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# Tree hollows are of conservation importance for a near-threatened python species

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## Abstract

Understanding microhabitat requirements for species vulnerable to anthropogenic threats can provide important information to conservation managers. This may be particularly true for ectotherms, where behaviour and physiology (e.g. digestion, responsiveness and activity patterns) are strongly influenced by thermal conditions of microhabitat retreat sites. Retreat sites selected by south-west carpet pythons (*Morelia spilota imbricata*) were identified through radiotracking 46 pythons over 3 years. Tree hollows appear to be a very important resource for pythons: 61% (22 of 36 individuals tracked over winter) used tree hollows as retreat sites (56% of all observations in winter), and remained in hollows for an average of  $124 \pm 49$  (range 34 to 210) days. If pythons did not use tree hollows over winter, they found refuge in one of four alternative microhabitats: low vegetation cover (26% of winter observations), ground cover (10%), on tree branches (6%) or in hollow logs on the ground (2%). We tested whether tree hollows provide a thermally distinct environment compared with alternative microhabitats, but found no difference in minimum, average, maximum or range of temperatures recorded between microhabitats. When within tree hollows over winter, pythons had colder daily average and maximum body temperatures (cf. pythons that used other microhabitats), but this did not give them an energy saving (in terms of body condition scores). Pythons ate very little over winter and we predict that animals sequestered within tree hollows do not access prey at this time. Tree

hollows provide a critical refuge over winter when python body temperature is low, and their responsiveness is limited, rendering individuals vulnerable to predation by terrestrial predators (e.g. introduced red fox). Destruction of hollows through fire, land clearing, competition with other fauna species and the significant age required for hollows to form in trees all contribute to the decline in availability of this important microhabitat.

**Keywords:** microhabitat; microclimate; *Morelia spilota imbricata*; predation; thermal biology; resource; snake

## Introduction

Tree hollows are an important resource for many vertebrate species. In the jarrah forest of Western Australia, 16 mammal, 21 bird and 5 reptile species use tree hollows for a variety of purposes (Abbott & Whitford, 2001). Tree hollows are used as diurnal or nocturnal retreat sites for sleeping, feeding, rearing young, thermoregulation, and to facilitate predator-safe dispersal and ranging behaviour (Saunders, Smith & Rowley, 1982; Smith & Lindenmayer, 1988; Inions, Tanton & Davey, 1989; Lindenmayer *et al.*, 1991; Gibbons & Lindenmayer, 2002; Glen & Dickman, 2006; Ruczynski, 2006; Koch, Munks & Driscoll, 2008). Sizeable hollows will usually only form in dead limbs or trunks of large trees (minimum of 45–50 cm over-bark tree diameter; Whitford & Williams, 2002). Limb breakage is an important contributor to hollow formation with 50% of hollows formed in this manner (Whitford, 2002). Trees of many species take over 130 years to reach a size where hollows will start to form, and some eucalypt species may need to be at least 400 years (Gibbons & Lindenmayer, 2002; Whitford & Williams, 2002). Removal of larger trees from the landscape (e.g. forestry, clearing due to farming or urbanization, and bushfires) therefore has important consequences for the availability and turnover of tree hollows (Bradshaw, 2000; Abbott & Whitford, 2001; Whitford, 2002; Whitford & Williams, 2002; Archibald *et al.*, 2006). Furthermore, aggressive competition for tree hollows with introduced species (e.g. European honeybee, *Apis mellifera*), as well as locally abundant native

species (e.g. galahs, *Eolophus roseicapillus*), can result in exclusion of threatened species (Gibbons & Lindenmayer, 2002). Competition and anthropogenic disturbance mean it is critical to understand the importance of tree hollow use for threatened species (Webb & Shine, 1997, 1998; Gibbons & Lindenmayer, 2002; Ruczynski, 2006; Ruczynski & Bogdanowicz, 2008).

Tree hollow use is reasonably well studied for birds, bats and other mammals; however, there is a dearth of information on tree hollow use by reptiles and amphibians (Lillywhite & Henderson, 1993). For example, broad-headed snakes *Hoplocephalus bungaroides* move from rocky outcrops to woodland areas and sequester in tree hollows with the onset of warmer weather (Webb & Shine, 1997, 1998), and tree hollows are therefore an important consideration in the conservation of this species.

The geographic distribution of the south-west carpet python (*Morelia spilota imbricata*) has contracted substantially since European settlement, and the species is currently listed as Near-Threatened (IUCN, 1998; Pearson, Shine & Williams, 2005; Henderson & Powell, 2007).

Understanding the biology of this animal is therefore a priority given the significant potential threats of anthropogenic environmental change (Webb & Shine, 1997, 1998; Webb, Brook & Shine, 2002). During a 3-year ecological study of *M. s. imbricata*, it was noted that the majority of individuals (28 of 46 individuals tracked; 61%) used tree hollows, spending a vast amount of time over winter sequestered in the hollows (56% of observations during winter months; June–August). Importantly, pythons often revisited and used the same tree hollow each year, despite the presence of other pythons using the same hollow or the same tree.

