

**ECOLOGY AND PHYSIOLOGY OF PYTHONS  
FROM THE NORTHERN TERRITORY OF  
AUSTRALIA**

**Gavin S. Bedford**

**B. Ec. (Flinders University), Grad. Dip. Sc. (NTU),  
M.Sc. (NTU)**

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## Dedication

One balmy summer's afternoon Peter Comber and I climbed to the top of the western facing cliff at Ormiston Gorge, west MacDonnell ranges. Hidden in the rocks on the cliff top were 5 Stimson's pythons just waiting to donate blood for isotope analysis. The idyllic scene of late afternoon sun painting the sky blue and orange, combined with blackfooted rock wallabies bounding everywhere was mesmerising. As usual we chatted while climbing the cliff until we reached a large cone shaped rock, 1 metre from the cliff edge. This rock was about 1 metre tall, sticking out of the ground like a fallen spire at a 45° angle to the ground and pointing away from the cliff edge. Beneath this rock according to the receiving signal was the first python. The radio receiving gear around my neck was heavy and in the way, so I bent down to place it on a rock behind me. Turning around I saw Pete standing on the cliff edge, hands on to the top of the rock spire, give an almighty heave back toward the cliff. NOOO I screamed, seemingly in slow motion, watching in horror as the rock broke into three pieces in his hands. His entire body momentum stopped at the same instant the rock broke. The smallest piece of rock, about the size of a football, was still in Petes' hands. Oblivious to what had just happened, Pete just went looking for the snake, unaware of his split second brush with a 40m free-fall onto rocks.

To this day it haunts me. The nightmare of having to tell his family he isn't coming home because he was helping me wakes me with monotonous regularity.

So much has been done by so many for me, to them I am most grateful, but the above incident has me questioning it's worth! Hopefully this thesis repays that help and provides some answers!

## AUTHOR'S DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

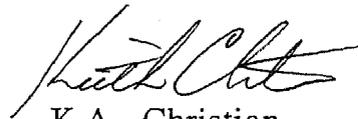
A handwritten signature in black ink, appearing to read 'G.S. Bedford', is centered on the page.

G.S. Bedford.

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## SUPERVISOR'S DECLARATION

I believe that this thesis is properly presented and conforms to the specifications of thesis presentation in the University and is prima facie worthy of examination.



K.A. Christian

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## Acknowledgments

Back in 1989 while working in a bank I had a chance meeting with Keith Christian that changed my life. From that meeting until now we have been a very effective team, producing some 22 published papers, with a number still to be published. Not only do I consider myself fortunate for that meeting, his supervision over three degrees and continued teamwork, but also for the reciprocated friendship. To him I am forever grateful.

Dr Brian Green and Keith Newgrain were great, helping with isotope analysis, manuscripts and sanity. My lovely wife Anna was an endless source of comfort and inspiration, presenting me with a baby boy some months before I had finished this thesis; obviously sick of waiting.

I would particularly like to thank Dr Tim Schultz, Peter and Jo Comber, Greg and Reg Fyfe, Steve Eldridge and Dr Rachel Paltridge all of whom helped in many ways. McCafferteys Bus Service provided free bus travel for me between Darwin and Alice Springs. They were courteous, friendly and always helpful, and I am extremely grateful for their help. Jim Hayes from 'Undoolya Station', allowed access to the study site in Alice. Northern Territory Parks and Wildlife Commission staff from the top down helped where they could and I thank them all including – Greg Fyfe, Peter Comber, Greg O'Neil, Dave Scammell, Barry Scott, Steve Eldridge, Beck Harmel, Michael Barrett, Roana O'Neil, Dr Lyn Day, Dr David Lawson, Dr Bill Freeland, Dr Tony Boland, Paul Caywood, Mike Haywood, Graham Horne and thanks also to any others I have missed. The many helpers who came for a herp, I thank you all. Dr Greg Leech and Graham and Dannielle Pritchard allowed access to the Botanic Gardens in Darwin. Pam Wickham and the staff at Windows on the Wetlands, an

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The three F's were a major inspiration: Family, Friends and Fish – I lost some of each along the way.

Grants were provided by the Australian Research Council and the Northern Territory University, while permits were provided by Parks and Wildlife NT and the Animal Experimentation Ethics Committee of the Northern Territory University.

Over this project I found new ways to lose pythons. This list is not exhaustive but includes: fire, flood, shot, stoned, stomped on, dehydrated, thermal shock, fell out of trees, eaten, bashed, run over, crushed under rocks, wedged in crevices, attacked by possum, flying fox, dog, cat, perentie, king brown snakes, attacked by people, etc. If my interference has in some way expedited their demise, I sincerely apologise.

*Live your dream, don't dream to live.*

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## Summary

Pythons are found over much of the Australian mainland and comprise a group of animals that have been poorly studied in the field to date. In this study, I investigated the biology of some python species (*Morelia spilota variegata*, *M.s.bredli*, *Antaresia childreni*, *A. stimsoni* and *Liasis fuscus*) that vary in habitat, size, climate and prey type using eco-physiological methods such as laboratory metabolism and energy expenditure in the field using isotopic techniques. With such obvious variation in life history variables between species, some aspects of their biology are inferred from experiments on a single species. This was due mostly to the logistical problem of obtaining sufficient numbers of each species for both field and laboratory investigation.

Laboratory techniques were used to investigate the metabolic rate of *Liasis fuscus* after feeding and while fasting. I found they are capable of reducing metabolic rate while fasting to a very low level, a level that can be considered a depressed metabolic rate. This low metabolic rate while fasting represents a new model for metabolic depression. After feeding, metabolic rate increased about 12 times standard metabolic rate, a level somewhat lower than reported for some other species of python.

To understand the energetics of these python species it was necessary to exercise them to obtain maximum metabolic rate ( $\dot{V}_{O_2 \max}$ ). Problems with pythons exercising on a treadmill in a manner similar to lizards forced me to investigate alternate methods. I therefore exercised pythons without a mask for a few minutes before placing the mask on them and keeping them moving. This process was repeated until the animal was exhausted. This method gave similar results to the conventional mask method and thus an overall value of  $\dot{V}_{O_2 \max}$  for each

species. These values were then incorporated in an energy budget for each species.

Pythons are among the very few reptiles that show parental care for their eggs. In fact, they not only protect the eggs, but in many instances they shiver around their clutch creating heat that is used to maintain a high clutch temperature until hatching. While investigating this phenomenon in the laboratory, I found that there were two different modes of shivering (mammal-like and pulse). Over the period of a minute, the mammalian method created approximately three times more heat, and this involved three times the time of muscle movement compared to the pulse method. I found that the metabolic rate of some pythons shivering on their eggs decreased as body temperature increased, a rare instance in the thermal sensitivity of metabolism ( $Q_{10} = -3.69$ ) in a vertebrate ectotherm.

It was necessary to have some understanding of the spatial and thermal ecology of the five species of pythons examined in this study so that the energy used could be apportioned to the various activities in an energy budget. Most pythons were found in high densities, with the carpet pythons being arboreal most of the time, children's and Stimson's pythons were arboreal some of the time, and the water python was entirely terrestrial. Many pythons spent considerable time (up to 330 days) in a single refuge site. I found that python body temperature correlated with air temperature through the day to allow them to attain a body temperature near 30°C immediately before dark each day except in winter for the desert carpet pythons.

Data from the first five chapters were incorporated into energy budgets for the five species of python. I found that there was a large difference in energy use in pythons between the wet-dry tropics and the arid zone species in the Northern Territory. Similarly there was a significant

difference in energy use between seasons in each of the python species investigated. Per year, the terrestrial water pythons used an amount of energy equivalent to a food consumption more than four times their body mass, and this was almost twice as much energy as the next highest species. In contrast, the desert species only needed to consume approximately their own body mass in food per year to survive.

Our understanding of the ecology of pythons has been enhanced by this study, with many new and exciting findings that have in some instances changed our understanding of these Australian super predators. The use of physiological tools to interpret general biology is not new, but this study highlights the need to revisit the ecology of python species from more extreme temperate regions in order to understand the extent of metabolic depression and its effect on the overall energy budget.



*Morelia spilota bredli* – This large python is found in the ranges of central Australia.

## **Introduction**

This thesis has been written as a series of papers that bring together the ecology and physiology of five species of python found in the Northern Territory of Australia. Each paper is a separate entity, but the papers are combined here as a thesis to give a more meaningful and global understanding of python biology. Although there will be obvious variation in some of the life history variables between species of python, some aspects of their biology are inferred from experiments on

a single species. This was due mostly to the logistical problem of obtaining sufficient numbers of each species for both field and laboratory investigation.

The first five Chapters expound different aspects of python biology which are then linked to overall energy use at both the individual and population level in Chapter six. Each paper has either been published or submitted for review in peer reviewed journals.

### **Chapter One**

Pythons are capable of consuming large food items compared to body mass, and this capacity is balanced by the extreme length of time pythons are capable of surviving without food. This chapter examines the extreme case of feeding and fasting in the Australian water python (*Liasis fuscus*).

### **Chapter Two**

The maximum metabolic rate ( $\dot{V}_{O_2\max}$ ) during exercise was examined in five species of python from the Northern Territory using a new method. Due to the inherent difficulty in convincing pythons to run on a treadmill in a manner similar to lizards, I investigated a new method of obtaining  $\dot{V}_{O_2\max}$  that I term the grab method.

### **Chapter Three**

Some pythons are able to raise body temperature while brooding eggs through a process known as shivering thermogenesis. Obtaining gravid pythons was difficult, but with a few animals, I was able to compare the metabolic costs of shivering thermogenesis among some species. This metabolic cost was also compared to the metabolic costs of feeding and exercise.

### **Chapter Four**

The spatial ecology and home ranges of four species of python were examined. The home ranges of only a few snakes and very few pythons have been determined. This paper examines the use of habitat in pythons from the tropical north and compares the results with habitat use in species from the desert. These species were latitudinally separated by over 1500 km.

### **Chapter Five**

Thermoregulation has occupied a significant part of the study of reptile biology for more than half a century, but to date there have only been two studies on the field body temperatures of pythons. I examined the seasonal aspects of temperature for four species of python. Some of these species were also geographically separated, so that both seasonal and latitudinal differences were investigated.

## **Chapter Six**

The field metabolic rate of pythons and the associated food, energy and water use in the field has never been examined. The total energy costs associated with feeding, fasting, exercise and temperature are integrated in an energy budget that compares seasonal and latitudinal differences for some species of python. These energy budgets allow conclusions to be drawn on other aspects of python biology such as the frequency of feeding, the use of habitat, level of activity and population density.

## **Synthesis**

I summarise the findings in each chapter and present a synthesis of conclusions on the ecology and physiology of pythons from two climatic zones from the Northern Territory of Australia.

## Chapter 1

### Metabolic response to feeding and fasting in the water python (*Liasis fuscus*)



An example of a python consuming a large meal, in this instance *Liasis olivaceus*

This Chapter has been published as follows:

Bedford, G. S., and Christian, K. A. (2001). Metabolic response to feeding and fasting in the water python (*Liasis fuscus*). *Australian Journal of Zoology* **49**:379-387.

**Abstract**

Compared to other reptiles, pythons have a relatively low standard metabolic rate (SMR) when post-absorptive, but metabolism increases substantially after feeding. This study examined the effects of feeding and fasting on adult and hatchling water pythons (*Liasis fuscus*). I compared ratios of peak digestive metabolic rate (PDMR) after feeding with the metabolic rate of both post-absorptive (SMR) and fasted water pythons. If metabolic rate of a fasting snake is taken as 'SMR', then the ratio PDMR/SMR becomes increasingly exaggerated as fasting continues. After 56 days of fasting in adults, or after 45 days in hatchlings, the metabolic rate of water pythons was significantly lower than that of post-absorptive animals. Peak digestive metabolic rate of post-absorptive adult water pythons was only 6.3 to 12.0 times SMR, but the ratio was twice that if fasted (metabolically depressed) animals were used to determine the "SMR" denominator. Thus, this ratio should be used with caution. Peak digestive metabolic rate after feeding increased with increasing meal size for meals less than 20% of body mass, but PDMR did not increase for meals between 20% and 39% of body mass for adult water pythons. Similarly, the PDMR did not increase significantly between 25% and 50% meal sizes for hatchlings. The digestive physiology of water pythons is apparently better suited to frequent meals of relatively small prey than the digestive physiology of some other pythons.

## Introduction

Standard metabolic rate (SMR) has been a useful benchmark in the study of ectotherms because it represents a repeatable minimum measure of the energy needed for life maintenance in reptiles (Bennett and Dawson 1976). Conventionally, SMR is measured from an ectotherm that is inactive and in a post-absorptive state (Kleiber 1975; Bennett and Dawson 1976; Niewiarowski and Waldschmidt 1992).

Pythons have both a very low SMR (Bennett and Dawson 1976; Andrews and Pough 1985; Chappell and Ellis 1987), and, under at least two circumstances, the capacity to raise their metabolic rate many times above SMR. Metabolic rate is substantially elevated up to 22 times SMR during the brooding of eggs (Harlow and Grigg 1984; Slip and Shine 1988a) and up to 45 times SMR after feeding (Benedict 1932; Secor 1995; Secor and Diamond 1995, 1997, 2000; Thompson and Withers 1999). In the Burmese python, the peak digestive metabolic rate (PDMR) is positively correlated with the amount of food eaten (Secor and Diamond 1997).

The increased metabolism during digestion is commonly referred to as specific dynamic action (SDA), and is characteristic of most animals. Generally, metabolism increases by 25 to 50% above SMR in mammals (Brody 1945), 60 to 160% in fish (Jobling 1981) and 200% in *Alligator mississippiensis* (Coulson and Hernandez 1979). Much larger increases in

metabolism after feeding were reported for pythons over half a century ago (Benedict 1932). Recently the peak digestive metabolic rate in pythons has been reported as being between seven and 45 times SMR (Secor and Diamond 1995, 1997).

The relatively large increase in oxygen consumption during digestion in pythons compared to mammals is attributable to three factors: (1) the relatively large meal size consumed by pythons, which can be more than 100% of their body mass (Pope 1961; Mavromichalis and Bloem 1994); (2) the low SMR of pythons (Andrews and Pough 1985; Chappell and Ellis 1987); and (3) the ability of pythons to atrophy the gut and other organs during periods of fasting (Secor and Diamond 1995, 2000). It is possible that considerable energy is needed to maintain the gut in an active mode. Presumably as a mechanism to conserve energy, pythons have refined the ability to atrophy the gut and other organs after digestion (Secor and Diamond 1995, 2000). Some large pythons have fasted for more than two years without obvious detrimental effects (Benedict 1932; Slip and Shine 1988b).

This study reports post-absorptive SMR, PDMR after feeding, and metabolic rate as a function of fasting duration for hatchling and adult water pythons (*Liasis fuscus*). I also examine the extent to which PDMR is affected by relative meal size, evaluate the index of metabolic increase as expressed by

PDMR/SMR, and discuss how the conditions under which SMR is measured can influence this index.

## **Materials and Methods**

### *Animals, maintenance and sampling*

Water pythons (*Liasis fuscus*) are medium sized pythons reaching a maximum length of three metres (Barker and Barker 1994). They are endemic to areas of high annual rainfall in the tropical northern part of the Australian mainland (Shine 1991; Cogger 2000). Water pythons, like most pythons, are nocturnal hunters that feed on birds and mammals (Barker and Barker 1994). This species is considered a sit-and-wait ambush predator, but may also actively forage when food is abundant (Madsen and Shine 1996a, personal observation).

Five adult *L. fuscus* were caught from the Fogg Dam area, 75 km east of Darwin, Northern Territory. All animals were at least 1 m long, with masses ranging from 314 to 2200 g and considered to be adult (Shine 1991). They were housed in individual plastic cages at the Northern Territory University. These cages were maintained in an outside animal house, and exposed to ambient shaded conditions for Darwin in the wet season (Christian and Bedford 1995). All animals were offered food once per week and were eating consistently before experiments commenced.

Twelve captive-hatched water pythons were housed in 4 L plastic containers and maintained at a temperature of 30°C in a constant temperature room for the duration of experiments. These animals were randomly selected from six clutches hatched from wild caught females in August. These hatchling water pythons had masses ranging from 25.0 to 60.5 g. Metabolic rate was determined at hatching. They were then fasted for six weeks before being fed dead laboratory mice equalling 10% of their mass, from which point feeding and fasting experiments commenced.

*Metabolic response to feeding*

Adult animals were fed meals consisting of 5%, 10%, 20% and 25% ( $\pm < 1\%$ ) of body mass and also fed more than 30% (range: 30 – 39%) of their body mass. Hatchlings were fed mice equalling  $25 \pm 2\%$ ,  $35 \pm 3\%$  and  $50 \pm 4\%$  of their body mass. Attempts were also made to feed hatchling animals meals of small mice totalling 75% of their body mass. The timing of each feeding event was at least two month intervals. Animals were fed the relative meal masses in no particular order. When feeding experiments were complete, fasting experiments began immediately.

During feeding and fasting experiments, each animal was placed in a perspex chamber inside a constant temperature cabinet (Forma Scientific) at 30°C. Open system respirometry was used to measure the metabolic response to digestion. Three animals were placed in

individual chambers with air samples drawn consecutively from each of the animal chambers for a period of two hours. Samples were drawn on a rotating basis over a 12 hour period during daylight hours therefore each animal was monitored for a total of four hours over the twelve hour period during the period when pythons are inactive. Metabolism was taken as the lowest stable measurements of oxygen consumption over a period of at least 40 minutes. Oxygen concentrations were measured with an Applied Electrochemistry S-3A oxygen analyser with rates of oxygen consumption calculated by the methods of Withers (1977).

To be certain that animals had completed the metabolic response to feeding, the period of 10 to 14 days after a moderate sized meal (30% or less of body mass) was selected to represent post-absorptive SMR (Bedford 1996; Thompson and Withers 1999).

Oxygen consumption was measured continuously over the first three days after feeding to obtain the peak level of consumption. However, in this and other unpublished studies of pythons, day two after feeding was consistently the time when oxygen consumption peaked at 30°C; thus measurements of PDMR were obtained from day two data.

### *Metabolic response to fasting*

To determine the effect of fasting on metabolism, adult and hatchling *L. fuscus* were fasted for 98 and 114 days respectively. They were given water once a week, but no food. Metabolic rate was measured at various intervals during fasting. Hatchling animals were placed in a constant temperature room at 30°C and given water once a week throughout the 114 days of their fast. No animal was measured during ecdysis.

### *Statistical analyses*

Measurements of metabolic rate immediately post-absorptive, after feeding, and after having fasted for some length of time were analysed statistically using analysis of covariance (ANCOVA) for adult water pythons, and repeated measures ANCOVA were used to analyse hatchling water pythons. All data were log-transformed, with log-mass as a covariate. Systat statistics package (Version 5.2 1992) was used for the repeated measures ANCOVA. All other data were analysed using Statview and SuperAnova statistics packages.

## **Results**

### *Adult Water Pythons*

There was no significant difference between post-absorptive SMR (measured between days 10 to 14 after feeding) and PDMR in pythons fed meals that were 5% or 10% of body mass (ANCOVA  $P > 0.05$ ). However, PDMR was significantly higher than post-absorptive SMR when animals were fed 20%,

25% or more than 30% of their body mass in food (ANCOVA  $F_{4,26} = 3.12$ ,  $P = 0.03$ ). The PDMR of oxygen consumption of pythons fed meals 20%, 25% or >30% of their body mass were not different from each other (ANCOVA  $P > 0.05$ ). Thus, it appears that oxygen consumption plateaus with meal sizes between 20% and 39% of body mass (Fig. 1.1).

Animals were fasted for 98 days, and oxygen consumption measurements were taken on the same day of the week at weekly intervals. Day 56 (six weeks after SMR measurements were taken) is the first measurement for which oxygen consumption had declined to a value which was significantly lower than SMR ( $F_{8,25} = 10.87$ ;  $P = 0.0001$ ; SMR =  $0.034 \text{ ml g}^{-1} \text{ h}^{-1}$ ;  $\pm 0.016$  s.d.; mean after 56 days =  $0.024 \text{ ml g}^{-1} \text{ h}^{-1}$ ;  $\pm 0.016$  s.d.). A post-hoc Fisher's test revealed that all days examined thereafter were significantly lower than SMR (Fig. 1.1).

The mean ratios determined by dividing PDMR by post-absorptive SMR are shown by the solid circles in Fig. 1.2. These ratios varied from no appreciable difference from SMR for animals that had consumed a meal equalling 5% of their body mass to a maximum of 8.3 for an animal that had consumed food equalling 20% of its body mass. The open circles in Fig. 1.2 are mean ratios calculated using PDMR divided by the metabolism of pythons fasted for 98 days. Although both ratios plateau with meal mass greater than 20% of body mass, the values calculated using the metabolism

of fasted animals as the denominator are almost twice those of data using the SMR in the denominator.

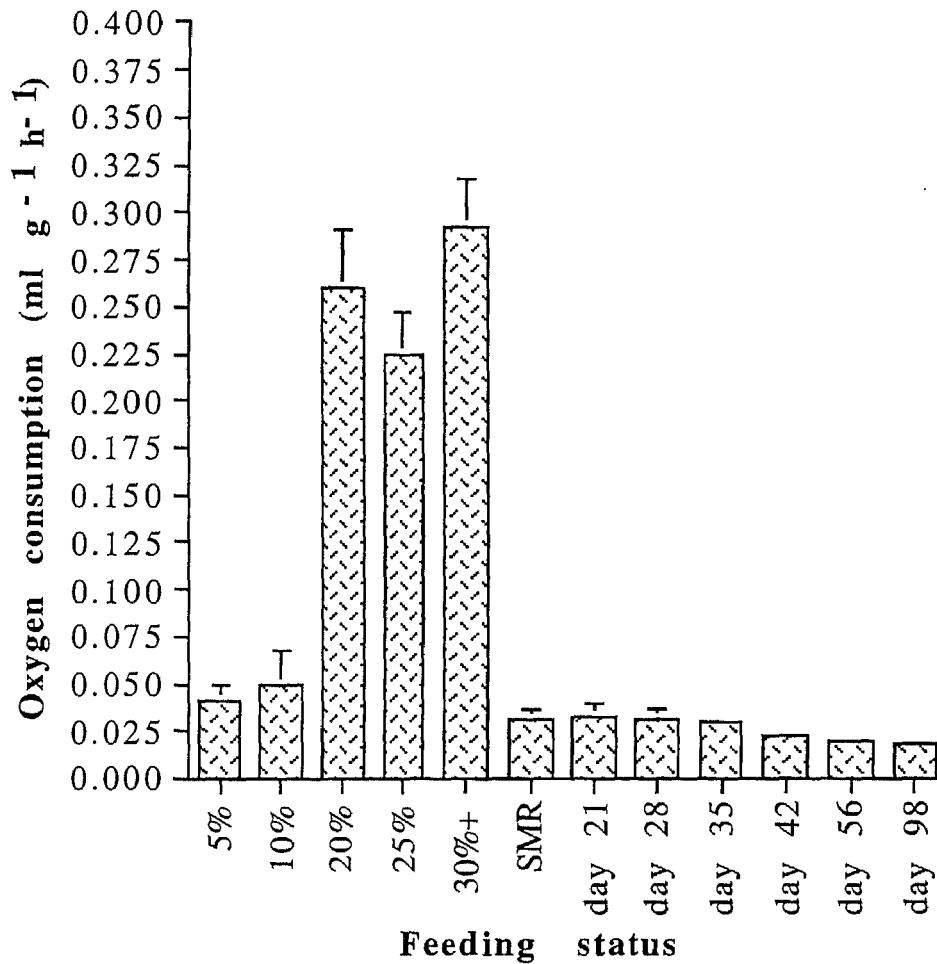


Figure 1.1. Metabolism after feeding (% values refer to size of meal relative to body size) and during a fasting period in adult water pythons (*Liasis fuscus*)(n = 5). Value of SMR was measured 10 to 14 days after a small meal (<10% body mass). Days 21 – 98 are days after a meal. Error bars indicate standard errors.

