Thermal biology of large snakes in cool climates: a radio-telemetric study of carpet pythons (*Morelia spilota imbricata*) in south-western Australia

David Pearson[a], Richard Shine[b,*], Andrew Williams[a]

[a] *Department of Conservation and Land Management, P.O. Box 51, Wanneroo, WA 6946, Australia*
[b] *School of Biological Sciences A08, University of Sydney, Sydney NSW 2006, 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 our 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 8-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.
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1. 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 and Madsen, 1996). For terrestrial reptiles in cooler and more variable climates, however, thermoregulation may be a critical facet of day-to-day existence (Bennett and 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 and Slatkin, 1976; Avery, 1982; Huey, 1982; Heatwole and 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 heating rates 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.

*Corresponding author. Tel.: +61-2-9351-3772; fax: +61-2-9351-5609.

E-mail address: rics@bio.usyd.edu.au (R. Shine).

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, then, 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 diamond pythons (*Morelia spilota spilota*) in eastern Australia indicate that adults of this taxon rely upon single long basking periods rather than the shuttling heliothermy of smaller reptiles; and thus, that large pythons display relatively smooth unimodal thermal profiles rather than an extended plateau that would result from shuttling between sun and shade (Slip and Shine, 1988c).

(ii) *Behavioural control over rates of heat exchange:* The ratio of surface area to volume will determine 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 and Shine, 1997). This effect might 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 and 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 and Dawson, 1976; Ellis and Chappell, 1987). Additionally, they downregulate ''unnecessary'' functions (such as digestive tract activity) during non-feeding periods (Secor and Diamond, 1995, 1997). Activity at relatively low body temperatures (Cogger and Holmes, 1960; Slip and Shine, 1988c) 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 and Barnard, 1978; Harlow and Grigg, 1984; Slip and Shine, 1988a; Bedford, 1996; Shine et al., 1996). Most studies on this topic have used captive snakes, but Slip and Shine (1988a, b, c) examined several brooding females as well as non-reproductive diamond pythons (*M. s. 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 and Grigg, 1984; Slip and Shine, 1988a).

Although diamond pythons have attracted intensive study, other subspecies of this wide-ranging taxon have attracted much less attention. We undertook a radio-telemetry study of two populations of the southwestern carpet python (*Morelia spilota imbricata*) in Western Australia. This subspecies grows larger and is more sexually dimorphic than diamond pythons, and occurs over a wider geographic area with correspondingly greater climatic diversity (Pearson et al., 2002a, b). Over a 5-year period, we 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.

2. Materials and methods

2.1. Study animal and study sites

Australian carpet pythons (*M. spilota*) are large non-venomous 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 and Barker, 1994). The southwestern 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 (Pearson et al., 2002a, b). *M. s. imbricata* displays strong sexual dimorphism, with females attaining much larger sizes than males (Pearson et al., 2002a, b).

We radio-tracked 70 of these pythons 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 1200 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 *Callitris priessii* and *Melaleuca lanceolata*, and other low shrublands (Pearson et al., 2002b). 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 (Pearson et al., 2002b).

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 (Pearson et al., 2002b; Figs. 1 and 2). Dryandra is approximately 125 km inland and experiences much greater daily and seasonal temperature variation, including subzero 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 3 months over winter (Pearson, 2002). 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 (Pearson, 2002).

