THE ECOLOGY AND CONSERVATION OF THE SOUTH-WESTERN CARPET PYTHON, *MORELIA SPILOTA IMBRICATA*

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ABSTRACT

Carpet pythons (*Morelia spilota*) are large nonvenomous snakes with a very broad geographic distribution across mainland Australia. Several subspecies have been recognised, of which one of the most distinctive is *Morelia spilota imbricata* from the south-western corner of the continent and adjacent offshore islands. This taxon has declined across much of its range over recent decades, and the present study was initiated to provide basic ecological information on this poorly-known animal. A better understanding of the snakes' body sizes, reproductive behaviour, diet, habitat use, home range sizes and movements may help to plan for the conservation of this important predator.

Unusually among reptiles, Australian carpet pythons display substantial geographic variation in mating systems and sexual size dimorphism. A detailed study of a population on Garden Island near Perth, Western Australia greatly expands the range of variation previously documented for populations of *M. spilota*. Unlike eastern Australian populations where sex differences in mean adult body size are relatively minor (< 10% in SVL, < 30% in mass), female *M. s. imbricata* grow to over twice the length and more than ten times the mass of adult males. Mean adult size averages 104 cm snout-vent length (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 the influence of 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. *Morelia spilota* displays the greatest geographic variation in sexual size dimorphism yet recorded for any vertebrate species.

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. Studies of one mainland and four insular Western Australian populations of carpet pythons revealed remarkable geographic variations 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. Reproductive biology was similar across these four populations, so that the high degree of geographic variation in sexually dimorphic aspects of body size and shape plausibly results from geographic variation in prey availability.

Radio-telemetry was used to study various aspects of the ecology of carpet pythons at Garden Island and Dryandra Woodland, sites with markedly different climates and habitats. Radio-transmitters were surgically implanted in 75 pythons and they were tracked for periods of 3 months to 4 years. The availability of miniature radio-transmitters has revolutionised the study of snake ecology with most workers surgically inserting transmitters into the animal's peritoneal cavity. Methods for surgical implantation of transmitters are now sophisticated and effective, but as more people use these techniques, new complications will undoubtedly appear. I found that free-ranging carpet pythons were able to rid themselves of surgically-implanted transmitters by incorporating the transmitter into the alimentary tract and then expelling it with faeces. Subsequent recapture of animals that had expelled transmitters confirmed that this process did not kill the snakes. Snakes that expelled transmitters covered a wide range of body sizes, included both sexes, and transmitters were carried for periods of 1 to 24 months before expulsion. Males expelled transmitters more frequently than females, but there was no significant difference between rates of expulsion between the two study areas. The most consistent correlate to explain expulsion may involve feeding. Eleven of the 14 expulsions were associated with faecal material, suggesting that they followed soon after the snake had taken a large prey item relative to its own body size. Massive temporal shifts in the size and activity of the alimentary tract in ambush predators means that they may be able to incorporate foreign objects during this rapid increase in size of the gut. If such abilities are widespread, there is an obvious caveat for interpretation of radio-telemetry studies. Researchers finding a transmitter in the field would be tempted to conclude that the animal carrying that telemeter had died and/or been consumed by a predator. Predation should not be assumed as the cause of death for radio-tracked snakes, unless the carcass (or part of it) is available.

The activity and movement patterns of pythons were also examined. Dryandra pythons remained inactive inside tree-hollows during cooler months (May-September), whereas some (especially small) pythons on Garden Island continued to move and feed. Overall weekly displacements (mean = 100 to 150 m) were similar at the two study sites and among age-sex classes, except that reproductive females were sedentary during summer while they were incubating eggs. Home ranges averaged between 15 ~~to~~ and 20 ha. Adult male pythons had larger home ranges than adult females at Dryandra, but not at Garden Island.

Some radio-tracked snakes exhibited high site fidelity, frequently returning to previously occupied sites after long absences. Pythons at Dryandra were found primarily in hollow logs and tree-hollows, whereas Garden Island snakes usually sheltered under shrubs. At both study sites, habitat usage was similar among different age/sex classes of snakes, except that juvenile pythons were more arboreal than adults. Although carpet pythons demonstrate great flexibility in habitat use, certain habitat elements may be critical for the persistence of viable populations. Fire plays a central role in this process, albeit in complex ways. For example, low-intensity fires reduce the availability of hollow logs on the ground at Dryandra, whereas paradoxically, high-intensity fires may fell trees and thus generate more logs - but might also threaten overwinter trees. Thus, disturbances such as wildfires that alter important microhabitats (such as vegetation cover on Garden Island or log availability at Dryandra) are likely to threaten python populations. At Dryandra, landscape management should include occasional fire events to generate new logs as well as shrub thickets used by prey. Strategic burning may also be required at Garden Island to regenerate some vegetation communities.

My radio-telemetric monitoring of 70 pythons also provided extensive data on the thermal ecology of free-ranging snakes. Body-temperature regimes were affected by season, time of day, location, microhabitat, size and sex, behaviour, and reproductive state. Over most of the year, pythons exhibited relatively smooth unimodal diel curves of heating and cooling, attaining maximal temperatures around 30°C. The smaller male snakes heated and cooled more rapidly than did the larger adult females. Climatic differences between my two study sites generated substantial shifts in mean body temperatures and thus, in the diel timing of ambush foraging behaviour.

Females wrapped tightly around their eggs after oviposition and brooded them throughout the ensuing seven to nine week incubation period. Throughout this time, females were facultatively endothermic, maintaining high constant temperatures through shivering thermogenesis. Females nesting in sites with relatively poor thermal buffering (under rootballs of fallen trees rather than rock crevices) supplemented endogenous heat production with occasional basking, and hence maintained lower and more variable incubation temperatures than did females with "better" nest-sites.

Knowledge of the life history attributes of a threatened species may assist in developing conservation management actions to negate or reduce negative factors acting upon it. Because the south-western carpet python is a

large ambush predator, of poorly known habitat requirements and with a preference for mammalian prey at maturity, it may be susceptible to direct (e.g. habitat clearance) or indirect (e.g. introduction of feral predators) anthropogenic habitat change. In order to provide information to guide conservation actions for this species, life history attributes were documented and examined to identify crucial times or events in the life cycle.

Female *M. s. imbricata* mature at large sizes and produce large clutches of eggs (range 9-30) in the wild. Reproduction is energetically expensive for females through lost feeding opportunities, vitellogenesis and incubation. Up to 31% of pre-reproductive weight may be lost and wild females take two or more years to recover condition sufficiently to breed again. The period after the hatching of their eggs is especially dangerous for female pythons. Thin and emaciated, with heavy parasite loads and reduced muscle tone and mass, they must quickly ambush prey to begin their recuperative journey. Males expend less energy in reproduction, but nonetheless face hazards associated with their wide-ranging movements in the breeding season. Management actions that preserve habitat integrity and continuity, reduce feral predators and maintain vigorous populations of prey species will substantially benefit the conservation of this python.

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A thesis with a gestation period as long as this one does not reach fruition (an explosive parturition?) without the assistance and generosity of many people.

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SVL and rectal sample?). During my candidature, we started a family. Josh has unwittingly become a key member of the python processing team as our weekends often involve measuring and marking pythons. Thank you Donna and Josh - you make my life special.

Addendum

1) Page 58, insert following text after line 10; Fire incidence is controlled at both sites. On Garden Island, fires are immediately suppressed to protect Naval installations and at Dryandra, there are limited strategic prescribed burns to prevent wildfires, typically undertaken in late winter and spring.

2) Page 60, insert text after line 11: These distances represent the minimum distance traveled over that period and so are likely to seriously underestimate daily movement patterns in the warmer months when the pythons are particularly active.

3) Page 63, insert text at line 15: The smoothing parameter reduces the impact of measurement error associated with the location of an animal.

4) Page 81, insert text after line 4: A notable exception occurs amongst tropical varanids, where some species thermoregulate more accurately than other species for reasons that remain unknown (Christian and Weavers 1996).

5) Page 93, insert text after line 19: Since juvenile female pythons eat more frequently than males, another explanation is that they are more often engaged in post-prandial basking.

6) Additional references:

Bureau of Meteorology (2001) Climate averages. Commonwealth of Australia. http://www.bom.gov.au/climate/averages.
Christian, K.A. and Weavers, B.W. (1996) Thermoregulation of monitor lizards in Australia: An evaluation of methods in thermal biology. *Ecological Monographs* 66:139-157.
Plummer, M.V. (1987) Geographic variation in body size in green snakes (*Opheodrys aestivus*). *Copeia* 1987:483-485.

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CHAPTER 1

Introduction

Carpet Pythons (*Morelia spilota*) are found across much of the land mass of mainland Australia, but are absent from the arid deserts and the most mesic and cool regions of the south-eastern corner. Reflecting their wide distribution, their abundance and (especially) their very large body size, carpet pythons are perhaps one of the best-known snake species for many Australians. Many people have stories of sightings while on holidays or visiting farms; or they know people who kept one as a pet; or they can recall a carpet python that raided their neighbour's chicken coop or ate the family "budgie". Nonetheless, the acquaintance between snakes and humans is relatively superficial: few people ever see more than one or two pythons in their lifetime. These charismatic predators appear briefly in view on the margins of our cities and farms and then seemingly disappear without trace.

It came as a surprise to me some years ago when reading through the "threatened fauna" schedule for Western Australia (WA) that four species of pythons were listed in this category. Even more surprisingly, one of the listed taxa was that seemingly ubiquitous and common snake, the carpet python. The disproportionate representation of pythons (4 of 11 species occurring in WA) on the schedule of threatened fauna stimulated my interest to find out what factors were responsible for their apparent declines, and what actions might be needed to improve their conservation status.

Australia has a sad record of mammal extinctions since European settlement. Since carpet pythons are large ambush predators of vertebrates (especially mammals), it could be anticipated that their populations would also decline as a consequence of both the loss of prey species and rapid habitat change. However, anecdotal accounts and some more detailed studies (Shine & Fitzgerald 1996; Fearn et al. 2001) have indicated that carpet pythons are able to adapt to changed habitat conditions (e.g. they can use buildings for shelter) and can take advantage of alternative prey (e.g. introduced species such as black rats and rabbits). Given this ecological flexibility, why then would pythons living in the southern regions of Western Australia - the woma (*Aspidites ramsayi*) and the south-western carpet python (*Morelia spilota imbricata*) - be threatened with extinction?

Searches of the literature revealed only fragmentary ecological information for these two species. The woma has declined throughout most of southern WA, particularly in the "Wheatbelt" region, that has been extensively cleared for cereal production (Smith 1981). The south-western subspecies of the carpet python has also apparently declined based on rate of accessions at the Western Australian Museum (Smith 1981). While the woma is not listed on State and Federal "threatened fauna" schedules (because of its wide distribution in arid Australia), the south-western carpet python is listed as "specially protected" in WA. This listing was based both on its apparent population decline and the perceived value of this python in the illicit pet-trade (it is illegal to keep reptiles without a licence in WA, and such licences are not issued for pets).

The lack of even basic biological information about these pythons made it clear that ecological study of one or more populations was necessary if we were to understand potential threatening processes. In an effort to locate suitable study populations, I initiated a sighting survey of pythons with the staff from the Department of Conservation and Land Management, amateur herpetologists and the general public. The findings of this survey have been published (Pearson 1993). No population of womas in south-western WA was reported, so I focussed my research efforts on the carpet python.

My primary research techniques were mark-recapture and radio-telemetry. I selected two study sites with apparently large populations of carpet pythons: Garden Island 45 km SW of Perth and Dryandra Woodland, 140 km SE of Perth. I also visited several island populations of *M. s. imbricata* for short periods to document the range of morphological and ecological characteristics within *M. s. imbricata*. Radio-telemetry was not used at these additional sites. Chapter 2 describes my detailed study of the Garden Island population of *M.s. imbricata*. Over 675 pythons were captured and morphometric, reproductive and dietary information collected. Necropsies of pythons killed on roads increased available data on age at maturity, diet and seasonal reproductive status. Previous research had indicated that this species of python displays substantial geographic variation in mating systems and sexual size dimorphism. I thus compared my data from Garden Island pythons with similar information from these previous studies in other parts of the continent. Unlike eastern Australian populations where sex differences in mean adult body size are relatively minor, female *M. s. imbricata* grow to over twice the length and more than ten times the mass of adult males. Reasons for these differences are considered in light of the observed variation in mating systems between subspecies. My data suggest that *Morelia spilota* displays the greatest geographic variation in sexual size dimorphism yet recorded for any vertebrate species.

Sexual dimorphism is typically interpreted in terms of reproductive adaptations, but the degree of sex divergence also may be affected by sex-based niche partitioning. In Chapter 3, I describe studies of one mainland and four insular Western Australian populations of carpet pythons. These comparisons revealed remarkable geographic variations in sexual size dimorphism (SSD) associated with differences in available prey resources.

Unexpectedly, my radio-telemetry studies at Garden Island and Dryandra revealed that pythons were able to expel surgically-implanted transmitters through their alimentary tract. Chapter 4 describes this phenomenon and its possible implications for fieldworkers interpreting the cause of death of telemetered snakes.

In Chapter 5, the activity and movement patterns of pythons and the sizes of home ranges are compared between the two study sites. These data provide a basis for suggestions about the effects of fire on the availability of hollow logs and overwinter trees at Dryandra, and suggestions are made for the management of these resources.

Thermoregulation is likely to be a major determinant of behaviour of pythons living in mid-latitudes, as they are subject to substantial differences in seasonal temperature profiles. Chapter 6 uses data from 70 telemetered pythons to describe the thermal ecology of *M. s. imbricata*. I focus particularly on the temperatures exhibited by reproductive females, and the role of nest-site selection in this respect.

Finally, Chapter 7 provides data on aspects of the reproductive biology of carpet pythons not covered in previous chapters. The emphasis here is on life history attributes relevant to the conservation of this threatened species. For example, I attempt to identify critical times, places or events that may render pythons vulnerable to disturbance or mortality.

Female reproduction appears to be one such event, and hence is the main focus of the chapter. I conclude with some suggested management actions that would aid the conservation of carpet python populations in south-western Australia.

CHAPTER 2

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

ABSTRACT

Unusually among reptiles, Australian carpet pythons (*Morelia spilota*) display substantial geographic variation in mating systems and sexual size dimorphism. I studied a population of the south-western subspecies (*M. s. imbricata*) of this widely distributed taxon, on Garden Island near Perth, Western Australia. My 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 SVL, < 30% in mass), female *M. s. imbricata* grow to over twice the length and more than ten times the mass of adult males. Mean adult size averages 104 cm snout-vent length (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" size

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* Pearson, D., Shine, R. & Williams, A. (2002). Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia*, in press.

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. *Morelia spilota* displays the greatest geographic variation in sexual size dimorphism yet recorded for any vertebrate species.

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 & 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 1991a; Heulin et al. 1999).

Analyses of mating systems and sexual size dimorphism in reptiles have generally relied upon much broader comparisons (e.g. Fitch 1981; King 1989a), but at least one species of snake has been found to exhibit geographic variation in both of these traits (Shine & 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 & Shine 1988a; Shine & Fitzgerald 1995). The correlation between mating system and sexual size dimorphism fits well with sexual-selection theory (e.g. Darwin 1871; Andersson 1994) and with the results of broader (interspecific) comparisons (Shine 1994a). 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 & Barker 1994). In the present study I 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) 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, pers. comm.).

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 & Barker 1994). This snake feeds on reptiles, birds and small mammals, including prey items as large as small wallabies (Wilson & 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

My 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 1100 ha (Marchant &

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 margin of Garden Island, limestone occurs as eroded sea cliffs and partially submerged reefs (McArthur & 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 prickle lily, *Acanthocarpus priessei* (McArthur & Bartle 1981). The vertebrate fauna is relatively depauperate, with introduced house-mice (*Mus musculus*) and tammar 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

I commenced a mark-recapture study of pythons in September 1995. Pythons were obtained from several sources. Road-driving after sunset (between 1800-2300 hr) 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). Snout-vent (SVL) and tail lengths 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 & Finster 1933; Spellerberg 1977; Madsen & Shine 1996). To aid the identification of recaptured snakes should their scale clips be unclear, three other characteristics were recorded. These were: (i) variations in the arrangement of subcaudal scales (these are usually paired but single and triple scales occur frequently); (ii) the arrangement of scales posterior to the parietal head shields; and (iii) 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.

I 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. 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 could not be induced to feed. The snakes were housed individually in glass-fronted wooden cages (50 x 40 cm and 40 cm high). Each cage had a layer of paper towel on the floor, a heat pad (35 x 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. I 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 sexual size dimorphism

I 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 2.1 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

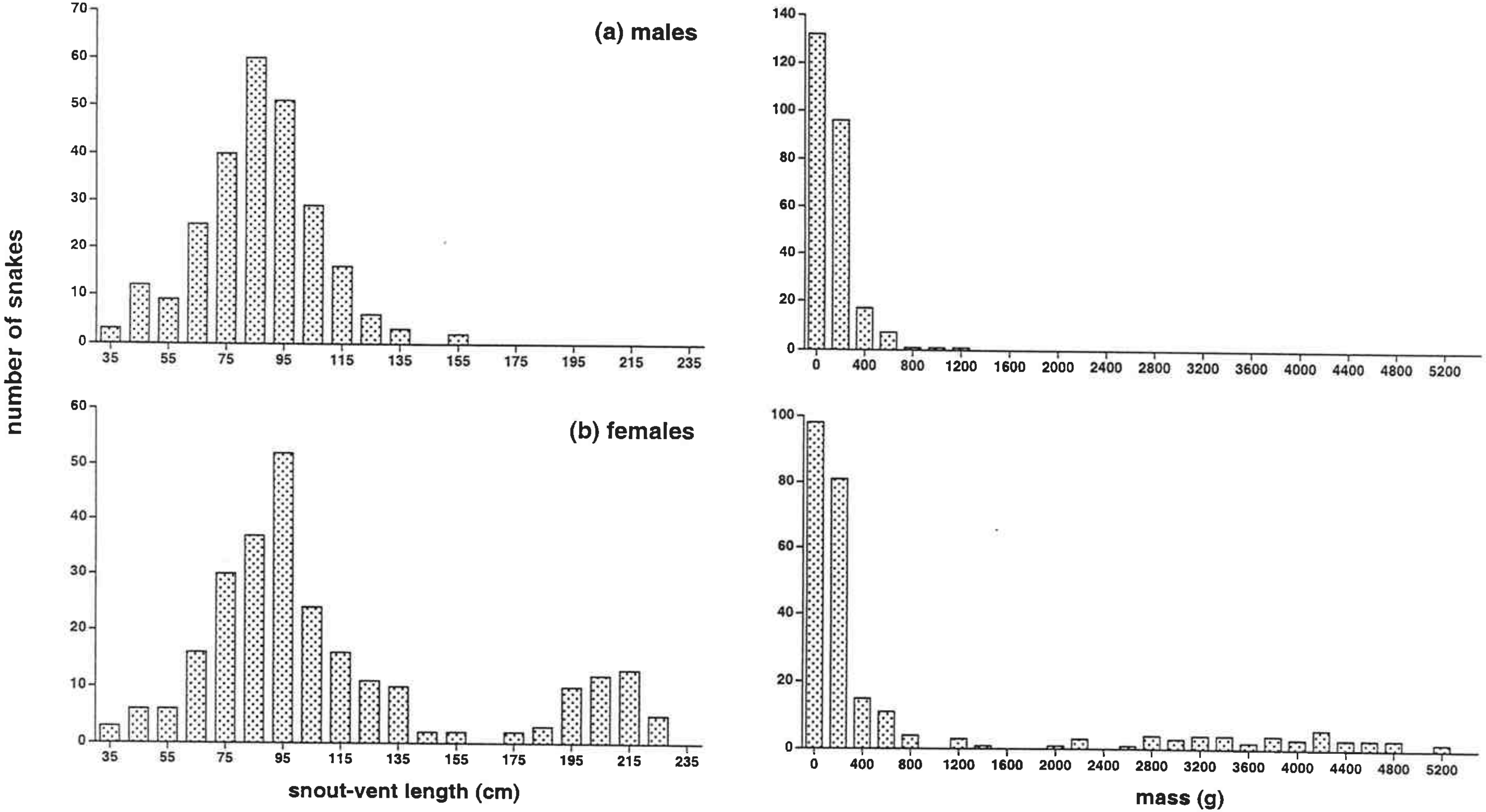

Figure 2.1. Body sizes of male (n = 256) and female (n = 262) carpet pythons (*Morelia spilota imbricata*) from Garden Island, Western Australia. Graphs on the left show frequency distributions of snout-vent lengths for males and females; and graphs on the right show frequency distributions of body mass for males and females.

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 my study ranged in size from 203.0 to 234.5 cm SVL, and weighed 4.25 to 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 2.1). 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 2.1).

Table 2.1. 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 females, 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 (n = 154)**	**Adult females (n = 39)**	**Statistical test**	***P***
SVL (mm)	1035.63 (135.77)	2139.54 (95.51)	$t = 47.82$	< 0.0001
Mass (g)	305.55 (170.42)	3935.13 (737.23)	$t = 55.86$	< 0.0001
Tail length (mm)	178.84 (25.61)	327.29 (18.18)	$t = 33.65$	< 0.0001
Jaw length (mm)	34.66 (4.27)	67.54 (2.81)	$t = 45.03$	< 0.0001
Head width (mm)	25.46 (3.67)	55.05 (3.09)	$t = 45.88$	< 0.0001
Head depth (mm)	11.95 (1.79)	26.14 (1.50)	$t = 45.16$	< 0.0001
Midbody diam. (mm)	26.86 (4.50)	63.11 (6.82)	$t = 39.31$	< 0.0001

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 ($\chi^2_1 = 112.12$, $P < 0.0001$). 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 & Lovich 1990). My recapture data allow me 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 recaptured once, seven twice, and eight on three or more occasions; 45 females were recaptured once, 10 twice, and four more than twice, $\chi^2_1 = 2.386$, $P = 0.303$). 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 and Shine 2002), and she was killed by a senseless human action.

Growth rates

I 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 2.2 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

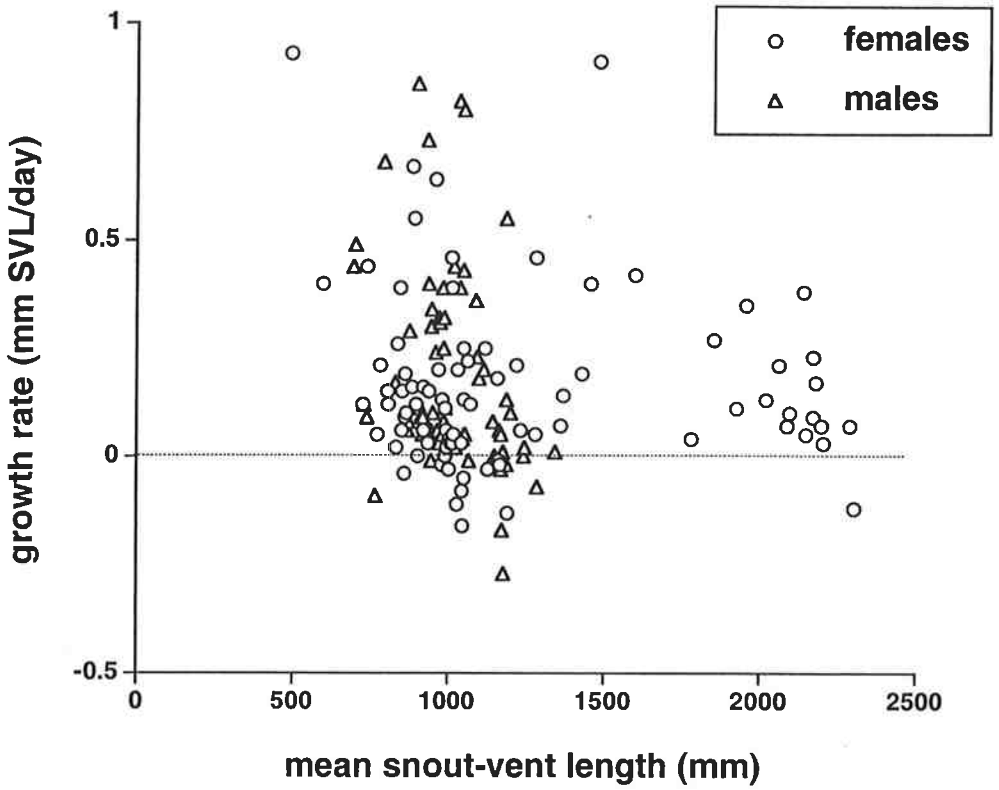

Figure 2.2. Growth rates of recaptured carpet pythons as a function of mean body size (snout-vent length) during the intervening period. See text for explanation and statistical tests.

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, $F_{1,145} = 0.5.61$, $P < 0.02$). 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 have low growth rates at this body size also, but some individuals continue to grow, sometimes quite rapidly (Fig. 2.2).

Why do the sexes differ in growth rate?

Given that the extreme sexual size dimorphism 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 & Shine 1988b). The snakes maintained in captivity provide more reliable information on this topic. I discarded data for two females and one male that were reluctant feeders, and hence lost mass during their period in captivity (Table 2.2). For the remaining animals (four males, four females), I recorded the number and mass of prey items consumed by each animal, and their consequent growth.

Table 2.2. 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 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	128.3	1757.5	243	0.420	73	0.126
Male 335	654	123	1583.5	184	0.281	96	0.147
Male 343	639	110.1	1147	197	0.308	187	0.293
Male 349	610	128.9	1487.5	80	0.131	82	0.134
Male 363	442	139.9	1029	-168	-0.380	39	0.088
Female 284	730	144.8	3604.4	724	0.992	311	0.426
Female 334	654	127.8	922	-52	-0.080	106	0.162
Female 337	654	147.8	3536	654	1.000	169	0.258
Female 373	424	149.8	3138	796	1.877	204	0.481
Female 379	404	134	3236.5	1030	2.550	303	0.750
Female 415	354	128.4	784.5	-7	-0.020	82	0.232

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 snout-vent length 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, I 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

My fieldwork provided 34 records of close male/female proximity or mating in free-ranging snakes (Table 2.3). All records came from spring and early

Table 2.3. 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 (#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
13 Oct 95	40*	195	2309	76	102	251	male coiled 3 m from loosely coiled female
25 Oct 95	50	206	4037	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 #50)
20 Sept 96	235	213	4731	83	129	608	tightly coiled beside each other
22 Nov 96	235			83			together in dense spiny shrub
21 Oct 96	79	197	3351	83			male coiled 2 m from female
31 Oct 96 0840 hr	79			83			male basking 1 m from female
31 Oct 96 1800 hr	79			83			male < 1 m from tightly-coiled 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

Table 2.3 cont.

Date	Female ID	SVL (cm)	Mass (g)	Male ID	SVL (cm)	Mass (g)	Comments
11 Nov 96	260	219	4824	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	4185	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	4233	259			together under dense shrub
16 Oct 97	56*	!	5200	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	5200	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	4253	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)
3 Dec 98	143	213	3394	471	106	224	coiled 10 m apart

summer (late September-mid December), indicating a strongly seasonal pattern of courtship and mating within the Garden Island population. I 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 & 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 2.3 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 snout-vent length 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, $t_{155} = 1.24$, $P = 0.22$). If the unusually small male is included in the sample of reproductive animals, the difference between the two groups is even smaller ($t_{156} = 0.17$, $P = 0.87$). Hence, there is no evidence that smaller males are excluded from mating opportunities within this population.

DISCUSSION

In conjunction with previous studies, my data reveal an extraordinary degree of geographic variation in sexual size dimorphism in carpet pythons

(*Morelia spilota*). One extreme occurs in carpet pythons (*M. s. mcdowelli*) from north-eastern New South Wales (Shine & 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 & Barker 1994; Shine & Fitzgerald 1995). The other extreme is represented by the study animals from Garden Island. Although *M. s. imbricata* is morphologically similar to *M. s. mcdowelli* (e.g. Barker & Barker 1994), its pattern of sexual size dimorphism 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 & Shine 1988a; Shine & Fitzgerald 1995).

To my knowledge, this geographic variation in sexual size dimorphism (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 & Ralls 1985; Plummer 1987 Schwaner & 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 1994a).

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 (1994a). Thus, intraspecific variation in SSD within *Morelia spilota* spans about as much variation as has hitherto been reported among snakes in general. Using the index of SSD proposed by Gibbons & Lovich (1990), indices for *M. spilota* range from -0.08 (*M. s. mcdowelli*) 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. My recapture data strongly falsify this interpretation: males are small because they differ from females in growth trajectories rather than in survival schedules (Fig. 2.2).

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 & Shine 1993a; Shine et al. 1999a). However, my 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 sexual size dimorphism 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 sexual size dimorphism should reflect the end result of a complex series of "costs" and "benefits" of different body sizes for each sex (Trivers 1976; Shine 1994a). 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 & Lovich 1990). Also, the higher maintenance costs of large body size may endanger the organism during episodes of chronic food shortage (e.g. Wilenski & 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 & 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 & Ford 1987; Slip & 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* (Table 2.3).

Interestingly, male "tactics" in this population resemble those of *M. s. spilota* in some respects (lack of male-male combat) and *M. s. mcdowelli* 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; see Table 2.3). Growth rates of recaptured animals (Fig. 2.2) 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 & Shine 1988a; Shine & Fitzgerald 1995; Chapter 7), 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 & Fitzgerald 1995).

These considerations support Shine & 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 sexual size dimorphism in carpet pythons is as follows:

(i) 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.

(ii) 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.

(iii) 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 1994a).

(iv) Evidence from other studies supports the plausibility of the putative selective pressures on male body size. Although I have no data on body size versus mating success in pythons, males found close to females were similar in size to other males (Table 2.3). In contrast, there is strong evidence of a large-male advantage in snake taxa exhibiting combat (e.g. Schuett & 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 & Shine 1993b). 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 & 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 ten times that of males at maturity. The absence of male-male combat and perhaps a restricted prey assemblage on Garden Island (Chapter 3; Pearson et al. 2002a) 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 & Shine 1994). Presumably males incur comparatively low costs associated with reproduction and are able to breed annually (see Table 2.3). 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 (Chapter 7).

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 (Table 2.3). 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 *Morelia 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.

CHAPTER 3

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

ABSTRACT

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. My studies of one mainland and four insular Western Australian populations of carpet pythons (*Morelia spilota*) reveal remarkable geographic 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.

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* Pearson, D.J., Shine, R. & How, R. (2002). Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*). *Biological Journal of the Linnean Society*, in press.

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. Reproductive biology was similar across these four populations, so that the high degree of geographic variation in sexually dimorphic aspects of body size and shape plausibly results from geographic variation in prey availability.

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, geographic 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, geographic 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. The local environment (and especially, the spectrum of available prey sizes) may often constrain the body sizes attained by organisms, with the degree of SSD varying geographically either (a) because local prey resources constrain both sexes to similar body sizes, thus preventing the expression of SSD coded in the genome (Madsen & Shine 1993a) 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, geographic 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 geographic variation in SSD than any other vertebrate species studied to date (Shine & Fitzgerald 1995). Adult males average heavier than females in some populations in eastern Australia (Shine & Fitzgerald 1995; Fearn et al. 2001), whereas females weigh ten times more than adult males in a western population (Chapter 2; Pearson et al. 2002b). 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 1994a; 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. 3.1). 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.

Here, I 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 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 colouration (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 1988c) 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

I obtained data from five populations of carpet pythons (Table 3.1, Fig. 3.1). 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 3.1) 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 2001). 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 3.1). 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 3 kg).

Table 3.1. Location and characteristics of study sites.

Study Site	**Dryandra Woodland (central block)**	**Garden Island**	**Mondrain Island**	**St. Francis Island**	**West Wallabi Island**
Latitude, Longitude (midpoint)	32° 47' S 117° 00' E	32° 12' S 115° 40' E	34° 08' S 122° 15' E	32° 36' S 133° 15' E	28° 28' S 113° 42' E
Area (ha)	12,192	1,200	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.

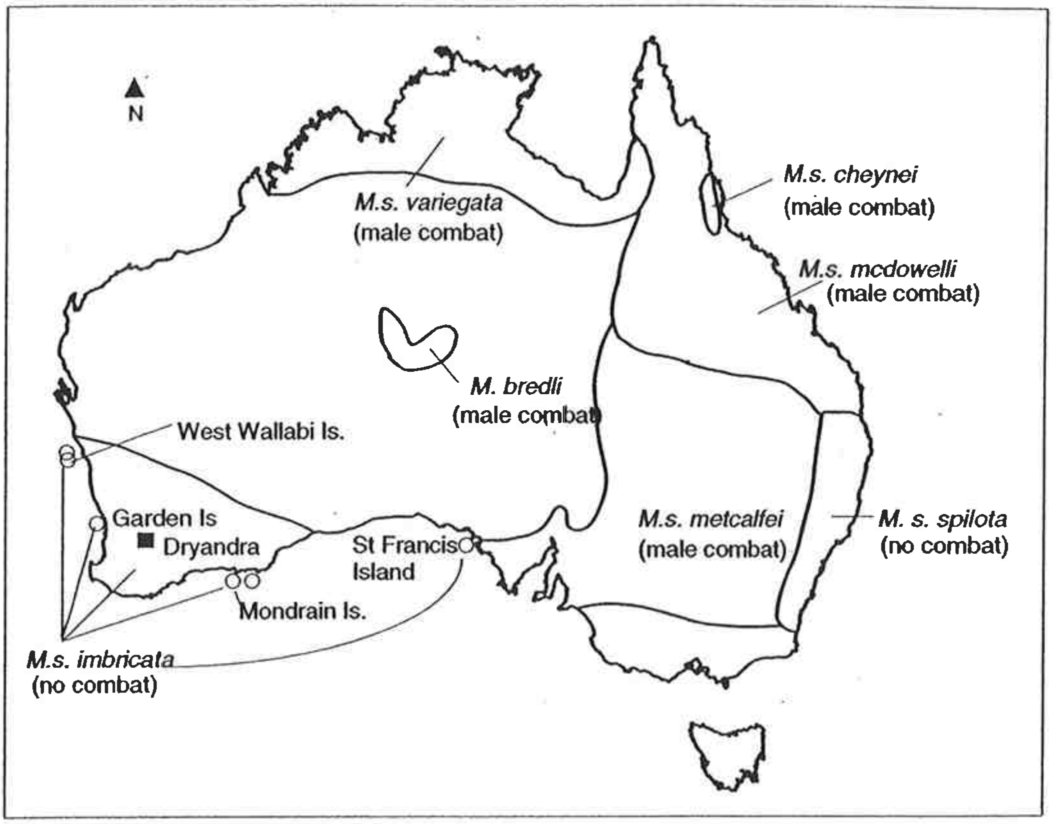

Figure 3.1. Map of Australia showing the various taxa of carpet pythons (*Morelia spilota*) recognised by Barker & Barker (1994), and their presumed mating systems. The locations of my five study populations in southern Australia are also shown.

Methods

I 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 I was conducting radio-telemetric studies on this species. The other populations were all on relatively inaccessible islands, and hence were only visited briefly during trips specifically organised for this purpose. For each captured animal I 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.

To estimate body sizes at sexual maturity, I 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, I 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 (smallest reproductive males 84 to 114 cm, with few animals in this "questionable" size range). For females, however, body sizes varied more and thus, I used actual sizes of the smallest reproductive female in each population as my 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, I classified all prey items into six categories: large (> 1 kg), medium (50 g - 1 kg) and small mammals (< 50 g), birds, and large ($\geq$ 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 3.2 shows mean values and standard errors for raw (untransformed) data, to facilitate intuitive comparisons. To compare relative proportions of animals from each population without confounding effects of geographic variation in absolute body size, I used residual scores from general linear regressions of ln-transformed variables. For example, I 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. I 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 3.3 and 3.4 show these indices based on residual scores (for ease of interpretation), my statistical comparisons relied on the more robust approach of ANCOVA, where I incorporated the independent variable as a covariate rather than using it to calculate a residual score (Sokal & Rohlf 1981; Seigel & Ford 1987).