We investigated four potential reasons that may determine the use of tree hollows by *M. s. imbricata* over winter. Because body temperature ( $T_b$ ) of ectotherms affects all biochemical rates (e.g. digestion and growth, sensory perception, and behavioural activity, such as movement, foraging and mate searching), thermal conditions of microhabitat retreats are likely to be extremely important for these animals (Huey, 1982; Kingsolver & Raymond, 2008), particularly for species that spend long periods sequestered in retreat sites (Huey *et al.*, 1989; Huey, 1991; Webb & Shine, 1998; Webb, Pringle & Shine, 2004). Therefore, firstly, the microclimate within tree hollows in large trees may buffer

temperature extremes, providing a warmer or more stable environmental temperature (Vonhof & Barclay, 1996). Secondly, pythons forfeit basking opportunities by sequestering inside a tree hollow and should experience body temperatures similar to temperatures within the hollow itself. Daily body temperatures of sequestering pythons may not fluctuate (cf. pythons that do bask and increase daily body temperature), allowing them to reduce their metabolic rate and therefore reduce their loss of body mass over winter. Thirdly, potential prey species (e.g. nesting birds, bats, possums, and quolls) use tree hollows for retreat and nest sites (Saunders *et al.*, 1982; Smith & Lindenmayer, 1988; Inions *et al.*, 1989; Lindenmayer *et al.*, 1991; Glen & Dickman, 2006; Ruczynski, 2006; Koch *et al.*, 2008). Predators, such as snakes, could arguably therefore enter a tree hollow to seek prey. Finally, being sequestered in an appropriately sized and shaped hollow (cf. roosting on branches, under vegetation cover or on the bare ground) may be an advantage in avoiding terrestrial predators. We analysed behavioural, temperature and dietary data to investigate whether there was support for each of these predictions to explain why the majority of *M. s. imbricata* used tree hollows as retreat sites over winter.

## **Materials and methods**

### **Study sites and environmental temperature**

Pythons were opportunistically captured from coastal woodland and jarrah forest of south-west 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, consisting of sandy soil, dominated by woodlands of *Banksia* spp. and *Agonis flexuosa*, with emergent tuart (*Eucalyptus gomphocephala*) trees (Trudgen, 1984). 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 region of Western Australia, where Archaean granite overlies metamorphic rocks capped by an extensive, but dissected lateritic duricrust (Churchward & Dimmock, 1989). The vegetation is dominated by jarrah (*Eucalyptus marginata*) and

marri (*Corymbia calophylla*), trees with a mosaic of woodland understory plant species, including grass trees (*Xanthorrhoea preissii*). Both habitat types experience Mediterranean climates with wet, cool winters and warm, dry summers, although the jarrah forest has slightly elevated rainfall (700–1100 mm per annum) compared with coastal woodland (600–1000 mm per annum).

Environmental air temperatures ( $T_a$ ; °C) were logged hourly by two 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 the south-west aspect of a vertical stake, approximately 1 m from the ground, and each was covered with a cardboard shelter to prevent rain damaging the device or direct solar radiation. Data were averaged for the two loggers for the jarrah forest and similarly for the two at the coastal woodland. For each month, the average of daily average air temperature ( $T_a$ ) was tested for differences between coastal woodland and jarrah forest using single-factor analysis of variance (ANOVA). Jarrah forest (JF) and coastal woodland (C) sites provided unique thermal environments (Fig. 1); therefore, study site (JF vs. C) was included in all analyses.

### **Tree hollow use by pythons – radiotelemetry**

Forty-six carpet pythons were radiotracked over a 3-year period. Body mass ( $M_b$ ) of the 46 pythons studied averaged  $1,030 \pm 564$  g (range: 136–3,730 g), and snout-to-vent length (SVL) averaged  $151 \pm 28$  cm (range: 90–223 cm). Pythons were surgically implanted with temperature-sensitive radiotransmitters (radiotransmitter selection for each individual was based on the individual's body mass). Five model types/sizes were used: SB-2T: 5 g (10 months battery life), S1-2T: 11.0 g (18 months battery life), S1-2T: 13.5 g, and A1-2T: 16.0 g (24 months battery life), and A1-2T: 25.0 g (36 months battery life) (Holohil® Systems Ltd, Ontario, Canada). Each python was anaesthetized using isoflurane (Forthane, Abbott Australasia Pty Ltd, Botany, NSW, Australia) inhalational anaesthesia, and radiotransmitters were aseptically inserted into the coelomic cavity following routine ventral coeliotomy. Transmitters were removed under reversal of this surgical procedure between October–November 2008 at the conclusion of the study (see Bryant *et al.*, 2010 for details). Radiotransmitters

were implanted for  $354 \pm 290$  (range 4–1,251) days; two pythons underwent radiotransmitter replacement due to battery expiry.

Pythons were released back to their point of capture and tracked on a weekly (or rarely fortnightly) basis on foot using a three-element Yagi aerial (Sirtrack Ltd, Havelock North, New Zealand) and receiver (R-1000 Telemetry Receiver, Communications Specialists, Inc. Orange, CA, USA). The exact position of each individual was determined using a differential GPS system (post-processing using Thales MobileMapper software, Thales Navigation, Santa Clara, CA, USA). Most pythons did not flee when approached, allowing direct behavioural observation, and, where possible, hand capture for measurement. Snout–vent length (SVL; cm) was recorded using a tape measure (sewing style) from the tip of the nasal bone to the cloacal opening along the ventral surface of the python. Body mass ( $M_b$ ) was calculated using calibrated spring balances (Pesola® AG, Rebmattli 19, CH-6340 Baar, Switzerland) when pythons were contained within a calico bag (bag weight was subtracted from the total). Values for  $M_b$  and SVL were  $\text{Log}_{10}$ -transformed for analyses.

Microhabitats used by pythons were classified as:

1. Tree hollows (TH) – pythons were radiotracked to a tree and either observed within a hollow, or, if the snake could not be visualized, strength of the radio signal indicated its presence within a hollow.
2. Tree branches (TB) – where a python was visible on a tree branch.
3. Hollow logs (HL) – pythons were radiotracked to and observed within a hollow log on the ground, or if it could not be visualized, the strength of the radio signal indicated its presence within the log.
4. Ground cover (GC) – where the python would lay coiled or stretched on ground debris exposed to potential sunlight radiation (e.g. leafy matter or low grass <5 cm in height).

5. Vegetation cover (VC) – where the python would have  $\geq 30\%$  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, with reduced exposure to sunlight radiation compared with GC, above.

Other microhabitats (e.g. burrows, small wetlands and roads) accounted for only a total of 4% of total observations; these were not included in analyses for the present study.