2.2. Transmitter implantation

Four types of temperature-sensitive transmitters (Holohil Systems Ltd., Canada) were used depending on the size of the python to be implanted. Pearson and Shine (2002) provide details on the units that we used, the methods of implantation, and the duration of radio-tracking. Transmitters were calibrated using a waterbath and circulating heater (Thermoline, Australia) against a
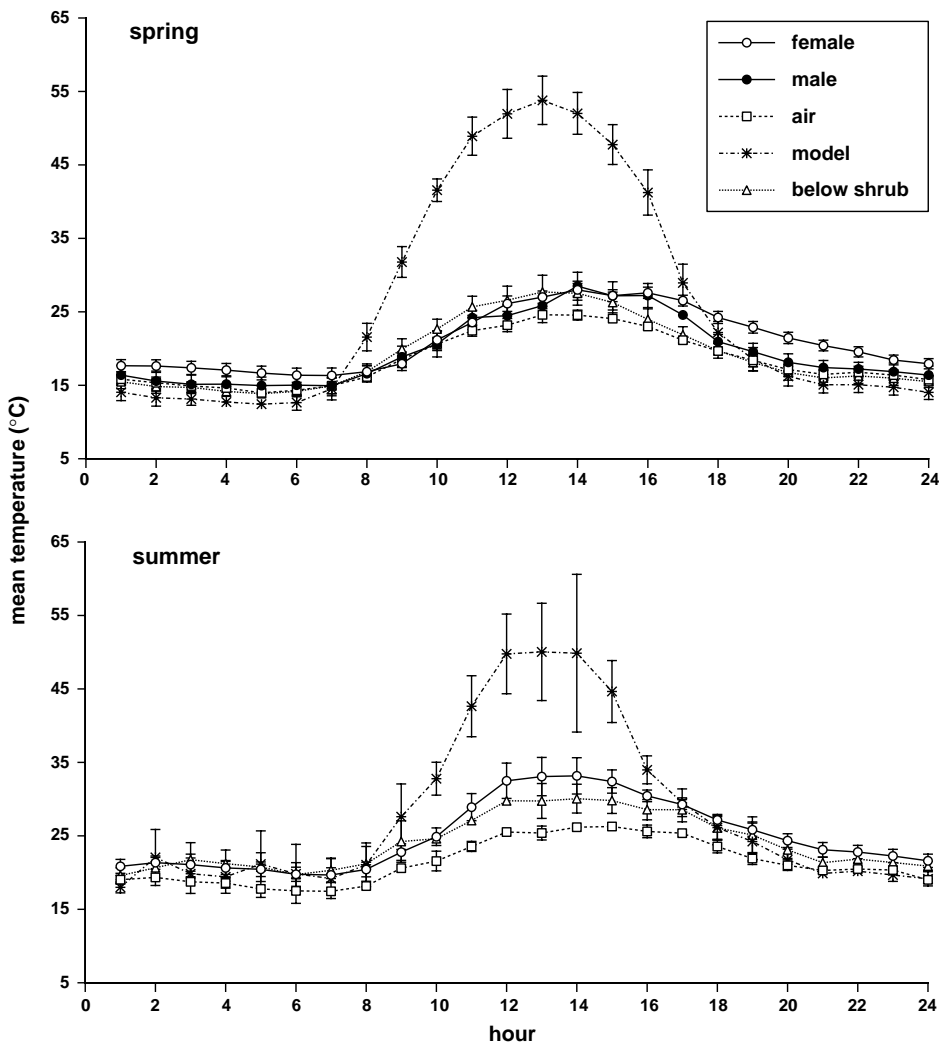

Fig. 1. Mean values, and associated standard errors, for ambient temperatures and body temperatures of radio-tracked carpet pythons on Garden Island during spring (a) and summer (b). These data were obtained using an automated system to receive telemetry signals and data from environmental probes. See text for explanation of symbols, definition of seasons and statistical analyses.
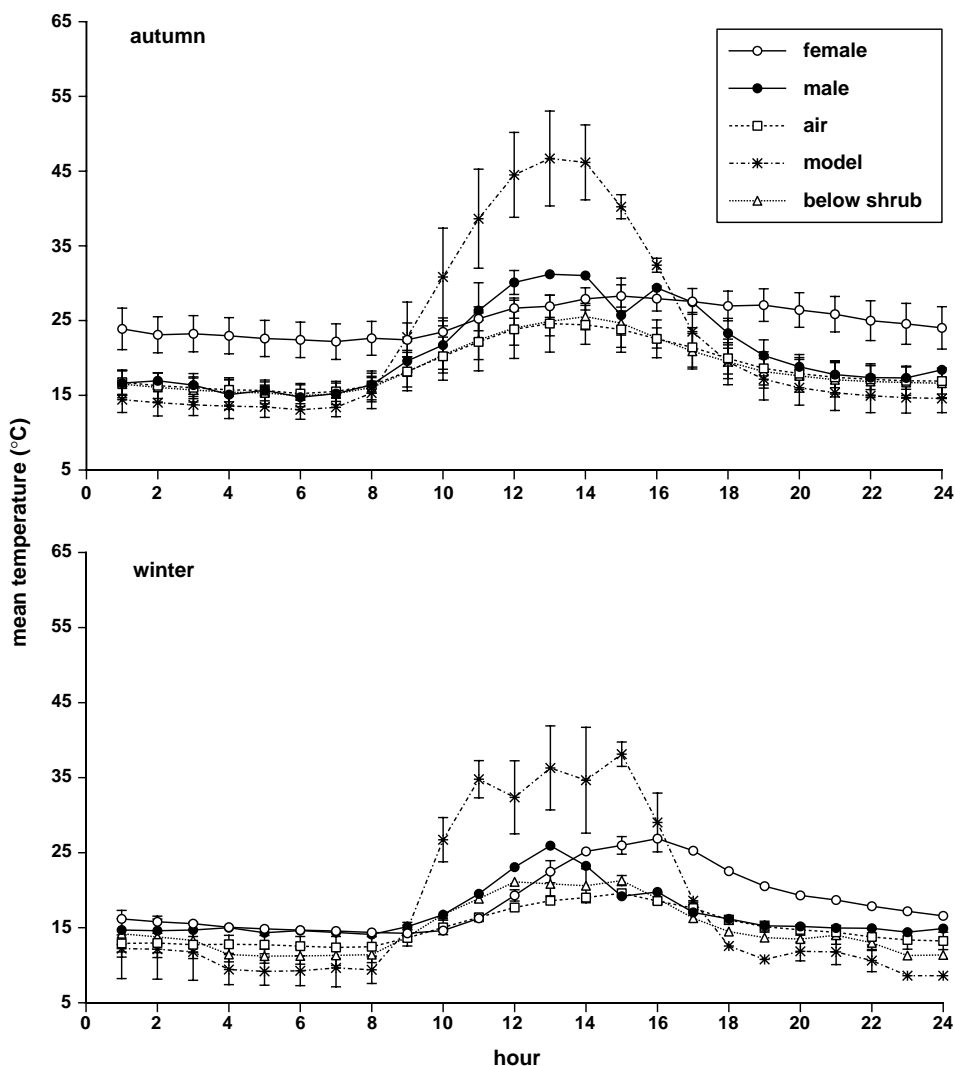
Fig. 2. Mean values, and associated standard errors, for ambient temperatures and body temperatures of radio-tracked carpet pythons on Garden Island during autumn (a) and winter (b). These data were obtained using an automated system to receive telemetry signals and data from environmental probes. See text for explanation of symbols, definition of seasons and statistical analyses.

