

Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*)

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Sexual dimorphism is usually interpreted in terms of reproductive adaptations, but the degree of sex divergence also may be affected by sex-based niche partitioning. In gape-limited animals like snakes, the degree of sexual dimorphism in body size (SSD) or relative head size can determine the size spectrum of ingestible prey for each sex. Our studies of one mainland and four insular Western Australian populations of carpet pythons (*Morelia spilota*) reveal remarkable geographical variation in SSD, associated with differences in prey resources available to the snakes. In all five populations, females grew larger than males and had larger heads relative to body length. However, the populations differed in mean body sizes and relative head sizes, as well as in the degree of sexual dimorphism in these traits. Adult males and females also diverged strongly in dietary composition: males consumed small prey (lizards, mice and small birds), while females took larger mammals such as possums and wallabies. Geographic differences in the availability of large mammalian prey were linked to differences in mean adult body sizes of females (the larger sex) and thus contributed to sex-based resource partitioning. For example, in one population adult male snakes ate mice and adult females ate wallabies; in another, birds and lizards were important prey types for both sexes. Thus, the high degree of geographical variation among python populations in sexually dimorphic aspects of body size and shape plausibly results from geographical variation in prey availability. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 113–125.

ADDITIONAL KEYWORDS: intraspecific variation – sexual size dimorphism – insular populations – snakes.

INTRODUCTION

In many species of animals, adult males and adult females differ considerably in body size and body shape (e.g. Darwin, 1871). In some cases, variations in the degree of sexual size dimorphism (SSD) occur even between different populations within a single species. Such cases of intraspecific variation in SSD offer powerful opportunities to identify the evolutionary forces affecting this trait (Harvey & Ralls, 1985; Andersson, 1994). Nonetheless, interpretation is difficult even in such apparently straightforward cases, because the degree of SSD within a population reflects the end result of a complex series of selective forces and direct

(proximate) environmental pressures. For example, geographical variation in mating systems may generate among-population differences in the intensity of sexual selection and/or fecundity selection on the body sizes of the two sexes (Andersson, 1994; Shine & Fitzgerald, 1995). In such cases, geographical variation in SSD may reflect adaptive responses of mating ‘tactics’ in each sex to local conditions.

Although reproductive correlates of SSD have attracted considerable scientific attention, another set of forces can also modify SSD. Even if selective forces related to reproduction strongly influence the direction and degree of SSD, the local environment (and especially, the spectrum of available prey sizes) may influence the body sizes attained by organisms. In such a situation the degree of SSD may vary geographically either (a) because local prey resources

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constrain both sexes to similar body sizes, thus preventing the expression of SSD coded in the genome (Madsen & Shine, 1993) or (b) because selection on foraging biology favours adaptations to different prey resources in males and females, and thus the evolution of sex differences in body size and/or in feeding structures and behaviour (Slatkin, 1984). Teasing apart the proximate effect (a) from the adaptive one (b) will be difficult without manipulative experiments. However, geographical variation in the relative size or shape of feeding structures would suggest an adaptive rather than direct role for environmental forces in this respect (e.g. Shine, 1989; Temeles *et al.*, 2000; but see Bonnet *et al.*, 2001).

Australian carpet pythons (*Morelia spilota*) show more geographical variation in SSD than any other vertebrate species studied to date (Shine & Fitzgerald, 1995; Pearson, Shine & Williams, 2002). Adult males average heavier than females in some populations in eastern Australia (Shine & Fitzgerald, 1995; Fearn *et al.*, 2001), whereas females weigh 10 times more than adult males in a western population (Pearson

et al., 2002). The broad direction of SSD (i.e. which sex grows larger) appears to be driven by the mating system. Males grow larger than females only in populations where males engage in vigorous physical battles for mating opportunities (Shine, 1994; Shine & Fitzgerald, 1995). These patterns are derived from studies at widely separated localities across Australia, and rely on comparisons among populations that are often referred to different subspecies (e.g. Barker & Barker, 1994; see Fig. 1). The broad-scale lability in SSD within carpet pythons suggests that they may also be suitable study animals for comparisons at a smaller spatial scale.

In this paper, we examine spatial (among-population) variation in aspects of diet, reproduction, morphology and SSD within the south-western subspecies of carpet pythons (*Morelia s. imbricata*). In addition to the advantages noted above, south-western carpet pythons occur on isolated islands which differ substantially in vertebrate prey resources. Hence, this taxon offers an ideal opportunity to examine the influence of prey resources on predator morphology, and in