Thirty-six pythons were observed over at least one winter period (five were observed over two winters; for these individuals, the length of time spent sequestered in tree hollows was averaged). The minimum duration of time pythons spent using tree hollows was recorded from the first incident where the python was radiotracked to a tree hollow (usually around April) until the python was first recorded back on the ground (usually September/October). These data have the caveat that only weekly observations were carried out and pythons could have moved about between observations. Only five pythons, however, were recorded to move position from a tree hollow over the winter months; one changed trees and hence tree hollows, and the remaining four were observed on the ground (nearing the end of winter) but subsequently retreated back into the same tree hollow. For some individuals, this descending/ascending behaviour was repeated over several weeks. The minimum amount of time spent sequestered in the tree hollow (days) was used for analyses and could therefore be a slight underestimate in such cases.

### **Do tree hollows provide a more favourable ambient temperature?**

#### ***Microhabitat temperatures***

To test whether tree hollows provide a thermally distinct environment to other microhabitats, over winter of the final field season (June–August 2008), data loggers (iButtons Thermochron iButtons DS1922L-F5, Maxim Integrated Products, Sunnyvale, CA, USA, logging hourly) were placed into the five microhabitat types. All iButtons were covered in two layers of inert wax (paraffin/elvax coating 130-0004-00, Mini-Mitter Respironics, Bend, OR, USA) and were attached to a string to facilitate retrieval. Four replicates of groups of five iButtons (one per microhabitat, within 10 m of each other) were placed at each of coastal and jarrah forest sites (i.e. 40 iButtons in total).

1. Tree hollows (TH) – seven iButtons were placed into tree hollows that animals were using at the time. Due to access reasons, two were placed into different hollows within the same tree, and in another case, a different tree as close as possible to a sequestered python was used. The last three tree hollows may or may not have contained a sequestered python (none of the radiotracked individuals were present but we could not preclude use by non-marked individuals). iButtons were placed as far into each hollow as possible (between 20 and 40 cm depth) by accessing the hollow with a tall ladder and additionally using 3–5 m telescopic aluminium poles.
2. Tree branch (TB) – 10 iButtons were placed on a branch adjacent to a visible python, or on the nearest branch proximate to the positions of the tree hollow iButtons.
3. Hollow logs (HL) – 10 iButtons were placed within a hollow log (as close as possible to each monitored tree hollow), approximately midway along its length (using telescopic aluminium poles).
4. Ground cover (GC) – 10 iButtons were placed in exposed locations on ground debris in the vicinity of each monitored tree hollow.
5. Vegetation cover (VC) – 10 iButtons were placed within vegetation and fallen branches in the vicinity of each monitored tree hollow.

To assess temperature differences between microhabitats, a mixed-model ANOVA was carried out with two fixed factors (site: JF vs. C and microhabitat: TH, TB, HL, GC or VC), and one random factor (iButton replicate number) to measure the temperature variables: daily minimum, daily average, daily maximum, and daily range (each treated as dependent factors).

### ***Python body temperature***

For 29 individuals that were large enough ( $M_b > 409$  g and  $SVL > 112$  cm), one or two additional temperature data loggers (iButtons) were implanted with the radiotransmitters. The iButtons were taped to the radiotransmitter, and the unit was dip-coated with three coats of inert wax. 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 2–23 months).

For the purpose of this study, we were interested in whether pythons wintering in tree hollows (TH) achieved different body temperatures compared with individuals that did not use tree hollows (all other microhabitats pooled as 'non-tree hollow', NTH). We therefore classified iButton temperature recordings according to the weekly microhabitat observations: pythons were classified as using a tree hollow or not (i.e. TH vs. NTH) each week. Eight of 10 (80%) jarrah forest pythons sequestered in tree hollows for winter, which meant only two pythons used other microhabitats (they remained in vegetation and used ground cover). Unfortunately, iButton temperature data could not be collected for these individuals (due to uncontrollable logistical issues at the time of implanting both animals); therefore, comparison of body temperature for TH versus NTH pythons over winter months was not possible for the jarrah forest.

Four measures of python body temperature (monthly averages of: daily average  $T_b$ , daily minimum  $T_b$ , daily maximum  $T_b$  and daily range in  $T_b$ ) were assessed for each month over a 6-month window. Data were analysed by two-way ANOVA (site: JF vs. C and microhabitat: TH vs. NTH as independent factors) for months where more than three pythons were recorded for each category (April, September and October). Single-factor ANOVA was used for May, June, July and August for C-NTH, C-TH and JF-TH (insufficient data for JF-NTH category over these months).

### **Is there an energy saving by using tree hollows?**

Python body condition score was calculated as the residual scores of  $M_b$  relative to body size (SVL), expressed as a percentage of predicted  $M_b$  (Madsen & Shine, 2002):

$$\text{BCS (\%)} = \frac{(\text{observed } M_b - \text{predicted } M_b)}{\text{predicted } M_b} \times 100$$

Effectively, body condition score (BCS) indicates how much a python deviates (positively or negatively) from a null model where the python's body mass is proportional to body length. Where SVL could not be measured (for many individuals, this required two persons to measure accurately) but body mass could, the average SVL for that python was used (<5% of records). There was no statistically significant sex difference in the relationship between  $\text{Log}_{10}\text{-}M_b$  and  $\text{Log}_{10}\text{-SVL}$  ( $F_{\text{slope } 1,42} = 0.19, P = 0.666$ , StatistiXL). Therefore, predicted  $M_b$  was calculated using a common equation derived from data collected for 45 individuals (average values for each individual excluding their first capture to reduce bias, as a number of pythons were initially caught because they had consumed a radiocollared prey; the only juvenile python was excluded from analysis) (Fig. 2;  $R^2 = 0.876$ ):