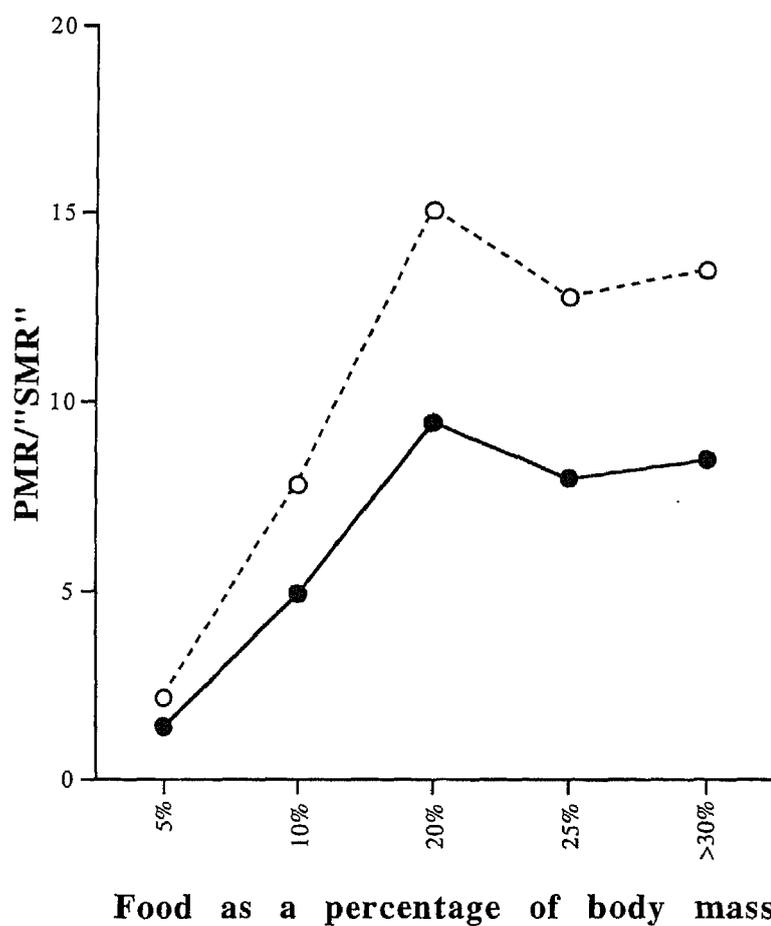


Figure 1.2. Mean PDMR/"SMR" ratios for increasing meal size relative to body mass in adult water pythons. Solid circles are mean values calculated using post-absorptive SMR (10 to 14 days after feeding) as the denominator, and open circles are mean ratios calculated using the metabolism of pythons after 98 days of fasting as the denominator.

### Hatchling Water Pythons

Peak digestive metabolic rate was significantly higher than post-absorptive SMR for hatchlings fed 25, 35 and 50% of their body mass in food (ANCOVA  $F_{3,13} = 6.9$ ,  $P = 0.005$ ). The rates of oxygen consumption of hatchlings fed 25%, 35% and 50% were not significantly different from each other (ANCOVA  $P > 0.05$ ) (Fig. 3). Metabolic rate within three days of hatching was high ( $0.274 \text{ mlg}^{-1}\text{h}^{-1}$ ,  $SD \pm 0.136$ ,  $n = 8$ ) but not significantly different from the feeding categories, 25, 35, and 50% (ANCOVA  $P > 0.05$ ).

When metabolic rate was measured forty-five days after the commencement of fasting, hatchling metabolic rate had declined to a level significantly lower than SMR (repeated measures ANCOVA  $F_{3,24} = 2.6$ ,  $P = 0.03$ ). One hundred and fourteen days after feeding, metabolic rate was only 32.4% of post-absorptive SMR (Fig. 1.3)

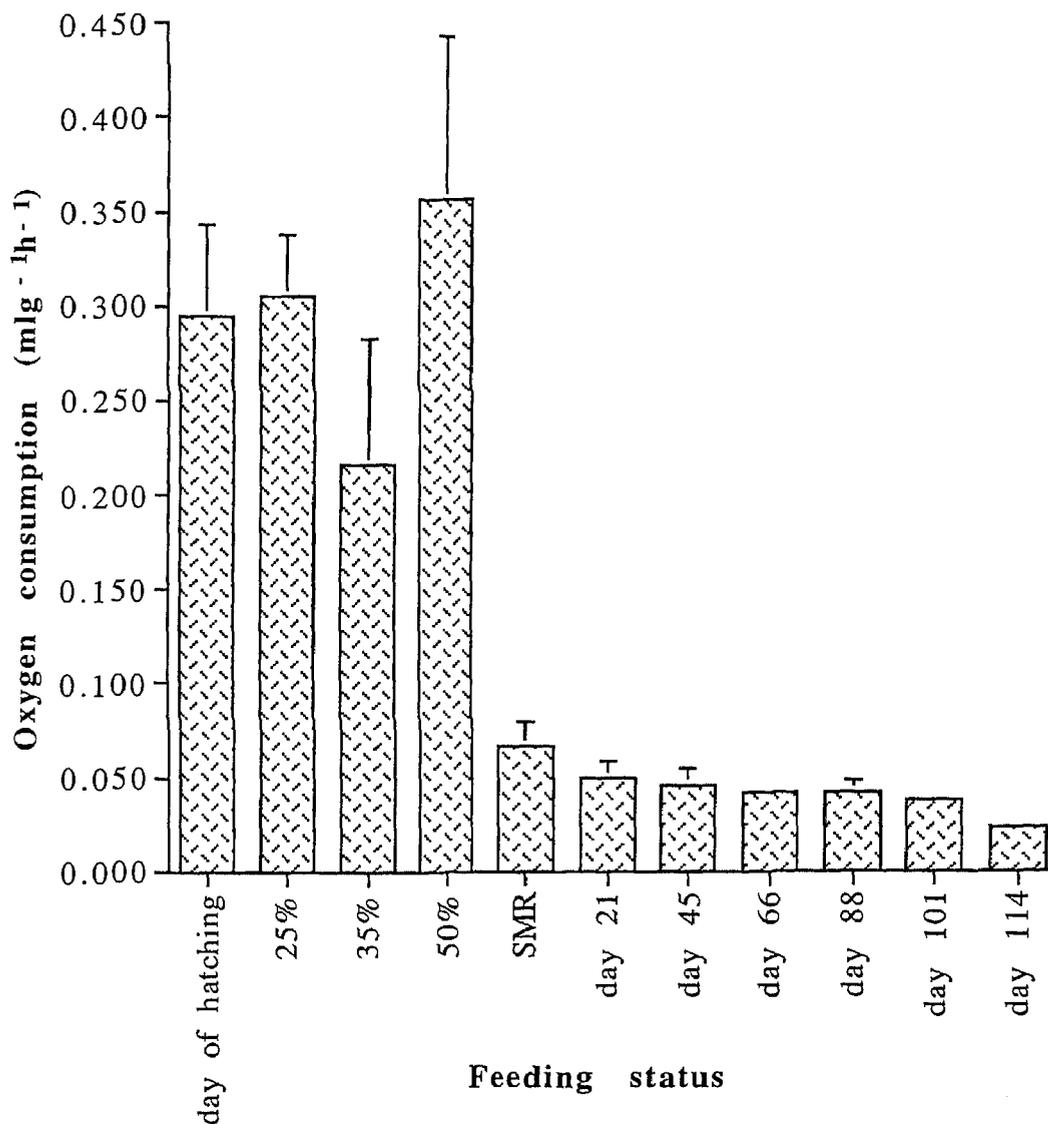


Figure 1.3. Metabolism on day of hatching, post-feeding and days during a fasting period in hatchling water pythons (*Liasis fuscus*) (n = 12). The % values refer to size of meal relative to body mass. SMR was measured 11 days after a meal of 10% body mass. Error bars represent standard error.

## Discussion

It is important to have a general protocol or standard that can be repeated when measuring physiological processes such as metabolism, particularly when there is large variability relating to feeding status, as in pythons. SMR in ectotherms should be measured while the animal is recently post absorptive (Kleiber 1975; Niewiarowski and Waldschmidt 1992; Thompson and Withers 1999). The magnitude of peak metabolism after feeding is dependent on the point at which "standard" metabolic rate is determined, and this has been noted in other studies on pythons (Bedford 1996; Thompson and Withers 1999). Results from this study indicate that at 30°C, after the peak, metabolism declines over time for adult and hatchling water pythons. Post-absorptive SMR for pythons should be measured at least 10 days after a meal, but before metabolism drops in response to extended fasting at 56 days for adults and 45 days in hatchlings. It should be noted however, that very large meals (> 50% of body mass) may result in longer periods of elevated metabolism (Secor and Diamond 1997). With a meal mass of 100% of body mass, metabolic rate returned to a pre-fed level 16 days after feeding (Secor and Diamond 1997).

At hatching, water python metabolism was very high, similar to that of animals which had consumed a meal larger than 20% of their body mass. I suggest that this may be due to the absorption of yolk into the body. Because hatchlings have a higher mass-specific metabolic rate than adult animals and because they expend more energy on growth, it

follows that hatchlings will expend their fat reserves at a faster rate than adult animals. It is therefore not surprising that the duration of stable post-absorptive SMR was shorter for hatchlings than adult animals (45 days vs 56 days).

During periods of reduced activity and feeding, the metabolic rate of many ectothermic animals gradually declines, presumably as a mechanism to conserve energy and water (Hochachka and Guppy 1987; Storey and Storey 1990; Guppy and Withers 1999). Among vertebrates, metabolic depression occurs in lungfish (Smith 1930; Fishman *et al.* 1986), every estivating amphibian that has ever been measured (Pinder *et al.* 1992; Withers 1993), inactive turtles (Seidel 1978; Kennett and Christian 1994; Hailey and Loveridge 1997), some over-wintering lizards (Tsuji 1988; Christian and Conley 1994), and tropical lizards during the dry season when food and water are scarce (Christian *et al.* 1996a, 1996b, 1996c, 1999). There is evidence that the lack of food is the stimulus for metabolic depression in lungfish (Smith 1930; Fishman *et al.* 1986), and there is circumstantial evidence that the lack of food (and water) is the stimulus for metabolic depression in some reptiles (Christian *et al.* 1996a, 1996b, 1996c, 1999), but not in an aestivating turtle (Kennett and Christian 1994).

Fifty-six and 45 days after feeding, in adult and hatchling water pythons respectively, was the duration after which metabolic rate had dropped significantly below a level that would be considered a conventional post-

absorptive SMR as determined within 10 – 14 days post feeding. Some ectothermic vertebrates for which metabolism has been monitored over time reach a state of metabolic depression in about a month after regular activity ceases (Fishman *et al.* 1986; Withers 1993; Kennett and Christian 1994).

After 114 days, the metabolism of fasting water pythons was depressed to 32% of SMR, which puts it in the range of metabolic depression (5 to 40%) most commonly found (Guppy and Withers 1999). The pattern of metabolism I describe here suggests that fasting water pythons have metabolic depression that is analogous to many other ectothermic vertebrates during periods of low food availability (Christian *et al.* 1996a, 1996b, 1996c, 1999, reviewed by Guppy and Withers 1999). Thus, the lack of food (and/or water) represents an environmental stress that triggers metabolic depression (Guppy and Withers 1999). This response is similar to animals exhibiting metabolic depression due to decreased food availability within a season, but because pythons feed opportunistically and infrequently, the ability to decrease metabolism has evolved to compensate for the uncertainty of feeding events throughout the year, rather than during a certain period within a year.

Not only can the gut atrophy after a meal in infrequent feeders like pythons, but also other metabolically expensive organs such as the liver, kidneys and heart (Secor and Diamond 2000). These organs

appear to use more energy per gram than other organs (Oikawa and Itazawa 1984; Secor and Diamond 2000). Atrophy of energetically expensive organs may occur in water pythons after digestion, and if this process is occurring in these animals, it would presumably contribute to the generally continuous and gradual decline in metabolic rate with fasting. However, atrophy of the gut, as experienced by Burmese pythons, has not been demonstrated in Australian pythons, so the observed metabolic decline with fasting may be due to some other mechanism. As noted by Guppy and Withers (1999), despite the documentation of a number of inter-related biochemical changes, the exact mechanism of metabolic depression is not known for any species. Determining the relative roles of morphological changes (atrophy of organs) and biochemical changes during metabolic depression is a formidable challenge for future python research.

When comparing *L. fuscus* data with those for *P. molurus* (Secor and Diamond 1997) there is a large difference in relative PDMR. For example, when consuming meals of 25% of body mass, the increase in metabolism is close to seven times SMR for the *L. fuscus*, whereas *P. molurus* has an increase of 16 times SMR (Secor and Diamond 1997). These two species have the same mass-specific SMR (*L. fuscus* and *P. molurus* SMR = 0.036 mlg<sup>-1</sup>h<sup>-1</sup>). Thus, the peak in metabolism after feeding in *L. fuscus* and Australian pythons in general (Bedford 1996; Thompson and Withers 1999) is moderate compared to *P. molurus*.

Peak digestive metabolic rate did not change for meal sizes between 20% and 39% of body mass in adult water pythons. Hatchling pythons that ate from 25 - 50% of their body mass in food did not significantly increase PDMR with increasing meal sizes, although there was a slight trend in this direction. These results indicate a plateau in PDMR for at least part of the range of meal sizes offered, possibly encompassing the relative meal sizes most often encountered in the wild by water pythons (Madsen and Shine 1996a). A plateau in PDMR exists in some fish (Jobling and Davies 1980), but PDMR in the Burmese python continues to increase with increasing meal mass even above 111% of body mass (Secor and Diamond 1997).

Why PDMR should plateau with increasing meal size in some Australian pythons but continue to increase with increasing meal size in *P. molurus* is unknown. The Burmese python can grow to gigantic body sizes of up to six m and over 100 kg (Pope 1961). Adult water pythons are less than one tenth of this mass, and most have a length of <3 m and a mass <3 kg. It is possible that the Burmese python has evolved an increasing digestive response to increasing meal size to exploit very large prey items. Water pythons, on the other hand, may have evolved in an environment where they feed on relatively small prey such as rats (Madsen and Shine 1996), and their body size may be an adaptation related to the available food resources (Shine and Slip 1990). Very rarely do water pythons have a full gut, and when they do, it is of relatively small prey items (Shine and Slip 1990). Therefore, both the body size and the meal size relative to body size

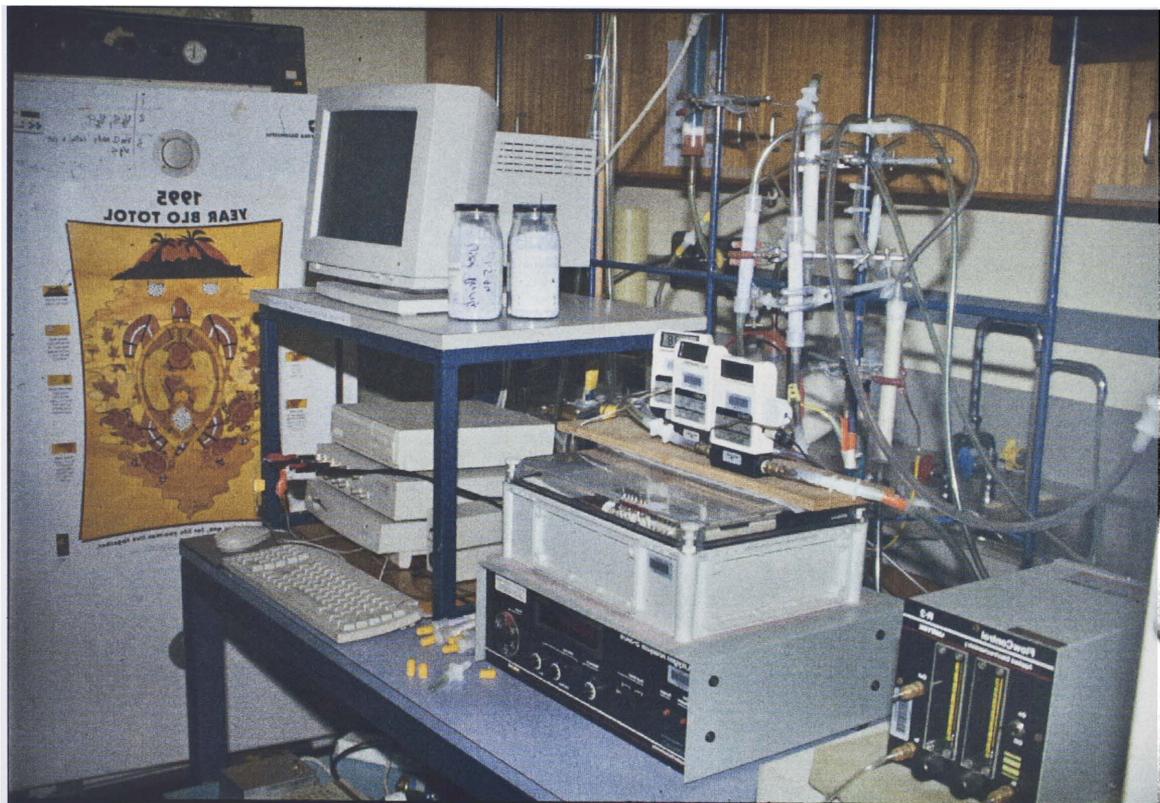
of water pythons may be related to the relative paucity of large prey items in water python environments.

Although adult water pythons were offered large amounts of food during the experiment involving meals in the >30% category, none of the snakes ate more than 39% of their body mass. The 12 hatchling water pythons were offered a meal 75% of body mass, but none were able to complete digestion. These observations may indicate that water pythons are unable to eat the relatively large meals that can be consumed by the gigantic Burmese python (*Python molurus bivittatus*), at least under the experimental conditions of 30°C. A thermophilic response to a large meal is an important aid in python digestion (Regal 1966; Slip and Shine 1988c). Determining the effect of increasing temperature on increasing meal size would be a valuable contribution to our understanding of the digestive physiology of pythons.

## Chapter 2

### Maximum oxygen consumption ( $\dot{V}_{O_{2\max}}$ )

### measurements in Australian pythons



Oxygen analyser, temperature controlled cabinet and MacLab logging system.

## Abstract

Energy used during activity differs between active and sit-and-wait foraging in some reptiles. I examined the activity metabolism of carpet pythons (*Morelia spilota variegata* and *M.s. bredli*), children's and stimson's pythons (*Antaresia childreni* and *A. stimsoni*) and the water python (*Liasis fuscus*). The  $\dot{V}_{O_{2\max}}$  values of five species of Australian python are similar, even though there are differences in foraging mode among the taxa. High lactate concentrations were reached in all animals during exercise, reflecting their sedentary existence and reluctance to move quickly. Respiratory exchange ratios (RER) were similar for all species examined, ranging from a low of 0.73 by *Morelia s. bredli*, to a high of 1.01 for *Liasis fuscus*.  $\dot{V}_{O_{2\max}}$  ranged between 7.1 and 11.7 times standard metabolic rate (SMR). The oxygen consumption resulting from exercise in these pythons is similar to oxygen consumption during digestion (six to 11 times SMR), but higher than thermogenesis during egg incubation (4.2 to 4.7 times SMR).

## Introduction

Reptilian metabolic rates are comparable to those of other terrestrial ectotherms, although an order of magnitude lower than those of endotherms (Bennett and Dawson 1976; Bennett 1982). The minimum measurement of metabolism, as measured through oxygen consumption ( $\dot{V}_{O_2}$ ), is the standard metabolic rate (SMR) in ectotherms, and it represents the energy requirement for survival in a fasted, quiescent state (Bennett and Dawson 1976; Secor and Diamond 1997). The maximum oxygen consumption ( $\dot{V}_{O_{2max}}$ ) represents the upper limit of energy use available during sustained exertion (Bennett 1978).

Some reptiles use anaerobic metabolism only at speeds greater than maximum sustained aerobic speed, while other reptile species routinely experience anaerobiosis with exercise (Bennett and Licht 1972; Bartholomew *et al.* 1976; Ruben 1976; Bennett *et al.* 1985; Gatten 1985; Gleeson 1991; Schultz 2002). Lactic acid, the by-product of anaerobic metabolism, may increase to lethal levels in some species of reptiles (Bennett *et al.* 1985), but is generally metabolized over a period of hours after exercise has ceased, and after metabolism has returned to resting levels (Mitchell *et al.* 1981; Bennett 1994).

Limbless locomotor costs have been determined for some reptiles (Bennett 1982, 1991), and early studies indicated that the cost of locomotion in terrestrial snakes was substantially less than that of

limbed terrestrial reptiles (Chowdrow and Taylor 1973 (cited in Bennett 1994); Gans 1975; Bennett and Dawson 1976). However, more recent studies have found that the cost of lateral undulation in snakes is similar to limbed locomotion of arthropods, lizards, birds and mammals of similar size (Walton *et al.* 1990; Bennett 1994).

The speed at which  $\dot{V}_{O_2\max}$  is reached is known as the maximal aerobic speed (Hertz *et al.* 1988; Bennett 1994). At greater speeds,  $\dot{V}_{O_2}$  remains constant, and energy is supplied via anaerobiosis (Bennett and John-Alder 1984). As speed increases further, exhaustion is reached rapidly. For a few reptiles, peak oxygen consumption is attained after exercise has ceased, during recovery (Schultz 2002).

Little is known about the maximal oxygen consumption rates in pythons. For Burmese pythons (*Python molurus*) exercising on a treadmill the  $\dot{V}_{O_2\max}$  is 6.2 times SMR (Secor and Diamond 1995). The metabolic increase with vigorous exercise is less than the increase resulting from digestion of a large meal in these snakes. After ingesting 100% of body mass in food, the metabolic rate can increase up to 45 times SMR (Secor and Diamond 1997, 2000). The metabolic response to thermogenesis during egg brooding, prevalent in a number of python species, increases metabolism from four to 22 times SMR (Vinegar *et al.* 1970; Van Mierop and Barnard 1976, 1978; Harlow and Grigg 1984;

Bedford and Christian unpub. data). Therefore, the metabolic increase associated with exercise in the only python species examined to date is modest compared to other attributes of python physiology such as digestion and brooding (Benedict 1932; Vinegar *et al.* 1970; Secor and Diamond 1997, 2000).