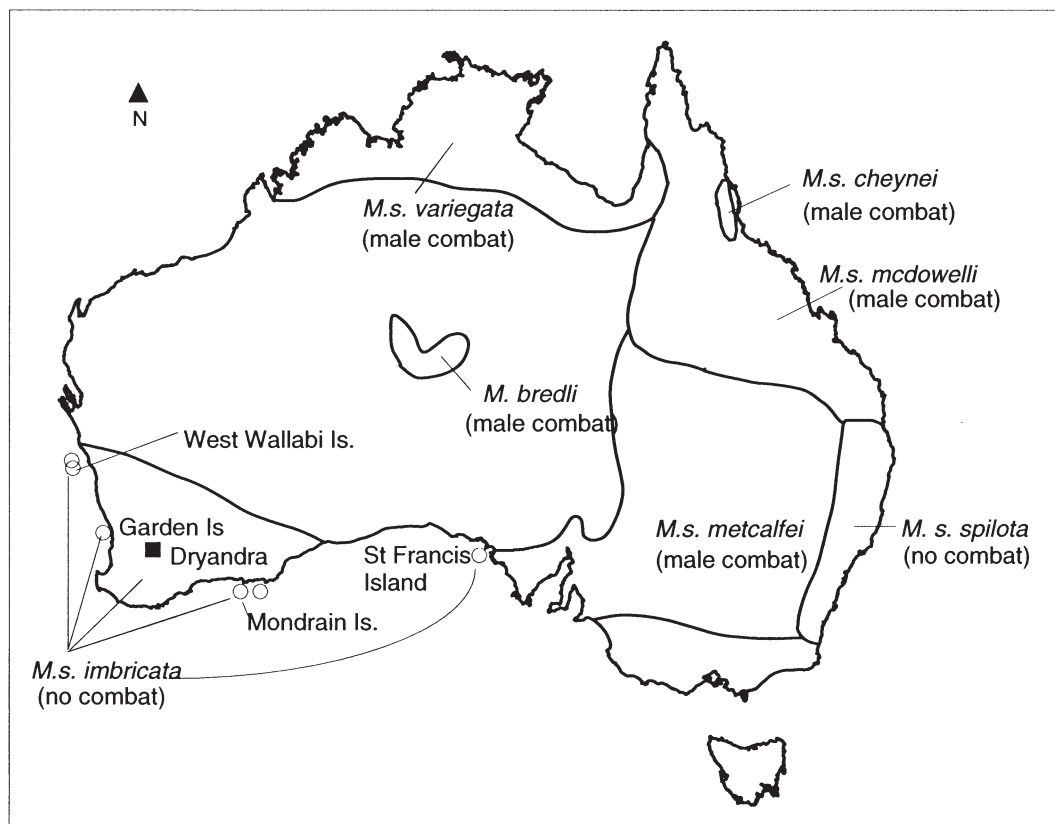


Figure 1. Map of Australia showing the various taxa of carpet pythons (*Morelia spilota*) recognized by Barker & Barker (1994), and their presumed mating systems. The locations of our five study populations in southern Australia are also shown.

particular to test the hypothesis that local variations in prey sizes can significantly modify sexual divergence in body sizes and feeding structures.

MATERIAL AND METHODS

STUDY SPECIES

Carpet pythons (*Morelia spilota*) are large heavy-bodied non-venomous snakes that kill their prey by constriction (Torr, 2000). The species is widely distributed across Australia, and shows strong regional differentiation in terms of habitats, body sizes and coloration (Barker & Barker, 1994). The south-western subspecies (*M. s. imbricata*) occurs in south-western Western Australia and six islands off the coast of South and Western Australia (Pearson, 1993; Barker & Barker, 1994). These snakes hunt mainly from ambush (Slip & Shine, 1988) and consume a wide variety of vertebrate prey. Juvenile carpet pythons typically consume mice, reptiles and birds whereas adults switch to larger mammalian prey (Torr, 2000).

STUDY AREAS

We obtained data from five populations of carpet pythons (Table 1, Fig. 1). One site was in an 'island' of eucalypt forest and heath surrounded by agricultural land in mainland Western Australia (Dryandra) whereas the other four populations occur on offshore islands over a range of 2500 km along the south-western and southern coasts of Australia. The sites differ in location and size (Table 1) but have broadly similar climatic conditions (cool wet winters, hot dry summers, with mean annual rainfall ranging from 292 to 715 mm: Robinson *et al.*, 1996; Smith & Johnstone, 1996; Bureau of Meteorology, <http://www.bom.gov.au>).

The array of potential prey species available shows substantial variation. The mainland site (Dryandra) has 20 species of mammals, 89 bird taxa and 51 reptiles, spanning a wide size range of potential prey items (Table 1). In contrast, prey-size spectra are much narrower in other sites (e.g. Saint Francis Island has <30 potential prey species) or wide but dichotomous. For example, Garden Island has only two mammalian taxa, and these differ enormously in mean adult body mass: mice (mean = 12 g) and wallabies (to 6 kg).

METHODS

We surveyed snake populations at each study area by hand-capture. Collecting effort differed substantially among localities, and was most intense at Garden Island and Dryandra where we were conducting radiotelemetric studies on this species. The other populations were all on relatively inaccessible islands, and hence were only visited briefly during trips specifically organized for this purpose. For each captured animal we recorded snout-vent length (SVL), tail length (for entire tails only), mass, mandible length (along the jaw, from the tip of the snout to the quadrate-articular joint at the rear of the mouth), maximum head width and maximum head depth. For analyses in the present study, data on mass exclude information from gravid females and from any snakes containing freshly ingested prey.

To estimate body sizes at sexual maturity, we used information on (1) morphology of gonads, from 135 dissected animals (found as roadkills), and (2) >40 observations of reproductive activity in the field. For males, we treated all individuals >85 cm SVL as adult, based on sperm in efferent ducts and observed participation in mating groups. There was little variation in this threshold size at maturity among populations (small-

Table 1. Location and characteristics of study sites

Study site	Dryandra Woodland (central block)	Garden Island	Mondrain Island	St. Francis Island	West Wallabi Island
Latitude	32° 47'S	32° 12'S	34° 08'S	32° 36'S	28° 28'S
Longitude (midpoint)	117° 00'E	115° 40'E	122° 15'E	133° 15'E	113° 42'E
Area (ha)	12 192	1200	780	809	619
Distance to mainland (km)	N/A	2	12	30	62
Rainfall (mm)	505	715	674	292	469
No. of species:					
terrestrial mammals	20	2*	2	2	2
reptiles	51	13	15	17	18
'landbirds'	89	18	13	8	7
Pythons collected (m:f)	36:38	533:527	17:11	46:68	52:36

Notes: * Feral cats and *Rattus rattus* are occasionally reported on Garden Island but have not established populations.

est reproductive males 84–114 cm, with few animals in this ‘questionable’ size range). For females, however, body sizes varied more and thus, we used actual sizes of the smallest reproductive female in each population as our estimate of size at maturity (132 cm SVL at St. Francis Island, 194 cm at Dryandra, 147 cm at Mondrain, 195 cm at Garden Island, and 183 cm at West Wallabi). To simplify analyses of dietary composition, we classified all prey items into six categories: large (>1 kg), medium (50 g–1 kg) and small mammals (<50 g), birds, and large (≥ 20 g) and small (<20 g) lizards.

The data were analysed on a Macintosh G4 computer, using the software programs Statview 5 (SAS Institute, 1998) and SuperANOVA 1.1 (Abacus Concepts, 1991). All continuous variables were ln-transformed prior to analysis, to improve their fit to assumptions (normal distributions, equal variances) of the relevant statistical tests. Figure 2 shows mean values and standard errors for raw (untransformed) data, to facilitate intuitive comparisons. To compare relative proportions of animals from each population, we used residual scores from general linear regressions of ln-transformed variables. For example, we regressed ln mass against ln SVL to obtain measures of the extent (and direction) to which a given individual snake deviated from the mass expected for a snake of that SVL. Negative residual scores thus indicate a snake that is lighter than average for its SVL. We used the same procedure to calculate indices of relative tail length (ln tail regressed against ln SVL), relative head length (ln head length vs. ln SVL), and head shape (ln head depth vs. ln head width, and ln head depth vs. ln head length). Although Figures 3 and 4 show these indices based on residual scores (for ease of interpretation), our statistical comparisons relied on the more robust approach of ANCOVA, where we incorporated the independent variable as a covariate rather than using it to calculate a residual score (Sokal & Rohlf, 1981; Seigel & Ford, 1987).