The BCS was calculated for every capture of each individual. Body condition could not be determined for animals that were sequestered in a tree hollow because they could not be hand-captured to measure. Therefore, to calculate the effects of utilizing tree hollows as a winter retreat or not, the change in body condition over time for each individual was calculated (StatistiXL): change in body condition was expressed as the slope or beta values ( $\beta$ ) for the relationship between body condition scores against real time (date) ( $\beta$ -BCS). Only individuals that had three or more records of BCS and only individuals that were monitored over a winter period were used in this analysis. Three multiple regression analyses were performed to ascertain:

1. Which factors influence the change in body condition ( $\beta$ -BCS)?  $\beta$ -BCS was used as the dependent variable, with study site (JF vs. C), sex (F vs. M), body size (average  $\text{Log}_{10}\text{-SVL}$ ) and tree hollow use (TH vs. NTH) as independent variables.
2. Which factors influence how long pythons stay sequestered in tree hollows? The length of time (days) was used as the dependent variable, with study site (JF vs. C), sex (F vs. M), body size (average  $\text{Log}_{10}\text{-SVL}$ ) and change in body condition ( $\beta$ -BCS) as independent variables.
3. Which factors affect the change in body condition ( $\beta$ -BCS) for pythons that use tree hollows over winter?  $\beta$ -BCS was used as the dependent variable, with study site (JF vs. C), sex (F vs.

M), body size (average  $\text{Log}_{10}\text{-SVL}$ ) and the time spent sequestered in tree hollows (days) as independent variables.

## **Diet**

A total of 87 scats were opportunistically collected from 34 individual pythons over the course of this study. 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  $\mu\text{m}$ , and 1.0  $\mu\text{m}$ ), 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. Prey species were classified according to whether they were arboreal or terrestrial based on species descriptions of their behavioural patterns (Van Dyck and Strahan 2008).

Statistical analyses were carried out using STATISTICA 8.0 (StatSoft Inc., 2007) and StatistiXL (statistiXL 1.8, 2007). Statistical significance was set to  $\alpha < 0.05$ . Values are shown as means  $\pm 1$  SD.

## **Results**

### **Tree hollow use by pythons**

A number of observations indicated that tree hollows are an important resource for *M. s. imbricata*. Firstly, a large number of pythons used tree hollows. Twenty-two (61%) of the 36 pythons (individuals that were monitored over 3 years and able to be tracked for at least one winter period) used tree hollows over winter months as their retreat site. At the coastal woodland site, 14 pythons used tree hollows and 12 did not, and in the jarrah forest, 8 pythons used tree hollows but only 2 did not. Average duration of retreat to a tree hollow was  $121 \pm 52$  days ( $n = 22$ ), ranging from a minimum of 34 days to a maximum of 210 days (7 months). Although pythons used tree hollows from April through to September, there was a clear increase in the proportion of observations of pythons using tree hollows over the winter months (June–August), with an average of 56% (max 65% in June alone)

of total winter observations tracking the individual python to a tree hollow (Fig. 3). The remainder of observations over winter (June–August) identified pythons as using vegetation cover (26%), ground cover (10%), tree branches (6%) and hollow logs (2%; Fig. 3).

Secondly, tree hollows were used repeatedly by the same individual: four of the five pythons tracked over two winters used the same hollows over consecutive years. Additionally, multiple individuals were found using the same tree hollow, or different hollows within the same tree.

### **Do tree hollows provide a more favourable ambient temperature?**

Air temperature was colder for the jarrah forest compared with coastal woodland ( $F_{11,12} = 28.2$ ,  $P < 0.001$ ) during June to September but was not different over the remaining months (Fig. 1). It was not, therefore, surprising that average daily temperature recorded for all five microhabitats was cooler for the jarrah forest compared with coastal woodland (site:  $F_{1,3,42} = 21.3$ ,  $P < 0.05$ ; Fig. 4). However, within each habitat type (jarrah forest and coastal woodland), there was no statistically significant difference in the minimum, average, maximum or range of daily temperatures recorded for each of the five microhabitats over winter (June–August; microhabitat:  $P > 0.05$ ).

In terms of python body temperature, jarrah forest pythons were colder compared with coastal pythons for three measures of body temperature (average  $T_b$ , minimum  $T_b$ , and maximum  $T_b$ ) from June through to September (Fig. 5a–c).

Comparison between body temperature for animals that either did or did not use tree hollows was carried out for animals in coastal woodland (as mentioned previously, iButtons had not been implanted into the two pythons that did not sequester in tree hollows in jarrah forest, which precluded the same comparison between pythons sequestering in tree hollows or an alternative microhabitat in this habitat). In coastal woodland, pythons that used tree hollows experienced similar minimum  $T_b$ . Pythons were colder on average (average  $T_b$ ; June to October; Fig. 5a) and experienced colder maximum  $T_b$  (over all months examined; Fig. 5c) than animals that did not use tree hollows. Therefore, the range of body temperatures (the monthly average of daily range calculated for each

individual) was greater for pythons that did not use tree hollows compared with pythons that sequestered in tree hollows (Fig. 5d).

### **Is there an energy saving by using tree hollows?**

We recorded a marked decline in body condition score for animals across this study. Since pythons that used tree hollows were colder than those that used alternative microhabitats, we predicted that a lower metabolic rate would mean that animals using tree hollows would show a slower rate of decline in body condition over winter (when, like most ectotherms, pythons rarely if ever feed). None of the four factors analysed, however (use of hollows, study site, sex, and body size), significantly affected python  $\beta$ -BCS (Table 1a). In terms of factors that influenced the length of time animals stayed in tree hollows, females spent longer in tree hollows ( $136 \pm 50.3$  days) compared with males ( $101 \pm 49.7$  days) ( $t_{17} = -2.23$ ,  $P = 0.040$ ), but the length of time was not affected by study site, body size (SVL) or their  $\beta$ -BCS (Table 1b; Fig. 6). The rate of decline in body condition differed between the sexes ( $t_{17} = -2.18$ ,  $P = 0.043$ ), with males that used tree hollows ( $\beta$ -BCS =  $-0.668 \pm 0.264$ ) showing greater decline in BCS than females that used tree hollows ( $\beta$ -BCS =  $-0.449 \pm 0.461$ ), but there was no significant effect of study site, body size or the amount of time sequestered in a tree hollow (Table 1c; Fig. 6).