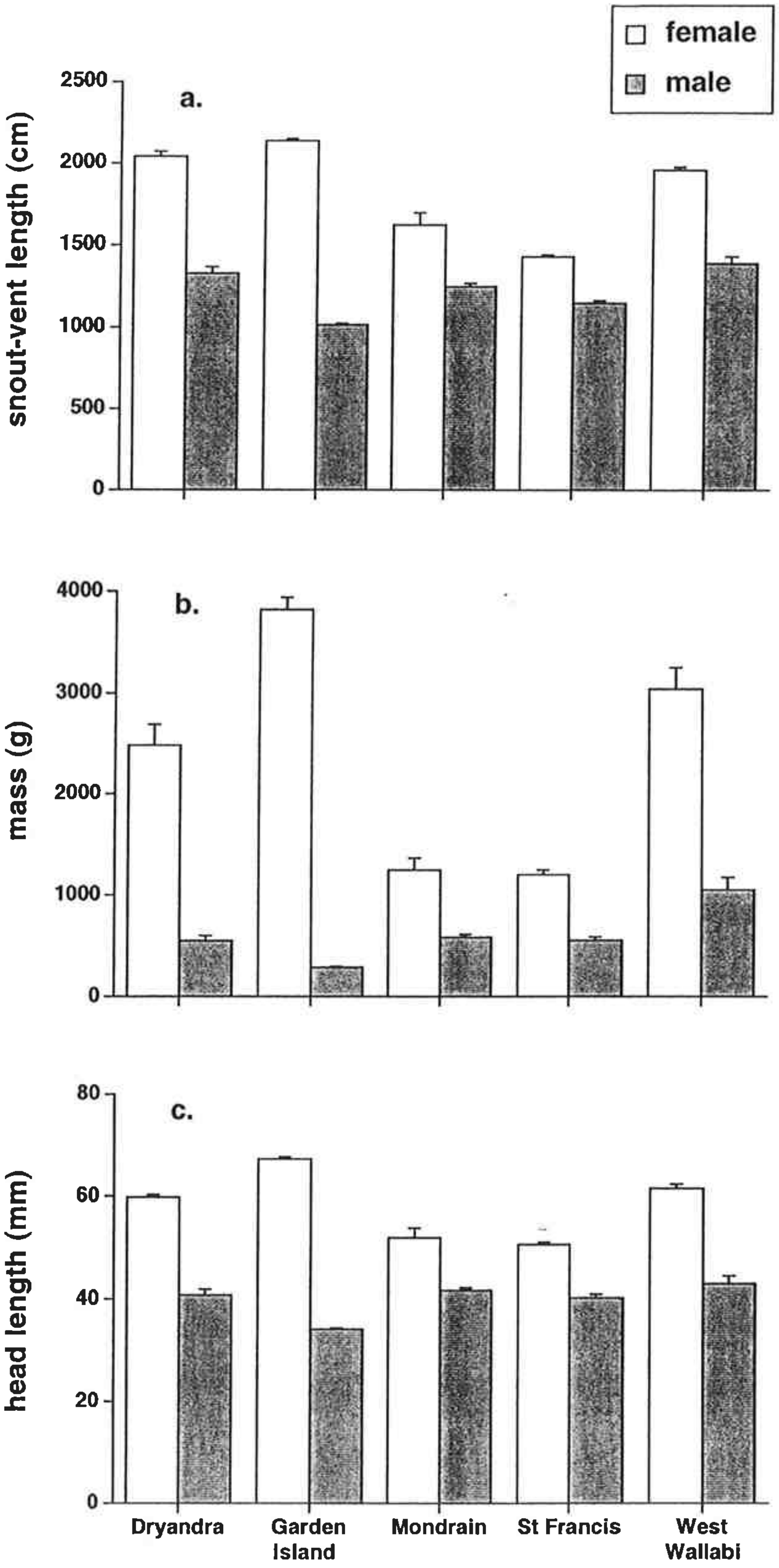

Figure 3.2. Geographic variation in mean body sizes and head sizes, and in the degree of sexual dimorphism in these traits, in adult carpet pythons *(Morelia spilota imbricata)* from five populations in south-western Australia. See Table 3.1 for sample sizes. See text for statistical analyses of these data.

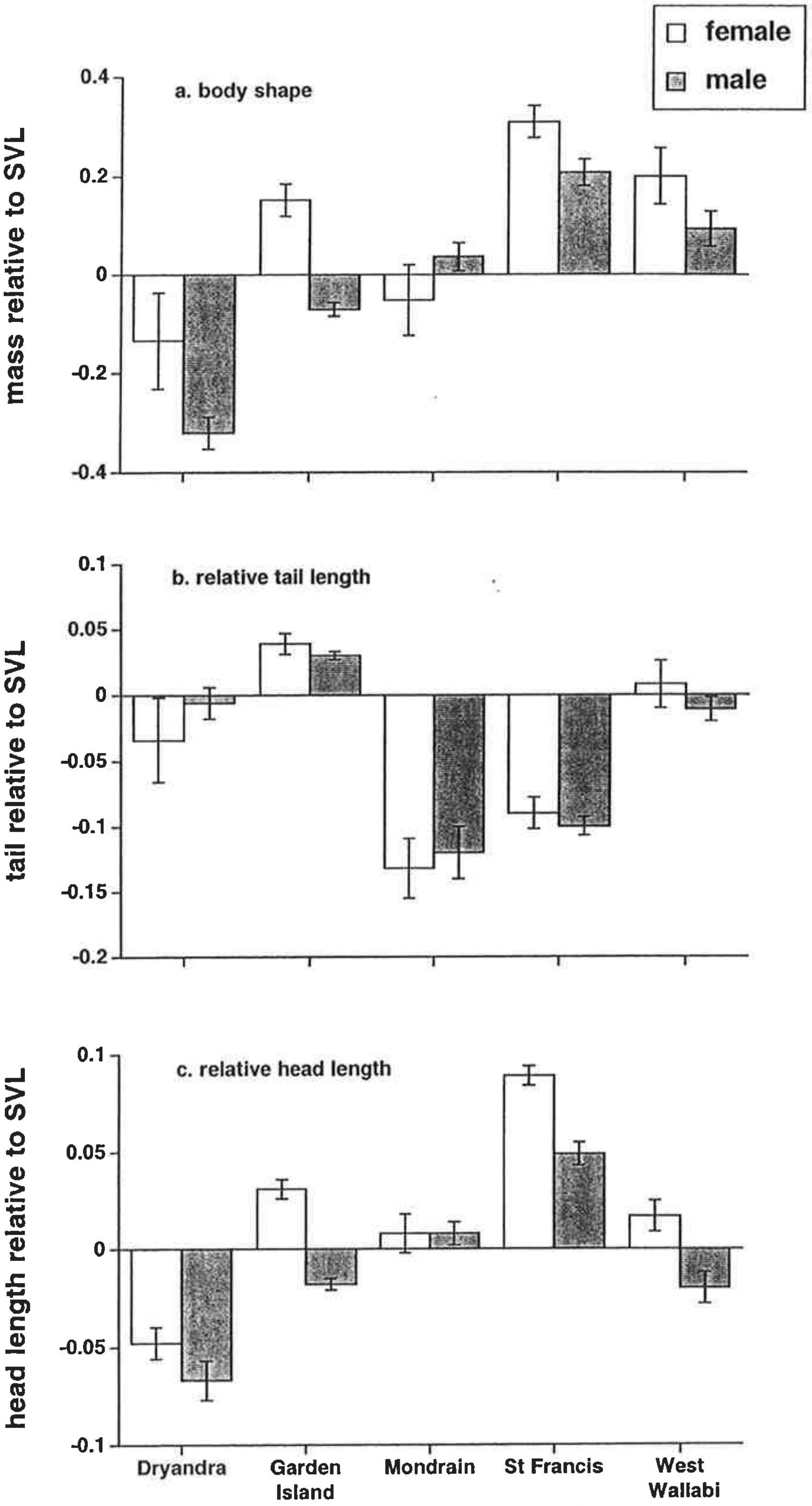

Figure 3.3. Geographic variation in body proportions, and in the degree of sexual dimorphism in these traits, in carpet pythons *(Morelia spilota imbricata)*from five populations in south-western Australia. See Table 3.1 for sample sizes. See text for statistical analyses of these data.

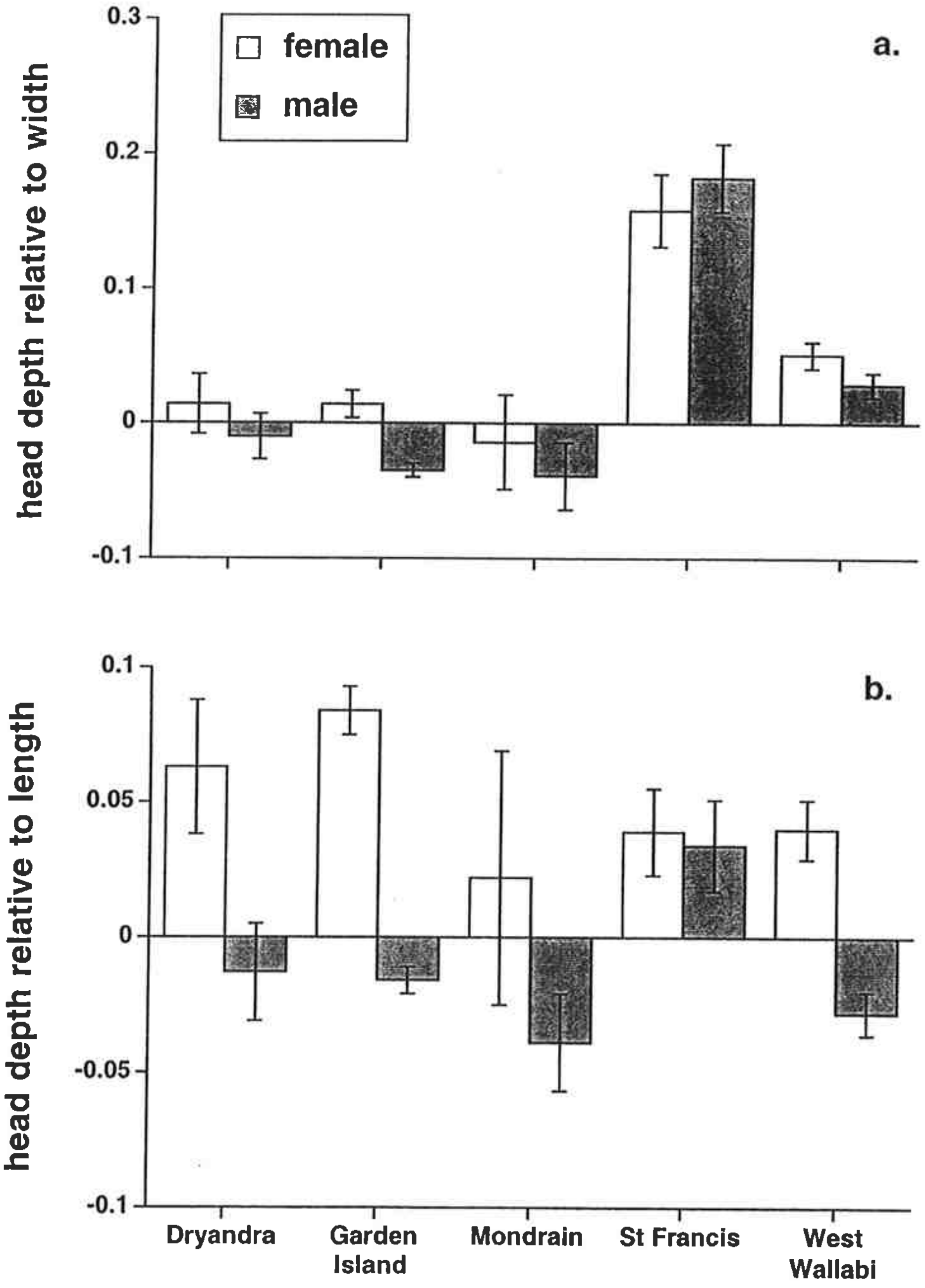

Figure 3.4. Geographic variation in head shape, and in the degree of sexual dimorphism in two measures of head shape, in carpet pythons *(Morelia spilota imbricata)* from five populations in south-western Australia. See Table 3.1 for sample sizes. See text for statistical analyses of these data.

RESULTS

Sample sizes and composition

I obtained data on 1364 carpet pythons (Table 3.1). 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, $\chi^2_4 = 43.4$, $P = 0.0001$; juveniles, $\chi^2_4 = 17.8$, $P = 0.0001$), as well as in age structure (proportions of juvenile snakes) among the samples ($\chi^2_4 = 113.3$, $P = 0.0001$).

Sexual and geographic variation in mean adult body size

In each of the five populations that I studied, female pythons grew to significantly larger body sizes than did their male counterparts (Fig. 3.2). Because a small increase in SVL can entail a large increase in mass, this sexual dimorphism was greater in terms of mass rather than body length (Fig. 3.2). Unsurprisingly (given the greater body size of females), the heads of females were larger than those of males (Fig. 3.2). 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 St. Francis Island (maxima of 5.4 vs 2.0 kg; see Fig. 3.2). 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 3.2). 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 average of 25.1% longer than males (St. Francis Island) to 111.3% longer than males (Garden Island). The variation in SSD was determined mainly by geographic variation in the body sizes of females rather than males (Fig. 3.2; 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 geographic sources of variation in body proportions

Are the sex and locality differences in traits such as head size (Fig. 3.2, Table 3.2) 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? I 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 ($P > 0.05$), I successively deleted such terms to increase the power of the analysis and look for differences in lower-order interactions or

Table 3.2. 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. 3.2 for graphical display. Table gives *F* values and associated probabilities (*P*) for main effects of population (4,474 df) and sex (1,474 df), and for the interaction between population and sex (4,474 df). The latter term tests for significant geographic variation in the degree of sexual dimorphism in each trait. See Table 3.1 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

main effects. I included all individuals, not just adult animals, in these analyses. Figures 3.3 and 3.4 provide the results of an alternative method of analysis (ANOVAs on size-corrected residual scores) for ease of interpretation. Below, I 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. 3.3a). For example, St. Francis snakes were more heavy-bodied than Dryandra animals, and males were thinner-bodied than females in all populations except for Mondrain Island (Fig. 3.3a).

(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 3.3b shows that this effect is due to shorter tails on the Mondrain and St. 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 St. 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. 3.3c).

(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 St. Francis snakes had wider heads relative to length, as well as longer heads relative to SVL, than did pythons from the other populations (Fig. 3.4a). Within each population except St. Francis, females had wider heads than males of the same head length (Fig. 3.4a).

(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. 3.4b). However, the degree of sexual dimorphism in this trait was less on Saint Francis Island than in the other populations (Fig. 3.4b).

Geographic variation in reproductive biology

My limited data do not reveal any substantial geographic variation in reproductive traits:

(i) Mating system

Pythons in all of my study populations appear to reproduce on a similar seasonal schedule (mating in spring, oviposition in summer). All male-female pairings were recorded in the period from September to November (observed in all study areas except Mondrain Island). Physical combat between rival males was never recorded (nor reported to me by others), and no bite scars were evident on adult males in any population (unlike the situation in eastern Australian populations of *M. spilota*, where male-male combat is frequently reported and most adult males show such scars: Shine & Fitzgerald 1995). Instead, I frequently recorded two or more males in close proximity to a female, without overt aggression (Chapter 2). The number of males in such aggregations ranged from two (recorded on Garden Island, Dryandra and West Wallabi Island) to five (recorded on Saint Francis Island). Anecdotal reports of multiple males from other mainland sites (T. Friend, M. Scanlon, pers. comm.) suggest that the broad outlines of the mating system are similar, and do not involve male-male combat, throughout the range of *M. s. imbricata*.

(ii) Reproductive output of females

If reproductive output increased more rapidly with female body size in some populations than others, fecundity selection might generate geographic differences in SSD (King 1989b). However, ANCOVA with population as the factor, ln SVL as the covariate, and clutch size as the dependent variable did not reveal any significant differences among populations either in the rate that clutch size increased with maternal SVL (slopes, $F_{2,10} = 0.62$, $P = 0.56$) or in clutch sizes at the same body size (intercepts, $F_{2,12} = 1.36$, $P = 0.29$; note that Mondrain Island animals were excluded from this analysis due to lack of data).

Sexual and geographic variation in dietary composition

Figure 3.5 shows composition of the diet in broad categories, and Table 3.3 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. 3.5). Contingency-table analyses confirm the statistical significance of these sex differences in dietary composition (separately for Garden Island, $\chi^2_3 = 168.84$, $P < 0.0001$; West Wallabi, $\chi^2_2 = 22.24$, $P < 0.0001$).

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 3.6 supports the former interpretation: mean SVLs of pythons eating different prey types 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 only because of SSD combined with the effect of body size on prey size.

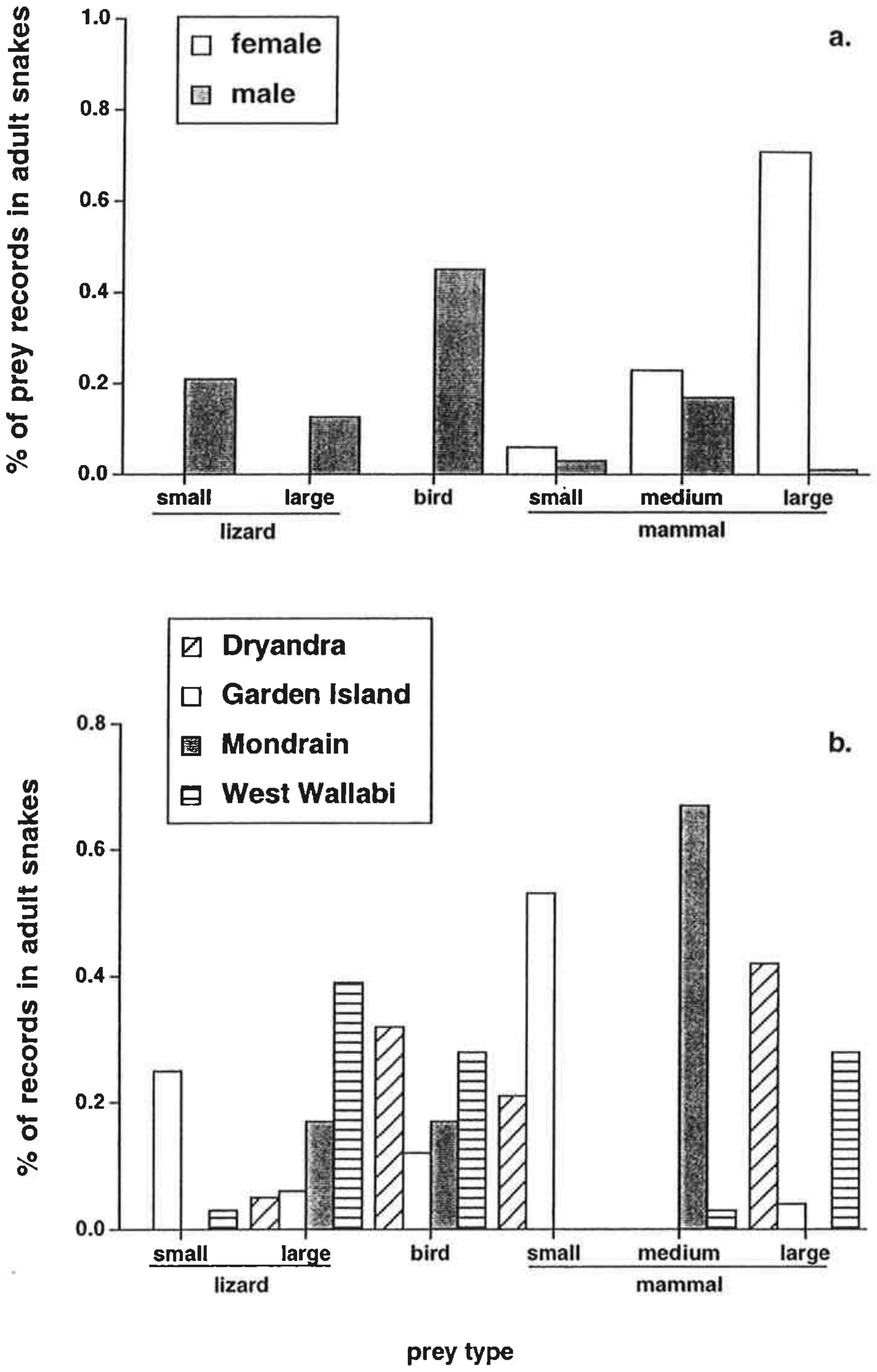

Figure 3.5. Composition of the diet of adult carpet pythons as a function of the snake's sex (a) and location (b). See text for definition of categories, and Table 3.3 for actual prey species in each category.

Table 3.3. 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 *Macropus eugenii* (subadult)	3000		4		7
House Mouse* *Mus domesticus*	12	34	77	100	
Birds					
Brush Bronzewing *Phaps elegans*	198			1	1
Laughing Dove* *Streptopelia senegalensis*	110		6	3	
Painted Button Quail *Turnix varia*	67		7	9	
Singing Honeyeater *Lichenostomus virescens*	28				
Golden Whistler *Pachycephala pectoralis*	25			1	
Grey Fantail *Rhipidura fuliginosa*	8	1	3	5	
Unidentified birds		2	5		
Reptiles					
Marbled Gecko *Christinus marmoratus*	3	4	8	2	
Spiny-tailed Gecko *Strophurus spinigerus*	6	23	61	22	
Fence Skink *Cryptoblepharus plagiocephalus*	1	1		1	
Acritoscincus trilineatum	5	1	7	1	
King Skink *Egernia kingii*	228	1	7	8	
Burton's Legless Lizard *Lialis burtonis*	11		3	4	
Morethia obscura	2	3	12	7	
Bobtail *Tiliqua rugosa*	300		4		
Unidentified gecko		3	8	2	
Python sloughed skin				1	
Unidentified skink			1	3	
Unidentified		19	16	13	

Table 3.3 cont.

	Mean prey mass (g)	**Juvenile**		**Adult**	
		Males	**Females**	**Males**	**Females**
DRYANDRA					
Mammals					
Woylie *Bettongia penicillata*	1500		1		
Numbat *Myrmecobius fasciatus*	425		1		
Brush-tailed Possum *Trichosurus vulpecula*	2000		1		1
Western Barred Bandicoot *Perameles bougainville*	300		1		
Mardo *Antechinus flavipes*	50				
Birds					
Purple-crowned Lorikeet *Glossopsitta porphyrocephala*	46	1			
Port Lincoln Parrot *Bernardius zonarius* (chick)	115		1		
Unidentified bird		1	1		
Unknown					1
MONDRAIN ISLAND					
Mammals					
Bush Rat *Rattus fuscipes*	71	3	6		2
Birds					
Unidentified bird				1	1
Reptiles					
King Skink *Egernia kingi*	228			2	
Unknown skink		1			
Unknown					1

Table 3.3 cont.

	Mean prey mass (g)	**Juvenile**		**Adult**	
		Males	**Females**	**Males**	**Females**
WEST WALLABI ISLAND					
Mammals					
Tammar Wallaby *Macropus eugenii*	3000		1	1	8
Bush Rat *Rattus fuscipes*	71	2		1	
Birds					
Brush Bronzewing *Phaps elegans*	198			1	
Painted Button Quail *Turnix varia scintillans*	67			3	
Unidentified bird			4	3	1
Reptiles					
King Skink *Egernia kingi*	228		2		
Stokes Skink *Egernia stokesii stokesii*	90		2	13	
Dwarf Bearded Dragon *Pogona minor minor*	41		1	1	
Unknown skink			1	1	
ST FRANCIS ISLAND					
Mammals					
Bandicoot *Isoodon obesulus nauticus*	300				1
Birds					
Singing Honeyeater *L. virescens*	18			1	
Painted Button Quail *T. varia*	106			1	
Buff-banded Rail *Gallirallus philippensis*	182				2
Unknown bird				1	
Reptiles					
Egernia multiscutata	16	1			

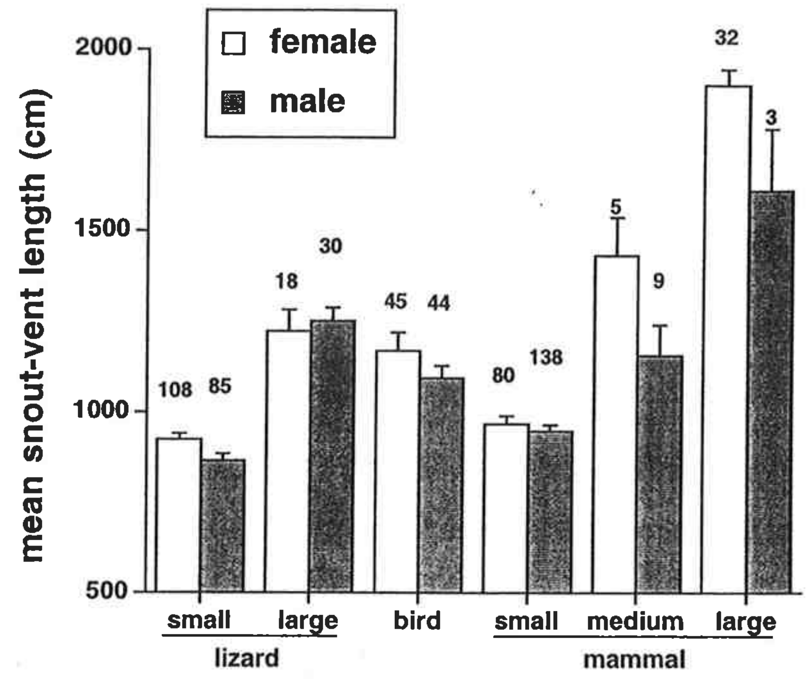

Figure 3.6. Mean snout-vent lengths (and associated standard errors) of carpet pythons recorded to consume various types of prey. Data combined for all study localities. Sample sizes shown above histograms. See text for statistical results, and Table 3.3 for actual prey species involved in each category.

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 geographic variation in the relative numbers of prey belonging to each of the major categories ($\chi^2_{12} = 207.97$, $P < 0.0001$). Lizards were the most commonly recorded prey items on West Wallabi, rats on Mondrain, mice on Garden Island and large mammals at Dryandra (Fig. 3.6).

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 versus 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 3.3). 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 to 120 cm SVL) do not. In contrast, we do not expect to see such an effect in other populations. Figure 3.7 summarises the relevant data on this question. Over the critical size range of 60 to 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 17.0% with prey, $\chi^2_1 = 40.78$, $P < 0.0001$),

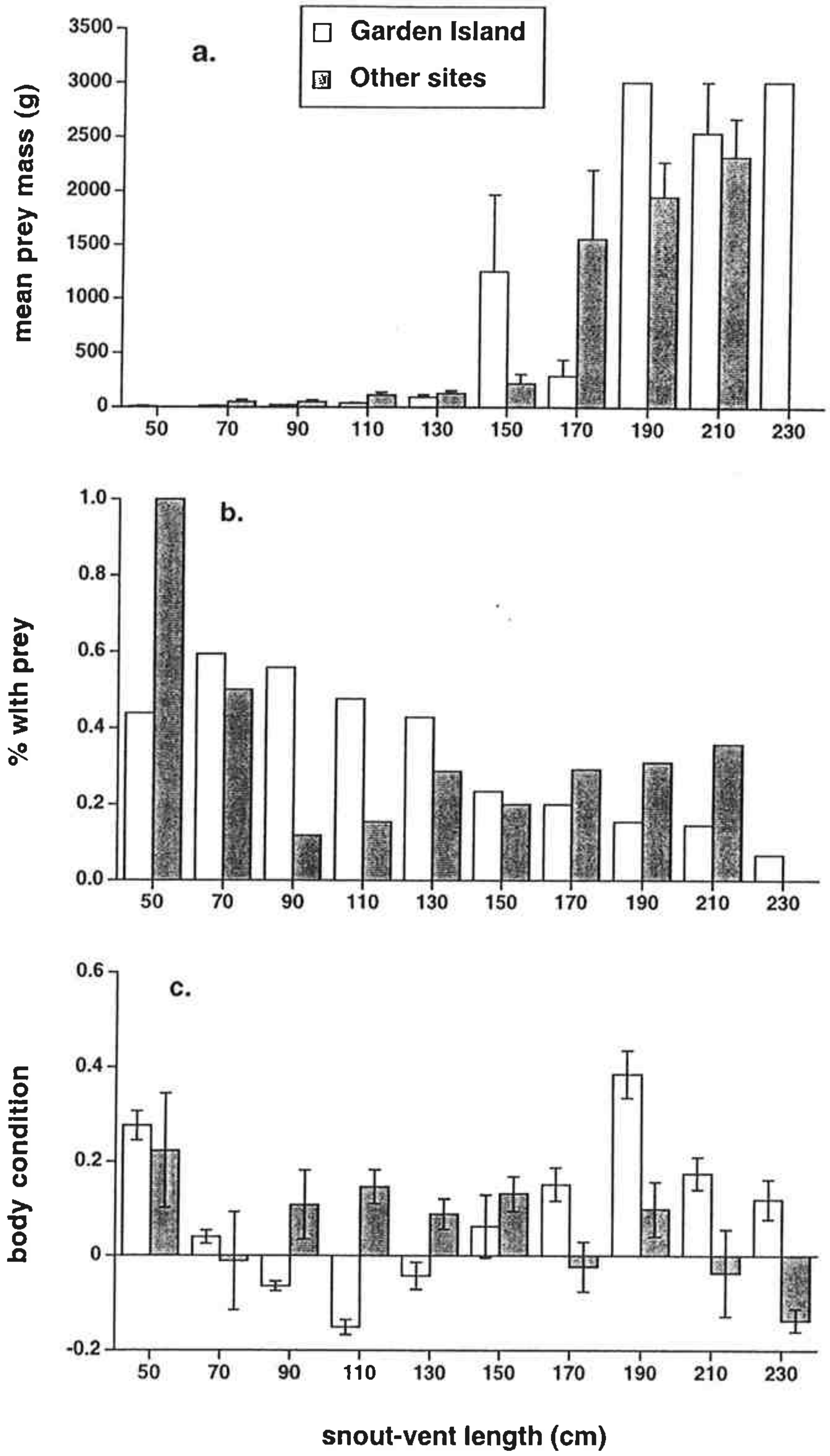

Figure 3.7. Effects of python body size (snout-vent length) on the size of prey items ingested (prey mass: a), the frequency of feeding (as indicated by the proportion of snakes containing identifiable prey items: b) and the body condition of the snakes (residual scores from the linear regression of 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).

pythons at this intermediate range of SVLs were significantly thinner-bodied than were pythons at my 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. 3.7). Pythons also grew very slowly over this range of body sizes, with some snakes failing to increase in mass over periods > 2 yr (Chapter 2).

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; Chapter 2). The present study reveals extensive geographic variation in SSD even among isolated populations within a single subspecies of this widespread taxon. My results support previous suggestions that the *direction* of sexual size dimorphism in snakes is determined by the mating system (Shine 1994a; Shine & Fitzgerald 1995). Females attained larger body sizes than males in all of my study populations, and there was no evidence of significant geographic variation in reproductive biology. Thus, the extensive variation in SSD among populations may reflect other factors, of which the most likely is geographic variation in prey resources.

Geographic differences in dietary composition 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 geographic variation in diets within *Morelia spilota imbricata* (Table 3.1). Many species that were eaten commonly by snakes at one site were absent from others (e.g. mice were found in Garden Island but not at most other sites) and thus, geographic 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 geographic variation in prey types correlate with the geographic variation in the body sizes 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 I 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 St. Francis; see Figs. 3.2 and 3.5). 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 geographic variation than did those of females (Fig. 3.2) and hence, why geographic 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. 3.7) and grew very slowly (Chapter 2). 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 1993a). In either case, SSD may mean that the sexes are differentially affected by prey-size spectra. This effect occurs on an extraordinary scale with my 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, geographic 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, I 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. 3.3). 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 non-adaptive processes such as genetic drift. Populations of carpet pythons in eastern Australia apparently do not display sex divergence in relative head sizes (Shine 1991a), whereas this was a consistent feature of the western populations (Fig. 3.3). This observation fits with the notion of adaptation to prey-size divergence, because the sex divergence in prey types is much greater for my 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* versus 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 geographic 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 geographic variation in SSD need to consider the role of ecological resources as well as reproductive pressures.

CHAPTER 4

Expulsion of intraperitoneally-implanted radiotransmitters by Australian pythons*

The availability of miniature radiotransmitters has revolutionised the study of snake ecology (Fitch 1987; Shine & Bonnet 2000). Most workers rely upon surgical insertion of transmitters into the animal's peritoneal cavity, and methods for the surgical implantation of transmitters are now sophisticated and effective (e.g. Reinert & Cundall 1982). As more workers use these techniques, new complications will undoubtedly appear. In this chapter I report a bizarre example of such a complication. Free-ranging carpet pythons (*Morelia spilota*) frequently rid themselves of surgically-implanted transmitters by incorporating the transmitter into the alimentary tract and then expelling it with the faeces.

Table 4.1 summarises 14 occasions when radio-telemetered pythons appear to have expelled transmitters in this way. The transmitters (Holohil models SI-2T and PD-2T) weighed 4 to 22 g, and constituted 0.7 to 3.3% of the mass of the snake into which they were implanted. The transmitters

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*Pearson, D.J. & Shine, R. (2002). Expulsion of intraperitoneally-implanted radiotransmitters by Australian pythons. *Herpetological Review*, in press.

Table 4.1. Cases in which radio-telemetered carpet pythons (*Morelia spilota imbricata*) expelled intraperitoneally-implanted transmitters. SVL = snout-vent length (cm). The Table shows the characteristics of snakes, the dates at which transmitters were surgically implanted and were later found in the field (without the snake), and whether or not snake faeces were present with the relocated transmitter. *For snake 22, the original transmitter was not found, but the snake was recaptured 25 Nov 1998 without its transmitter. Note that snake 80 was also recaptured 14 Nov 1995 and reimplanted after voiding its first transmitter.

Snake ID#	**Location**	**Date implanted**	**Date recovered**	**Days before expulsion**	**Sex**	**SVL (cm)**	**Mass (g)**	**Transmitter found in faecal pellet**
2	Dryandra	9 Jan 1995	10 Feb 1995	32	F	172	1401	yes
3	Dryandra	5 Apr 1997	30 Dec 1997	269	F	196	1620	yes
10	Dryandra	31 Mar 1995	27 Feb 1996	333	M	147	905	yes
17	Dryandra	8 Mar 1995	22 Dec 1997	196	M	130	633	no
18	Dryandra	10 Dec 1995	22 Sept 1996	287	M	145	712	yes
22	Dryandra	7 Feb 1996	?	?	M	113	248	*
25	Dryandra	5 Apr 1996	12 Nov 1996	221	M	146	693	yes
30	Dryandra	3 Dec 1996	22 May 1998	535	F	179	2389	no
32	Dryandra	23 Feb 1997	30 Dec 1997	310	M	160	955	yes
36	Dryandra	29 Oct 1997	30 Dec 1997	62	M	152	960	yes
80	Garden Is.	1 Dec 1995	9 Feb 1996	70	M	134	744	yes*
80	Garden Is.	14 Nov 1995	29 Jan 1997	442	M	135	759	yes
83	Garden Is.	1 Dec 1995	22 Dec 1997	752	M	129	608	no
40	Garden Is.	15 Apr 1995	16 Feb 1996	307	F	195	2309	yes

were inserted under isoflurane anaesthesia, via a midventral incision approximately 10% of the snake's snout-vent length anterior to the vent. The entire unit (transmitter plus 19-30 cm antenna) was placed inside the peritoneal cavity, with the body of the transmitter positioned anterior to the antenna. The transmitter was not sutured to a rib. The incision was sutured closed, and the snake released 1 to 14 days after surgery.

In the course of the study, many telemetered snakes were recaptured for transmitter replacement. In all such cases except those described below, the transmitter had remained in place within the peritoneum, and was surrounded by fibrous tissue. In the cases listed in Table 4.1, however, attempts to relocate snakes in the field revealed only the transmitter, usually in conjunction with faecal material from the snake. Python faeces are very easily distinguished from those of other large predators because the python faeces are distinctive in shape, are always associated with uric acid deposits, and detailed examination reveals the presence of python teeth. Large carnivorous mammals (e.g. cats, dogs, foxes) are absent from the Garden Island study area and very rare (because of a prolonged control program) at the Dryandra site. Subsequent recapture of two of these free-ranging pythons that had lost their telemeters confirmed that the snake was in good health, and showed no scarring that would indicate loss of the transmitter through the body wall. Evidence of the route of transmitter expulsion was available for two additional snakes. First, an adult diamond python (*Morelia spilota spilota;* not listed in Table 4.1) was captured and kept in captivity after several months radio-tracking, prior to surgery to remove the transmitter. Before I could remove it, the snake defecated the transmitter in its cage. Second, I dissected a radio-tracked carpet python (*M. s. imbricata;* again not listed in Table 4.1) that died in the field after 22 months of radio-tracking.

The transmitter in this snake was partially incorporated into the stomach, but the antenna remained attached in the peritoneal cavity. It appeared that faecal impaction may have led to the snake's death.

Data in Table 4.1 show that cloacal expulsion of transmitters was relatively frequent, although by no means universal (these snakes were 14 of 75 pythons radio-tracked during the study). The snakes that expelled transmitters covered a wide range of body sizes, included both sexes, and carried the transmitters prior to expulsion for periods of 1 to 24 months. At the Dryandra study site, 3 female and 7 male pythons expelled their transmitters from a total of 48 transmitters implanted. This involved 33 individual pythons, as some females were implanted twice. At the Garden Island study site, 1 female and 3 male pythons expelled their transmitters from a total of 52 transmitters implanted (consisting of 42 individual pythons).

To examine correlates of transmitter expulsion, I conducted a logistic regression on data from all radio-tracked pythons. Although some snakes were fitted with more than one transmitter in succession during my study, each animal appeared only once in the data set to avoid pseudoreplication. The dependent variable was whether or not the transmitter was expelled, and the independent variables were the snake's sex and snout-vent length. I excluded four cases where I had less reliable evidence for expulsion (no faeces with transmitters: see Table 4.1) but inclusion or exclusion of these data did not change any of the conclusions from the analysis. The regression was based on 38 female snakes (3 of which expelled transmitters) and 36 males (7 of which expelled transmitters). Likelihood ratio tests from this regression showed that the probability of expulsion was linked both to the snake's sex ($\chi^2_1 = 6.75$, $P < 0.01$) and its body length ($\chi^2_1 = 4.90$, $P < 0.03$).

Males expelled transmitters more frequently than did females (7 of 36, = 19% of males, vs 3 of 38, = 8% of females). The mean snout-vent lengths of snakes that expelled transmitters were larger than those of other snakes, in both sexes (males: 145 vs 119 cm; females, 188 vs 175 cm). There was no significant difference in rates of expulsion between the two study areas.

The most consistent correlate of expulsion involved feeding. Ten of the 14 expulsions were associated with faecal material (Table 4.1), suggesting that transmitters were expelled soon after the snake had consumed a large prey item. Although many of the other radio-tracked snakes took equally large meals and did not expel transmitters afterwards, I suspect that there is a functional link between feeding on a large meal, and transmitter expulsion. Not only was transmitter loss linked to feeding events (Table 4.1), but the sexes and sizes of snakes that most frequently expelled transmitters (large specimens, and males rather than females) are those that tend to take very large prey (relative to snake size) in my study populations (unpubl. data).

Why should a snake consuming a large meal be likely (or indeed, able) to transfer an object in its peritoneal cavity into its alimentary tract? This ability may be linked to massive temporal shifts in size and activity of the alimentary tract in ambush predators such as pythons (Secor & Diamond 1995), including carpet pythons (Bedford 1996). The gut shrinks during non-feeding periods, but is massively up-regulated soon after a prey item is ingested. It may be able to incorporate foreign objects during this rapid increase in size. This ability may function in removal of objects such as fish spines that can penetrate the stomach wall and lodge in the peritoneum (Shine 1991b).

