

Giant snakes in tropical forests: a field study of the Australian scrub python, *Morelia kinghorni*

S. Fearn^{A,C}, L. Schwarzkopf^A and R. Shine^{B,D}

^ASchool of Tropical Biology, James Cook University, Townsville, Qld 4811, Australia.

^BSchool of Biological Sciences A08, University of Sydney, NSW 2006, Australia.

^CCurrent address: 8 Diana Court, Riverside, Launceston, Tas. 7250, Australia.

^DCorresponding author. Email: rics@bio.usyd.edu.au

Abstract. Studies on species that attain very large body sizes provide a powerful opportunity to clarify the ecological correlates and consequences of body size, but logistical obstacles mean that most 'giant' species have attracted little field-based research. The Australian scrub python, *Morelia kinghorni* (= *M. amethistina* in earlier literature), is the largest Australian snake. Our three-year field study in the Tully River Gorge of tropical north-eastern Australia provides the first detailed ecological data on this species. Snakes aggregate in the gorge during the wet season for reproductive activities (combat, courtship and mating), and these aggregations consist primarily of large adult males. Dry-season samples from a nearby road contained more females, and more juvenile animals. Body temperatures of diurnally active pythons averaged 25.2°C, and were highly correlated with air and substrate temperatures. Larger snakes were cooler than smaller conspecifics, perhaps reflecting their slower heating rates. Recapture of marked individuals suggests that pythons of both sexes and all body sizes maintain fixed home ranges, as the distance from initial capture did not increase through time; most animals were recaptured <100 m from their initial capture point, but some dispersed at least 1.5 km. Adult male pythons spanned a massive range in body sizes (1.3–3.76 m in snout–vent length, 0.30–11 kg in mass), and larger males were more likely to engage in combat, exhibit combat-related injuries (bite wounds) and obtain matings. Presumably reflecting the reproductive advantage of larger body size, males attained much larger maximum sizes than did females within our study population.

Introduction

An organism's body size profoundly influences many facets of its biology, ranging from abiotic variables (e.g. the kinds of shelters it can use, its rate of thermal and hydric exchange with the surrounding environment) to predator–prey relationships (e.g. the types and sizes of prey that it consumes, the kinds of predators to which it is vulnerable) through to life-history traits (e.g. fecundity, offspring size, relative body size at maturation, sexual size dimorphism: Calder 1984; Shine *et al.* 1998a). The influence of body size on ecological parameters is likely to be most evident in ectothermic vertebrates (for which rates of thermal exchange determine the range of available body temperatures) and gape-limited predators (because a shift in predator size may induce major changes in prey sizes, prey types and foraging tactics: Arnold 1993; Shine *et al.* 1998b). If such a population contains individuals that span a wide range of body sizes, as occurs in species with large absolute body size, we can also examine body-size effects on ecological and reproductive traits within that population. For all of these reasons, giant snakes provide a powerful opportunity to examine the ways in which absolute body size influences an organism's ecology (Shine *et al.* 1998a).

This research opportunity has rarely been exploited. Although massive snakes in tropical rainforests have always attracted considerable popular attention, and are the subjects of numerous wildlife documentaries and popular books (Pope 1975; Murphy and Henderson 1997), scientific research on these animals has lagged far behind. Logistical obstacles have been primary causes for this disparity; not only because giant snakes are rare and are difficult to capture and handle, but also because they occur in areas far from most research-oriented universities, and often in places where the infrastructure is inadequate to support a major research program. The consequent lack of detailed information on these charismatic animals has significantly affected our ability to understand the true diversity of ecological traits exhibited by squamate reptiles (Murphy and Henderson 1997).

Nonetheless, the situation is changing. Although pioneering studies of snake ecology were heavily biased towards small-bodied cool-temperate taxa (especially Northern Hemisphere viperids and natricine colubrids), recent years have seen significant changes to this situation. Thus, our understanding of snake ecology increasingly derives from a broader phylogenetic, ecological and geographic array of

taxa (Shine and Bonnet 2000). As part of that broadening focus, giant snakes have attracted more scientific attention. For example, quantitative ecological data are now available for large pythons in Indonesia (Shine *et al.* 1998a, 1998b), India (Starin and Burghardt 1992; Goodyear 1994) and Africa (Luiselli and Angelici 1998), anacondas in Venezuela (Rivas and Burghardt 2001), and boa constrictors in Argentina (Bertona and Chiaraviglio 2003). Nonetheless, many taxa remain virtually unstudied. The most poorly known 'giant' snakes have been the scrub pythons (*Morelia amethystina* group) of Australia and south-east Asia (Pope 1975; Murphy and Henderson 1997). Indeed, only recently has the phylogeny of this lineage been examined in any detail, resulting in recognition of five separate species within what had previously been a monotypic taxon (Harvey *et al.* 2000). The present study focuses on the sole Australian taxon within this lineage, to provide the first detailed field-based information on sexual dimorphism, population structure, reproduction and behaviour in this species.

Methods

Study species

The scrub python, *Morelia kinghorni* (= *Morelia amethystina kinghorni* in earlier literature) is by far the largest Australian snake, attaining body lengths >5 m (Barker and Barker 1994; Fearn 2002a; Fearn and Sambono 2000). This relatively slender-bodied, large-headed snake occurs through coastal and near-coastal areas of tropical north-eastern Australia, and feeds on a variety of birds and mammals. Published reports of dietary items include an array of birds and mammals (summarised by Barker and Barker 1994; Fearn 2002b); four animals in our own study disgorged one bird, one bushrat (*Rattus fuscipes*) and two brown bandicoots (*Isodon macrourus*). Available ecological and behavioural data on *M. kinghorni* are limited, and based on anecdotal reports (e.g. Loop *et al.* 1995; Martin 1995; Handasyde and Martin 1996; Sues and Shine 1999), observations of captive specimens (Charles *et al.* 1985; Grow *et al.* 1988; Ross and Marzec 1990; Barker and Barker 1994), and dissection of preserved museum specimens (Shine and Slip 1990). Although valuable, these sources cannot provide an overall picture of scrub python ecology. For example, anecdotal reports will be biased towards exceptionally large individual specimens or spectacular behaviours such as male–male combat; captivity can strongly modify behaviours, growth rates and reproductive output (Seigel and Ford 1991), and museum collections are heavily biased because larger animals are less likely to be preserved (Barker and Barker 1994).