### **Do pythons access more arboreal prey?**

Behavioural observations suggest that pythons did feed while in trees, as pythons were observed in ambush position in trees. However, it should be noted that pythons did not feed regularly over winter (when they were using tree hollows extensively). As part of the broader radiotelemetry study on this species, behavioural observations (where pythons were observed or palpated to check whether they had recently fed) revealed that pythons very rarely fed during winter (7.5% of field observations) compared with warmer months (31.5% of summer, 12.6% of autumn and 10.4% of spring observations; Bryant *et al.* in press). Overall, only 29% of prey species in python scats were identified as being arboreal or mostly arboreal, whereas over 71% were principally terrestrial (Table 2).

### **Do tree hollows offer protection from predation?**

There are at least six potential predator species of pythons in Western Australian jarrah forest and coastal woodland. Most of these predators are terrestrial, including the introduced red fox (*Vulpes vulpes*) and native varanid lizards (Table 3). Two of the 13 deaths recorded as part of the broader ecological study on *M. s. imbricata* resulted from predation (or scavenging following death). Red fox DNA was confirmed for one of the carcasses and the bite marks on the implanted radiotransmitter from the second also suggest fox predation.

## **Discussion**

South-west carpet pythons display distinct patterns of microhabitat selection, with over half the individuals tracked using tree hollows as winter retreats for an average of 3 months, but for as long as 7 months of the year. Observational data revealed numerous pythons using hollows in the same tree, repeated use of the same tree hollows over consecutive years, and even numerous pythons sharing the same hollow. These observations provide strong indication that tree hollows could be a limiting resource for this python species. Given the high level of use of tree hollows over winter months, we investigated whether tree hollows may provide a thermally distinct or physiologically advantageous environment compared with alternative microhabitats. We also investigated whether pythons utilize a large proportion of arboreal prey and could therefore have greater access to prey if they use tree hollows, or whether they have need of protection from predation. We discuss these alternative explanations for tree hollow use below.

### **Do tree hollows provide a more favourable ambient temperature?**

Our data did not support the hypothesis that tree hollows provide a stable or warmer thermal environment, since the thermal properties inside tree hollows were not different from those of other microhabitats used by pythons. Similarly, studies of diurnal roost sites used by microbats found trunk hollows had significantly larger entrances and internal volumes than knot-hole cavities, and

temperatures within trunk hollows were much less stable, often fluctuating in the same way as ambient temperature (Sedgeley, 2001). The large dimensions necessary to allow a python entry would therefore expose these hollows to ambient conditions. Additionally, heat transfer (convection, radiation, and conduction) and thus the microclimate of a tree hollow may be affected by differing thickness of the hollow walls, the size of the hollow entrance and the amount of solar radiation reaching the tree (Bakken & Kunz, 1988). Early-decaying branches or trunks will have thicker hardwood surrounding the internal hollow (Whitford & Williams, 2002), but the hollows are likely to be too small for a python to occupy. Larger, older hollows suitable for a python are likely to be located in a completely decayed branch or trunk, will have thinner hardwood surrounds (Gibbons & Lindenmayer, 2002; Whitford, 2002; Whitford & Williams, 2002), and this may reduce the thermal insulating properties (Sedgeley, 2001). Possibly even more importantly, having a sufficiently large entrance and internal dimensions to allow a python residence is likely to result in rapid heat exchange with air temperature, and therefore these tree hollows are likely to exhibit temperatures similar to air temperature, with only minimal buffering of temperature fluctuations. In summary, there was no indication that tree hollow temperatures differed from air temperature, and therefore we have no data to suggest that this microhabitat provides a more favourable thermal environment over winter compared with other microhabitats used by pythons.

### **Is there an energy saving by using tree hollows?**

While sequestered inside a tree hollow, pythons forfeit basking opportunities that would enable them to increase their body temperature. The choice to remain sequestered inside a tree hollow and forgo basking over winter was reflected in python body temperature measurements. Both monthly average and maximum values of body temperatures were colder for pythons sequestering inside tree hollows compared with pythons that did not use tree hollows. Pythons experienced a greater range of body temperature when they utilized other microhabitats compared with pythons that sequestered in tree hollows.

It could be argued that an ectotherm attempting to minimize energy losses should select temperatures as low as possible (Huey, 1991). Because pythons that used tree hollows had lower body temperatures

(cf. animals occupying other microhabitats) we predicted there may be an energy saving to using a tree hollow over winter by decreasing metabolic rate and consequently reduce their rate of body condition decline. However, our data do not support this prediction. We observed no difference in the overall decline in body condition of pythons using tree hollows compared with pythons using alternative winter microhabitats. Our prediction assumed that none of the pythons feed over winter (Slip & Shine, 1988a); we note that because pythons that remained on the ground achieved higher maximum body temperatures, they may have taken more prey over this time than animals sequestered in a hollow. Taking this caveat into account, however, we have no support for a slower rate of body condition decline for pythons that used tree hollows.

### **Do pythons access more arboreal prey?**

It is possible that pythons use tree hollows because they provide a source of accessible prey. It is difficult to be certain that pythons, particularly those that spent many months sequestered in hollows, did not have access to prey. However, even though birds and arboreal mammals use tree hollows for retreat and nesting sites, it is unlikely that pythons are using tree hollows at this time of year in order to gain access to prey, since we suspect these animals were unlikely to be feeding at this time. Usually at  $T_b < 10^\circ\text{C}$ , digestion is inhibited, and snakes will regurgitate their food (Lillywhite, 1987). Pythons that used tree hollows were colder, and, therefore, less likely to feed compared with animals that remained on the ground. Furthermore, our radiotelemetry data indicated that pythons fed infrequently over winter, and that the majority of prey species consumed by pythons were terrestrial with only a small percentage of prey species identified as largely arboreal.