RESULTS

SAMPLE SIZES AND COMPOSITION

We obtained data on 1364 carpet pythons (Table 1). Sample sizes differed considerably among populations, and because some snakes were found as roadkills, sample sizes also differed among traits (i.e. some attributes could not be measured for some specimens). Sex differences in sizes (ages) at maturity (see above) meant that sex ratios were generally male-biased in adult snakes (77% male), but strongly female-biased among juveniles (76% female). Contingency-table analyses revealed differences among sites in the sex ratios of both adult and juvenile snakes (adults,

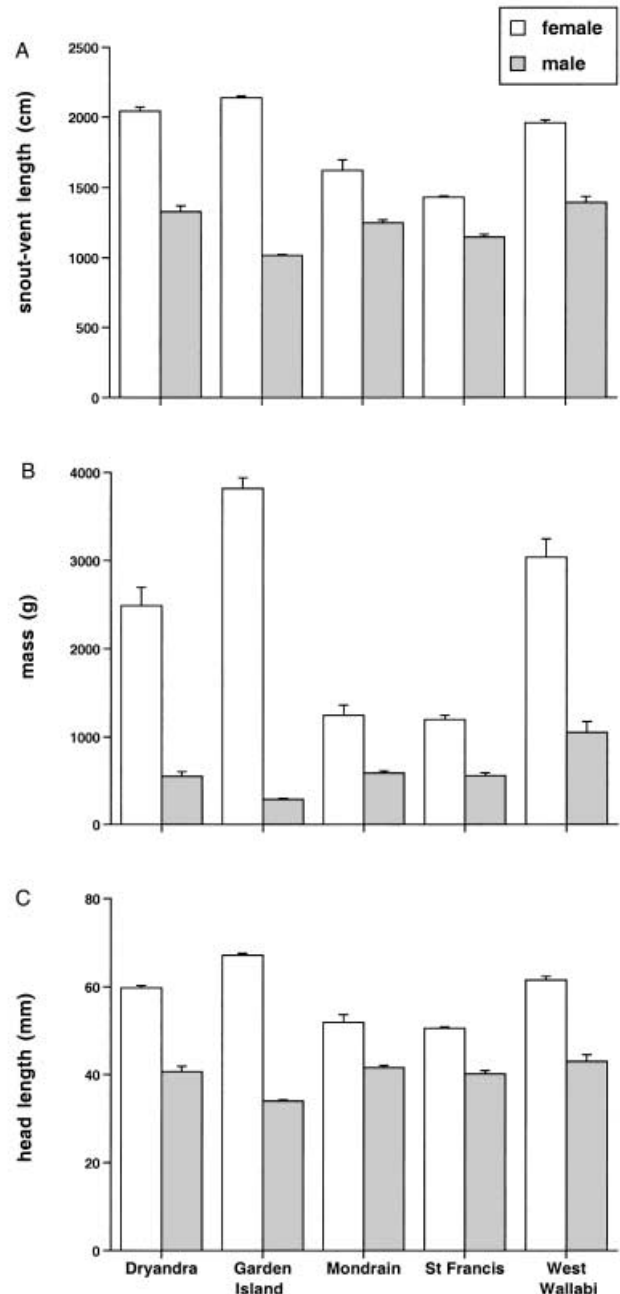


Figure 2. Geographic variation in mean body sizes and head sizes, and in the degree of sexual dimorphism in these traits, in adult carpet pythons (*Morelia spilota imbricata*) from five populations in south-western Australia. See Table 1 for sample sizes. See text for statistical analyses of these data.

$\chi^2 = 43.4$, 4 df, $P = 0.0001$; juveniles, $\chi^2 = 17.8$, 4 df, $P = 0.0001$), as well as in age structure (proportions of juvenile snakes) among the samples ($\chi^2 = 113.3$, 4 df, $P = 0.0001$).

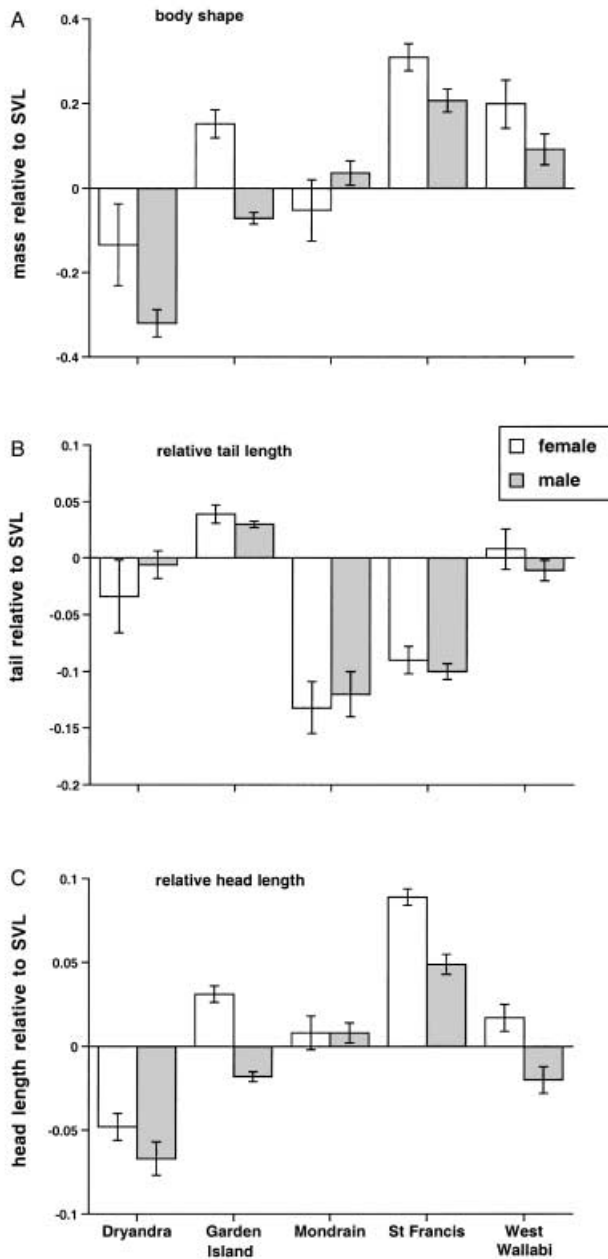


Figure 3. Geographic variation in body proportions, and in the degree of sexual dimorphism in these traits, in carpet pythons (*Morelia spilota imbricata*) from five populations in south-western Australia. See Table 1 for sample sizes. See text for statistical analyses of these data.