Study area and methods

Between May 2000 and July 2003, specimens of *M. kinghorni* were collected along two transects, meeting at a central point (the Kareeya Power Station) in the vicinity of the Tully River Gorge (17°46'S, 145°35'E), 40 km north-west of Tully in north Queensland. The local area has very high annual precipitation (mean = 3721 mm per annum), with ~50% of this rain falling during a three-month wet season (January–March). Temperatures are mild to hot year-round (diel range 15–25°C during the dry season, 25–32°C during the wet season: Australian Bureau of Meteorology). During the wet season, snakes were collected nocturnally by driving along the terminal 20 km of Cardstone Road, which runs north-west from Tully, following the Tully River, and terminates at the Kareeya Power Station 1.5 km from the river's source at the foot of Tully Falls. During the dry season, snakes

were captured by walking a 1.5-km transect along the western edge of the Tully River Gorge upstream from the power station. Aggregations of *M. kinghorni* occur seasonally on the rocky shoreline of the gorge (as recorded for other sites by Worrell 1958; Shine 1991). Both the Cardstone Road and Tully River Gorge transects are bordered on both sides by notophyll vine forest. We used these two transects at these two times of year because access to the gorge was impossible during the wet season for safety reasons (flooding, steep cliffs and slippery rocks), and snakes were never seen on Cardstone Road during the dry season.

We recorded dates and times of capture, and the snake's activity and location. Immediately after capture, the sex of each snake was determined by eversion of hemipenes, and its snout–vent length (SVL) and tail length were measured by stretching the animal out along a tape measure. The snake was also weighed, and permanently identified with a Passive Integrated Transponder (PIT) tag injected into dorso-lateral musculature anterior to the vent. Shaded ambient (air) temperature was taken 1.5 m above ground at the point of capture, and substrate temperature was taken on the place the snake was first seen. Body temperatures were taken by inserting the digital thermometer into the snake's cloaca. All snakes were released at their site of capture after processing.

Results

Body sizes and sexual size dimorphism

On the basis of dissection of preserved snakes and records from captive animals, male scrub pythons mature at ~1.29 m SVL, and females at 2.27 m SVL (Shine and Slip 1990; Barnett 1993). We assigned snakes as adult or juvenile on the basis of these size criteria. In total, we collected 80 different adult males (captured a total of 122 times, up to 5 captures per snake), 24 different adult females (total of 37 captures, up to 5 per snake), 50 subadult females (up to 4 captures per snake) and 13 juveniles (≤12 months old, based on SVL; not individually marked). Our analyses of sexual size dimorphism (below) treat each capture record as an independent data point because many snakes grew significantly between captures and hence this approach best reflects the size spectra encountered in the field. None of our major conclusions are modified by restricting analysis to a single record per individual.

Male and female scrub pythons are broadly similar in body shape: thus, mass relative to SVL did not differ between the sexes (ANCOVA with sex as factor, $\ln(\text{SVL})$ as covariate, $\ln(\text{mass})$ as dependent variable: interaction, $F_{1,194} = 0.34$, $P = 0.56$; intercepts, $F_{1,195} = 0.86$, $P = 0.35$). However, males have longer tails than do females at the same body length (restricting analysis to animals with complete tails, ANCOVA with sex as factor, SVL as covariate, tail length as dependent variable: interaction, $F_{1,142} = 17.07$, $P < 0.0001$). Partial tail loss occurred with equal frequency (21%) in males and females (17 of 80 males; 15 of 72 females).

Male scrub pythons mature at smaller body sizes than females (1.29 v. 2.27 m SVL, from dissections by Shine and Slip 1990; see also Barnett 1993 for data on captive snakes) but males grow to much greater sizes in terms of both SVL and mass. Fig. 1 plots the size distributions of captured snakes. Adult male scrub pythons in our sample averaged 2.91 m SVL (5.1 kg) whereas adult females averaged 2.68 m

(3.4 kg) (SVL, $F_{1,157} = 5.75$, $P < 0.02$; mass, $F_{1,157} = 12.46$, $P < 0.001$). Applying the method of Lovich and Gibbons (1992) to these data yields a sexual size dimorphism index of -0.34 . However, this simple calculation ignores the fact that males matured at smaller sizes than females, and thus the estimate of mean male size incorporates many small animals (well below the size at female maturation); adult males thus covered a much wider size range than did adult females, and the largest 25% of animals were all males (Fig. 1).

Mean body lengths differed between localities (seasons of collection) as well as between sexes. Snakes collected in the gorge during the dry season averaged larger than those found on the road during the wet season (Fig. 2) (two-factor ANOVA with sex and location as factors, SVL as the dependent variable: sex effect, $F_{1,217} = 55.38$, $P < 0.0001$; location effect, $F_{1,217} = 127.06$, $P < 0.0001$). This geographic and seasonal difference in mean body sizes was evident in both

sexes at both locations (interaction sex \times location, $F_{1,217} = 1.29$, $P = 0.26$). The body condition of captured snakes also differed between these two locations. Although mass relative to body length did not differ between the sexes in the combined sample (above), males were in better condition in the gorge than on the road whereas the reverse was true for females (Fig. 3) (ANOVA with sex and location as factors: interaction sex \times location, $F_{1,200} = 5.06$, $P < 0.03$).