### **Do tree hollows offer protection from predation?**

Tree hollows may provide pythons protection from predators over winter, when their minimum body temperatures averaged  $6.25 \pm 2.73^\circ\text{C}$  (jarrah forest) and  $9.84 \pm 2.36^\circ\text{C}$  (coastal woodland). At such low temperatures, the perception of a predator and response to its presence (i.e. flight or fight response) would undoubtedly be hindered. For example, tongue-flicking is necessary for chemoreception in snakes (Peterson, Gibson & Dorcas, 1993), and in numerous species, optimal body

temperature is important for effective prey detection and may also be important for predator detection, escape and defensive behaviour (Dorcas & Peterson, 2007). Defensive behaviours (e.g. hissing, striking and biting) are exhibited more often in three species of colubrid snakes at high air temperatures (between 20–30°C; Vincent, Herrel & Irschick, 2004), and increasing body temperature exponentially increases both the crawling and escape speeds (reaching and hiding its body in a rock crevice) of rubber boas (*Charina bottae*; Dorcas & Peterson, 2007). Cold pythons would therefore be more vulnerable to predation. For many reptile species, the risk of predation is significantly increased if individuals bask in the open such as on rocks or in open vegetation (Dorcas & Peterson, 1998; Martin & Lopez, 1999). Tree hollow retreats may therefore provide a safehouse over winter while python body temperatures are at their minimum, and hence behavioural and physiological responses are slowest.

A number of potential predator species were evident at these study sites, including the introduced red fox and varanid lizards (Table 3). Most of the predators identified at these sites are terrestrial hunters. It could be argued that hollow logs on the ground have similar features as tree hollows, and therefore provide similar habitat for pythons. However, while hollow logs are used extensively over summer months (Fig. 3), only 2% of observations of pythons showed that they used hollow logs in winter (cf. 56% of observations over winter were for tree hollows). While there is no difference in the thermal conditions inside hollow logs cf. tree hollows there is likely to be a very different predation risk to pythons. While it would be difficult for a terrestrial predator to remove a python from a tree hollow, over past centuries, man and now extinct carnivorous marsupials may easily have hunted and captured a cold-bodied python sequestered in a hollow log, as can terrestrial predators present today. Although we have no direct evidence to suggest that tree hollows offer protection from predation, this hypothesis warrants further investigation.

Our results highlight the importance of understanding this threatened species' physiology and ecology for improving conservation management outcomes. Tree hollows appear to provide pythons with an important resource over winter months. We have no evidence to suggest that tree hollows provide a more stable thermal environment, although pythons sequestered within tree hollows maintain lower

and less variable body temperature. Although this should have resulted in a lowered metabolic rate, we did not find a statistically significant saving in terms of reduced decline in body condition over winter. It is unlikely that pythons use tree hollows as a source of prey (since they feed infrequently if at all over winter), but they are likely to provide a safe retreat from predators. The presence of numerous predators at both study sites, including mammals such as red foxes and feral cats, suggests there is a risk of predation. Tree hollows are a limited resource due the long time for hollows to form in trees (Whitford & Williams, 2002), the vast expanses of land clearing for forestry, housing and other infrastructure, along with competition with other fauna. Their importance to a wide variety of animal species needs to be recognized and taken into account as part of conservation management.

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Figure 1. Average ( $\pm 1$  SD) daily air temperature at the coastal woodland and jarrah forest study sites were similar for most of the year except during winter/early spring months (June–September), where the jarrah forest has lower daily average ambient temperatures. \*Indicates significant difference between the study sites  $P < 0.001$ .

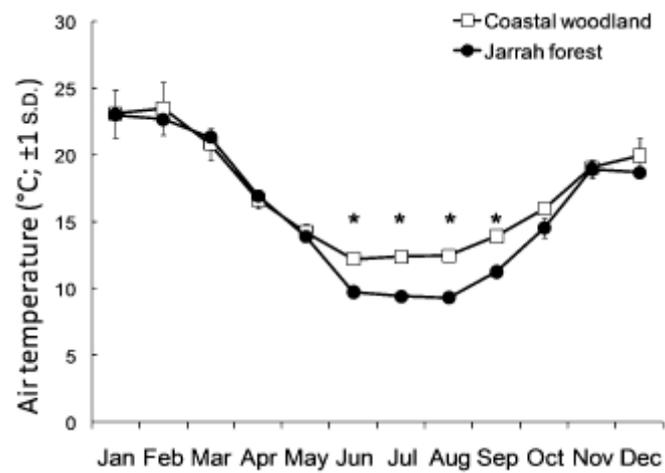


Figure 2. Scatter plot of the body mass ( $M_b$ , g) of *Morelia spilota imbricata* relative to their snout-vent length (SVL, cm). There was no statistically significant difference between equations describing males ( $X$ :  $M_b = 2.43 \times \text{SVL} - 2.36$ ,  $R^2 = 0.66$ ,  $n = 21$ ) and females ( $\Delta$ :  $M_b = 2.40 \times \text{SVL} - 2.23$ ,  $R^2 = 0.65$ ,  $n = 24$ ;  $F_{\text{slope } 1,42} = 0.19$ ,  $P = 0.666$ ), so the common equation was used. The least-squares linear regression of best fit is shown by the line, where Predicted  $\text{Log}_{10}\text{-}M_b$  (g) =  $2.90 \times \text{Log}_{10}\text{-SVL}$  (cm) - 3.34,  $R^2 = 0.876$ .

