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Does body size influence thermal biology and diet of a python 
(Morelia spilota imbricata)?

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FLEMING¹

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Abstract

Current theory predicts that larger-bodied snakes not only consume larger prey (compared 
with smaller individuals), but may also have a different range of prey available to them due to 
their thermal biology. It has been argued that smaller individuals, with lower thermal inertia 
(i.e. faster cooling rates at nightfall when air temperature falls and basking opportunities are 
limited), may be thermally restricted to foraging and hunting during the day on diurnally 
active prey, and have reduced capacity to hunt crepuscular and nocturnal prey species. This 
predictive theory was investigated by way of dietary analysis, assessment of thermal biology
and thermoregulation behaviour in an ambush forager, the south-west carpet python (Morelia spilota imbricata, Pythonidae). Eighty-seven scats were collected from 34 individual pythons over a 3-year radiotelemetry monitoring study. As predicted by gape size limitation, larger pythons took larger prey; however, 65% of prey items of small pythons were represented by nocturnally active, small mammals, a larger proportion than present in larger snakes. Several measures of thermal biology (absolute body temperature, thermal differential of body temperature to air temperature, maximum hourly heating and cooling rates) were not strongly affected by python body mass. Additionally, body temperature was only influenced by the behavioural choice of microhabitat selection and was not affected by python body size or position, suggesting that these behavioural choices do not allow smaller pythons to vastly increase their temporal foraging window. By coupling dietary analysis, measures of body temperature and behavioural observations of free-ranging animals, we conclude that, contrary to theoretical predictions, a small body size does not thermally restrict the temporal window for ambush foraging in M. s. imbricata. An ontogenetic or size-determined switch from ambush feeding to actively foraging on slower prey would account for the differences in prey taken by these animals. The concept of altered foraging behaviour warrants further investigation in this species.

**Keywords:** ambush predator; body temperature; dietary analysis; foraging; thermoregulation
INTRODUCTION

Most snake species are unable to dismember their food, and consequently swallow their prey whole. Snakes are therefore ‘gape-limited predators’, where their maximum ingestible prey size is limited by their head size (Forsman & Lindell 1993; Shine & Thomas 2005). It is not surprising, therefore, that many studies reveal an ontogenetic shift in the size of prey consumed as snake body size increases (Mushinsky et al. 1982; Chiszar et al. 1986; Shine et al. 1998; Rodríguez-Robles et al. 1999) which is largely determined by physical size restriction. However, there are also indirect effects of snake body size on prey type selection, since body size plays a significant role in a snake's ability to capture and ingest prey.

Body size influences a complex interplay between thermoregulation and feeding capacity. Prey detection and capture success is increased when snakes have higher body temperatures (Ayers & Shine 1997), and temperature therefore plays a significant role in foraging strategies of snakes. Ectotherms behaviourally regulate their body temperature by moving between sun and shade or hot and cold microenvironments to alter heat flux, by modifying posture to alter surface areas exposed to heat sources or sinks, and by regulating activity times (Huey 1974). Such behaviour allows snakes to achieve an elevated body temperature which will optimize feeding success or physiological functions such as digestion.

Thermal inertia is affected by body size, and therefore in a varying environment, body size may influence a snake's ability to maintain a stable, optimal body temperature. For example, maximum rates of heating and cooling are inversely correlated with body mass and length in
the southern African python (*Python natalensis*), with small pythons heating and cooling twice as quickly as large pythons (Alexander 2007). Theoretically, larger snakes with a higher thermal inertia (Slip & Shine 1988c; Pearson *et al.* 2003) can therefore retain more heat in a cooling environment (e.g. at nightfall when air temperatures decline and basking opportunities are absent) and could therefore have an increased temporal window for feeding, with greater capacity to hunt on crepuscular and nocturnal prey species. By contrast, it has been argued that smaller individuals (with lower thermal inertia and therefore faster cooling rates at the end of the day) may be restricted to feeding during the day on diurnally active prey (Slip & Shine 1988a,c; Ayers & Shine 1997).

