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Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae)

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Abstract Unusually among reptiles, Australian carpet pythons (*Morelia spilota*) display substantial geographic variation in mating systems and sexual size dimorphism. We studied a population of the south-western subspecies (*M. s. imbricata*) of this widely distributed taxon, on Garden Island near Perth, Western Australia. Our data greatly expand the range of variation previously documented for populations of this species. Unlike eastern Australian populations where sex differences in mean adult body size are relatively minor [$<10\%$ in snout-vent length (SVL), $<30\%$ in mass], female *M. s. imbricata* grow to over twice the length and more than 10 times the mass of adult males. Mean adult size averages 104 cm SVL (305 g) for males versus 214 cm SVL (3.9 kg) for females. This sex difference is a consequence of cessation in growth by males, in turn due to a reduced rate of feeding. Males display low feeding rates even in captivity, suggesting that their “dwarf” sizes reflect genetic control rather than local prey availability. Observations of free-ranging snakes suggest that males do not engage in overt agonistic interactions during the mating season, and that larger body size does not enhance male mating success. These results fit well with previous interpretations of the relationship between mating systems and sexual size dimorphism in snakes, including other populations of carpet pythons. *M.s. spilota* displays the greatest geographic variation in sexual size dimorphism yet recorded for any vertebrate species.

Keywords Intraspecific geographic variation · Mating system · Reptile · Sexual selection · Snake

Introduction

In recent years, evolutionary biologists have changed the ways in which they attempt to test ideas about adaptation. Broad interspecific comparisons have been largely replaced by methods that take phylogeny into account when testing adaptationist hypotheses (e.g. Harvey and Pagel 1991). These comparative approaches focus upon phylogenetic changes in character states, to overcome the problem that many character states show strong phylogenetic conservatism. That is, organisms display many traits because of events during their ancestry, not as adaptations to current conditions. If we want to understand why a trait has evolved, the strongest evidence will come from comparisons between closely related taxa that differ in the trait of interest but not in other traits.

This methodological shift has highlighted the significance of intraspecific variation. If two populations of the same species differ significantly in some biological trait, they provide an ideal opportunity to understand the causes and consequences of that phylogenetic transition. Recent research has identified many “model systems” of this kind and provided important insights into the biological significance of a range of traits. Reptiles have been the study organisms for several such studies and have provided examples of intraspecific variation in traits such as body sizes, modes of reproduction, and offspring sizes (Andrews 1979; Forsman 1991; Heulin et al. 1999).

Analyses of mating systems and sexual size dimorphism (SSD) in reptiles have generally relied upon much broader comparisons (e.g. Fitch 1981; King 1989), but at least one species of snake has been found to exhibit geographic variation in both of these traits (Shine and Fitzgerald 1995). In populations of carpet pythons (*Morelia spilota*) from north-eastern Australia, males grow larger than females and exhibit vigorous male-male combat during the breeding season. In contrast, populations of the same species from south-eastern Australia have males slightly smaller than females, with no evidence of agonistic interactions among breeding males (Slip and Shine 1988a; Shine and Fitzgerald 1995).

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The correlation between mating system and SSD fits well with sexual-selection theory (e.g. Darwin 1871; Andersson 1994) and with the results of broader (inter-specific) comparisons (Shine 1994). The intraspecific lability within *M. spilota* means that mating systems and dimorphism in other populations of this taxon are of interest as well. This species is well-suited to such analyses, because it occurs as a series of morphologically distinctive forms (often accorded subspecific status) across a large geographic area in Australia (e.g. Barker and Barker 1994). In the present study we present information on the south-western form of *M. spilota* and compare it to previously studied populations from eastern Australia.

Materials and methods

Study species

South-western carpet pythons (*Morelia spilota imbricata*) are moderately sized (up to 2.5 m snout-vent length, SVL) non-venomous snakes, distributed in the south-western corner of Western Australia, along the southern coastline of both Western Australia and South Australia, and on several offshore islands (Smith 1981; Schwaner et al. 1988; Pearson 1993; L. Rawlings, personal communication).

The ecology of *M. s. imbricata* is poorly known. It occurs in a variety of habitats ranging from coastal heathland, open woodlands, rock outcrops and tall forests to semi-arid shrublands (Pearson 1993; Barker and Barker 1994). This snake feeds on reptiles, birds and small mammals, including prey items as large as small wallabies (Wilson and Knowles 1988). The only information on reproduction comes from observations of captive specimens. Mating has been recorded in September and November, with egg deposition in early January (Bush 1988, 1997). Like other members of the genus *Morelia*, females typically produce large clutches (16–17, $n=3$; Bush 1997).