SEXUAL AND GEOGRAPHICAL VARIATION IN MEAN ADULT BODY SIZE

In each of the five populations that we studied, female pythons grew to significantly larger body sizes than did their male counterparts (Fig. 2). Because a small increase in SVL can entail a large increase in mass, this sexual dimorphism was greater in terms of mass

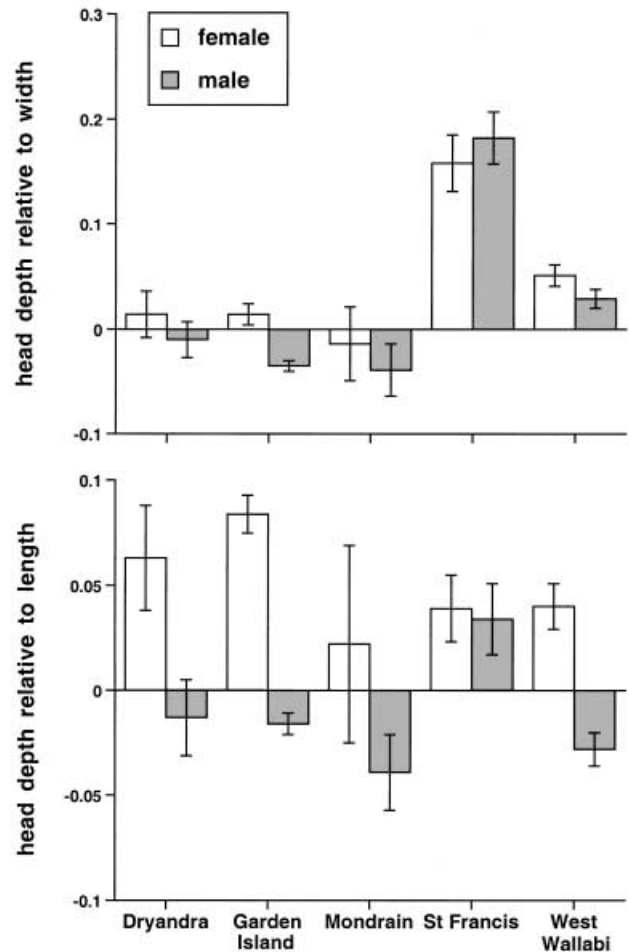


Figure 4. Geographic variation in head shape, and in the degree of sexual dimorphism in two measures of head shape, in carpet pythons (*Morelia spilota imbricata*) from five populations in south-western Australia. See Table 1 for sample sizes. See text for statistical analyses of these data.

rather than body length (Fig. 2). Unsurprisingly (given the greater body size of females), the heads of females were larger than those of males (Fig. 2). Mean adult body sizes also varied among the five populations, especially in females. For example, female pythons on Garden Island grew much larger than those on Saint Francis Island (maxima of 5.4 vs. 2.0 kg; see Fig. 2). Statistical analysis of these data with a two-factor ANOVA confirmed that body sizes and head sizes of carpet pythons were affected not only by sex and population, but by a significant interaction between these two factors (Table 2). That is, the degree to which females exceeded males in head and body sizes was greater in some populations than others.

The degree of SSD in adult pythons within each population was quantified using the method of Lovich & Gibbons (1992), and ranged from females being an

Table 2. Results of two-factor ANOVA (with population and sex as factors) on morphology of south-western Australian carpet pythons. These analyses are based only on adult animals; see text for maturation criteria, and Fig. 2 for graphical display. Table gives F -values and associated probabilities (P) for main effects of population (4474 df) and sex (1474df), and for the interaction between population and sex (4474 df). The latter term tests for significant geographical variation in the degree of sexual dimorphism in each trait. See Table 1 for sample sizes for each sex for each population

Trait	Population effect		Sex effect		Interaction: Population*Sex	
	F	P	F	P	F	P
ln SVL	44.3	0.0001	478.0	0.0001	78.0	0.0001
ln tail	78.3	0.0001	263.0	0.0001	42.1	0.0001
ln mass	25.4	0.0001	564.6	0.0001	87.1	0.0001
ln head length	12.5	0.0001	449.7	0.0001	64.8	0.0001
ln head width	48.2	0.0001	427.2	0.0001	53.4	0.0001
ln head depth	5.2	0.0004	405.0	0.0001	61.7	0.0001

average of 25.1% longer than males (Saint Francis Island) to 111.3% longer than males (Garden Island). The variation in SSD was determined mainly by geographical variation in the body sizes of females rather than males (Fig. 2; Spearman rank correlation $N = 5$, $\rho = 1.00$, $P < 0.046$ for SSD vs. mean SVL of adult females; $N = 5$, $\rho = 0.70$, $P = 0.16$ for SSD vs. mean SVL of adult males).

SEXUAL AND GEOGRAPHICAL SOURCES OF VARIATION IN BODY PROPORTIONS

Are the sex and locality differences in traits such as head size (Fig. 2, Table 2) simply due to overall differences in body size, or are there divergences (between sexes or among populations) in traits such as head mass relative to SVL, or body mass relative to SVL? We analysed this question using two-factor ANCOVA, with sex and location as factors and a morphological variable (such as ln SVL) as the covariate. If higher-order interaction effects were non-significant ($P > 0.05$), we successively deleted such terms to increase the power of the analysis and look for differences in lower-order interactions or main effects. We included all individuals, not just adult animals, in these analyses. Figures 3 and 4 provide the results of an alternative method of analysis (ANOVAs on size-corrected residual scores) for ease of interpretation. Below, we cite only 'significant' effects from the ANCOVA analyses (i.e. $P < 0.05$).