Body size therefore affects snake foraging behaviour and thermal biology and should also influence the type of prey taken in addition to prey size. We investigated the effects of body size upon the foraging ecology of the south-west carpet python (*Morelia spilota imbricata*, Pythonidae). A long-term radiotracking study enabled concurrent recording of diet, thermoregulatory behaviour and body temperature for free-ranging individuals of a range of body sizes. We tested the theoretical prediction that body size influences not only prey size, but also the type of prey taken. More specifically, we tested the hypothesis that small individuals are thermally restricted in their ability to take nocturnal prey.

**METHODS**

**Study sites and ambient conditions**

Pythons were opportunistically captured from coastal woodland and jarrah forest in Western Australia. The coastal woodland (Martin's Tank, Yalgorup National Park 32°51'S, 115°40'E,
and Leschenault Peninsula Conservation Park, 33°26′S, 115°41′E 40 km further south) is on
the Swan Coastal Plain where sandy soils are dominated by Banksia spp. and Agonis
flexuosa woodlands, with emergent tuart (Eucalyptus gomphocephala) trees (Trudgen
1984; CALM 1995, 1998). Animals sourced from the jarrah forest were located within State
Forest surrounding the township of Dwellingup (32°43′S, 116°4′E). This area lies within the
northern jarrah forest, where Archaean granite overlies metamorphic rocks capped by an
extensive, but dissected lateritic duricrust (Churchward & Dimmock 1989). The vegetation
comprises of jarrah (Eucalyptus marginata) and marri (Corymbia calophylla) trees with a
mosaic of understory woodland plant species. Both study sites experience Mediterranean
climates with cool, wet winters and warm, dry summers. The jarrah forest has slightly
elevated rainfall (700–1100 mm per annum), compared with the coastal woodland (600–
1000 mm per annum).

Environmental air temperatures (\(T_a; ^{\circ}C\)) were logged hourly using temperature and humidity
loggers (HOBO H8 Pro Series, H08-032-08; Onset Computer Corporation, Bourne, MA,
USA) placed at a location central in each site (one at each of the two coastal areas and two
loggers within the jarrah forest positioned approximately 70 km apart). HOBO loggers were
attached to a vertical stake and positioned approximately 1 m from the ground in a southwest-
facing direction and covered with a cardboard shelter to prevent rain damaging the device or
direct solar radiation. Daily air temperature for the jarrah forest averaged \(21.5 \pm 0.20^\circ C\) in
summer and \(9.49 \pm 0.12^\circ C\) in winter, and coastal woodland averaged \(22.2 \pm 1.72^\circ C\) in
summer and \(12.4 \pm 0.26^\circ C\) in winter (averaged over the 3 years of the study; 2006–2008).
The jarrah forest experienced colder air temperature in winter months (June to September)
compared with coastal woodland, but there was no difference in air temperature for the rest of
the year (Bryant et al. 2011).
**Study animal**

Forty-six carpet pythons were radiotracked over a 3-year period. Body mass ($M_b$) of the 46 pythons studied averaged $1030 \pm 564$ g (range: 136–3730 g) and snout-to-vent length (SVL) averaged $151 \pm 28.3$ cm (range: 90.0–223 cm). Where possible, individual body mass values were used in statistical analyses. For graphical representation and for the purposes of testing the hypothesis that smaller pythons demonstrated different diet selectivity and thermal biology, two size classes were distinguished: small pythons ($<1000$ g; average $599 \pm 229$ g) and large pythons ($>1000$ g; average $1480 \pm 448$ g).