certified mercury bulb thermometer ($\pm 0.1^{\circ}$C). Temperature was increased by 5°C increments from 5°C to 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 when pythons were located during fieldwork. Body temperatures of snakes were determined by applying third order polynomial equations derived from calibration data (mean $r^2 = 0.998$, range 0.994–1.0). 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 $>1^{\circ}$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 three element Yagi aerial (Sirtrack, New Zealand). Because carpet pythons typically did not flee from our 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. We defined a snake to be in "ambush posture" if its neck

was bent into a tight "s-shape" in readiness to strike with the head and body held immobile. 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 a week in the first 2 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 1998 and then sporadically in 1998 and 1999, mostly to record temperatures of incubating female pythons. We collected data for 7–20 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 V 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 min.

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 over-wintering 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 we 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. We used the software program SuperANO-VA (AbacusConcepts, 1991) for these calculations. We then divided the year into four biologically relevant seasons. Spring was defined as September 1–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 August 31. We 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 and Didrichson, 1994) without the problems of statistical non-independence.

3. Results

3.1. 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-2 T 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-telemetered snakes, plus 858 hourly mean values for associated environmental temperatures. Because these records span the entire 24 h diel cycle, they provide the most robust basis from which to identify general patterns in snake thermal biology. We 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 we measured pulse intervals (and thus, could estimate body temperatures) whenever a radio-telemetered snake was located, we also have an extensive dataset 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.

3.2. General patterns at Garden Island

Ambient temperatures displayed marked seasonal variation at Garden Island (Figs. 1 and 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 >7 h in summer (typically reaching $>50°C$: Fig. 2). Air temperatures averaged around $15°C$ in winter to $25°C$ in summer (Figs. 1 and 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. 1 and 2).

Body temperatures of the radio-tracked pythons also showed substantial diel and seasonal variation (Figs. 1 and 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 males during the morning, but also cooled more slowly than males during the afternoon and evening (Figs. 1 and 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. 2; females higher for 19 of 25 hourly means, against a null of 50%, $\chi_1^2 = 6.76$, $P < 0.05$). 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).

We also calculated patterns of hourly variation in body temperatures and associated ambient temperatures from the automated records. Figs. 3 and 4 show that in warmer months (spring through autumn), the snakes were generally less variable thermally than the environmental temperatures that we 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 we 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. 3).

3.3. Effects of location and sex on body temperature

The records of pulse interval taken when we located radio-tracked snakes provided an extensive data set with which to compare male and female snakes at 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. 5) and males (Fig. 6), body temperatures were typically about 2–5°C lower at Dryandra than at Garden Island ($F_{13,842} = 180.3$, $P < 0.0001$). Ambient temperatures measured at the same time revealed the same pattern: mean air temperatures were higher at Garden Island than Dryandra for spring ($20.9°C$ vs $19.8°C$), autumn ($21.4°C$ vs $19.3°C$) and winter ($16.6°C$ vs $13.7°C$), but in summer mean temperatures were very similar ($25.6°C$ vs $25.8°C$; location effect, $F_{13,824} = 86.62$, $P < 0.0001$).

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). 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, $F_{33,824} = 20.08$, $P < 0.0001$; on body temperatures, $F_{33,836} = 11.66$, $P < 0.0001$).