Study area

Our study was conducted on Garden Island (32°16'S, 115°40'E), 45 km south-west of the city of Perth. The island is of moderate size, extending north-south for approximately 10 km and reaching 2 km at its widest point (Bell et al. 1987). It occupies a total area of around 1,100 ha (Marchant and Abbott 1981) and was connected to the mainland prior to a rise in sea level 6,000–7,000 years ago (Main 1961). The island consists of a basement of limestone overlain by white sands, which in places form large dunes. Around the fringe of Garden Island, limestone outcrops as eroded sea cliffs and partially submerged reefs (McArthur and Bartle 1981).

Despite a brief period of occupation by European settlers in 1829, Garden Island has been little impacted by development until recent times. A causeway linking the island to the mainland was completed in 1973 and a naval base, HMAS Stirling, was commissioned on the island in 1978. About 20% of the island is currently devoted to buildings or other naval infrastructure (McArthur 1966). The remainder is managed for nature conservation and public recreation.

The island experiences a mild maritime climate, with hot summer days tempered by afternoon south-westerly winds. Winters are wet, with 64% of annual rainfall (average total 715 mm) falling between May and August (Bureau of Meteorology, Perth). The mean maximum and minimum temperatures for the hottest month (February) at nearby Rockingham are 28.5°C and 18.3°C, while the equivalent temperatures for the coldest month (August) are 17.5°C and 10.3°C respectively. Reliable afternoon sea breezes

ensure that Garden Island experiences less extreme temperatures than the adjacent mainland.

The island is primarily covered by low woodlands and shrublands with a variable but often dense under-storey dominated by prickly lily (*Acanthocarpus priessei*) (McArthur and Bartle 1981). The vertebrate fauna is relatively depauperate, with introduced house-mice (*Mus musculus*) and tamar wallabies (*Macropus eugenii*) the only resident mammalian species on the island (Wykes et al. 1999). Apart from pythons, the island supports tiger snakes (*Notechis scutatus*) and 12 taxa of lizards (9 skinks, 2 geckoes, and 1 pygopodid). Ninety-five species of birds are known to occur on Garden Island (Wykes et al. 1999).

Methods

We commenced a mark-recapture study of pythons in September 1995. Pythons were obtained from several sources. Road-driving after sunset (between 1800 and 2300 hours) was carried out weekly during spring and summer and any pythons observed were collected. Some pythons were captured opportunistically during other fieldwork. Rangers and Naval Police captured many pythons on roads, in vehicles and buildings. Pythons were also collected by contractors spraying for weeds, by work crews from the Department of Juvenile Justice and by other researchers working on the island.

Following capture, pythons were brought to the ranger's office and kept there in cages or calico bags until processed. Prior to any measurements, the lower gut of each python was palpated to remove faecal material. Faeces were stored in 70% ethanol for later dietary analysis. If food items were present in the stomach, their identity was determined by gentle palpation. Pythons were then weighed with a Mettler electric balance (± 1 g) if less than 5 kg; or if over 5 kg, with a Salter spring balance (± 50 g). SVL and tail length were obtained by stretching pythons along a tape measure (± 1 mm). Measurements of the head and mid-body diameter (average of two perpendicular measures) were made with calipers (± 0.5 mm).

Each python was sexed by eversion of hemipenes or by insertion of a lubricated blunt probe into the base of the tail to determine the presence or otherwise of hemipenes. The depth the probe could be inserted was scored in terms of the number of overlying subcaudal scales. Males probed to depths equivalent to 7–20 subcaudals and females from 1–5 subcaudals. Reproductive information was also collected at this time, particularly the presence of sperm in reproductive males, or the existence of sperm around the cloaca of recently inseminated females. Females of reproductive size were palpated for enlarged follicles in the ovary or fertilised eggs in the oviduct. The body of each python was examined for scarring and parasites, then given a unique number by the removal of half a ventral scale and several of its adjoining lateral scales with a scalpel. This numbering technique has been successfully used on other snakes without any apparent problems (Blanchard and Finster 1933; Spellerberg 1977; Madsen and Shine 1996). To aid the identification of recaptured snakes should their scale clips be unclear, three other characteristics were recorded. These were: (1) variations in the arrangement of subcaudal scales (these are usually paired but single and triple scales occur frequently); (2) the arrangement of scales posterior to the parietal head shields; and (3) scoring white subcaudal scales starting at the vent and counting down the tail for 30 scales. The latter proved to be an almost unique identifier. Each python was then released at its site of capture.