The thermal biology of these animals was examined in the following two ways:

1. *Temperature-sensitive radiotransmitter data*

   Temperature-sensitive radiotransmitters (Holohil Systems Ltd, Canada) were surgically implanted into the coelomic cavity using a surgical technique under general anaesthesia (Bryant *et al.* 2010). After recovery from surgery, pythons were released back to their point of capture. Pythons were subsequently radiotracked weekly (or fortnightly) on foot using a three-element Yagi aerial (Sirtrack Ltd, Havelock North, New Zealand) and receiver (R-1000 Telemetry Receiver; Communications Specialists, Inc., USA). Most pythons did not flee when approached, allowing direct behavioural observation and, where possible, capture to measure SVL and $M_b$. 
Each radiotransmitter was calibrated to a unique temperature calibration curve prior to surgical implantation (and confirmed after surgical removal). Python body temperature could therefore be calculated and directly compared with air temperature (to the nearest hour, see details for recording above) and behavioural observations each time the python was located through radiotelemetry. Animals were categorized as located within one of five microhabitats: (i) hollow log – within a hollow log on the ground; (ii) ground cover – where the python would lay on ground debris exposed to potential sunlight radiation (e.g. leafy matter or low grass <5 cm in height); (iii) vegetation cover – where the python would have ≥30% of its body under or in piles of dead branches/sticks or vegetation (e.g. bushes) or was lying on top of logs or fallen branches (<2 m in height), with reduced exposure to sunlight radiation compared with ground cover; (iv) tree branch – resting on a tree branch elevated above the ground; or (v) tree hollow – radiotracked to a tree and either observed within a hollow or if the snake could not be visualized, the strength of the radio signal indicated its presence within a hollow. Python body position was scored as: (i) stretched; (ii) very loose coil; (iii) loose coil; (iv) coil; or (v) tight coil. If the python was sequestered in a tree hollow or hollow log and therefore not directly observed, it was assumed to be in a tight coil.

We used 5 × 2 contingency Pearson's chi-squared analyses to compare the likelihood of observing small and large pythons in each of the five microhabitats and in each of the five body position categories. Observations were compared with expected values calculated assuming an equal proportion of pythons observed in each category was small or large individuals.
Multiple regression was used to determine what factors influenced python body temperature (dependent variable). Independent factors included python body mass ($\log_{10} M_b$; average value for each individual over all captures), study site (coastal woodland or jarrah forest, recorded as 1 or 0), month (using a sine function of the calendar month, with maximum values during summer and minimum values over winter), sex (male or female), the unique python identification (ID) code (as a fixed factor to account for multiple measures made on each individual), air temperature (recorded for the nearest hour to each observation), microhabitat (one of five categories) and body position (one of five categories).

2. Temperature data loggers

For 29 individuals that were large enough ($M_b > 409$ g and SVL > 112 cm), one or two additional temperature data loggers (Thermochron iButtons DS1922L-F5; Maxim Integrated Products, Sunnyvale, CA, USA) were implanted with the radiotransmitters. The iButtons were taped to the radiotransmitter and the unit was dip-coated with three coats of inert wax (paraffin/elvax coating 130-0004-00; Mini-Mitter Respironics, OR, USA). The implanted radiotransmitter and iButton package was <5% of the individual's body mass. The two (or one for smaller animals or individuals captured close to the end of the study) iButtons recorded python body temperature hourly; the second was set with a delayed start to commence logging when the first had reached memory capacity. Individuals were monitored for body temperature using iButtons over $6.38 \pm 3.20$ months (range 2 to 23 months).

Three aspects of thermal biology were calculated from the iButton data for each python:
Thermal differential—hourly records of body temperature ($T_b$) for each individual were compared with air temperature ($T_a$) recorded simultaneously (as outlined above). The hourly thermal differential ($T_b - T_a$) was averaged for each month.

Maximum heating rate—hourly changes in body temperature ($\Delta T_b$) were calculated as $\Delta T_b = T_b(\text{Hour}_{i+1}) - T_b(\text{Hour}_i)$. For each day, the maximum heating rate (i.e. daily maximum hourly $\Delta T_b$) was extracted and then averaged for each month.

Maximum cooling rate—daily minimum $\Delta T_b$ (i.e. daily maximum cooling rate) was extracted and then averaged for each month.

Multiple regression analyses were performed for these three (dependent) factors. Independent factors for the analyses included individual python body mass ($\log_{10} M_b$), study site, month, sex and the unique python ID code (as a fixed factor).