Sex ratio

Overall numbers of captures of males and females were similar (127 captures of males, 91 of females, v. a null of 50% male, $\chi^2_1 = 5.94$, $P < 0.02$; but deleting recapture records, $n = 82$ males, 74 females, so $\chi^2_1 = 0.41$, $P > 0.50$). Nonetheless, sex ratios differed between our two collection localities. Males dominated in samples from the gorge (90 of 135 records, 55 of 82 individuals) but females were more common

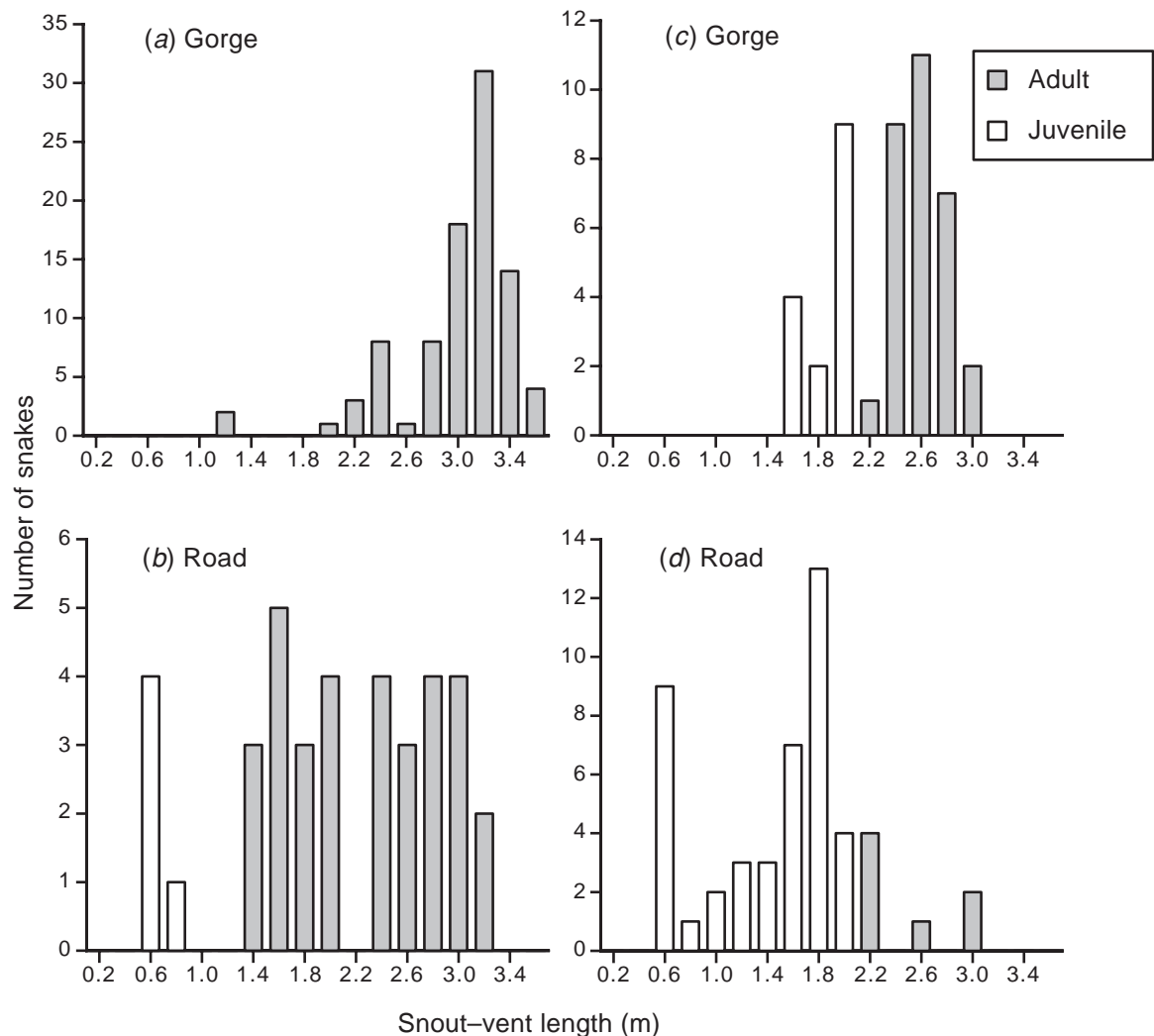


Fig. 1. Frequency distributions for snout-vent lengths of male and female scrub pythons (*Morelia kinghorni*) captured at two areas (Tully River Gorge and Cardwell Road) in tropical north-eastern Australia. Assessment of sexual maturity was based on body sizes of smallest mature animals in museum dissections (Shine and Slip 1990).

in samples taken along the road (49 of 86 records, 44 of 74 individuals) (using all records, $\chi^2_1 = 11.07$, $P < 0.001$; based on initial captures only, $\chi^2_1 = 10.00$, $P < 0.002$).

Activity patterns

The numbers of snakes collected varied significantly among months, with >60% of the total sample being collected in a three-month period each year (139 of 222 during June–August). The sex ratio also varied significantly among months ($\chi^2_{11} = 21.38$, $P < 0.03$), reflecting the seasonal shift documented above.

If we restrict attention to snakes collected in the gorge (because road-driving was conducted only at night), hourly variation in sex ratios was statistically significant ($\chi^2_7 = 14.69$, $P < 0.04$), reflecting a trend for males to be found mostly in the morning whereas females were found throughout the day (Fig. 4).