The aim of this study was to determine the  $\dot{V}_{O_{2max}}$  associated with exercise for a number of Australian python species. I used two methods to determine  $\dot{V}_{O_{2max}}$ , and I compare the results with the physiologically expensive processes of digestion and thermogenesis during brooding. Lactic acid concentrations in the blood were measured before and after exercise to test for anaerobic activity during the exertion.

### **Materials and Methods**

Adult pythons were wild caught by hand in the Northern Territory. Three species collected from the tropical north included the carpet python (*Morelia spilota variegata*) (n = 3), children's (*Antaresia childreni*) (n = 3) and water (*Liasis fuscus*) pythons (n = 12). Two species from the desert included the central carpet python (*Morelia spilota bredli*) (n = 4) and stimson python (*A. stimsoni*) (n = 3) from the Alice Springs area. Animals were held in an outside animal house at the Northern Territory University and experienced ambient shaded temperatures during the dry season, which has a mean minimum and

maximum of 19°C and 30.4°C respectively (unpublished data compiled and supplied by the Commonwealth Bureau of Meteorology, Darwin). All animals were maintained in captivity and fed a small meal of rodents (<10% of body mass) then allowed 10 days before metabolic measurements were made to ensure they were post absorptive and in good health (Bedford 1996; Bedford and Christian 1998; Thompson and Withers 1999). No animals were in either a reproductive state or ecdysis.

#### Measurement of Oxygen Consumption

All pythons were maintained at 30°C for at least six hours before measurements began. This temperature approximates the preferred body temperature of most Australian pythons (Bedford and Christian 1998). I used a flow through respirometry system to measure gas exchange during exercise on a treadmill (Christian *et al.* 1995; Christian and Conley 1994). Air was pumped (Reciprotor, Denmark) through the system, with the flow rate measured using a flow meter (Top-Track, Sierra Instruments USA). The flow meter was calibrated against a soap bubble burette (Long and Ireland 1985). Downstream of the animal the air was dried using Dryrite®, before entering the oxygen analyser (Applied Electrochemistry S-3A/111, Ametek, USA) and then the carbon dioxide analyser (Fuji Electrics, Japan). The flow rates used in exercise experiments ranged from 500 mL min<sup>-1</sup> for the *Antaresia* spp. to 1600 mL min<sup>-1</sup> for *Morelia* and *Liasis* sp. Data were recorded at 0.05 Hz on a

MacLab system (8e, ADInstruments, Australia). Metabolic rates were calculated using the equations of Withers (1977), and the fractional concentration of oxygen did not fall below 0.2.

The usual method used to measure  $\dot{V}_{O_2\max}$  is to place the head of the animal in a flow through acetate mask, then run the animal on the motorized treadmill until exhausted (Christian and Conley 1994; Christian *et al.* 1995, 1996a,b, 1999; Thompson and Withers 1997). I refer to this method as the “mask” method. I encouraged the animals to move at treadmill speed by pinching them mid body and on the tail. Treadmill speed was set at one km h<sup>-1</sup>, at which snakes were able to crawl at a fast pace without tiring too quickly.

Many snakes did not co-operate during experiments using the “mask” method, and consistently attempted to remove the acetate mask. These snakes exercised freely on the treadmill when not masked, thus I also tested a modified technique which I termed the “grab” method. For this method the pythons exercised on the treadmill without a mask for a period of two minutes, then the mask was placed on the animal for one minute while still prodding and pinching the animal to maintain locomotion. After a minute of measurements the mask was removed for another two minutes of unhindered exercise before being replaced for a further minute. This sequence of events was continued until the animal was exhausted. I compared the two methods using 12 water pythons

(*Liasis fuscus*) measured using both techniques. Exercise experiments ceased when the animal lost the righting response. The  $\dot{V}_{O_{2max}}$  was determined from the lowest oxygen measurements over 60 seconds.

Standard metabolic rates were determined from the allometric equation of Bedford and Christian (1998) for Australian pythons at 30°C:

$$\text{SMR (mLh}^{-1}\text{)} = 0.394M^{.76}$$

Where M is mass in grams.

#### Lactates

A blood sample of approximately 0.1 mL was taken by cardiac puncture from all snakes prior to exercise. The pythons were then exercised on the treadmill and a second blood sample of 0.1 mL was taken immediately after exercise. Whole blood was spun in a centrifuge to separate plasma and red blood cell fractions, then frozen in Eppendorf tubes at -20°C. Lactate concentration was determined using the Sigma diagnostic lactate procedure 735 (Sigma Diagnostics®).

After metabolic data were log-transformed, they were analysed using analysis of covariance with log-mass as a covariate (Zar 1984) to test the two methods of obtaining  $\dot{V}_{O_{2max}}$  and the effect of exercise among different species. Metabolic data are presented as mL g<sup>-1</sup> h<sup>-1</sup> and mL h<sup>-1</sup>, with standard deviations representing errors. A comprehensive phylogeny has not been determined for all Australian pythons, so I

have not tested for this effect in the few species I examine; however, data are presented so that this can be incorporated when further species have been investigated. Duration of treadmill exercise comparing both methods of measuring  $\dot{V}_{O_{2max}}$  was analysed using paired t-tests ( $\text{mL h}^{-1}$ ). Factorial scope of oxygen consumption was calculated by  $\dot{V}_{O_{2max}}/\text{SMR}$  (Seymour 1973). Respiratory exchange ratios (RER) ( $\dot{V}_{CO_2}/\dot{V}_{O_2}$ ) were arc-sin transformed (Zar 1984) before being analysed using analysis of variance. Data for each species were analysed using Statview 5.0 and SuperANOVA programs on a Macintosh computer ( $\text{mL g}^{-1} \text{h}^{-1}$ ), with statistics presented at the 5% level of probability.

## Results

Maximum oxygen consumption was determined for 25 pythons from five species (Table 2.1). Maximum oxygen consumption during most runs was obtained within the final few minutes before the loss of the righting response. There was no difference in  $\dot{V}_{O_{2max}}$  measurements between the "mask" and "grab" methods in *L. fuscus* (Paired t-test  $P > 0.05$ )(Table 2.1), enabling all data from *L. fuscus* to be combined in further analyses. The consumption of oxygen using the grab method during the minute of readings results in a plateau, and this plateau was similar to that obtained using the conventional mask approach. The mean duration of treadmill movements using the continuous mask

method (12.2 minutes, SD = 2.2) did not differ from that of the grab method (14.6 minutes, SD = 5.0) ( $P > 0.05$ ,  $n = 12$ ).  $\dot{V}_{O_{2\max}}$  for all other species of python were obtained by the “grab” method. There was no difference in  $\dot{V}_{O_{2\max}}$  among species (ANCOVA  $P > 0.05$ ).

The factorial scope ranged from a low of 7.1 times SMR in *L. fuscus* to a high of 11.7 times SMR in *M. s. variegata* (Table 2.1). The respiratory exchange ratios were significantly different among the species ( $F_{4,29} = 5.767$ ,  $P = 0.002$ ), and a Fisher's post hoc test indicated that RER in *Liasis fuscus* was significantly higher than in *A. stimsoni*, *A. childreni* and *M. s. bredli*.

Table 2.1. Gas exchange during exercise in five species of Australian python at 30°C. Whole-animal (mL h<sup>-1</sup>) and mass specific (mL g<sup>-1</sup> h<sup>-1</sup>)  $\dot{V}_{O_{2max}}$ , whole-animal  $\dot{V}_{CO_{2max}}$ , factorial scope ( $\dot{V}_{O_{2max}}/SMR$ ) and respiratory exchange ratio (RER) are included. Metabolic data gathered for *Liasis fuscus* are denoted by 1 (mask) and 2 (grab) to indicate method. Values are presented as means ( $\pm 1$  SD).

Species	n	Mass (g)	$\dot{V}_{O_{2max}}$ (mL h <sup>-1</sup> )	$\dot{V}_{O_{2max}}$ (mL g <sup>-1</sup> h <sup>-1</sup> )	$\dot{V}_{CO_{2max}}$ (mL h <sup>-1</sup> )	Factorial scope	RER
<i>Morelia s.</i>	4	787.7 (105.4)	585.3(80.0)	0.691(0.32)	334.5(134.1)	7.8(2.3)	0.73 (0.33)
<i>bredli</i>							
<i>M. s. variegata</i>	3	942.0 (228.8)	1080(690.7)	0.849(0.50)	410.9(101.1)	11.7(6.7)	0.77 (0.52)
<i>Antaresia</i>	3	165.7 (135.6)	200.5 (47.2)	1.322(0.78)	134.2(26.3)	10.3(5.0)	0.86 (0.11)
<i>childreni</i>							
<i>A. stimsoni</i>	3	170.2 (87.4)	260.6 (104.8)	0.725(0.15)	161.0(56.4)	8.5(3.0)	0.79 (0.04)
<i>Liasis fuscus</i> 1	12	1463.4 (416.7)	963.8 (190.0)	0.584(0.26)	548.3(141.0)	8.3(2.9)	1.01 (0.31)
<i>L. fuscus</i> 2	12	1463.4 (416.7)	953.9 (200.2)	0.565(0.25)	486.4(97.5)	7.1(1.3)	0.91 (0.15)

Lactate production was not significantly different between methods (mask vs grab) for *L. fuscus* ( $P > 0.05$ ). A two factor ANOVA with rest or exercise and species as factors, indicates that lactate production after exercise was significantly elevated compared to resting lactate concentrations (ANOVA  $F_{1,63} = 62.1$ ,  $P = 0.0001$ ). Lactate production was not significantly different among the species at rest or after activity (ANOVA  $P > 0.05$ ) (Table 2.2).

Table 2.2. Lactate concentrations of five species of python at rest and after exercise. Sample sizes are given in Table 2.1. Means are presented ( $\pm 1SD$ ).

Species	N	Rest lactate (mg mL <sup>-1</sup> of plasma)	Exercise lactate (mg mL <sup>-1</sup> of plasma)
<i>M.s. bredli</i>	4	0.034 (0.062)	0.225 (0.300)
<i>M. s. variegata</i>	3	0.002 (0.054)	1.089 (0.654)
<i>A. childreni</i>	3	0.038 (0.074)	1.261 (0.211)
<i>A. stimsoni</i>	3	0.010 (0.059)	0.885 (0.934)
<i>L. fuscus</i>	12	0.032 (0.056)	1.139 (0.517)

## Discussion

In the laboratory, it is important for physiologists to assess the actions of an animal in an experiment, and where possible ensure these emulate actions that might occur in nature (Bauwens *et al.* 1995;

Gregory 2001). For this reason I spent some time assessing the ability of snakes to exercise on the treadmill, and compared this with standard techniques of lizard treadmill exercise (Christian *et al.* 1996a,b).

Although most lizards are willing to exercise on a treadmill after being fitted with an acetate face-mask, the pythons would only do so rarely. This may be related to behaviour differences: pythons retreat when confronted by a predator or aggressor, and if the harassment continues, they tend to strike out viciously (pers. obs.). With few options open to pythons on the treadmill and the moderately heavy acetate mask firmly in place, most animals were more intent on ridding themselves of the mask than they were on crawling. However, after removal of the mask, all animals moved continuously on the treadmill at a steady pace until near exhaustion.

Carpet pythons, both the desert dwelling *M.s. bredli* and the tropical *M.s. variegata*, are mostly arboreal, sit-and-wait foragers that move infrequently (Shine 1991; Chapter 4). The desert inhabiting *A. stimsoni* (Cogger 2000) is also a sedentary species, although it may move up to 150 metres in one night (pers. obs.). The tropical *A. childreni* (Cogger 2000) is a sedentary forager but can move up to 300 metres in one night between ambush sites (per. obs.). The tropical *Liasis fuscus* is highly mobile and can move more than 12 km between seasons (Madsen and Shine 1996a), and appears to hunt actively rather than being a sit-and-wait predator; it may switch foraging modes depending

on the availability of food resources (Shine 1991; Madsen and Shine 1996a; Chapter 4).

Examination of standard metabolic rate between the extremes in foraging mode (active foraging versus sit-and-wait) has revealed that active foraging reptiles expend and consume more energy than sit-and-wait reptiles (Bennett *et al.* 1984; Dmi'el 1986; Chappell and Ellis 1987). Similarly, animals relying on a sit-and-wait foraging mode generally have a proportionately lower  $\dot{V}_{O_2\max}$  than their active foraging counterparts (Kamel and Gatten 1983; Dmi'el 1986; Beaupre *et al.* 1993; Secor and Nagy 1994; Wang and Abe 1994; Thompson and Withers 1997). Metabolic rate in some lizards (Kamel and Gatten Jr 1983; Bennett *et al.* 1984; Thompson and Withers 1997; Schultz 2002) and snakes (Ruben 1976; Secor and Nagy 1994; Secor 2001) has been correlated with foraging mode. Results in this study suggest that irrespective of foraging mode, the amount of energy used during exercise was similar among these species of Australian python.

Pythons have a low SMR compared to other squamates; however, this is not significantly different from other reptile groups (Bennett and Dawson 1976; Andrews and Pough 1985). Most reptiles do not routinely engage in maximal oxygen consumption (Hertz *et al.* 1988), and during field work, as part of a larger study, I found that pythons actively moving between sites did not move quickly, so it is doubtful

this locomotion would require a high  $\dot{V}_{O_2}$ . On many occasions, *M.s.variegata* and *M.s. bredli* were found climbing trees and buildings. This activity is possibly an energetically expensive exercise and may represent the highest level of voluntary oxygen consumption in these pythons, although this was not tested. Male-male combat occurs for short periods during the breeding season and may also be aerobically expensive (Barker and Barker 1994; Greer 1997); however, this also was not measured.

Active foraging species of snake increase metabolic rate from 4.1 to 10 times SMR during vigorous exercise on a treadmill (Walton *et al.* 1990; Secor *et al.* 1992, 1994; Peterson *et al.* 1998), while the range of maximal metabolic increase with exercise in sit-and-wait foraging snakes appears slightly higher. For example, *Crotalus cerastes* was found to increase oxygen consumption 8.7 times SMR when forced to exercise vigorously on a treadmill. This species is a sit-and-wait viper, and the increase in oxygen consumption was similar to that of sit-and-wait foraging pythons. The  $\dot{V}_{O_{2max}}$  (mL g<sup>-1</sup>h<sup>-1</sup>) of Burmese pythons forced to crawl vigorously increased oxygen consumption from six to 10 times SMR (Secor and Diamond 1997; Secor *et al.* 2000). In this study Australian pythons were able to increase their metabolic rates from seven to almost 12 times SMR when forced to exercise on a treadmill. The increase in metabolic rate resulting from exercise in Australian pythons is similar to the peak digestive metabolic rate (PDMR) (5.0 -

12.2 times SMR) of day two post-feeding metabolic rate during digestion of a meal (Bedford and Christian 2001), and above the metabolic rate during brooding (4.2 – 4.6 times SMR) (Chapter 3) (Table 2.3), but is well short of 45 times SMR observed in PDMR in digesting Burmese pythons (Secor and Diamond 2000).

Table 2.3. The SMR and cost of digestion or thermogenesis during incubation in some pythons, along with the peak factorial scope of incubation (I) and digestion (D) after consuming different meal sizes expressed as a percentage of snake body mass (%).

Python	SMR (mL g <sup>-1</sup> h <sup>-1</sup> )	Incubation/Digestion (mL g <sup>-1</sup> h <sup>-1</sup> )	Factorial Scope
<i>M.s. bredli</i>	0.016	0.074 (I)	4.6 (I)
<i>L. fuscus</i>	0.017	0.070 (I)	4.1 (I)
<i>L. fuscus</i> (adult)	0.023	0.28 (D-20%)	12.2 (D)
<i>L. fuscus</i> (juv)	0.07	0.35 (D-50%)	5.0 (D)
<i>L. olivaceus</i> (juv)	0.037	0.34 (D- 75%)	9.2 (D)

It seems likely that the maximum level of  $\dot{V}_{O_2}$  in these Australian pythons is similar for different physiological processes such as digestion, brooding and exercise. This is an interesting finding, because the pathways of energy use are different, with muscular exercise being dominant in both shivering and treadmill exercise, while digestion involves gut biochemistry and the energy cost of specific dynamic

involves gut biochemistry and the energy cost of specific dynamic action. Elevated metabolic rates due to exercise and digestion do not occur at the expense of each other in a python and a varanid, but rather these two processes are additive (Secor *et al.* 2001; Bennett and Hicks 2001). This suggests that the Australian pythons in this study may be able to achieve even higher levels of oxygen consumption under some conditions involving a combination of digestion and exercise, but further research is needed to determine if a higher  $\dot{V}_{O_{2max}}$  is possible.

An increase in lactate with exercise is common in many lower vertebrates (Bennett and Licht 1972; Bennett 1978, 1982; Baldwin *et al.* 1989; Gleeson 1991; Baldwin *et al.* 1995), including snake species (Ruben 1976). After exercise, blood lactates in the five species of Australian python were on average 32.3 times greater than resting rates (99.2 vs 3.08 mg dL<sup>-1</sup>), indicating that anaerobiosis was used extensively by all species during exercise (Ruben 1976; Bennett 1994). The increase in lactates with exercise is similar to that found in other reptiles (Coulson and Hernandez 1980).

This is the first study to investigate and compare  $\dot{V}_{O_{2max}}$  in the laboratory for animals from the sub-family Pythonidae. Because pythons are relatively sedentary, cryptic and slow moving, it is

unknown to what extent  $\dot{V}O_{2\max}$  is attained during nocturnal locomotion. In the future, with more data from the field and the laboratory, it would be interesting to determine the cost of activity at ecologically relevant speeds.

## Chapter 3

# The energetics of brooding in Australian pythons



*Liasis olivaceus* coiled around eggs during incubation in the laboratory

## Abstract

While all pythons coil around their eggs during incubation, some use shivering thermogenesis to increase egg temperature above ambient and maintain a relatively constant clutch temperature during this time. Egg brooding was examined in tropical and temperate species of Australian python, and two methods of shivering thermogenesis were identified. Some large temperate pythons appear to shiver continuously for 3.2 seconds in a single burst, analogous to mammalian shivering. The large tropical species that shiver use a pulsing method that involves a single muscular spike of 0.36 seconds, then a short period of quiescence (1.2 seconds) before another spike. Oxygen consumption per unit time was four to five times SMR for both shivering modes, but the 'mammal-like' method of prolonged shivering produced almost three times more heat than pulse shivering over the same time, although this method does involve a three fold increase in muscle movements per minute. Brooding water pythons (*Liasis fuscus*), a tropical species, were only able to raise their body temperature 2 - 2.5°C above ambient over extended periods of time. Carpet pythons (*Morelia spilota bredli*) from arid, temperate regions were able to raise body temperature by over 3°C, but at least one other taxon of Australian python of similar size (*M.s.spilota*) is able to elevate body temperatures by up to 7 - 9°C above ambient. The metabolic and thermal differences between these two shivering methods may be related to the geographic radiation of pythons in Australia. 'Mammal-

like' shivering python species occur at higher latitudes where temperatures during the breeding season are lower than in tropical regions where resident pythons either do not shiver or use a pulse method.

## Introduction

For many years reptiles have been regarded as simple 'lower' vertebrates, making them ideal study organisms of evolutionary developments (Bennett and Dawson 1976) and this has been strengthened by the surge in reptile experiments over recent decades (Nagy 1983a&b; Shea 1993). Increased study has given insight into reptile behaviours, some of which are as complex as behaviours in 'higher' vertebrates. Python behaviour involves some complex features, including a recognised social hierarchy (Barker, Murphy and Smith 1979), conspecific recognition and combat (Bedford and Sullivan 1993; Greer 1997) and parental care (Benedict 1932; Ellis and Chappell 1987; Shine 1988; Shine 1995; Greer 1997).

Maternal parental care in pythons involves the coiling around and maintenance of eggs from the time of oviposition until hatching, after which no further attention is paid to the hatchlings (Benedict 1932; Ross and Marzec 1990; Barker and Barker 1994). During egg brooding, muscular shivering results in an increase in metabolic rate and the production of heat, which allows regulation of egg temperature (Benedict 1932; Hutchison, Dowling and Vinegar 1966; Vinegar, Hutchison and Dowling 1970; Harlow and Grigg 1984; Slip and Shine 1988 a,b). Diurnal basking, in which body temperature increases through absorption of solar energy, may be used in conjunction with shivering thermogenesis (Slip and Shine 1988a,b,c; Shine 1991). The

heat is subsequently transferred to the clutch via conduction when the female returns to the eggs (Harlow and Grigg 1984; Slip and Shine 1988a; Madsen and Shine 1996b).

Shivering thermogenesis, although thought to be universal among Australian pythons (Greer 1997), has not been observed in all species examined to date (Ross and Marzec 1990). Some Australian pythons have evolved a smaller body size compared to many non-Australian python species (Ross and Marzec 1990), possibly as a result of selection for smaller prey (Shine and Slip 1990; Shine 1991). The evolution of small body size appears at odds with the use of shivering thermogenesis as a method of egg incubation. Thermal inertia increases with body mass; therefore, a larger mass would facilitate the maintenance of a more constant temperature in a thermally variable environment. In non-Australian species of python, shivering thermogenesis has been documented for the Indian python complex (*Python molurus* ssp.); however, it has not been recorded in other large species such as *Python reticulatus* or *Python sebae* (Benedict 1932; Vinegar *et al.* 1970). *Python reticulatus* and *Python sebae* grow >5 m, and have many eggs (Ross and Marzec 1990), so shivering thermogenesis might seem plausible. *Python regius*, a small African species is not known to shiver during brooding (Ellis and Chappell 1987).

Although shivering thermogenesis during egg incubation is not universal, almost all Australian pythons coil around their egg mass during this period (reviewed in Greer 1997). A documented exception is that of the water python (*Liasis fuscus*), which occasionally lays eggs in varanid lizard burrows and leaves them to incubate in the confines of the burrow, where the temperature and humidity are thought to be optimal (Madsen and Shine 1996). This strategy has a number of advantages, the most significant of which is the ability of the female to resume feeding immediately post-oviposition rather than fasting over approximately 60 days of egg brooding (Madsen and Shine 1996b, 1999a).

Many reptiles in the wild seek a relative humidity of around 96% for their eggs (Packard and Packard 1988) to prevent desiccation during incubation. Female pythons invest considerable time and energy in reproduction, expending 5-6 months and the equivalent of up to 66% of body mass in reproduction (Shine 1991; Barker and Barker 1994). It would therefore be anticipated that a female python would do 'all she could' to maximise embryo survival (Slip and Shine 1988a,b; Shine 1991). This may include reducing water loss by coiling tightly around the eggs (Vinegar *et al.* 1970; pers obs). When eggs desiccate to some critical level it might be expected that the female would provide additional moisture through either body water or water from an external source (Ross and Marzec 1990; Shine 1991). In this study, I

investigate the behavioural means used by brooding water pythons to regulate temperature and humidity around the egg mass to ensure successful egg incubation.