Diet analysis

Thirty-five scats were collected for dietary analysis from pythons when they were initially brought into captivity to have radiotransmitters implanted, and 52 scats were collected over the course of the study when radiotracking animals in the field – 45 through gentle palpation of python's rectum during field telemetry work, one was found lying adjacent to an animal's known refuge and six were collected opportunistically when found in close association to expelled radiotransmitters (Bryant et al. 2010). In total, these 87 samples enabled the diet assessment for 34 individual pythons. The months were pooled into seasons for graphical presentation and analyses: summer (December to February), autumn (March to May), winter (June to August), and spring (September to November).
Each scat was carefully washed with gentle running water through a series of stainless steel or brass mesh sieves of three aperture sizes (2.0 mm, 250 µm and 1.0 µm), dried and then sorted (macroscopically) into bird, reptile or mammal samples. Mammal species were identified by microscopic analysis of hair samples (Triggs & Brunner 2002), reptiles by the size of undigested scales and limbs, and birds were identified by the shape and size of undigested beaks, skulls, feet and feather colour.

As pythons eat their prey whole, prey items found within the scats represent a whole animal. Therefore, where two or more species were found in a single scat, each prey item was confidently classified as representing a whole individual animal, eaten sequentially. However, where successive scats were collected from an individual (i.e. 1 or 2 weeks between sample times) and analysis identified the same prey species present in the scats, only the first record of the prey species was used for analysis, since it could not be assumed that this would represent a new prey item.

We used a 4 × 2 contingency Pearson's chi-squared analysis to compare the proportions of scats collected over each season and the number of times pythons were captured, comparing observed numbers with expected values calculated assuming an equal number of scats each season. Similarly, the proportions of each prey type consumed each season were compared by a 4 × 4 contingency chi-squared analysis with expected values calculated assuming an equal proportion of each prey type. The four prey type classes were: (i) small mammals (range 18 to 300 g); (ii) large mammals (range 1 to 4.5 kg); (iii) reptiles (principally bobtail lizards, *Tiliqua rugosa*); and (iv) birds (for a full species list, including average adult body mass, see Appendix S1). Finally, we used a 4 × 2 contingency chi-squared analysis to
determine if small pythons (<1000 g, n = 18) consume different types of prey from large pythons (>1000 g, n = 16); expected values were calculated assuming that the proportion of each prey category was the same between small and large pythons.

Multiple regression analysis was performed to investigate factors that influenced prey body size (dependent variable; average body mass of adults reported in the literature; Appendix S1). Independent variables included individual python body mass (Log10 - Mb), study site, month, python sex and the individual python ID code (as a fixed factor).

Data are presented as means ± 1 SD throughout.

**RESULTS**

**Diet analysis**

Because of the distance (approximately 150 km) and habitat differences between jarrah forest and the coastal woodland, prey data are indicated for these two areas separately (Appendix S1). A greater number of python scats were obtained for warmer months (summer, spring and autumn) and very few for winter months when the snakes were less frequently captured ($\chi^2_3 = 23.64, P < 0.001$). Despite these differences in sample size, there were no differences in the proportions of small mammal, large mammal, reptile or bird prey consumed across the four seasons ($\chi^2_9 = 11.05, P = 0.272$; Fig. 1).
Python body mass was the strongest influence in determining the size of prey (reported average adult mass) consumed by pythons (MR analysis: $t_{72} = 3.58$, $P < 0.001$); study site, month, sex or python ID did not influence the mass of prey consumed (all $P > 0.05$). As python body mass increased, so did the size of the prey consumed ($y = 1.25x - 1.45$, $R^2 = 0.197$; Fig. 2).