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 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 ($\chi_1^2 = 0.44$, $P = 0.51$). 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, $= 29\%$; $\chi_1^2 = 30.65$, $P < 0.0001$). Why should
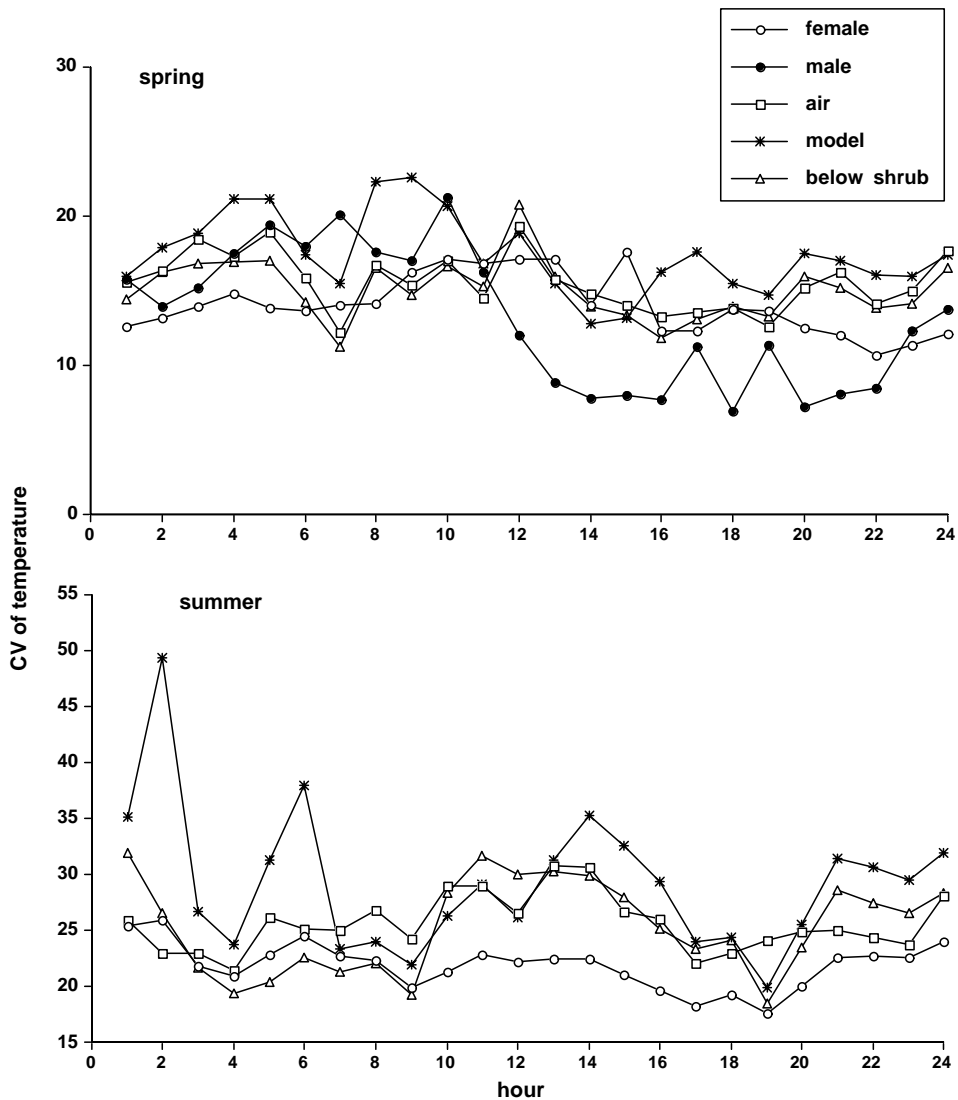
Fig. 3. Mean values, and associated standard errors, for the coefficient of variation in ambient temperatures and body temperatures of radio-tracked carpet pythons on Garden Island during spring (a) and summer (b). These data were obtained using an automated system to receive telemetry signals and data from environmental probes. See text for explanation of symbols, definition of seasons and statistical analyses.

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 (Pearson et al., 2002a), 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 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%, $\chi_1^2 = 155.48$, $P < 0.0001$; for Dryandra, 12% vs 3%, $\chi_1^2 = 9.97$, $P < 0.002$). Thus, one reason for lower basking frequencies in male pythons, especially on Garden Island, was their more frequent adoption of ambush poses.