Thermal biology

Body temperatures of snakes ranged from 17.1 to 35.1°C (for gorge snakes only, because they were captured during day-

light hours when they were able to regulate their own temperatures: mean = 25.2, s.d. = 0.45°C), averaging higher than either air ($19.91 \pm 0.27^\circ\text{C}$) or substrate ($23.71 \pm 0.53^\circ\text{C}$) temperatures in this respect (paired *t*-tests: body *v.* air, $t_{95} = 13.68$, $P < 0.0001$; body *v.* substrate, $t_{95} = 3.17$, $P < 0.003$; see Fig. 5). To identify sources of variation in body temperatures, we used ANCOVA with sex and location (road *v.* gorge) as factors, and ambient temperatures and snake body size (SVL) as covariates. No interaction terms were significant (all $P > 0.12$) so we deleted these terms and recalculated main effects. Unsurprisingly, body temperatures were strongly influenced by air temperature ($F_{1,155} = 85.96$, $P < 0.0001$). At the same body size, males and females had similar body temperatures relative to air temperature ($F_{1,155} = 1.26$, $P = 0.26$) but road-caught snakes were warmer than gorge snakes ($F_{1,155} = 32.46$, $P < 0.0001$) and larger snakes were cooler than smaller conspecifics (SVL effect, $F_{1,155} = 6.17$, $P < 0.015$). Identical conclusions were derived from analyses using substrate rather than air temperature as a covariate.

Because we recorded whether or not snakes in the gorge were basking at the time of capture, we can also examine the determinants of this behaviour. Multiple logistic regression with 'basking or not' as the dependent variable, revealed that whether or not a snake was basking when sighted varied with substrate temperature ($\chi^2_1 = 14.77$, $P < 0.0001$; basking occurred when substrates were warmer) and time of day ($\chi^2_1 = 5.19$, $P < 0.03$; basking was most common during the morning hours), but did not differ between the sexes ($\chi^2_1 = 0.62$, $P = 0.43$) or according to body length ($\chi^2_1 = 2.22$, $P = 0.14$).

Movements

We recaptured marked pythons on 61 occasions (38 recaptures of 25 males, 23 recaptures of 13 females) over inter-



Fig. 2. Mean snout-vent lengths and body masses (and associated standard errors) for male and female scrub pythons collected in two adjacent areas: in the Tully River Gorge (during the dry season) and along Cardstone Road (during the wet season).

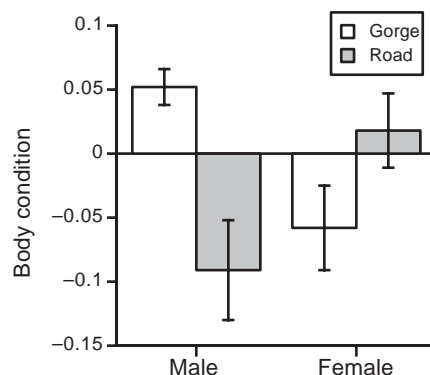


Fig. 3. Mean body condition (and associated standard errors) for male and female scrub pythons collected in two adjacent areas: in the Tully River Gorge (during the dry season) and along Cardstone Road (during the wet season). Body condition indices are residual scores from the linear regression of \ln -transformed (body mass) *v.* \ln (snout-vent length) (to show patterns), but statistical analyses in the text are based on analysis of covariance.

vals of 1–696 days (mean = 126.9 days). Most (38 of 61 = 62%) displacements were <100 m from the previous capture; these relatively short-distance displacements were recorded from captures averaging 105 days apart (range = 1–696 days). Overall, the range of displacement distances recorded was similar in the two sexes (males, 0–1.3 km; females, 0–1.5 km). Analysis showed that mean displacement distance was not significantly affected by the python's sex (ANCOVA: $F_{1,56} = 0.19$, $P = 0.67$), its body length ($F_{1,56} = 1.89$, $P = 0.17$), by the interval between capture and recaptures ($F_{1,56} = 0.92$, $P = 0.34$) nor by any interaction between these factors (all $P > 0.05$). The only significant difference apparent from our analyses was that distances moved were greater (relative to the time between captures) for female snakes captured on the road than for females captured in the gorge ($F_{1,19} = 15.88$, $P < 0.001$; means 550 m for 5 snakes v. 22.3 m for 18 snakes). Males showed the same pattern, but it fell well short of statistical significance ($F_{1,33} = 0.92$, $P = 0.34$).

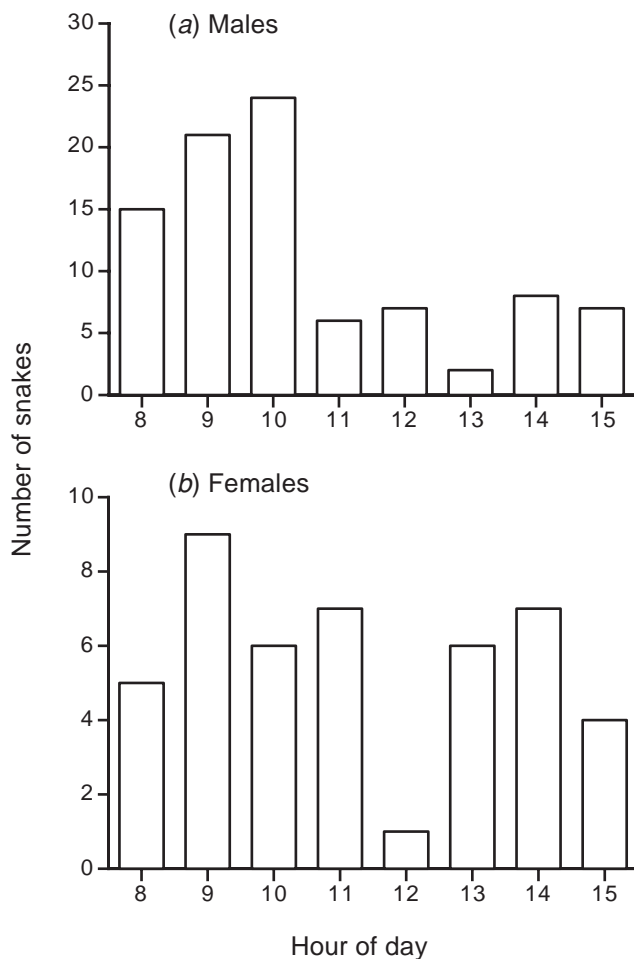


Fig. 4. Times of day at which male and female scrub pythons were collected in the Tully River Gorge during the dry season.