(i) *Body mass relative to SVL*: After deletion of a non-significant three-way interaction, the ANCOVA revealed three significant two-way interaction terms: between location and SVL ($F_{4,966} = 3.78$, $P = 0.005$), sex and SVL ($F_{1,966} = 60.06$, $P = 0.0001$) and sex and

location ($F_{4,966} = 2.87$, $P = 0.02$). That is, the rate at which ln body mass increased with ln SVL differed among populations, was higher in females than males, and differed between the two sexes among locations (see Fig. 3A). For example, Saint Francis snakes were more heavy-bodied than Dryandra animals, and males were thinner-bodied than females in all populations except for Mondrain Island (Fig. 3A).

(ii) *Tail length relative to SVL*: The ANCOVA detected no significant interaction terms, but a highly significant main effect of locality on relative tail length ($F_{4,975} = 102.4$, $P = 0.001$). Figure 3B shows that this effect is due to shorter tails on the Mondrain and Saint Francis snakes than in other populations.

(iii) *Head length relative to SVL*: After deletion of a non-significant three-way interaction, the ANCOVA revealed two significant two-way interaction terms: between location and SVL ($F_{4,966} = 3.99$, $P = 0.003$) and between sex and SVL ($F_{1,966} = 9.38$, $P = 0.002$). Snakes from Saint Francis Island had larger heads (relative to SVL) than did conspecifics from other populations, and females generally had larger heads than males of the same body length (Fig. 3C).

(iv) *Head width relative to head length*: Results for this variable were similar to those for relative head length (above). After deletion of a non-significant three-way interaction, the ANCOVA revealed two significant two-way interaction terms: between location and SVL ($F_{4,966} = 4.97$, $P = 0.001$) and between sex and SVL ($F_{1,966} = 46.0$, $P = 0.0001$). The Saint Francis snakes had wider heads relative to length, as well as longer heads relative to SVL, than did pythons from the other populations (Fig. 4A). Within each population except

Saint Francis, females had wider heads than males of the same head length (Fig. 4A).

(v) *Head depth relative to head length*: A significant three-way interaction term (location*sex*SVL: $F_{4,962} = 5.45$, $P = 0.0002$) complicates interpretation of this result. Some populations had deeper heads than others, and females generally had deeper heads than males of the same head length (Fig. 4B). However, the degree of sexual dimorphism in this trait was less on Saint Francis Island than in the other populations (Fig. 4B).

SEXUAL AND GEOGRAPHICAL VARIATION IN DIETARY COMPOSITION

Figure 5 shows composition of the diet in broad categories, and Table 3 provides more detail on the species consumed. These data reveal a strong divergence between the sexes in dietary composition. Restricting analysis to adult snakes, the clear pattern is that adult females fed primarily on large mammals (22 of 31 prey items = 71%), whereas this group comprised only 3 of 231 prey (1%) for adult males. The remainder of the diet in adult male pythons was diverse (e.g. 107 rodents = 46%; 77 lizards = 33%; 40 birds = 17%; see Fig. 5). Contingency-table analyses confirm the statistical significance of these sex differences in dietary composition (separately for Garden Island, $\chi^2 = 168.84$, 3 df, $P < 0.0001$; West Wallabi, $\chi^2 = 22.24$, 2 df, $P < 0.0001$).

Is this sex divergence in prey types a simple consequence of the sex divergence in body sizes, or do males and females eat different kinds of prey even at the same body sizes? Figure 6 supports the former interpretation: mean SVLs of pythons eating different prey type were different, but males and females displayed very similar patterns in this respect (interaction term between sex and prey type in two-factor ANOVA with ln SVL as the dependent variable, $F_{5,564} = 1.32$, $P = 0.26$). This ANOVA thus shows that body size is the main determinant of prey type ($F_{5,564} = 46.15$, $P = 0.0001$), with diets differing between the sexes because of SSD combined with the effect of body size on prey size.

Diets also showed strong spatial variation. Again restricting analysis to adult snakes (because the proportion of juveniles was much higher in some locations than others), contingency-table analysis shows significant geographical variation in the relative numbers of prey belonging to each of the major categories ($\chi^2 = 207.97$, 12 df, $P < 0.0001$). Lizards were the most commonly recorded prey items on West Wallabi, rats on Mondrain, mice on Garden Island and large mammals at Dryandra (Fig. 5).

DO PREY RESOURCES INFLUENCE PYTHON BODY SIZES?

The strongest opportunity to answer this question comes from a comparison of pythons of various body sizes on Garden Island vs. other sites. The Garden Island snakes are distinctive in that two prey taxa (mice and wallabies) comprise almost the entire adult diet, and these prey differ enormously in mass (approx 10 g vs. 3 kg). Snakes from other populations consume a wider variety of prey types and sizes (Table 3). If the size of available prey items influences the energy balance of pythons, we should see such an effect strongly on Garden Island because small and large pythons have 'appropriately sized' prey available, but intermediate-sized snakes (60–120 cm SVL) do not. In contrast, we do not expect to see such an effect in other populations. Figure 7 summarizes the relevant data on this question. Over the critical size range of 60–120 cm SVL, Garden Island snakes consumed smaller prey items (means of 84.6 vs. 24.5 g; $F_{1,414} = 23.30$, $P < 0.0001$). Although they ate more often (presumably because small mice are abundant on Garden Island: 54% vs. 17% with prey, $\chi^2 = 40.78$, 1 df, $P < 0.0001$), pythons at this intermediate range of SVLs were significantly thinner-bodied than were pythons at our other study sites (mean residual scores -0.8 vs. $+0.13$; heterogeneity of slopes test with location as factor, ln SVL as covariate and ln mass as dependent variable, $F_{1,891} = 23.36$, $P < 0.0001$; Fig. 7). Pythons also grew very slowly over this range of body sizes (Pearson *et al.*, 2002), with some snakes failing to increase in mass over periods >2 years (Pearson, unpubl. data).

DISCUSSION

Comparisons among carpet python (*Morelia spilota*) subspecies across Australia have shown that this species exhibits massive variation in the degree of sexual dimorphism in mean adult body size (Shine & Fitzgerald, 1995; Pearson *et al.*, 2002). The present study reveals extensive geographical variation in SSD even among isolated populations within a single subspecies of this widespread taxon. Our results support previous suggestions that the *direction* of sexual size dimorphism in snakes is determined primarily by the mating system (Shine, 1994; Shine & Fitzgerald, 1995). Females attained larger body sizes than males in all of our study populations, and there was no evidence of significant geographical variation in reproductive biology (Pearson, 2002). Thus, the extensive variation in SSD among populations may reflect other factors, of which the most likely is geographical variation in prey resources.