3.4. 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
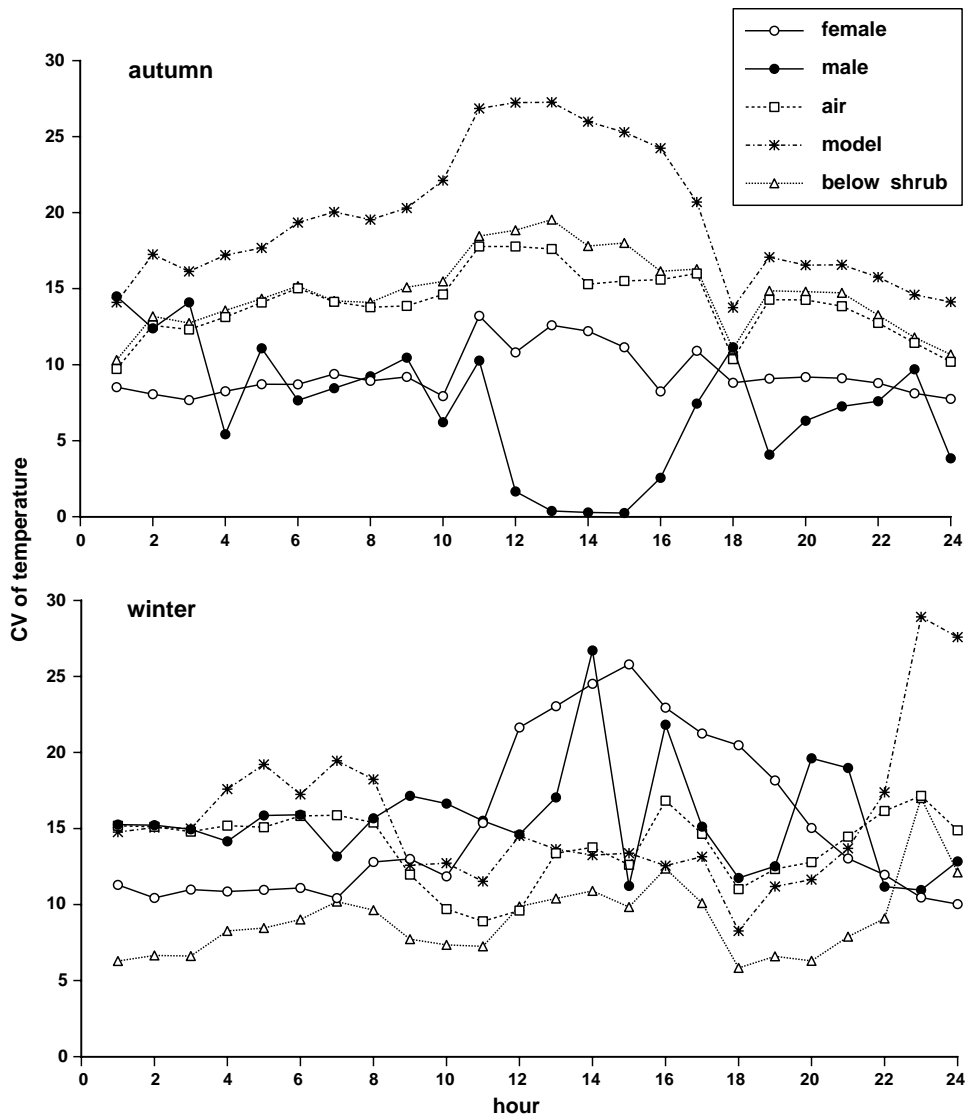
Fig. 4. Mean values, and associated standard errors, for the coefficient of variation in ambient temperatures and body temperatures of radio-tracked carpet pythons on Garden Island during autumn (a) and winter (b). These data were obtained using an automated system to receive telemetry signals and data from environmental probes. See text for explanation of symbols, definition of seasons and statistical analyses.

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.

3.5. 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 and Shine, 1988c; Ayers and Shine, 1997). To investigate this
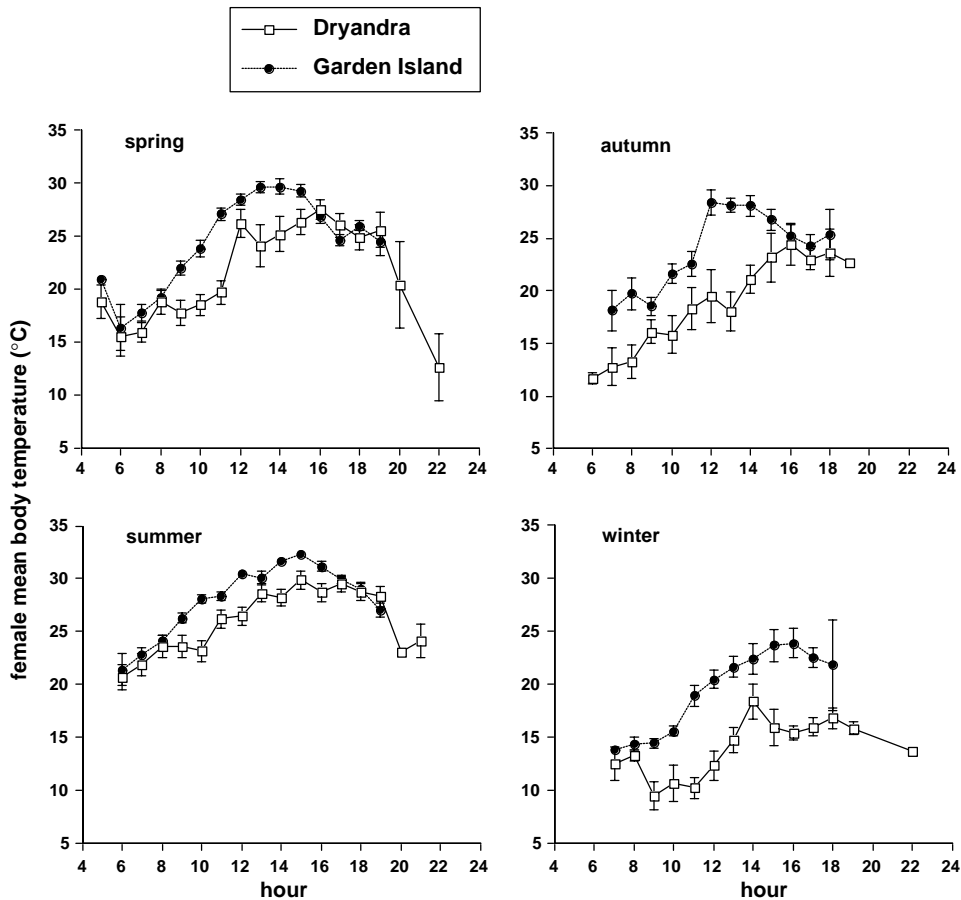
Fig. 5. Body temperatures of female carpet pythons at two study areas and during four seasons. These data were obtained by recording pulse intervals from telemetry signals whenever a radio-tracked snake was located in the field.