Reproductive behaviour

In the course of the study, we recorded two instances of copulation and one of male–male combat. One copulation (male 3.61 m SVL, 9.8 kg; female 2.74 m, 5 kg) was recorded at 1025 hours on 16 June 2001. The other was inferred from the close proximity of a male (3.76 m; 9.9 kg) and female (2.8 m, 4.5 kg) on 8 July 2000; blood in the female's cloaca provided strong evidence of recent mating (Charles *et al.* 1985). The two males found in combat at 1445 hours on 5 Sept 2000 were also very large (SVLs 3.45 and 3.36 m; masses 8.2 and

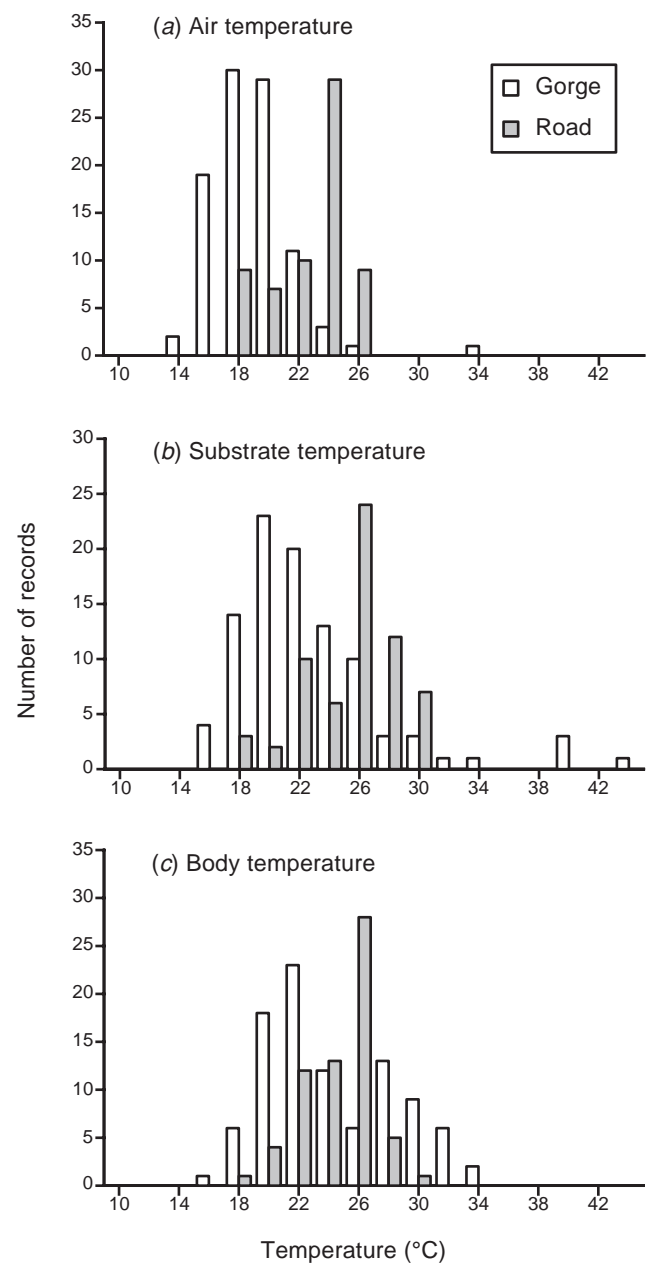


Fig. 5. Frequency distributions for air temperatures, substrate temperatures and body temperatures (and associated standard errors) taken at the time of capture of scrub pythons (*Morelia kinghorni*).

8.0 kg). Eight males showed obvious combat injuries, inflicted by bites from rival males (Charles *et al.* 1985; Sues and Shine 1999). These males averaged larger (range 3.0–3.6 m, 5.1–11 kg) than 113 males without overt bite-wounds (range 1.39–3.76 m, 0.38–10 kg).

We used multiple logistic regression to ask whether a male's body size affected his probability of being found in combat, mating, or showing combat injuries. Despite low sample sizes, all of these patterns were significant: larger males were more likely than smaller adult males to obtain matings (likelihood ratio test: $\chi^2_1 = 14.54$, $P < 0.0001$), to engage in combat ($\chi^2_1 = 2.84$, $P = 0.09$; but because the *a priori* prediction is that successful males should be larger, we can use a one-tailed test of the hypothesis, so $P = 0.045$), and exhibit bite marks from rival males ($\chi^2_1 = 6.45$, $P < 0.04$).

Discussion

Although our sample sizes for some traits were relatively small, our dataset provides the first detailed information on ecology of scrub pythons in the field. The data clarify many facets of the behavioural ecology of these giant pythons, including population structure, seasonal habitat use, movements, thermal biology, mating system and sexual dimorphism. Below, we discuss these aspects in light of previous literature, and with particular reference to the ecological correlates of body size.

Species of snakes with a larger absolute mean adult body size also have a wider size range of body sizes overall, and among adult specimens (Shine *et al.* 1998a). Larger snake species have offspring that are smaller relative to adult body size; these taxa mature at a lower proportion of maximum body size than do smaller species, and the proportion of juvenile animals is lower in males than in females (Shine *et al.* 1998a). Our data on scrub pythons fit all of these patterns. On the basis of capture rates, the population of scrub pythons in our study area consisted mostly of adult males and adult plus juvenile females. The sex divergence in the proportion of adult animals reflects sex differences in the body size (and presumably age) at sexual maturation, rather than by a sex bias at hatching. Wet-season samples included several animals close to hatchling size (63.3–72.9 cm SVL; Barker and Barker 1994) and then a peak at close to 2 m (Fig. 1). Captive snakes grow to ~2 m length in one year (Barnett 1993; Barker and Barker 1994) and thus these animals presumably are one-year-olds. Hence, scrub pythons mature rapidly despite their large body size: we infer that male scrub pythons in our population mature at one year of age, and females at two years. Captive snakes continue to grow rapidly, with one captive attaining 4.8 m in four years (Barnett 1993).