Shivering thermogenesis, while a prominent behaviour in the life history of some Australian pythons, proved challenging to study. Where possible, I measured the maternal metabolic rates during incubation. From these data I identified two methods of shivering thermogenesis, for which I compare the energetic cost and heat production. The humidity needed for successful incubation and the ability of water pythons to facilitate this are also described. Finally, I discuss the relationship between the types of shivering and the geographic ranges of Australian pythons.

## **Methods**

Metabolism was measured from female pythons that were post-brooding and, where possible, brooding eggs on moist vermiculite (Barker and Barker 1994). The ratio of vermiculite to water was 1:0.9, which gives an approximate relative humidity of 96% (Packard and Packard 1988). Pythons and eggs were placed individually in one of three chambers with air samples drawn consecutively from each of the animal chambers for a period of two hours on a rotating basis over a 24 hour period using open system respirometry. Therefore, each animal was monitored for eight hours over a twenty-four hour period.

Each chamber was maintained in a constant temperature cabinet (Forma Scientific) at 30°C ( $\pm 0.5^\circ\text{C}$ ) most of the time; however experimental temperatures of 22, 24, 26, 28, 30 and 33°C were used to examine the relationship between shivering and temperature in the different python species. These temperatures were chosen to represent the range of preferred active temperatures of pythons obtained from laboratory thermal gradients (Bedford and Christian 1998). Not all experimental temperatures were examined for all species of python due to the biological constraint of pythons failing to shiver.

Metabolism was determined using the lowest stable measurements of oxygen consumption over a period of at least 40 minutes. A full description of this system is detailed elsewhere (Bedford 1996; Christian *et al.* 1996a; Christian, Griffiths and Bedford 1996b). Oxygen concentrations were measured using an Applied Electrochemistry oxygen analyser (S-3A), with rates of oxygen consumption ( $\dot{V}_{\text{O}_2}$ ) calculated using the methods of Withers (1977).

#### *Metabolism of brooding pythons*

Metabolic measurements were made on two *L. olivaceus* while coiled around their eggs at 24, 28, 30 and 33°C.

The metabolism of four brooding female children's pythons (*Antaresia childreni*) was measured at three temperatures (24, 30 and 33°C).

Measurements commenced within one week of oviposition, and continued intermittently throughout the subsequent 8 weeks of incubation. Adult females remained in the metabolic chambers until the young began to emerge. The adults were offered water each week, but not food, because gravid and brooding pythons rarely eat (Ross and Marzec 1990; Barker and Barker 1994). After hatchlings were removed from the chamber, the metabolic rate of the post-brooding female was measured at all temperatures.

Eight wild caught gravid water pythons (*Liasis fuscus*) were placed in individual chambers on moist vermiculite inside a constant temperature cabinet (Forma Scientific). Data were collected during both day and night (24, 26, 28, 30 and 33°C).

The oxygen consumption of a single carpet python (*Morelia s. variegata*) was examined in the laboratory at 26, 28, 30 and 33°C. This animal was coiled around its eggs over the entire period of experiments.

One brooding central carpet python (*Morelia s. bredli*) was studied in Alice Springs. A portable oxygen analyser (Servomex model 572: Sussex, England) was used to measure oxygen consumption. The animal was placed in a box on moist vermiculite. This was housed in an airconditioned shed. Ambient conditions in Alice Springs at that time

(February 2000) were extreme, with day temperatures above 40°C, and night-time temperatures around 36°C. Although operating at maximum capacity the shed airconditioner was only able to reduce the ambient temperature to 28°C during the day and the snake container reached 24°C for a short period early in the morning. This was sufficient to determine the metabolic rate during brooding but not cool enough to determine the lower extent of shivering thermogenesis with decreasing temperature.

The *M.s. bredli* was housed in a sealed 60 L plastic box, with room air drawn into the box, past the animal then out of the box and into a column of CO<sub>2</sub> absorbent (Dragersorb 800, Germany) and through a drying column (Drierite, USA). The air was then passed through a Top Trak flow-meter (Sierra Instrument, USA) before being drawn into the oxygen analyser with a reciprotor 506r pump (Denmark).

The measurement of metabolism during brooding occurred soon after eggs were laid. The metabolic rate of embryos associated with newly laid eggs is negligible (unpublished data) so this cost has not been removed from the total cost of metabolism associated with brooding female pythons.

*Thermal increase and metabolic sensitivity to temperature during shivering*

Air temperatures ( $T_a$ ) were measured using a Fluke thermocouple thermometer. Body temperatures ( $T_b$ ) were measured using an infra-red thermometer (Raynger PM, Raytek, Santa Cruz, USA) before and after metabolic measurements to obtain the temperature differential during bouts of shivering. These temperature differences were then incorporated in the metabolic cost of shivering.

Thermal sensitivity ( $Q_{10}$ ) is the rate at which oxygen consumption increases as temperature increases by  $10^\circ\text{C}$  (Bennett and Dawson 1976). The thermal sensitivity for brooding water pythons over the range  $26\text{-}33^\circ\text{C}$  was determined using the equation:

$$Q_{10} = \left( \frac{\dot{V}_{\text{O}_2(2)}}{\dot{V}_{\text{O}_2(1)}} \right)^{\frac{10}{T_2 - T_1}}$$

(Eq. 1)

In this equation  $\dot{V}_{\text{O}_2(2)}$  and  $\dot{V}_{\text{O}_2(1)}$  are oxygen consumption at the higher and lower temperatures respectively, and  $T_1$  and  $T_2$  are the upper and lower temperatures ( $^\circ\text{C}$ ) respectively (Schmidt-Nielsen 1990).

*Comparison of shivering thermogenesis*

Data from the two species of pythons that shivered consistently on eggs in this study (*Liasis fuscus* and *Morelia spilota bredli*) were examined. A digital video camera (Sony CCD) was used to record shivering in both *L. fuscus* and *M.s. bredli*. The video was used to examine the patterns of shivering, and analysed in slow motion using the timing function to obtain measurements of the duration of shivering bouts. The brooding data from this study were then compared to brooding data obtained for another Australian python, *M. s. spilota* (Harlow and Grigg 1984).

*Desiccation of water python eggs during brooding.*

During incubation, water pythons were initially maintained in a constant temperature cabinet at 33°C on moist vermiculite with high relative humidity during the metabolic experiments. After the metabolic experiments were completed, the brooding water pythons were moved to a constant temperature room at 30°C.

Humidity in the constant temperature room was approximately 50%, measured using a hand held humidity sensor (Model: AM34, Vaisala, Finland). Each python was placed in a 60 L plastic container on a newspaper substrate. A soup ladle filled with 200 ml of water was easily accessible from the coiled brooding position of the female. The handle of the ladle was hooked over the edge of the container so that it

hung half way down within the box so that water could not be spilt. Water was provided to each brooding water python *ad libitum* and all animals were observed to drink from that source. I aimed to determine whether pythons were able to supplement nest humidity directly using water from the ladle or from excretion after drinking water.

### *Statistical analyses*

Metabolic rates were analysed between species of python using analysis of covariance (ANCOVA) on log transformed data, with log mass as a covariate, and metabolic data for *Liasis fuscus* on eggs measured day and night were analysed using a repeated measures analysis of variance (RMANOVA). Probability level was 0.05. Desiccation data on brooding pythons was interpreted visually and not statistically investigated.

## **Results**

### *Thermal increase and metabolic sensitivity to temperature during shivering*

*Liasis fuscus* shivered at night almost exclusively, with night time metabolic rate significantly different to day time metabolic rate while brooding eggs at 28°C (RMANOVA  $F_{1,8} = 12.96$ ,  $P = 0.007$ ). Therefore only night time metabolic rates of brooding *L. fuscus* are presented; however there was no difference between day and night time brooding metabolic rates at other temperatures examined ( $P > 0.05$ ) because

daytime metabolism was highly variable. Brooding *Liasis fuscus* were maintained in the laboratory and subjected to decreasing experimental temperatures. At 33°C, there was no evidence of shivering, and pythons were draped loosely over their eggs. Shivering thermogenesis commenced when the temperature fell below 31°C, and *L. fuscus* maintained an incubation temperature of 32.6°C (s.d. 0.8, n = 4) when subjected to temperatures between 30 and 32.5°C. When ambient temperature fell to 28°C, *L. fuscus* were able to maintain a clutch temperature of 30.2°C. When ambient temperature fell below 26°C, clutch temperature fell to 28.3°C. At an ambient temperature of 24°C shivering ceased and clutch temperature fell toward the ambient temperature over the following hours.

*Liasis fuscus* at 28°C pulse shivered 38 times per minute (mean for 5 minutes, n = 3 pythons), to give a temperature differential of 2.5°C above ambient. At 30°C, mean  $\dot{V}_{O_2}$  was 0.073 ml g<sup>-1</sup> h<sup>-1</sup> (s.d. = 0.042) which is 4.2 times the SMR for a non-brooding water python with a similar mass of 2.2 kg (Bedford and Christian 1998).

The temperature differential ( $T_b - T_a$ ) for the *M.s. bredli* was 2.2°C, at a  $T_a$  of 28°C. The temperature differential increased to 3°C when  $T_a$  in the metabolic chamber fell to 26°C, although it was not sustained.

*Morelia s. bredli* at 28°C shivered 14 times per minute (mean for 5 minutes), which brought  $T_b$  to 31°C. This temperature differential was

associated with a maximum  $\dot{V}_{O_2}$  during shivering of  $0.074 \text{ ml g}^{-1} \text{ h}^{-1}$  for a 3 kg snake. The SMR for this animal when non-gravid was  $0.016 \text{ ml g}^{-1} \text{ h}^{-1}$  then the ratio of shivering metabolic rate divided by SMR was 4.6.

#### *Metabolism of brooding pythons*

During this study two olive pythons brooded their eggs, however only one shivered. The shivering animal did so at intervals which were not consistent with either changing temperatures or time of the day, therefore the metabolic results were not examined in detail. The shivering was identical to the pulse shivering described for *L. fuscus*, but the fact that they are capable of shivering is worthy of note. The animal that did shiver ceased shivering whenever disturbed, often taking hours before recommencing. Inspection of the metabolic data for the single olive python reveals a trend for an elevated metabolic rate at high temperatures (Fig. 3.1). Further data would be needed to understand the relationship between brooding and temperature in this species.

None of the four *A. childreni* shivered while brooding, and they did not exhibit a significant difference in metabolic rate over the three experimental temperatures of 24, 30 and 33°C (ANCOVA  $P > 0.05$ ) (Fig. 3.2). There was a significant difference between brooding metabolic rate of children's pythons and that of brooding water pythons at each temperature (ANCOVA  $F_{1,24} = 13.8$ ,  $P = 0.001$ ), with water pythons

having a higher metabolic rate at each temperature. Due to the relationship between metabolism and body temperature in pythons (Bedford and Christian 1998) it would be anticipated that standard metabolic rate (SMR) would increase with increasing temperatures, and while this trend was evident, it was not significant (Table 3.2). There was no difference in metabolic rate in *A. childreni* that were post-brooding, gravid or brooding at any of the three experimental temperatures, although these data were highly variable (ANCOVA  $P > 0.05$ ).

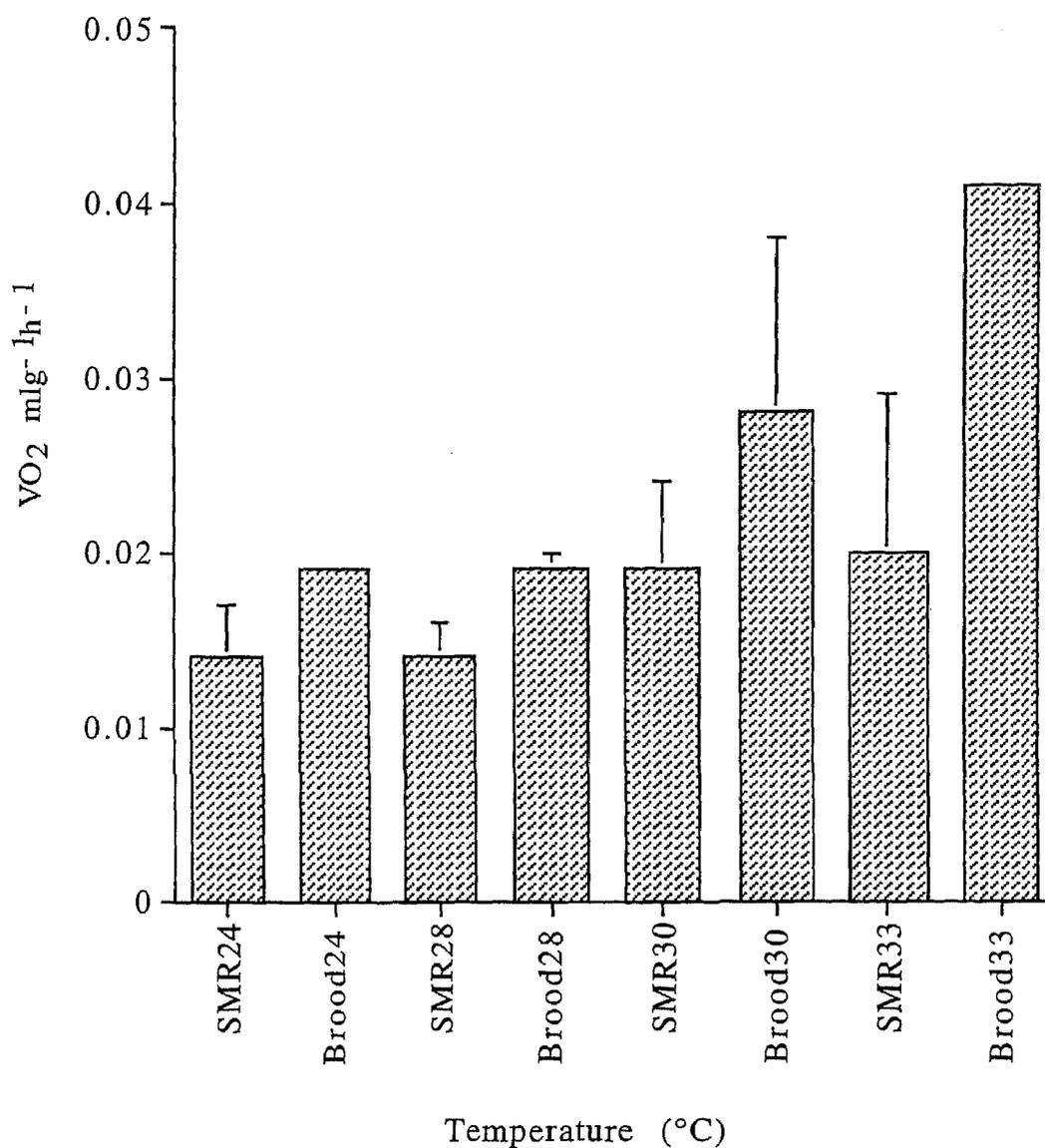


Figure 3.1. Standard metabolic rate and brooding metabolic rate of olive pythons at temperatures from 24 - 33 $^{\circ}C$ . Only two animals were obtained with eggs but only one animal that would shiver. Error bars ( $\pm SD$ ) are for indication only.

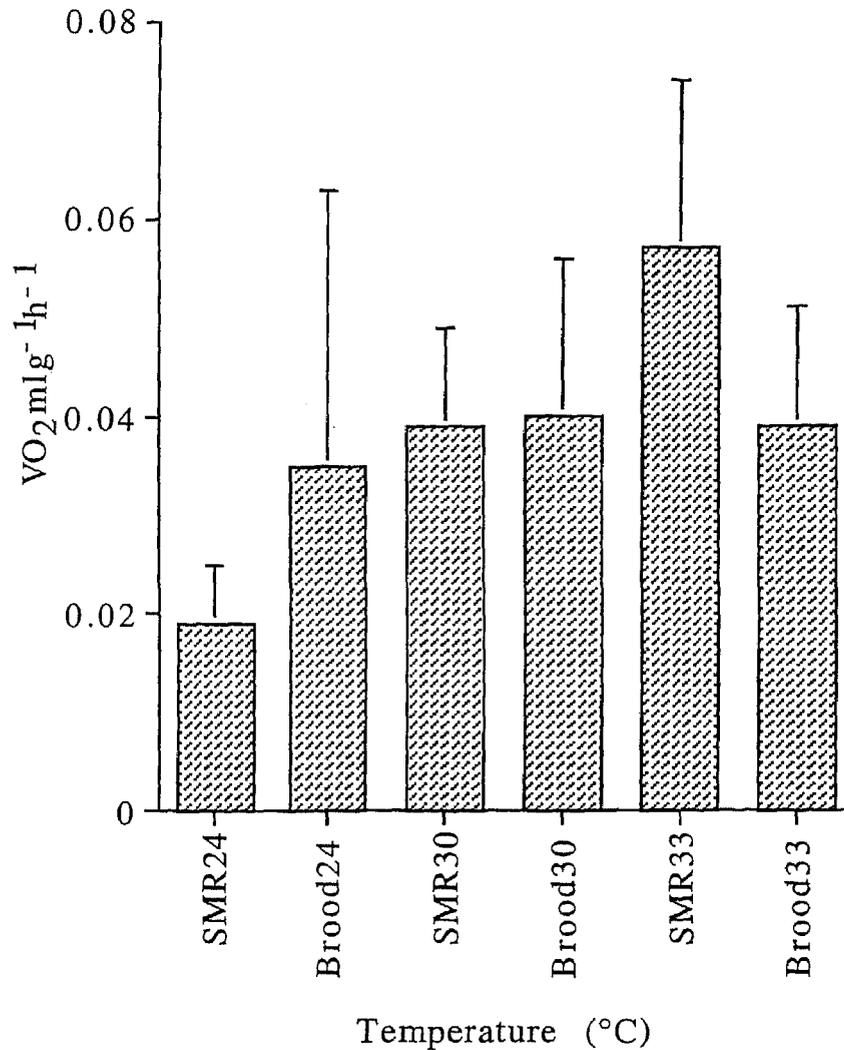


Figure 3.2. Children's python metabolism while brooding at different temperatures ( $\pm$ SD) ( $n = 4$ ).

Most water pythons shivered while coiled around their eggs at ambient temperatures below 31°C. At 33 and 30°C there were no significant differences among SMR, gravid, brooding or immediate post-brooding metabolic rate (ANCOVA  $P > 0.05$ ) (Fig. 3.3). The metabolic rate of

shivering pythons brooding at 26°C was 4.2 times greater than SMR (ANCOVA,  $F_{1,12} = 9.288$ ,  $P = 0.002$ ). At 24°C there was no evidence of shivering, and no significant differences ( $P > 0.05$ ) among SMR, gravid, brooding or immediate post-brooding metabolic rates in water pythons.

Visual inspection of a single 1560 g *Morelia s. variegata* coiled around her eggs did not reveal any shivering during either day or night. The metabolic rate at the three experimental temperatures was similar to data for SMR (26°C = 0.006 mL g<sup>-1</sup> h<sup>-1</sup>; 28°C = 0.012 mL g<sup>-1</sup> h<sup>-1</sup>; 30°C = 0.029 mL g<sup>-1</sup> h<sup>-1</sup>).

Visual inspection of the single *Morelia s. bredli* coiled around her eggs indicated that this species was using shivering thermogenesis to heat the clutch mass. Brooding metabolic rate at 28°C was 4.6 times SMR (shivering metabolic rate = 0.074 mL g<sup>-1</sup> h<sup>-1</sup>; SMR = 0.016 mL g<sup>-1</sup> h<sup>-1</sup>).

#### *Thermal sensitivity of brooding metabolism*

Thermal sensitivity ( $Q_{10}$ , Eq. 1) of oxygen consumption during brooding in water pythons was calculated to be -3.69 using equation 1 (Fig. 3.4). The negative sign is used to indicate that for an increase in ambient temperature, metabolic rate was met with a decrease over the 7°C temperature range (26 - 33°C).

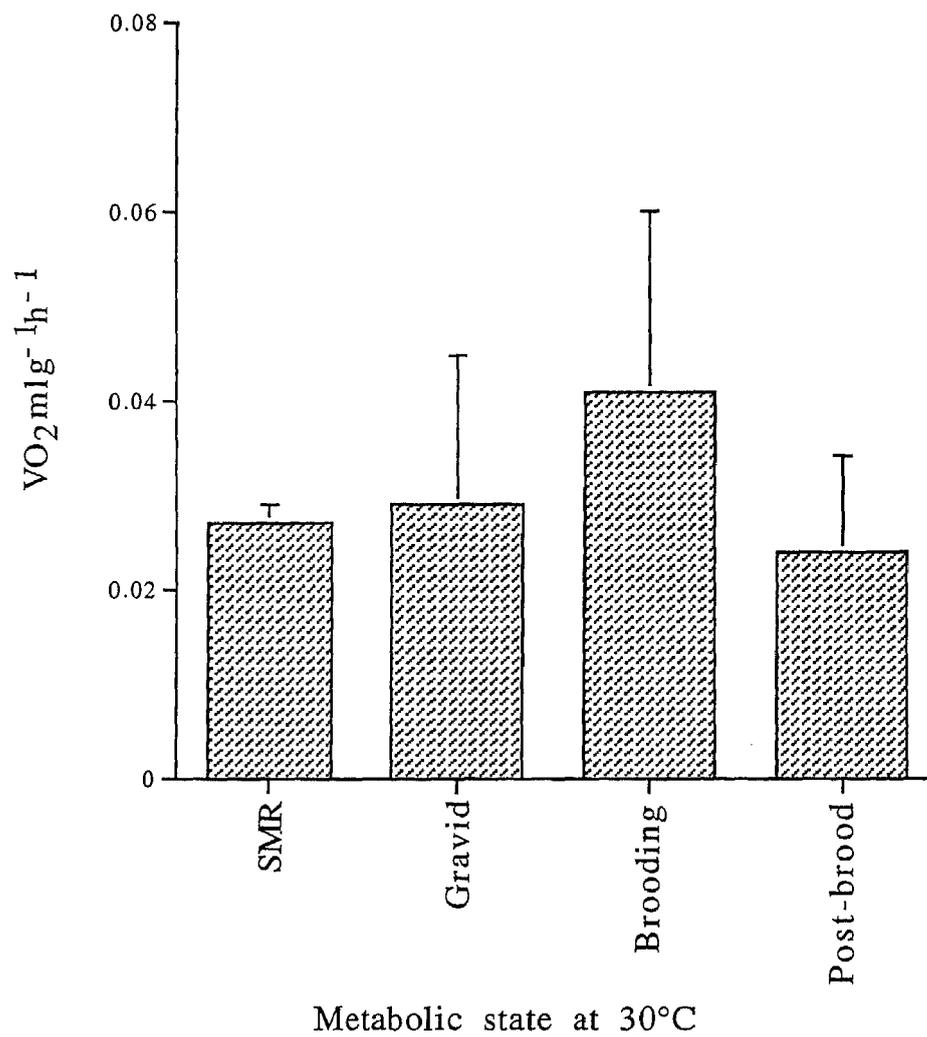


Figure 3.3. Water python metabolism showing SMR, gravid pythons, brooding and post-brooding at 30°C ( $\pm$ SD) (n = 8).