possibility, we examined the body temperatures of snakes found in this posture compared to others. Because location and sex also influence body temperatures in this species, we 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 post-hoc PLSD tests, all comparisons have $P < 0.05$). When these data were analysed separately by season, we 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.

3.6. Overwinter body temperatures in relation to shelter sites

Fig. 7 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
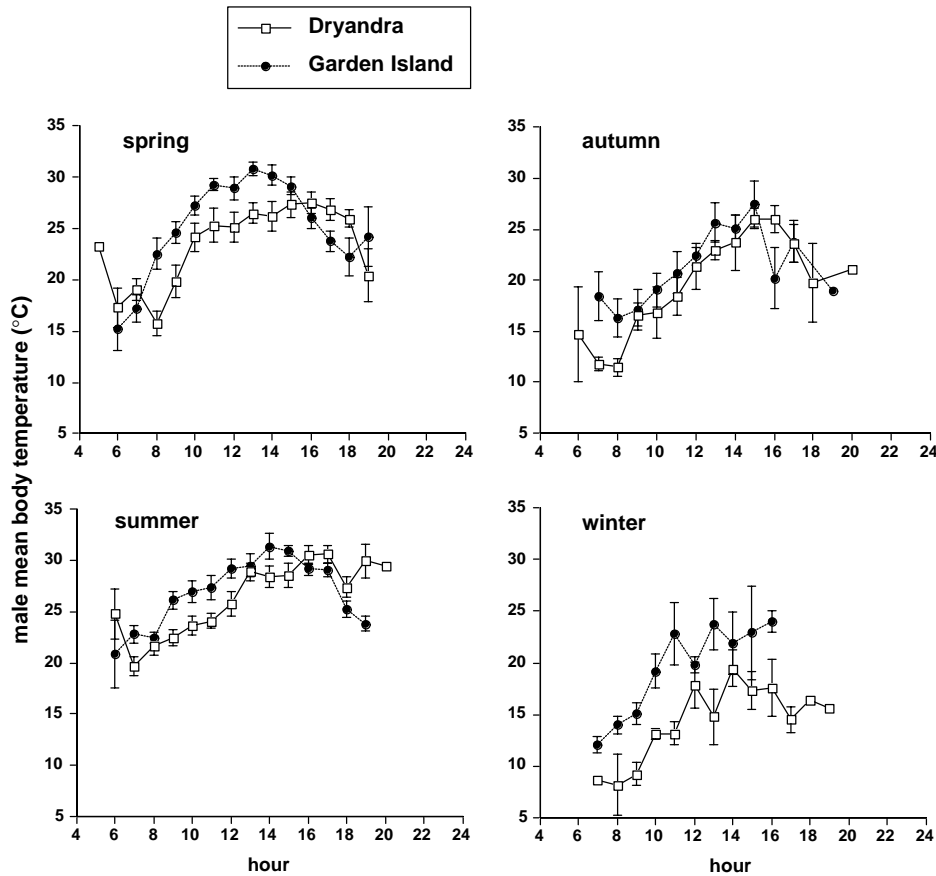
Fig. 6. Body temperatures of male carpet pythons at two study areas and during four seasons. These data were obtained by recording pulse intervals from telemetry signals whenever a radio-tracked snake was located in the field.

above ground, respectively, displayed more variable body temperatures. However, they 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 we 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.

3.7. 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. 8). For example, Fig. 8a 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. 8a).