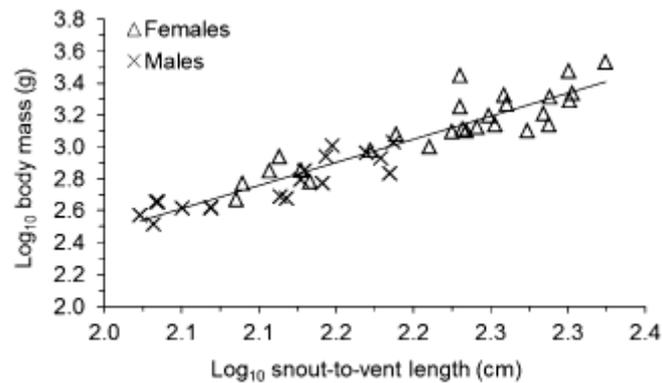


Figure 3. The use of five microhabitats by *Morelia spilota imbricata* shown by calendar month. Tree hollow use increased during winter months, while use of hollow logs decreased. See methods for detailed description of each microhabitat. Data is collated over 3 years of radiotelemetry monitoring of 46 pythons at both coastal woodland and jarrah forest sites.  $N$  = total number of pythons observed each month.

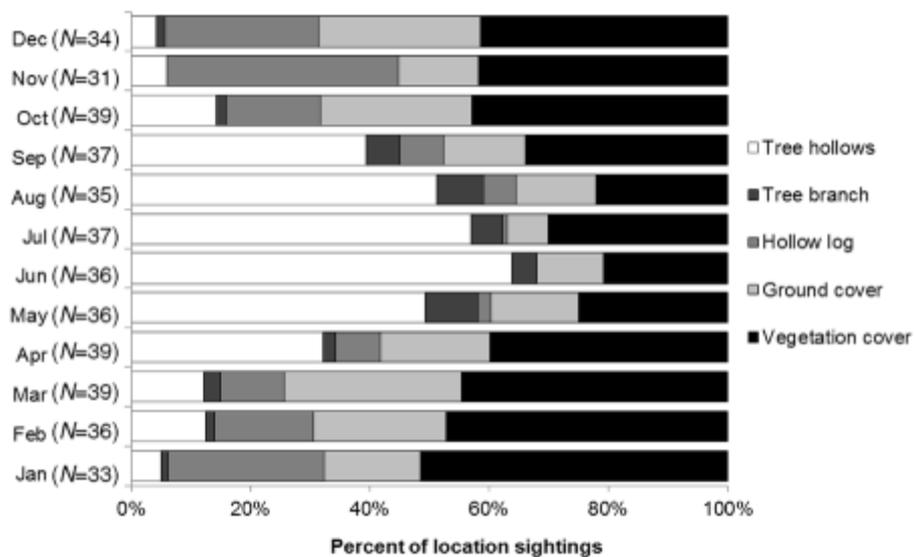


Figure 4. Box plot illustrating temperature for the five microhabitats used by *Morelia spilota imbricata*. There was no measureable difference in the winter (June–August) in daily average, minimum and maximum or range of temperatures for five microhabitat types ( $P > 0.06$ ). Jarrah forest daily average temperatures for the five microhabitats were, however, colder than experienced in coastal woodland ( $F_{1,3,42} = 21.32, P < 0.05$ ). The median is identified by a line inside the box. The length of the box is the interquartile range (IQR). \*Indicates outlier values more than 1.5 the interquartile range (IQR), but less than 3 IQR's from the end of the box. \*Indicates values more than 3 IQR's from the end of the box.

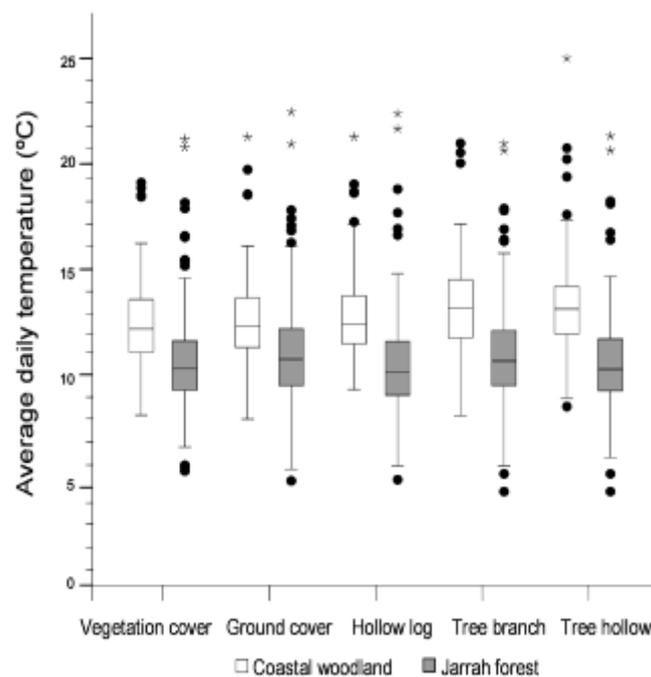


Figure 5. Four measures of python body temperature recorded over a 7-month period (April–October) when *Morelia spilota imbricata* made use of tree hollows. Average ( $\pm 1$  sd) monthly body temperature (a), maximum body temperature (c) and the range in body temperature recordings (d) were lower for pythons sequestered inside tree hollows compared with those that did not use a tree hollow over this period. There was no difference for minimum body temperature (b). The closed symbols represent jarrah forest pythons, open symbols represent coastal pythons. Circles indicate pythons using tree hollows (TH); squares indicate pythons that did not use tree hollows (NTH) (ground to <2 m-level vegetation). Letters link groups that are not significantly different ( $P > 0.05$ ). Data is shown where there are three or more pythons for each category for each month, as indicated in the table below the figure.