The same ability to expel intraperitoneally-implanted transmitters through the gut has been reported in fishes (Chisholm & Hubert 1985; Marty

& Summerfelt 1986), and may prove to be widespread. The only analogous phenomenon in snakes (to my knowledge) involves passive integrated transponder microchips surgically implanted in the necks of corn snakes (*Elaphe guttata*); the tags frequently (and sometimes rapidly) moved posteriorly through the body and were expelled in the faeces (Roark & Dorcas 2000). If such abilities are widespread, there is an obvious caveat for interpretation of radio-telemetry studies. Researchers finding a transmitter in the field would be tempted to conclude that the animal carrying that telemeter had died and/or been consumed by a predator. Marks on a transmitter left by teeth or claws of a predator species would be interpreted as evidence for such an event, but may have been inflicted after expulsion of the unit. I advocate caution in inferring predation as a cause of death of radio-tracked snakes, unless the carcass (or part of it) is available.

Studies on fishes have attempted to determine whether changes in factors such as the size or coating of a transmitter can reduce the probability of expulsion. Smaller transmitters were less likely to be expelled (Marty & Summerfelt 1986), but the transmitters used in my own study were smaller relative to snake body mass (< 4%) than is the case in most such studies. Anchoring the transmitter by suturing it to a rib during the initial surgery or by running the antenna subcutaneously (e.g. Reinert & Cundall 1982; Reinert 1992) is one obvious solution, but experimental work on fishes found that anchoring the transmitters greatly increased the rate at which they were expelled via rupturing the animal's body wall (Marty & Summerfelt 1986).

My results are interesting not only in providing a cautionary note about interpreting cases of transmitter loss, but also in revealing a hitherto-unsuspected ability of snakes to encapsulate and expel a foreign object from the peritoneum. The apparent link between expulsion and feeding (and especially to ingestion of prey that are very large relative to the predator), in a lineage of snakes known to show massive fluctuations in size and activity of the alimentary tract, strongly suggests the ability to regulate organ size in this way may have more diverse consequences than has been previously recognised.

CHAPTER 5

Spatial ecology of a threatened python (*Morelia spilota imbricata*) from south-western Australia

ABSTRACT

Carpet pythons (*Morelia spilota imbricata*) have declined across much of south-western Australia due to habitat clearance and degradation. Information on habitat use, home range sizes and movements may help to plan for the conservation of this important predator. I studied pythons at two study sites (Garden Island and Dryandra Woodland) with markedly different climates and habitat types. I surgically implanted radio-transmitters in 75 pythons and tracked them for periods of 3 months to 4 years. Dryandra pythons remained inactive inside tree-hollows during cooler months (May-September), whereas some (especially small) pythons on Garden Island continued to move and feed. Overall weekly displacements (mean = 100 to 150 m) were similar at the two study sites and among sex/age classes, except that reproductive females were sedentary during summer while they were incubating eggs. Mean Home ranges averaged 15 to 20 ha. Adult

male pythons had larger home ranges than adult females at Dryandra, but not at Garden Island. Some radio-tracked snakes exhibited high site fidelity, frequently returning to previously occupied sites after long absences. Pythons at Dryandra were found primarily in hollow logs and tree-hollows, whereas Garden Island snakes usually sheltered under shrubs. At both study sites, habitat usage was similar among different sex/age classes of snakes, except that juvenile pythons were more arboreal than adults. Although carpet pythons demonstrate great flexibility in habitat use, certain habitat elements may be critical for the persistence of viable populations. Fire plays a central role in this process, albeit in complex ways. For example, low-intensity fires reduce the availability of hollow logs on the ground at Dryandra, whereas paradoxically, high-intensity fires may fell trees and thus generate more logs - but might also threaten overwinter trees. Thus, disturbances (such as wildfires) that alter important microhabitats (such as vegetation cover on Garden Island or log availability at Dryandra) are likely to threaten python populations. At Dryandra, landscape management should include occasional fire events to generate new logs as well as shrub thickets used by prey. Strategic burning may also be required at Garden Island to regenerate some vegetation communities.

INTRODUCTION

In order for wildlife populations to persist, they need access to suitable habitat of sufficient size and contiguity to provide adequate resources (i.e. food, shelter, etc.) and to cope with environmental perturbations. Habitat destruction and fragmentation can reduce the ability of wild populations to persist and/or to reinvade after major natural and anthropogenic disturbances. Some types of animals may be particularly vulnerable to such changes, and among snakes large ambush predators may be at most risk (Webb & Shine 1998). Such species depend upon vegetation structure for concealment from potential prey and predators, and even minor modifications to habitat can have serious effects on their population viability (Reed & Shine 2002). Also, habitat changes may alter the composition and abundance of prey assemblages and so reduce hunting success.

The south-western carpet python (*Morelia spilota imbricata*) is a large ambush predator with a wide distribution across southern Australia (Pearson 1993). It is considered a threatened taxon (Cogger et al. 1993) and a "specially-protected taxon" under State legislation (Western Australian Wildlife Conservation Notice 1999) on the basis of declines in parts of its range, due presumably to habitat destruction (Smith 1981). The diet consists of vertebrates, particularly mammals, and logs are important for shelter (Barker & Barker 1994). Thus, this taxon is likely to be vulnerable to any reduction in ground cover (and therefore ambush opportunities) or in the abundance and/or diversity of vertebrate prey (Shine 1994b). Although carpet pythons from eastern Australian have attracted considerable ecological research (Slip & Shine 1988a,b,c,d,e,f; Shine & Fitzgerald 1995, 1996), the south-western subspecies has been virtually unstudied. Because information on the spatial ecology of this python can guide decisions regarding its conservation and management, I undertook a detailed radio-telemetry study of two populations of this species in south-western Australia.

Despite the proximity of my two study sites (separated by 130 km; 35' of latitude), they differ markedly in climate, landform, vegetation types, prey resources and potential shelter sites. This contrast allowed me to compare activity patterns, seasonal movements, habitat use and home ranges in an effort to identify the ways in which habitat and climatic diversity influence python ecology. To this end, I radio-tracked juvenile pythons, adult males and reproductive and non-reproductive female pythons over several years. An understanding of how pythons use the varying resources of these two sites should clarify their responses to environmental change and disturbances such as fire, logging and land clearance.

MATERIALS AND METHODS

Study animal

The south-western carpet python (*M.s. imbricata*) is a large non-venomous snake, measuring up to 2.5 m in total length with a mass of up to 6 kg. It is an ambush predator of vertebrates including birds, reptiles and mammals ranging in size up to small wallabies. The sexes are strongly size dimorphic with adult females averaging > 10 times the mass of adult males in some populations (Chapter 3). Mating occurs from October to mid-December, eggs are laid in December and the female coils around the eggs and incubates them until hatching in March. Adult males are probably reproductively active every year, but females only breed every second year or less frequently due to the time required for emaciated post-reproductive females to rebuild energy stores (Chapter 7).

Carpet pythons use a range of habitats including coastal shrublands, heath, forest, woodlands, the margins of agricultural land and outer metropolitan areas (where they sometimes utilise the roof spaces of buildings: Slip & Shine 1988d; Shine & Fitzgerald 1996; Fearn et al. 2001). Despite this flexibility, the south-western carpet python has disappeared from large tracts of its historic range. It is now rarely recorded in most of the "Wheatbelt Region", an area of intensive cereal production in inland Western Australia, and the Swan Coastal Plain, now largely covered by metropolitan development around the city of Perth (Smith 1981; Pearson 1993).

Study areas

Garden Island (32°12'S, 115°40'E) lies 15 km south-west of the port of Fremantle and has an area of 1100 ha. It experiences hot dry summers, tempered by reliable afternoon sea breezes and mild wet winters. Figure 5.1 summarises the mean maximum and minimum temperatures and mean monthly rainfall data for Kwinana (from 1955 to 2001), situated on the mainland adjacent to Garden Island.

Garden Island is connected to the mainland by a causeway built in 1973 to service the HMAS Stirling naval base. Public access is restricted, resulting in a lower incidence of fire than the adjacent mainland and hence vegetation communities are well preserved (Keighery et al. 1997). The island is covered by low forests and shrublands (McArthur 1957; McArthur & Bartle 1981). All telemetry work was undertaken on the northern section of

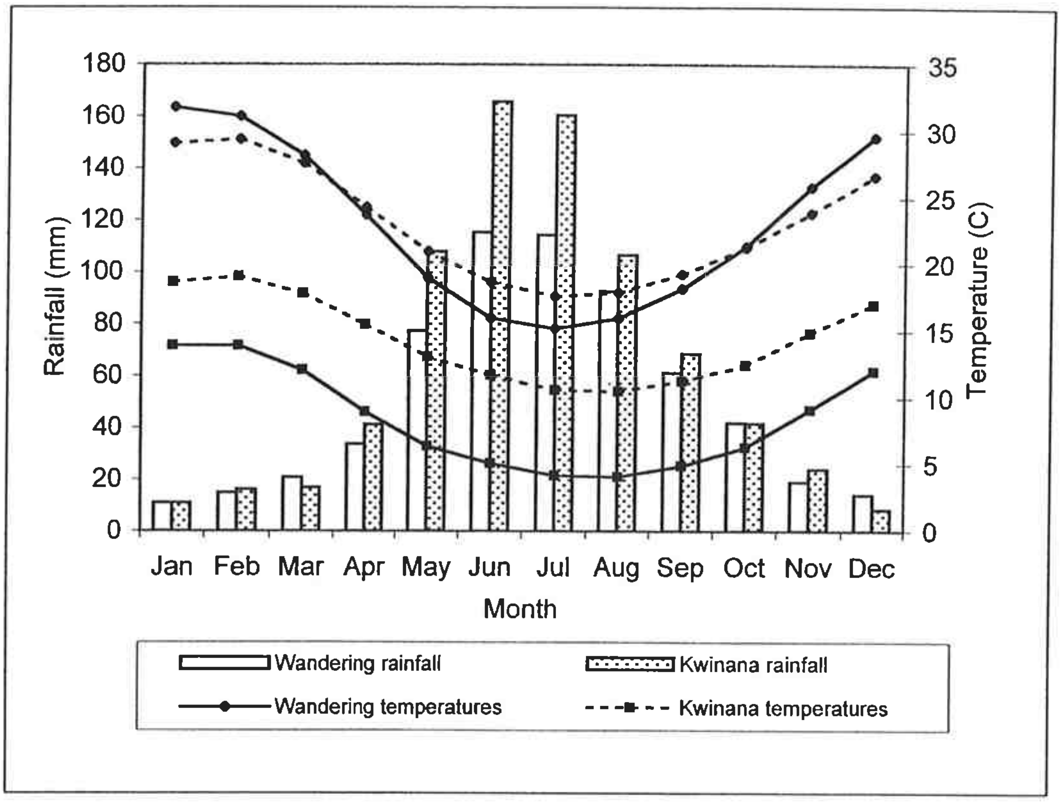

Figure 5.1. Climate data for the closest meteorological station to the two study sites in south-western Australia (Kwinana near Garden Island; Wandering near Dryandra). Note the greater extremes of temperature experienced at Dryandra.

the island away from naval facilities. Major vegetation communities in this area were as follows: (i) low (8-10 m) dense forest of native pine *Callitris preissii* and *Melaleuca lanceolata* on wind-protected sites on deeper sands, with a sparse understorey of shrubs and herbs; (ii) shrublands of *Acacia rostellifera* with a thick understorey of prickle lily (*Acanthocarpus preissii*) and a variety of other shrubs on dune sands; (iii) mixed low forest of *C. preissii, M. lanceolata, Melaleuca hueglii* and *A. rostellifera* with *A. preissii* understorey on undulating sandplain; (iv) low (0.5-1.5 m) heath dominated by *Alyxia buxifolia, Scaevola crassifolia* and *Olearia axillaris* on shallow soils over limestone or in exposed positions along the west coast. There are also minor areas of littoral shrubland of variable composition around the coastal margin (McArthur & Bartle 1981). Trees on Garden Island only grow to a maximum height of 10 m, with few tree hollows or hollow logs.

The second site, Dryandra Woodland (32°47'S, 116°55'E) lies 140 km SE of Perth and 130 km ESE of Garden Island. Dryandra also experiences hot, dry summers, but without mediating maritime influences. Winters are cold and wet. Figure 5.1 summarises climatic data for the town of Wandering, 28 km NW of Dryandra. It has lower rainfall than Garden Island and more pronounced temperature extremes than Garden Island. Dryandra Woodland (formerly Dryandra Forest) consists of 24 fragmented woodland and forest blocks separated by areas cleared for wheat production (Coates 1993). The total area of the State Forests that make up Dryandra Woodland is 28066 ha, but my study was carried out entirely within the largest contiguous area of the Woodland (in areas known as Dryandra, Frank and Peters forest blocks). This area is vegetated by: (i) undulating open woodlands of wandoo (*Eucalyptus wandoo*) with a variable understorey of poison bush (*Gastrolobium* spp.) and heath; (ii) areas of residual lateritic plateau vegetated by tall *Dryandra* spp.-dominated heath (to 3 m) with occasional marri, *Corymbia calophylla*; (iii) mixed woodlands of powderbark wandoo *Eucalyptus accedens*, with scattered mallet *Eucalytpus astringens* and *C. calophylla* on the erosional slopes of these plateaux; (iv) low woodland of rock oak, *Allocasuarina huegeliana* and emergent *E. wandoo* with little understorey on granitic soils; and (v) areas of mallet plantation (*E. astringens* and *E. gardneri*) planted on areas where natural woodlands were cleared from the late 1920s to the 1940s for tannin production (Coates 1993). Wandoo and powderbark wandoo are susceptible to termites, so these woodlands are rich in hollow branches and logs.

See Addendum

Capture of study animals

Most pythons were captured at night by road-driving, but some were captured by naval police, rangers, other researchers, and weed-spraying contractors. Several pythons at Dryandra were captured after they consumed radio-telemetered mammals. Over 650 pythons were captured, marked and released on Garden Island during the study (1995-2000) and 42 of these animals were implanted with transmitters (Table 5.1). Of the 63 pythons captured at Dryandra, 33 were fitted with transmitters.

Implantation of radio-transmitters

Four sizes of implantable transmitters (Holohil Systems Ltd., Canada) were used depending on the size of the python; all transmitters were < 5% of the

Table 5.1. Sexes, body sizes, duration of radio-tracking and other traits for south-western carpet pythons used in this study. (Age: A=adult, S= subadult, J=juvenile; see text for relative sizes).

Snake No.	Location	Sex	Age	SVL (cm)	Mass (g)	Start date	Finish date	Days radio-telemetered	No. locations	Fate
1	Dryandra	M	A	171.5	1156	19-Jan-95	09-Jan-97	721	104	Reimplanted
1	Dryandra	M	A	176.5	1244	20-Jan-97	09-Feb-98	385	38	Died
2	Dryandra	F	S	172.0	1401	07-Jan-95	10-Feb-95	34	11	Expelled transmitter
3	Dryandra	F	A	187.5	2294	20-Jan-95	02-Apr-97	803	106	Reimplanted
3	Dryandra	F	A	195.5	1618	10-Apr-97	22-Dec-97	256	23	Expelled transmitter
4	Dryandra	F	J	105.6	216	05-Mar-95	29-Oct-96	604	85	Removed transmitter
5	Dryandra	F	J	96.7	189.7	05-Mar-95	26-Sep-95	205	24	Fail
6	Dryandra	F	S	146.5	658	05-Mar-95	17-Nov-97	988	122	Removed transmitter
7	Dryandra	M	A	130.2	402	11-Mar-95	14-Oct-96	583	66	Reimplanted
7	Dryandra	M	A	137.0	645	22-Oct-96	12-Nov-97	386	38	Lost/Fail
9	Dryandra	F	S	155.5	1023	01-Apr-95	23-Apr-97	753	96	Reimplanted
9	Dryandra	F	A	183.5	2167	02-May-97	05-Aug-98	460	36	Removed transmitter
10	Dryandra	M	A	147.2	905	01-Apr-95	20-Feb-96	325	49	Expelled transmitter
11	Dryandra	F	A	182.0	2575	21-Apr-95	12-Feb-97	663	96	Died
12	Dryandra	M	A	133.5	441	21-Aug-95	20-Dec-95	121	24	Lost/Fail
13	Dryandra	M	A	120.5	322	21-Nov-95	28-May-96	189	33	Lost/Fail
14	Dryandra	F	A	189.0	1803	12-Dec-95	12-Jan-98	762	89	Reimplanted
14	Dryandra	F	A	195.5	1433	13-Jan-98	23-Nov-99	679	23	Died
15	Dryandra	F	A	200.0	2353	12-Dec-95	10-Feb-98	791	91	Died
16	Dryandra	M	A	109.6	547	24-Jun-96	18-Nov-96	147	18	Lost/Fail
16	Dryandra	M	A	111.1	312	20-Nov-95	21-May-96	183	29	Reimplanted
17	Dryandra	M	A	143.1	618	12-Dec-95	06-Jun-97	542	69	Reimplanted

Table 5.1 cont.

Snake No.	Location	Sex	Age	SVL (cm)	Mass (g)	Start date	Finish date	Days radio-telemetered	No. locations	Fate
17	Dryandra	M	A	143.8	623	26-Jun-97	15-Dec-97	172	29	Expelled transmitter
18	Dryandra	M	A	145.4	712	12-Dec-95	24-Jan-96	43	5	Expelled transmitter
22	Dryandra	M	A	113.1	248	08-Apr-96	02-Sep-96	147	16	Expelled transmitter
23	Dryandra	M	J	94.4	141	08-Apr-96	24-Jun-96	77	10	Lost/Fail
24	Dryandra	F	A	193.8	1775	25-Mar-96	11-Nov-97	596	64	Fail
25	Dryandra	M	A	146.0	693	08-Apr-96	03-Nov-96	209	25	Expelled transmitter
28	Dryandra	M	A	113.5	404	22-May-96	18-Nov-96	180	21	Lost/Fail
29	Dryandra	M	A	142.6	637	18-Nov-96	31-Dec-97	408	42	Lost/Fail
30	Dryandra	F	A	178.5	2389	04-Dec-96	18-Mar-98	469	53	Expelled transmitter
31	Dryandra	M	A	132.0	527	05-Dec-96	12-Jan-98	403	43	Removed transmitter
31	Dryandra	M	A	136.8	551	13-Jan-98	18-Feb-99	401	20	Died
32	Dryandra	M	A	159.5	955	27-Feb-97	23-Dec-97	299	22	Expelled transmitter
34	Dryandra	F	A	188.1	2710	08-May-97	13-Jan-99	615	42	Expelled transmitter
35	Dryandra	F	J	72.2	94	17-Sep-97	18-Mar-98	182	20	Lost
36	Dryandra	M	A	151.5	960	30-Oct-97	22-Dec-97	53	9	Expelled transmitter
37	Dryandra	F	A	205.7	3253	11-Nov-97	27-Mar-00	867	37	Removed transmitter
38	Dryandra	F	A	193.9	2698	11-Nov-97	05-Nov-98	359	25	Removed transmitter

Table 5.1 cont.

Snake No.	Location	Sex	Age	SVL (cm)	Mass (g)	Start date	Finish date	Days radio-telemetered	No. locations	Fate
39	Dryandra	M	A	134.2	522	18-Nov-97	05-Jan-99	413	24	Removed transmitter
46	Dryandra	F	J	124.5	380	06-Jan-98	04-Nov-98	302	17	Removed transmitter
9	Garden Is.	F	J	86.3	153	22-Jan-95	15-Aug-95	205	28	Removed transmitter
10	Garden Is.	F	J	80.6	124	29-Dec-94	04-Aug-95	218	26	Removed transmitter
14	Garden Is.	F	J	95.5	184	22-Jan-95	15-Apr-95	83	10	Fail/Removed
17	Garden Is.	F	J	102.8	246	15-Jan-95	04-Aug-95	201	28	Removed transmitter
18	Garden Is.	F	J	126.2	444	11-Feb-95	06-Jun-96	481	71	Died
34	Garden Is.	M	A	107.9	310	15-Apr-95	30-Jun-95	76	12	Died
39	Garden Is.	M	A	100.9	218	15-Apr-95	13-Jul-95	89	13	Lost/Fail
40	Garden Is.	F	S	195.0	2309	15-Apr-95	09-Feb-96	300	49	Expelled transmitter
50	Garden Is.	F	A	206.0	4037	23-Apr-95	04-Apr-97	712	116	Reimplanted
50	Garden Is.	F	A	211.4	3524	12-Apr-97	27-Apr-99	745	73	Removed transmitter
53	Garden Is.	F	J	146.0	938	13-Jul-95	25-Apr-97	652	108	Reimplanted
53	Garden Is.	F	S	174.5	2038	10-May-97	05-Jun-99	756	59	Removed transmitter
56	Garden Is.	F	A	204.0	3392	25-Aug-95	06-Oct-97	773	121	Removed transmitter
56	Garden Is.	F	A	207.5	5200	10-Oct-97	29-Dec-99	810	65	Removed transmitter
62	Garden Is.	M	A	105.6	288	11-Sep-95	03-Nov-95	53	11	Fail/Removed
67	Garden Is.	F	J	136.2	618	06-Oct-95	31-Oct-96	391	65	Died

Table 5.1 cont.

Snake No.	Location	Sex	Age	SVL (cm)	Mass (g)	Start date	Finish date	Days radio- telemetered	No. locations	Fate
76	Garden Is.	M	A	101.6	251	01-Dec-95	13-Feb-97	440	76	Lost/Fail
79	Garden Is.	F	A	196.5	3351	01-Dec-95	19-Mar-98	839	136	Reimplanted
79	Garden Is.	F	A	222.0	5163	02-Apr-98	24-Feb-00	693	37	Removed transmitter
80	Garden Is.	M	A	134.2	744	01-Dec-95	09-Feb-96	70	10	Expelled transmitter
80	Garden Is.	M	A	134.5	759	15-Nov-96	23-Jan-97	69	17	Expelled transmitter
81	Garden Is.	F	S	184.0	2429	01-Dec-95	27-Nov-97	727	97	Removed transmitter
83	Garden Is.	M	A	129.0	608	01-Dec-95	27-Dec-96	392	84	Expelled/ predation?
87	Garden Is.	F	A	217.0	4233	22-Dec-95	09-Jan-98	749	107	Reimplanted
87	Garden Is.	F	A	222.4	5200	16-Jan-98	31-Mar-98	74	49	Removed transmitter
143	Garden Is.	F	A	213.0	3394	25-Apr-97	27-Apr-99	732	67	Reimplanted
143	Garden Is.	F	A	206.0	4185	10-Jul-95	22-Apr-97	652	113	Removed transmitter
165	Garden Is.	M	A	157.0	1011	29-Mar-96	12-Apr-97	379	61	Died
212	Garden Is.	F	A	213.5	2639	11-May-96	05-Jan-97	239	59	Killed
218	Garden Is.	F	A	225.8	3224	09-Aug-96	01-Oct-98	783	101	Reimplanted
218	Garden Is.	F	A	231.8	4423	02-Oct-98	29-Jun-99	270	18	Removed transmitter
235	Garden Is.	F	A	212.6	4731	03-Oct-96	02-Jan-98	456	69	Lost/Fail
259	Garden Is.	M	A	107.1	328	15-Nov-96	13-Nov-97	363	58	Lost/Fail
260	Garden Is.	F	A	219.2	4824	15-Nov-96	28-Jan-99	804	83	Removed transmitter
266	Garden Is.	M	A	106.7	311	04-Dec-96	19-Feb-98	442	59	Lost/Fail

Table 5.1 cont.

Snake No.	Location	Sex	Age	SVL (cm)	Mass (g)	Start date	Finish date	Days radio-telemetered	No. locations	Fate
313	Garden Is.	M	A	107.2	326	23-Jan-97	06-Mar-98	407	51	Lost/Fail
317	Garden Is.	F	A	213.6	4162	23-Jan-97	04-Feb-99	742	71	Removed transmitter
347	Garden Is.	F	A	199.8	3199	12-Apr-97	27-Apr-99	745	65	Removed transmitter
368	Garden Is.	F	A	226.8	4460	06-Oct-97	25-Nov-99	780	53	Removed transmitter
371	Garden Is.	M	J	86.6	218	17-Oct-97	06-Feb-98	112	17	Lost/Fail
374	Garden Is.	M	A	105.5	306	05-Nov-97	16-Jan-98	72	14	Lost/Fail
375	Garden Is.	F	A	203.0	4253	06-Nov-97	31-Mar-00	876	69	Removed transmitter
381	Garden Is.	F	A	212.3	4854	16-Nov-97	18-Feb-00	824	58	Removed transmitter
382	Garden Is.	F	A	221.7	5200	16-Nov-97	09-Mar-00	844	62	Removed transmitter
383	Garden Is.	M	A	121.4	313	26-Nov-97	03-Jan-98	38	7	Died
471	Garden Is.	M	A	105.2	245	14-Oct-98	18-Feb-99	127	34	Removed transmitter
474	Garden Is.	M	A	94.7	209	21-Oct-98	04-Feb-99	106	11	Removed transmitter
574	Garden Is.	M	A	98.5	191	24-Nov-99	02-Mar-00	99	14	Removed transmitter
575	Garden Is.	M	A	95.6	189	09-Dec-99	12-Mar-00	94	13	Removed transmitter
577	Garden Is.	M	A	105.8	234	28-Nov-99	18-Feb-00	82	23	Removed transmitter

python's mass. Snakes > 100 cm snout-vent length (SVL) were fitted with SI-2T transmitters (13 or 21 g with a life of 18 to 24 mo, depending on battery size). Smaller snakes were fitted with either BD-2T or PD-2T transmitters (3 and 5 g, with battery lives of 28 and 35 weeks respectively). Aerials were encased in 2 mm non-toxic Silastic® tubing and the entire unit sealed with 734 flowable sealant (Dow Corning Corporation).

For surgery, pythons were maintained under isoflurane ("Forthane", Abbott Pty. Ltd.) anaesthesia while the transmitter and aerial were inserted into the peritoneum through a mid-lateral incision 10% of the snake's SVL anterior to the vent (Pearson & Shine, 2002). Absorbable sutures were used to close the incision and the python was released 1-3 days later. A few of these pythons later excreted their transmitters through the alimentary tract (Pearson & Shine, 2002). When possible, snakes were recaptured close to the end of battery life and the transmitter was removed or replaced. To quantify reproductive frequency, several large females were tracked for > four years each. In contrast, the smaller transmitters implanted in males limited the duration of tracking, although some were reimplanted and monitored for up to two years.

Radio-telemetry

During the first two years of the study (1995 and 1996), I located most pythons on a weekly basis. In later years, Dryandra pythons were located fortnightly for most of the year but less often during their sedentary overwintering period. Pythons were tracked on foot using a 3-element yagi aerial (Sirtrak Ltd., New Zealand) and receiver (RX3, Biotelemetry Services, Australia). Most pythons did not flee from observers, allowing direct observation of microhabitat use. The exact position of pythons in trees was determined by scaling the tree, or by using a directional antennae attached to an extendable pole. When pythons were found, the location was marked with flagging tape. Distances and directions to previous locations were determined by compass and pacing at the start of the study and later with a rangefinder. A differential GPS system (Omnistar using an Optus satellite signal) was used to determine accurate positions (± 1-3 m) of most locations. Remaining locations were calculated from distances and directions to known points using the program "Numtrack" (M. Choo, pers. comm.).

See addendum

Movement patterns

To compare how far pythons moved at various times (seasons) of the year, I calculated distances between locations at approximately weekly intervals (defined as 5-8 days since the previous location). These distances represent the minimum distance travelled over that period; some pythons may have wandered extensively between the two points. I divided the year into four general time periods based on biological criteria, as follows:

(i) *Winter (June, July and August)* - Pythons at Dryandra usually retired to tree hollows for winter while those at Garden Island stayed on the ground and sheltered below shrubs. The end of the winter period was defined for Dryandra pythons as the last time they were located in their overwinter tree and for Garden Island pythons, it was arbitrarily defined as the end of August.

(ii) *Spring (breeding season)* - For Dryandra pythons, the start of the spring period was defined as the first time they were located on the ground away from their overwinter tree and for Garden Island, arbitrarily on September 1. For pythons at both sites, spring was deemed to finish on December 15 each year, around the latest date reproductive activity was ever observed (mating or close male-female proximity was noted from October 13 to December 20 with only one observation after December 15). I distinguished between reproductive and non-reproductive females, but all males were considered reproductive (Chapter 2).

(iii) *Summer* - This season was defined as December 16 to the end of March at both sites. Reproductive females during this period were developing eggs, with oviposition in mid-December to early January and incubation of eggs into March. Males and non-reproductive adult and juvenile females feed extensively during this period.

(iv) *Autumn (April, May)* - A time of cooler days and nights, when reproductive females have left their nests following the hatching of eggs, with feeding occurring by both sexes but particularly by post-incubation females.

Due to differences in transmitter battery life and the duration of tracking, data were available for only one season for some snakes ($n = 5$), but up to 16 seasons for other individuals (Table 5.1 lists the duration of tracking for each python). Extensive simulations show that treating successive seasons of data from the same snake as independent should not invalidate statistical analyses so long as the differences in movement patterns across seasons within a single animal are similar in magnitude to (or larger than) the variation among individual animals within a single season (Leger & Didrichson 1994). My data fulfil this assumption (see below), and so I treated the mean movement distances for each python in each season of each year that it was radio-tracked as independent for the purposes of my analyses.

Home range analysis

I followed Burt's (1943) definition of "home range" as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young", but noted the need to include a temporal component when reporting home ranges (White & Garrott 1990). A wide range of home range estimators are available, with the accuracy of calculated home ranges depending on the characteristics of the sampling techniques used, particularly the number of fixes (Jennrich & Turner 1969; Seaman et al. 1999), the interval between fixes (Swihart & Slade 1985a), how the locations were determined (e.g. trapping, triangulation of telemetry fixes; Otis & White 1999) and the home range estimator used (White & Garrott 1990; Garton et al. 2001). In this study, I was interested in determining the seasonal movements of pythons, yearly home ranges, habitat use in terms of broad vegetation/habitat types and microhabitat preferences. Where sample sizes permit, I compare these factors between sexes, between juvenile and adult pythons and between the two study sites. Rather than employ a calendar year that would divide the activity season in half, I calculated yearly home ranges from July 1 to June 30.

I employed three home range estimators (as recommended by Harris et al. 1990; Kernohan et al. 2001) available within Ranges V (Kenward & Hodder 1995). The Minimum Convex Polygon (MCP; Mohr 1947) has been widely reported in the literature and so was calculated to enable general comparison with other studies on snake home ranges. However, MCP only uses a proportion of location data, is sensitive to outliers and sample size, provides no information on an animal's use within the home range, and incorporates large areas that may never be used (White & Garrott 1990; Seaman et al. 1999; Powell 2000). The advantages of MCP are its simplicity and its lack of reliance on any statistical distribution (Seaman et al. 1999). I also employed the Harmonic Mean estimator (Dixon & Chapman 1980) because it has been commonly used in previous studies on snake home ranges (e.g. McCartney et al. 1988; Secor 1994). The third estimator used was the Kernel method (Worton 1987, 1989), recommended by recent reviews (Powell 2000; Kernohan et al. 2001). A fixed band width and least squares cross validation (Worton 1995) were applied to select the smoothing parameter; this method provides more accurate estimates than the adaptive kernel (Seaman & Powell 1996; Seaman et al. 1999). See addendum

The number of fixes required to estimate the home range accurately depends on the type of estimator used, the degree of autocorrelation between fixes and the time period under investigation. Seaman et al. (1999) suggested that robust kernel estimates required 30-50 observations per animal. However, the wide temporal spacing of data collection during my study (predominantly 7-14 days between fixes; see below) means that fewer fixes are needed than if the time between successive locations was shorter (Swihart & Slade 1985b; Hansteen et al. 1997; Kernohan et al. 2001). I arbitrarily set 20 fixes (equivalent to around 20 weeks telemetry) as the minimum required for the calculation of home range, with the additional proviso that most locations were obtained during the active season. The pythons do not undertake any regular seasonal migrations, so that the seasonal timing of data acquisition within the active season is relatively unimportant for calculating home ranges. The use of 20 fixes as a criterion allowed me to retain data on juvenile and male pythons that could only be fitted with short-term transmitters.

For the calculation of data on distances moved, I used fixes taken 5 to 8 days apart (see above). For home range calculations, I relaxed this requirement to a minimum time between fixes of three days. Pythons are capable of traversing their entire home ranges within a three-day day period.

Habitat and microhabitat type scoring

Whenever I located telemetered pythons, I recorded a range of physical and biotic features of the surrounding habitat as well as data on snake behaviour. Vegetation was described in terms of general classes defined by McArthur & Bartle (1981) for Garden Island and Coates (1993) for Dryandra Woodland. The type of microhabitat occupied was originally classified into one of 14 categories, but reduced to four categories for data analysis: (i) in tree hollows; (ii) in or under shrubs, leaf litter, or fallen branches; (iii) in logs; or (iv) underground.

RESULTS

General activity patterns

Telemetered pythons at the two sites displayed similar general activity patterns, with some variation apparently due to climatic differences. Adult males at both sites were active and moving in search of females in spring (October to mid-December) and continued to move around and feed during summer. In winter, Dryandra adult male and female pythons typically retreated up trees to shelter in hollow limbs, apparently ceased to feed and were occasionally observed basking near their overwinter refuge (see Discussion below). Dryandra experiences minimum temperatures close to freezing throughout winter and pythons were able to escape severe conditions at ground level by utilising elevated refuges where they were able to bask when conditions were suitable.

In contrast, all Garden Island adult males continued to move about on the ground and feed during winter. Adult female pythons at both sites moved extensively in spring and summer, although reproductive individuals (< 30% of the group) were more sedentary and eventually stationary during the incubation of their eggs. While adult females at Garden Island did not retreat to overwinter refuges like their Dryandra counterparts, they reduced their movements and most lay coiled under shrubs or under fallen timber, occasionally emerging to bask on sunny days. They were not observed to feed at this time.

Movement patterns

I calculated mean weekly movements for each snake in each season, and analysed the resulting data using a three-factor ANOVA (Table 5.2). The factors were: (i) sex/age class (juveniles, adult females, adult males); (ii) season (spring, summer, autumn, winter); and (iii) site (Dryandra, Garden Island). The analysis did not identify any significant three-way interaction between these factors ($F_{6,201} = 0.42$, $P = 0.86$), but did generate a significant two-way interaction between sex/age class and season ($F_{6,201} = 2.28$, $P = 0.037$), as well as highly significant main effects of season ($F_{3,201} = 11.63$, $P = 0.0001$) and sex/age class ($F_{2,201} = 5.33$, $P = 0.006$). There was no significant difference between the two study sites in terms of mean distances moved per week ($F_{1,201} = 0.19$, $P = 0.66$). Due to the significant interaction term, I then tested seasons separately to look at whether sex/age classes differed in any season. There was a marginally significant difference between sex/age classes in winter ($F_{2,30} = 3.32$, $P = 0.05$), and strong differences in summer ($F_{2,66} = 5.67$, $P = 0.005$).

Closer inspection of these data reveals the reasons for these significant results. Mean distances moved were remarkably similar at the two study sites, despite their considerable divergence in climate and vegetation cover (Table 5.2, Fig. 5.2). Unsurprisingly, snakes moved about less in winter than in the warmer seasons. Mean weekly movements of adult male snakes and reproductive females were similar in spring (the mating season) as in summer, but reproductive females were highly sedentary in summer (by this time, they were incubating their eggs; see Fig. 5.2).

Table 5.2. Mean weekly distances moved by radio-tracked carpet pythons (*Morelia spilota imbricata*) at two study sites in south-western Australia. Data for adult female snakes in summer are separated into snakes that were incubating eggs, and those that did not reproduce in the summer they were radio-tracked. See text for further explanation, definitions of seasons and statistical analysis.