The times of day at which we collected pythons largely reflect our own activity schedules, which were enforced by logistics (e.g. it was too dangerous to traverse the gorge at night) as well as snake activity (e.g. we rarely saw pythons

along the road by day). Within the gorge sample, however, the sex difference in activity times (Fig. 4) cannot be attributed to sampling artefacts. Females may remain active through the afternoon (or, at least, in exposed situations) to maintain high and constant temperatures to accelerate vitellogenesis and/or embryogenesis, as has been observed in many other snake species (e.g. Gier *et al.* 1989; Blazquez 1995). The lower body temperatures of larger snakes may be due to sex differences also (because males are larger than females) or, alternatively, the slower heating rates of larger animals (Ayers and Shine 1997) may require more prolonged basking.

Recaptures showed that these snakes usually moved relatively short distances (generally <100 m, but occasionally up to 1.5 km), despite their large body sizes. Displacement did not increase with time, suggesting that each animal lives within a relatively fixed home range, as is generally true for previously studied snakes (Gregory *et al.* 1987). Our recaptures were too infrequent to quantify day-to-day movements; presumably, some animals traversed long distances before being recaptured at sites close to their original location. Perhaps the most interesting question about movement patterns in this population is the seasonal shift from the road to the gorge. Pythons may occur in the gorge during the wet season also, but frequent severe flooding means that most animals must move to higher ground. In keeping with this inference, we never saw snakes along the road during the dry season. However, only a single snake (a 3.3-m male) was recorded to move between these two sites during our study.

Previous reports of dry-season aggregations of scrub pythons in sites like the Tully River Gorge generally have posited a thermoregulatory function for this behaviour, with snakes leaving the dense wet forest to bask in sunny exposed rocky habitats during the coldest time of the year (Worrell 1958; Shine 1991). However, the strong shift in sex ratios and body sizes between our wet-season and dry-season samples (Fig. 2) suggests a different explanation. The snakes encountered in the gorge during the dry season were mostly males, especially large animals, and we recorded both mating and male–male combat in these situations. Thus, we suggest that the dry-season aggregations of scrub pythons primarily reflect reproductive activity (see also Barker and Barker 1994). Thermal advantages may well explain why reproductive females move to these sites (note that females were found in the open over a larger part of the day than were males, and that smaller snakes (thus, females) generally were warmer than larger animals). In turn, the concentration of these females would serve to attract reproductive males to the area. The absence of juvenile males from these sites suggests that thermoregulation alone is not the causal factor drawing snakes to the gorge. The elevated body condition of males captured in the gorge (Fig. 3) fits well with the idea that these animals are in reproductive condition, but the lower body condition of females is surprising in this respect,

and suggests that non-reproductive as well as reproductive female snakes are present in the gorge during the dry season.

Male–male combat has been previously reported for scrub pythons, both in captivity (Barker and Barker 1994) and in the field (Sues and Shine 1999; Lloyd and Fearn 2004). Nonetheless, actual physical contests may be rare: in 90 encounters with male pythons in the gorge, we found males in physical combat only once. The restriction of bite wounds to large snakes suggests that small adult males may avoid physical confrontations with rivals. This inference is supported by previous records of male–male combat in scrub pythons and in the closely related carpet python, *Morelia spilota*; in all cases, the only animals involved were unusually large males (Shine and Fitzgerald 1995; Sues and Shine 1999; Lloyd and Fearn 2004). Given that larger males almost invariably win combat bouts in the few snake species studied to date (Madsen *et al.* 1993; Schuett 1997), a small male may be unlikely to defeat a larger opponent (potentially, a male more than 10-fold heavier than himself) and may face substantial risk of injury from such a battle. Accordingly, male mating tactics may shift with body size, with smaller males searching for unaccompanied females, whereas larger conspecifics are prepared to battle for mating opportunities. Similar ontogenetic shifts in male tactics may be widespread in snakes (Madsen *et al.* 1993; Shine *et al.* 2001).

The enhanced mating opportunities afforded by larger body size in males may have been a critical selective factor favouring the evolution of extreme male-biased sexual size dimorphism in *M. kinghorni*. Adult males were 34% longer, on average, than adult females, and 50% heavier. Thus, the degree of male-biased SVL dimorphism in this population (34%) is higher than in most other snake species; for example, it is exceeded by only two taxa (both colubrids) in Shine's (1994) compilation of sexual size dimorphism (SSD) in 375 species of snake. In other respects, males and females of *M. kinghorni* resemble previously studied snake species; for example, male and female snakes generally are similar in overall body shape, but males have relatively longer tails than conspecific females (King 1989).

Phylogenetically based analyses show that male-biased SSD among snakes is strongly associated with male–male combat (Shine 1994) and that, in turn, male–male combat is most common in lineages that constrict their prey (Schuett *et al.* 2001). *M. kinghorni* fits both of these patterns, and the extreme SSD may relate to the fact that combat in this population is more vigorous, and more capable of causing severe injury, than is the case for most other snake species (Sues and Shine 1999). Even our relatively small sample was able to detect size-related shifts among males in combat, injury, and mating success. This is one of only a few empirical demonstrations of a relationship between body size and reproductive success in free-ranging male snakes (Madsen *et al.* 1993; Brown and Weatherhead 1999; Shine *et al.* 2000; Blouin-Demers *et al.* 2004). The degree of sex-based divergence in

mean adult body size within snakes also is influenced by niche partitioning, and thus upon local prey resources (Pearson *et al.* 2002a). Because the energetically feasible range of snake body sizes depends upon prey sizes, the two sexes cannot attain very different body sizes unless there is a broad size range of potential prey sizes (Madsen and Shine 1993). Thus, local prey resources constrain the SSD generated by sexual selection in geographically isolated populations of carpet pythons exposed to different prey spectra (Pearson *et al.* 2002a). The broad mammal diversity in tropical Queensland thus may have facilitated body-size divergence between male and female scrub pythons.