Geographic differences in dietary composition

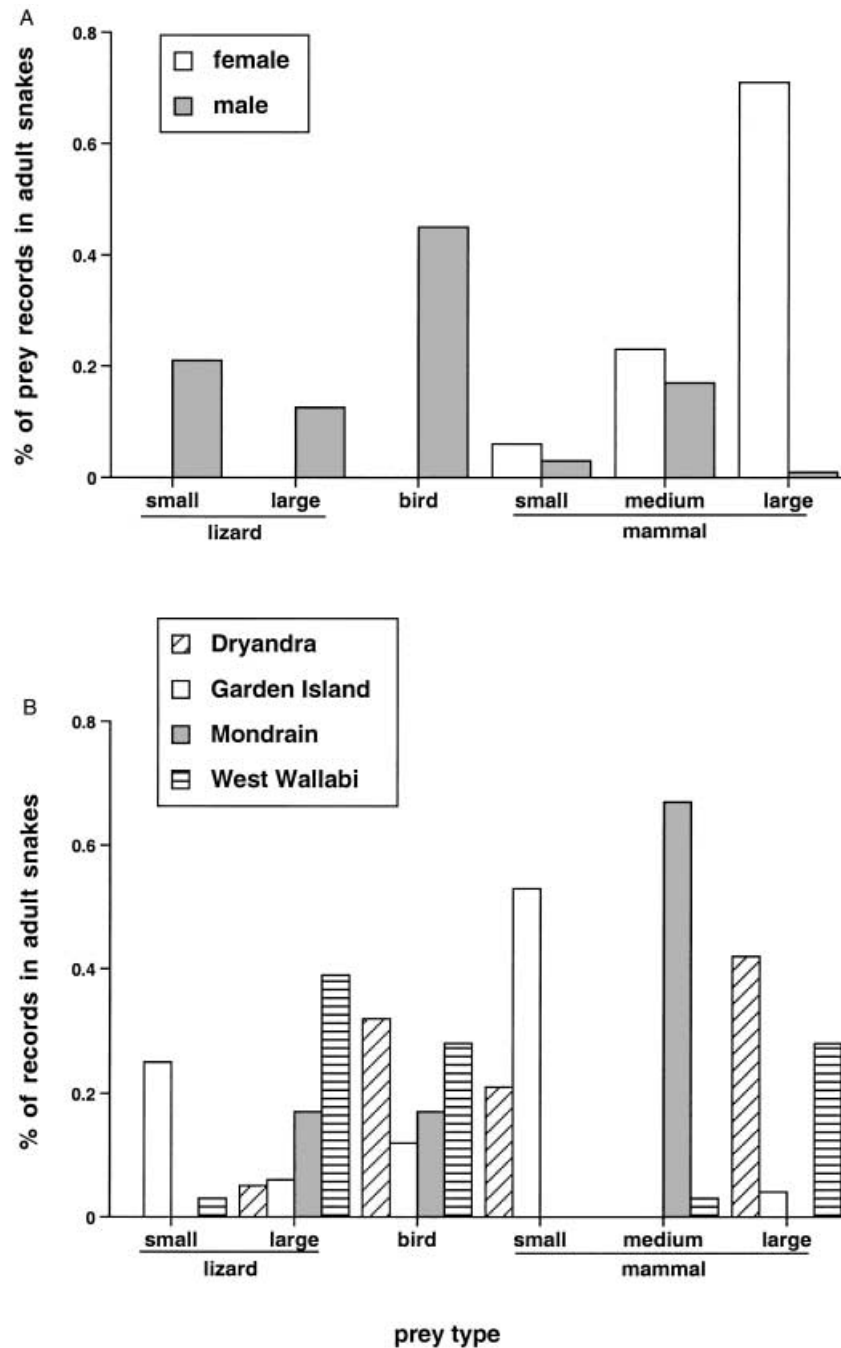


Figure 5. Composition of the diet of adult carpet pythons as a function of the snake's sex (A) and location (B). See text for definition of categories, and Table 3 for actual prey species in each category.

among isolated populations are widespread in snakes as in other kinds of animals, and generally are attributable to differences in the availability of different kinds of prey (e.g. Mushinsky, 1987). This is clearly the explanation for the geographical variation in diets within *Morelia spilota imbricata* (Table 1). Many species that were eaten commonly by snakes at one site were absent from others (e.g. mice were

found on Garden Island but not at most other sites) and thus, geographical differences in prey types are inevitable. Of more interest are the ways in which this heterogeneity in trophic resources has influenced the attributes of the pythons that prey upon these diverse taxa.

Does the geographical variation in prey types correlate with the geographical variation in the body sizes

Table 3. Prey items recorded from alimentary tracts of free-ranging carpet pythons (*Morelia spilota imbricata*) from five populations in south-western and southern Australia. The table shows mean mass for prey items of each species, and the number of snakes in which each prey type was recorded. Prey masses for most reptile and mammal species were means calculated from trapping data (Pearson, unpubl.). Masses for birds were taken from Keast (1985), Boles (1988) and Johnstone & Storr (1998). * introduced (non-native) species