We also captured and maintained 12 pythons in captivity to examine the relative growth rates of adult males and similarly sized female pythons when offered known amounts of food. The duration of captivity varied among snakes, because of difficulties in capturing appropriately sized animals (Table 1). Six male and six female pythons (ranging from 100.6 cm to 137.9 cm SVL) were kept under identical conditions at the ranger's office on Garden Island. Due to naval quarantine regulations, the pythons could not be removed from the island. One male was subsequently released as it

Table 1 Sexual size dimorphism in adult carpet pythons (*Morelia spilota imbricata*) from Garden Island, Western Australia. The table shows mean values (with SD in parentheses) for adult males and fe-

males, and the results of statistical tests (unpaired *t*-tests with 191 *df*) and associated probability values for differences between the sexes. *SVL* Snout-vent length

Trait	Adult males (<i>n</i> =154)	Adult females (<i>n</i> =39)	Statistical test (<i>t</i>)	<i>P</i>
SVL (mm)	1,035.63 (135.77)	2,139.54 (95.51)	47.82	<0.0001
Mass (g)	305.55 (170.42)	3,935.13 (737.23)	55.86	<0.0001
Tail length (mm)	178.84 (25.61)	327.29 (18.18)	33.65	<0.0001
Jaw length (mm)	34.66 (4.27)	67.54 (2.81)	45.03	<0.0001
Head width (mm)	25.46 (3.67)	55.05 (3.09)	45.88	<0.0001
Head depth (mm)	11.95 (1.79)	26.14 (1.50)	45.16	<0.0001
Midbody diameter (mm)	26.86 (4.50)	63.11 (6.82)	39.31	<0.0001

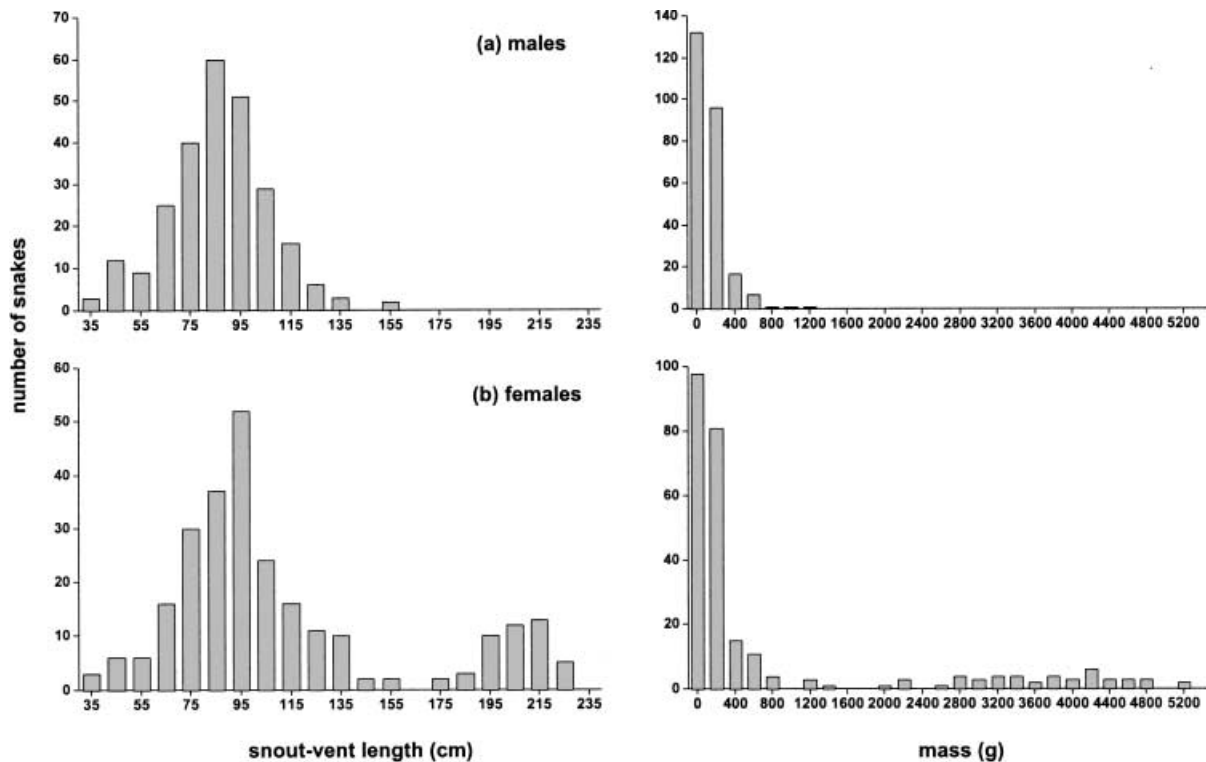


Fig. 1 Body sizes of male and female carpet pythons (*Morelia spilota imbricata*) from Garden Island, Western Australia. *Left-hand-side* graphs show frequency distributions of snout-vent lengths for males and females; and *right-hand-side* graphs show frequency distributions of body mass for males and females

could not be induced to feed. The snakes were housed individually in glass-fronted wooden cages (50×40 cm and 40 cm high). Each cage had a layer of paper towel on the floor, a heat pad (35×20 cm; Thermofilm, Victoria) which provided a constant warm spot (28–30°C), a cardboard box for shelter and a water dish.