Weekly distance moved (m)		**Dryandra**			**Garden Island**		
Sex/age class	Season/activity	N	Mean	SE	N	Mean	SE
adult female	SPRING (reproductive)	7	123.31	64.69	10	78.25	16.33
adult female	SPRING (non-reproductive)	7	149.73	61.83	15	98.67	16.88
adult female	SUMMER (reproductive)	5	1.00	1.00	8	1.55	1.55
adult female	SUMMER (non-reproductive)	8	164.45	18.82	15	154.09	18.07
adult female	AUTUMN	6	90.69	27.83	12	89.08	9.84
adult female	WINTER	6	22.10	6.26	7	9.13	3.22
adult male	SPRING	11	128.62	20.50	13	107.79	14.92
adult male	SUMMER	10	135.86	24.03	14	109.00	11.40
adult male	AUTUMN	9	116.77	28.68	8	78.53	16.54
adult male	WINTER	7	44.27	14.94	5	43.34	12.96
juvenile female	SPRING	3	69.51	28.39	6	88.71	10.84
juvenile female	SUMMER	4	108.18	34.67	8	134.20	28.67
juvenile female	AUTUMN	2	68.65	6.22	8	71.17	11.69
juvenile female	WINTER	3	8.56	2.70	8	25.68	7.31

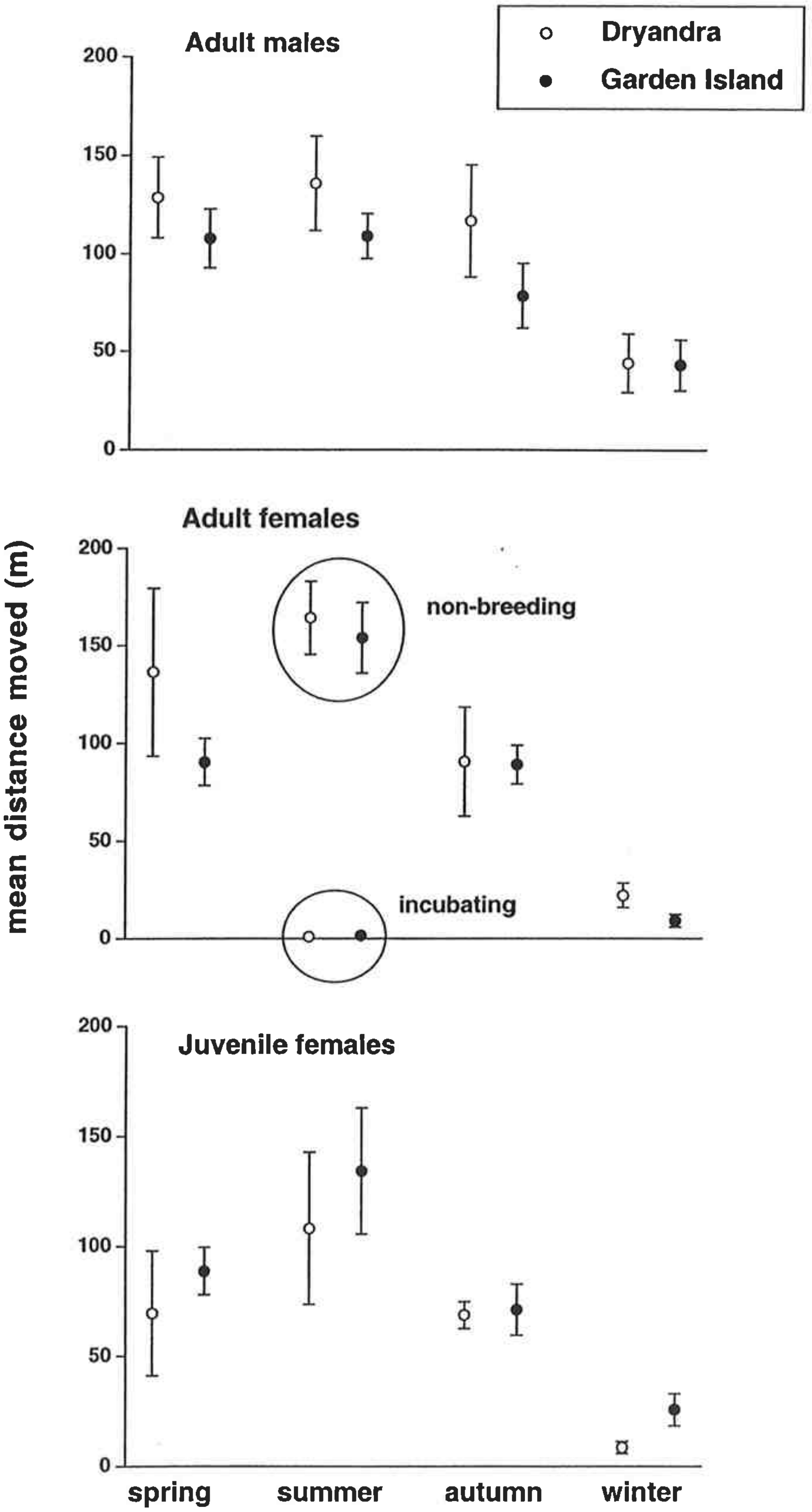

Figure 5.2. Mean weekly movements by radio-tracked carpet pythons at two study locations in south-western Australia. Data for adult female snakes in summer are separated into snakes that were incubating eggs, and those that did not reproduce in the summer they were radio-tracked. See text for further explanation and statistical analysis.

Site fidelity

Telemetered pythons were sometimes observed to return to sites where they had been previously located. At Garden Island, such observations were relatively rare (33 observed from a total sample of 2672 locations; or 1.2%), appeared to have no seasonal pattern and only two pythons (one male, one juvenile female) were observed to return to the same site on more than two occasions. In comparison, when I excluded overwinter trees from the analysis (since Garden Island pythons did not utilise them, but see below), Dryandra pythons still revisited previously occupied sites more often (154 of 1743 records; or 8.8%), but not significantly so ($z = 1.14$, $P = 0.25$). Most revisited sites were logs (51%) and hollows in trees (37%), with all other microhabitats (including burrows, under rocks and below shrubs) comprising the remaining 12%. There was considerable individual variation, with one subadult female (#6) reusing a few hollows on 15 occasions within her small home range of only 3.73 ha.

The timing of revisitation of previously occupied sites may reveal seasonal movements. Dryandra telemetry data were scanned to identify and extract non-overwinter refuges that were occupied on > 2 occasions. There were seven instances (1 adult male, 2 juvenile females and 4 adult females) of repeated visitation to logs or tree hollows during the active months. Some pythons did revisit certain refuges over several years and often these visits occurred at similar times each year, particularly in spring and early summer.

Overwinter refuge fidelity

At both sites, adult males and females and juvenile females reduced their movements during winter. The retreat to overwinter refuges by Dryandra Woodland pythons was the most striking difference in habitat use and seasonal activity patterns between the two studied populations. Most of the overwinter refuges used by Dryandra pythons were hollows in trees (see Table 5.3) and many of the pythons displayed strong fidelity, returning to the same hollow in consecutive years. Sample sizes were too small to detect any differences in site fidelity among the three sex/age groupings of pythons, but all used overwinter refuges. The duration of time spent in the overwinter refuge differed between sex/age groups at Dryandra. Minimum overwinter refuge durations averaged 96 days for adult males, 129.8 days for adult females and 131.3 days for juvenile females (one-factor ANOVA, $F_{2,37} = 3.81$, $P = 0.03$, but Tukey-Kramer posthoc pairwise comparisons found no significant difference between any pair of means).

At Garden Island, adult females reduced their movements markedly during winter. Several sheltered under the same shrubs for up to 67 days, although most continued to move small distances to new clumps of shrubs throughout winter. No radio-tracked adult female python on Garden Island returned to the same area in consecutive winters.

Table 5.3. Overwinter refuge fidelity of carpet pythons at Dryandra Woodland, including minimum and possible maximum duration of use, type of refuge and reuse of refuges between years. The snake column includes the sex and age class of each python: AM = adult male, AF = adult female, JF = juvenile female. Site fidelity refers to whether a python returned to the same overwinter refuge as used in the previous year.

Snake No.	Year	Date first at o'w refuge	Last date at o'w refuge	Min. o'winter time	Max. possible o'winter time	Type of refuge	Site fidelity
AM1	1995	22-May-95	3-Sep-95	104	112	tree hollow	
AM1	1996	21-May-96	19-Aug-96	90	104	tree hollow	y
AM1	1997	21-May-97	17-Sep-97	119	132	tree hollow	y
AF3	1995	6-Jun-95	3-Oct-95	119	133	tree hollow	
AF3	1996	24-Apr-96	15-Oct-96	174	182	tree hollow	y
AF3	1997	21-May-97	17-Sep-97	119	132	tree hollow	y
JF4	1995	14-May-95	9-Oct-95	148	156	tree hollow	
JF4	1996	7-May-96	24-Jun-96	48	49	tree hollow	y
JF4	1996	9-Jul-96	15-Oct-96	98	113	tree hollow	
JF6	1995	6-May-95	18-Sep-95	135	150	tree hollow	
JF6	1996	29-Apr-96	15-Oct-96	169	174	tree hollow	y
JF6	1997	21-May-97	23-Oct-97	155	169	tree hollow	y
AM7	1995	14-May-95	2-Oct-95	141	149	tree hollow	
AM7	1996	12-May-96	19-Aug-96	99	105	tree hollow	n
AM7	1997	21-May-97	27-Aug-97	98	112	tree hollow	n
JF9	1995	14-May-95	18-Sep-95	127	135	tree hollow	
JF9	1996	1-Apr-96	7-Oct-96	189	196	tree hollow	y
AF9	1997	7-May-97	23-Oct-97	169	174	tree hollow	
AM10	1995	14-May-95	24-Jul-95	71	79	tree hollow	
AF11	1995	6-May-95	18-Sep-95	135	150	log	
AF11	1996	7-May-96	2-Sep-96	118	125	tree hollow	n
AF14	1996	24-Apr-96	24-Oct-96	183	191	tree hollow	
AF14	1997	8-May-97	17-Sep-97	132	138	tree hollow	y
AF14	1998	3-Jun-98	5-Aug-98	63	75	log	n
AF15	1996	7-May-96	24-Oct-96	170	177	tree hollow	

Table 5.3 cont.

Snake No.	Year	Date first at o'w refuge	Last date at o'w refuge	Min. o'winter time	Max. possible o'winter time	Type of refuge	Site fidelity
AF15	1997	8-May-97	14-Oct-97	159	174	tree hollow	y
AM17	1996	7-May-96	19-Aug-96	104	105	tree hollow	
AM22	1996	15-Apr-96	2-Sep-96	140	146	tree hollow	
AF24	1996	28-May-96	16-Sep-96	111	118	tree hollow	
AF24	1997	21-May-97	1-Oct-97	133	147	tree hollow	y
AM25	1996	24-Apr-96	17-Sep-96	146	154	wallspace	
AM29	1997	6-Jun-97	27-Aug-97	82	97	tree hollow	
AF30	1997	10-Apr-97	17-Sep-97	160	167	tree hollow	
AM31	1997	2-Jul-97	29-Jul-97	27	33	log	
AM31	1998	15-Jun-98	28-Aug-98	74	85	tree hollow	n
AM32	1997	8-May-97	26-Jun-97	49	64	tree hollow	
AF34	1997	21-May-97	27-Aug-97	98	111	log	
AF34	1998	22-May-98	5-Aug-98	75	112	log	n
AF37	1998	4-Aug-98	23-Sep-98	50	61	log	
AF38	1998	3-Jun-98	24-Sep-98	113	125	tree hollow	
AM39	1998	22-May-98	5-Aug-98	75	112	tree hollow	
JF46	1996	3-Jun-98	24-Sep-98	113	125	tree hollow	

Home ranges

Mean home ranges as estimated by the alternative methods were broadly similar, and showed similar patterns with respect to the effects of location and sex/age class on home range size (Table 5.4, Fig. 5.3). MCP estimates averaged 17.6 ha, harmonic mean (95%) estimates averaged 19.3 ha, and kernel (95%) methods averaged 19.9 ha. All three were highly correlated with each other ($r > 0.68$, $P < 0.0001$). Two-factor ANOVA with location and sex/age class as factors revealed a significant interaction term (for MCP, $F_{2,87} = 5.81$, $P < 0.005$; for harmonic mean, $F_{2,87} = 5.45$, $P < 0.006$); that is, the effect of sex/age class on home range size differed between the two study areas. This interaction term reflects the fact that adult male pythons had very large home ranges at Dryandra, but small home ranges on Garden Island (Fig. 5.3). To further investigate these patterns, I conducted one-factor ANOVAs (with sex/age class as the factor) separately for data from each location. In each case, home ranges did not differ significantly among adult males, adult females and juveniles at Garden Island, but did so at Dryandra. This was true both for MCP estimates (Dryandra, $F_{2,29} = 5.76$, $P < 0.001$; Garden Island, $F_{2,58} = 2.07$, $P = 0.14$) and for harmonic mean estimates (Dryandra, $F_{2,29} = 3.38$, $P < 0.05$; Garden Island, $F_{2,58} = 1.44$, $P = 0.25$).

Reproductive females had slightly smaller home ranges than non-reproductive females, but not significantly so (mean (SD) of home ranges using MCP estimate: Garden Island reproductive 14.15 (9.71) ha vs non-reproductive 22.26 (18.21) ha; $t_{36} = 1.21$, $P = 0.24$ and Dryandra 6.51 (5.2) ha vs 14.27 (12.1) ha; $t_{11} = 1.34$, $P = 0.21$).

Table 5.4. Yearly home ranges of radio-tracked carpet pythons at two study sites in south-western Australia, determined by three home range estimators. See text for further explanation and statistical analysis. Notes. M = male, F = female, A = adult, J = juvenile. * indicates reproductive year for females. MCP = Minimum Convex Polygon, HM = Harmonic Mean, Kernel = Kernel analysis. All % figures refer to isopleths containing either 50% of locations (= core area) or 95% of locations (= yearly home range; see text for further details).

Snake No.	Sex	Age Class	Year	No. of locations	MCP 100%	HM 95%	HM 50%	Kernel 95%	Kernel 50%
Dryandra									
3	F	A	95/6	41	34.17	42.05	1.30	41.78	1.18
3	F	A	96/7*	36	14.97	7.32	0.48	29.02	1.98
9	F	A	97/8	27	4.16	3.11	0.17	3.71	0.19
11	F	A	95/6*	43	5.89	2.00	0.20	6.53	1.22
11	F	A	96/7	26	31.91	29.69	2.70	46.14	13.23
14	F	A	95/6	26	6.64	7.98	0.79	10.87	1.24
14	F	A	96/7*	38	1.10	1.46	0.08	1.09	0.10
14	F	A	97/8	26	3.32	14.92	2.31	13.19	3.22
15	F	A	95/6	26	13.91	12.45	0.61	19.00	4.40
15	F	A	96/7	38	8.89	6.68	0.64	12.33	2.56
15	F	A	97/8*	21	3.87	0.75	0.04	4.36	0.20
24	F	A	96/7	39	11.14	11.08	1.59	11.46	2.27
34	F	A	97/8*	25	6.72	1.93	0.34	8.50	0.44
4	F	J	95/6	44	3.14	2.77	0.41	3.70	0.77
6	F	S	95/6	44	6.84	7.24	0.21	4.11	0.23
6	F	S	96/7	40	9.85	10.45	0.16	3.35	0.21
9	F	S	95/6	41	9.37	5.90	0.80	6.74	1.93
9	F	S	96/7	35	8.64	6.07	1.38	8.11	1.78
30	F	J	96/7	23	19.61	17.21	1.33	27.61	3.98
30	F	J	97/8	23	25.63	26.85	0.65	34.39	5.07
1	M	A	95/6	42	25.18	27.01	0.86	24.56	0.83
1	M	A	96/7	38	28.15	22.57	2.42	49.36	10.63
7	M	A	95/6	44	11.68	7.31	1.02	10.21	1.60

Table 5.4 cont.

Snake No.	Sex	Age Class	Year	No. of locations	MCP 100%	HM 95%	HM 50%	Kernel 95%	Kernel 50%
Dryandra									
7	M	A	96/7	35	69.24	61.42	3.59	52.23	7.20
10	M	A	95/6	28	17.68	19.90	0.85	19.57	2.64
13	M	A	95/6	28	9.20	7.11	0.05	9.69	0.33
16	M	A	95/6	28	29.64	188.00	2.62	117.43	2.37
17	M	A	95/6	25	8.69	4.70	0.30	8.31	0.37
17	M	A	96/7	37	29.85	51.39	2.04	55.95	8.50
29	M	A	96/7	25	38.94	37.40	2.44	50.95	2.68
31	M	A	96/7	22	27.63	24.03	5.92	74.47	13.71
31	M	A	97/8	29	29.51	41.45	5.53	47.87	9.34
Mean				32.59	17.35	22.19	1.37	25.52	3.33
SD				7.70	14.43	34.10	1.48	25.92	3.84
Garden Island									
50	F	A	95/6*	57	25.99	19.15	1.19	34.90	1.52
50	F	A	96/7	47	34.18	28.27	0.59	27.29	0.74
50	F	A	97/8	38	83.29	94.95	7.26	79.66	10.04
50	F	A	98/9	24	56.73	41.29	4.06	70.88	12.87
56	F	A	95/6	48	6.34	3.62	0.51	3.87	0.86
56	F	A	96/7	54	11.58	12.44	0.81	11.14	1.88
56	F	A	97/8	39	11.04	9.35	1.15	13.23	3.02
56	F	A	98/9	22	7.16	6.68	0.65	13.22	1.76
79	F	A	95/6	30	20.28	16.84	1.81	16.44	5.58
79	F	A	96/7*	56	15.22	9.27	1.49	18.15	5.27
79	F	A	97/8	35	28.43	25.33	2.74	11.24	2.92
79	F	A	98/9	21	12.18	8.30	1.28	15.82	3.30
87	F	A	95/6	26	5.01	4.52	0.46	4.70	0.50
87	F	A	96/7*	55	3.82	1.74	0.21	1.68	0.21
87	F	A	97/8	31	13.05	7.06	1.25	8.94	1.30

Table 5.4 cont.

Snake No.	Sex	Age Class	Year	No. of locations	MCP 100%	HM 95%	HM 50%	Kernel 95%	Kernel 50%
Garden Island									
87	F	A	98/9	22	15.32	18.66	2.31	14.89	3.21
143	F	A	95/6	55	6.65	5.21	0.74	4.33	0.62
143	F	A	96/7*	56	10.04	9.89	0.61	3.48	0.35
143	F	A	97/8	35	12.61	10.17	1.25	17.52	2.02
143	F	A	98/9*	26	3.00	3.11	0.25	4.26	0.72
212	F	A	96/7	34	13.79	12.28	0.40	11.42	0.58
218	F	A	96/7	45	13.10	6.04	1.62	9.13	4.40
218	F	A	97/8	38	13.39	15.04	0.98	14.84	1.37
218	F	A	98/9	26	16.55	14.41	2.05	19.94	3.83
235	F	A	96/7*	41	9.52	13.69	0.43	17.75	1.49
235	F	A	97/8	21	5.25	2.26	0.41	0.71	0.93
260	F	A	96/7*	30	15.77	14.83	1.67	11.25	1.97
260	F	A	97/8	34	33.98	26.12	3.99	8.50	9.74
317	F	A	97/8	35	27.68	22.45	4.26	29.32	4.89
347	F	A	97/8	35	58.64	46.19	3.95	69.07	9.08
347	F	A	98/9	23	24.68	28.48	2.91	26.31	5.39
268	F	A	97/8	26	34.43	32.52	4.21	15.26	5.16
375	F	A	97/8*	28	29.84	28.60	1.65	28.29	2.54
375	F	A	98/9	21	42.03	51.63	0.51	95.71	0.66
381	F	A	97/8	21	23.71	11.85	1.88	12.48	5.13
381	F	A	98/9	22	13.17	8.40	0.66	18.10	4.59
382	F	A	97/8	21	15.79	12.21	0.22	22.05	0.41
382	F	A	98/9	23	7.76	6.47	0.62	9.70	0.92
9	F	J	94/5	21	2.22	0.80	0.14	2.40	0.83
10	F	J	94/5	22	12.25	10.30	0.06	5.50	0.07
17	F	J	94/5	23	0.51	0.35	0.07	0.31	0.05
18	F	J	95/6	52	3.62	2.97	0.54	1.25	0.99

Table 5.4 cont.

Snake No.	Sex	Age Class	Year	No. of locations	MCP 100%	HM 95%	HM 50%	Kernel 95%	Kernel 50%
Garden Island									
40	F	J	95/6	38	48.72	69.87	2.15	28.66	2.58
53	F	S	95/6	53	7.15	7.12	1.02	7.77	1.08
53	F	S	96/7	52	5.73	6.45	0.37	6.00	0.67
53	F	A	97/8	33	8.04	6.51	0.46	8.78	1.33
53	F	A	98/9	21	23.83	101.20	2.32	13.45	1.06
67	F	J	95/6	40	6.12	3.84	0.46	6.99	1.00
67	F	J	96/7	21	2.08	1.92	0.12	0.49	0.18
81	F	S	95/6	32	35.09	52.30	4.75	28.49	3.14
81	F	S	96/7	48	44.15	42.41	9.11	40.41	7.47
76	M	A	95/6	32	10.27	10.72	1.14	14.30	3.67
76	M	A	96/7	39	20.01	25.74	1.09	23.09	0.98
83	M	A	95/6	31	7.29	8.67	1.09	5.90	1.40
83	M	A	96/7	35	18.21	14.05	3.34	20.75	4.77
165	M	A	96/7	43	8.23	6.03	0.46	5.40	0.65
259	M	A	96/7	34	16.38	10.14	3.01	8.88	3.04
266	M	A	96/7	30	3.18	3.49	0.52	4.34	0.69
266	M	A	97/8	30	2.13	1.48	0.30	2.12	0.71
313	M	A	96/7	19	4.98	4.17	0.27	1.97	0.36
313	M	A	97/8	31	5.66	4.30	0.60	1.26	0.87
Mean				34	17.65	17.77	1.58	16.95	0.61
SD				11	16.08	20.78	1.74	19.12	0.28

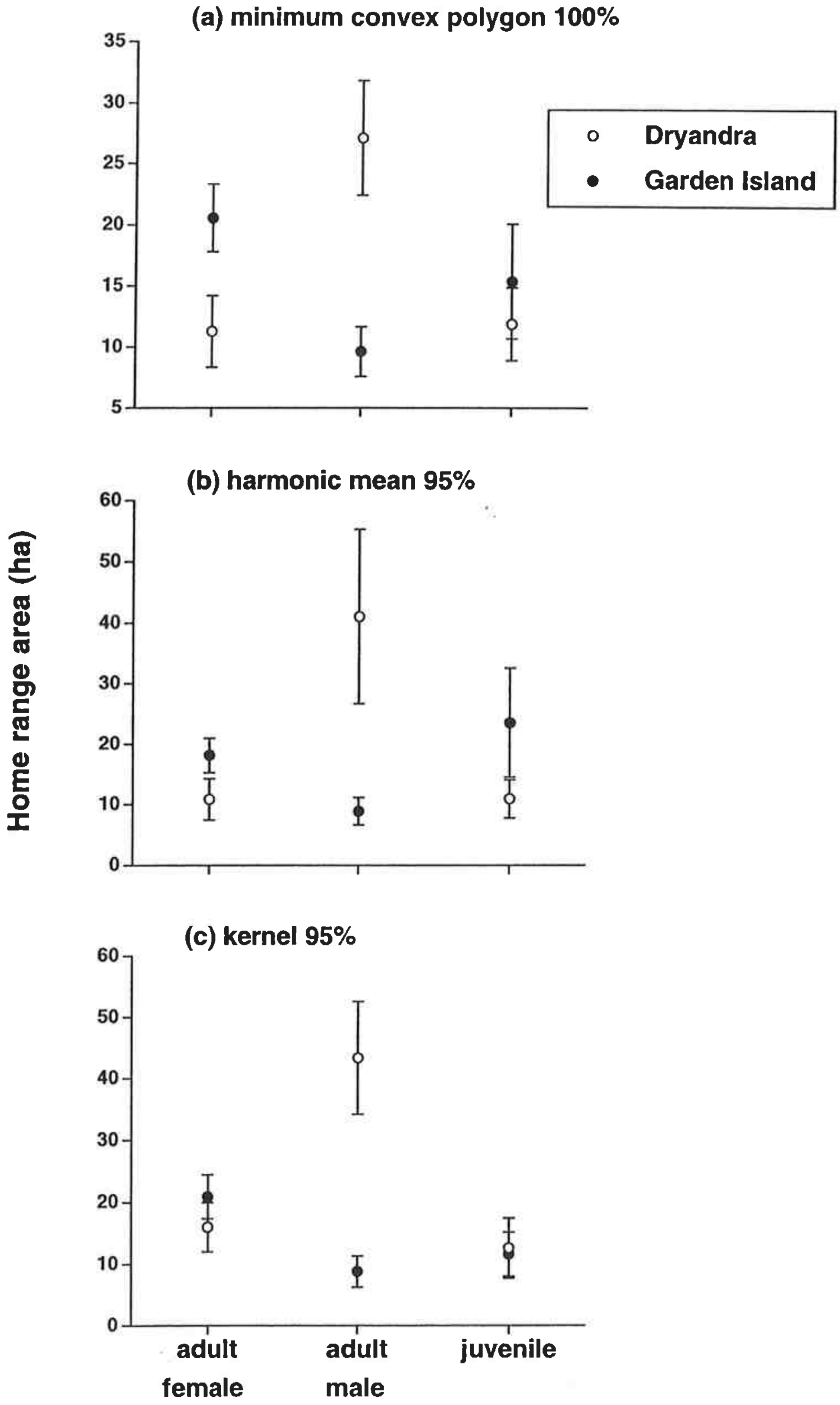

Figure 5.3. Yearly home ranges of radio-tracked carpet pythons at two study locations in south-western Australia, derived by three methods of calculation. See text for further explanation and statistical analysis.

Patterns in macrohabitat use

Because habitat availability at the two study sites differed profoundly, so did habitat usage by the pythons. Dryandra snakes were located primarily in open wandoo woodland (65.6% of 1504 records) and powderbark wandoo woodland (15.2%); with the remainder in heath, rock oak/wandoo communities or in disturbed habitats such as mallet plantation and in huts. In contrast, pythons on Garden Island were found mainly in vegetation associations dominated by *Acacia rostellifera* (shrublands and low forest: 68% of 2451 locations) or native pine/*Melaleuca* forest (23%).

I examined whether habitat selection by pythons was occurring between these broad groups by comparing observed use with availability of the various vegetation associations. For the Dryandra Woodland study site, the relative proportions of vegetation units (determined from the maps of Coates 1993) were compared with telemetry observations. Assuming that pythons had similar access to all vegetation types (a reasonable assumption given the fine-scale interdigitating vegetation pattern of the study area), pythons showed a high level of habitat selection (analysis of contingency table listing the five major habitat types: wandoo, powderbark wandoo, rock oak/wandoo woodlands, heath and mallet plantations; $\chi^2_4 = 359.21$, $P < 0.001$). Wandoo woodland was a preferred habitat type (66% of python locations vs availability of 35%); other major habitats were used in approximate proportion to their availability (powderbark woodland 15% vs 19%; and rock oak/wandoo woodland 10% vs 6%). However, mallet plantations were avoided (8% usage vs 32% availability; test of proportions, z

= 15.11, $P < 0.001$). None of the snakes I tracked had home ranges completely within the mallet plantations; all made extensive use of neighbouring native woodlands.

Areas occupied by the various vegetation types in the Garden Island study area were determined by interrogation of available Department of Defence digital vegetation mapping (based on the units of McArthur & Bartle 1981). Python usage of the four major types; *Acacia rostellifera*-dominated shrubland or woodland, native pine/*Melaleuca lanceolata* forest, heath and littoral communities proved to be significantly different to availability ($\chi^2_3 = 926.92$, $P < 0.001$). Pythons showed a preference for communities dominated by *A. rostellifera* (68% usage vs 41% availability) and heath (8.3% vs 4%), but native pine/*M. lanceolata* forest (22.7% usage vs 41% availability) and littoral communities (0.1% vs 13.5%) were used less than expected from their availability.

Within each of the study sites, my analyses did not detect any differences between sex/age groups in macrohabitat use. At Garden Island, one-factor ANOVA with sex/age class as the factor revealed no significant differences among juveniles, adult males and adult females in terms of the proportion of radio-tracking records when snakes were found in *Acacia rostellifera* habitats ($F_{2,38} = 1.72$, $P = 0.19$), heath ($F_{2,38} = 0.35$, $P = 0.71$), native pine/*Melaleuca* ($F_{2,38} = 2.00$, $P = 0.15$) or the littoral zone ($F_{2,38} = 1.36$, $P = 0.27$). At Dryandra, the three sex/age classes also used the major habitat types in similar frequencies (wandoo, $F_{2,28} = 2.55$, $P = 0.10$; powderbark wandoo, $F_{2,28} = 1.37$, $P = 0.27$; rock oak, $F_{2,28} = 0.46$, $P = 0.64$; heath, $F_{2,28} = 0.47$, $P = 0.63$; disturbed habitat, $F_{2,28} = 0.77$, $P = 0.47$). The trees used by pythons at Dryandra were larger than those at Garden Island (mean DBH = 62 vs 13 cm;

$F_{1,35}$ = 190.0, $P < 0.0001$), but the sizes of trees used by radio-tracked snakes did not differ between adult males, adult females and juveniles ($F_{2,35}$ = 0.08, P = 0.92).

Patterns in microhabitat use

To facilitate comparisons between snakes at my two study sites, I classified microhabitats into four broad categories: (i) in logs; (ii) in or under shrubs or fallen branches; (iii) in tree hollows; or (iv) underground. I analysed these data (mean proportions in each category for each snake) using two-factor ANOVA, with factors being location and sex/age class (see Fig. 5.4 for graphical presentation). Unsurprisingly, the proportion of snakes located in logs was higher at Dryandra than Garden Island (means of 46 vs 4%; $F_{1,66}$ = 73.67, $P < 0.0001$), but there was no difference among sex/age classes in this respect ($F_{2,66}$ = 0.66, P = 0.52), nor any significant interaction between the two factors ($F_{2,66}$ = 2.17, P = 0.12). Exactly the reverse pattern was evident for the proportion of snakes located in or under shrubs, with means of 12% at Dryandra versus 91% at Garden Island ($F_{1,66}$ = 841.0, $P < 0.0001$) and again, no sex/age class difference ($F_{2,66}$ = 1.28, P = 0.28) or significant interaction ($F_{2,66}$ = 0.32, P = 0.73). Usage of tree hollows showed a more complex pattern, differing not only between sites ($F_{1,66}$ = 59.28, $P < 0.0001$), but also between sex/age classes ($F_{2,66}$ = 3.30, $P < 0.045$; see Fig. 5.4c). The interaction between the two factors was also close to statistical significance ($F_{2,66}$ = 3.07, P = 0.05). Posthoc Tukey-Kramer tests showed that juvenile snakes differed significantly from adult females in this respect ($P < 0.05$). The final microhabitat category involved snakes that were underground when located.

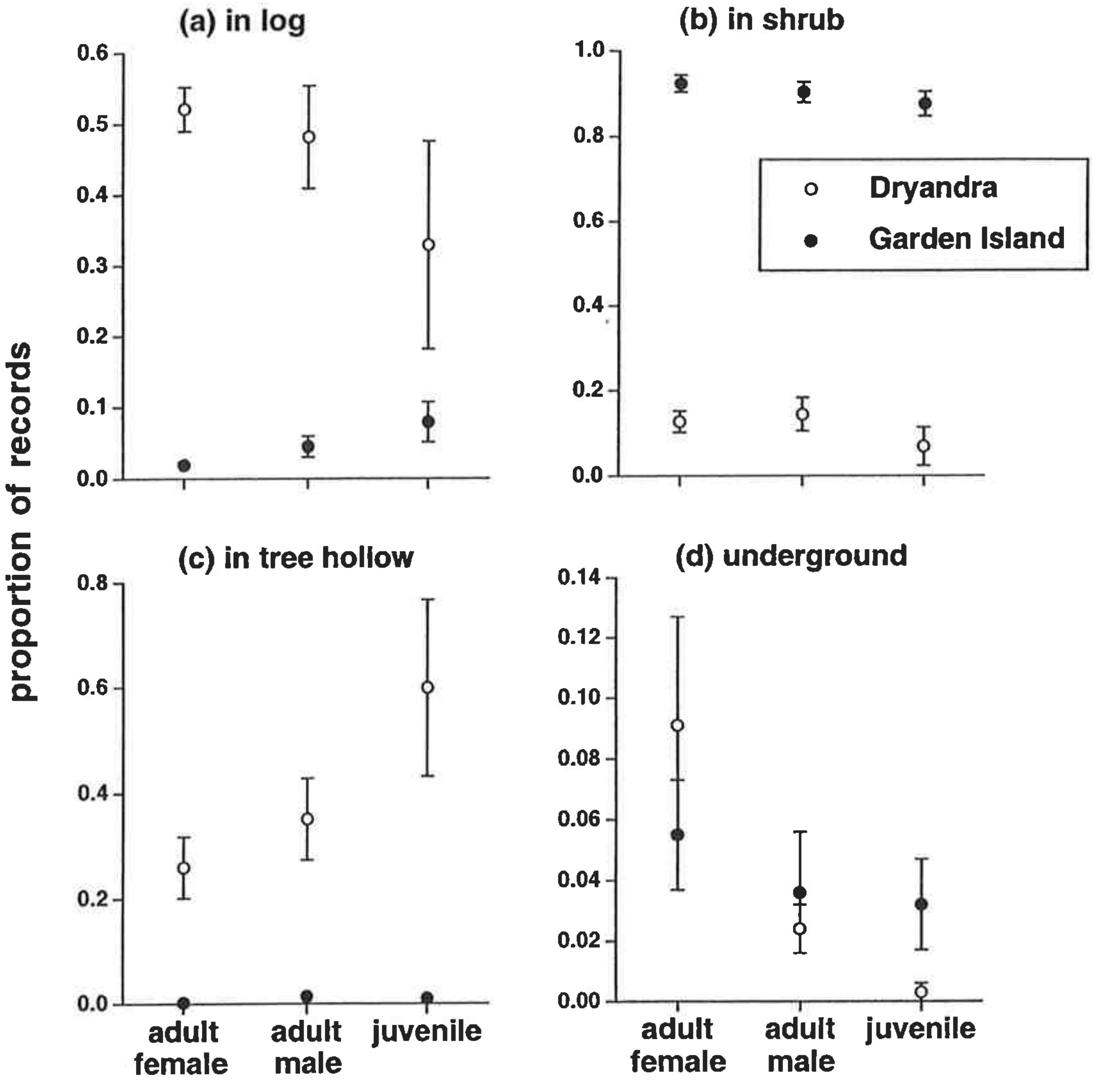

Figure 5.4. Microhabitat use by radio-tracked carpet pythons at two study locations in south-western Australia. See text for further explanation and statistical analysis.

The proportion of snakes in holes or burrows did not differ between the two study sites (4% in both; $F_{1,66} = 0.01$, $P = 0.92$), but was higher in adult females than in other sex/age classes (Fig. 5.4d; $F_{2,66} = 3.76$, $P < 0.03$; but Tukey-Kramer posthoc tests non-significant). Additional data on microhabitat variables at Dryandra allow me to examine effects of snake size and sex on log use. The three sex/age classes did not differ in the sizes of logs that they used (log diameter, $F_{2,23} = 2.58$, $P = 0.10$; log length, $F_{2,23} = 0.34$, $P = 0.72$).

DISCUSSION

My study provides the first detailed ecological data on carpet pythons in south-western Australia, and is the largest data set of its kind for a radio-telemetric study on any Australian snake species. The unusually large number of snakes radio-tracked ($n = 75$), and the use of two study areas that differ markedly in climate and habitat types, provide an opportunity to tease apart the influences of environmental factors versus attributes of the snake (sex/age class) on variables such as movement patterns and home range sizes. Although my study revealed many such effects, perhaps the most striking aspect is the broad similarity in overall patterns. Snakes at the two sites perforce used very different habitats, but they did so in relatively similar ways. Thus, a snake's sex and body size influenced its behaviour only within relatively narrow limits (e.g. Fig. 5.2).

Telemetered *Morelia s. imbricata* typically moved approximately 100 m per week during the active season, similar to distances reported for adults in the eastern subspecies *Morelia s. mcdowelli* in a densely forested area (Shine &

Fitzgerald 1996). My study animals also remained relatively sedentary during winter, as has been reported for eastern subspecies of carpet pythons (Slip & Shine 1988d; Shine & Fitzgerald 1996). The cooler night and day time temperatures at Dryandra Woodland presumably result in all python sex/age classes retreating to overwinter shelters for on average over three months, as well as the apparent cessation of feeding. Garden Island male and juvenile pythons continue to move and feed during winter and consequently might be expected to be able to maintain more rapid growth rates than their inland conspecifics. The most pronounced feature of movement patterns was the differences between non-reproductive and reproductive adult females, the latter remaining sedentary throughout the period when they were incubating eggs (Fig. 5.1). The same phenomenon occurs in all egg-brooding pythons (Shine 1988). Thus, overall patterns of movement for females were influenced more strongly by differences in reproductive state within a single population, than by major differences in habitat type across my two study areas, or even thousands of km from south-western to eastern Australia.

One apparent paradox when comparing the data for Garden Island versus Dryandra Woodland animals was that home ranges of adult male pythons were much larger than those of females at the latter site but not the former (Fig. 5.3), despite the fact that mean weekly distances moved were similar in both sexes in both areas (Fig. 5.2). This difference reflects the tendency for adult male pythons at Dryandra to undertake long distance movements to locate a female, but then to remain with her for a long period (up to a few weeks). In contrast, adult male pythons at Garden Island typically moved shorter distances, but did not stay with each female for long and instead, visited several females during the mating season (Chapter 2).

The end result was a broad similarity in mean weekly displacements for adult males at the two sites (Table 5.2; 128.62 m at Dryandra vs 107.79 m at Garden Island), but this similarity masks a substantial difference in the distances and frequency of mate-searching activities. The likely reason for this difference is the much higher density of snakes (including reproductive females) at Garden Island than at Dryandra (note that I captured > 10 times as many snakes at the former site as the latter). Thus, a mate-searching male at Garden Island would be likely to locate a female without having to undertake a major search. Given this high density, males may also be more likely to leave a female after mating because they are very likely to soon encounter another one. The same hypothesis has been used to explain divergence in male mate-searching tactics between populations of eastern Australian carpet pythons (Shine & Fitzgerald 1995).

Home ranges of my radio-tracked snakes were broadly similar between the two study areas (means = 17.3 and 17.7 ha), and similar to previous MCP estimates from studies on eastern Australian carpet pythons (mean home range of 17 ha for female *M. s. spilota*, Slip & Shine 1988d; and 22 ha for *M. s. mcdowelli*, Shine & Fitzgerald 1996). However, male *M. s. spilota* travelled over larger areas (mean = 43 ha; Slip & Shine 1988d). At both sites, exclusive territories were not apparent, with the home ranges of male, female and juvenile pythons showing extensive overlap (as was reported for *M. s. spilota*, Slip & Shine 1988d). Given the strong geographic variation both in sexual size dimorphism and in mating systems within this species (Chapters 2 and 3), such differences in spatial ecology are not surprising.

My estimates of home range size in south-western carpet pythons fit within the general range of those reported for other ambush predators in the recent literature (where radio-telemetry has been used; for a review of reported home ranges up to 1987, see McCartney et al. 1988). Many viperids tend to have very small home ranges (MCP 0.19 to 8.0 ha), but others such as *Crotalus horridus* have home ranges as large as 207.4 ha, although this figure includes migratory movements to hibernacula (McCartney et al. 1988; Beck 1995). My data for carpet pythons show some similarity to patterns described by Secor (1994) for sidewinders, *Crotalus cerastes.* Males moved greater distances than females in breeding periods, however mean home ranges of both sexes and subadults were similar (means 22.9, 19.0 and 22.3 ha respectively). It is interesting to note that reported mean home range sizes of snakes are all comparatively small (typically < 1-25 ha, although there is considerable individual variation), and those of ambush predators such as viperids and carpet pythons are within the same range as active foragers amongst the colubrids (Madsen 1984; McCartney et al. 1988; Weatherhead & Hoysak 1989) and elapids (Shine 1987).