	Mean prey mass (g)	Juvenile		Adult	
		Males	Females	Males	Females
GARDEN ISLAND					
MAMMALS					
Tammar wallaby <i>Macropus eugenii</i> (subadult)	3000		4		7
House mouse* <i>Mus domesticus</i>	12	34	77	100	
BIRDS					
Brush Bronzewing <i>Phaps elegans</i>	198			1	1
Laughing Dove* <i>Streptopeli senegalensis</i>	110		6	3	
Painted Button Quail <i>Turnix varia</i>	67		7	9	
Singing Honeyeater <i>Lichenostomus virescens</i>	28				
Golden Whistler <i>Pachycephala pectoralis</i>	25			1	
Grey Fantail <i>Rhipidura fuliginosa</i>	8	1	3	5	
Unidentified birds		2	5		
REPTILES					
Marbled gecko <i>Christinus marmoratus</i>	3	4	8	2	
Spiny-tailed gecko <i>Strophurus spinigerus</i>	6	23	61	22	
Fence skink <i>Cryptoblepharus plagiocephalus</i>	1	1		1	
Cool-skink <i>Acritoscincus trilineatum</i>	5	1	7	1	
King skink <i>Egernia kingii</i>	228	1	7	8	
Burton's legless lizard <i>Lialis burtonis</i>	11		3	4	
Morethia <i>Morethia obscura</i>	2	3	12	7	
Bobtail <i>Tiliqua rugosa</i>	300		4		
Unidentified gecko		3	8	2	
Python sloughed skin				1	
Unidentified skink			1	3	
Unidentified		19	16	13	
DRYANDRA					
MAMMALS					
Woylie <i>Bettongia penicillata</i>	1500		1		
Numbat <i>Myrmecobius fasciatus</i>	425		1		
Brush-tailed possum <i>Trichosurus vulpecula</i>	2000		1		1
Western barred bandicoot <i>Perameles bougainville</i>	300		1		
Mardo <i>Antechinus flavipes</i>	50				
BIRDS					
Purple-crowned Lorikeet <i>Glossopsitta porphyrocephala</i>	46	1			
Port Lincoln Parrot <i>Bernardius zonarius</i> (chick)	115		1		
Unidentified bird		1	1		
Unknown					1

Table 3. (Continued)

	Mean prey mass (g)	Juvenile		Adult	
		Males	Females	Males	Females
MONDRAIN ISLAND					
MAMMALS					
Bush rat <i>Rattus fuscipes</i>	71	3	6		2
BIRDS					
Unidentified bird				1	1
REPTILES					
King skink <i>Egernia kingii</i>	228			2	
Unknown skink		1			
Unknown					1
WEST WALLABI ISLAND					
MAMMALS					
Tammar wallaby <i>Macropus eugenii</i>	3000		1	1	8
Bush rat <i>Rattus fuscipes</i>	71	2		1	
BIRDS					
Brush Bronzewing <i>Phaps elegans</i>	198			1	
Painted Button Quail <i>Turnix varia scintillans</i>	67			3	
Unidentified bird			4	3	1
REPTILES					
King skink <i>Egernia kingii</i>	228		2		
Stokes skink <i>Egernia stokesii stokesii</i>	90		2	13	
Dwarf bearded dragon <i>Pogona minor minor</i>	41		1	1	
Unknown skink			1	1	
ST FRANCIS ISLAND					
MAMMALS					
Bandicoot <i>Isoodon obesulus nauticus</i>	300				1
BIRDS					
Singing Honeyeater <i>L. virescens</i>	18			1	
Painted Button Quail <i>T. varia</i>	106			1	
Buff-banded Rail <i>Gallirallus philippensis</i>	182				2
Unknown bird				1	
REPTILES					
Sand-skink <i>Egernia multiscutata</i>	16	1			

and sexual dimorphism of the pythons? Unfortunately, such a comparison is difficult to make in any quantitative fashion. Numbers of prey items provide no information on the importance of different prey types in terms of overall nutrient intake (a 4-kg wallaby is more important than a 10-g mouse). Although we do not have quantitative data on prey abundance, the overall pattern is that pythons attain larger body sizes in localities where larger prey are more abundant. Garden Island has tammar wallabies at high densities and pythons at that site attain body masses >5 kg. Large mammals are much less abundant at the other study areas, and the snakes are smaller. Notably,

adult female pythons do not attain large body sizes on islands where they do not consume large mammals (Mondrain and Saint Francis: see Figs 2 and 5). In contrast, the availability of these large prey items is irrelevant to the body sizes of adult male snakes, because almost all males are too small to consume such prey (the sole exception was a 1.73-m male on West Wallabi Island that had eaten a tammar wallaby). The fact that small pythons have access to suitable prey (generally lizards) at all sites may explain why the mean adult body sizes of male pythons showed less geographical variation than did those of females (Fig. 2) and hence, why geographical

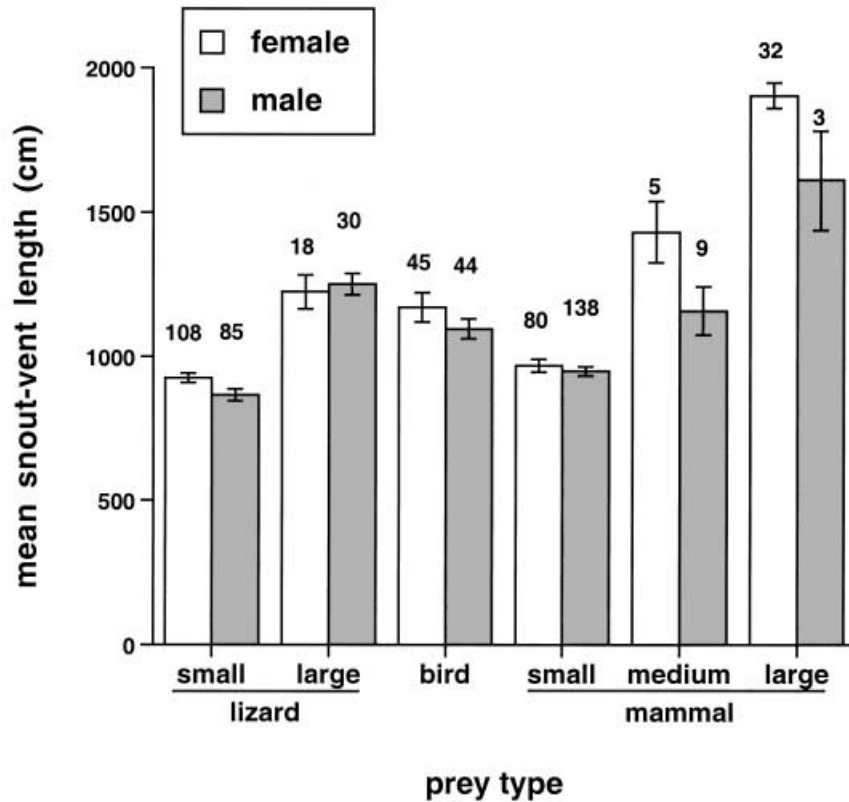


Figure 6. Mean snout–vent lengths (and associated standard errors) of carpet pythons recorded to consume various types of prey. Data combined for all study localities. Sample sizes shown above histograms. See text for statistical results, and Table 3 for actual prey species involved in each category.

variation in SSD was driven primarily by variation in the sizes of females rather than males (see above).