All pythons were weighed and measured at the time of capture (the same measurements as outlined above) and then regularly (usually monthly) for the remainder of the study. Once a week, all pythons were offered the same type of prey item, usually a dead mouse or rat (5–70 g), but occasionally dead chicks (30–40 g). If this item was eaten, another was offered until each python appeared satiated. Uneaten food items were removed several hours after being offered, usually the following morning. Reluctant feeders were tempted with freshly killed mice. We recorded the mass of food items eaten, faeces produced and sloughed skins. At the conclusion of the study, the pythons were released at their sites of capture.

Results

Body sizes and SSD

We collected data on 518 free-ranging carpet pythons (256 males, 262 females), ranging from 39 cm SVL (18 g) to 213 cm SVL (5.4 kg). Figure 1 presents body-size distributions of these animals and shows that females attain very much larger sizes than do males. The largest male python measured 159 cm SVL and weighed 1.24 kg, whereas the largest female was 231 cm SVL and 5.35 kg. Thus, there was no overlap in adult body sizes between the two sexes: no male grew to 160 cm SVL, whereas all adult females exceeded this size.

Body sizes at sexual maturation were established by dissection of roadkills and by observation of free-ranging snakes. Dissection of 85 male pythons showed that most males >88 cm SVL (mass approx. 230 g) possessed thickened opaque efferent ducts, indicating the presence

of sperm. Occasional smaller snakes (down to 78.2 cm SVL) may also have been adult. The smallest male found copulating with a female in the field was 101.6 cm SVL (251 g), but much smaller males (to 61.1 cm SVL and 60 g) were found close to females during the mating season and may have been engaged in reproductive activity. Very few large female snakes were available for dissection, so our estimate of size at maturation is based on the smallest reproductive female located in the field. She measured 195.3 cm SVL and weighed 4.21 kg when gravid (2.91 kg after oviposition). Another eight gravid females found during our study ranged in size from 203.0 to 234.5 cm SVL and weighed 4.25–5.4 kg.

Because females mature at much larger sizes than males and grow to much larger maximum sizes, the mean values for all morphological traits were substantially greater in adult females than in adult males (Table 1). This difference was approximately twofold for body length and for other linear measures (such as head size and mid-body diameter). Snakes grow much heavier as they increase in length, however, so the dimorphism was much greater when calculated in terms of mass. An average adult female python weighed approximately 13 times as much as an average male (Table 1).

Sex ratios

Sex ratios were heavily female-biased among juveniles (221 females, 101 males), but male-biased among adults (39 females, 155 males). Contingency-table analysis confirms that sex ratios differ significantly between juveniles and adults ($\chi^2=112.12$, $df=1$, $P<0.0001$). However, it may be misleading to compare between groups in this way, because females mature at much larger sizes (and presumably, at greater ages) than do males. In the overall sample (i.e. combining adults and juveniles), the sex disparity is negligible (260 females, 256 males).

Determinants of sex differences in mean adult body size

Males and females may display differences in mean adult body size either because the sexes diverge in growth trajectories, or because one sex experiences higher survival rates than the other. In the latter situation, individuals of the higher-survival sex will tend to be larger simply because they are (on average) older (e.g. Stamps 1983; Gibbons and Lovich 1990). Our recapture data allow us to evaluate the magnitude of sex differences in rates of growth and survival.

Survival rates

Capture data for all marked snakes (but excluding those fitted with radio-transmitters) indicated no significant differences in the numbers of male and female pythons recaptured over the 33 months of the study (35 males were

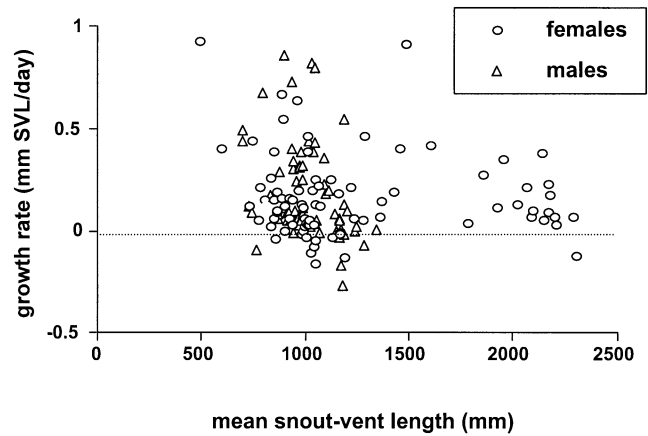


Fig. 2 Growth rates of recaptured carpet pythons as a function of mean body size (snout-vent length) during the intervening period. See text for explanation and statistical tests

recaptured once, seven twice, and eight on three or more occasions; 45 females were recaptured once, 10 twice, and four more than twice; $\chi^2=2.386$, $df=1$, $P=0.303$). However, the few recaptures of non-telemetered adult females (only three of 24 marked) suggest that either this group has higher mortality or is less likely to be recaptured than smaller snakes due to different behavioural traits. The latter appears the most likely explanation, because the mortality rate of 16 telemetered adult females was very low during the study. Only one of 16 adult females died during telemetry (over a cumulative total of 11,872 days of monitoring; Pearson et al., unpublished data), and she was killed by a senseless human action.