Macrohabitat use by the pythons was highly flexible, responding to the great disparity in available habitat types in my two study areas. Pythons at Garden Island were almost always terrestrial, generally sheltering beneath prickle lily shrubs that cover most of the island. In contrast, pythons at Dryandra were usually found in hollows, either in standing trees or in logs on the ground. The proportion of arboreal records at the two sites thus spans the diversity reported in previous studies from widely separated localities (16% for *M. s. spilota*, 45% in *M. s. mcdowelli*), and reveals a high degree of flexibility in habitat use by these large snakes. The common factor is concealment; pythons were rarely found in exposed situations, and instead sheltered within whatever type of retreat was available. This result fits well with previous reports of carpet pythons utilising a broad range of habitat types, including the highly modified habitats of suburbia (e.g. Fearn et al. 2001).

Despite this apparent flexibility, carpet pythons at Dryandra avoided mallet plantations. The small diameter of mallet trees, their lack of hollows, logging practices that remove them at small diameters (the timber is used primarily for tool handles), and the suppression of undergrowth in dense plantations restricts the number of shelter and potential ambush sites available to pythons. When I did locate pythons in mallet plantations, they were almost invariably in logs (76 of 103 locations) or lying under bushes in close proximity to logs. Of particular importance is the origin of these logs. I never found pythons in mallet logs (they are rarely of sufficient diameter) and all the logs occupied by pythons were from wandoo or powderbark wandoo trees cut down during the establishment of the plantation or in subsequent thinning. Most of these logs are now extremely old (some > 70 years) and many are in advanced states of decay. This observation suggests that mallet plantations will become increasingly unsuitable for pythons with the loss of logs and no possibility of replacement. The loss of logs in mallet plantations is also likely to impact heavily on various mammals (and hence, python prey) in Dryandra Woodland including such species as the threatened numbat (*Myrmecobius fasciatus*). While the management of these plantations is primarily for timber production, their value to pythons would be increased by retaining the small patches of native vegetation that have regrown in some areas, avoiding the use of fire (which will destroy existing logs) and retaining the fallen canopies (branches and leaves) of cut mallet trees as these provide some shelter for pythons.

Much of the behavioural diversity that I observed is readily interpretable in light of the characteristics of the snakes and the study areas.

For example, the reasons why juvenile snakes were more arboreal than adults at Dryandra (Fig. 5.4) probably involves the availability of suitably-sized prey (juveniles take birds and small arboreal mammals whereas adults concentrate on larger terrestrial mammals: Chapter 3) and refuges (adult female pythons are too large to fit into many tree-hollows). The potential role of predators (primarily the introduced fox, *Vulpes vulpes* and feral cats) in determining habitat use by pythons remains unresolved and may warrant further study.

The general picture that emerges from my study is of a species that displays extreme ecological flexibility. It uses whatever habitats are available, at both macro and micro scales. Although the massive disparity in body sizes (lengths) between hatchling (25 cm) and adult (> 200 cm) snakes inevitably requires shifts in traits such as retreat-site selection, ambush location and prey types (Mushinsky 1987), the same general patterns of spatial ecology are seen in individuals over a substantial range of body sizes and habitat types. The same is true for comparisons across my two very dissimilar study areas, as well as for wider comparisons that encompass previously-studied populations of *M. spilota* in eastern Australia (Slip & Shine 1988d; Shine & Fitzgerald 1996).

The ability of carpet pythons to utilise such a wide range of habitat types and prey taxa suggests that these snakes would fare well in anthropogenically disturbed habitats, and indeed this is the case in coastal areas of eastern Australia (Shine 1994b). Paradoxically, however, this flexible generalist has disappeared from much of its range in south-western Australia (Smith 1981; Pearson 1993) as well as in semi-arid to arid parts of its range in eastern Australia (Shine 1994b). My study suggests that one of the critical resources needed for populations of this large predator is the availability of suitable hiding places in which the snakes can shelter, from which they can ambush prey, and in which they can brood their eggs. Well-watered coastal habitats with uneven topography typically provide such places (often in densely-forested gullies within disturbed landscapes), whereas agricultural development often removes extensive areas of habitat in semi-arid areas with little topographic relief (as in the Western Australian Wheatbelt, where only 7% of the native vegetation remains; Saunders 1979).

Although land-clearing for agriculture has undoubtedly played a major role in the destruction of python habitat, wildfires may also be significant. There is a substantial complexity to the effects of fire, however. Because of the great spatial diversity in the types of retreat-sites and ambush-sites used by carpet pythons, fires would substantially reduce the availability of critical ground cover in some areas but not in others. Also, the timescale over which the cover items regenerate would differ considerably depending on the habitat involved (e.g. logs vs shrubs), the area and its climate. The seasonal timing (and thus, intensity) of fire may also be significant. Relatively "cool" fires used for prescribed fuel reduction at Dryandra Woodland may destroy logs (and thus, remove the pythons' primary places of concealment). On the other hand, "hot" fires while burning many logs, also kill and fell standing trees thus resulting in a new generation of logs. "Hot" fires may also remove many of the hollow limbs used as overwintering sites (often, year after year) by snakes. These complexities suggest that we need a much clearer understanding of the processes that determine the abundance of potential shelter-sites (especially, logs) in semi-arid areas. The keys to maintaining populations of carpet pythons may be twofold: sufficient mammals of the appropriate size to be prey for adult snakes, and sufficient protected refuges at ground level for effective shelter and ambush predation.

CHAPTER 6

Thermal biology of carpet pythons (*Morelia spilota imbricata*) in south-western Australia

ABSTRACT

Radio-telemetric monitoring of 70 free-ranging carpet pythons (*Morelia spilota imbricata*) at two sites in south-western Australia provided extensive data on the body temperatures exhibited by these animals. The snake's thermal regimes were affected by season, time of day, location, microhabitat, size and sex, behaviour, and reproductive state. Over most of the year pythons exhibited relatively smooth unimodal diel curves of heating and cooling, attaining maximal temperatures around 30°C. The (small) male snakes heated and cooled more rapidly than did the (larger) females. Climatic differences between my two study sites generated substantial shifts in mean body temperatures and thus, in the diel timing of ambush foraging behaviour. Females wrapped tightly around their eggs after oviposition and brooded them throughout the ensuing eight week incubation period. Throughout this time, females were facultatively endothermic, maintaining high constant temperatures through shivering thermogenesis. Females nesting in sites with relatively poor thermal buffering (under rootballs of

fallen trees rather than rock crevices) supplemented endogenous heat production with occasional basking, and hence overall maintained lower and more variable incubation temperatures than did females with "better" nest-sites. See Addendum

INTRODUCTION

For many species of tropical reptiles, temporal and spatial variation in environmental temperatures may not have much influence on the animal's activities, because the relatively benign environmental temperatures permit extensive thermoconformity (Shine & Madsen 1996). For terrestrial reptiles in cooler and more variable climates, however, thermoregulation may be a critical facet of day-to-day existence (Bennett & Nagy 1977; Hertz et al. 1993). Perhaps for this reason, studies on the thermal ecology of reptiles have concentrated primarily on temperate zone diurnal lizards (Huey 1974; Huey & Slatkin 1976; Avery 1982; Huey 1982; Heatwole & Taylor 1987). These studies provide abundant evidence that small temperate-zone reptiles employ a variety of strategies to avoid daily temperature extremes while maintaining body temperatures to meet a raft of (at times) conflicting objectives such as foraging, predator avoidance, and mate location. The thermal biology of very large squamate reptiles in cool, highly seasonal environments has attracted less scientific attention, perhaps because there are far fewer species in this category. Nonetheless, the temperature relations of large snakes in cool climates are of great interest for at least four reasons:

(i) Body size and thermal inertia. - Because rates of heat exchange (heating and cooling) depend upon absolute body size (Grigg et al. 1979; Seebacher et al. 1999), large animals need to bask for very long periods to achieve high body temperatures. Intuition suggests that this constraint may be a reason why most very large reptile species (giant pythons, varanid lizards, crocodiles, sea turtles) tend to be found primarily in tropical regions. How do very large temperate-zone reptiles manage to maintain effective body-temperature regimes in the face of diel fluctuations in the ambient thermal environment? Studies on the eastern subspecies of carpet pythons (*M. s. spilota*) indicate that adults of this taxon rely upon single long basking periods rather than the shuttling heliothermy of smaller reptiles; and so, large pythons display relatively smooth unimodal thermal profiles rather than an extended plateau that would result from shuttling between sun and shade (Slip & Shine 1988e).

(ii) Behavioural control over rates of heat exchange. - The ratio of surface area to volume determines the rate of heat exchange, and large snakes thus have extensive behavioural control over the rate of heat transfer by means of changing postures. A tightly coiled python has a much lower ratio of surface area to volume than does a snake that is stretched out; and hence, the coiled animal will heat and cool much more slowly (Ayers & Shine 1997). This effect may be biologically significant for pythons, allowing large (but not small) snakes to maintain high body temperatures (and thus, effective striking ability) late into the evening as ambient temperatures decline (Ayers & Shine 1997).

(iii) Low metabolic rates. - Perhaps related to a widespread dependence upon ambush predation, pythonid snakes possess physiological adaptations that minimise rates of energy expenditure. They have lower metabolic rates

than most other reptiles, even at the same body temperatures (Bennett & Dawson 1976; Ellis & Chappell 1987). Additionally, they downregulate "unnecessary" functions (such as digestive tract activity) during non-feeding periods (Secor & Diamond 1995, 1997). Activity at relatively low body temperatures (Cogger & Holmes 1960; Slip & Shine 1988e) may also reduce energy expenditure, and we might thus expect to see voluntary hypothermia during times when the snakes do not directly benefit from high body temperature.

(iv) Facultative endothermy. - Uniquely among squamate reptiles, female pythons use metabolic heat production (shivering thermogenesis) to maintain high and stable body temperatures throughout the period when they are incubating their eggs (Hutchison et al. 1966; Van Mierop & Barnard 1976, 1978; Harlow & Grigg 1984; Slip & Shine 1988f; Bedford 1996; Shine et al. 1996). Most studies on this topic have used captive snakes, but Slip & Shine (1988f) examined several brooding females as well as non-reproductive diamond pythons (*Morelia spilota spilota*) in the field. The brooding females maintained body temperatures within a narrow range (27-32°C), up to 13°C above ambient. The use of oviposition sites insulated by leaf litter, occasional bouts of basking (usually daily) and endogenous heat production through shivering thermogenesis enabled these diamond pythons to maintain high temperatures throughout embryonic development (Harlow & Grigg 1984; Slip & Shine 1988f).

I undertook a radio-telemetry study of two populations of the south-western carpet python (*M. s. imbricata*) in Western Australia. Over a five-year period, I collected field body temperatures from free-ranging pythons using temperature-sensitive radio-transmitters to describe patterns of temperature regulation in these animals, and to investigate potential influences on the thermal regimes of free-ranging snakes.

MATERIALS AND METHODS

Study animal and study sites

Australian carpet pythons (*M. spilota*) are large nonvenomous snakes (up to 3 m long and 10 kg mass) with a wide geographic distribution in Australia, extending from the tropics (11°S) to mid-latitudes (37°S) and occupying mesic to arid habitats. Several subspecies are recognised (Barker & Barker 1994). The south-western subspecies (*M. s. imbricata*) occurs in mid-latitudes in south-western Western Australia, along the southern coastline in South Australia (Mark Hutchinson, pers. comm.) and on six oceanic islands (see Chapter 3). *Morelia spilota imbricata* displays strong sexual dimorphism, with females attaining much larger sizes than males (Chapter 2).

I radio-tracked 70 of these pythons (see Table 5.1 in Chapter 5) between 1995 and 2000 at two study sites near Perth in Western Australia. Garden Island (32°12'S, 115°40'E) lies 15 km south-west of the port of Fremantle and covers an area of 1100 ha. It is linked to the mainland by a causeway constructed for a naval base on the island. All telemetry was carried out on the northern end of the island in largely undisturbed areas of *Acacia* shrubland, low forests of native pine *Callitris priessii* and *Melaleuca lanceolata* and other low shrublands (Chapter 5). The second study site, Dryandra Woodland (32°47'S, 116°55'E), is 140 km south-east of Perth. It is an area of fragmented woodland surrounded by agricultural land. Pythons were tracked in wandoo (*Eucalyptus wandoo*) and powderbark wandoo (*E. accedens*) woodlands, heath (dominated by proteaceous species) and mallet (*E. astringens* and *E. gardneri*) plantations (Chapter 5).

The two sites differ markedly in climate despite their relatively close proximity (Dryandra is 130 km ESE of Garden Island). Garden Island has warm dry summers and wet cool winters, with temperature extremes tempered by cool maritime breezes (Chapter 5). Dryandra is approximately 125 km inland and experiences much greater daily and seasonal temperature variation, including sub-zero minima in winter and frequent summer maxima over 38°C. This climatic difference is reflected in activity patterns of the pythons. At Dryandra, most pythons retreated to tree hollows (typically 5-10 m above ground) for at least three months over winter (Chapter 5). In contrast, on Garden Island, large female pythons were sedentary under shrubs for a few weeks in winter (there are very few logs and no large tree hollows on Garden Island), while males and juveniles continued to be active (Chapter 5).

Transmitter implantation

Four types of temperature-sensitive transmitters (Holohil Systems Ltd., Canada) were used depending on the size of the python to be implanted. Chapter 5 provides details on the units that I used, the methods of implantation, and the duration of radio-tracking. Transmitters were calibrated using a waterbath and circulating heater (Thermoline, Australia) against a certified mercury bulb thermometer (± 0.1°C). Temperature was increased by 5°C increments from 5-40°C. The period between pulses was recorded using a Period/PPM meter (Titley Electronics, Australia) as well as the time taken to hear 10 pulses using a stopwatch. The former measure was used for calculating body temperatures from an automated telemetry system and the latter for data collected during fieldwork. Body temperatures of snakes were determined by applying 3rd order polynomial equations derived from calibration data (mean $r^2 = 0.998$, range 0.994 to 1.0). Transmitters were recalibrated following removal from pythons to ensure there had not been significant drift in calibration. The calibration of two transmitters was found to have drifted by > 1°C and data for the snakes into which these were implanted were excluded from analysis.

During fieldwork, pythons were located using a RX3 receiver (Biotelemetry Services, Australia) and a 3-element Yagi aerial (Sirtrak, New Zealand). Because carpet pythons typically did not flee from my approach, it was possible to record their behaviour (basking, ambush position, moving, etc.), posture (loosely or tightly coiled, stretched out), proportion of body in the sun, cloud cover and aspects of the microhabitat. I defined a snake to be in "ambush posture" if its neck was bent into a tight "s-shape" and the head and body was held immobile ready to strike. Typically, the anterior two-thirds of the body was stretched out and the posterior third was coiled, often around an anchoring point such as a branch. Pythons in ambush posture were found both on the ground and hanging from shrubs. A reference shaded air temperature at 1.5 m above ground and a shaded soil temperature were taken close to each python and the snake's body temperature was estimated by recording the time for 10 pulses of the transmitter (with a stopwatch) for later calculation of temperature. Pythons were usually located once weekly in the first two years of study but then fortnightly at Dryandra and less frequently during winter when the pythons were inactive.

An automated telemetry station was used on a monthly basis from March 1997 to March 1998 and then sporadically in 1998 and 1999, mostly to record temperatures of incubating female pythons. I collected data for 7 to 20 days each month. The telemetry station consisted of a Telonics TR-2 receiver (Telonics, Mesa, Arizona) to scan and receive signals, a Telonics TDP-2 digital processor and a Campbell CR-10 datalogger (Campbell Scientific, Logan, Utah), powered by a 12-volt car battery. At Garden Island, this station was placed on top of a large sand dune (Mt Haycock) that was reasonably central to the study area. A 10 m omni-directional radio-mast was erected and the datalogger and receiver placed inside a locked box. This mast could receive transmitter signals within a range of around 1 km in the absence of geographic barriers. When pythons moved into dune swales or limestone cliffs or beyond this distance, signal was lost for varying periods of time.

An added problem was the proximity of the site to major metropolitan areas with radio interference from diverse sources including courier companies and a Greek folk music station. Radio disturbance was particularly pronounced during daylight hours and data files were scanned to remove spurious records. Thermocouples were run from the datalogger to measure various environmental temperatures (shaded air, open leaf litter and below shrub) and to a thermal model made from a 60 cm-long copper pipe painted with matt brown paint of similar colour to an adult female carpet python. This model was placed in an open position on bare soil on the top of Mt Haycock, positioned on its north-eastern side sheltered from the regular south-west sea breezes, so that it could approximate the maximum temperature achievable by a python if it lay continuously in the open. The "below shrub" thermocouple provided an approximate indication of the minimum temperature of microhabitats available to most snakes. Environmental temperatures, thermal model and snake telemetry signals were recorded every 15 minutes.

Detailed data on the temperatures of incubating females and nearby non-reproductive females were also collected by placing the automated telemetry station alongside nest sites in a weatherproof box with a Yagi aerial tied into a tree. Temperature data for overwintering pythons at Dryandra Woodland were collected in June and July 1998 using this same assembly. Raw data were stored and calibration equations fitted in Excel spreadsheets. The massive size of these data-sets, and the non-independence of repeated measures of the same variable from the same animals at short intervals, introduce substantial difficulties for statistical analysis. To overcome these problems, I reduced the size of the data-sets by calculating means and standard errors for the body temperatures of each snake for each hourly period over which it was monitored. I used the software program SuperANOVA (Abacus Concepts 1991) for these calculations. I then divided the year into four biologically relevant seasons. Spring was defined as September 1 to December 15, around the last date that mating was observed; summer covered the period from December 15 to March 31; autumn, the months of April and May; and winter from June through to September 15 (see Chapter 5 for further explanation). I used these divisions to calculate mean hourly temperatures per snake per season, thus generating a data-set of manageable size and (because the variance in temperatures through time within a single snake was much greater than the variance in mean temperatures among snakes: Leger & Didrichson 1994) without the problems of statistical non-independence.

RESULTS

Sample sizes and data-sets

Much of the automatically-recorded thermal data had to be discarded due to excessive interference from other radio sources. This problem disproportionately affected data from male snakes, because the signals from their smaller transmitters were more often affected by radio interference. No useful data for males were collected during summer. In contrast, the larger transmitters implanted in adult female pythons (Holohil SI-2T model) provided relatively continuous temperature data for several females over many months.

In total, the automatic data-recording system on Garden Island yielded 1139 valid records of hourly mean body temperatures of radio-tracked snakes, plus 858 hourly mean values for associated environmental temperatures. Because these records span the entire 24-hour diel cycle, they provide the most robust basis from which to identify general patterns in snake thermal biology. I thus used them for this purpose. Detailed continuous monitoring using this automated system also provides the most extensive information on the effects of reproductive state (incubating versus non-reproductive females) and hibernation-site selection on body temperatures.

Because I measured pulse intervals (and thus, could estimate body temperatures) whenever a radio-tracked snake was located, I also have an extensive data-set on temperatures of snakes from both Garden Island (*N* = 2350 records) and Dryandra (*N* = 1494 records). These data were almost all taken during daylight hours, and provide an opportunity to compare the thermal regimes exhibited by snakes of different sexes and body sizes in the two study areas.

General patterns at Garden Island

Ambient temperatures displayed marked seasonal variation at Garden Island (Figs. 6.1 and 6.2). Overnight minima averaged about 12°C in winter and 18°C in summer. Maximum temperatures inside copper models exposed to full sunlight attained > 35°C at midday in all seasons, and exceeded this level for > seven hours in summer (typically reaching > 50°C: Fig. 6.2). Air temperatures averaged around 15°C in winter to 25°C in summer (Figs. 6.1 and 6.2). Thermal probes in deep shade beneath shrubs (the most widespread python habitat on the island) showed much less diel fluctuation than did exposed models, typically varying only from 11 to 20°C in winter and 20 to 28°C in summer (Figs. 6.1 and 6.2).

Body temperatures of the radio-tracked pythons also showed substantial diel and seasonal variation (Figs. 6.1 and 6.2). Mean hourly temperatures ranged from 14°C (overnight in winter) to 32°C (mid-afternoon in summer). Body temperatures were at their lowest near dawn, and typically were maximal relatively late in the day. This pattern was especially pronounced for female pythons, which typically heated more slowly than

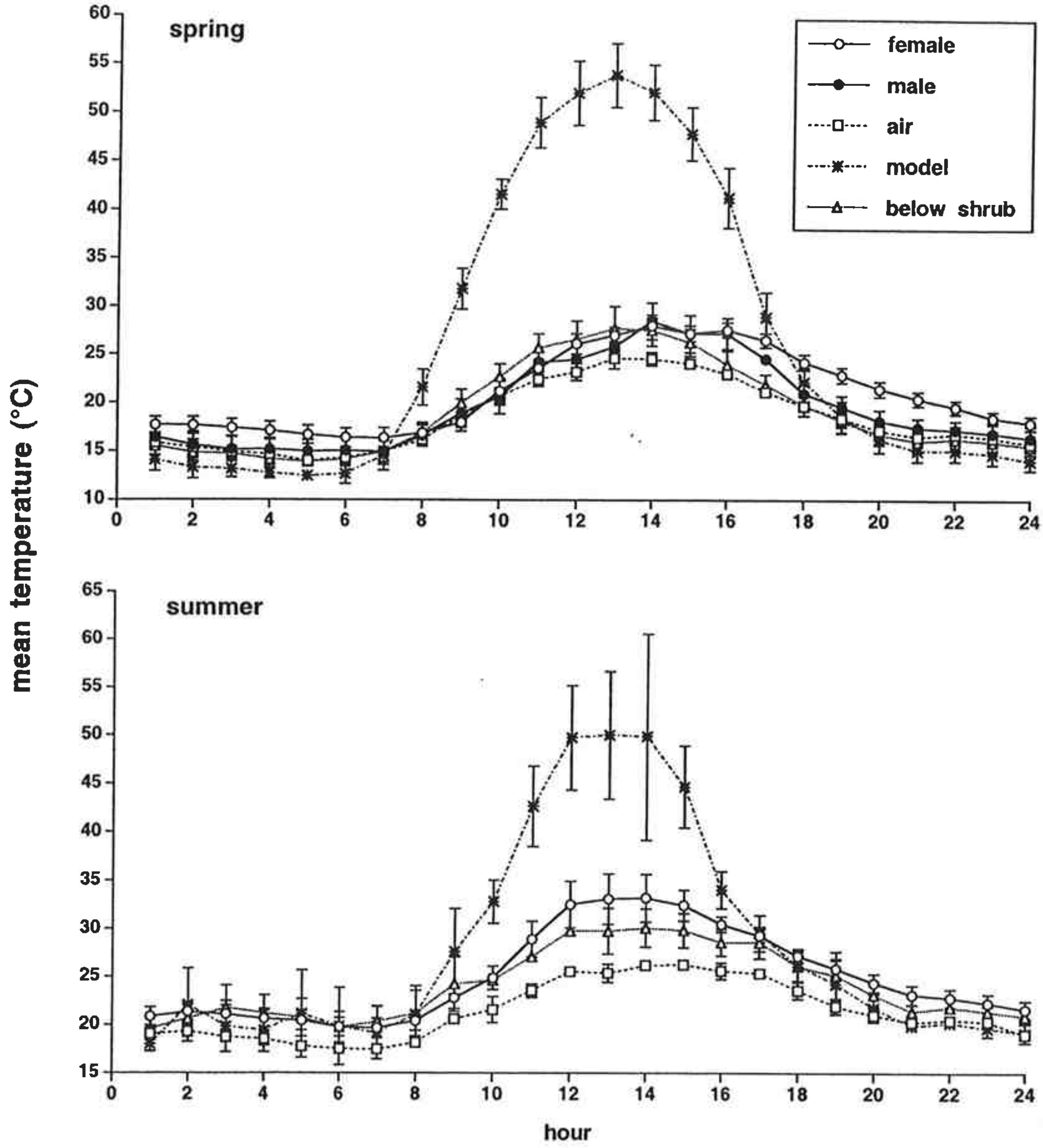

Figure 6.1. Mean values, and associated standard errors, for ambient temperatures and body temperatures of radio-tracked carpet pythons on Garden Island during spring (a) and summer (b). These data were obtained using an automated system to receive telemetry signals and data from environmental probes. See text for explanation of symbols, definition of seasons and statistical analyses.

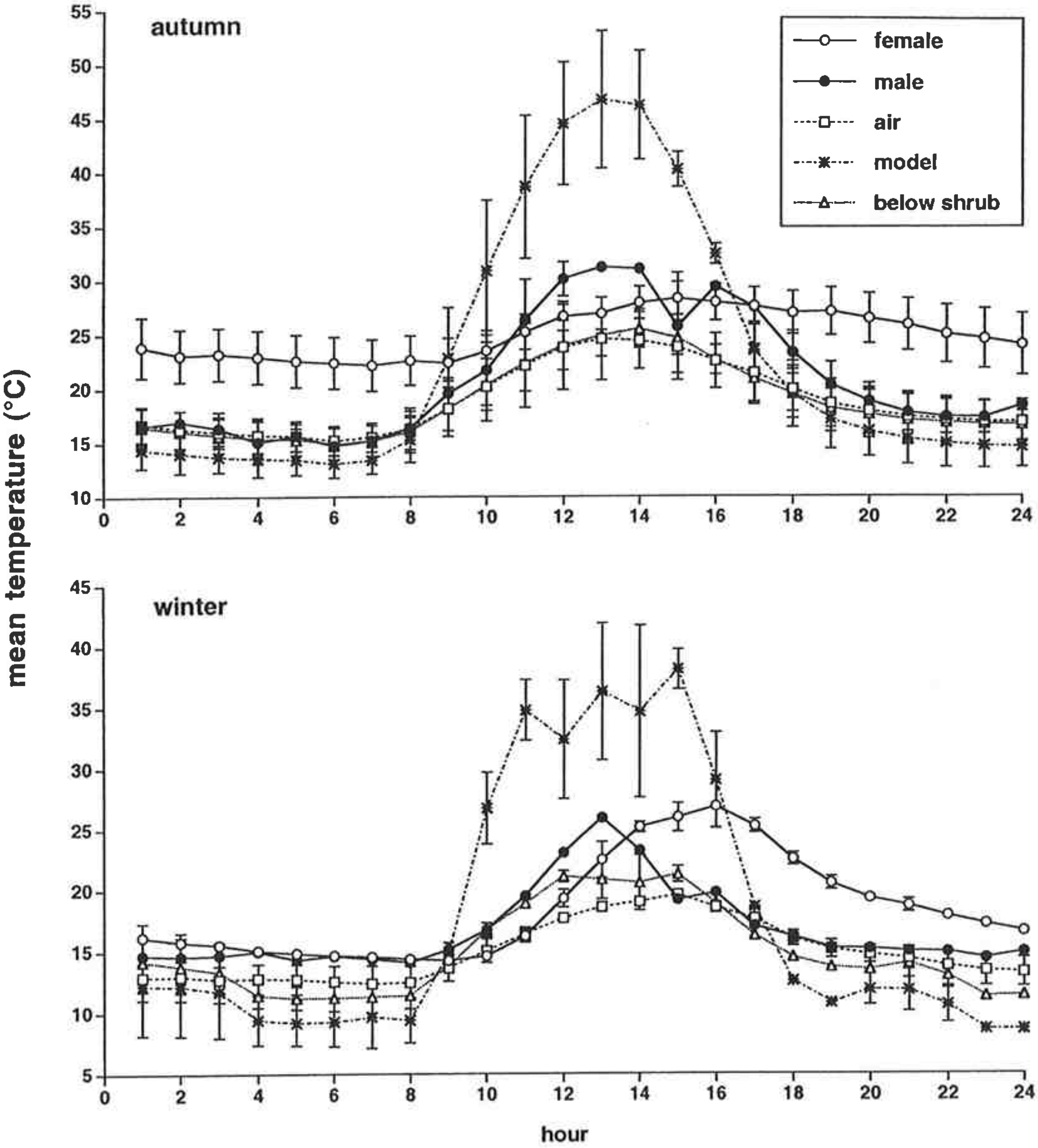

Figure 6.2. Mean values, and associated standard errors, for ambient temperatures and body temperatures of radio-tracked carpet pythons on Garden Island during autumn (a) and winter (b). These data were obtained using an automated system to receive telemetry signals and data from environmental probes. See text for explanation of symbols, definition of seasons and statistical analyses.

males during the morning, but also cooled more slowly than males during the afternoon and evening (Figs. 6.1 and 6.2). Thus, female temperatures tended to vary less than male temperatures over the course of a day; this pattern was particularly evident in autumn, when the radio-telemetered females maintained higher, less variable temperatures than did males throughout most of the day except for the hottest times around midday and the early afternoon (Fig. 6.2; females higher for 19 of 25 hourly means, against a null of 50%, $\chi^2_1 = 6.76$, $P < 0.05$). Overall, both males and females typically exhibited relatively smooth diel curves in heating and cooling, rather than maintaining a stable plateau temperature throughout daylight hours as is often seen in shuttling heliotherms (Avery 1982).

I also calculated patterns of hourly variation in body temperatures and associated ambient temperatures from the automated records. Figures 6.3 and 6.4 show that in warmer months (spring through autumn), the snakes were generally less variable thermally than the environmental temperatures that I monitored. However, snakes exhibited highly variable temperatures in the middle of the day in winter, reflecting their frequent emergence to bask at these times and thus, the rapid rise (and then fall) in body temperatures. Male pythons displayed highly variable body temperatures during the morning hours in spring (the only season and time of day that I regularly saw males basking), but this pattern shifted partway through the day. During spring afternoons, male pythons generally exhibited more stable body temperatures than did females (Fig. 6.3).

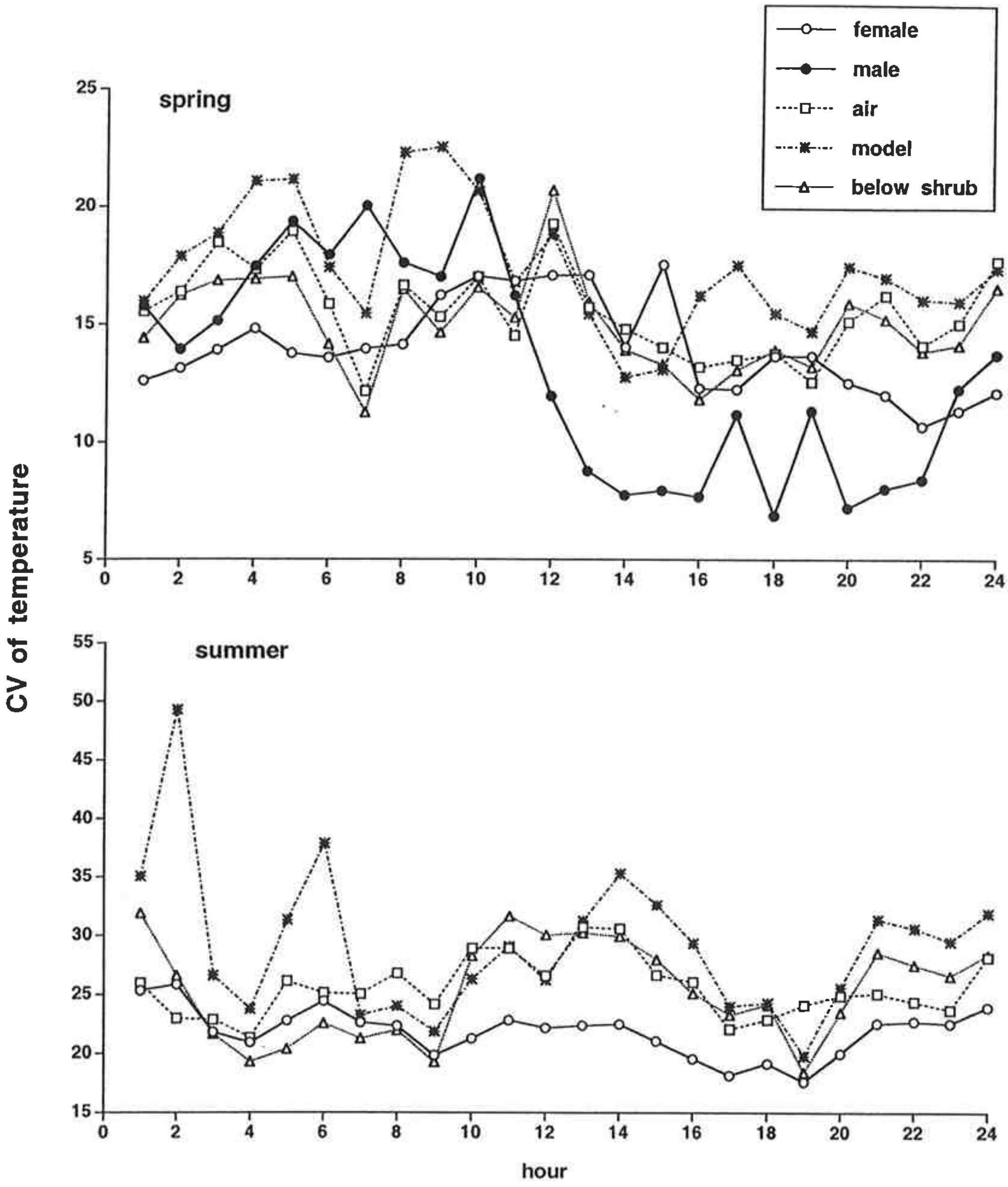

Figure 6.3. Mean values, and associated standard errors, for the coefficient of variation in ambient temperatures and body temperatures of radio-tracked carpet pythons on Garden Island during spring (a) and summer (b). These data were obtained using an automated system to receive telemetry signals and data from environmental probes. See text for explanation of symbols, definition of seasons and statistical analyses.

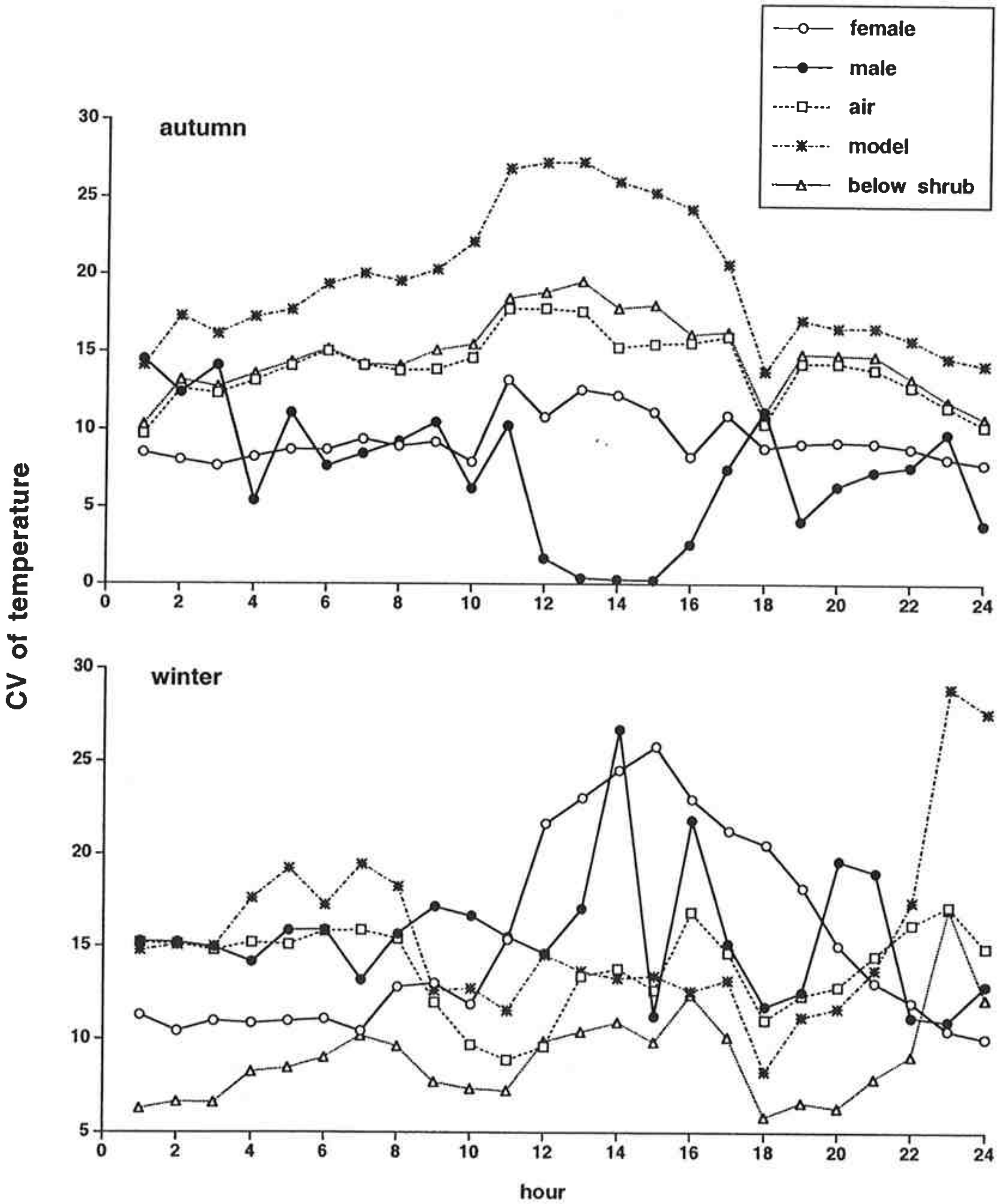

Figure 6.4. Mean values, and associated standard errors, for the coefficient of variation in ambient temperatures and body temperatures of radio-tracked carpet pythons on Garden Island during autumn (a) and winter (b). These data were obtained using an automated system to receive telemetry signals and data from environmental probes. See text for explanation of symbols, definition of seasons and statistical analyses.