Small mammals represented in the pythons' diet included carnivorous marsupials (*Sminthopsis griseoventer, Sminthopsis* spp. and *Antechinus flavipes*) as well as introduced eutherian rodents (*Mus musculus* and *Rattus rattus*). Small mammal prey species were all nocturnally active species but may exhibit some crepuscular activity. The large mammals consumed were mostly nocturnally active and included two possum species (*Pseudocheirus occidentalis* and *Trichosurus vulpecula*), a macropod (*Bettongia penicillata ogilbyi*) and introduced eutherian species (*Oryctolagus cuniculus* and *Felis catus*). Diurnally active prey consumed by large and small pythons included both reptiles (principally *Tiliqua rugosa*; other skink species were taken but were not identifiable to species level from remains) and bird species. The array of prey type categories differed significantly between small and large pythons ($\chi^2_3 = 17.14$, $P < 0.001$; Fig. 3). Small mammals made up the majority (65%) of small python diets. Large pythons consumed a wider range of prey size and type; the greatest proportion of the diets of large pythons was made up of large mammals (41%).

**Thermoregulation**

*Thermal differential*—heavier pythons were able to maintain a larger thermal differential ($t_{229} = 2.24$, $P = 0.025$). However, by contrast with other factors, the effect of body mass was
small: the thermal differential was more strongly influenced by study site, month and sex (all \( P < 0.001 \)), but not by individual differences (python ID; Table 1). Python body mass accounted for only 4% of the difference in \( T_b - T_a \) (\( y = 1.75x - 2.57, R^2 = 0.044; \) Fig. 4A).

*Heating rate* – the maximum heating rate was influenced by study site, month, python sex and ID (Table 1). When all the factors were taken into account, python body mass was not a statistically significant influence (\( t_{239} = 1.39, P = 0.166 \)). The equation describing heating rate compared with body mass (\( y = -3.26x + 22.79, R^2 = 0.032; \) Fig. 4B) indicates that only 3% of the variation in heating rate was attributed to body mass.

*Cooling rate* – the maximum cooling rate was influenced by study site, month, python sex and ID (Table 1). Python body mass was not a statistically significant influence on cooling rates (\( t_{239} = -1.33, P = 0.186 \)). Only 4% of the variation in cooling rate was attributed to body mass (\( y = -2.10x + 12.61, R^2 = 0.042; \) Fig. 4C).

*Thermoregulatory behaviour* – even though python body temperature (as measured through data collected during field observation by implanted temperature-sensitive radiotransmitters) was influenced by their behavioural choice of microhabitat (\( t_{189} = -2.09, P = 0.038 \)) (and air temperature; \( t_{189} = 6.18, P < 0.001 \)), body temperature was not affected by the size of the python (body mass), body position (Fig. 5C), study site, month, sex or python ID (all \( P > 0.05 \); Table 1). Pythons were warmest if they were located in hollow logs or ground cover and cooler when they were found within tree hollows (Fig. 5A). There was a significant difference in the microhabitat use between small and large pythons.
(χ²₄ = 33.14, P < 0.001; Fig. 5B). There was no difference between the proportion of observations of small and large pythons in the different body positions (χ²₄ = 6.17, P = 0.187; Fig. 5D).

**DISCUSSION**

An ontogenetic shift in prey size for snakes is predicted based on their physical restrictions on prey ingestion. However, a number of studies have also reported an ontogenetic shift in prey type (e.g. fish consumed by juvenile colubrids but amphibians as adults; Kjaergaard 1981; Mushinsky et al. 1982; Chiszar et al. 1986, lizards consumed by juvenile vipers and death adders but mammals as adults (Shine 1980, but see some exceptions, e.g. Vincent et al. 2004). Given they are capable of consuming larger prey, the range of prey available to larger individuals is greater than that available to smaller individuals (Arnold 1993).