Growth rates

We calculated growth increments (final SVL minus initial SVL) for all recaptured snakes and divided these increments by the number of days between captures (they continued to feed throughout winter) to provide a measure of the daily rate of growth over the intervening period. Figure 2 shows these growth rates plotted against the animal's mean SVL over the period of growth. Growth rates declined with increasing mean SVL in male pythons (regression of growth rate versus mean SVL, $n=65$, $r=-0.30$, $P<0.02$), but not in females ($n=84$, $r=-0.09$, $P=0.41$). Thus, growth rates were higher overall in females than in males. A heterogeneity of slopes test on these data (with sex as the factor, mean SVL as the covariate and growth rate as the dependent variable) shows that growth rates declined more rapidly with increasing SVL in males than in females (slopes $F_{1,145}=0.561$, $P<0.02$). These data show that the massive sex disparity in body sizes of carpet pythons on Garden Island reflects the fact that male snakes virtually cease growing at approximately 100 cm SVL. Most females also have low growth rates at this body size, but some individuals continue to grow, sometimes quite rapidly (Fig. 2).

Table 2 Changes in snout-vent length, head length, growth rates and prey intake of captive Carpet Pythons. SVL snout-vent length (cm)

Snake ID	Days as captive	SVL at capture	SVL mean over study period	Prey intake (g)	Change in mass (g) over study period	Increase rate in mass (g/day)	Change in SVL (mm) over study period	Increase rate in SVL (mm/day)
Male 42	579	124.6	128.3	1,757.5	243	0.420	73	0.126
Male 335	654	118.2	123	1,583.5	184	0.281	96	0.147
Male 343	639	100.7	110.1	1,147	197	0.308	187	0.293
Male 349	610	124.8	128.9	1,487.5	80	0.131	82	0.134
Male 363	442	137.9	139.9	1,029	-168	-0.380	39	0.088
Female 284	730	129.2	144.8	3,604.4	724	0.992	311	0.426
Female 334	654	122.5	127.8	922	-52	-0.080	106	0.162
Female 337	654	139.3	147.8	3,536	654	1.000	169	0.258
Female 373	424	139.6	149.8	3,138	796	1.877	204	0.481
Female 379	404	118.8	134	3,236.5	1,030	2.550	303	0.750
Female 415	354	124.3	128.4	784.5	-7	-0.020	82	0.232

Why do the sexes differ in growth rate?

Given that the extreme SSD in this python population is caused by sex differences in growth rates, it is of interest to investigate why such differences occur. One plausible sex difference in this respect involves the rate of feeding: females might grow faster than males simply because they feed more frequently. Field data are difficult to interpret in this respect, because small prey items may be difficult to detect by palpation in these muscular snakes, and because feeding may alter a snake's behaviour and, thus, its vulnerability to capture (e.g. Slip and Shine 1988b). The snakes maintained in captivity provide more reliable information on this topic. We discarded data for two females and one male that were reluctant feeders, and hence lost mass during their period in captivity (Table 2). For the remaining animals (four males, four females), we recorded the number and mass of prey items consumed by each animal, and their consequent growth. At the commencement of the trial, body sizes were similar in the two sexes (female mean SVL=131.7 cm, male 117.1 cm; from one-factor ANOVA, effect of sex on SVL $F_{1,6}=3.80$, $P=0.10$). The females each consumed an average of 3.4 kg of prey during the trial (mean=6.4 g per day, $SD=1.50$), whereas the captive males each consumed an average of only 1.5 kg (mean=2.4 g per day, $SD=0.51$; from one-factor ANOVA, effect of sex on daily food intake $F_{1,6}=25.86$, $P<0.003$). In consequence, females grew more rapidly than males. Daily growth in mass for females averaged 1.61 g ($SD=0.78$) whereas males gained an average of only 0.29 g ($SD=0.12$) per day ($F_{1,6}=11.94$, $P<0.02$). Corresponding figures for SVL were 0.48 mm/day ($SD=0.20$) for females and 0.18 mm/day ($SD=0.08$) for males ($F_{1,6}=7.70$, $P<0.04$). We can also compare the two sexes in terms of how much they grew relative to how much they ate. To do this, we performed an ANCOVA with sex as the factor, mean daily prey intake as the covariate, and growth rate as the dependent variable. Males and females did not differ significantly in growth rates relative to food intake either for mass increase (slopes

$F_{1,4}=3.42$, $P=0.14$; intercepts $F_{1,5}=1.79$, $P=0.24$) or SVL increase (slopes $F_{1,4}=3.40$, $P=0.14$; intercepts $F_{1,5}=0.03$, $P=0.88$). Overall, these data suggest that growth rates of the pythons are determined by rates of food intake; and that males grow less than females because they eat less frequently.