Effects of location and sex on body temperature

The records of timed pulses taken when I located radio-tracked snakes provided an extensive data set with which to compare male and female snakes in Dryandra and Garden Island. Patterns of thermal variation were generally similar to those obtained from the automated telemetry system. The effect of location was very clearcut: for both females (Fig. 6.5) and males (Fig. 6.6), body temperatures were typically about 2 to 5°C lower at Dryandra than at Garden Island ($F_{1,3842} = 180.3$, $P < 0.0001$). Ambient temperatures measured at the same time revealed the same pattern: mean air temperatures for each season were higher at Garden Island (spring, 20.9; summer, 25.6; autumn, 21.4; and winter 16.6°C) than at Dryandra (19.8; 25.8; 19.3; 13.7°C respectively; location effect, $F_{1,3824} = 86.62$, $P < 0.0001$).

The magnitude of the geographic difference in thermal regimes also varied among seasons. For example, male pythons at the two sites exhibited similar body temperatures in autumn, whereas the Garden Island snakes were much warmer than their Dryandra counterparts in other seasons (Fig. 6.6). The discrepancy between the two sites was greatest in winter, reflecting the mild maritime climate at Garden Island compared to the severely cold continental climate at Dryandra (interaction between season and location in a two-factor ANOVA on air temperatures, $F_{3,3824} = 20.08$, $P < 0.0001$; on body temperatures, $F_{3,3836} = 11.66$, $P < 0.0001$).

The data on behaviours of snakes at the times they were located also provide insight into thermoregulatory tactics. The most striking result in this respect is an interaction between sex and location in determining the incidence of overt basking behaviour. In the relatively open woodland

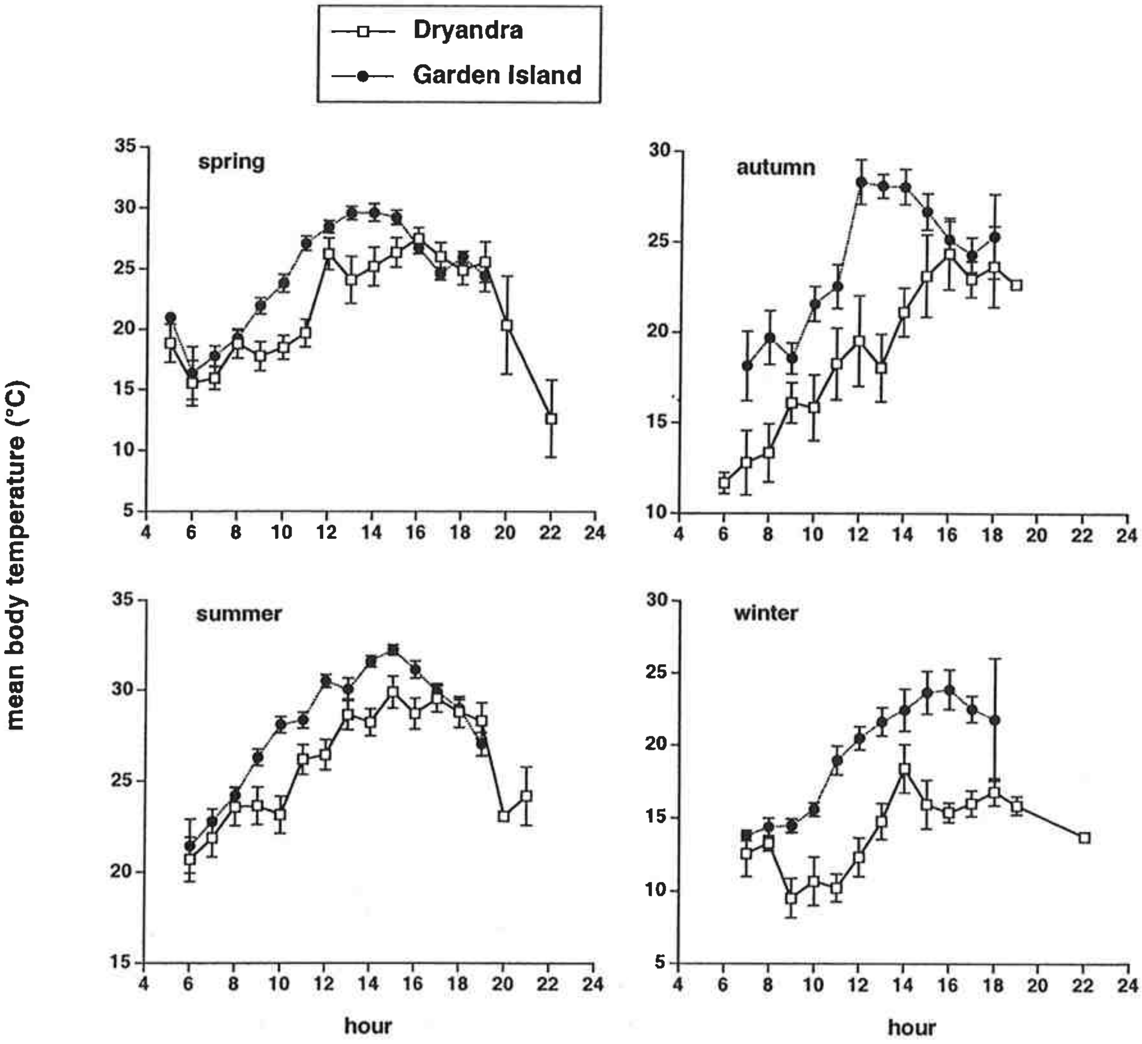

Figure 6.5. Body temperatures of female carpet pythons at two study areas and during four seasons. These data were obtained by recording pulse-intervals from telemetry signals whenever a radio-tracked snake was located in the field.

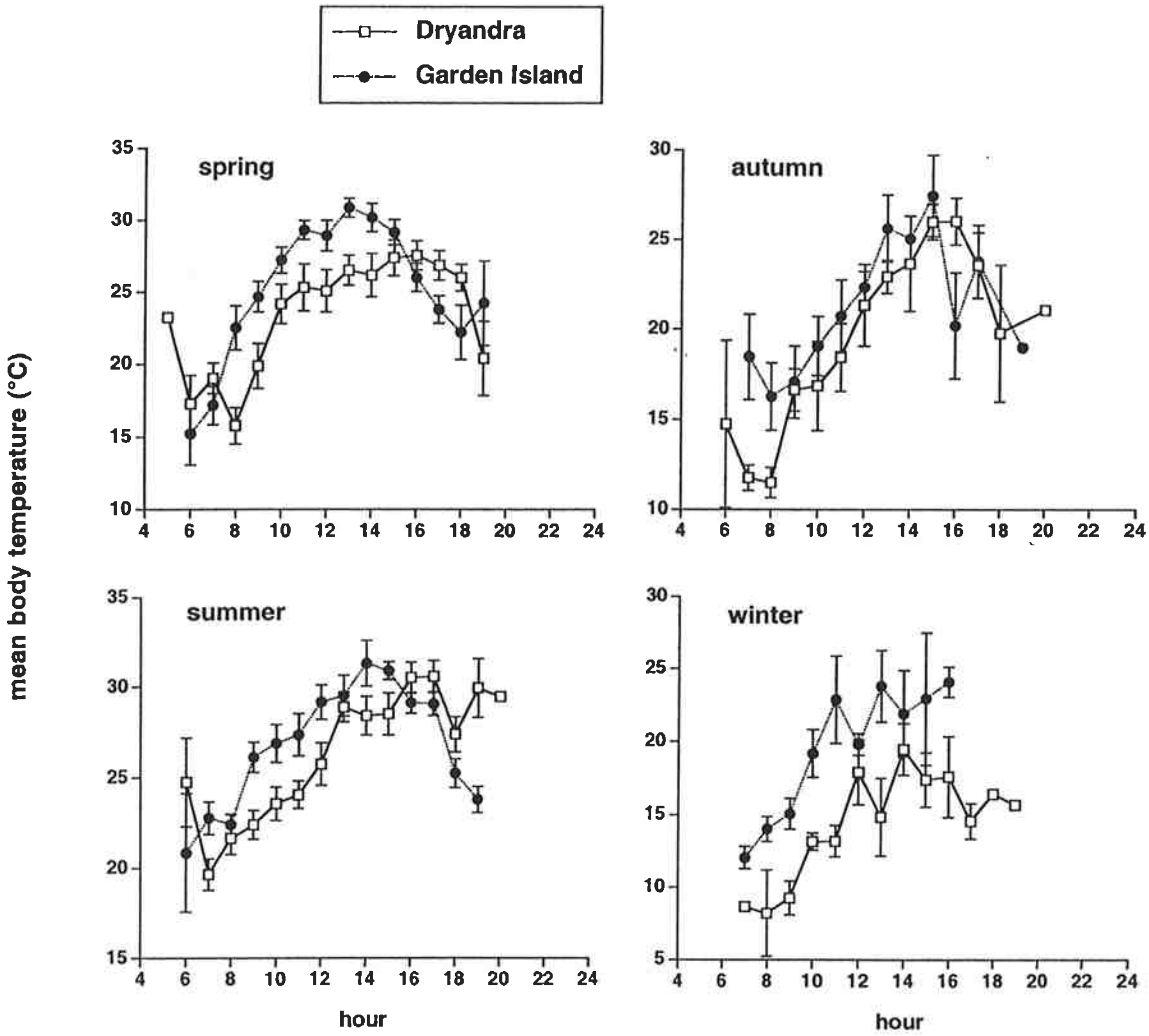

Figure 6.6. Body temperatures of male carpet pythons at two study areas and during four seasons. These data were obtained by recording pulse-intervals from telemetry signals whenever a radio-tracked snake was located in the field.

habitats of Dryandra, snakes were observed basking quite rarely (64 of 215 records for female snakes, = 30%; 62 of 234 records for males, = 27%). These data do not show any significant sex difference in basking frequencies (χ^2_1 = 0.44, $P = 0.51$). In the dense shrub habitats of Garden Island, however, female pythons were often found basking (599 of 1296 records, = 46%), whereas male snakes were not (94 of 324 records, = 29%; $\chi^2_1 = 30.65$, $P < 0.0001$). Why should female snakes bask more often than males at Garden Island but not at Dryandra? Because the Garden Island females were larger animals than the Dryandra females (Chapter 3), one possibility is body size. However, more detailed inspection shows that basking frequencies were as high for juvenile female pythons (< 195 cm SVL) on Garden Island (132 of 302, = 44%) as for adult females (467 of 994, = 47%).

The amount of time that an individual snake spends basking also depends upon the amount of time that it spends involved in other activities. Radio-tracked male pythons spent a much higher proportion of time in ambush postures during the day than did females (for Garden Island, 26 vs 4%, $\chi^2_1 = 155.48$, $P < 0.0001$; for Dryandra, 12 vs 3%, $\chi^2_1 = 9.97$, $P < 0.002$). Thus, one reason for lower basking frequencies in male pythons, especially on Garden Island, was their frequent adoption of ambush poses instead.

Relationship between body size and body temperature

Visual analysis revealed no consistent differences between adult and juvenile pythons in thermal profiles, despite the very large difference in body size between these animals. Correlation analysis showed no difference between these size classes in terms of the degree to which body temperatures were related to air temperatures. Correlation coefficients for the relationship between snake temperatures and air temperatures for juvenile and adult snakes at Dryandra were 0.78 and 0.75 respectively; at Garden Island the corresponding coefficients were 0.69 and 0.67. Correlation coefficients between snake temperatures and soil temperatures at Dryandra were 0.77 and 0.75 for juvenile and adult snakes (Garden Island 0.66 and 0.70). Thus, pythons of all body sizes showed relatively similar thermal profiles.

Relationship between ambush posture and body temperature

Previous authors have suggested that retention of relatively high body temperatures may be an important benefit of "ambush" postures in foraging pythons, due to the low surface area of coiled snakes (Slip & Shine 1988e; Ayers & Shine 1997). To investigate this possibility, I examined the body temperatures of snakes found in this posture compared to others. Because location and sex also influence body temperatures in this species, I included these two variables, along with posture, in a three-factor ANOVA with body temperature as the dependent variable. There were no significant interactions among the factors (all $P > 0.05$), simplifying interpretation of the main effects. Pythons at Dryandra overall were cooler than those at Garden Island ($F_{1,2064} = 9.99$, $P < 0.002$), and the sexes did not differ in mean body temperature ($F_{1,2064} = 2.68$, $P = 0.10$). Posture was strongly associated with body temperature ($F_{3,2064} = 9.42$, $P < 0.0001$). Temperatures of snakes found in ambush postures (mean = 22.4°C) were significantly lower than for those found stretched out (24.0°C), which in turn were cooler than those found in tight coils (25.1°C) or loosely coiled (26.1°C; in posthoc PLSD tests, all comparisons have $P < 0.05$).

When these data were analysed separately by season, I detected significant interactions between posture and location (Dryandra vs Garden Island) in both spring ($F_{3,888} = 5.47$, $P < 0.001$) and summer ($F_{3,627} = 3.08$, $P < 0.03$), and an almost-significant interaction in autumn ($F_{3,249} = 2.56$, $P < 0.06$). These interaction terms reflect a pattern whereby in each season, snakes in ambush postures were much warmer at Garden Island than Dryandra; the thermal difference between the two sites was less marked for other postures. These effects stimulated me to look more closely at the times and places where snakes were found in ambush posture. Analysis showed that pythons at Dryandra were found in ambush postures mostly in the afternoon and evening, whereas Garden Island snakes were found in ambush poses throughout the day (Fig. 6.7; dividing the day into 10 equal periods to compare between the two sites, contingency-table test $\chi^2_9 = 22.00$, $P < 0.01$).

Overwinter body temperatures in relation to shelter sites

Figure 6.8 shows data from simultaneously-monitored snakes and ambient probes at Dryandra during winter (June 15-July 3 1998). Over this period, a large female python (SVL 194 cm, mass 2.7 kg) ensconced in a tree hollow 12 m above the ground displayed relatively high and stable temperatures. A smaller juvenile female python (SVL 124.5 cm, mass 380 g) and a male (SVL 136.8 cm, mass 551 g) also in tree hollows 5 and 8 m above ground respectively displayed more variable body temperatures. However, they

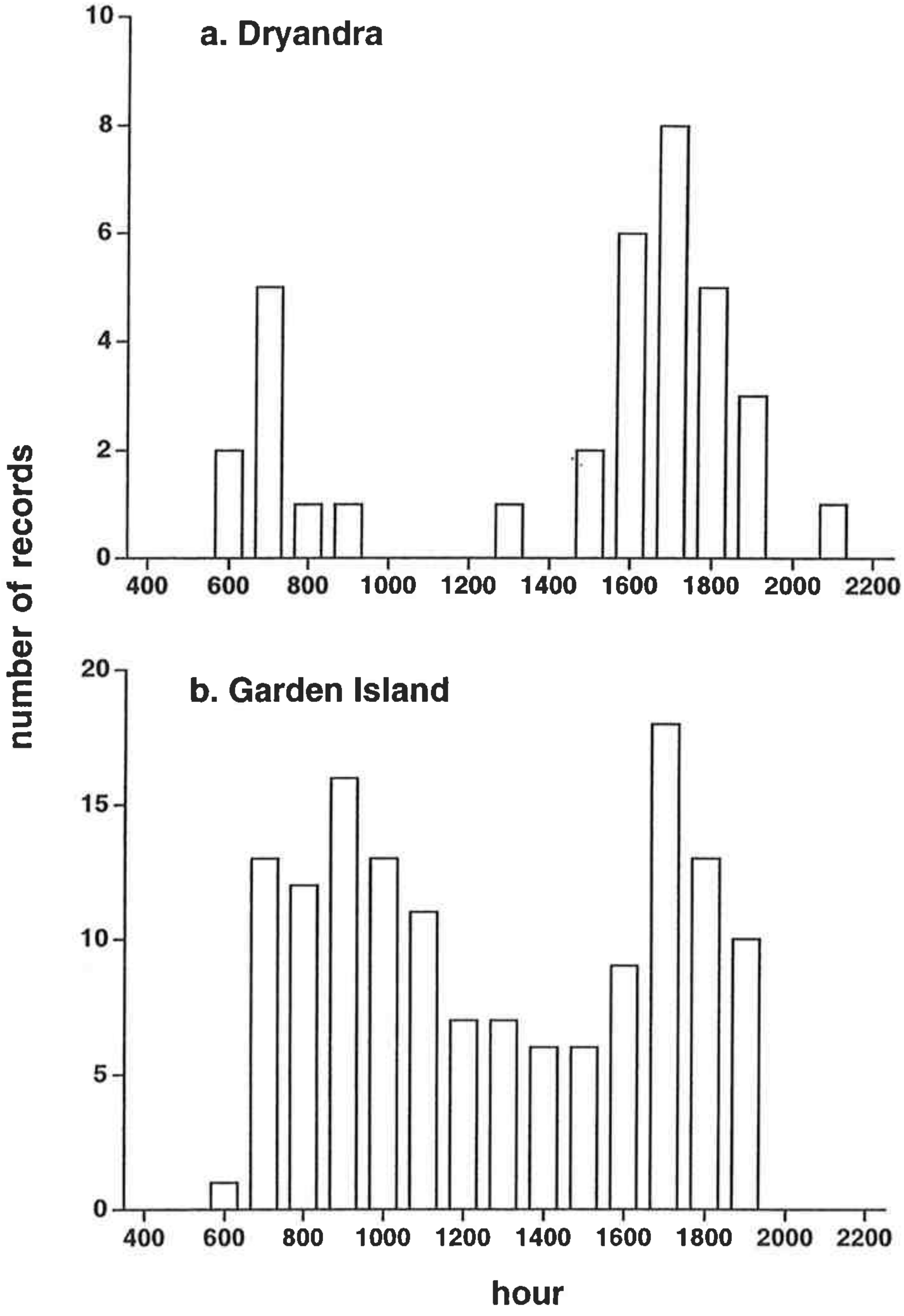

Figure 6.7. Times of day during which radio-tracked carpet pythons were in ambush postures when located. Data are shown separately for snakes from (a) Dryandra Woodland and (b) Garden Island.

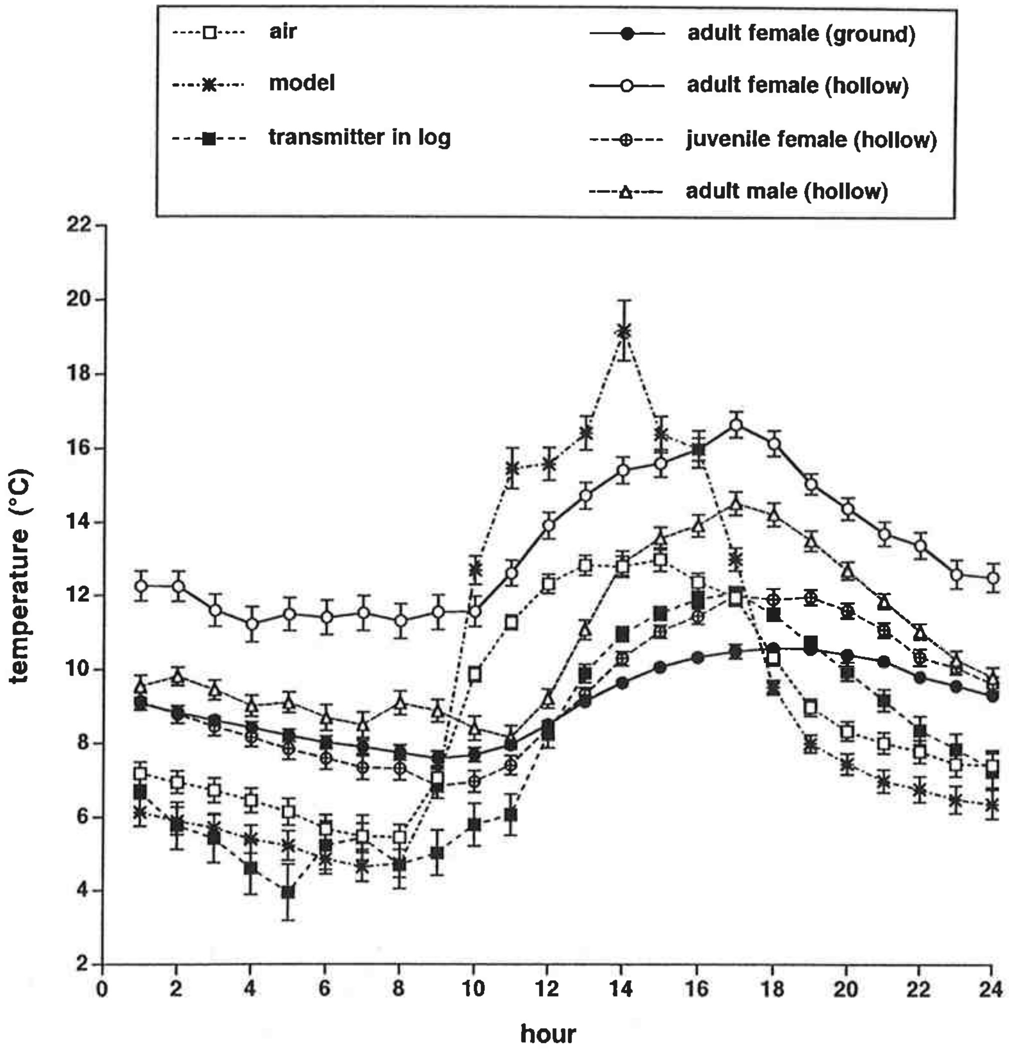

Figure 6.8. Body temperatures of radio-tracked carpet pythons and associated environmental temperatures recorded over an 18-day period in Dryandra Woodland during winter (June-July 1998). The graphs show hourly means and associated standard errors for each snake or environmental probe.

were able to maintain higher and less variable thermal regimes than a large female python (SVL 206 cm, mass 3.25 kg) sheltering on the ground in logs and under fallen branches and a reference transmitter placed in a log. Although I do not have replication in terms of multiple snakes in each kind of overwinter site, the data suggest that tree-hollows provide relatively warm, thermally buffered retreat-sites for snakes in this location.

Effect of reproductive status on body temperature

Automatic data-recording for temperatures of female pythons during the period when they were incubating their eggs reveals a very significant increase in mean temperature, and a decrease in thermal variance, compared to other snakes monitored at the same time (Fig. 6.9). For example, Figure 6.9a shows thermal data for a female that oviposited in a crevice in a north-west facing limestone cliff exposed to the sun for much of the day. She was never observed to bask. The thermal differential between the incubating and non-incubating females averaged > 4°C (Fig. 6.9a).

South-western carpet pythons use a range of microhabitats as nesting sites, and these sites may differ substantially in the degree of thermal buffering available to the python and her clutch. Figure 6.9b shows thermal data for a female that oviposited under leaf litter and shrubs on a west-facing dune slope under low woodland canopy cover. She was also never observed to bask. Thermal data for a female that oviposited under the rootball of a fallen *Callitris* tree is shown in Fig. 6.9c. The temperatures of these two pythons were much more variable than were those of females that oviposited in the limestone cliff crevice. In particular, the body temperature of the

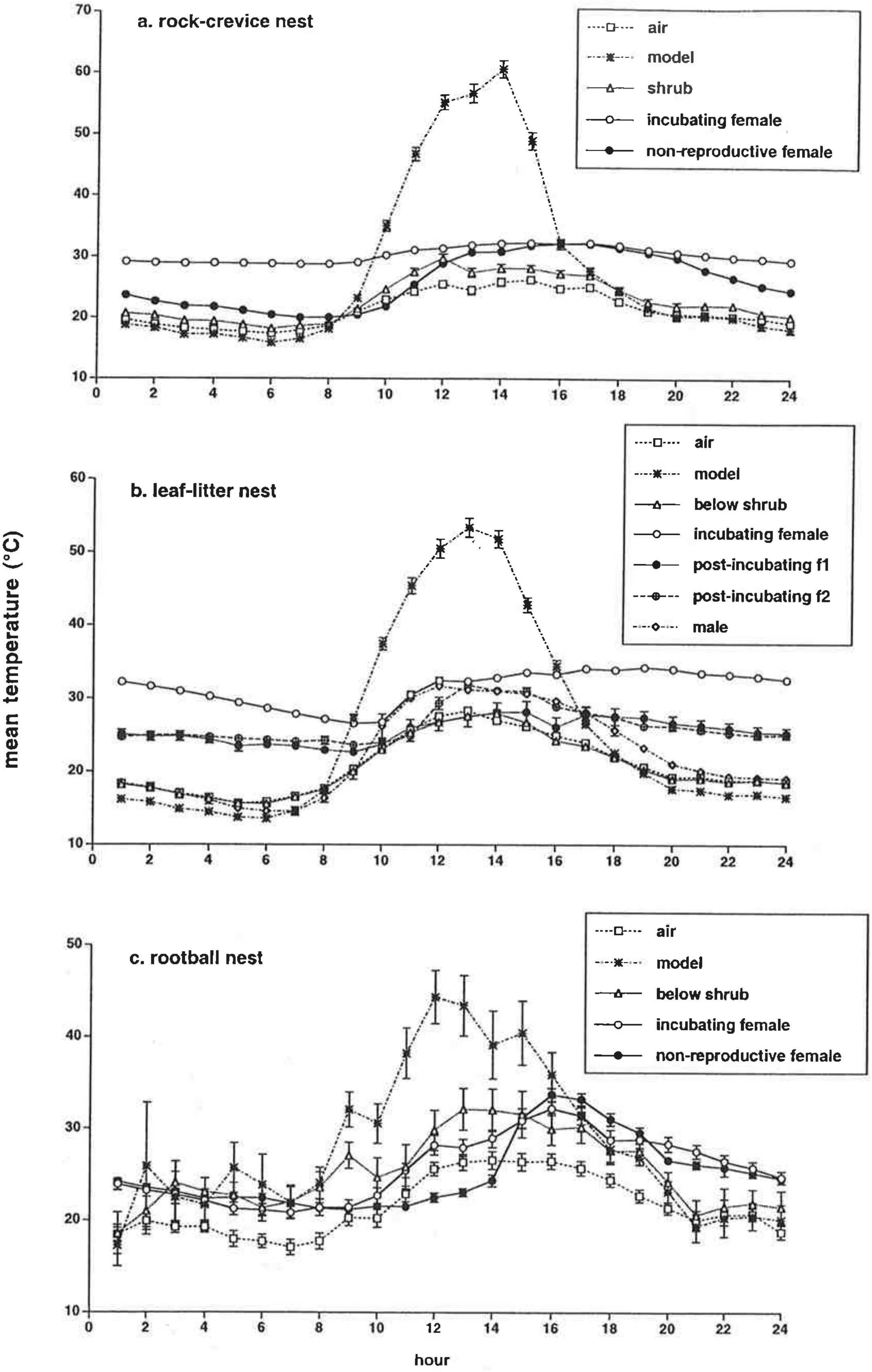

Figure 6.9. Body temperatures of radio-tracked carpet pythons and associated environmental temperatures at Garden Island, showing the differences between non-reproductive pythons and others incubating their eggs. Pythons were monitored by an automatic recording system over the same period and in the same general location. Graphs show hourly means and associated standard errors for each snake or environmental probe. Graph (a) shows thermal data for the period February 22 to March 29, 1999; for an incubating female in a crevice in a cliff, a free-ranging non-reproductive adult female and environmental probes. Graph (b) shows thermal data for the period 9 to 31 March 1998; for a female incubating in a "nest" under leaf litter and shrub cover, plus data for two post-incubation females, a male snake and environmental probes. Graph (c) shows thermal data for the period 23 February to 19 March 1998; for a female incubating under the rootball of a fallen tree, plus data for a non-reproductive adult female and environmental probes.

female that nested under the rootball fell precipitously overnight, and direct observations confirm that she raised her temperature mid-morning by basking before retreating to the clutch to presumably recommence shivering thermogenesis.

DISCUSSION

The extensive data set from radio-telemetric monitoring of 70 snakes over five years identifies several influences on the body-temperature regimes of the radio-tracked snakes. Ideally, studies on thermal biology of free-ranging reptiles should also incorporate information on thermal preferenda of the animals, so that one can judge the degree to which the thermal profiles of the reptiles conform to these preferenda (Hertz et al. 1993). Although I did not conduct such a study, previous work on the same species has documented mean selected temperatures of 29-32°C (Cogger & Holmes 1960; Webb & Heatwole 1971; Johnson 1972; Slip & Shine 1988e,f; Bedford & Christian 1998), increasing slightly after feeding (Slip & Shine 1988b). Most of the radio-tracked snakes were generally much cooler than this "preferred" level, especially during the night, even in the relatively benign ambient thermal environment of Garden Island (Figs. 6.1 and 6.2). Thus, in strong contrast to tropical pythons (Shine & Madsen 1996), the radio-tracked snakes in my study exhibited highly variable thermal regimes. Clearly, part of that variation was directly induced by fluctuations in the ambient thermal environment, whereas part was due to thermoregulatory (and other) behaviours of the snakes. Below, I examine some of the factors that generated that variation in body temperatures.

(i) Season. - Mean body temperatures during daylight hours (arbitrarily, 0700 to 1800 h) varied substantially among seasons; combining data from both study areas, mean values were 27.2°C in summer, 25.0°C in spring, 21.9°C in autumn and 17.3°C in winter. This variation very clearly reflects the highly seasonal climate in south-western Australia; corresponding values for air temperature were 26.0°C in summer, 20.8°C in spring, 20.5°C in autumn and 15.6°C in winter.

(ii) Time of day. - Strong diel rhythms in body temperature were evident in both study sites and in all seasons (Figs. 6.3, 6.4). Unsurprisingly, snake body temperatures fell during the night and increased during the day (Figs. 6.1, 6.2). This diel variation reflects temporal shifts in ambient temperatures and especially, in incident radiation (note thermal profiles for exposed models, which often ranged from < 20°C overnight to > 50°C by day). Much of the diel variation in body temperatures within each season directly resulted from the snake's behavioural thermoregulation (selection of sites exposed to full or partial sunlight), rather than being a secondary consequence of ambient thermal fluctuations.

(iii) Location. - Although the overall patterns of diel cycles in body temperatures were similar at the two study areas, snakes at Garden Island were consistently a few degrees warmer than were those at Dryandra (Figs. 6.5, 6.6). This geographic difference resulted primarily from differences in climatic conditions at the two sites, but was exaggerated by a difference in thermoregulatory behaviour of snakes in the two areas. In male pythons, basking was observed about as often at Garden Island as at Dryandra (29 vs 27% of records of snake behaviours), but for females the Garden Island

animals basked much more frequently (46% of records) than did the Dryandra females (30%). Thus, thermoregulatory behaviour was affected by a significant interaction between sex and location. Similar phenomena probably occur in males also. For example, body temperatures of male pythons were similar at the two sites in autumn, but differed considerably in other seasons (Fig. 6.6). Part of this difference probably reflects climatic factors (notably, the much lower winter temperatures at Dryandra), but part may also reflect thermoregulatory opportunities and thus, be influenced by the behaviour of the snakes.

(iv) Sex and body size. - I cannot easily separate these two factors, because most of the "small" (< 1 kg) snakes in my study were males, whereas all of the "large" snakes (> 1.3 kg) were females. However, differences in the frequency of overt basking behaviour were related to sex rather than body size, with juvenile females resembling adult females rather than adult males more similar to their own body sizes (see above). Part of this difference may reflect the higher incidence of ambush postures in males, presumably relating to their reliance on frequent small meals rather than occasional large meals (see Chapter 3).

Overall, the two sexes displayed relatively similar body temperatures (e.g. Figs. 6.1, 6.2). The most obvious difference lay in rates of thermal exchange, presumably mediated via body size. Male pythons heated more rapidly than females in the morning, and cooled more rapidly in the evening (Figs. 6.1, 6.2). This effect may well be biologically significant. For example, Figure 6.2a shows that adult female pythons on Garden Island maintained mean hourly body temperatures > 22°C throughout the night in autumn, whereas males fell below this level before dusk (by 1800 h) and did not regain high temperatures until partway through the following morning. The resulting thermal differential between the sexes during the evening (a prime time for ambush predation on mammals and gekkonid lizards) averaged > 5°C. Laboratory studies suggest that such a difference can substantially reduce the python's ability to detect and capture prey (Ayers & Shine 1997). Thus, the thermal inertia generated by large body size plus postural control of surface area, may provide important thermal advantages for large snakes in relatively cool climates.

(v) Posture. - Mean body temperatures of snakes varied according to the snake's posture when located, with animals in ambush posture significantly cooler than all other groups. Given that sensory and motor skills decline at lower temperatures (Ayers & Shine 1997), we might expect snakes to be most effective foragers at relatively high temperatures. However, the crepuscular and nocturnal habits of many of the main prey species (Chapter 3) create a conflict in this respect. In particular, the low overnight ambient temperatures at Dryandra mean that snakes are generally very cool in the mornings and hence, may not be able to ambush prey effectively at this time. Presumably for this reason, pythons at Dryandra were found in ambush postures mainly in the late afternoon and evening, whereas pythons at the warmer Garden Island site were able to forage in this way throughout the day (Fig. 6.7). This factor also interacts in a complex way with other features of the animal's biology: for example, male pythons at Garden Island were recorded in ambush postures much more frequently than were females.

(vi) Habitat. - In areas with considerable spatial variation in operative temperatures (as was certainly the case in both of my study areas: see Figs. 6.1a,b and 6.2a,b), a snake's selection of habitats will almost inevitably influence its body temperature regimes. The most obvious example of this

phenomenon in my study involved the selection of overwintering sites at Dryandra; snakes in elevated positions (tree hollows) maintained higher, less variable temperatures than did snakes on the ground (Fig. 6.8). It is difficult to judge whether such thermal factors (as opposed to protection from predators, etc.) comprise causal (selective) factors for the snakes' general selection of arboreal rather than terrestrial overwintering sites at Dryandra. Maintenance of higher temperatures at this time will increase the overall metabolic costs of overwintering, but might also increase the animal's ability to respond to the approach of danger.

(vii) Reproductive status. - Body temperatures of female pythons were very different during the incubation period compared to those at any other time (Fig. 6.9). As in previous studies of incubating diamond pythons in eastern Australia (Slip & Shine 1988f), brooding females maintained remarkably high, stable temperatures for long periods of time. Also in accord with previous work (Slip & Shine 1988f; Madsen & Shine 1999), natural nest sites appear to vary significantly in the degree of thermal buffering that they provide for the female and her clutch. A less protected nest-site may increase the female's vulnerability to predators (e.g. Shine & Fitzgerald 1996), as well as increasing the metabolic costs of shivering thermogenesis, and exposing the eggs to lower and more variable temperatures (Fig. 6.9). Such modifications to incubation regimes may significantly influence hatching success and/or phenotypic traits of the hatchlings (Shine et al. 1996). Thus, maternal nest-site selection may be under intense selection in pythons. The limestone cliff crevices on Garden Island were used annually by several pythons, including two telemetered pythons that shared a crevice in one season. Every December between 1996

and 2000, I found recently-sloughed skins of large females and old egg shells from freshly excavated nest sites at this site.

In summary, my study revealed substantial spatial and temporal variation in the body temperatures exhibited by free-ranging carpet pythons, as well as effects related to the snake itself (size, sex, reproductive status). As in many other ecological traits of this species - notably sexual size dimorphism (Chapters 2 and 3), dietary habits (Chapter 3) and movement patterns (Chapter 4) - the overall impression from my data on thermal ecology is of an extremely flexible organism that is able to modify major facets of its biology to exploit habitats that are highly heterogeneous in space and time.

CHAPTER 7

Life history attributes of a threatened python, *Morelia spilota imbricata* (Serpentes: Pythonidae)

ABSTRACT

Knowledge of the life history attributes of a threatened species may assist in developing conservation management actions. The south-western carpet python (*Morelia spilota imbricata*) is a large (up to 2.8 m in total length and 6 kg in mass) ambush predator. Particular life-history traits, and reliance upon specific habitat features for reproduction, may render such a species particularly vulnerable to anthropogenic processes. In the course of a wide-ranging mark-recapture and radio-telemetric study of two populations of carpet pythons, I gathered data on several facets of their biology relevant to this issue. Female *M. s.imbricata* mature at large body sizes and produce large clutches of eggs (range 9-30, mean 19.1), but reproduce on a less-than-annual schedule. Reproduction is energetically expensive for females through lost feeding opportunities, vitellogenesis and maternal brooding throughout incubation. Up to 31% of pre-reproductive weight may be lost and wild females take two or more years to recover condition sufficiently to breed again. The period after the hatching of their eggs may be especially

dangerous for female pythons. Emaciated and with heavy parasite loads, they must quickly ambush prey to begin their recuperative journey and may be vulnerable to several sources of mortality at this time. Although male pythons expend less energy in reproduction, they are at risk from their wide-ranging movements in the breeding season. Frequent re-use of specific thermally-distinctive nesting sites by several snakes suggest that such sites may be rare in the landscape, and critical to long-term viability of python populations. Management actions should ensure habitat integrity and continuity, reduce feral predators and maintain vigorous populations of prey species.

INTRODUCTION

Large predators appear to be particularly vulnerable to extinction, especially if they have specific habitat requirements, specialised diets, low rates of growth and reproduction, or if they rely on ambush or feed primarily on other threatened taxa (Reed & Shine 2002). Problems facing the conservation of large mammalian predators are well known, but those facing large ectothermic species have attracted much less scientific attention (but see Brown 1993; Shine et al. 1995, 1999b). In many parts of the world, giant constricting snakes of the families Boidae and Pythonidae comprise a significant component of the large-predator fauna. Throughout a diverse array of habitat types across much of Africa, Asia and Australia, pythons are among the largest and most abundant predators (Greene 1997; Torr 2000). These animals are undoubtedly important predators on a wide range of vertebrate prey, and hence may play a significant ecological role. Any threat to their continued existence may thus have serious consequences for other components of these ecosystems.