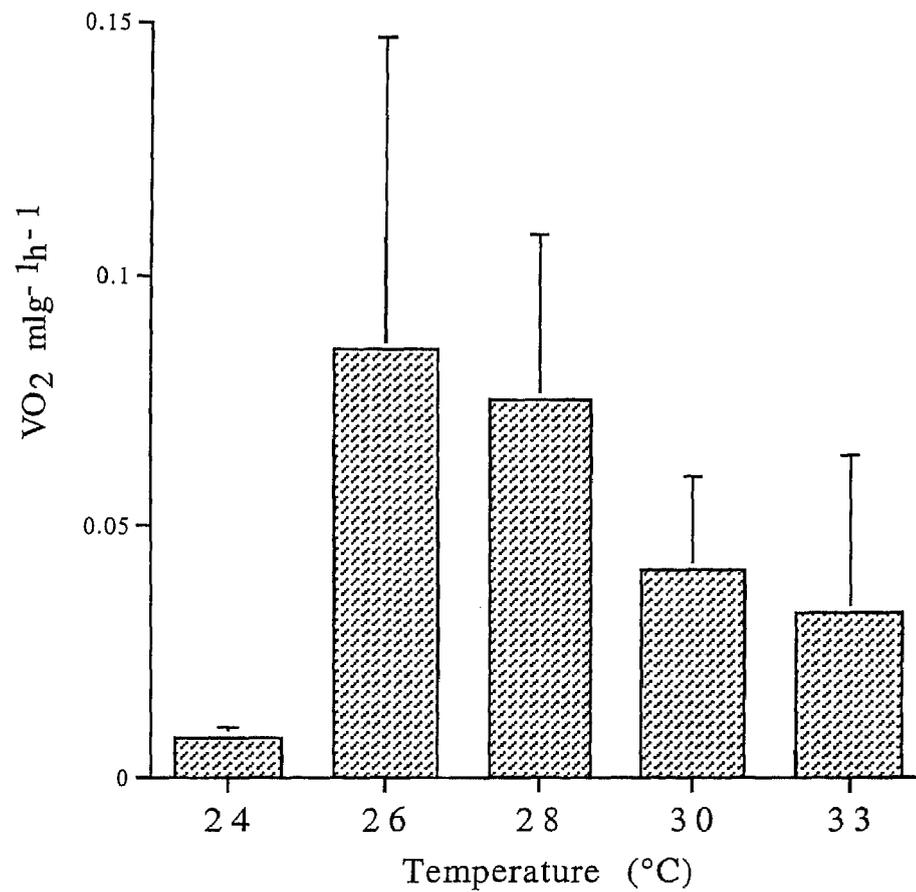


Figure 3.4. Metabolic rate of brooding water pythons at different temperatures showing metabolic decrease with increasing temperatures between 26°C and 33°C ( $\pm$ SD) ( $n = 8$ ).

### *Comparison of shivering thermogenesis*

Two modes of shivering thermogenesis were observed during this study. The first was a pulse method employed by both water and olive pythons, and involved a single pulse of the entire body. The momentum produced a single spike of movement 0.36 s in duration (range 0.3 - 0.5, n of *L. fuscus* = 5); there was a short quiescent period of 1.2 s (range 0.4 - 2.5 s, n of 10 samples from a single animal). The second type of shivering was observed in *M.s. bredli*, and involved a rolling of the body, consisting of a number of shivering events in each movement. Thus, the muscles along the body contracted in a prolonged movement, with a mean duration of 3.2 s (range 2 - 4 s, n of measurements = 5 in a single animal) with a period of 3.1 s quiescence between shivering bouts (range 1.7 - 4.8 s, n of 10 samples from a single animal).

### *Behavioural maintenance of clutch humidity*

At no time during the maternal incubation of eggs in a desiccating environment did *L. fuscus* attempt to increase the humidity of the clutch or surroundings with urine, direct water contact or regurgitation of water. The six water pythons (mean clutch size = 15, range 12 - 17) shivered sporadically for the first week while coiled tightly around the eggs. As the time spent in a desiccating environment increased, pythons coiled as tightly as possible and ceased shivering completely. Five weeks post oviposition it became apparent that the eggs were

desiccating, even though each female had access to water and remained coiled tightly around the eggs. By week six, three clutches of eggs had desiccated to the point of embryo death. The remaining three clutches were removed from the females and placed in a mixture of 1:1 vermiculite to water, and most subsequently survived.

### **Discussion**

Pythons have a low  $V_{O_2}$  compared to other reptiles (Bennett and Dawson 1976; Andrews and Pough 1985; Chappell and Ellis 1987). However, metabolic rate increases substantially during digestion and while brooding. When digesting a meal, the metabolic rate of the large *Python molurus* increases by up to 45 times SMR (Secor and Diamond 1997). The smaller Australian pythons have a more modest increase due to digestion of about six - 12 times SMR (Bedford 1996; Thompson and Withers 1999; Bedford and Christian 2001). Similarly, another species of Australian python (*Morelia s. spilota*) exhibits an increase in metabolic rate many times above SMR during brooding (Harlow and Grigg 1984). This increase in metabolism during brooding is due, in part, to an increase in body temperature through shivering thermogenesis. The increase in  $T_b$  allows pythons to maintain the egg mass at a relatively constant temperature even when ambient temperatures decline.

The advantages of a higher constant temperature during incubation are that duration of incubation is reduced (Packard and Packard 1988; Slip and Shine 1988a), and thus, embryos experience fewer deformities (Ross and Marzec 1990). In some instances, an increase in temperature of three degrees (from 29 to 32°C) has resulted in the incubation period being reduced by more than ten days (Greer 1997). The shorter incubation period also allows the female to commence feeding sooner in a cooler climate where opportunities for feeding and digestion are highly seasonal (Slip and Shine 1988b).

Although shivering thermogenesis has resulted in an elevated metabolic rate 22 times SMR in the Australian Diamond python, *Morelia s. spilota* (Harlow and Grigg 1984), and 10 - 20 times SMR in the Burmese python, *Python molurus bivittatus* (Vinegar *et al.* 1970; Van Mierop and Barnard 1978), the increase found in this study was more moderate and similar in energy cost to the digestion of a moderate sized meal.

#### *Children's pythons*

Shivering thermogenesis is energetically expensive (Vinegar *et al.* 1970; Harlow and Grigg 1984; Slip and Shine 1988a), and has not been documented in the small (<350 g) children's python (*Antaresia childreni*). Shivering is occasionally observed during brooding in some species of the *Antaresia sp.* complex (*A. maculosus* and *A. stimsoni*),

but it is rare and of short duration (< 5 minutes)(pers.obs, P. Comber, pers. comm.). There was an increase in MR at low temperatures in at least two individual *A. childreni*, but there was no evidence of shivering. Thus, it appears that small pythons such as the *Antaresia childreni* complex and the African species, *Python regius*, may be too small to effectively increase body and clutch temperature when ambient temperature declines. To date three wild *Antaresia childreni* nests have been observed and all were well insulated in soil burrows at least 40 cm below ground (Bedford and Christian unpub. data). The selection of a thermally optimal nest site with high humidity may reduce the need to shiver (Madsen and Shine 1999a).

#### *Water pythons*

The temperature at which eggs are incubated had, until recently, been seen as critical to the successful development and hatching of pythons (Branch and Patterson 1975; Ross and Marzec 1990; Barker and Barker 1994). A recent study of the incubation of water python eggs using three temperature regimes (stable, hot fluctuating and cold fluctuating) showed that a stable temperature is not necessary for successful hatching (Shine *et al.* 1997). If temperature were critical in determining egg mortality, it might be postulated that all pythons would shiver, unless it became too costly (metabolically) or ambient temperature made shivering unnecessary (Shine and Madsen 1996). Brooding water pythons maintained in the laboratory at 33°C displayed

no evidence of shivering, and they draped loosely over the eggs. When temperature declined to 30°C the animals coiled more tightly around their eggs. In a cooling environment this behaviour would increase the thermal inertia, thereby reducing the rate at which the female and egg mass loses heat (Cogger and Holmes 1960).

When possible, water pythons maintain a preferred nest temperature of 32.2-32.4°C (Shine *et al.* 1997), higher than that traditionally used for captive incubation of python eggs, which is usually 30°C (Ross and Marzec 1990; Barker and Barker 1994). It has been suggested that some water pythons have lost the ability to shiver and thus must use the near optimal conditions found in goanna warrens (Shine *et al.* 1997, Madsen and Shine 1999a). In this study I collected three gravid *L. fuscus* from goanna warrens and allowed them to care for their clutch in the laboratory. Without exception, when the animals had no means of laying in the benign environment of the goanna warren, they carefully regulated egg temperature using the pulse method of shivering thermogenesis. Thus, shivering thermogenesis is facultative in this species, depending on the thermal characteristics of the nest.

#### *Carpet pythons*

Using mammal-like (Harlow and Grigg 1984) shivering, a *M.s. bredli* was able to increase body temperature 3°C above ambient with 14 shivers per minute. Harlow and Grigg (1984) indicate that 'mammal-

like' shivering pythons are capable of increasing  $T_b$  at least  $7^\circ\text{C}$  above ambient with 50 shivers per minute. Pulse shivering animals are capable of up to about 60 shivers per minute, but generally, 30 - 40 per minute can be maintained and results in a temperature differential of  $2 - 2.5^\circ\text{C}$  for a 2 - 3 kg water python.

#### *Evaluation of shivering methods*

A small Burmese python (14.25 kg) using pulse shivering (pers. obs.) could maintain egg temperatures  $4.7^\circ\text{C}$  above ambient (Vinegar *et al.* 1970), while a 20.7 kg Burmese python could create a differential due to pulse shivering up to  $8.3^\circ\text{C}$  (Van Mierop and Barnard 1978) (Table 3.1). Water pythons weighing 2 - 3 kg could only increase body temperature by about  $2^\circ\text{C}$  above ambient, thus there is a correlation between heat generated using pulse shivering thermogenesis and maternal mass (regression  $T_b = 1.21 + 0.312 \times M$ ;  $R^2 = 0.91$ ). However, it appears that for a given number of shivers per minute the 'mammal-like' method generates three times more heat than pulse shivering for a similar energetic cost. However, when the time spent shivering is considered per minute I found that the pulse method was only enacted for 33% of the time that the mammal-like method was employed (mammal-like time shivering was 3.2 seconds x 14 events per minute at  $28^\circ\text{C}$  = 44.8 s of movement compared to the pulse method where each pulse was 0.36 s x 38 events per minute at  $28^\circ\text{C}$  to give 13.7 s, approximately one third the time in movement per minute). A

diamond python of 4 kg was able to raise its body temperature almost 7°C above ambient using ‘mammal-like’ shivering (Harlow and Grigg 1984), which is approximately three times the heat expected to be generated using the regression equation describing the relationship between the heat generated and mass of the pulse shivering python species. As there is a disparity between the heat generated by the different modes of shivering, it will be important in future studies to ensure that the mode of shivering is considered when comparing endogenous heat production in pythons.

The factorial scope of brooding  $\dot{V}_{O_2}$  divided by SMR for a diamond python (Harlow and Grigg 1984) is given as 22; however, SMR values given for the 4 kg post-brooding diamond python (0.0039 mL g<sup>-1</sup> h<sup>-1</sup>; Harlow and Grigg 1984) are considerably lower than both recent laboratory data (*Morelia s. spilota*, 0.032 mL g<sup>-1</sup> h<sup>-1</sup>, s.d. 0.01, n = 12, mean mass 1331g s.d. 236 g @ 30°C and 0.026 mL g<sup>-1</sup> h<sup>-1</sup>, s.d. 0.01, n = 12, mean mass 1193 g s.d. 149g @ 27°C, Bedford 1996), and SMR predicted from allometric equations for pythons (Andrews and Pough 1985; Chappell and Ellis 1987; Bedford and Christian 1998). If SMR is estimated from allometric equations rather than using the very low SMR reported by Harlow and Grigg (1984), the ratio of brooding metabolism/SMR (0.088/0.007) is 12.6 rather than 22, indicating that the cost of brooding in the diamond python may not be as expensive as calculated by these authors.

Table 3.1. Temperature differential ( $T_b - T_a$ ) produced by different pythons using two methods of shivering thermogenesis.

Species	Mass (kg)	Temperature differential (°C)	Shivering mode	Reference
<i>A. childreni</i>	0.3	none	none	This study
<i>M.spilota</i> <i>variegata</i>	1.6	none	none	This study
<i>Liasis olivaceus</i>	>4.0	none	Pulse sporadic	This study
<i>Morelia spilota</i>	4.0	7.0	'mammal-like'	Harlow and Grigg 1984
<i>M.s.bredli</i>	3.0	3.0	'mammal-like'	This study
<i>Liasis fuscus</i>	3.0	2.5	Pulse	This study
<i>Python molurus</i>	14.3	4.7	Pulse	Vinegar et al. 1970
<i>Python molurus</i>	20.7	8.3	Pulse	Van Mierop and Barnard 1978

#### *Thermal sensitivity of metabolism*

This study demonstrates that, as temperature increased, metabolic rate of brooding water pythons decreased, resulting in a  $Q_{10}$  above three that indicates that metabolism was upregulating with the change in temperature. This relationship between temperature and metabolism is unexplored in ectotherms, although some ectotherms are able to produce endogenous heat (Heinrich 1977; Hayes and Garland 1995).

This relationship between metabolism and temperature appears necessary for brooding pythons to maintain a relatively constant body and clutch temperature when ambient temperature falls. In all pythons investigated, when ambient temperatures fell to 24°C, shivering ceased and the metabolic rate quickly fell to a level similar to SMR at the lower temperature. This may indicate that temperatures of 24°C and lower make heat production too costly or impossible for some brooding pythons. Metabolism continued to increase when  $T_a$  fell from 30 to 26°C, with heat production increasing also. Thus "heat produced" is not independent of  $T_a$  – it increases with decreasing  $T_a$  indicating that heat production over the temperature range of 30 to 26°C has increased to compensate for the increased heat loss.

Pythons in the tropics have access to microhabitats that are both warm and humid (Madsen and Shine 1999b) and therefore would be less likely to require shivering thermogenesis to maintain optimal egg incubation temperatures than animals in arid or temperate zones. Therefore tropical conditions would suit either not shivering, or using pulse shivering to maintain nest temperature.

Pythons in the tropics are thought to have access to an abundance of food (Shine 1991; Madsen and Shine 1999a,b), and often increase mass after reproduction. They can also reproduce most years, being limited only in abnormal rainfall years (Madsen and Shine 1996b, 1999a). In

contrast, pythons from the temperate or arid zones only breed biennially or less frequently, most likely due to high costs of reproduction for females and the short feeding season (Harlow and Grigg 1984, Slip and Shine 1988a,b, Shine and Slip 1990; Shine 1991). Thus, large, temperate pythons appear unable to increase body mass sufficiently to reproduce every year (Harlow and Grigg 1984; Slip and Shine 1988a,b). The amount of parental care given to a clutch of eggs may be dependent on the frequency and cost of reproduction.

'Mammal-like' shivering may represent the maximum energy available to ensure the survival of a clutch of python eggs, and this mode of incubation is confined to python species that are large from temperate areas and breed infrequently.

#### *Nest humidity*

Although it has been previously reported that brooding pythons supplement sub-optimal nest humidity conditions with water obtained from outside the nest (Ross and Marzec 1990; Shine 1991), I found no evidence of this behaviour in captivity. From our observations, it is doubtful that water pythons would supplement nest humidity in a deliberate manner with extraneous water, however it is important to recognise that the small sample size may considerably affect these conclusions.

*Shivering mode and geographic radiation of pythons in Australia*

Australian pythons that shiver can be divided into two groups on the basis of their method of shivering. Pulse shivering pythons include *Liasis fuscus*, *L. olivaceus*, *Antaresia stimsoni*, *A. maculosus*, *Morelia amethestina* (N. Charles pers. com.), *M. s. cheynei* (K. Ailand, pers. com.) and *M. viridis* (B. Withey pers. com.). The 'mammal-like' shivering pythons include most of the *Morelia spilota* complex such as *M.s. spilota*, *M.s. imbricata*, *M.s. bredli*, *M.s. mcdowellii*, *M.s. metcafei* (J. Bell, B. Bush, P. Comber, N. Charles, G. Fyfe, pers. com.), and the woma (*Aspidites ramsayi*) (G. Fyfe pers. com.). Female pythons may remain coiled around their eggs after oviposition but not actually use shivering thermogenesis to maintain a constant temperature of the clutch. This suggests that they are acting as a guardian until the eggs have hatched, and integral to this may be the female mass which adds thermal inertia to the clutch and the decreased egg surface area exposed to desiccating conditions.

Although common, shivering thermogenesis is not universal among pythons, with some Australian pythons having either a limited ability to shiver (*L. olivaceus*, (this study), *A. stimsoni* (P. Comber, pers. com.) and *A. maculosus* (pers. obs)), or being unable to do so (*Aspidites melanocephalus* (T. Sullivan and S. Lee pers. com.), *Antaresia childreni* (pers. obs.), *Antaresia perthensis* (B. Bush, pers. com.), *Morelia oenpelliensis* (P. Krauss pers. com.), *M. carinata* (J. Weigel pers.com.

only one animal observed) and *M. s. variegata* (Darwin form, pers. obs.)).

The geographic radiation of Australian pythons appear to correlate with the mode of shivering used. The pulse method is associated with only a moderate radiation from the tropics, with most species (*Liasis olivaceus*, *L. fuscus*, *Antaresia childreni*, *Morelia amethestina*, *Morelia viridis*) confined to the hot tropics. A "mammal-like" shivering method is more cost effective in terms of energy used per unit of heat produced and is associated with a radiation into colder latitudes. It is interesting to note that "mammal-like" shivering has evolved independently in two Australian genera (*Aspidites* and *Morelia*). However, there are taxa within each genus which use either pulse shivering or do not shiver at all, and these taxa are confined to the tropical north.

Animals which exhibit 'mammal-like' shivering are medium to large species found in temperate climates (*A. ramsayi*, *M.s.spilota*, *M. s. variegata*, *M. s. imbricata*, *M.s. metcalfei*, *M. s. mcdowellii*). Animals that have either no propensity to shiver (*M. oenpelliensis*, *M. carinata*, *A. childreni*) or use pulse shivering (*L. fuscus*, *M. amethestina*, *M. viridis*) appear to have a limited tropical distribution, although *A. melanocephalus* has a more widespread, though still tropical, distribution. Pythons that do not use shivering to maternally incubate

eggs even though there may be some remnant of this strategy include:

*L. olivaceus*, *A. stimsoni*, and *A. maculosus*. These are pythons that have a larger distribution than the pulse shivering species, and may have more tolerance to the climatic variation associated with high latitude.

## Chapter 4

### The Spatial Ecology of pythons in the Northern Territory of Australia



Darwin Botanic Gardens – study site for *Morelia spilota variegata*



Roe creek flood out – Alice Springs study site for *M. s. bredli*

**Abstract**

Sit-and-wait foraging may be a relatively inefficient way to obtain prey, but many Australian python species successfully employ this low energy foraging strategy to meet their modest energetic needs. Energy is conserved and survival is enhanced when a python can remain concealed from predators but still access both prey and a high stable body temperature. In this study, I investigated the home range of four species of python from the Northern Territory of Australia that differed in size, level of arboreality, and climate. I found that some members of the genus *Morelia* were primarily arboreal (88 - 92% of time) while some of the small *Antaresia* species were mostly terrestrial (69.2 - 95.2% of time). Home range differed inter-specifically, but this was due to the increased distance between trees for the desert arboreal species, with available refuge sites for *Morelia spilota bredli* being further apart than refuge sites for the other species. Pythons in this study inhabited single refuge sites for periods of between one and 11 months. In particular, *Morelia s. variegata* in the Darwin Botanic Gardens used selected refuge sites in home ranges that were small and overlapping. This overlap in space was accompanied by temporal separation, with different snakes using the same refuge site at different times. This spatial overlap of refuge sites was not found in other species of python examined, although there was a significant overlap in home ranges within each of the species.

## **Introduction**

Home range is the total area an animal occupies in its day to day movements (Burt 1943; Harris *et al.* 1990) and varies in size both within (Rose 1982; Van Sluys 1997; Webb and Shine 1997a), and between species (Christian and Waldschmidt 1984; Harris *et al.* 1990).

A number of factors influence home range, including gender, size of animal, size of habitat patches, time of year, trophic level, foraging behaviour, population density, energetic requirements, the thermal environment, social behaviour and mate availability (McNab 1963; Turner *et al.* 1969; Barker *et al.* 1979; Rose 1982; Mace and Harvey 1983; Christian and Waldschmidt 1984; Christian and Tracy 1985a; Shine 1987; Stamps 1987, 1994; Donnelly 1989; Auffenberg *et al.* 1991; Bedford and Sullivan 1993; Secor and Nagy 1994; Van Sluys 1997; Kelt and Van Vuren 1999).

A sedentary lifestyle in snakes is generally linked to a plentiful and predictable food supply (Gregory *et al.* 1987). The Australian landscape rarely has plentiful or predictable food resources (Flannery 1994), and this would seem at odds with a sedentary lifestyle. Here I investigate movements and the use of space by some Australian pythons, and comment on a sedentary lifestyle that is associated with a low food intake and low energy use.

Australian pythons have a low preferred body temperature compared to most Australian lizards and some other Australian snakes (Greer 1989, 1997; Bedford and Christian 1998). They also have a slightly lower standard metabolic rate (Bedford and Christian 1998), attributes which might assist them to cope with a low energy existence. Pythons are mostly nocturnal, secretive and sedentary animals (Slip and Shine 1988a,b,c; Shine 1991; Shine and Fitzgerald 1996) that will survive provided there are abundant places to hide and a sufficient food supply (Shine and Fitzgerald 1996). They can spend weeks, and in some cases months, in a single location (Slip and Shine 1988a; Shine and Fitzgerald 1996). In this study I examine the use of secure retreat sites from which pythons hunt using sit-and-wait (ambush) predation (Slip and Shine 1988a,b,c).

Snakes, having a discrete home range as opposed to random movements, or a nomadic lifestyle (Shine and Lambeck 1985; Slip and Shine 1988a; Shine and Fitzgerald 1996), may exhibit site fidelity, that may in turn affect their susceptibility to human induced habitat disturbance (Webb and Shine 1997a). Many terrestrial and arboreal species of python persist in areas that have been affected by severe habitat modification (Slip and Shine 1988a,c; Shine and Fitzgerald 1996; Shine *et al.* 1999). It is becoming increasingly obvious that in order to understand the impact of human development on a species of reptile, it is necessary to understand their spatial requirements (Cogger

*et al.* 1993; Pearson 1993; Torr 2000). With extensive land clearing forecast for the Northern Territory of Australia, a basic understanding of the spatial ecology of pythons would allow planning authorities to initiate adequate reserves and conservation areas to ensure future survival of the various taxa.

In this study, I investigate the home range of four taxa of python from the Northern Territory of Australia. These species are differentiated by size, level of arboreality, and the climate of two geographic zones.