Mating system

Our fieldwork provided 34 records of close male/female proximity or mating in free-ranging snakes (Table 3). All records came from spring and early summer (late September to mid-December), indicating a strongly seasonal pattern of courtship and mating within the Garden Island population. We did not record overt agonistic behaviour among males, and in one case a male was found close to a courting pair. No male python was found with bite-scars on the body; such scars are common in populations of *M. spilota* that exhibit male-male combat (Shine and Fitzgerald 1995). These observations suggest that male *M. s. imbricata* do not engage in physical combat for mating opportunities.

In snake species with male-male combat, larger males may reduce the smaller animals' access to females (e.g. Madsen et al. 1993). If this happened with the Garden Island pythons, it should be reflected in the body sizes of courting males. Data in Table 3 reveal that the males found courting and copulating were similar in mean body size to other adult males in the population [mean size of courting males=109.5 cm, $SD=14.2$, $n=8$ excluding one very small individual only 61.1 cm in SVL which may not have been engaged in reproduction; compared to all other adult (>88 cm SVL) males, mean size=103.3 cm, $SD=13.6$, $t=1.24$, $df=155$, $P=0.22$]. If the unusually small male is included in the sample of reproductive animals, the difference between the two groups is even smaller ($t=0.17$, $df=156$, $P=0.87$). Hence, there is no evidence that smaller males are excluded from mating opportunities within this population.

Table 3 Observations of python reproductive behaviour on Garden Island, 1995–1998. Few records are actual mating events; most document the close proximity of sexually mature males and females. Female pythons marked * were telemetered females that failed to oviposit (nos. 40 and 56) during November or December following these observations. (! indicates measurement not made)

Date	Female ID	SVL (cm)	Mass (g)	Male ID	SVL (cm)	Mass (g)	Comments
1995							
13 Oct 95	40*	195	2,309	76	102	251	Male coiled 3 m from loosely coiled female
25 Oct 95	50	206	4,037	80	134	774	Both in loose coils with male on top, mating?
29 Oct 95	50			83	129	608	Male stretched out on a branch basking 2 m from female
8 Dec 95	50			80			Together under a dense spiny shrub
14 Dec 95	50			83			Loosely coiled with male lying on top
7 Dec 95	Unknown			80			Male draped over large female (probably no. 50)
1996							
20 Sept 96	235	213	4,731	83	129	608	Tightly coiled beside each other
22 Nov 96	235			83			Together in dense spiny shrub
21 Oct 96	79	197	3,351	83			Male coiled 2 m from female
31 Oct 96	79			83			Male basking 1 m from female
9 Nov 96	79			83+261	61	60	Male 83 draped over tightly coiled female, male 261 coiled 1.5 m away
13 Nov 96	79			259	107	328	Coiled 2 m apart
19 Nov 96	79			83			tightly coiled 9 m apart under thick scrub
20 Nov 96	79			83			Male in thick shrub 3 m from tightly coiled female
22 Nov 96	79			259			Male coiled 1 m from female
26 Nov 96	79			259			Male 15 m from female
26 Nov 96	79			83			Male moving rapidly 10 m from female
30 Nov 96	79			259			Together under dense shrub
6 Dec 96	79			259			Male basking 5 m from female
11 Nov 96	260	219	4,824	83			Female captured near male, sperm visible around her vent
20 Dec 96	260			83			Together under a limestone slab
14 Nov 96	143	206	4,185	80	135	759	Mating; loosely coiled male lying on top of female with vents joined
27 Nov 96	143			80			Male coiled on top of female
1 Dec 96	143			266	107	311	Male basking 1.5 m from female
13 Dec 96	143			266			Male near female
30 Nov 96	87	217	4,233	259			Together under dense shrub
1997							
16 Oct 97	56*	!	5,200	371	87	218	Male moving 0.5 m from female
2 Nov 97	56			374	106	306	Male coiled 7 m from female
14 Nov 97	382	222	5,200	374			Male lying on tightly-coiled female
17 Nov 97	382			374			Both coiled under thick shrubs 12 m apart
5 Nov 97	375	203	4,253	259			Male coiled 1 m from female; sperm around her vent
27 Oct 97	Unknown			259			Male basking 0.3 m from large female (latter not captured)
1998							
3 Dec 98	143	213	3,394	471	106	224	Coiled 10 m apart