Although the degree of sex divergence in mean adult body sizes is influenced by ecological factors, male-biased SSD in snakes is seen only under strong sexual selection exerted via male–male combat (Shine 1994). The extreme male-biased SSD of scrub pythons thus accords well with adaptationist arguments about sexual selection and the mating system, and with previous research on the closely related carpet python, *M. spilota*. Mating systems and SSD vary geographically within the latter species: males attain larger mean adult body sizes than females in tropical populations where male–male combat is common, but do not grow as large as females in temperate-zone populations where male–male combat is absent (Shine and Fitzgerald 1995; Pearson *et al.* 2002b). Although the association between combat and male-biased dimorphism is unusually clear within this clade, the relationship between SSD and absolute body size is more confusing. Among snakes in general, larger absolute body size is correlated with an increasingly male-biased SSD, and our data for *M. kinghorni* fit almost perfectly with the situation predicted for a species of its mean adult body size (Shine *et al.* 1998a). Remarkably, however, empirical evidence on other pythonids reveals the reverse pattern, whereby SSD becomes increasingly female-biased, not male-biased, in larger species (Shine *et al.* 1998a). Clearly, allometric patterns in SSD can vary even between closely related (confamilial) lineages, and pythons may provide an excellent model system in which to investigate such divergences.

In summary, field research on giant snakes poses significant logistical obstacles, but can provide valuable insights. The ecology of these charismatic animals is of interest not simply because they attract massive public interest, but also because they play an important ecological role as top predators in complex tropical food webs. Additionally, even modest datasets on these unusually large animals can clarify the ecological correlates of absolute body size, and thus identify allometric patterns in both intraspecific and interspecific comparisons. Giant snakes will never be popular study organisms for field-based researchers, but information on these spectacular creatures is essential if we are ever to comprehend the full diversity of ecological tactics within squamate reptiles.

Acknowledgments

Sincere thanks to our field assistants, especially Dane Trembath, Damian King, David Frier and Joe Sambono; and to the staff of the Kareeya Power Station, particularly Rodney Dodds, for assistance and accommodation. Funding was supplied by the Rainforest CRC, the Peter Rankin Trust Fund for Herpetology, and the Australian Research Council. This work was conducted under Queensland Department of Environment permits N0/001446/98/SAB and F1/000330/00/SAA and Ethics Review Committee number A661_01.

References

- Arnold, S. J. (1993). Foraging theory and prey-size-predator-size relations in snakes. In 'Snakes. Ecology and Behavior'. (Eds R. A. Seigel and J. T. Collins.) pp. 87–116. (McGraw-Hill: New York.)
- Ayers, D. Y., and Shine, R. (1997). Thermal influences on foraging ability: body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*. *Functional Ecology* **11**, 342–347. doi:10.1046/j.1365-2435.1997.00093.x
- Barker, D. G., and Barker, T. M. (1994). 'Pythons of the World. Volume 1. Australia.' (Advanced Vivarium Systems: Lakeside, CA.)
- Barnett, B. (1993). The amethystine python (*Morelia amethystina*). Captive keeping, reproduction, and growth. *Monitor* **4**, 77–128.
- Bertona, M., and Chiaraviglio, M. (2003). Reproductive biology, mating aggregations, and sexual dimorphism of the Argentine boa constrictor (*Boa constrictor occidentalis*). *Journal of Herpetology* **37**, 510–516.
- Blazquez, M. C. (1995). Body temperature, activity pattern and movements by gravid and non-gravid females of *Malpolon monspessulanus*. *Journal of Herpetology* **29**, 264–266.
- Blouin-Demers, G., Gibbs, H. L., and Weatherhead, P. J. (2004). Genetic evidence for sexual selection in black ratsnakes (*Elaphe obsoleta*). *Animal Behaviour* **XXX**, 000–000.
- Brown, G. P., and Weatherhead, P. J. (1999). Female distribution affects mate searching and sexual selection in male northern water snakes (*Nerodia sipedon*). *Behavioral Ecology and Sociobiology* **47**, 9–16. doi:10.1007/s002650050644
- Calder, W. A. (1984). 'Size, Function and Life History.' (Harvard University Press: Boston, MS.)
- Charles, N., Field, R., and Shine, R. (1985). Notes on the reproductive biology of Australian pythons, genera *Aspidites*, *Liasis* and *Morelia*. *Herpetological Review* **16**, 45–48.
- Fearn, S. (2002a). Notes on a maximal sized scrub python *Morelia amethystina* (Serpentes: Pythonidae) from Kuranda, north east Queensland. *Herpetofauna* **32**, 2–3.
- Fearn, S. (2002b). *Morelia amethystina* (scrub python). Diet. *Herpetological Review* **33**, 58–59.
- Fearn, S., and Sambono, J. (2000). A reliable size record for the scrub python *Morelia amethystina* (Serpentes: Pythonidae) in north east Queensland. *Herpetofauna* **30**, 2–6.
- Gier, P. J., Wallace, R. L., and Ingerman, R. L. (1989). Influence of pregnancy on behavioral thermoregulation in the Northern Pacific rattlesnake *Crotalus viridis oreganus*. *Journal of Experimental Biology* **145**, 465–469.
- Goodyear, N. C. (1994). *Python molurus bivittatus* (Burmese python). Movements. *Herpetological Review* **25**, 71–72.
- Gregory, P. T., Macartney, J. M., and Larsen, K. W. (1987). Spatial patterns and movements. In 'Snakes: Ecology and Evolutionary Biology'. (Eds R. A. Seigel, J. T. Collins, and S. S. Novak.) pp. 366–395. (McGraw-Hill: New York.)
- Grow, D., Wheeler, S., and Clark, B. (1988). Reproduction in the amethystine python *Python amethystinus kinghorni* at the Oklahoma City Zoo. *International Zoo Yearbook* **27**, 241–244.
- Handasyde, K. A., and Martin, R. W. (1996). Field observations on the common striped possum (*Dactylopsila trivirgata*) in north Queensland. *Wildlife Research* **23**, 755–766.
- Harvey, M. B., Barker, D. G., Ammerman, L. K., and Chippindale, P. T. (2000). Systematics of pythons of the *Morelia amethystina* complex (Serpentes: Boidae) with the description of three new species. *Herpetological Monograph* **14**, 139–185.
- King, R. B. (1989). Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint? *Biological Journal of the Linnean Society* **38**, 133–154.
- Lloyd, R., and Fearn, S. (2004). Intraspecific combat in free ranging scrub pythons *Morelia kinghorni* (Serpentes: Pythonidae) in north-east Queensland. *Herpetofauna* **XXX**, 000–000.
- Loop, K. A., Millar, J. D., and Pollard, D. (1995). Observations of the amethyst python (*Morelia amethystina*) feeding on rainbow bee-eaters (*Merops ornatus*). *Memoirs of the Queensland Museum* **38**, 504.
- Lovich, J. E., and Gibbons, J. W. (1992). A review of techniques for quantifying sexual size dimorphism. *Growth, Development, and Aging* **56**, 269–281.
- Luiselli, L., and Angelici, F. M. (1998). Sexual size dimorphism and natural history traits are correlated with intersexual dietary divergence in royal pythons (*Python regius*) from the rainforests of south-eastern Nigeria. *Italian Journal of Zoology* **65**, 183–185.
- Madsen, T., and Shine, R. (1993). Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution* **47**, 321–325.
- Madsen, T., Shine, R., Loman, J., and Håkansson, T. (1993). Determinants of mating success in male adders, *Vipera berus*. *Animal Behaviour* **45**, 491–499. doi:10.1006/anbe.1993.1060
- Martin, R. W. (1995). Field observation of predation on Bennett's tree-kangaroo (*Dendrolagus bennettianus*) by an amethystine python (*Morelia amethystina*). *Herpetological Review* **26**, 74–76.
- Murphy, J. C., and Henderson, R. W. (1997). 'Tales of Giant Snakes: A Historical Natural History of Anacondas and Pythons.' (Krieger: Malabar, FL.)
- Pearson, D., Shine, R., and How, R. (2002a). Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*). *Biological Journal of the Linnean Society* **77**, 113–125. doi:10.1046/j.1095-8312.1999.00075.x
- Pearson, D., Shine, R., and Williams, A. (2002b). Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia* **131**, 418–426. doi:10.1007/s00442-002-0917-5
- Pope, C. H. (1975). 'The Giant Snakes.' (Alfred A. Knopf: New York.)
- Rivas, J., and Burghardt, G. M. (2001). Understanding sexual size dimorphism in snakes: wearing the snake's shoes. *Animal Behaviour* **62**, F1–F6. doi:10.1006/anbe.2001.1755
- Ross, R. A., and Marzec, G. (1990). 'The Reproductive Biology of Pythons and Boas.' (Institute for Herpetological Research: Stanford, CA.)
- Schuett, G. W. (1997). Body size and agonistic experience affect dominance and mating success in male copperheads. *Animal Behaviour* **54**, 213–224. doi:10.1006/anbe.1996.0417
- Schuett, G. W., Gergus, E. W. A., and Kraus, F. (2001). Phylogenetic correlation between male-male fighting and mode of prey subjugation in snakes. *Acta Ethologica* **4**, 31–49. doi:10.1007/s102110100043
- Seigel, R. A., and Ford, N. B. (1991). Phenotypic plasticity in the reproductive characteristics of an oviparous snake, *Elaphe guttata*: implications for life history studies. *Herpetologica* **47**, 301–307.