While some degree of prey switching may therefore simply reflect prey availability, it has also been suggested that switching prey type may reflect thermal biology. It was suggested that smaller snakes, with a lower thermal inertia, would cool quicker in the evenings and therefore have a shorter temporal window for foraging on crepuscular and nocturnal prey (Slip & Shine 1988a,c; Ayers & Shine 1997). Slip and Shine (1988a) examined stomach contents (museum specimens) of juvenile *Morelia spilota spilota* pythons, a subspecies to our study species and found that small, nocturnal mammals comprised 70% of their diet; the remaining portion of the diet was diurnally active reptiles and birds. The diet of adult pythons (determined through faecal sampling of radiotracked individuals) also included principally mammals (crepuscular and nocturnal species) and the occasional bird, but no reptiles. The
absence of reptiles (diurnally active prey) in the diet of adults led the authors to infer a shift in the time of day juveniles and adults fed. This was expanded in a subsequent thermoregulation study, where larger-bodied snakes resting in a coiled body posture demonstrated increased thermal inertia and therefore slower cooling rates; the authors argued that this would allow larger individuals to ambush forage on crepuscular and nocturnally active prey (Slip & Shine 1988c). In contrast, it was explained that small individuals (i.e. juveniles), which could not maintain sufficiently elevated body temperatures to allow them to ambush hunt on nocturnal species, are therefore more likely to forage on diurnally active species (e.g. reptiles).

Our research is generally consistent with Slip and Shine's (1988a) observations for *M. s. spilota*, with small *M. s. imbricata* consuming a large proportion of small mammals (which made up 65% of their diet) and larger individuals consuming a broader range of sizes and type of prey. However, smaller *M. s. imbricata* were clearly not restricted in terms of their temporal window from foraging on crepuscular and nocturnal prey, since the majority of prey items taken by small pythons were nocturnally active species. Pearson *et al.* (2002) also found that both juveniles and adult male pythons mainly consumed nocturnally active prey including *M. musculus* and spiny-tailed geckos (*Strophurus spinigerus*).

The selection for mammalian (nocturnally active) rather than reptilian (diurnally active) prey observed in the present study does not simply reflect overall prey availability, since data available for the coastal site indicated that although reptiles made up only 14% of small python diet, an abundance of 21 reptile species were present (Wentzel 2011). About 91% of these reptiles weighed <20 g (Wentzel 2011) and were therefore available as prey to small
pythons (although fossorial species may not have been). Prey consumed therefore clearly did not simply reflect availability.

In addition to the activity patterns of prey species taken, we also examined the thermal biology of *M. s. imbricata* to test the hypothesis that smaller individuals may be thermally restricted in their temporal hunting patterns. Our data indicate little difference in three measures of thermal biology (thermal differential, maximum heating and cooling rates) due to body mass (*M*<sub>b</sub> accounted for only 3% or 4% of the variability in these values). Similarly, correlation analysis of adult and juvenile animals of the same species at Garden Island and Dryandra Woodland in Western Australia showed no difference between these size classes in terms of the degree to which body temperatures were related to air temperatures (Pearson *et al.* 2003). Although there were differences in the thermoregulatory behaviour of small and large individuals in the present study, these differences were unlikely to counter the potentially lower thermal inertia of small individuals (since smaller animals were apparently selecting microhabitats that resulted in cooler, not warmer, body temperatures, which is contrary to the prediction that smaller pythons may use behavioural thermoregulation to elevate their body temperature). We therefore found little evidence for a thermal limitation restricting small individuals from feeding on crepuscular or nocturnal prey.

There is a considerable range of opportunities for ectotherms to regulate their body temperature within their environment (e.g. through microhabitat selection or body position), which may increase or stabilize body temperature, minimizing the effects of thermal inertia due to body size alone (Christian *et al.* 2006). This was clearly observed in the wide range of body temperatures achieved by both small and large pythons located in a range of
microhabitats. Behavioural choices may therefore allow small individuals to regulate and maintain their thermal energy (i.e. higher body temperature), and may critically extend their nocturnal foraging window allowing the capture of crepuscular or nocturnally active mammals (Christian et al. 2006). Additionally, differences in thermal inertia may only operate over a matter of minutes, not hours, following sunset (Christian et al. 2006). Individual python behaviour coupled with the stochastic nature of ambush foraging (driven by prey availability, seasonal activity patterns, etc.) may make the detection of differences between small and large snakes extremely difficult.