A number of pythonid species worldwide are known to have declined (Dodd 1993). In Australia, several pythons are listed as threatened (Cogger et al. 1993), and pythons are disproportionately represented on schedules of threatened fauna in Western Australia. Four pythons from a total of 11 taxa that occur in that State are listed as "threatened" under wildlife legislation. The justifications for that listing vary among taxa. For some species, their perceived commercial value for the illegal pet trade has led to listing; others have clearly declined in distribution and/or abundance (Smith 1981; Pearson, 1993; Barker & Barker 1994) and two species occur in remote areas and have been poorly surveyed.

One python taxon that has shown substantial decline is the south-western subspecies of the widespread carpet python (*Morelia spilota*). Although carpet pythons are frequently displayed in zoos and wildlife parks, and are popular pets in North America and Europe as well as many parts of Australia, our knowledge of the biology of wild populations is based primarily on only two studies. Both of these studies were conducted in the extreme eastern part of the species' broad geographic range, near Sydney NSW, (*M. s. spilota*: Slip & Shine 1988a) and near Mullumbimby in northern NSW (*M. s. mcdowelli*: Fitzgerald & Shine 1995, 1996). There is surprisingly little ecological information available for the south-western subspecies, *Morelia spilota imbricata* (Maryan 1994). Some information has been published on the captive reproduction of this species (Bush 1988; Barker & Barker 1994) but none is available for wild snakes.

The reasons for reported declines of pythons are unclear; processes such as habitat destruction, predation by feral animals, commercial harvesting and overcollection for the pet trade have been suggested to play a role (Smith 1981; Ehmann & Cogger 1985; Groombridge & Luxmoore 1991; Pearson 1993). The same uncertainties are present for the reasons behind the decline of south-western carpet pythons. Teasing apart the relative importance of such factors is difficult, especially if the species of interest is rare, cryptic and long-lived. Under these circumstances, impacts may take many years to become apparent. An alternative approach is to focus on the animal's life-history traits and specific habitat requirements, because these may provide a basis not only for predicting species vulnerability (Reed & Shine 2002) but also for identifying critical management priorities. In the course of a five-year ecological study on south-western Australian carpet pythons, I gathered extensive data on such traits. Although the information is difficult to use in any direct tests of hypotheses, it may be helpful for future conservation planning. Thus, this chapter presents information on life-history traits of carpet pythons, and in particular on the ways in which they use specific habitats during the course of the reproductive cycle.

MATERIALS AND METHODS

Study animal and study sites

Morelia spilota imbricata is a large (up to 2.4 m snout-vent length, 6 kg mass) python occupying shrubland, woodland and forest in the south-western region of Western Australia and along the southern coastline to South Australia. The species also occurs on five islands off Western Australia, and on St. Francis Island and the adjoining mainland in South Australia (Smith 1981; M. Hutchison pers. comm.; Chapter 3). I undertook detailed studies of carpet pythons at two sites, Garden Island and Dryandra Woodland (Chapters 2, 3 and 5). Long-term mark-recapture and radio-telemetry studies were conducted. Short visits were made to most of the island populations (Mondrain, West Wallabi and St. Francis Islands) to collect morphometric, dietary and reproductive data. These sites are described in detail in Chapter 3.

Populations of pythons in sufficient numbers for detailed study could not be found in areas where habitat had been extensively cleared or modified, or where feral predators (European foxes *Vulpes vulpes* and feral cats *Felis catus*) were abundant. This latter pattern is not surprising, because these two feral species have been implicated as potential reasons for python population declines (Smith 1981; Pearson 1993). Garden Island has occasional incursions of foxes and feral cats, presumably across the causeway built in 1973 to service a naval base on the island. On each occasion, they have been quickly exterminated by trapping or fluoracetate ("1080") baiting (J. Maher, pers. comm.). The other island sites have no introduced predators. On the mainland, broadscale aerial and ground-based fox baiting has been occurring throughout most of the forested regions and many of the larger nature conservation areas in the south-west of Western Australia, including Dryandra Woodland since the mid 1980s (T. Friend, pers. comm.). I saw only two foxes and one feral cat during five years of regular fieldwork at the Dryandra Woodland site.

Adult pythons seem to be taken only rarely by native predators; indeed, I never recorded any instances of such an event during my own study. However, since I was able to implant radio-transmitters only in pythons > 800 mm SVL, I may have failed to detect predation on smaller snakes even if it occurred. In the absence of direct evidence on predation, all that I can do is identify situations in the biology of pythons that may render them especially vulnerable to a variety of potential sources of mortality. At all my study sites, pythons fed on a diverse array of small vertebrates (geckoes, native and introduced rodents, lizards and birds; Chapter 3), but adult females in two populations (Garden and West Wallabi) fed almost exclusively on a threatened macropod species (the tammar wallaby *Macropus eugenii*). This species is abundant on both these islands (pers. obs.), but is rare and has declined both in distribution and abundance on the adjacent mainland (Smith 1983). Pythons at Dryandra Woodland prey on a much wider variety of mammal species including the threatened numbat (*Myrmecobius fasciatus*) and woylie (*Bettongia penicillata*) (see Chapter 3).

Methods

I used three main techniques to obtain data on demography, growth, survivorship, diet and reproduction. These data were collected from December 1995 to March 2000.

(i) Mark-recapture

Pythons were captured either by searching on foot by day or at night (with a head-torch), road-driving at night (where road access was possible) or opportunistically during radio-telemetry fieldwork. At Garden Island and Dryandra, I was aided by Naval Police, rangers and researchers who captured pythons on roads or in buildings or on other naval infrastructure. Each python was processed (measured and weighed) according to the same protocol, given a unique individual number by ventral scale clipping (Blanchard & Finster 1933; Spellerberg 1977; Chapter 3) and released at its site of capture.

Sex was determined by eversion of hemipenes of males or the use of a lubricated probe to check for their presence. The lower gut was gently palpated to obtain faecal material and remove it prior to weighing (dietary information is presented in Chapter 3). Reproductive status could usually be assessed in males by examining for the presence of sperm when the hemipenes were everted. The lower abdomen of each adult female python was palpated to search for follicles or oviductal eggs.

To aid in the process of identification of recaptured pythons, I drew diagrams of head scales posterior to the frontal, the arrangement of subcaudal scales and the distribution of white pigment on the first 30 subcaudals posterior to the vent. The latter trait proved to be an especially valuable identification tool. Indeed, recaptures of marked snakes showed that this feature alone could establish individual identity.

(ii) Radio-telemetry

Surgically implanted transmitters were used to track pythons at both sites (see Chapter 5 for details). A total of 42 individual pythons were implanted at Garden Island (7 had transmitters changed once and one twice), and tracked for periods ranging in duration from 31 to 876 days. At Dryandra, 33 pythons were implanted (8 on two occasions) and tracked for

22 to 990 days. During the warmer months when most activity was occurring, pythons were located weekly on Garden Island and fortnightly at Dryandra. In winter, tracking was less frequent after the first year.

(iii) Necropsies

Carpet pythons found dead on roads were collected and frozen, and later dissected and their reproductive condition assessed. Dietary items were recovered from the stomach and intestinal tract. Males were classified as mature if the testes were enlarged and the efferent ducts were thickened and convoluted. Females were considered as reproductive if the ovaries contained enlarged follicles (> 10 mm), oviducal eggs or thickened and folded oviducts.

(iv) Other evidence

Eggshells from the clutches of telemetered female pythons were collected where possible after hatching. Some clutches could not be retrieved because to do so would destroy the nesting site, especially when they were situated under huge rocks or in crevices under a limestone cliff. On two occasions on Garden Island, gravid pythons were captured close to oviposition and kept until they deposited eggs. These were then artificially incubated.

Data on the causes of python mortality were collected from volunteers and Department of Conservation and Land Management staff who responded to a survey of python sightings over the period 1993-2000, as well as personal observations of pythons in the metropolitan area of the city of Perth. The latter included one male python captured at Lake Joondalup in the northern suburbs of Perth that was implanted with a transmitter and tracked for a period of 240 days until its death (Pearson & Wright, unpubl. data).

RESULTS

The structure of python populations

A total of 802 pythons were captured and measured during the study. Table 7.1 lists the number of individual pythons examined, their origin, and the proportions of juvenile and adult pythons of each sex at each location. A further 146 roadkills were salvaged and necropsies were carried out to provide information on size at maturity, reproduction and diet (reported in Chapter 3). Of these roadkills, 111 were in sufficiently good condition to allocate collection numbers and will be lodged at the Western Australian Museum.

On Garden Island, 675 individual pythons were captured and marked during the period January 1995 to March 2000. The structure of this population was examined in some detail in Chapter 2. Two striking features of the Garden Island population are the pronounced sexual size dimorphism of adults (with females on average twice as long and ten times heavier than males) and the large proportion of juvenile pythons. The capture of such a high proportion of juveniles may be an artifact of the primary sampling technique (road-driving at night) used on Garden Island. Only one adult female was collected during road-driving searches at night and she was caught under atypical conditions (observed with a hand-held spotlight away

Table 7.1. Carpet pythons captured and examined during this study from sites in Western Australia and South Australia (excluding recaptures). Pythons were classified as adults or juveniles by snout-vent length based on the size of smallest reproductive individuals. No reproductive female was captured on Mondrain Island, so the minimum adult size of St. Francis Island females was applied to this population. See text for further explanation.

Site	**No. of captures**	**Latitude**	**Longitude**	**Juvenile male**	**Adult male**	**Juvenile female**	**Adult female**
Garden Island	518	32° 12' S	115° 40' E	101	155	221	39
Dryandra Woodland	58	32° 47' S	117° 00' E	0	28	21	9
West Wallabi Island	86	28° 28' S	113° 42' E	3	46	27	10
Mondrain Island	26	34° 08' S	122° 15' E	0	17	2	9?
St. Francis Island	102	32° 36' S	133° 15' E	2	40	18	42
Other mainland sites	12			0	9	3	0

from the road). Only 4 of 56 captures of adult females (snout-vent length > 195 cm, see Chapter 2) were captured on the road (one hit by a car) and all were crossing during daylight hours. About half were found when moving through the scrub during weekly radio-telemetry sessions and four were captured with telemetered male pythons during the breeding season. The remainder were opportunistically captured by people who were walking through the vegetation (the Island's Ranger and Juvenile Justice work teams and contractors spraying weeds).

In contrast, juvenile female and male pythons were frequently captured along roads at night, often lying on the margin of the sealed road in ambush positions waiting for passing geckoes. The other source of small pythons was via their removal from Naval buildings and other infrastructure by the Ranger and Naval Police. These observations suggest that the proportion of Garden Island adult females in the population is higher than my capture results would imply (47 of 675 initial captures to the end of March 2000 or 6.9% of the population).

Data sets on other carpet python populations are much smaller (Table 7.1), but the capture of small juvenile pythons was relatively rare elsewhere. Carpet python neonates are around 39-41 cm in SVL (see below). At Dryandra Woodland, no juvenile male pythons were captured (smallest of 28 males captured was 89 cm SVL; minimum male size at maturity 88 cm SVL; Chapter 2), while 21 females were considered juveniles (< 195 cm SVL; smallest female 67.2 cm SVL) and only nine were adult size. On West Wallabi Island, the smallest female of 36 captured was 57 cm SVL and all but three males were adults (smallest 64.1 cm SVL). The smallest male python captured on St. Francis Island was 70.4 cm SVL, but of 42 captured only two were juvenile. Among the females, the smallest captured was 83.1 cm SVL and there were 18 juveniles and 42 adults (based on the minimum size of reproductive females of 132 cm SVL on this island; Chapter 3). Only two neonate pythons were caught on Garden Island suggesting that this cohort of pythons grows rapidly, or is highly cryptic, or suffers high mortality. I have no data to illuminate the fate of hatchling pythons; this age class might be vulnerable to a variety of predators.

Sources of mortality

Of the anthropogenic sources of mortality for pythons, death on roads was by far the most frequently recorded. For example, I collected > 150 fresh roadkills on Garden Island over a six year period; many more dead snakes were not picked up because they were too damaged or decayed. Several roadkills were found at Dryandra. Roadkills were strongly biased towards males and juvenile pythons (no adult female fatalities in > 170 roadkill snakes). As noted above, this bias may be due to the adult females' behavioural avoidance of roads, as well as to the extensive movements undertaken by adult males during the breeding season, and also perhaps the large size of adult female pythons that makes them easier for motorists to see and thus to avoid. Pythons living in metropolitan areas may be particularly at peril from traffic. I implanted a male python at Lake Joondalup in the northern metropolitan area of Perth. Over the eight-month period that he was radio-tracked, he often moved out of bushland around Lake Joondalup and crossed roads to neighbouring patches of bush. He was eventually run-over and killed by a motor vehicle.

Carpet pythons periodically are also killed by people in other ways, either accidentally or deliberately. Several pythons on Garden Island were fatally injured in roller doors or air-conditioning units. One large telemetered female python was killed by a visiting boat-owner. The python (which had recently eaten a wallaby) was killed with numerous blows to the head and then dragged down onto the beach and left.

I made only one observation of possible predation of a carpet python by natural predators during the study. A neonate (420 mm SVL) was found on a beach at Garden Island in April 1996. Its body was contorted and muscle and skin had been torn, suggesting that an avian predator may have dropped it. Several birds of prey have been recorded on the Island and butcherbirds (*Cracticus* sp.) and corvids may be predators of small pythons.

On the mainland at sites such as Dryandra Woodland, there are more potential predators of pythons, including marsupial carnivores (*Dasyurus geoffroii*), other reptiles (*Varanus rosenbergi*) and a range of birds. No telemetered pythons were lost to predators at Dryandra so their impact on python populations remains unknown. Colleagues who work on fox diets report finding numerous skinks in fox stomachs but have not observed remains of large snakes (J. Sinagra and P. de Tores, pers. comm.).

Reproductive and post-reproductive females have other potential sources of mortality. One telemetered female died while incubating her eggs, and a post-incubation female that was extremely emaciated was found dead with no overt injuries. For both of these cases, it seems likely that the animals simply exhausted their energy reserves. Another post-reproductive animal died after it became jammed in a log entrance after eating a possum.

Disturbance of reproductive behaviour by capture and transmitter implantation

Although adult female pythons proved difficult to locate, particularly at Garden Island (see above), I sometimes located females beside telemetered males during the breeding season. I took advantage of this situation to catch these females to obtain morphometric and dietary data (Chapter 2) and to implant transmitters (Chapter 5). In an effort to minimise disturbance of these reproductive pythons, they were quickly processed and implanted. At Garden Island, implanted pythons were usually released the same day or the day after capture, but at Dryandra (much further from the laboratory), they were returned to the field five to seven days after initial capture.

Whereas males typically returned to reproductive activities soon after release following transmitter implantation (Chapter 4), the response of adult females was varied (Table 7.2). Two females captured at Dryandra in the company of male snakes during the mating season (Dec 4 and Nov 7) failed to produce clutches in the following summer, but a female on Garden Island (#375) did nest successfully after her capture with a male on November 11. This snake had already been inseminated (sperm observed around the vent area), so perhaps the other two had not yet mated and the disturbance of capture and implantation was sufficient to deter further reproductive activity. Another adult female python (#38) was captured in the breeding season at Dryandra, but not in the company of a male. When palpated (Chapter 2), well-developed ova could be detected, but she failed to reproduce that year. Perhaps the duration of time that female pythons were held was important in determining whether or not they resumed reproductive activities upon release, since the three Dryandra pythons were held for longer periods than the Garden Island individual that subsequently bred. Obviously, such potential interruption to reproductive activities needs to be remembered when estimating reproductive frequency (see below).

Seasonality of reproduction

The south-western carpet python is a highly seasonal breeder, with matings observed from October 13 to December 20 in the wild (45 observations of male-female proximity), oviposition occurring in late December to early February (see below) and hatchlings emerging in March and April. Occasional late clutches may be produced in the wild. J. Maher (pers. comm.) observed a female coiled around eggs in early April on Garden Island, but it may be difficult for incubating females to maintain adequate clutch temperatures after March due to declining ambient temperatures (see Chapter 6).

Frequency of reproduction

Based on necropsies and the extrusion of sperm when male pythons were handled during spring, the vast majority of adult males seem to be capable of annual reproductive activity (Chapter 2). However, some males may not participate in reproductive activities in some years. Unfortunately, the cryptic behaviour of pythons (particularly when mating), the short duration of the transmitters I could implant in males, the comparatively brief mating season and infrequent monitoring of snakes (weekly or fortnightly) made it difficult to determine if males were sexually active. Several of the telemetered males on Garden Island were observed engaging in reproductive behaviour on an annual basis (Chapter 2), but only one male at Dryandra was observed to do so (see below).

Clearly, it is easier to determine if females are reproductive and mate successfully because they will eventually oviposit and incubate their eggs. In captivity, female *M. s. imbricata* can be induced to breed annually (R. Browne-Cooper, pers. comm.). However, my data on female pythons in the field suggest a much less frequent pattern. Table 7.2 lists adult females for the two study sites by reproductive years (July through June, because mating occurs in spring and incubation takes place during the summer of the next calendar year). At Dryandra during the five years of my study, the proportion of reproductive females among telemetered adult females was low (0 of 4 in 1995-6, 2 of 6 in 1996-7, 5 of 8 in 1997-8, 0 of 2 in 1998-9 and 1 of 2 in 1999-2000). Although the proportion of telemetered females that reproduced at Dryandra thus varied among years, the variation was not great enough to reject the null hypothesis of equal proportions of reproductive females among years ($\chi^2_4 = 5.98$, $P = 0.20$). No telemetered females at Dryandra bred on more than one occasion during my study, partly due to the mortality rate of post-reproductive females. The low number of reproductive females in each season and the absence of any telemetered female breeding twice (despite some being tracked for up to three years) suggests that adult females at Dryandra breed infrequently; perhaps every three years at a maximum .

On Garden Island, two telemetered females were observed to breed biannually (Table 7.2; #87 and 143). Breeding occurred less frequently for other adult females including some monitored for three and four years that failed to reproduce (#56, 218, 381), or those that did not reproduce in the three years following the successful rearing of a clutch (#50, 79). Only eight of the 14 (57%) telemetered adult females monitored over two or more breeding seasons reproduced and, as at Dryandra, annual proportions varied greatly (1 of 5 in 1995-6, 5 of 8 in 1996-7, 1 of 14 in 1997-8, 1 of 13 in 1998-9, and 3 of 5 in 1999-2000). Sample sizes were larger at Garden Island, however, permitting robust rejection of the null hypothesis of equal proportions of reproductive females each year ($\chi^2_4 = 13.99, P < 0.01$). The overall proportion of reproductive females did not differ significantly between the two sites ($\chi^2_1 = 0.54, P = 0.46$).

Observations of matings and possible matings

(i) Garden Island

During autumn and winter (May-August), adult female pythons on Garden Island were sedentary, sheltering under thick bushes or fallen timber (Chapter 5) and emerging to bask mid-morning in sunny weather. By September, females that will not breed in the subsequent months begin to take prey and are frequently observed with large stomach bulges indicating recent meals of tammar wallabies. Reproductive females were not observed to start feeding until after their eggs had hatched in March. Thus, reproductive females go without food for 10 or more months during the reproductive cycle. Observations of python mating behaviour and male-female proximity on Garden Island were reported in Chapter 2. In brief, matings were observed from mid-October to mid-December. Males were observed to visit more than one female during a breeding season and to revisit reproductive females over a period of several weeks. They remained with females for a short time and pairs of males were seen close to females. No aggression between courting males was observed and the absence of scarring on adult male snakes ($n = 155$) suggests an absence of male-male combat. Most males appear to be capable of reproductive activity every year based on necropsies and observations of telemetered snakes on Garden Island (Chapter 2).

(ii) Dryandra Woodland

Dryandra pythons predominantly spend the late autumn, winter and early spring (May to October) in tree hollows 5-12 m above ground. Males retreated to overwinter trees later in autumn and typically returned to the ground sooner in spring (September) than did females (late September to October). A few pythons spent the winter on the ground sheltering in logs or under piles of fallen branches (Chapter 5). Observations of pythons mating or of males and females in close proximity to each other during spring are summarised in Table 7.3.

Some males were observed to make long distance movements from their usual areas of activity to locate females. On one occasion, a male (#39) moved 2 km to a female. Males appeared to remain with females only a short time (maximum 4 days), but the infrequency of sampling precluded the detailed collection of data on this aspect of reproduction. No males were found with more than one female in a breeding season and only one male (#17) was found with reproductive females in two consecutive years.

Table 7.3. Observations of python reproductive behaviour at Dryandra Woodland, 1995-1997.

Date	Female ID	SVL (mm)	Mass (g)	Male ID	SVL (mm)	Mass (g)	Comments
7 Nov 1995	11	1820	2575*	17	1431	618	Laying loosely coiled over female in small depression; male captured for transmitter implantation (*on 5 Apr 1997)
29 Oct 1996	Not captured			28	1135	404	Mating; coiled on top of female with tails aligned in a log
12 Nov 1996	Not captured			7	1370	645	Coiled on top of female inside a log; both still in log the following morning
13 Nov 1996	30	1785	2389	17	1438	623	Moving towards basking reproductive pair (other male #29, 1426 mm SVL, 637 g); both implanted
24 Oct 1997	34	1881	2710*	36	1515	960	Captured basking near female and implanted with a transmitter; released 28 Oct 1997 (*on 6 May 1997)
20 Nov 1997	34			36			Found coiled together in a log and remained there until at least 1940 hr, 21 Nov 1997
24 Nov 1997	34			36			Both had moved to a rock cavity 26 m away and remained there until 25 Nov 1997. Male left about 1430 hr.
6 Nov 1997	Not captured			29	1426	637	Male coiled on top of tightly coiled female inside log; uncoiled and retreated further into log
7 Nov 1997	37	2057	3253	31	1370	645	Both basking beside a log; female had sperm around her vent; female captured and transmitter implanted
12 Nov 1997	Not captured			7			Mating; coiled on top of female inside log
11 Nov 1997	24	1938	1775*	39	1342	522	Coiled together and entwined basking in weak hazy sun (*on 31 Dec 1996)
26 Nov 1997	15	2000	2353*	43	1215	347	Male captured at entrance of log occupied by female (*on 19 Oct 1995)

Groupings of a female with more than one male (as observed on Garden and St. Francis Islands, Chapters 2 and 3) were not observed, although male #17 did appear to be moving towards a reproductive pair when captured. No evidence of male-male aggression in the form of body scarring was seen on any males examined from Dryandra (*n* = 28).

Nest sites and incubation behaviour

Following mating, female pythons moved comparatively little and were frequently observed basking. On one occasion, a gravid female on Garden Island was seen basking under a tangle of branches in an inverted position, lying on its back with its ventral surface oriented towards the sun, a position reported occasionally in other species of pythons in captivity (Barker & Barker 1994). Some of the radio-tracked females visited their eventual nesting site prior to oviposition. At Dryandra, female #3 oviposited in a log she had visited for at least a week in December the previous year, and female #37 also used a log visited in March the previous year. The remaining four females used sites where I had not previously located them, but all were within their normal home range (Chapter 5). At least three of the nine nesting females on Garden Island also visited their future nest sites, but usually only a few weeks to a month before oviposition.

Types of nest sites varied markedly between my two study sites (Table 7.4). At Dryandra, three pythons oviposited in logs, two in burrows or crevices in outcrops of lateritic rock and one in the disused burrow of a numbat (*Myrmecobius fasciatus*). The logs chosen were large (395-530 mm diameter). Two of the three logs were formed from the trunks of trees that

Table 7.4. Nest sites of carpet pythons, incubation behaviour and inferred minimum (min. inc.) and maximum (max. inc.) incubation periods (in days). No. obs. refers to the number of times the nesting site was visited.

Python No.	**Location**	**Year**	**Earliest date at nest site**	**min. inc.**	**max. inc.**	**No. obs.**	**No. basking obs.**	**Nest site**
11	Dryandra	1996	11 Dec 1995	45	58	10	0	Disused numbat burrow, length 2.4 m with leaf lined nest, 36 cm below ground level
3	Dryandra	1997	9 Jan 1997	62	92	10	0	Felled wandoo bole in mallet plantation; 7 m long, 465 mm diameter, 2 entrances at one end
14	Dryandra	1997	17 Dec 1996	64	79	10	0	Wandoo log; 4 m long, 530 mm diameter, 1 entrance; natural fall tree bole
15	Dryandra	1998	22 Dec 1998	!	!	7	0	Former goanna burrow in laterite outcrop in open position
34	Dryandra	1998	30 Dec 1997	64	73	8	0	In crevice on top of a laterite outcrop; top of crevice filled with leaf litter and sticks
37	Dryandra	2000	19 Jan 1999	68	126*	4	0	Powderbark wandoo log; natural fall bole, 4 m long, 395 mm diameter, 2 entrances
50	Garden Island	1996	6 Jan 1996	68	84	12	0	Under huge limestone boulder; old python eggs at entrance; slide marks indicated basking
87	Garden Island	1997	13 Jan 1997	60	74	10	1	Under leaf litter and dense *Acanthocarpus* shrub; basking 13 Jan 1997
260	Garden Island	1997	29 Jan 1997	66	78	11	0	Under dense sword sedge and *Acanthocarpus* shrub
143	Garden Island	1997	16 Jan 1997	50	60	8	0	In crevice in limestone cliff with another incubating female (#79)
79	Garden Island	1997	13 Jan 1997	59	76	10	0	In crevice in limestone cliff with #143
235	Garden Island	1997	29 Jan 1997	61	72	10	1	Under limestone boulder at base of west-facing scree slope and only 5 m above sea level; basking 1440 hr 13 March 1997

Table 7.4 cont.

Python No.	Location	Year	Earliest date at nest site	min. inc.	max. inc.	No. obs.	No. basking obs.	Nest site
375	Garden Island	1998	29 Jan 1998	63	76	12	4	Under rootball of fallen *Callitris* tree; slide marks at entrance and seen basking at; 1020 hr 29 Jan 1998, 1045 hr 26 Feb 1998, 0925 hr 5 Mar 1998, 0910 hr 2 Apr 1998
143	Garden Island	1999	29 Jan 1999	66	78	11	0	Under dense sword sedge and *Acanthocarpus* on east-facing dune slope
87	Garden Island	2000	3 Feb 2000	41	77	7	0	Buried in leaf litter under a tangle of fallen branches and *Acanthocarpus*
375	Garden Island	2000	6 Jan 2000	70	92	10	2	Under rootball of fallen *Callitris* tree; seen basking 0820 hr 19 Jan 2000 and 1610 hr 24 Feb 2000
382	Garden Island	2000	10 Feb 2000	^	^	4	0	Under leaf litter and dense *Acanthocarpus* 2 m from an access track; on 2 Mar 2000 had moved and dessicated eggs were strewn around her

! 10 Feb 98 found dead still coiled around eggs; they had failed to hatch

* infrequently checked

^ eggs abandoned; female probably disturbed by people passing on nearby access track had naturally toppled over, whereas the other had been cut down during clearing to establish a mallet plantation. The nest logs were lying horizontally and their structure was still robust (i.e. the log had not extensively weathered, begun to collapse or fill with sand). The length of the hollow section of the logs ranged from 4 to 7 m and only one end was open. The pythons coiled and incubated their eggs at the blind end of these logs. Once the female had left the nest log, I cut out a small section of wood with a chainsaw to access the interior of the log to collect eggshells for clutch size data, and later replaced the block of wood.

Nest sites in the outcropping laterite (highly weathered and chemically altered granite) at Dryandra provided a warm microenvironment, since there was little canopy cover above the outcrop and it was exposed to direct sunlight for most of the day. The rocks overlying the crevice and burrow were loose and cracks between them were filled with leaf litter and sticks. Once the pythons finished incubation, it was easy to pull up the loose rock to recover the vacated eggshells.

At Garden Island, reproductive female pythons used three main types of nest sites; under rocks, below leaf litter and dense vegetation (usually prickle lily *Acanthocarpus preissii* or sword sedge *Lepidosperma gladiatum*) and along the root tunnels of fallen trees. One area of cliff on the western side of Garden Island was an especially important site for python reproduction with three of my telemetered pythons (of 11 recorded nests of 9 individual pythons) ovipositing there. A few crevices were available under a 6 m high limestone cliff facing north-west and some associated boulders that had fallen from this cliff. The site was protected from prevailing south-west afternoon sea breezes by another cliff and tall trees and provided a warm (sometimes hot) microclimate. The entrances to the crevices were small (<

200 mm diameter) and surrounded by prickle lily bush. I tried to locate and observe the pythons inside these crevices during their nesting using a video camera on a 3 m flexible conduit (purpose-built for inspecting pipes in the Navy's torpedo bunkers) and a fibre-optic light source and camera. However, the passage into the nesting chambers was convoluted and ascended through rock and deep sand preventing the cameras reaching the python's nesting chamber.

Females #79 and #143 nested within a metre of each other in this limestone cliff in 1997, perhaps in the same crevice. Another python, #50, had nested under a huge limestone boulder approximately 30 m away in 1996. Prior to oviposition, #143 had also visited this boulder, but by then it was already occupied (indicated by the nearby fresh slough of a large (and unknown) female, freshly excavated dirt containing fragments of old python eggs and a large slide mark at the entrance). The three telemetered pythons that used this area to nest were never observed to bask, presumably because of the thermal characteristics of the limestone cliff (Chapter 6) and the site's protection from cooling south-west afternoon winds. However, I did occasionally observe fresh slide marks at the entrance of these crevices, so the incubating females may have left their eggs occasionally. I monitored this site every breeding season since 1996, and every year several pythons used it to nest. I was unable to locate any other site on Garden Island during my fieldwork that supported such densities of incubating females.

The other nest sites used on Garden Island were more dispersed and I found no evidence that they had been used previously by pythons. Female #235 chose an unusual site under a limestone boulder at the base of a steep west-facing scree slope. The site did not receive direct sun until late morning and the nest was only 5 m above waves crashing onto the base of the limestone pavement supporting the boulder. Nonetheless, the female successfully incubated her eggs through to hatching. I visited the nest shortly after she had left her eggs following incubation (1630 hr on 5 April 1997). In fading daylight and steady rain, she was about 40 m away from the nest and moving upslope. When I inspected the nest, there was a neonate at the entrance, another in the nest chamber and several other hatchlings had pipped their eggs but not yet escaped their confines. This observation suggests that under natural conditions, female pythons may leave their eggs as soon as the hatchlings begin to pip their eggs.

One python (#375) nested twice in underground cavities formed under the rootball of fallen *Callitris* trees, but not in the same location. The first site used in 1998 was in an area of dense low forest with fairly continuous canopy cover and appeared to be a cool and therefore unsuitable site to nest. However, her nest was located under the rootball of a large tree that had brought down some of the surrounding trees when it had fallen and so opened up a small area in the canopy. During incubation, her body temperature (and presumably clutch temperature) varied over a much greater range than telemetered pythons nesting in cliffs and under leaf litter/dense *Acanthocarpus* (Chapter 6). She was also observed to bask more frequently than any of the other telemetered incubating females (4 of 12 observations), but was only observed basking in the morning as the site was well shaded in the afternoon.

A previous study on tropical pythons (*Liasis fuscus*) explored maternal nest-site selection in great detail, including the consequences of selecting sites with cooler and more variable thermal regimes (Shine & Madsen 1996; Madsen & Shine 1999). Because females in such sites expended more energy in brooding, they were in poor condition by the end of incubation, were less likely to survive than females breeding in warmer nest-sites, and postponed subsequent reproduction even if they did survive (Madsen & Shine 1999). It might be surmised that the female carpet python described above (#375) would experience all of these costs. Despite this scenario, however, female #375 bred again two years later, and was one of only two pythons to display biannual reproduction during my study. The second nest site of female #375 in 2000 appeared to be in a more suitable site, again situated under the rootball of a fallen tree, but near the top of a north-west facing dune slope with a large canopy opening overhead. She was seen basking on two of the 10 occasions the nest site was visited (0820 hr Jan 19, 2000; 1610 hr Feb 24, 2000).

The remaining nests were located in dense thickets of *Acanthocarpus,* often intermixed with sword sedge. Pythons were partially or totally buried in leaf litter under these thickets. Only one of the four pythons that nested in such a site was observed to bask (#87 on Jan 13, 1997), but this may have been prior to oviposition. These nests were usually situated such that the thicket received many hours of sunlight, either in places with very open canopy or near roads. One of these pythons (#382, Table 7.4) placed her nest less than 2 m from the edge of a road frequented by visitors to the island who had landed by boat. People passing close to the nest may have led to her disturbance and eventual abandonment of the eggs.

Duration of incubation

Because pythons were not located on a daily basis (usually weekly or fortnightly) and incubating pythons could be observed only rarely, I could not determine the exact duration of the incubation period. An estimate of the minimum possible duration of incubation was calculated from the first time that a reproductive python was detected at the nest site until the last time it was found there (Table 7.4), while a maximum possible duration of incubation represents the time elapsed between the last time the python was located before occupying the nest site and the first time it was located away from the nest post-incubation. The actual duration of incubation lies somewhere between these two figures but absolute upper and lower limits cannot be more accurately determined. The lowest possible maximum was 58 days (#11 at Dryandra), with most incubation events for regularly monitored pythons in the range of 58 to 78 days.

Incubation times of eggs removed from captive pythons (based on Bush 1997 and unpublished data of J. Stuart and R. Browne-Cooper) and one wild-caught gravid female on Garden Island are presented in Table 7.5. The Garden Island female laid her eggs over a period of 9 days (one on Feb 2, one on Feb 7 and the remainder between Feb 9 and 11). These were placed in a tray of moist vermiculite and incubated at 30-31°C. The first two eggs failed and those eggs that hatched successfully did so between April 2 and 3. This gives an incubation time of 50 to 53 days. In the captive clutches, higher incubation temperatures resulted in shorter incubation times. The shortest incubation was 44 days for eggs incubated at 31.5°C and the longest was 72-75 days for those incubated at 28°C.

Table 7.5. Maternal sizes, clutch sizes and hatching success for *Morelia spilota imbricata* at Garden Island and Dryandra Woodland and for captive pythons (Bush 1997; Robert Browne-Cooper unpublished; Jamie Stuart, unpublished). "slugs" refer to infertile, usually smaller than average eggs.

Python #	**Location**	**Year**	**SVL (mm)**	**Pre-oviposition mass (g)**	**Post-oviposition mass (g)**	**Clutch mass (g)**	**Clutch size (g)**	**No. hatched**	**Inc. period (days)**	**Comments**
11	Dryandra	1996	1887				20	20		
14	Dryandra	1997	1935				11	8		
3	Dryandra	1997	1955				11	11		1 slug
15	Dryandra	1998	2065				14	0		female died coiled around eggs; all were fertile
34	Dryandra	1998	1899				20.	16		
37	Dryandra	2000	2125				16	13		
139; wild caught	Garden Island	1996	2218	4684	3502	1149	22	17		captured 10 Jan 1996; gravid, retained to lay (2 Feb 1996)
50	Garden Island	1996	2114				-	-		Egg shells not recovered
289; wild caught	Garden Island	1997	1953	4205	2907	973	24	0		Captured 3 Jan 1997; gravid, retained to lay. All eggs failed; 2 slugs
87	Garden Island	1997	2224				30	26		
260	Garden Island	1997	2215				18	16		
143	Garden Island	1997	2130				-	-		egg shells not recovered
79	Garden Island	1997	2220				-	-		egg shells not recovered
235	Garden Island	1997	2126				17	5		10 were fertile but failed to hatch, 2 were infertile
375	Garden Island	1998	2130				18	16		
143	Garden Island	1999	2164				-	-		egg shells not recovered
87	Garden Island	2000	2322				26	26		1 slug

Table 7.5 cont.

Python #	Location	Year	SVL (mm)	Pre-oviposition mass (g)	Post-oviposition mass (g)	Clutch mass (g)	Clutch size (g)	No. hatched	Incubation time (days)	Comments
375	Garden Island	2000	2130				19	16		1 slug
382	Garden Island	2000	2312				20	0		disturbed; 12 fertile, 8 half size, 5 slugs
1	captive	1994	1730	2500	2100	758	17	14	63-71	Bush (1997); python from Norseman, WA; date of oviposition 15 Jan 1994
1	captive	1996	1810	-	1900	656	17	16	63-74	Bush (1997); same python as above; date of oviposition 27 Dec 1995; 1 slug
2	captive	1996	1710	1960		751	17	12	62-75	Bush (1997); python from Woodvale, WA; date of oviposition 18 Nov 1995
1A	captive	2000	-	2506	1484	628	15	12		Stuart, pers. comm.; date of oviposition 10 Feb 2001; 3 slugs
6B	captive	2000		2921	2061	337	10	7		Stuart, pers. comm.; date of oviposition 10 Feb 2001; 3 slugs
5A	captive	2001		2110	1324	516	13	7		Stuart, pers. comm.; date of oviposition 11 Feb 2001; 6 infertile
R1	captive	1997	1980	2961	2049		23	18	44	Browne-Cooper, pers. comm.; python from Neerabup, WA; 1 slug
R1	captive	1998		3335	2490		22	14	49	Browne-Cooper, pers. comm.; 17 fertile eggs
R1	captive	1999	2100	4236	3111		28	16	51	Browne-Cooper, pers. comm.; 25 fertile eggs
R2	captive	2000		2285	1588		17	16		Browne-Cooper, pers. comm.; 16 fertile eggs; progeny of R1 born March 1998

Maternal size and the costs of reproduction

The possibility that handling wild pythons during the breeding season could modify their behaviour (see above) precluded their regular capture and weighing during the breeding season. Thus, I was unable to collect data on body mass loss during oviposition and incubation from telemetered snakes. However, some data were available on the costs of egg production from captive pythons and two wild caught pythons (Table 7.5).

The small sample size of wild snakes (*n* = 2) prevented statistical comparison against captive snakes. Because the general figures were similar (25% and 30% mass loss versus 25-41% for captives), data for wild and captive snakes were combined for further analyses. Loss of body mass of females following oviposition ranged from 25-41% of pre-oviposition body mass (mean 31%). Fewer data are available on clutch mass as a proportion of maternal body mass, because the clutch masses of some captive snakes were not recorded. Clutch mass as a function of pre-oviposition mass ranged from 12-25% (mean 22%, *n* = 5).

