of Burmese pythons (including notes on other large pythons)*. Lakeside, California: The Herpetocultural Library.
- Ellis, T. M. & Chappell, M. A. (1987). Metabolism, temperature relations, maternal behaviour, and reproductive energetics in the ball python (*Python regius*). *J. Comp. Physiol.* **157**: 393–402.
- Erdelen, W. (1991). Conservation and population ecology of monitor lizards: The water monitor *Varanus salvator* (Laurenti, 1768) in south Sumatra. *Mertensiella* **2**: 120–135.
- Fitch, H. S. (1970). Reproductive cycles in lizards and snakes. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* **52**: 1–247.
- 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. *J. Herpetol.* **27**: 70–78.
- Gibbons, J. W. & Lovich, J. E. (1990). Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetol. Monogr.* **4**: 1–29.
- Glissmeyer, H. R. (1951). Egg production of the Great Basin rattlesnake. *Herpetologica* **7**: 24–27.
- Harvey, P. H. & Harcourt, A. H. (1984). Sperm competition, testes size, and breeding system in primates. In *Sperm competition and the evolution of animal mating systems*: 589–600. Smith, R. L. (Ed.). New York: Academic Press.
- Harvey, P. H. & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford Studies in Ecology and Evolution. May, R. M. & Harvey, P. H. (Eds). Oxford: Oxford University Press.
- Henderson, R. W. (1994). A splendid quintet: The widespread boas of South America. *Lore* **44**: 2–9.
- James, C. & Shine, R. (1985). The seasonal timing of reproduction: A tropical-temperate comparison in Australian lizards. *Oecologia (Berl.)* **67**: 464–474.
- King, R. B. (1989). Sexual dimorphism in snake tail length: Sexual selection, natural selection, or morphological constraint? *Biol. J. Linn. Soc.* **38**: 133–154.
- Leamy, L. & Atchley, A. (1984). Static and evolutionary allometry of osteometric traits in selected lines of rats. *Evolution* **38**: 47–54.
- Lovich, J. E. & Gibbons, J. W. (1992). A review of techniques for quantifying sexual size dimorphism. *Growth Dev. Aging* **56**: 269–281.
- Madsen, T. & Shine, R. (1996). Determinants of reproductive output in female water pythons (*Liasis fuscus*, Pythonidae). *Herpetologica* **52**: 146–159.
- Madsen, T., Shine, R., Loman, J. & Håkansson, T. (1993). Determinants of mating success in male adders, *Vipera berus*. *Anim. Behav.* **45**: 491–499.
- Parker, W. S. & Plummer, M. V. (1987). Population ecology. In *Snakes: ecology and evolutionary biology*: 253–301. Seigel, R. A., Collins, J. T. & Novak, S. S. (Eds). New York: Macmillan.
- Pope, C. H. (1975). *The giant snakes*. New York: Alfred A. Knopf.
- Ross, R. (1978). *The python breeding manual*. Stanford, California: Institute for Herpetological Research.
- Ross, R. A. & Marzec, G. (1990). *The reproductive biology of pythons and boas*. Stanford, California: Institute for Herpetological Research.
- Seigel, R. A. & Ford, N. B. (1987). Reproductive ecology. In *Snakes: ecology and evolutionary biology*: 210–252. Seigel, R. A., Collins, J. T. & Novak, S. S. (Eds). New York: Macmillan.
- Shine, R. (1978). Growth rates and sexual maturation in six species of Australian elapid snakes. *Herpetologica* **34**: 73–79.
- 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. (1991). Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *Am. Nat.* **138**: 103–122.
- Shine, R. (1992). Relative clutch mass and body shape in lizards and snakes: Is reproductive investment constrained or optimized? *Evolution* **46**: 828–833.
- Shine, R. (1993). Sexual dimorphism. In *Snakes: ecology and behaviour*: 49–86. Seigel, R. & Collins, J. (Eds). New York: McGraw-Hill.
- Shine, R. (1994a). Allometric patterns in the ecology of Australian snakes. *Copeia* **1994**: 851–867.
- Shine, R. (1994b). Sexual size dimorphism in snakes revisited. *Copeia* **1994**: 326–346.
- Shine, R. (1996). Life-history evolution in Australian snakes: A path analysis. *Oecologia (Berl.)* **107**: 484–489.
- Shine, R. & Charnov, E. L. (1992). Patterns of survival, growth and maturation in snakes and lizards. *Am. Nat.* **139**: 1257–1269.
- Shine, R. & Seigel, R. A. (1996). A neglected life-history trait: clutch-size variance in snakes. *J. Zool. (Lond.)* **239**: 209–233.
- 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*). *J. Herpetol.* **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. *Biol. Cons.* **77**: 125–134.
- Shine, R., Harlow, P., Keogh, J. S. & Boeadi (In press). The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. *Funct. Ecol.*
- Slip, D. J. & Shine, R. (1988). The reproductive biology and mating system of diamond pythons, *Morelia spilota* (Serpentes, Boidae). *Herpetologica* **44**: 396–404.
- Vitt, L. J. & Vangilder, L. D. (1983). Ecology of a snake community in northeastern Brazil. *Amphibia-Reptilia* **4**: 273–296.
- Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**: 687–690.
- Williamson, M. A. (1967). Notes on the growth rate of *Python reticulatus* (Serpentes: Boidae). *Herpetologica* **23**: 130–132.