Because most pythons are sit-and-wait predators, I examined the length of time the pythons spent in any one refuge. It might be expected that the longer an animal can remain hidden but still obtain all needed resources, the more successful it will be in surviving at minimal cost while exploiting its environment. I would expect the tropical species to have access to more food and water than their arid zone counterparts and therefore have a smaller home range while maintaining a secretive, low energy existence. However, the warmer year round ambient temperatures in the tropics would result in a higher metabolic rate and therefore increase the demand for food. I also discuss the potential effect of disturbance and habitat fragmentation on the python species of the Northern Territory of Australia.

## Methods

In this study two species (one large and one small) of tropical python and two species (one large and one small) of python from the temperate, arid zone were examined. The larger species were the top end carpet python (*Morelia spilota variegata*), studied in the Darwin Botanic Gardens approximately three km east of Darwin city (study area 5.94 ha<sup>-1</sup>) and the central carpet python (*M.s. bredli*), studied in Roe Creek, 25 km south of Alice Springs, Northern Territory (study area 180.8 ha<sup>-1</sup>). Both species grow to three m, and they consume mostly endothermic prey (Shine and Slip 1990; Cogger 2000). The two smaller species were the northern children's python (*Antaresia childreni*), studied on the Adelaide River flood plain and Beatrice Hill, 75 km east of Darwin (study area 22.3 ha<sup>-1</sup>) and the stimson's python (*A. stimsoni*), studied in Ormiston Gorge, 180 km west of Alice Springs (study area 5.8 ha<sup>-1</sup>). These smaller species are generally less than one m in total length and consume mostly ectothermic prey such as frogs and lizards (Shine and Slip 1990; Cogger 2000).

Darwin Botanic Gardens consists of a small sandstone escarpment, approximately 10 m high on its western boundary, and is home to both remnant native and some non-native vegetation. The surrounding area is low lying, mainly flat with many large tree species, and planted with an under-story of grass. This mosaic of native and non-native plants has been watered and maintained for nearly 100 years. Trees of

significance are African Rain-trees (*Samanea saman*) because they are the largest and oldest non-native plants in the Botanic Gardens (G. Pritchard pers. com.). This site is bordered on the west side by a major road, on the east and south sides by housing and on the north side by a school. Thus, it is an apparent hard edged vegetative oasis among buildings (Stamps 1987).

Roe Creek is, for the most part, a dry watercourse bordered by large river red gum trees (*Eucalyptus camaldulensis*). This study site continues for 1.5 km south of the Stuart highway before opening into a flood plain. At this junction, the vegetation changes to be dominated by coolibah trees (*Eucalyptus microtheca*). The under-story of the entire region appears to be introduced buffel grass, although some native grasses survive during seasons with good rains. For at least the previous seven years, cattle and horse grazing allowed only approximately 5-15% of the ground to have a buffel grass cover with no obvious natural grasses (pers. obs.). Most trees along the water-course were live, but dead trees were interspersed throughout. Wild passionfruit bushes (*Capyrus* sp.) grow near some of the *E. camaldulensis* in the creek. In a creek system affected by drought throughout much of the study, these bushes were the only low lying plants that appeared green and succulent.

The Adelaide River flood plain that was the study site for *A. childreni* was a flat treeless black-soil expanse adjacent to the western bank of the Adelaide River. This floodplain extends uninterrupted for more than 20 km and is approximately two km wide with a dominant vegetation of sedges (*Eleocharis*) and wild rice (*Oryza*) (Cowie *et al.* 2000). Beatrice Hill is a series of small isolated hills that rise from the floodplain, with remnant rainforest and bamboo stands found in the gullies between these hills.

The Ormiston Gorge study site for *A. stimsoni* is a creek lined with river red gum trees (*E. camauldulensis*) coursing through a gorge with spinifex (*Triodia* sp.) studded hills on either side. Each side of the creek has a scree slope below a vertical cliff to the top. The approximate height of these cliffs is 60 m.

More than 80 pythons, including at least 12 in each taxa were implanted with Holohil (ST-2I or PD-2T) temperature sensitive transmitters using a previously outlined technique (Shine and Fitzgerald 1996; Webb and Shine 1997b). These transmitters were calibrated in a water bath using a thermometer traceable to a standard. Due to transmitter problems only approximately 25% of implanted pythons were used in experiments (number of animals for each species presented in tables 4.1-4.3).

Home range data were collected by locating individual pythons and each animal location was noted on a map with notes to indicate tree, burrow or building. These data were collected whenever possible throughout the year, with some pythons being monitored every month over two years, while others were monitored daily over periods of two weeks. A location on any one day was assumed to be the static location for that day, and when an animal was found in a single location over many months, I assume that it had not moved from that location. The mean distance moved for each python in each species was compared using ANOVA and indicates the distance each species moved between refuge sites.

Home ranges of each of three species of python (*M.s. variegata*, *M.s. bredli*, *A. childreni*) were determined using the Minimum Convex Polygon (MCP) method on the computer package Calhome (Kie *et al.* 1994). I examine the 95% isopleths as a robust estimate of home range size, and this allowed comparison with other studies (Harris *et al.* 1990; White and Garrott 1990). 50% of total area MCPs were examined to investigate whether a core home range incorporated most data points with only a few outside this area making up the balance of the total home range. Home range of the fourth species of python (*A. stimsoni* at Ormiston Gorge) was not calculated because of the lack of movement in both summer and winter, but I discuss other aspects of space use by this species. Because most species of python are sedentary sit-and-wait

foragers, I determined how long pythons of each species spent in one place before moving. The amount of time an animal spent in one position was determined in three *M.s.variegata*, seven *M.s. bredli* and four *A. childreni*. Six *A. stimsoni* were tracked in both summer and winter.

The positions of individual snakes were used to estimate the duration each species spent either on the ground or above the ground in either a tree or building. These data were then expressed as percentage of total time the animal was observed. Major refuge sites are described as a site used by an animal for substantial periods (ie: > one month), and within a home range, a python may have multiple major retreat sites.

Pythons are extremely long lived (15-20+ years, Greer 1997), reproduce infrequently (Chapter 3) and have a variable and uncertain food supply. For these reasons I used a conservative estimate of density of pythons, consisting of the number of animals marked at each study site over a four year period as the total number of animals in that site. This assumes that the population is in a steady state over time with no recruitment, export or import in any one year. This was done in order to give some workable estimate of population size because most of the assumptions used to estimate population size from mark-recapture data were violated (Seber 1982). Coupled with the cryptic nature of pythons was the fact that some animals were fitted with transmitters, introducing a bias when searching the study sites. The total number of

animals caught in each taxa was used to give a representative mean mass of pythons in each study site. This estimate of python biomass was divided by the total area of each study site to give an estimate of mass per m<sup>2</sup>.

Analysis of variance on log-transformed data was used to examine the home range of each species, with comparisons between species, sexes, distances moved and tropical versus temperate climatic region. All statistics are evaluated at the 0.05% level of probability.

## Results

Analysis of variance revealed a significant difference in size of home range among python species ( $F_{2,16} = 3.74$ ,  $P = 0.046$ ). A Fisher's post hoc test revealed that *M.s. bredli* had a larger home range than *A. childreni* but not *M.s. variegata* (Tables 4.1-4.3). There was no effect of sex in home range size ( $P > 0.05$ ).

There was a significant difference in the distance moved by species (ANOVA  $F_{2,16} = 14.1$ ,  $P = 0.0003$ ). Multiple comparisons, using Fisher's post hoc test, indicated that *M.s. bredli* moved further between sites within their home range than the other species (*M.s. variegata* and *A. childreni*). There was no significant difference in 50% isopleth home range between species, between sexes or with different mass (ANOVA  $P > 0.05$ ) There was however a difference in area between the 50 and

95% isopleths for two of the three species of python examined, with the two carpet pythons having a considerably smaller core area when compared to total home range (*M.s.bredli* paired t-test,  $t_{1,6} = 7.54$ ,  $P = 0.0003$ ; *M.s.variegata* paired t-test,  $t_{1,6} = 7.17$ ,  $P = 0.0004$ ), while this relationship was not significant for *A. childreni* (paired t-test,  $P > 0.05$ ). Major retreat sites were 461.2 m (s.d. 236.1 m) apart for *M.s. bredli*, 183.8 m (s.d. 246.1 m) apart for *A. childreni* and 190.3 m (s.d. 76.5 m) apart for *M.s.variegata*. There was no significant difference among species when comparing the distance between major retreat sites (ANOVA  $P > 0.05$ ). However, when one extraordinary *A. childreni* distance is removed, distances between major retreat sites were significantly different ( $F_{2,9} = 6.2$ ;  $P = 0.02$ ), with a Fisher's post hoc test revealing that major retreat sites for *M.s. bredli* were further apart than either *M.s. variegata* or *A. childreni*.

The percentage of time spent either on the ground or in an elevated refuge site suggests that the two *Morelia* species were predominantly arboreal, while the small *Antaresia* sp. were mostly terrestrial. *Morelia s. variegata* spent 70.4% of the time in trees, 22.2% in buildings and 7.4% on the ground. *Morelia s. bredli* were found in trees 87.7% of the time and on the ground only 12.3% of the time. *Antaresia childreni* were found on the ground 69.2% of the time and in buildings 30.8% of the time. *Antaresia stimsoni* were found on the ground most of the time (95.2%) and only infrequently in trees (4.8%).

*Morelia s. variegata* were tracked for two to 24 months, and the data encompassed all months of the year. During this time, three individuals moved from one position to another between tracking periods (ie: number of locations is equal to the number of fixes), although two of these animals were only tracked for a short time during the late dry season when reproduction occurs. The other four *M.s.variegata* moved less frequently, with three females and one male being sedentary over at least part of the monitoring period (Table 4.1). *M.s.variegata* spent from 62 up to 330 days in one place (Table 4.1). Of these animals that spent a number of days in one place, two spanned most seasons, while the third was sedentary only during the dry season.

*Morelia s. bredli* were tracked for seven to 12 months, incorporating all seasons in central Australia. All *M.s. bredli* had periods of sedentary behaviour, with the number of fixes greater than the number of locations for these fixes (Table 4.2). Time in one place ranged from 35 to 95 days in *M.s. bredli* (Table 4.2). Of the animals that were sedentary for a period of time, five were sedentary in winter, two in spring, and two in summer.

Table 4.1. Home range (HR) for top end carpet pythons (*M.s. variegata*) using the minimum convex polygon method. Included are numbers of locations and fixes, maximum time in a single location, months with movement of pythons between refuges, and home range as a percentage of total study site. Standard deviations are presented in parenthesis.

ID	Sex	Mass (g)	N of Locations	N of Fixes	Duration of Tracking	Max. Time in Single Location (days)	Months	95% MCP (m <sup>2</sup> )	50% MCP (m <sup>2</sup> )	Movement (m)	HR/Total Area %
11	Male	717	15	15	4 months	Nil.	Sept-Dec	2369.8	446.9	43.5	4.0
12	Male	1654	20	20	12 months	Nil.	Jan-Dec	2449.8	162.0	57.0	4.1
16	Male	3738	28	51	24 months	330	Jan-Dec	10582.1	1861.4	34.4	17.6
18	Female	2590	43	62	24 months	270	Jan-Dec	5830.2	332.1	44.3	9.7
23	Female	3641	16	29	12 months	62	Jan-Dec	3534.2	463.3	36.1	5.9
15	Female	2902	8	8	2 months	Nil.	Sep-Oct	1408.4	188.6	42.6	2.4
02	Female	1658	19	25	7 months	71	Sep-Mar	1679.0	840.5	33.2	2.8
Mean		2414.3						3979.1	613.5	41.6	6.6
S.D.		(1122.2)						(3267.3)	(594.8)	(8.2)	(5.4)

Table 4.2. Home range (HR) for central carpet pythons (*M.s.bredli*) using the minimum convex polygon method. Included are numbers of locations and fixes, maximum time in a single location, months with movement of pythons between refuges, and home range as a percentage of total study site. Standard deviations are presented in parenthesis.

ID	Sex	Mass (g)	N of Locations	N of Fixes	Duration of Tracking	Max. Time in Single Location (days)	Months	95% MCP (m <sup>2</sup> )	50% MCP (m <sup>2</sup> )	Movement (m)	HR/Total Area%
12	Female	961	19	25	8 months	60	Feb-Sep	11117.6	2911.3	160.3	6.2
24	Female	975	15	23	9 months	73	Dec-Aug	10103.8	1123.4	186.3	5.6
14	Female	1330	19	28	10 months	49	Dec-Sep	23605.1	828.9	248.0	13.1
25	Male	1091	7	11	7 months	58	Mar-Sep	7069.2	164.4	328.8	3.9
17	Female	817	20	31	12 months	95	Jan-Dec	3685.3	726.1	146.6	2.0
10	Female	2062	25	36	12 months	90	Jan-Dec	49717.3	4288.1	286.3	27.5
9	Female	1342	15	24	9 months	60	Dec-Aug	3096.2	164.4	113.7	1.7
Mean		1225.4						15484.9	1458.1	210.0	8.6
S.D.		(416.7)						(16579.9)	(1555.2)	(79.3)	(9.2)

Table 4.3. Home range (HR) for children's pythons (*Antaresia childreni*) using the minimum convex polygon method. Included are numbers of locations and fixes, maximum time in a single location, months with movement of pythons between refuges, and home range as a percentage of total study site. Standard deviations are presented in parenthesis.

ID	Sex	Mass (g)	N of Locations	N of Fixes	Duration of Tracking	Time in Single Location (days)	Seasons	95% MCP (m <sup>2</sup> )	50% MCP (m <sup>2</sup> )	Movement (m)	HR/Total Area %
379	Male	330.5	10	19	6 months	80	Sep-Jan	43295.9	23268.8	84.5	194.0
206	Female	217.4	4	15	3 months	63	Sep-Nov	65.3	65.3	14.4	0.29
258	Male	428.6	8	8	4 months	Nil.	Sep-Dec	3585.1	51.5	81.2	16.1
438	Female	376.9	19	28	4 months	81	Sep-Dec	576.9	175.1	13.9	2.6
556	Male	528.0	11	17	2 months	45	Oct-Nov	30.9	6.9	3.7	0.14
Mean		376.3						9510.8	4713.5	54.8	42.6
S.D.		(115.2)						(18943.7)	(10372.4)	(54.2)	(84.9)

*Antaresia childreni* were tracked mostly over the buildup and wet seasons, for two to six months. Four of the five animals remained sedentary and did not move between tracking periods, and one animal moved between every tracking period (Table 4.3). *A. childreni* spent from 45 to 81 days in one place (Table 4.3).

*Antaresia stimsoni* occupied the same refuge sites for some months each time they were released. Some animals did not move between sites, but the number of locations was small with the number of fixes high for each refuge site. *A. stimsoni* spent a mean of 63 days in the winter, and at least 90 days in summer in one place, but transmitters failed after this time.

Of the 19 pythons examined in all species, 15 remained sedentary over at least part of the release period. The number of pythons per hectare ranged from 0.15 in *M.s. variegata* to a high of 3.4 for *A. stimsoni* (Table 4.4).

Table 4.4. Number of pythons caught for each species, with sexes, mass and density of pythons per hectare.

Species	Male	Female	Total	Mean Mass (g)	Snake mass per area (kg ha <sup>-1</sup> )	Snakes per ha <sup>-1</sup>
<i>M. s. variegata</i>	9	11	20	1888.9	6.3	0.3
<i>Ms. bredli</i>	13	43	56	1059.8	3.3	0.15
<i>A. childreni</i>	23	27	50	213.1	4.8	1.7
<i>A. stimsoni</i>	8	14	22	138.2	5.2	3.4

## Discussion

Pythons in this study had a predominantly sedentary activity pattern, and at least two species had a core home range similar to that exhibited in some lizards (Christian *et al.* 1986). All species of python examined here selected many refuge sites; however it is difficult to compare refuge selection of pythons with that of a core area identified in other studies in which the species are prepared to defend an area or site (Christian *et al.* 1986; Heatwole and Taylor 1987; Johnston 1997).

The economics of foraging suggests that animals should try to maintain an optimal distance between each other so that a food resource is maximised (Ake Norberg 1977; Beachly *et al.* 1995), indicating that pythons should ambush prey from widely spaced refuge locations. Some species of snakes use the same refuge sites as con-specifics, but with temporal separation (Webb and Shine 1997a; Whittaker unpub. data). In this study, many individual *M.s.variegata* used the same tree

hollow refuge sites, and these sites were visited by a number of conspecifics. The fact that individual *M.s.variegata* would occupy a site before or after a conspecific, but not at the same time, indicates refuge site recognition and conspecific avoidance. The recognition of the suitability of refuge sites, such as whether prey are present or whether a conspecific currently resides in it, is possibly done using chemical cues (Graves and Halpern 1991; Gregory *et al.* 1987; Bedford 1992; Bull *et al.* 1993, 2000). Whether an occupant can recognise the prey attributes of a site is unknown. However, it is possible that because these snakes are able to go for long periods of time without food (Bedford and Christian 2001), most sites have a similar probability of encountering prey.

*Morelia s. bredli* is arboreal, living in both river red gum and coolibah trees along the Roe creek watercourse. These pythons had a larger home range than the other species of python examined, and they moved farther between major retreat sites. These differences appear due to the distance that separates the tree canopy in the desert. Generally, more than 20 m separates trees; therefore, snakes must move over open ground between trees. Free-standing water was only available once during a flood in this four year study period. However, these snakes are able to drink from their coils during rain while in a tree canopy (Fyfe 1994). There was a high density of pythons at the

study site, and this may, in part, be due to the refuge sites available and the proximity to prey.

*Antaresia childreni* were mostly terrestrial, living among rocks in open areas, underground or in buildings. Food was plentiful and water was never more than 200 m away, but in most cases was within 50 m. These pythons had a small home range, but were able to move long distances when needed. These pythons are presumably at risk of predation on Beatrice Hill and surrounds, due to their small size and the prevalence of predators. However, they were found in large numbers, which may have been due to the refuge sites in a rock wall erected as part of a prison complex some decades ago.

*Antaresia stimsoni* were terrestrial and in this study confined to the rocky watercourse of Ormiston Gorge in the West Macdonnell Ranges. Although mostly terrestrial, they were occasionally found on trees such as river red gums (*Eucalyptus camaldulensis*). During spring and summer they were found within 50 m of the creek in the gorge. This meant they had access to both water and food (frogs and birds) (unpub. data). During this study *Antaresia stimsoni* moved from the valley floor to the cliff tops each April-May for the winter months. Seasonal movement in reptiles has been found in crocodiles (Webb *et al.* 1982), elapid snakes (Webb and Shine 1997a,b), acrochordid snakes (Shine and Lambeck 1985; Houston and Shine 1994) and pythons (Slip

and Shine 1988a,b; Madsen and Shine 1996a). Five of the six *A. stimsoni* moved to the top of the cliffs at Ormiston gorge during May and stayed there until the transmitters failed (approx. four months later). Of the six *A. stimsoni*, five moved to a cliff with a western facing aspect, while the sixth animal moved half-way up the opposite hill with an eastern facing aspect. After these snakes selected a refuge site, they sealed the entrance with soil during the cold months (Bedford and Comber 2000).

There is a positive allometric relationship between home range size and mass (Turner *et al.* 1969; Christian and Waldschmidt 1984) in lizards, but no similar relationship was found in this study, even though the smaller species of python were only 17% of the mass of *M.s.variegata* and 33% of the mass of *M.s. bredli*. The fact that there was no difference in home range size between species when all data were compared appears due to the large variation in home range size within each species. This may suggest that over the study period, some pythons occupied an area that had significant food and water resources and animals did not have to move around, while other pythons were forced to move over large distances to secure these (or other) resources. It was not possible to measure home range for each season, so some of the intra-specific variation may be related to seasonal changes in home range.

A large variation in home range has been found in other Australian snake species, with ranges from 0.003 to 1.12 ha<sup>-1</sup> for *Hoplocephalus bungaroides* (Webb and Shine 1997a) and from 0.002 to 4.0 ha<sup>-1</sup> for the Australian black snake (*Pseudechis porphyriacus*) (Shine 1987). The arafura filesnake (*Acrochordus arafurae*) has a small home range (0.01 to 0.47 ha<sup>-1</sup>), that is less variable than most other snake species studied to date (Shine and Lambeck 1985; Houston and Shine 1993). In general, home ranges of the pythons in this study were similar to the home ranges of other species of Australian snake. However, the home range of the diamond python (*Morelia s. spilota*) is comparatively large, and for one male python was 12.4 ha<sup>-1</sup> and for a female was 8.2 ha<sup>-1</sup> (Slip and Shine 1988a). The home ranges of these diamond pythons are more than an order of magnitude greater than the home range of pythons from this study. This difference may be due to the seasonal movement in spring of *M.s.spilota*. It is probable that *M.s.spilota* moves large distances between both food and mates, and both resources may be in low numbers and distributed relatively evenly over the forest habitat. The pythons in our study appear to be concentrated within a habitat type (ie: remnant rainforest for *M.s. variegata* or riverine edge for *M.s. bredli*) and may have continuous access to both food and conspecifics. Even though prey may be in very low densities at times, there may be an energy saving by not moving from an area that provided resources in the past.

Significant sexual differences in home range are found in some snakes (Weatherhead and Hoysak 1988; Webb and Shine 1997a) including some species of python (Slip and Shine 1988a; Shine and Fitzgerald 1996). Differences between sexes were not found in this study, although this may have been an artefact of small sample sizes.

Carpet python taxa (*Morelia* sp.) are distributed almost continuously around the coast of Australia (reviewed in Barker and Barker 1994), but *Morelia s. bredli* is geographically separated from the coastal *Morelia* taxa. The amount of time each taxon within the genus *Morelia* spends on the ground varies with latitude. Southern populations (*M.s. imbricata*) are entirely terrestrial and confined to cliffs and burrows (St Frances Island population, South Australia, S. Stone pers. com.).

Diamond pythons (*M.s. spilota*) are mostly terrestrial, being arboreal only 16% of the time (Slip and Shine 1988a). Carpet pythons from the north coast of New South Wales are arboreal 45% of the time (Shine and Fitzgerald 1996). The Queensland *Morelia* populations are more arboreal, with the northern sub species, *M.s. cheynei* being almost entirely arboreal (Barker and Barker 1994).

*Morelia spilota variegata* (this study) were almost entirely arboreal, living in both trees and buildings. The buildings that carpet pythons inhabit are connected in most instances to the surrounding tree canopy. Thus, a continuous artificial canopy negates the need for *M.s. variegata* to traverse open ground when moving between trees. Food

items were also arboreal, including birds, rats and fruit bats (Appendix 1).

Pythons of all four species spent more than one month in at least one retreat site (excluding periods of inactivity by gravid or brooding animals). The fact that this behaviour was not just confined to the cool or cold months of the year suggests that the pythons were obtaining some benefit from it. Possible benefits include a constant food supply or a well-insulated refuge site that allow concealed thermoregulation (Schlesinger and Shine 1994; Webb and Shine 1997a,b; Kearney and Predavec 2000).

A single *Morelia s.variegata* that remained in the same refuge for 330 days was inside a roof space. Over the time this animal was monitored, five con-specifics spent from a few days to a few months in the same roof. Although the other snakes did not have implanted transmitters, our observations suggest that they were not aggregated in the roof and that the roof space was sufficiently large to allow spatial separation. These results are similar to the sedentary nature of the diamond python (*M.s.spilota*), in which individuals spent up to 80 days in a single site in almost all seasons (Slip and Shine 1988a).