Apart from egg production, other major costs include those associated with incubation of eggs over a period of 50+ days, including shivering thermogenesis and forgone opportunities to feed (Slip & Shine 1988f; Madsen & Shine 1999, 2000). Females at the end of their egg incubation were often captured to remove and replace transmitters and on these occasions, I examined their body condition. At both study sites, such females were emaciated with ribs prominent and reduced muscle tone (they did not strongly resist handling) and often with large numbers of ticks. These snakes took considerable time to recover body condition and appeared to suffer higher mortality than did non-reproductive females (see above).

Clutch size

Eggshells from most nests could be recovered once the female had finished incubation and the neonates had dispersed, so clutch size could be determined. The nests in crevices under the limestone cliff on Garden Island could not be readily accessed and to do so may have destroyed them. Thus, no clutch size information is available from these nests (Table 7.5). Pythons typically produce three types of eggs in clutches; fertile eggs which develop normally and hatch if incubation conditions are suitable; inviable eggs of varying sizes and shapes which are usually yolked, do not develop and usually become infected with bacteria and fungi; and small often hard rubbery "slugs" (infertile eggs). Reported clutch sizes in Table 7.5 excluded "slugs", which can be easily distinguished by their size and shape, but not inviable eggs which may be difficult to distinguish from failed fertile eggs.

Recorded clutch sizes for *M. s. imbricata* range from a minimum of seven eggs from a captive snake (J. Stuart, Table 7.5) and nine for the smallest wild python, a St. Francis Island female (Chapter 3), through to 30 for a Garden Island female (#87). The calculation of a mean clutch size across all populations of *M. s. imbricata* is of little value given the huge observed range and its probable correlation with maternal body size. Such a correlation is very widespread (virtually ubiquitous) among snakes, including other populations of carpet pythons (Seigel & Ford 1987; Slip & Shine 1988a; Shine & Fitzgerald 1995). Data from the present study revealed a significant correlation between maternal body size and clutch size for captive snakes ($n = 5$, $r = +0.96$, $P < 0.02$) but not for wild snakes (Garden Island, $n = 9$, $r = +0.18$, $P = 0.65$; Dryandra, $n = 6$, $r = -0.35$, $P = 0.50$). The small sample sizes make it very difficult to interpret this lack of statistical significance, but the results suggest that clutch sizes in wild pythons may vary as a function of traits (such as maternal body condition) other than simply maternal body length.

Sex ratios of neonates

Sex ratios of hatchlings based on one clutch from Garden Island (5 males: 7 females) and three captive clutches (9:9, 7:7, 8:8; Browne-Cooper, pers. comm.) do not suggest any bias in sex ratios at hatching.

Size of neonates

Data on the size of neonates at the time of hatching was available for eight clutches of eggs (involving 116 individual neonates; Table 7.5). Mean mass of neonates from each clutch ranged from 22.1 to 26.9 g and the mean snout-vent length (on a reduced sample of four clutches) was 351 to 393 mm.

DISCUSSION

Many of the general life history attributes of *M. s. imbricata* are similar to those reported for other subspecies of carpet pythons (Slip & Shine 1988a,b,c,d,e,f; Shine & Fitzgerald 1995). Similarities include the mean adult body sizes of females, the seasonal timing of reproduction (spring mating, summer nesting), the low reproductive frequency of adult females, the large clutch sizes and the incubation of eggs in thermally- buffered microenvironments. There are however, some significant differences. In contrast to eastern subspecies, *M. s. imbricata* males mature at much smaller sizes (SVL of 88 cm vs 149 cm for *M. spilota spilota*, Slip & Shine 1988a; Chapter 2) and sexual size dimorphism among adults is thus much more pronounced than in the eastern populations. Mating systems differ also, but it is difficult to determine exactly what happens during the mating season. I have never recorded male combat within *M. s. imbricata*, so in this sense the south-western subspecies resembles *M. s. spilota* rather than *M. s. mcdowelli* (Shine & Fitzgerald 1995). However, there may be significant diversity even among the non-combative python populations. For example, males of *M. s. spilota* remain in mating aggregations with females for several weeks (Slip & Shine 1988a) whereas males of *M. s. imbricata* tended to move on after a few days. Also, it is striking that the largest breeding aggregation was recorded from St. Francis Island, a site from which relatively few records were obtained. The much larger data sets from Garden Island and Dryandra generally included records of only one or at most two males per female.

The reproductive strategy of male pythons in Dryandra Woodland (this chapter) is difficult to interpret given the relatively infrequent monitoring at this site. Males moved from their usual area of foraging activity to locate females, sometimes travelling up to 2 km (this Chapter). Reproductive females remained in their usual home ranges (see Chapter 5) and did not move away to particular areas for courtship or nesting. Mating occurred in late October to mid-December, usually involving only one male and one female python. I did not observe male pythons at Dryandra visiting more than one female in a season, but this may occur. Some males were certainly reproductively active on an annual basis, but some male pythons that were tracked over up to three mating seasons were never observed with female pythons and did not make any long range movements. Perhaps these pythons were able to secure matings with females within their home range and the timing of my visits did not coincide with mating events. Alternatively, some adult males may not be reproductively active every year, due to poor body condition or some other unknown factor. Certainly there is great variation in growth rates and body condition of male pythons (at least on Garden Island; Chapter 2) and males may forgo mating opportunities in order to feed. One adult male at Dryandra Woodland was observed to capture and eat a large numbat in mid-October, at a time when other males were locating females to mate and thus, were not feeding. Further work is required to clarify the reproductive cycles of male pythons.

For female *M. s. imbricata*, reproduction is infrequent and requires an enormous commitment of body resources. These pythons are capable of breeding annually in captivity with an abundant food supply and constant heating, but the less favourable thermal and feeding regimes in the wild result in slower recuperation after egg incubation and hence, a less-than-annual frequency of reproduction. At Garden Island, two females bred on a biennial basis (this Chapter), but most bred less frequently, perhaps every third or fourth year. The abundance of tammar wallabies on Garden Island and its relatively mild weather in March and April allows post-reproductive females an opportunity to feed before the onset of winter (Chapters 3 and 6). Two telemetered females were observed in ambush positions within weeks of completing egg incubation. Female #79 was recorded at her nest site for the last time on 13 March 1997. She was located a few weeks later in an ambush position and on 4 May 1997 had a tammar in her stomach. Another post-reproductive female (#143) left her nest site sometime after 25 March 1999 and was observed in an ambush position on 27 April 1999. I found only one other adult female (non-reproductive) in an ambush position in April and no others until late August. So, post-reproductive females are able to feed before the onset of winter and begin feeding again after winter, as early as August.

In contrast, autumn night-time temperatures are cool at Dryandra (average minimum < 10°C; Chapter 5) and probably preclude pythons from eating large meals at this time. I have no records of adult female pythons eating, in ambush positions or with food items in their stomach from May to October (8 records of adult females in ambush positions from November to April and 6 records of faecal material between October and May; but note that the digestion of large items may take several weeks and faecal material may be retained for long periods after a meal). None of the radio-tracked female pythons at Dryandra reproduced more than once during my study, suggesting that reproduction may be very infrequent (> 3 years), possibly because thermal restrictions and less abundant food reduce the rate at which post-reproductive females can regain body condition.

Carpet pythons have fairly generalised nesting requirements, selecting a wide range of microhabitats that provide relatively stable thermal regimes and good concealment. During this study, females nested in large logs, in burrows and rock crevices and under leaf litter and dense shrubs. At Dryandra where there are many logs, it would seem that there are abundant possible nesting sites. The logs that were selected were very large (395-530 mm in diameter), typically the main trunks of fallen trees, and were long and blocked at one end. Logs with these characteristics may be relatively rare, but I do not have any data on their availability. Given the importance of large trees as overwinter sites and for providing suitable logs for nesting, research into their availability and the continued maintenance of trees of these dimensions will benefit the conservation of pythons. The other nest sites (a numbat burrow, a goanna burrow and a rock crevice) used at Dryandra illustrate the flexibility of these snakes. Previous reports of nesting sites in carpet pythons reveal the same kind of flexibility; for example, females of this species have been recorded to nest under a sheet of corrugated iron (Charles et al. 1985) and in the roofspace of a building (Barker & Barker 1994).

Although female pythons at Garden Island demonstrated flexibility in the selection of nest sites, some individuals displayed year-to-year consistency in the types of nest-sites that they used. For example, two telemetered pythons bred twice during the study period; one nested on both occasions under leaf litter and *Acanthocarpus* shrubs and the other twice nested under the rootballs of fallen trees. Neither returned to the earlier nest site, choosing instead to oviposit in a new but nearby location. Both these pythons had home ranges that overlapped the small limestone cliff used by numerous other pythons for nesting during the study, but neither used this popular site.

The small limestone cliff where three of my telemetered pythons nested was a scene of intense female activity every summer. The few available crevices were cleaned out by gravid females removing past eggshells and depositing them around the crevice entrances. Sloughed skins lay discarded on shrubs near the crevices and slide-marks of large female pythons were common. This site appears to be unique on Garden Island and is used by several females to oviposit every year. The structure of the crevices may be important in this respect, as they provide a high degree of physical protection for brooding snakes. However, the thermal characteristics of the site are likely to be equally important. The cliff is exposed to sun from around 0900 to 1830 hr during summer and is protected from prevailing cool afternoon breezes. Data from telemetered pythons monitored by the automated telemetry system show that the snakes were able to maintain higher and more consistent body temperatures than were females using other types of nests (Chapter 6). In terms of conservation, the presence of such important incubation sites may be important for other populations of carpet pythons in environments where there are limited other options. For example, some offshore islands that support carpet pythons populations have very few or no large trees, and hence few or no logs. Dense low vegetation and leaf litter in which to oviposit may also be rare. It would be particularly interesting to know where carpet pythons nest on islands such as West Wallabi and St. Francis Islands (with low open vegetation but no logs) or Mondrain Island (with large smooth granite outcrops and low forest with little undergrowth).

Reproduction for female carpet pythons is a long and exhausting journey; they lose up to 41% of their body mass through the deposition (this Chapter) and more through subsequent incubation of eggs (Slip and Shine 1988a). At the conclusion of incubation they are emaciated, with reduced muscle mass and presumably strength. Often they are inflicted with numerous ectoparasites such as ticks. They must find and capture prey and begin to recuperate. The choice of incubation site could presumably have a major influence on body condition at the end of incubation. A nest site with a warm and fairly stable thermal regime would reduce the need to use shivering thermogenesis to maintain clutch temperatures, and also minimise the need to engage in potentially risky basking behaviour.

Why have populations of south-western carpet pythons declined over much of their geographic range within the last half-century (Smith 1981; Pearson 1993)? The answer is undoubtedly complex and multifactorial. In common with other ambush predators, carpet pythons display a suite of life-history traits that may make them particularly vulnerable to habitat change (Webb & Shine 1998; Reed & Shine 2002). Essentially, many ambush predators tend to have relatively low rates of food intake, and hence have "slow" life-histories (slow growth, delayed maturation, infrequent reproduction) that threaten their ability to withstand an increase in mortality rates caused by humans or feral pests. Ambush predators also depend upon relatively dense vegetation, or other potential shelter-sites at ground level; anthropogenic disturbance of this layer may pose a serious threat to the snakes (Reed & Shine 2002). The very large body size of carpet pythons introduces additional points of vulnerability. For example, these pythons require assemblages of prey from small to large items to cope with ontogenetic diet shifts (Chapter 2). Reproductive females grow to large sizes and require a large, relatively abundant mammalian prey species; such taxa themselves are frequently threatened by habitat modification. Large body size also poses thermal challenges, with the maintenance of high and stable body temperatures a difficult task in cooler times of the year. These thermal problems are reflected in the disproportionate significance of thermally optimal nest-sites, which may be relatively rare and widely scattered in the landscape. Despite these points of vulnerability, however, the major picture that emerges from my study is of an immensely flexible ecological generalist with a remarkable ability to exploit even highly modified habitats. We will need to plan carefully if we are to maintain carpet pythons in the fragmented habitats of south-western Australia, especially in the semi-arid regions where vegetative cover at ground level and the availability of logs as shelter sites are under threat from agricultural activities and fire regimes. Although the challenges are considerable, my study suggests that carpet pythons may well prove to be more resilient than many of the other vertebrate taxa that have disappeared from their original habitats across the Australian continent.

REFERENCES

Abacus Concepts (1991) *SuperANOVA v. 1.11.* Abacus Concepts Inc., Berkeley, California.

Andersson, M. (1994) *Sexual Selection.* Princeton University Press, New Jersey.

Andrews, R.M. (1979) Evolution of life-histories: a comparison of *Anolis* lizards from matched island and mainland habitats. *Breviora* 454:1-51.

Avery, R.A. (1982) Field studies of body temperatures and thermoregulation. In: *Biology of the Reptilia, Volume 12* (Ed. by C. Gans & F.H. Pough), pp. 93-166. Academic Press, New York.

Ayers, D.Y. & 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.

Barker, D.G. & Barker T.M. (1994) *Pythons of the World. Volume 1, Australia.* Advanced Vivarium Systems, Lakeside, California.

Beck, D.B. (1995) Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. *Journal of Herpetology* 29:211-223.

Bedford, G.S. (1996) Metabolic physiology, digestive efficiency and energetics of some Australian pythons. Unpublished MSc dissertation, Faculty of Science, Northern Territory University.

Bedford, G.S. & Christian, K.A. (1998) Standard metabolic rate and preferred body temperatures in some Australian pythons. *Australian Journal of Zoology* 46:317-328.

Bell, D.T., Moredoundt J.C. & Loneragan, W.A. (1987) Grazing pressure by the tammar (*Macropus eugenii* Desm.) on the vegetation of Garden Island, Western Australia, and the potential impact on food reserves of a controlled burning regime. *Journal of the Royal Society of Western Australia* 69:89-94.

Bennett, A.F. & Dawson, W.R. (1976) Metabolism. In: *Biology of Reptilia, Volume 5* (Ed. by C. Gans & W.R. Dawson), pp. 127-223. Academic Press, New York.

Bennett, A.F. & Nagy, K.A. (1977) Energy expenditure in free-ranging lizards. *Ecology* 58:697-700.

Blanchard, F.N. & Finster, E.B. (1933) A method of marking living snakes for future recognition, with a discussion of some problems and results. *Ecology* 14:334-347.

Boles, W.E. (1988) *The Robins and Flycatchers of Australia.* Angus & Robertson, Sydney.

Bonnet, X., Shine, R., Naulleau, G. & Thiburce, C. (2001) Plastic vipers: genetic and environmental influences on the size and shape of Gaboon vipers, *Bitis gabonica. Journal of Zoology (London)* 255:341-351.

Brown, W.S. (1993) Biology, status and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. *Herpetological Circulars* 22:1-78.

*See Addendum

Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.

Bush, B. (1988) An unsuccessful breeding record for the Western Australian Carpet Python, *Morelia spilota imbricata. Herpetofauna* 18:30-31.

Bush, B. (1997) Captive reproduction in the south western Carpet Python, *Morelia spilota imbricata,* including an exceptional fasting record of a reproductively active female. *Herpetofauna* 27:8-12.

Charles, N., Field, R., & Shine, R. (1985) Notes on the reproductive biology of Australian python, genera *Aspidites, Liasis* and *Morelia. Herpetological Review* 16:45-48.

Chisholm, I.M. & Hubert, W.A. (1985) Expulsion of dummy transmitters by rainbow trout. *Transactions of the American Fisheries Society* 114:766-767.

See addendum

Coates, A. (1993) *Vegetation Survey of Dryandra Forest*. Unpublished report for the Department of Conservation and Land Management, Perth, Western Australia.

Cogger, H.G., Cameron, E.E., Sadlier, R.A. & Eggler, P. (1993) *The Action Plan for Australian Reptiles*. Australian Nature Conservation Agency, Canberra.

Cogger, H.G. & Holmes, A. (1960) Thermoregulatory behaviour in a specimen of *Morelia spilota variegata* Gray (Serpentes: Boidae). *Proceedings of the Linneaan Society of NSW* 85:328-333.

Crews, D., Diamond, M., Whittier, J. & Mason, R. (1985) Small male body size in garter snakes depends on testes. *American Journal of Physiology* 249:62-66.

Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*. Murray, London.

Dixon, K.R. & Chapman, J.A. (1980) Harmonic mean measure of animal activity areas. *Ecology* 61:1040-1044.

Dodd, C.K.Jr. (1993) Strategies for snake conservation. In: *Snakes. Ecology and Behavior* (Ed. by R.A. Seigel & J.T. Collins), pp. 363-394. McGraw-Hill, New York.

Ehmann, H. & Cogger, H. (1985) Australia's endangered herpetofauna: a review of criteria and policies. In: *The Biology of Australasian Frogs and*

Reptiles (Ed. by G. Grigg, R. Shine & H. Ehmann), pp. 435-447. Royal Zoological Society of New South Wales, Sydney.

Ellis, T.M. & Chappell, M.A. (1987) Metabolism, temperature relations, maternal behavior, and reproductive energetics in the ball python (*Python regius*). *Journal of Comparative Physiology* 157:393-402.

Fearn, S., Robinson, B., Sambono, J. & Shine, R. (2001) Pythons in the pergola: the ecology of "nuisance" carpet pythons (*Morelia spilota*) from suburban habitats in south-eastern Queensland. *Wildlife Research* 28:573-579.

Feaver, P.E. (1977) *The Demography of a Michigan Population of* Natrix sipedon *with Discussions of Ophidian Growth and Reproduction*. University of Michigan Press, Ann Arbor.

Fitch, H.S. (1970) Reproductive cycles of lizards and snakes. *Miscellaneous Publications of the Museum of Natural History, University of Kansas* 52:1-247.

Fitch, H.S. (1981) Sexual size differences in reptiles. *Miscellaneous Publications of the Museum of Natural History, University of Kansas* 70:1-72.

Fitch, H.S. (1987) Collecting and life-history techniques. In: *Snakes: Ecology and Evolutionary Biology* (Ed. by R.A. Seigel, J.T. Collins & S.S. Novak), pp. 143-164. Macmillan, New York.

Forsman, A. (1991a) Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *Journal of Animal Ecology* 60:253-267.

Forsman, A. (1991b) Adaptive variation in head size in *Vipera berus* L. populations. *Biological Journal of the Linnean Society* 43:281-296.

Forsman, A. & Lindell, L.E. (1993) The advantage of a big head: swallowing performance in adders, *Vipera berus*. *Functional Ecology* 7:183-189.

Garton, E.O., Wisdom, M.J., Leban, F.A. & Johnson, B.K. (2001) Experimental design for radiotelemetry studies. In: *Radio-tracking and Animal Populations* (Ed. by J.J. Millspaugh & J.M. Marzluff), pp. 15-42. Academic Press, San Diego, California.

Ghiselin, M.T. (1972) Models in phylogeny. In: *Models in Paleobiology* (Ed. by T.J.M. Schopf), pp. 130-145. Freeman & Cooper, San Francisco.

Gibbons, J.W. & Lovich, J.E. (1990) Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs* 4:1-29.

Greene, H.W. (1997) *Snakes. The Evolution of Mystery in Nature*. University of California Press, Berkeley.

Grigg, G.C., Drane, C.R. & Courtice, G.P. (1979) Time constants of heating and cooling in the eastern water dragon, *Physignathus lesueurii* and some generalisations about heating and cooling in reptiles. *Journal of Thermal Biology* 4:95-103.

Groombridge, B. & Luxmoore, R. (1991) Pythons in South-east Asia. A review of distribution, status and trade in three selected species. Report to CITES Secretariat.

Hansteen, T.L., Andreassen, H.P. & Ims, R.M. (1997) Effects of spatiotemporal scale on autocorrelation and home range estimators. *Journal of Wildlife Management* 61:280-290.

Harlow, P.S. & Grigg, G. (1984) Shivering thermogenesis in a brooding diamond python, *Python spilotes spilotes*. *Copeia* 1984:959-965.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woolard, T. & Wray, S. (1990) Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of animals. *Mammal Review* 20:97-123.

Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.

Harvey, P.H. & Ralls, K. (1985) Homage to the null weasel. In: *Evolution: Essays in Honour of John Maynard Smith* (Ed. by P.J. Greenwood, P.H. Harvey & M. Slatkin), pp. 155-171. Cambridge University Press, Cambridge.

Heatwole, H.F. & Taylor, J. (1987) *Ecology of Reptiles*. Surrey Beatty & Sons, Sydney.

Hertz, P.E., Huey, R.B. & Stevenson, R.D. (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *American Naturalist* 142:796-818.

Heulin, B., Surget-Groba, Y., Guiller, A., Guillaume, C.P. & Deunff, J. (1999) Comparisons of mitochondrial DNA (mtDNA) sequences (16 rRNA gene) between oviparous and viviparous strains of *Lacerta vivipara*: a preliminary study. *Molecular Ecology* 8:1627-1631.

Huey, R.B. (1974) Behavioral thermoregulation in lizards: Importance of associated costs. *Science* 184:1001-1003.

Huey, R.B. (1982) *Temperature, Physiology and the Ecology of Reptiles*. Academic Press, London.

Huey, R. & Slatkin, M. (1976) Costs and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51:363-384.

Hutchison, V.H., Dowling, H.G. & Vinegar, A. (1966) Thermoregulation in a brooding female Indian python, *Python molurus bivittatus. Science* 151:694-696.

Jennich, R.I. & Turner, F.B. (1969) Measurements of non-circular home range. *Journal of Theoretical Biology* 22:227-237.

Johnson, C.R. (1972) Thermoregulation in pythons. I. Effect of shelter, substrate type and posture on body temperature of the Australian Carpet Python, *Morelia spilotes variegata*. *Comparative Biochemistry and Physiology* 43A:271-278.

Johnstone, R.E. & Storr, G.M. (1998) *Handbook of Western Australian Birds. Volume 1. Non-passerines*. Western Australian Museum, Perth.

Joy, J.E. & Crews, D. (1988) Male mating success in red-sided gartersnakes: size is not important. *Animal Behaviour* 36:1839-1841.

Keast, A. (1985) Bird community structure in southern forests and northern woodlands: a comparison. In: *Birds of Eucalypt Forests and Woodlands: Ecology, Conservation and Management* (Ed. by A. Keast, H.F. Recher, H. Ford & D. Saunders), pp. 97-116. Surrey Beatty & Sons, Chipping Norton.

Keighery, B., Gibson, N. & Keighery, G. (1997) *The Regional Significance of the Flora and Vegetation of Garden Island*. Proceedings of the Environment and Energy Conference, April 14 - 15, 1997. HMAS Stirling, Garden Island, Western Australia.

Kenward, R.E. & Hodder, K.H. (1995) *Ranges V: An Analysis System for Biological Location Data*. Institute of Terrestrial Ecology, Wareham, Dorset.

Kernohan, B.J., Gitzen, R.A. & Millspaugh, J.J. (2001) Analysis of animal space use and movements. In: *Radio-tracking and Animal Populations* (Ed. by J.J. Millspaugh & J.M. Marzluff), pp. 126-166. Academic Press, San Diego, California.

King, R.B. (1989a) Sexual dimorphism in snake tail length: sexual selection, natural selection or morphological constraint? *Biological Journal of the Linnean Society* 38:133-154.

King, R.B. (1989b) Body size variation among island and mainland snake populations. *Herpetologica* 45:84-88.

Leger, D.W. & Didrichson, I.A. (1994) An assessment of data pooling and some alternatives. *Animal Behaviour* 48:823-832.

Lovich, J.E. & Gibbons, J.W. (1992) A review of techniques for quantifying sexual size dimorphism. *Growth, Development and Aging* 56:269-281.

Luiselli, L. (1996) Individual success in mating balls of the grass snake, *Natrix natrix*: size is important. *Journal of Zoology* 239:731-740.

McArthur, W.M. (1957) Plant ecology of the coastal islands near Fremantle, W.A. *Journal of the Royal Society of Western Australia* 40:46-63.

McArthur, W.M. (1966) *The Effects of Fire on the Vegetation of Garden Island, Western Australia, and the Impact of Grazing Tammars* (Macropus eugenii) *on Subsequent Regeneration*. HMAS Stirling Environmental Working Paper 10, Department of Defence.

McArthur, W.M. & Bartle, G.A. (1981) *The Landforms, Soils and Vegetation as a Basis of Management of Garden Island*. CSIRO Division of Land Resource Management Service Bulletin No. 7, Perth.

McCartney, J.M., Gregory, P.T. & Larsen, K.W. (1988) A tabular survey of data on movements and home ranges of snakes. *Journal of Herpetology* 22:61-73.

Madsen, T. (1984) Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in southern Sweden. *Copeia* 1984:707-713.

Madsen, T. & Shine, R. (1993a) Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution* 47:321-325.

Madsen, T. & Shine, R. (1993b) Temporal variability in sexual selection on reproductive tactics and body size in male snakes. *American Naturalist* 141:167-171.

Madsen, T. & Shine, R. (1994) Costs of reproduction influence the evolution of sexual size dimorphism in snakes. *Evolution* 48:1389-1397.

Madsen, T. & Shine, R. (1996) Seasonal migration of predators and prey - a study of pythons and rats in tropical Australia. *Ecology* 77:149-156.

Madsen, T.R.L. & Shine, R. (1999) Life-history consequences of nest-site variation in tropical pythons. *Ecology* 80:989-997.

Madsen, T. & Shine, R. (2000) Energy versus risk: costs of reproduction in free-ranging pythons in tropical Australia. *Austral Ecology* 25:670-675.

Madsen, T., Shine, R., Loman, J. & Håkansson, T. (1993) Determinants of mating success in male adders, *Vipera berus*. *Animal Behaviour* 45:491-499.

Main, A.R. (1961) The occurrence of Macropodidae on islands and its ecological and climatic implications. *Journal of the Royal Society of Western Australia* 44:84-89.

Marchant, N.G. & Abbott, I. (1981) Historical and recent observations of the flora of Garden Island, Western Australia. *Western Australian Herbarium Research Notes* 5:49-62.

Marty, G.D. & Summerfelt, R.C. (1986) Pathways and mechanisms for expulsion of surgically implanted dummy transmitters in channel catfish. *Transactions of the American Fisheries Society* 115:577-589.

Maryan, B. (1994) The Western Australian Carpet Python (*Morelia spilota imbricata*): how little we know about it. *Herpetofauna* 24:30-32.

Mohr, C.O. (1947) Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37:223-449.

Mushinsky, H.R. (1987) Foraging ecology. In: *Snakes: Ecology and Evolutionary Biology* (Ed. by R.A. Seigel, N.B. Ford & S.S. Novak), pp. 302-334. Macmillan, New York.

Otis, D.L. & White, G.C. (1999) Autocorrelation of location estimates and the analysis of radio-tracking data. *Journal of Wildlife Management* 63:1039-1044.

Parker, G.A. (1984) Sperm competition and the evolution of animal mating strategies. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R.L. Smith), pp. 1-60. Academic Press, Orlando, Florida.

Pearson, D.J. (1993) Distribution, status and conservation of pythons in Western Australia. In: *Herpetology in Australia: A Diverse Discipline* (Ed. by D. Lunney & D. Ayers), pp. 393-395. Royal Zoological Society of New South Wales, Sydney.

Pearson, D.J. & Shine, R. (2002) Expulsion of interperitoneally-implanted radiotransmitters by Australian pythons. *Herpetological Review,* in press.

Pearson, D., Shine, R. & Williams, A. & How, R. (2002a) Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*). *Biological Journal of the Linnean Society,* in press.

Pearson, D., Shine, R. & Williams, A. (2002b) Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia (Berlin),* in press.

See addendum

Powell, R.A. (2000) Animal home ranges and territories and home range estimators. In: *Research Techniques in Animal Ecology: Controversies and Consequences* (Ed. by L. Boitani & T.K. Fuller), pp. 66-110. Columbia University Press, New York.

Reed, R.N. & Shine, R. (2002) Lying in wait for extinction? Ecological correlates of conservation status among Australian elapid snakes. *Conservation Biology*, in press.

Reinert, H.K. (1992) Radiotelemetric field studies of pitvipers: data acquisition and analysis. In: *Biology of the Pitvipers* (Ed. by J.A. Campbell & E.D.J. Brodie), pp. 185-197. Selva, Tyler, Texas.

Reinert, H.K. & Cundall, D. (1982) An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702-705.

Roark, A.W. & Dorcas, M.E. (2000) Regional body temperature variation in corn snakes measured using temperature-sensitive passive integrated transponders. *Journal of Herpetology* 34:481-485.

Robinson, A., Canty, P., Mooney, T. & Ruddock, P. (1996) *South Australia's Offshore Islands*. Australian Heritage Commission, Canberra.

SAS Institute. (1998) *Statview 5*. SAS Institute, Cary, Indiana.

Saunders, D.A. (1979) The availability of tree hollows for use as nest sites by white-tailed black cockatoos. *Wildlife Research* 6:205-216.

Schuett, G.W. & Gillingham, J.C. (1989) Male-male agonistic behaviour of the copperhead, *Agkistrodon contortrix*. *Amphibia-Reptilia* 10:243-266.

Schwaner, T., Francis, M. & Harvey, C. (1988) Identification and conservation of carpet pythons (*Morelia spilota imbricata*) on St Francis Island, South Australia. *Herpetofauna* 18:13-20.

Schwaner, T.D. & Sarre, S.D. (1988) Body size of tiger snakes in southern Australia, with particular reference to *Notechis ater serventyi* (Elapidae) on Chappell Island. *Journal of Herpetology* 22:24-33.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. (1999) Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739-747.

Seaman, D.E. & Powell, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075-2085.

Secor, S.M. (1994) Ecological significance of movements and activity range of the Sidewinder, *Crotalus cerastes. Copeia* 1994:631-645.

Secor, S.M. & Diamond, J. (1995) Adaptive responses to feeding in Burmese pythons: pay before pumping. *Journal of Experimental Biology* 198:1315-1325.

Secor, S.M. & Diamond, J. (1997) Effects of meal size on postprandial responses in juvenile Burmese pythons (*Python molurus*). *American Journal of Physiology* 272:R902-R912.

Seebacher, F., Grigg, G.C. & Beard, L.A. (1999) Crocodiles as dinosaurs: behavioural thermoregulation in very large ectotherms leads to high and stable body temperatures. *Journal of Experimental Biology* 202:77-86.

Seigel, R.A. & Ford, N.B. (1987) Reproductive ecology. In: *Snakes: Ecology and Evolutionary Biology* (Ed. by R.A. Seigel, J.T. Collins & S.S. Novak), pp. 210-252. McGraw-Hill, New York.

Semlitsch, R.D. & Gibbons, J.W. (1982) Body size dimorphism and sexual selection in two species of water snakes. *Copeia* 1982:974-976.

Shine, R. (1986) Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae. Oecologia* 69:260-267.

Shine, R. (1987) Intraspecific variation in thermoregulation, movements and habitat use by Australian blacksnakes, *Pseudechis porphyriacus* (Elapidae). *Journal of Herpetology* 21:165-177.

Shine, R. (1988) Parental care in reptiles. In: *Biology of the Reptilia, Volume 16* (Ed. by C. Gans & R.B. Huey), pp. 275-330. Alan R. Liss, New York.

Shine, R. (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* 64:419-461.

Shine, R. (1991a) Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* 138:103-122.

Shine, R. (1991b) *Australian Snakes. A Natural History*. Reed Books, Sydney.

Shine, R. (1994a) Sexual size dimorphism in snakes revisited. *Copeia* 1994:326-346.

Shine, R. (1994b) *The Biology and Management of Diamond Pythons (*Morelia s. spilota*) and Carpet Pythons (*M. s. variegata*)*. Species Management Report, New South Wales National Parks and Wildlife Service, Sydney.

Shine, R., Ambariyanto, Harlow, P.S. & Mumpuni (1999a) Reticulated pythons in Sumatra: biology, harvesting and sustainability. *Biological Conservation* 87:349-357.

Shine, R., Ambariyanto, Harlow, P.S. & Mumpuni. (1999b) Ecological attributes of two commercially-harvested python species in northern Sumatra. *Journal of Herpetology* 33:249-257.

Shine, R. & Bonnet, X. (2000) Snakes: a new "model organism" in ecological research? *Trends in Ecology and Evolution* 15:221-222.

Shine, R. & 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.

Shine, R. & Fitzgerald, M. (1996) Large snakes in a mosaic rural landscape: the ecology of carpet pythons, *Morelia spilota* (Serpentes: Pythonidae) in coastal eastern Australia. *Biological Conservation* 76:113-122.

Shine, R., Harlow, P., Keogh, J.S. & Boeadi. (1995) Biology and commercial utilization of acrochordid snakes, with special reference to karung (*Acrochordus javanicus*). *Journal of Herpetology* 29:352-360.

Shine, R. & Madsen, T. (1996) Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiological Zoology* 69:252-269.

Shine, R., Madsen, T., Elphick, M. & Harlow, P. (1996) The influence of nest temperatures and maternal thermogenesis on hatchling phenotypes of water pythons. *Ecology* 78:1713-1721.

Shine, R., Olsson, M.M., Moore, I., Le Master, M.P., Greene, M. & Mason, R.T. (2000) Body size enhances mating success in male gartersnakes. *Animal Behaviour* 59:F4-F11.

Slatkin, M. (1984) Ecological causes of sexual dimorphism. *Evolution* 38:622-630.

Slip, D.J. & Shine, R. (1988a) The reproductive biology and mating system of diamond pythons, *Morelia spilota* (Serpentes, Boidae). *Herpetologica* 44:396-404.

Slip, D.J. & Shine, R. (1988b) Thermophilic response to feeding of the diamond python, *Morelia s. spilota* (Serpentes, Boidae). *Comparative Biochemistry and Physiology* 89A:645-650.

Slip, D.J. & Shine, R. (1988c) Feeding habits of the diamond python, *Morelia s. spilota*: ambush predation by a boid snake. *Journal of Herpetology* 22:323-330.

Slip, D.J. & Shine, R. (1988d). Habitat use, movements and activity patterns of free-ranging diamond pythons, *Morelia s. spilota* (Serpentes: Boidae): a radiotelemetric study. *Wildlife Research* 15:515-531.

Slip, D.J. & Shine, R. (1988e) Thermoregulation of free-ranging diamond pythons, *Morelia spilota* (Serpentes, Boidae). *Copeia* 1988:984-995.

Slip, D.J. & Shine, R. (1988f) Reptilian endothermy: a field study of thermoregulation by brooding diamond pythons. *Journal of Zoology (London)* 216:367-378.

Smith, L.A. (1981) A revision of the python genera *Aspidites* and *Python* (Serpentes: Boidae) in Western Australia. *Records of the Western Australian Museum* 9:211-226.

Smith, L.A. & Johnstone, R.E. (1996) Biogeography of the herpetofauna of the Archipelago of the Recherche, Western Australia. *Journal of the Royal Society of Western Australia* 79:165-173.

Smith, M.J. (1983) Tamar Wallaby In: *The Australian Museum Complete Book of Mammals* (Ed. By R. Strahan), pp. 232-233. Angus & Robertson, Sydney.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry, 2nd Edition.* WH Freeman & Co., New York.

Spellerberg, I.F. (1977) Marking live snakes for identification of individuals in population studies. *Journal of Applied Ecology* 14:137-138.

Stamps, J.A. (1983) Sexual selection, sexual dimorphism, and territoriality. In: *Lizard Ecology: Studies of a Model Organism* (Ed. by R.B. Huey, E.R. Pianka & T.W. Schoener), pp. 169-204. Cambridge University Press, Massachusetts.

Swihart, R.K. & Slade, N.A. (1985a) Testing for independence of observations in animal movements. *Ecology* 66:1176-1184.

Swihart, R.K. & Slade, N.A. (1985b) Influence of sampling interval on estimates of home range size. *Journal of Wildlife Management* 49:1019-1025.

Temeles, E.J., Pan, I.L., Brennan, J.L. & Horwitt, J.N. (2000) Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science* 289:441-443.

Torr, G.A. (2000) *Pythons of Australia: A Natural History*. University of New South Wales Press, Sydney.

Trivers, R.L. (1976) Sexual selection and resource-accruing abilities in *Anolis garmani*. *Evolution* 30:253-269.

Van Mierop, L.H.S. & Barnard, S.M. (1976) Thermoregulation in a brooding female *Python molurus bivittatus* (Serpentes: Boidae). *Copeia* 1976:398-401.

Van Mierop, L.H.S. & Barnard, S.M. (1978) Further observations on thermoregulation in the brooding female *Python molurus bivittatus* (Serpentes: Boidae). *Copeia* 1978:615-621.

Weatherhead, P.J., Barry, F.E., Brown, G.P. & Forbes M.R.L. (1995) Sex ratios, mating behavior and sexual size dimorphism of the northern water snake, *Nerodia sipedon*. *Behavioral Ecology and Sociobiology* 36:301-311.

Weatherhead, P.J. & Hoysak, D.J. (1989) Spatial and activity patterns of black rat snakes (*Elaphe obsoleta*) from radiotelemetry and recapture data. *Canadian Journal of Zoology* 67:463-468.

Webb, G. & Heatwole, H. (1971) Patterns of heat distribution within the bodies of some Australian pythons. *Copeia* 1971:209-220.

Webb, J.K. & Shine, R. (1998) Ecological characteristics of a threatened snake species, *Hoplocephalus bungaroides* (Serpentes, Elapidae). *Animal Conservation* 1:185-193.

White, G.C. & Garrott, R.A. (1990) *Analysis of Radio-tracking Data*. Academic Press, San Diego, California.

Wilenski, M. & Thom, C. (2000) Marine iguanas shrink to save El Nino. *Nature* 403:37-38.

Wilson, S.K. & Knowles, D.G. (1988) *Australia's Reptiles*. Collins, Sydney.

Worton, B.J. (1987) A review of models of home range for animal movement. *Ecological Modelling* 38:277-298.

Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home range studies. *Ecology* 70:164-168.

Worton, B.J. (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794-800.

Wykes, B.J., Pearson, D.J. & Maher, J. (1999) *Fauna Survey of Garden Island, Western Australia 1996-1997*. HMAS Stirling Environmental Working Paper 12, Department of Defence.