Discussion

In conjunction with previous studies, our data reveal an extraordinary degree of geographic variation in SSD in carpet pythons (*Morelia spilota*). One extreme occurs in carpet pythons (*M. s. mcdowelli*) from north-eastern New South Wales (Shine and Fitzgerald 1995) and south-eastern Queensland (Fearn et al. 2001). In these areas, males average approximately 10% longer and 30% heavier than conspecific females. A similar condition apparently occurs in carpet pythons from tropical areas (*M. s. variegata*) and in the closely related *M. bredli* from arid Australia (Barker and Barker 1994; Shine and Fitzgerald 1995). The other extreme is represented by our study animals from Garden Island. Although *M. s. imbricata* is morphologically similar to *M. s. mcdowelli* (e.g. Barker and Barker 1994), its pattern of SSD is remarkably different. Males average less than half the

length, and less than one-tenth the mass, of conspecific females. Under a commonly used definition, the males of *M. s. imbricata* would qualify as “dwarf males” (Ghiselin 1972). The only other subspecies of carpet python for which data are available – the diamond python *M. s. spilota* – is intermediate between these extremes: females grow slightly larger than males (Slip and Shine 1988a; Shine and Fitzgerald 1995).

To our knowledge, this geographic variation in SSD is more extreme than has previously been recorded in any other vertebrate species. Geographic variation in SSD has been reported in many taxa, but generally involves relatively modest differences in the proportional sizes of males and females (e.g. Harvey and Ralls 1985; Schwaner and Sarre 1988). Certainly, the variation within *M. spilota* is unparalleled within snakes. A review of published data on SSD in 374 species of snakes revealed extremes from males 50% larger than females in mean

adult SVL, to females 58% longer than males (Shine 1994).

Although the degree of male size superiority in north-eastern populations does not approach the maximum values for SSD recorded in other snake species, the degree to which females exceed males in mean adult body size is much greater for the Garden Island pythons than in any of the 374 species reviewed by Shine (1994). Thus, intraspecific variation in SSD within *M. spilota* spans about as much variation as has hitherto been reported among snakes in general. Using the index of SSD proposed by Gibbons and Lovich (1990), indices for *M. spilota* range from -0.08 (*M. s. mcdowellii*) through 0.16 (*M. s. spilota*) to 1.07 (*M. s. imbricata*).

The causes for the extreme sex disparity in body sizes of adult *M. s. imbricata* can be examined at both proximate and ultimate levels. On a proximate level, females attain larger sizes than males because they continue to increase in size well past the point at which males have ceased to grow. The only plausible alternative explanation for this effect would be if adult males experienced very high rates of mortality, so that their small body size reflected an age structure biased towards young animals. Our recapture data strongly falsify this interpretation: males are small because they differ from females in growth trajectories rather than in survival schedules (Fig. 2).

Why do males grow slowly and cease growing at approximately 100 cm SVL? Various alternatives are plausible; for example, differences in habitat use, and thus prey availability, between the sexes could generate such effects (e.g. Madsen and Shine 1993b; Shine et al. 1999). However, our experiment with captive snakes indicates that the answer lies in some intrinsic difference between the sexes in propensity to feed, rather than in local conditions of resource availability. Growth rates are (unsurprisingly) related to food consumption rates; and even when offered ad libitum opportunities, male pythons fed less frequently than did females of the same range of body sizes. Similar anorexia in male snakes compared to conspecific females has been reported in previous studies of North American natricine snakes, both in the field (Feaver 1977) and captivity (Crews et al. 1985). These results suggest that males of at least some snake species (or populations) may be "hard-wired" to remain relatively small-bodied, regardless of prey availability.

Given that the SSD of the Garden Island snakes reflects these kinds of sex differences in foraging behaviour, what selective forces may have been involved in the evolution of these traits? Although ultimate causes for observed patterns of phenotypic variation are difficult to demonstrate unequivocally, our data accord well with existing ideas and data on this topic. Life-history theory suggests that the direction and degree of SSD should reflect the end result of a complex series of "costs" and "benefits" of different body sizes for each sex (Trivers 1976; Shine 1994). In turn, these costs and benefits result from the ecological and reproductive consequences of body size.

In ecological terms, small body size may confer significant advantages. It permits earlier maturation and allocation of resources to reproduction rather than growth (Gibbons and Lovich 1990). Also, the higher maintenance costs of large body size may endanger the organism during episodes of chronic food shortage (e.g. Wikelski and Thom 2000). In reproductive terms, larger body size may enhance fitness in females by increasing clutch sizes. If maternal body volume constrains reproductive output (Semlitsch and Gibbons 1982), then larger females can produce more or larger offspring. Increased fecundity with increasing maternal body size has been reported in many snake species, including *M. spilota* (Fitch 1970; Seigel and Ford 1987; Slip and Shine 1988a). Larger body size can also enhance male reproductive success, but only in mating systems that reward physical strength in males or where females actively select larger partners (Andersson 1994). If males tolerate each others' presence during courtship, and male success is determined by factors such as chance, mate-finding ability, or persistence or effectiveness in courtship, then there is no reason to expect larger males to obtain more matings. This appears to be the situation in *M. s. imbricata*.