Some aspects of python physiology suggest that they are able to eat and digest food at almost any time during the year (Bedford and

Christian 2000), and they are also capable of a reduced metabolism when food and/or water are limited (Bedford and Christian 2001). Major refuge sites may allow pythons to conserve energy by being confined in a safe haven during times of reduced metabolism, but still able to continue ambush foraging from the refugia. Four *M.s. bredli* had more than one major refuge site. Thus, over the duration of the study they were found in one refuge for a month or more and after they moved they were found in another site for a month or more. In addition to being related to the spatial distribution of trees in the desert habitat, the large distance between refuge sites may also be related to the probability of obtaining food from any one site when the density of conspecifics in the entire riverine habitat is high.

Site selection in sit-and-wait predators is affected by factors that influence the economics of the foraging strategy (Beachly *et al.* 1995), and some factors that affect the viability of a particular site include recognition of site quality, and travel time between sites (Caraco and Gillespie 1986; Beachly *et al.* 1995). It is obvious that if all resources are abundant in one site and they diminish with movement away from that site, there is no need to move.

Pythons that used either the same or neighbouring major retreat sites had considerable overlap in home ranges. Many *M.s. variegata* visited shared refuge sites over the duration of this study. The overlap of five

*M.s.variegata* resulted from the shared use of a single African rain-tree in the middle of the Botanic Gardens (Fig. 4.1). In many instances, a *M.s.variegata* would leave a refuge site and within one month, another would take its place. Other than during the breeding season, no two animals shared a single site, other than through loose association in a roof space. Thus, they appeared to be temporally separated, despite the shared use of the same refuge sites.

No *M.s. bredli* were found in a refuge site that had been recently evacuated by a con-specific even though they occasionally occupied the same tree. Thus, *M.s. bredli* were both temporally and spatially separated.

The availability of food does not appear to be limiting in the tropics, and is, for the most part, seasonally available (Shine 1991; Shine and Madsen 1997; Madsen and Shine 1999). Thus, although prey may be scarce at various times of the year, the prey are predictably available at some time during the year. However, a factor that might limit survival for some tropical python species such as *M.s.variegata* is the availability of refuge sites. The tropical *A. childreni* did not appear limited by food or refuge sites, although this was not quantified.

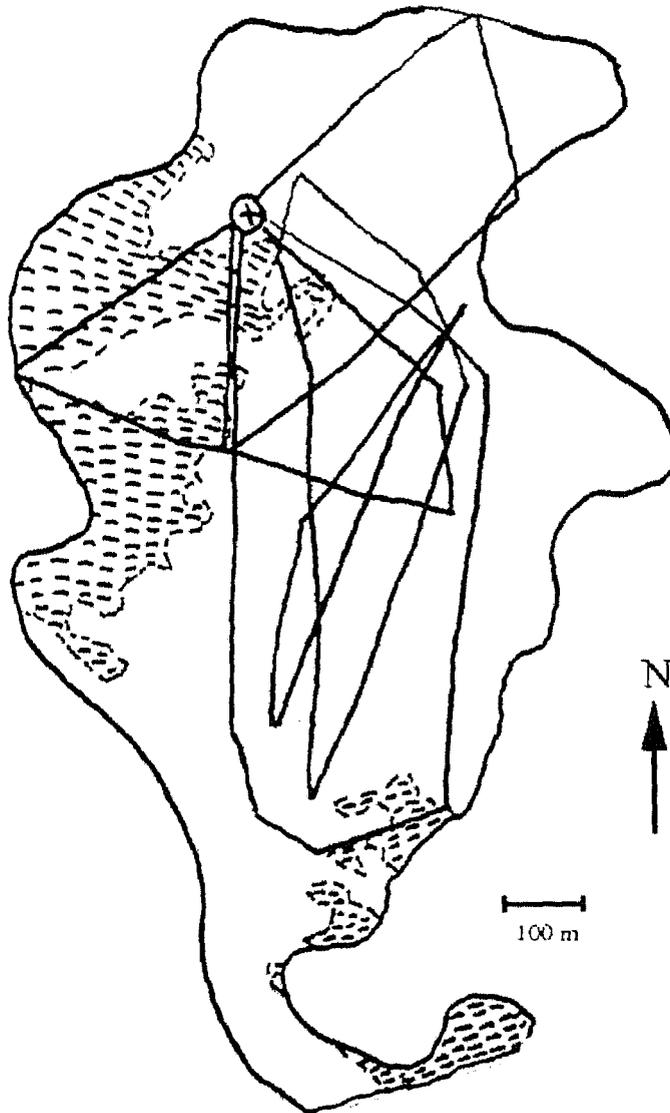


Figure 4.1. Darwin Botanic Gardens study site, showing five *M.s. variegata* home ranges and the overlap with a single tree hollow used by three animals (indicated by X). All pythons were adults. The hatched area indicates areas without tree canopy.

The home ranges for some species examined here were not two dimensional. *A. stimsoni* in some cases only moved 20 m horizontally, but up to 150 m vertically up a cliff face. Similarly, *M.s. bredli*, have to descend one tree before being able to climb another. If the distance between trees is 20 metres and the height of a tree is 10 metres then the distance measured is 20 metres, but the reality is that the animal has moved 40 metres. Thus, a comparison of species such as *A. childreni* and *M.s. bredli* is difficult due to the two dimensional nature of the home range of the former and the three dimensional nature of the latter.

Land clearing has caused a decline in diversity and abundance of birds (Hobbs *et al.* 1992), a number of mammal species (Morton and Baynes 1985; Caughley and Gunn 1995) and reptiles (Cogger *et al.* 1993). With home range being linked to size of animal in both mammals and some reptiles, the degree of decline in animal species will be in some part dependent on the size of the animals and the extent of fragmentation of habitat (Christian and Waldschmidt 1984; Pearson 1993; Stamps 1988; Kelt and Van Vuren 1999). Survival of a species will depend on its ability to cope with reduced habitat and how it moves between suitable areas of habitat (Stamps 1987; Mittermeier *et al.* 1992; Shine and Fitzgerald 1996).

The impact that habitat reduction would have on populations of *M.s.variegata* may be less damaging than to *M.s. bredli* due to the latter species' need for large trees and a large home range, the open spaces over which they must traverse, and the general patchiness and uncertainty of resources in the desert habitat. Food resources are often associated with the abundance of vegetation (Madsen and Shine 1999a) and can be markedly reduced through a small reduction in habitat. Habitat reduction will have its strongest impact in years with below average rainfall. How habitat reduction would affect the smaller species of *Antaresia* is less clear. A small home range is common to both species, although there were exceptions. Both species of *Antaresia* fall victim to large predators, and with human disturbance and land clearing comes introduced predators that would possibly impact heavily on these species. Predation pressure may not be increased if these species have access to secure refuge sites from which they can hunt and move between sites while concealed. However, if refuge sites are removed with clearing, these species will be adversely affected. Because of their secretive habits, it is doubtful that many pythons would be found during fauna surveys, particularly if populations are small. Therefore, the sit-and-wait foraging strategy of pythons can make them invisible to planning authorities and vulnerable to habitat fragmentation if key refuge sites are removed (Wilcove *et al.* 1986; Weins 1994).

## **Chapter 5**

# **Seasonal body temperatures in four species of Australian python**

**Abstract**

Pythons in this study remained cryptic and possibly used passive thermoregulation to obtain a preferred body temperature range. By remaining sequestered in a refuge that results in appropriate  $T_b$ s during the day, pythons do not expend energy actively thermoregulating or expose themselves to predation. Body temperature peaked immediately before nightfall in both hot and cool seasons for most python species. Changes in python  $T_b$  between seasons may be due, in part, to the change in thermal characteristics of a retreat, and the position of the python within it.

## Introduction

Thermoregulation at a preferred body temperature ( $T_b$ ) by reptiles is thought to optimise physiological and ecological processes such as digestion, sprint speed, social behaviour, prey consumption, predator avoidance, defence, mate searching and shelter seeking (Greenwald 1974; Christian and Tracy 1981; Hertz *et al.* 1982; Huey 1982; Troyer 1987; Slip and Shine 1988a,b; Huey and Kingsolver 1989; Garland *et al.* 1990; Rosen 1991; Hertz 1992; Weatherhead and Robertson 1992; Bauwens *et al.* 1995; Webb and Shine 1998; Shine *et al.* 2000; Shine *et al.* 2002). Thus, the study of thermoregulation (Cowles and Bogert 1944) has occupied the forefront of herpetological research for more than 50 years. Shuttling in and out of a heat source allows the maintenance of a constant  $T_b$  or range of temperatures (Cowles and Bogert 1944; Huey and Pianka 1977), but there are a raft of thermoregulatory strategies used by reptiles, representing a continuum between the avoidance of extremes to very precise regulation.

Generally, diurnal reptile species have a higher preferred  $T_b$  than nocturnal reptiles (Huey and Bennett 1987; Greer 1989, 1997).

However, in Australia many diurnal elapids have preferred  $T_b$ s similar to nocturnal pythons (Shine 1991; Bedford 1996; Greer 1997) indicating that even when not using solar radiation to bask pythons can still achieve a high body temperature. Some snakes thermoregulate as precisely as some lizards (Peterson 1987; Charland 1995), but at least

one species of large tropical python (*Liasis fuscus*) is under no thermal constraints and apparently does not actively thermoregulate (Shine and Madsen 1996), but they do avoid extreme body temperatures.

Ectotherms that remain concealed while maintaining a preferred body temperature can be termed cryptic thermoregulators. This is a recognised strategy for temperature maintenance when the animal is small and may be subject to strong predation pressure (Bustard 1967; Schleisinger and Shine 1994; Christian and Bedford 1996; Webb and Shine 1998; Kearney and Predavec 2000). However, if little threat from predators exists, there would be little need to regulate body temperature cryptically (King and Green 1993; Heger and Heger 1994). Larger reptiles such as most pythons may therefore be able to bask overtly (Slip and Shine 1988a), whereas smaller species and juvenile pythons of large species may be inclined to regulate  $T_b$  cryptically.

In this study, I investigate the thermal relations of four species of nocturnal python. In the wet-dry tropics of northern Australia, the thermal regime has been described as benign, with a temperature range capable of supporting activity all year round (Shine and Madsen 1996). In the arid desert region, where the temperature is highly variable both within and between seasons, activity and feeding periods are periodically limited. I therefore investigated differences in  $T_b$ s between species, zones and seasons in python species.

## Materials & Methods

### *Animals and study sites*

The top end carpet python (*Morelia spilota variegata*) and central carpet python (*M.s. bredli*) are large (to three m), mostly arboreal species that eat predominantly small mammals and birds (Shine and Slip 1990; Shine 1991; Greer 1997). The stimson's python (*Antaresia stimsoni*) and children's python (*A. childreni*) are small terrestrial species (<one m) that consume mostly lizards and frogs (Shine and Slip 1990; Greer 1997).

Both tropical species of python (*M.s. variegata* and *A. childreni*) inhabit the wet-dry tropics of the Northern Territory within 250 km of the coast (Barker and Barker 1994). In this climatic zone, approximately 80% of the 1600 mm mean annual rainfall occurs during the "wet season" months from December to March (Taylor and Tullock 1985). The wet season is characterised as having high humidity with mean minimum and maximum diel temperatures of 25.3°C to 33.1°C respectively. The dry season minimum and maximum diel temperatures are 19.0°C and 30.4°C respectively with lower humidity (Taylor and Tullock 1985).

Python species in central Australia (*Morelia s. bredli* and *Antaresia stimsoni*) are subject to a thermally variable desert environment, both within and across the four seasons. The mean annual rainfall is 268 mm

and usually falls in winter (James 1991a&b). Climatic anomalies such as rain depressions associated with cyclones can dramatically alter the total annual rainfall, with the entire annual rainfall having fallen within 48 hours (James 1991b). Thus, temperatures and rainfall are unpredictable. Mean monthly summer maximum temperatures vary from 29° to 37°C, while mean minimum temperatures vary from 15 to 22°C (Slatyer 1962). Mean monthly winter maximum temperatures vary from 17.6 to 24.2°C, while mean minimum temperatures vary from 1.1 to 9.8°C. During this study the annual rainfall exceeded the mean annual rainfall in three of the five years (1997, 1998 and 2000) (Commonwealth Bureau of Meteorology, Alice Springs, unpub. data).

*Morelia spilota variegata* were tracked in the Darwin Botanical Gardens, 3 km east of the centre of Darwin for between two and 24 months.

*Antaresia childreni* were caught and monitored for between two and six months at Beatrice Hill, 75 km east of Darwin. *Morelia s. bredli* were monitored for between seven and 12 months in Roe creek, 25 km south of Alice Springs, and *A. stimsoni* were found at Ormiston Gorge, 180 km west of Alice Springs and monitored for between two and four months.

Darwin is located near 12°S latitude, while Alice Springs is approximately 1500 km south near 23°S latitude.

### *Temperature measurements*

Temperature sensitive transmitters (Holohil PD-2T or ST-2I) were implanted in the abdominal cavities of pythons of the four taxa. Transmitter temperatures were calibrated against a standard thermometer in a water bath, with temperature determined by transmitter pulse rate on an interval pulse counter (Telonics, USA). All animals were released at their point of capture after three weeks of monitoring to ensure they were not affected by surgery. Each group of animals was subsequently located and temperature data were recorded by hand from the transmitter pulse interval readouts over a 24 hour period in both the wet/summer and dry/winter.

A single day was chosen to represent each season for each python species, with air and body temperatures recorded by hand for each. Summer and wet season data were collected in January for each species while winter and dry season data were obtained in July for all species except *A. stimsoni*, for which data were obtained in May. Body temperature data were collected on clear, sunny days that would allow the 'maximum temperatures' during each season.

Air temperatures ( $T_a$ ) were measured in the shade at a height of 1.5 m using a Fluke thermocouple thermometer in conjunction with a 30 gauge thermocouple that had its tip painted white, to reduce extra absorbed radiation (Christian and Tracy 1985b). Ground temperature

was measured in the sun and shade using a Raytek infrared thermometer (Raynger PM, Raytek, Santa Cruz, USA). There were four *M.s.variegata* monitored in both the wet and dry seasons, six wet season and five dry season *A. childreni*, seven *M.s.bredli* in summer and winter and four *A. stimsoni* in summer and five in winter.

Most pythons in this study were active at night, with very few found moving or basking during the day in any season. Preferred body temperatures of pythons used in this study were obtained from animals in a laboratory thermal gradient (Bedford 1996; Bedford and Christian 1998).

### *Statistics*

Repeated measures analysis of variance (RMANOVA) was used to compare temperatures between seasons and species ( $P < 0.05$ ). Python body temperatures and air temperatures were collected throughout the 24 h day. Visual inspection of the body temperature data for each python species indicated a general pattern of warming throughout the day and cooling throughout the night in both seasons. To investigate the relationship between warm and cool body temperatures and ambient temperature, some of the data were separated into two temperature extremes, a cool sample period before dawn (0200 – 0600 h) and a warm sample period before dark (1300 – 1800 h). These two time periods were selected to represent the warmest and coolest periods for python Tb as determined from visual inspection of the Tb

data over the entire day. Other periods throughout the day appear to follow a near linear increase and decrease in  $T_b$  and as such were possibly of little value in the overall understanding of python  $T_b$  except as part of the general daily pattern already described. Without a direct measure of all environmental parameters (solar radiation, wind speed, conduction, etc) the warming and cooling periods are difficult to compare. One-group t-tests were used to compare the temperature obtained by snakes over the four hours before sunset (1300-1800 h) and the mean temperature obtained in a laboratory temperature gradient for each python species in each season (Bedford and Christian 1998).

## Results

### *Morelia s. variegata*

Comparing the five hour period from 1300 to 1800 h between seasons, *Morelia s. variegata* had a significantly lower  $T_b$  in the dry season than in the wet season (paired t-test:  $t_{1,4} = 22.1$ ,  $P < 0.0001$ )(Fig. 5.1).

Similarly, the pre-dawn temperatures were significantly lower in the dry season than in the wet season (paired t-test  $t_{1,4} = 38.8$ ,  $P < 0.0001$ ). (Fig. 5.1)

### *M.s.bredli*

Summer  $T_b$  was significantly higher than winter  $T_b$  throughout the day for *M.s.bredli* (Paired t-test:  $t_{1,21} = 70.7$ ,  $P < 0.0001$ ), with the difference

being around 14°C (Fig. 5.2). Pre-dawn Tbs were also significantly higher in the summer (paired t-test,  $t_{1,4} = 67.0$ ,  $P < 0.0001$ ).

(Fig. 5.2)

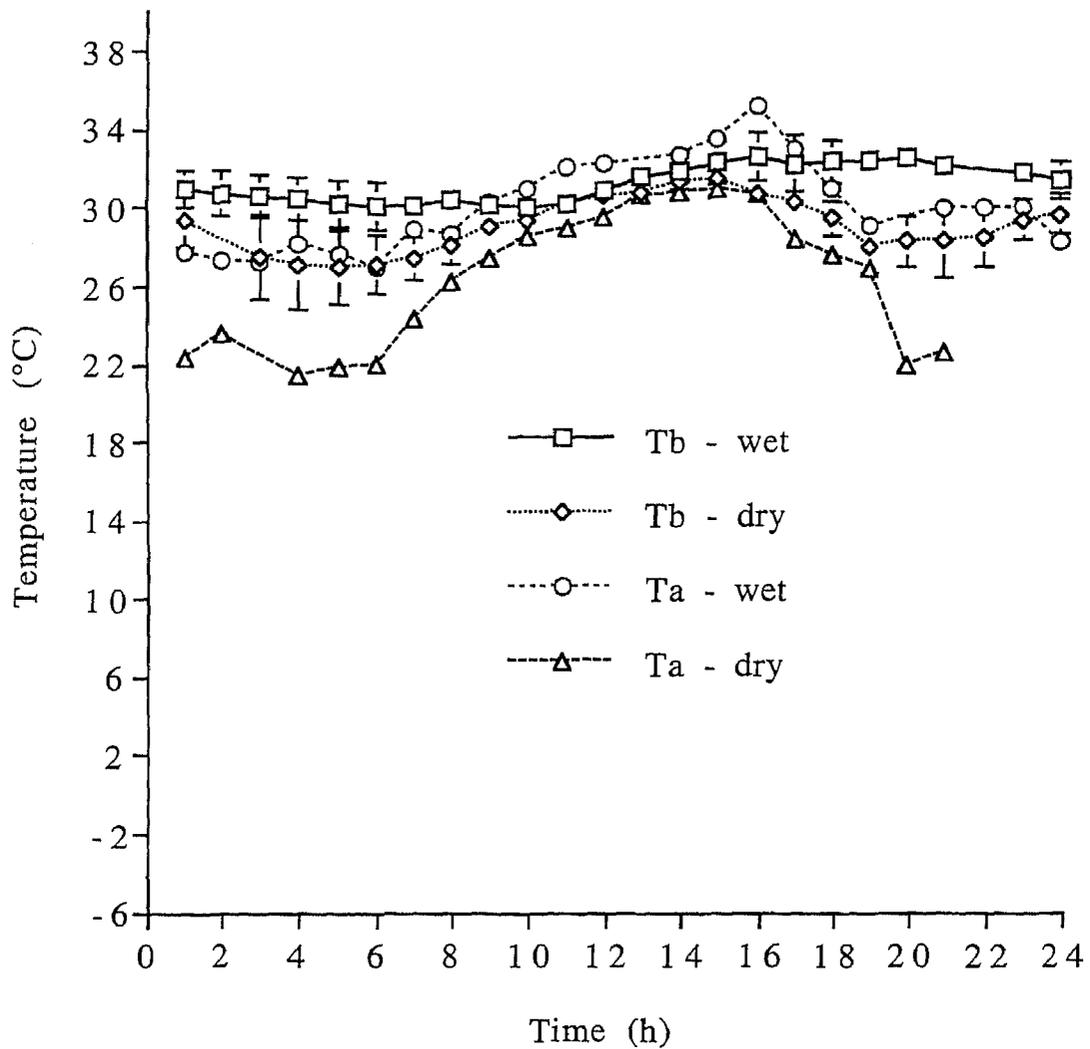


Figure 5.1. Body temperatures of *M.s.variegata* in the wet (diamonds,  $n = 6$ ) and dry (squares,  $n = 6$ ) seasons. Air temperatures for wet and dry seasons are also presented. Error bars represent standard errors.

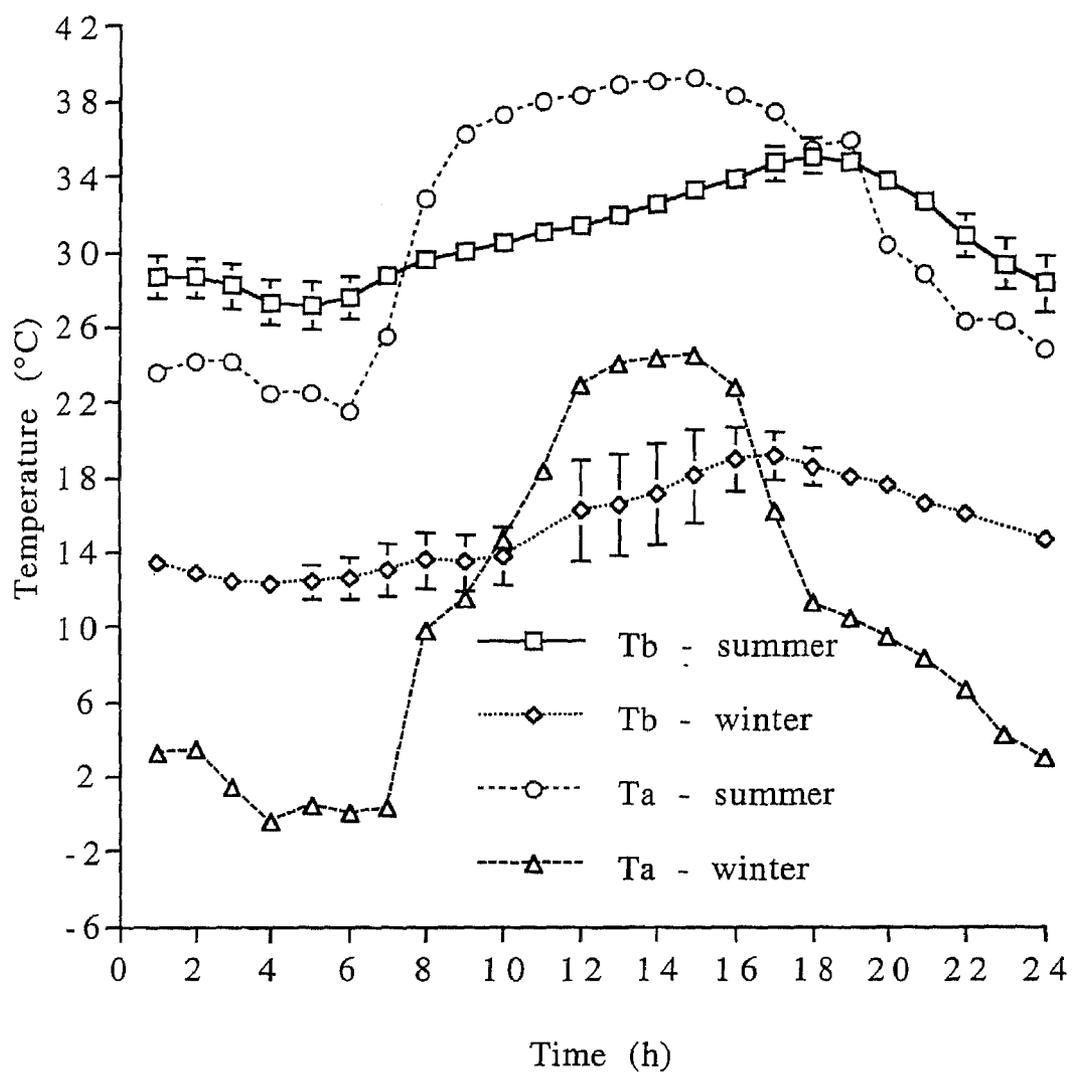


Figure 5.2. Body temperatures of *M.s.bredli* in the summer (diamonds,  $n = 7$ ) and winter (squares,  $n = 7$ ). Air temperatures for summer and winter seasons are also presented. Errors represent standard errors.