South-western carpet pythons use a range of micro-habitats as nesting sites, and these sites may differ substantially in the degree of thermal buffering available to the python and her clutch. Fig. 8b 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 are shown in Fig. 8c. 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 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 recommence shivering thermogenesis.
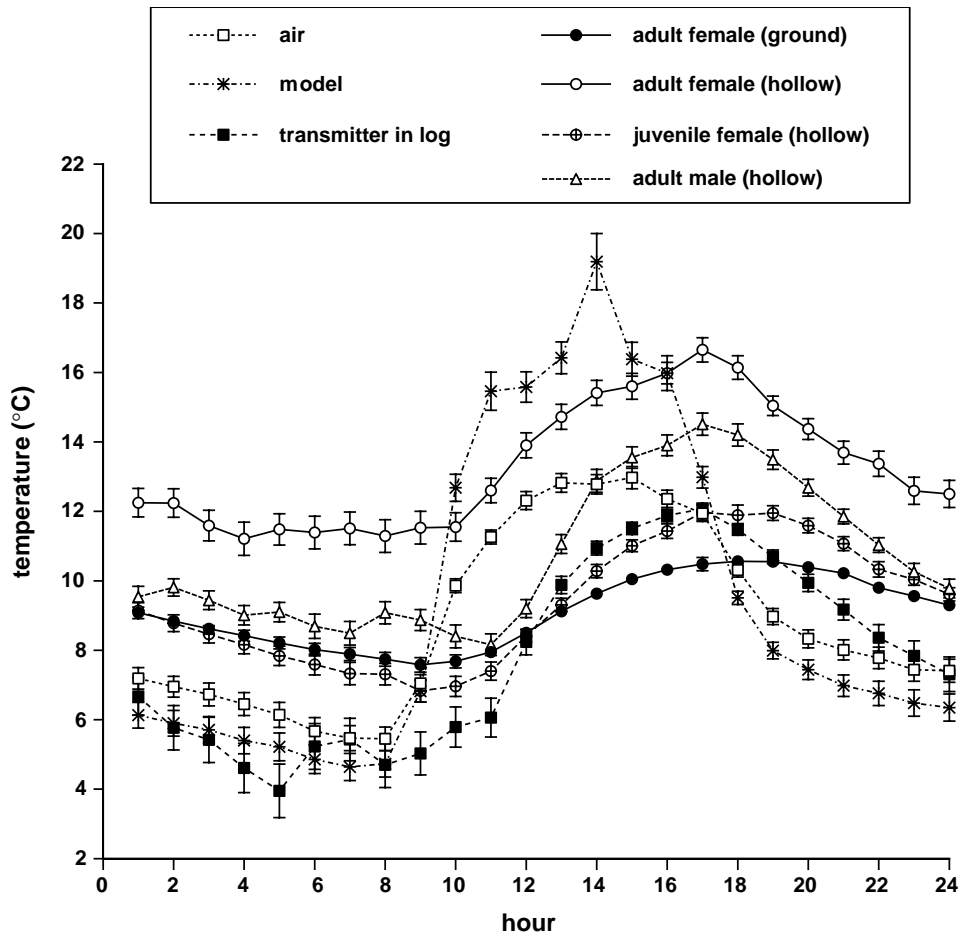
Fig. 7. Body temperatures of radio-tracked carpet pythons and associated environmental temperatures recorded over an 18-day period in Dryandra Woodland during winter (June–July 1998). The graphs show hourly means and associated standard errors for each snake or environmental probe.

4. Discussion

The extensive data set from radio-telemetric monitoring of 70 snakes over 5 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 we did not conduct such a study, previous work on the same species has documented mean selected temperatures of 29–32°C (Cogger and Holmes, 1960; Webb and Heatwole, 1971; Johnson, 1972; Slip and Shine, 1988a, c; Bedford and Christian, 1998), increasing slightly after feeding (Slip and 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. 1 and 2). Thus, in strong contrast to tropical pythons (Shine and Madsen, 1996), the radio-tracked snakes in our 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, we examine some of the factors that generated that variation in body temperatures:

(i) *Season*: Mean body temperatures during daylight hours (arbitrarily, 0700–1800 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
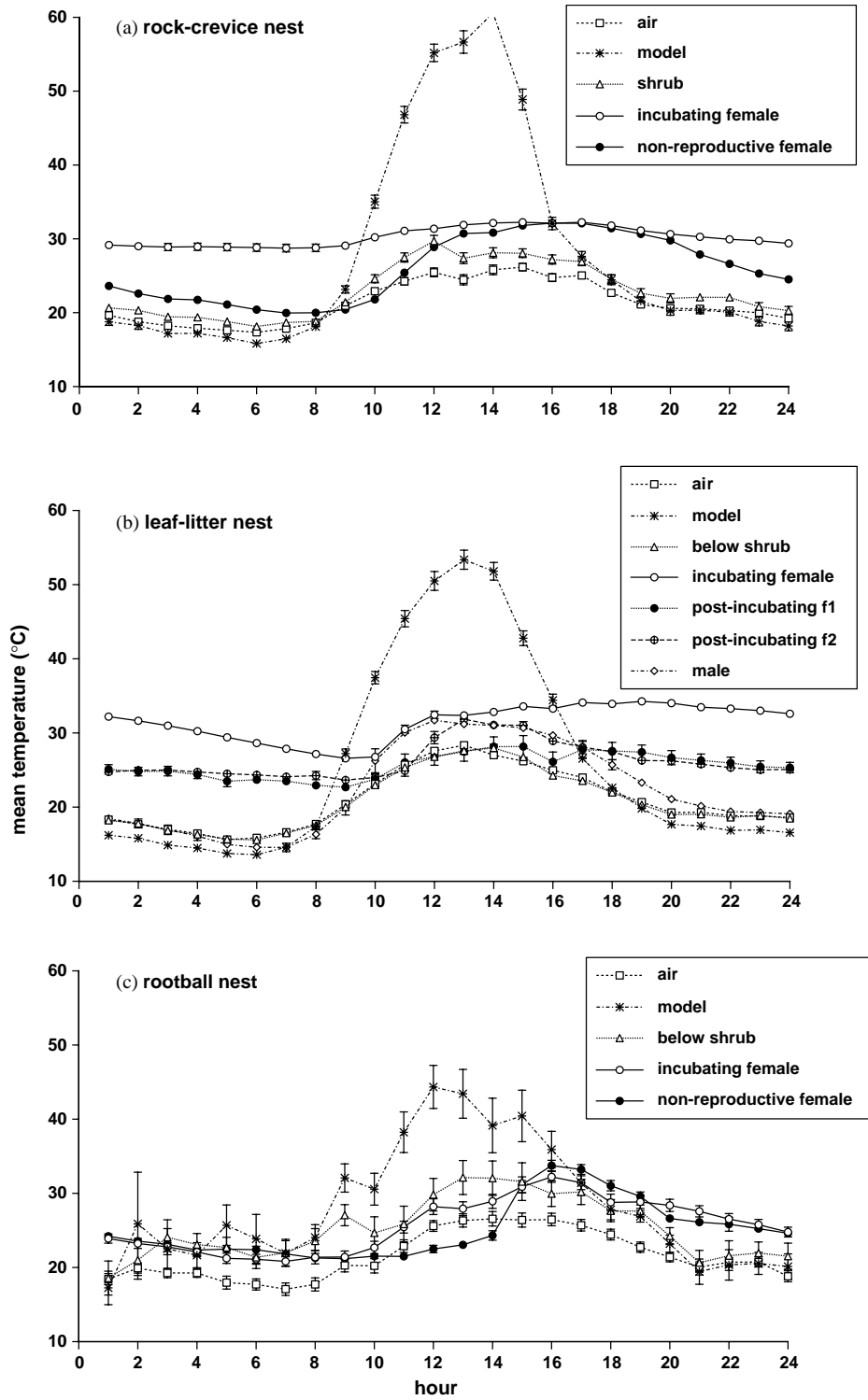
temperature were 26.0°C in summer, 20.8°C in spring, 20.5°C in autumn and 15.6°C in winter.

(ii) *Time of day*: Strong diel rhythms in body temperature were evident in both study sites and in all seasons (Figs. 3 and 4). Unsurprisingly, snake body temperatures fell during the night and increased during the day (Figs. 1 and 2). This diel pattern reflects temporal shifts in ambient temperatures but 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 thus resulted from the snake's 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 temperature were similar at the two study areas, snakes at Garden Island were consistently a few degrees warmer than were those at Dryandra (Figs. 5 and 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). 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*: We cannot easily separate these two factors, because most of the "small" (<1 kg) snakes in our 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). Juveniles may bask to increase growth rates (Lillywhite et al., 1973). Part of the sex 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 Pearson et al., 2002b).

Overall, the two sexes displayed relatively similar body temperatures (e.g. Figs. 1 and 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. 1 and 2). This effect may well be biologically significant. For example, Fig. 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 and 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 and 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 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. This factor also interacts in a complex way with other features of the animal's biology: for example, male

Fig. 8. Body temperatures of radio-tracked carpet pythons and associated environmental temperatures, showing the differences between female pythons that were incubating their eggs compared to other non-brooding pythons monitored by an automatic recording system over the same period and in the same general location. The graphs show hourly means and associated standard errors for each snake or environmental probe. The three graphs show data for females incubating their eggs in different microhabitats. The upper graph (a) shows data from Garden Island over the period February 22–March 29, 1999; with plots of thermal data for an incubating female in a crevice in a cliff, a free-ranging non-reproductive adult female and environmental probes. The middle graph (b) shows data from Garden Island over the period 9–31 March 1998, with plots of thermal data for a female incubating in a "nest" under leaf litter and shrub cover, plus data for two non-reproductive (post-incubation) females, a male snake and environmental probes. The lower graph (c) shows data for Garden Island over the period 23 February–19 March 1998, with plots of thermal data for a female incubating under the rootball of a fallen tree, plus data for a non-reproductive adult female and environmental probes.

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 our study areas: see Figs. 1a, b and Figs. 2a, b), a snake's selection of habitats will almost inevitably influence its body temperature regimes. The most obvious example of this phenomenon in our 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. 7). 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 over-wintering, 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. 8). As in previous studies of incubating diamond pythons in eastern Australia (Slip and Shine, 1988a), the brooding females maintained remarkably high, stable tempera-tures for long periods of time. Also in accord with previous work (Slip and Shine, 1988a; Madsen and Shine, 1999), natural nest sites appear to vary signifi-cantly 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 and Fitzgerald, 1996), as well as increasing the metabolic costs of shivering thermogen-esis, and exposing the eggs to lower and more variable temperatures (Fig. 8). 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, we found recently sloughed skins of large females and old egg shells from freshly excavated nest sites at this site.

In summary, our 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, dietary habits and movement patterns (Pearson et al., 2002a, b; Pearson, 2002)—the overall impression from our 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.

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