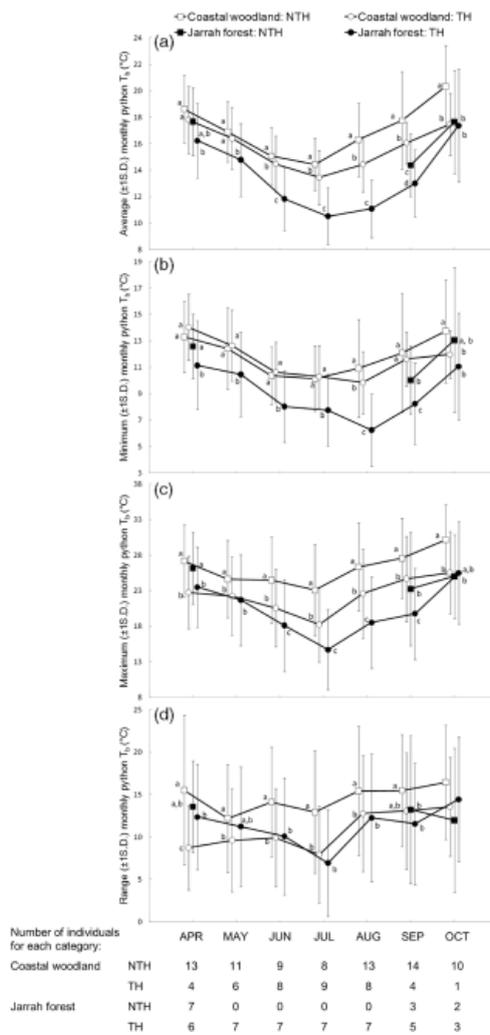


Figure 6. The rate of body condition decline ( $\beta$ -BCS) was not significantly reduced for *Morelia spilota imbricata* that used tree hollows over winter compared with those that did not (NTH; average  $\pm$  1 sd). For pythons that used tree hollows over winter, males spent less time ( $101 \pm 49.7$  days) in tree hollows compared with females ( $136 \pm 50.3$  days), yet showed a faster decline in body condition (lower  $\beta$ -BCS) compared with females.

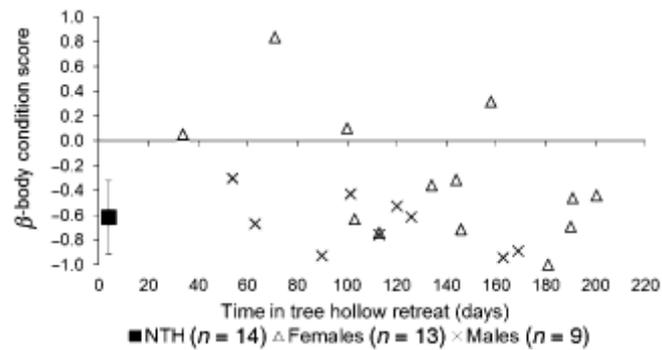


Table 1. Multiple regression output for analyses addressing three questions: (1) Which factors influence the change in body condition ( $\beta$ -BCS)? (2) Which factors influence how long pythons stay sequestered in tree hollows? and (3) Which factors affect the change in body condition ( $\beta$ -BCS) for pythons that use tree hollows over winter?

Independent factors:	(1) Change in body condition ( $\beta$ -BCS; $n = 36$ )		(2) Length of time in tree hollow (days; $n = 22$ )		(3) Change in body condition ( $\beta$ -BCS) for tree hollow users ( $n = 22$ )	
	$t_{31}$	$P$ -value	$t_{17}$	$P$ -value	$t_{17}$	$P$ -value
Study site (C or JF)	-1.65	0.11	1.6	0.129	-0.624	0.541
Sex (F or M)	-1.33	0.194	-2.23	0.04	-2.18	0.043
Body size (Log <sub>10</sub> avg. SVL)	1.33	0.194	-0.871	0.396	1.09	0.292
Tree hollow user or not	0.542	0.592	-	-	-	-
Change in body condition ( $\beta$ -BCS)	-	-	-1.64	0.12	-	-
Time in tree hollow (days)	-	-	-	-	-1.64	0.12

Table 2. The spatial ecology of prey species identified from *Morelia spilota imbricata* scats opportunistically collected from radiotracked individuals in coastal woodland and jarrah forest of Western Australia

<b>Spatial ecology of prey species</b>	<b>Examples of prey species identified</b>	<b>Total no. of scats (% of total)</b>
Arboreal	<i>Pseudocheirus occidentalis</i>	18 (21%)
Mostly arboreal	Parrots <i>Trichosurus vulpecula</i>	7 (8%)
Ground dwelling to mid-storey vegetation	<i>Antechinus flavipes</i> <i>Felis catus</i> <i>Mus musculus</i>	7 (8%)
Mostly ground dwelling	<i>Rattus rattus</i> <i>Sminthopsis griseoventer</i> <i>Betongia pencillata ogilbyi</i>	31 (35%)
Ground dwelling	<i>Oryctolagus cuniculus</i>	24 (28%)
Total	<i>Tiliqua rugosa rugosa</i>	87

Table 3. Possible predators of *Morelia spilota imbricata* pythons at the two study sites in south-west Western Australia and evidence for predation upon *M. s. imbricata* and *M. s. spilota* (eastern Australia)

Predator	Species	Jarrah forest	Coastal woodland	Habitat	Evidence for predation	Reference
Lizards	<i>Varanus gouldii</i>	Present	Present	Terrestrial	Yes	<i>V. rosenbergi</i> attempted predation on <i>M. s. imbricata</i> (This study, Bryant pers. obs.)
	<i>Varanus rosenbergi</i>	Present	Present			<i>V. varius</i> predating on <i>M. s. spilota</i> (Shine & Fitzgerald, 1996)
Feral mammals	<i>Vulpes vulpes</i>	Present	Present	Terrestrial	Yes	Fox DNA found on radiotransmitter and body of dead python (This study)
	<i>Felis catus</i>	Present	Present			Semi-arboreal
Birds of prey	<i>Aquila audax</i>	Present	Present	Aerial	Limited (very few snake remains found in scats/pellets)	Cherriman, (2008)
	<i>Haliastur sphenurus</i>	Uncommon	Present			Limited (small reptiles)