The strongest evidence that the array of available prey sizes constrains the range of achievable (energetically viable) body sizes for pythons comes from the correlated size-related shifts in prey mass and body condition in the Garden Island snakes. Over an intermediate range of body sizes where the only ingestible prey were small relative to predator size, the pythons on Garden Island were emaciated (Fig. 7) and grew very slowly (Pearson *et al.*, 2002). No such effect was seen in other populations, where a more continuous range of prey sizes was available to the snakes. This comparison strongly supports the idea that the body sizes of pythons in an area are affected by the size range of available prey.

It may generally be true that snakes attain larger body sizes in places where they can obtain larger prey (e.g. Schwaner & Sarre, 1988; Forsman, 1991a,b). The mechanism that generates this correlation might be adaptive, or simply reflect phenotypically plastic responses of growth trajectories to rates of food intake (Madsen & Shine, 1993). In either case, SSD may mean that the sexes are differentially affected by prey-

size spectra. This effect occurs on an extraordinary scale with our carpet pythons, notably on Garden Island where mean prey sizes for adult male and female snakes differed by a factor of 300 (10 g vs. 3 kg).

In a gape-limited predator, geographical differences in the availability of prey of different sizes may impose selection not only on mean body sizes of predators, but also on the relative size of the trophic apparatus (Forsman, 1991a,b; Forsman & Lindell, 1993). In keeping with this prediction, we found significant variation among study populations not only in the relative size and shape of the pythons' heads, but also in the nature and magnitude of sexual dimorphism in these traits (Fig. 3). Unfortunately, it is difficult to correlate such morphological variation with underlying prey-size spectra. It is possible that these differences reflect adaptations to foraging biology (e.g. longer tails in more arboreal snakes; larger heads in snakes eating relatively larger prey) but equally, the divergence might reflect nonadaptive processes such as genetic drift. Populations of carpet pythons in eastern Australia apparently do not display sex divergence in relative head sizes (Shine, 1991), whereas this was a consistent feature of the western populations (Fig. 3).

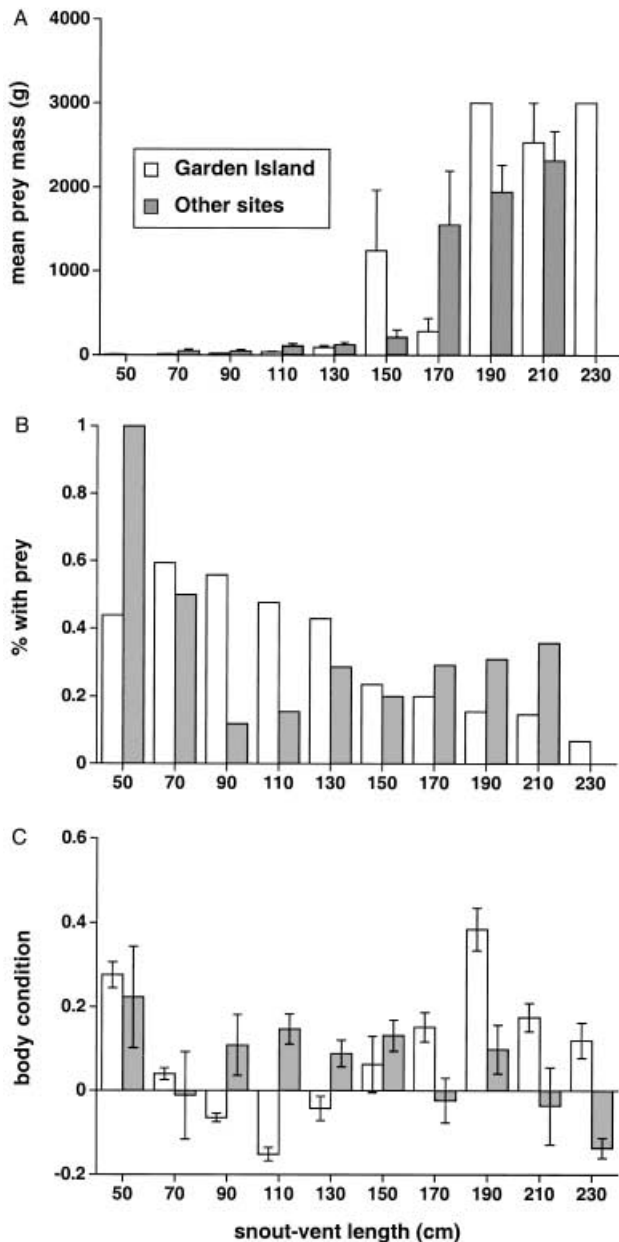


Figure 7. Effects of python body size (snout-vent length) on the size of prey items ingested (prey mass: A), the frequency of feeding (as indicated by the proportion of snakes containing identifiable prey items: B) and the body condition of the snakes (residual scores from the linear regression of \ln mass to \ln SVL: C). Pythons on Garden Island (where the sizes of available mammalian prey are dichotomous) are compared to those of the other four localities combined (where prey sizes are more continuously distributed).

This observation fits with the notion of adaptation to prey-size divergence, because the sex divergence in prey types is much greater for our populations than for those in eastern Australia (Fearn *et al.*, 2001). However, the evidence is necessarily weak. There seems to have been only a single evolutionary origin (or loss) of sex dimorphism in relative head size within carpet pythons (i.e. *M. s. imbricata* vs. the other subspecies). Also, the sex divergence in relative head sizes within *M. s. imbricata* might be an effect of, rather than an adaptation to, sex divergence in prey sizes (Bonnet *et al.*, 2001).

Despite these uncertainties, the isolated populations of south-western carpet pythons provide a remarkable example of correlated intraspecific divergence in morphology, sexual dimorphism and ecology (food habits). The magnitude of sex divergence in dietary habits, especially in the Garden Island population, is extraordinary. The presence of significant sexual dimorphism in several aspects of body shape as well as absolute body size (and of geographical variation in both of these aspects), fits well with this extreme sex-based niche divergence. Although we need experimental studies to tease apart the roles of adaptation and phenotypic plasticity in generating such complex patterns, these snakes provide strong support for the hypothesis that SSD in natural populations is determined by ecological factors as well as by sexual and fecundity selection. Thus, explanations for geographical variation in SSD need to consider the role of ecological resources as well as reproductive pressures.

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