If there is no evidence for a thermal restriction on hunting activities, and prey selection does not directly reflect prey availability, what alternative explanations may be offered? It is possible that the lack of reptiles in the diet of adult *M. s. spilota* (Slip & Shine 1988a) reflects that larger snakes prefer larger or more active prey, dropping small or less active prey from their diet completely (Plummer & Goy 1984; Shine 1987; Arnold 1993; Shine et al. 1998). While active foraging snakes move about in search of suitable prey, ambush predators sit and wait in an area where prey are likely to pass (e.g. adjacent to an animal passage; Slip & Shine 1988b,c; Ayers & Shine 1997). Ambush predators are therefore more likely to feed on fast-moving endothermic prey such as birds and mammals that have field metabolic rates approximately 10–30 times higher than ectothermic reptiles, since there is a higher likelihood of these prey passing the snake's ambush position (Shine 1980; Huey & Pianka 1981; Arnold 1993; Ayers & Shine 1997; Nagy et al. 1999). Small reptiles may therefore be less likely to be detected and captured. Alternatively, the consumption of particular prey types (e.g. *Tiliqua rugosa* skinks or *Pseudocheirus occidentalis* possums) may suggest that larger pythons are selecting slower prey (compared to small mammal prey taken by smaller pythons) which may
reflect size-dependent locomotory patterns. The potential for different feeding strategies between small and large pythons warrants further investigation.

We conclude that while body size directly affects the size of prey that can be taken, the link with selection of prey type is less obvious. The significant proportion of nocturnally active mammals found in the diet of smaller pythons (both the present study and that of Slip & Shine 1988a) suggests that small pythons are certainly able to ambush nocturnally active prey. There is also little support for an effect of body size on temperature regulation of *M. s. imbricata*, and therefore little chance that these animals are differentially influenced in terms of thermal biology. Small body size does not thermally restrict the temporal window for ambush foraging in the south-west carpet python. The ontogenetic shift in prey type consumed by *M. s. imbricata* therefore does not appear to reflect their thermal biology or prey availability, but possibly a shift in foraging behaviour in this species. Future studies could investigate potential physical restrictions of strike rate and prey speed for larger snakes.

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AEC54/2006) and was financially supported by the Invasive Animal Cooperative Research Council Australia, Department of Environment and Conservation and Murdoch University.

REFERENCES


Figure 1. Seasonal changes in the type of prey consumed by *Morelia spilota imbricata*. 
Figure 2. Comparison between prey body mass (reported Log$_{10}$ adult average) and individual carpet python body mass.
Figure 3. Differences in the type of prey consumed by small and large *Morelia spilota imbricata* pythons.
Figure 4. Relationship between python body mass and three measures of thermal biology. The measures shown are the (A) thermal differential (difference of python body temperature above air temperature), (B) maximum hourly heating rates and (C) maximum cooling rate. Each column of data points represents monthly values for an individual python (separated by their overall average body mass measures).
Figure 5. The proportion of observations (B,D) and average (±SD) body temperature (A,C) of small (white) and large (black) pythons observed in each of five microhabitat categories (left-hand panel) and in five body positions (right-hand panel).
Table 1. Results of multiple regression analyses testing for the effect of environmental, individual and behavioural factors on four measures of thermal biology of south-west carpet pythons

<table>
<thead>
<tr>
<th>Variable</th>
<th>Temperature-sensitive radiotransmitters</th>
<th>iButton temperature loggers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Body temperature ($T_b$)</td>
<td>Thermal differential ($T_b - T_a$)</td>
</tr>
<tr>
<td></td>
<td>$t$</td>
<td>$P$</td>
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<td>Body mass (Log$_{10}$ – $M_b$)</td>
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<td>Study site (coastal woodland/jarrah forest)</td>
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<td>Month (sine values of calendar month)</td>
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<td>Python ID code</td>
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<tr>
<td>Air temperature ($T_a$, °C)</td>
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<td>Microhabitat category</td>
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<tr>
<td>Body position category</td>
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</tbody>
</table>

Table gives $t$-values and associated probabilities ($P$). –, independent variables not included in analysis.