- Shine, R. (1991). 'Australian Snakes. A Natural History.' (Reed Books: Sydney.)
- Shine, R. (1994). Sexual size dimorphism in snakes revisited. *Copeia* **1994**, 326–346.
- Shine, R., and Bonnet, X. (2000). Snakes: a new “model organism” in ecological research? *Trends in Ecology & Evolution* **15**, 221–222. doi:10.1016/S0169-5347(00)01853-X
- Shine, R., and Fitzgerald, M. (1995). Variation in mating systems and sexual size dimorphism between populations of the Australian python *Morelia spilota* (Serpentes: Pythonidae). *Oecologia* **103**, 490–498. doi:10.1007/BF00328688
- Shine, R., and Slip, D. J. (1990). Biological aspects of the adaptive radiation of Australasian pythons (Serpentes: Boidae). *Herpetologica* **46**, 283–290.
- Shine, R., Harlow, P. S., Keogh, J. S., and Boeadi, X. (1998a). The allometry of life-history traits: insights from a study of giant snakes (*Python reticulatus*). *Journal of Zoology* **244**, 405–414. doi:10.1017/S0952836998003112
- Shine, R., Harlow, P. S., Keogh, J. S., and Boeadi, X. (1998b). The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. *Functional Ecology* **12**, 248–258. doi:10.1046/j.1365-2435.1998.00179.x
- Shine, R., Olsson, M. M., Moore, I., Le Master, M. P., Greene, M., and Mason, R. T. (2000). Body size enhances mating success in male gartersnakes. *Animal Behaviour* **59**, F4–F11. doi:10.1006/anbe.1999.1338
- Shine, R., O'Connor, D., LeMaster, M. P., and Mason, R. T. (2001). Pick on someone your own size: ontogenetic shifts in mate choice by male garter snakes result in size-assortative mating. *Animal Behaviour* **61**, 1133–1141. doi:10.1006/anbe.2001.1712
- Starin, E., and Burghardt, G. M. (1992). African rock pythons (*Python sebae*) in the Gambia: observations on natural history and interactions with primates. *Snake* **24**, 50–62.
- Sues, L., and Shine, R. (1999). *Morelia amethystina* (Australian scrub python). Male–male combat. *Herpetological Review* **30**, 102.
- Worrell, E. (1958). 'Song of the Snake.' (Angus and Robertson: Sydney.)

Manuscript received 20 September 2004, accepted 16 March 2005