Interestingly, male "tactics" in this population resemble those of *M. s. spilota* in some respects (lack of male-male combat) and *M. s. mcdowellii* in others (males do not remain for long periods with a single female, but instead move around and may return to her at a later date). Growth rates of recaptured animals (Fig. 2) suggest that males and females grow at fairly similar rates during the first few years of life. Thus, the massive sex difference in size at maturity translates into a difference in age at first reproduction, and a consequent skew in the adult sex ratio (4:1 male:female). This strong bias in adult sex ratio will be further exacerbated by the fact that female *M. spilota* reproduce less-than-annually (Slip and Shine 1988a; Shine and Fitzgerald 1995; Pearson, unpublished data for *M. s. imbricata*), whereas (based on the presence of sperm in efferent ducts) all adult males are capable of breeding annually. Thus, the operational sex ratio is likely to be very highly male-biased in the Garden Island pythons. Under such circumstances, male-male combat may be ineffective in assuring access to reproductive females, thus selecting against such behaviour (Parker 1984; Shine and Fitzgerald 1995).

These considerations support Shine and Fitzgerald's (1995) suggestion that geographic variation in SSD within *M. spilota* reflects geographic variation in selective pressures on male body size associated with the mating system. In populations where males fight for access to reproductive females, genes that produce large body size in males have been favoured by sexual selection, and the end result has been that males tend to exceed females in mean adult body size. In contrast, male fitness has been enhanced by smaller rather than larger body size in populations that do not display overt male-male rivalry, with the consequence that females exceed males in mean body size.

Such adaptationist scenarios are difficult to test in any rigorous way, although the tight phylogenetic focus of the comparisons adds considerably to their power. The evidence in favour of a causal link between mating systems and SSD in carpet pythons is as follows:

1. Concurrent variation in the two traits: females grow larger than males in two subspecies without male-male combat, but are smaller than males in at least three subspecies in which combat is known to occur. Unfortunately, we know too little about intraspecific phylogenies to assess the direction of evolutionary changes in mating systems and SSD, or the numbers of independent evolutionary shifts involved.
2. Mean body sizes (SVLs) of adult females are relatively similar in the three carpet python subspecies studied thus far (ranging from 180 to 210 cm), whereas mean adult male body sizes are more variable (means of 100 to 200 cm). This pattern suggests that it is male rather than female body sizes that have shifted over evolutionary time, during the adaptive radiation of this species across Australia. In turn, this result fits the idea that it is selection on male rather than female sizes that has been most important in generating shifts in SSD.
3. The intraspecific correlation between mating systems and SSD mirrors the same pattern at higher phylogenetic levels; the evolution of male-male combat in snakes has been consistently associated with shifts towards male-biased size dimorphism (Shine 1994).
4. Evidence from other studies supports the plausibility of the putative selective pressures on male body size. Although we have no data on body size versus mating success in pythons, males found close to females were similar in size to other males (Table 2). In contrast, there is strong evidence of a large-male advantage in snake taxa exhibiting combat (e.g. Schuett and Gillingham 1989; Madsen et al. 1993). In European adders, the intensity of selection on male body size varies from year to year, correlated with (and, presumably, depending upon) the degree to which success in male-male combat determines a male's mating opportunities (Madsen and Shine 1993a). Similarly, studies on snake species that do not display male-male combat have reported only minor (or no) effects of increased male body size on mating success (Shine 1986; Joy and Crews 1988; but see Weatherhead et al. 1995; Luiselli 1996; Shine et al. 2000).

The pythons of Garden Island display an incredible degree of SSD, with females attaining an average mass over 10 times that of males at maturity. The absence of male-male combat and perhaps a restricted prey assemblage on Garden Island (Pearson and Shine, unpublished data) seems to remove any selective advantage for males to attain large body size. The divergence in body sizes of adult male and female pythons is probably driven by relative differences in the costs of reproduction for the sexes (Madsen and Shine 1994). Presumably males incur comparatively low costs associated with reproduction

and are able to breed annually. In contrast, female pythons mature at much larger sizes and experience high reproductive costs associated with egg production, incubation and missed opportunities to feed during the breeding cycle. Consequently they have not been recorded to breed annually, but rather every second or third year (Pearson et al., unpublished data).

Comparatively small body size might confer significant benefits to males due to the particular nature of the mating system of pythons on Garden Island. Reproductively active males travel considerable distances and may visit (and revisit) numerous females over the several weeks of peak mating activity (Pearson, unpublished data). Easier passage through thick and prickly vegetation, avoidance of avian predation and a reliance on small prey (lizards, mice and birds) might reinforce the advantages of small body size in males. SSD in this population appears to be controlled genetically, with males growing smaller than females because they consume fewer prey. The geographic range of *M. spilota* across the Australian continent and associated islands, and the wide variation in SSD across this range, provides an ideal opportunity to further clarify mechanisms involved in the evolution of sexual size dimorphism.

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