*Antaresia childreni*

There was no significant difference in Tbs between wet and dry seasons in *A. childreni* during the period immediately before dark (paired t,  $P > 0.05$ ). However, the pre-dawn Tbs in the dry season were significantly lower than in the wet season (paired t-test,  $t_{1,4} = 27.3$ ,  $P < 0.0001$ ).

(Fig. 5.3)

*A. stimsoni*

In *A. stimsoni* there were no significant differences in Tbs between seasons in either the period immediately before dark or the period pre-dawn (paired t-test,  $P > 0.05$ ).

(Fig. 5.4)

There were significant differences in python body temperatures between species and between seasons (RMANOVA, species  $F_{3,32} = 579.3$ ,  $P < 0.0001$ ; season  $F_{3,32} = 1372.1$ ,  $P < 0.0001$ ). A Fisher's means separation test revealed that the Tb of *M.s.bredli* in the cool season was cooler than all other species, while the Tb of *A. childreni* in the cool season was lower than the Tb of both *A. stimsoni* and *M.s.variegata*. Python body temperatures were significantly higher in the late afternoon (1300 – 1800) than in the early part of the day (0200 – 0600) (RMANOVA,  $F_{1,32} = 290.5$ ,  $P < 0.0001$ ). Similarly, a Fisher's post-hoc test revealed that python Tbs in the warm season (summer/wet)

were higher than  $T_b$ s in the cool season (winter/dry) when all species and seasons were analysed.

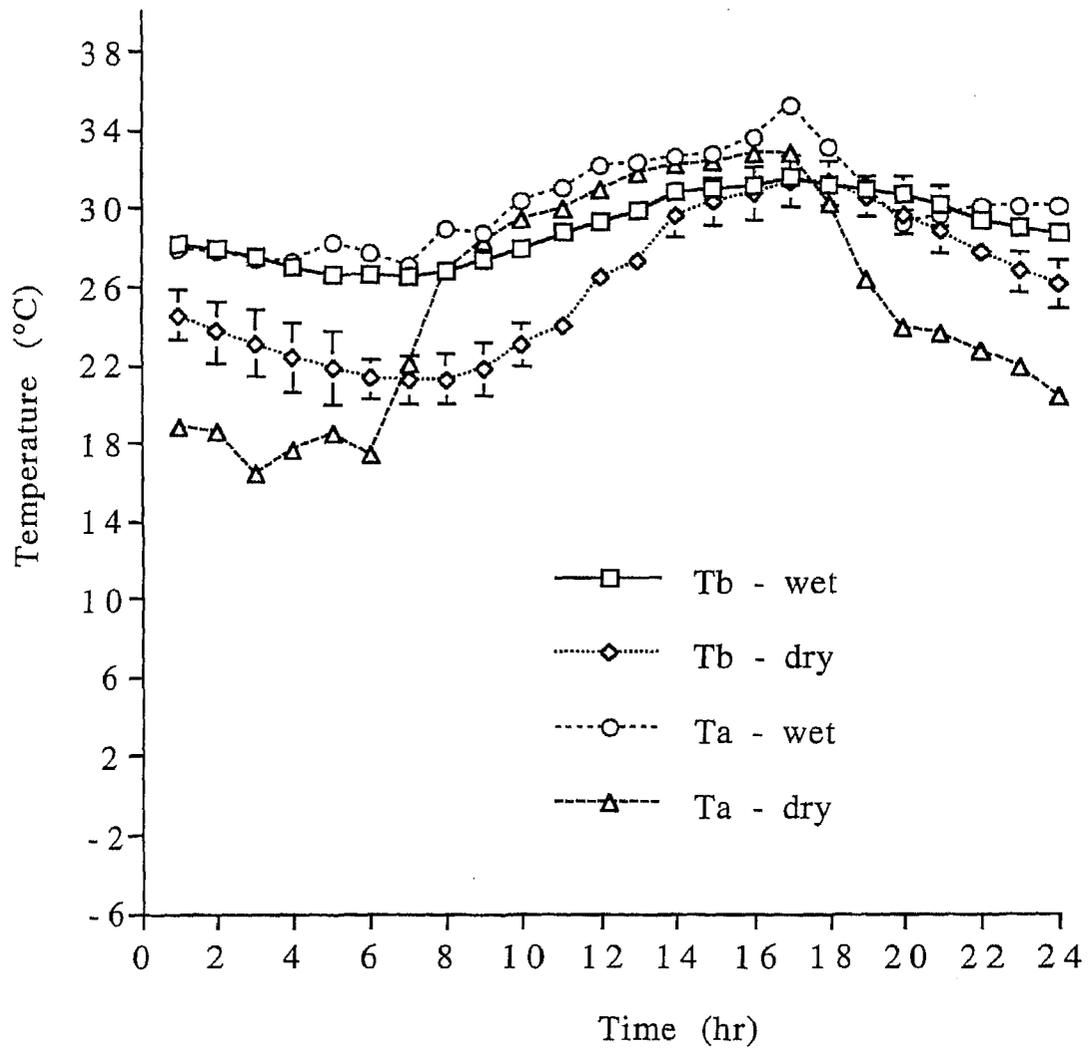


Figure 5.3. Body temperatures of *A. childreni* in the wet (diamonds,  $n = 6$ ) and dry (squares,  $n = 5$ ) seasons. Air temperatures for wet and dry seasons are also presented. Error bars represent standard errors.

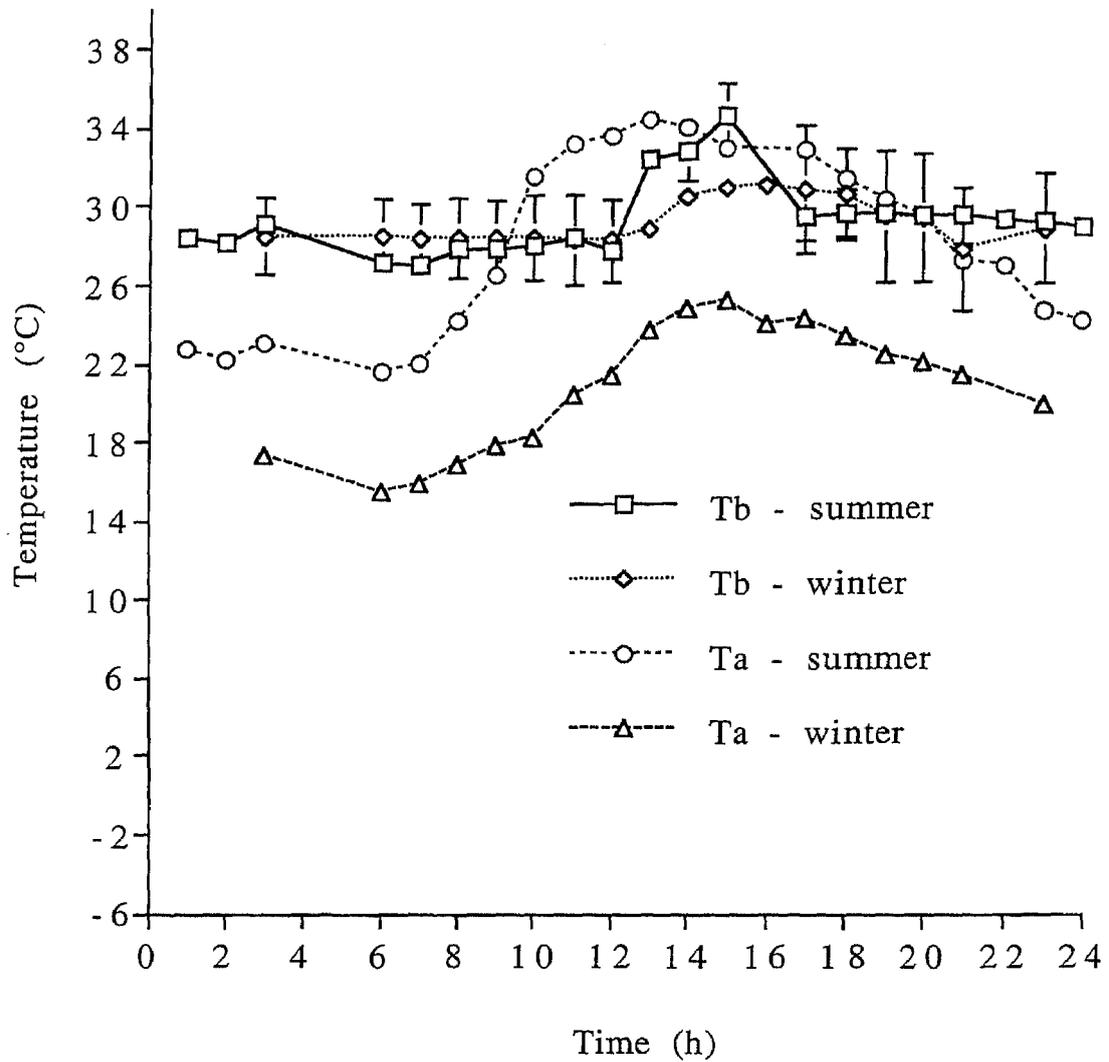


Figure 5.4. Body temperatures of *A. stimsoni* in summer (diamonds,  $n = 4$ ) and winter (squares,  $n = 5$ ). Air temperatures for summer and winter seasons are also presented. Error bars represent standard errors.

Pythons that experienced a winter season (*M.s. bredli* and *A. stimsoni*) had significantly lower Tbs in the hours before dark (1300 – 1800) during winter when compared with all other seasons (wet, dry, summer) ( $F_{3,56} = 11.6, P < 0.0001$ ).

The warmest body temperatures immediately before dark in the wet/summer season were significantly different among the four species of python ( $F_{3,36} = 11.6, P = 0.03$ ). The mean separation test revealed that Tbs for *A. childreni* were lower than Tbs for either *M.s.bredli* or *A. stimsoni*, but not different from *M.s.variegata*. Similarly, there was a significant difference in Tb immediately before dark among species of python in the dry/winter season ( $F_{3,16} = 241.3, P = 0.0001$ ), with a Fisher's means separation test indicating that *M.s.bredli* had a lower Tb in that season than all other species. This similarity in Tbs between *A. childreni* and *A. stimsoni* is interesting given that the cool season for *A. stimsoni* is much cooler than that for *A. childreni*.

In the period before dawn during the wet/summer season, there was a significant difference among species ( $F_{3,16} = 23.4, P < 0.0001$ ), with *A. childreni* having a lower Tb than *M.s.variegata* and *A. stimsoni*. *A. stimsoni* and *M.s.bredli* also had a lower Tb than *M.s.variegata*. During the same pre-dawn period for all species in the dry/winter season, there was also a significant species effect ( $F_{3,16} = 637.8, P < 0.0001$ ).

*M.s.bredli* had a lower winter Tb than all other species and *A. childreni* was lower than *M.s.variegata* and *A. stimsoni*.

The Tbs in the larger carpet python species (*M.s.variegata* and *M.s.bredli*) were less variable than Ta, and increased to be higher than Ta by 1800 – 1900 h in the wet/summer season, and 1700 – 1800 h in the dry season (Figs. 5.1 and 5.2). The smaller species of python (*A. childreni* and *A. stimsoni*) had Tbs in the wet/summer season that were higher than Ta by 1900 – 2000 h. Python Tbs in the dry/winter season were above Ta throughout the day (Figs. 5.3 and 5.4). For all species, Tb did not decline to the same extent as Ta in the cooler part of the day before dawn.

#### *Laboratory versus field body temperatures*

There was a significant difference between the mean Tb of *M.s.variegata* in the laboratory and the field in both the wet and dry seasons ( $t_{1,19} = 5.9, P < 0.0001$ , wet;  $t_{1,19} = 11.0, P < 0.0001$ , dry) with the laboratory temperature lower than field temperatures over the five hours before sunset (29.5<sub>lab.</sub> vs 32.1<sub>field.</sub>, wet; 29.1<sub>lab.</sub> vs 30.7<sub>field.</sub>, dry (°C)). The mean laboratory Tb of *M.s.bredli* in summer was lower than Tbs measured in the field (29.5<sub>lab.</sub> vs 33.0<sub>field.</sub> (°C)) ( $t_{1,34} = 10.5, P < 0.0001$ ). The mean laboratory Tb of *M.s.bredli* in a thermal gradient in winter was significantly higher than the mean field Tb in winter (29.1<sub>lab.</sub> vs 17.2<sub>field.</sub> (°C)) ( $t_{1,34} = -11.2, P < 0.0001$ ). *Antaresia childreni* had a significantly

lower mean wet season Tb measured in a thermal gradient than mean Tb measured in the field ( $29.3_{\text{lab.}}$  vs  $30.6_{\text{field}}$  ( $^{\circ}\text{C}$ )) ( $t_{1,29} = 4.9$ ,  $P < 0.0001$ ), but there was no difference between the mean laboratory Tb ( $29.5^{\circ}\text{C}$ ) and the mean field Tb ( $28.9^{\circ}\text{C}$ ) in the dry season ( $P > 0.05$ ). There was no difference between mean laboratory ( $31.5^{\circ}\text{C}$ ) and mean field Tbs ( $32.9^{\circ}\text{C}$ ) in the summer season for *A. stimsoni* ( $P > 0.05$ ), but this species had a significantly higher mean Tb in the laboratory in winter when compared to field body temperatures ( $31.5_{\text{lab.}}$  vs  $30.3_{\text{field}}$  ( $^{\circ}\text{C}$ ) ( $t_{1,23} = -2.4$ ,  $P = 0.03$ ).

## Discussion

Thermoregulation in large tropical reptiles has been a subject for discussion over recent years (Shine and Madsen 1996). Some large tropical lizards thermoregulate precisely (Christian and Weavers 1996), others less precisely (Christian *et al.* 1996c), while at least one large tropical python apparently does not thermoregulate at all, having Tbs similar to ambient temperatures through their daily activities (Shine and Madsen 1996). In this study, I found that pythons appear to increase Tbs throughout the day until immediately before nightfall with no animal seen outside their refuge, thus they appear to remain hidden during the period they are heating. The temperature achieved during the warm season (summer/wet) was similar for all species irrespective of the ambient temperature or climatic zone. Tbs for each species of python appears to correlate with changes in  $T_a$  throughout the day.

However  $T_b$ s in each season were either higher or lower than  $T_a$  but follow a similar pattern to diel  $T_a$ . It appears that most pythons in this study were achieving body temperatures prior to nightfall that were different to the preferred  $T_b$ s observed in each of the species in a laboratory thermal gradient (Bedford 1996, Bedford and Christian 1998). A disparity between python temperatures attained in the laboratory and field may reflect possible differences between individuals, other constraints may include the time of year, the maximum heat obtained from solar radiation on any particular day, the light levels between field and laboratory, or even the threat of predation. Most of these field temperatures were within a few degrees of the laboratory temperatures and possibly would not have impeded their activity patterns.

The general daily pattern in python  $T_b$ s in this study was an increase over the day, until immediately before dark, when it peaked, before declining over the subsequent hours to a minimum around dawn. In acquiring all heat directly from the refuge, the heating pattern of pythons tended to lag behind that of  $T_a$ . This general pattern was exhibited by all species of python in all seasons and appears to give the maximum heat energy for movement early in the night. This strategy for heating and cooling may also give pythons access to the highest number of prey items immediately after dark because many mammals, reptiles and amphibians are nocturnal in the Northern Territory. This

strategy may be analogous to that of an active forager which is at a preferred temperature over a period of a few hours during which it seeks to obtain as much food as possible (Huey and Pianka 1981). In this case, however, the python obtains a sufficient  $T_b$  for all activities such as movement and predation, and seeks to be in the right place at the right time to intercept the maximum number of prey items.

The maximum  $T_b$  in the wet/summer season was lower than maximum air temperatures, whereas maximum  $T_b$  in the dry/winter season was higher than maximum  $T_a$  in that season for most species. In this study, few animals basked or moved between retreat sites during the day, which is characteristic of nocturnal species (Shine 1991; Greer 1997). However, the thermal profiles here may be indicative of animals using a refuge such as a building, tree branch or rock which allows them to heat up over the day, as seen in some other species of reptile (Schleisinger and Shine 1994; Christian and Bedford 1996; Webb and Shine 1998).

Although there were significant differences in  $T_b$  between seasons, generally the  $T_b$  was high enough in both seasons for physiological activities such as prey capture, movement, and reproduction for all species except possibly *M.s. bredli* in winter. However, even in the coldest months, *M.s. bredli* was warmer than  $T_a$  for 75% of the 24 h day, and may have been able to obtain body temperatures sufficient for

physiological activities (Bedford and Christian 2000). One animal consumed prey on a night when the  $T_a$  was 16°C (pers. obs.), indicating that even during winter this species was able to feed.

Body temperatures may change between seasons because of limitations of the thermal environment in the dry/winter season, or because of a behavioural shift in preferred  $T_b$  related to energy conservation. A lower body temperature results in a lower metabolic rate, and therefore, requires a lower energy intake to maintain energy balance. Some reptiles select lower  $T_b$ s in the cooler dry/winter seasons when resources are scarce (Christian *et al.* 1983; Christian and Bedford 1995; Christian and Bedford 1996). Further investigation would be needed to determine whether the metabolic savings associated with a drop in  $T_b$  in a cool season is due only to a decline in refuge temperatures or whether it is due to a deliberate selection of a lower temperature in the cool season.

A sit-and-wait foraging strategy is thought to be less efficient (energy gained per time period) in obtaining food than an active foraging strategy (Huey and Pianka 1981). Some active foraging snakes consume more than twice the amount of sit-and-wait foraging species (Secor and Nagy 1994). However, a high, though variable,  $T_b$  maintained by pythons in this study including *Morelia s. bredli* over the 24 hours of a day in both seasons, indicates that they are capable of consuming prey

at any time of the day, throughout the year, except perhaps in extreme conditions during winter. It is possible that sit-and-wait python foragers may be able to hunt by being vigilant in a refuge even though they are at lower  $T_b$ s than active foraging snakes require to hunt (Shine *et al.* 2002). Active foraging species of reptile generally have a high preferred  $T_b$  and a small window of activity on any one day (Huey and Pianka 1981). Pythons may therefore have a higher probability of encountering and consuming prey than their active foraging counterparts over the entire year, an aspect that invites further investigation.

Very small animals cool faster than they heat (Frazer and Grigg 1984), but larger ectotherms tend to cool more slowly than they heat. For nocturnal reptiles, a larger body size allows a longer time for activity after a preferred  $T_b$  has been achieved (King and Green 1993). Many secretive snakes spend hours hidden from the sun by remaining sequestered in diurnal retreat sites (Slip and Shine 1988a; Webb and Shine 1997a,b). For large pythons the most important factors relating to body temperature regulation are: 1) the posture of the snake (Johnston 1972, 1973; Ayers and Shine 1997; Shine 1991; Slip and Shine 1988a), 2) mass of the animal (Ayers and Shine 1997) and 3) the level of insulation afforded by the refuge site being occupied (Johnston 1972; Slip and Shine 1988a; Huey 1991; Ayers and Shine 1997). Remaining in a refuge allows only limited opportunity to

thermoregulate, and gives a different body temperature profile over a day compared to snakes which are active, diurnal and heliothermic (Shine 1979, 1987). The thermal characteristics of a refuge may accrue benefits for a python in terms of energy conservation through obtaining a preferred  $T_b$  lower than many other reptiles for the few hours immediately before nightfall when compared to reptiles that thermoregulate actively to a higher  $T_b$  over most of the day. The energy used to thermoregulate to a high  $T_b$  for many hours of the day may exceed the short term food energy intake of sit-and-wait foragers (Huey and Slatkin 1976; Hertz 1974; Lee 1980; Rummary *et al.* 1995) such as pythons. Although it is probable that pythons could have achieved a high body temperature earlier in the day through basking (Slip and Shine 1988a), similar to the  $T_b$ s of large lizards found in similar climatic conditions (Christian and Weavers 1996; King and Green 1993), the fact that they did not suggests advantages in this thermal regime, the most obvious of which is energy conservation through a lower  $T_b$ . Overt basking by pythons would expose them to both predators (although they have few) and to prey. If pythons are relying on crypsis to forage, and they have access to temperatures over which foraging can occur, then the most economical strategy appears to forage constantly and take advantage of significant thermal retreats that allow both foraging and high body temperatures.

Season, weather, microhabitat, time of day, reproductive state, activity type and level of predation all act as thermoregulatory constraints (Huey 1982; Rosen 1991; Webb and Shine 1998, 1997a,b). By affecting activity time, temperature has the ability to affect survival (Adolph and Porter 1993), so pythons would have fewer energetic and ecological costs associated with foraging from a refuge that provides an acceptable thermal environment, thereby enhancing survival. Obviously, if no food presents itself the animals starve.

The Tb profile displayed by pythons in this study reflects the thermal characteristics of the refuge site (tree branch or rock wall) and the temperature of the day and is similar to that experienced by *Liasis fuscus* (Shine and Madsen 1996). Maximum daytime Tbs for *M.s. variegata* during the dry were similar to those for the wet season, but night-time body temperatures were up to 4°C cooler. However, the decrease in temperature was not to the point where movement or feeding ceased (pers. obs.). For *A. childreni*, maximum daytime Tbs were similar between seasons, but Tbs dropped to near Ta overnight in both seasons, resulting in a lower night-time body temperature in the dry season. This indicates that *A. childreni* possibly did not select retreat sites that are well insulated, although this may not be important because night time Ta in both dry and wet seasons was warm enough for feeding and movement.

Conversely, ambient temperatures in the desert during the winter nights were too low for many physiological processes, with temperatures falling below zero on some nights. Body temperatures varied between seasons for *M.s. bredli*, but the small variation in  $T_b$  during winter days, even with large fluctuations in  $T_a$ , suggest a well insulated retreat site. *Morelia s. bredli* used either tree hollows or rabbit burrows as retreat sites and remained hidden throughout the day. The effect of well insulated refugia was also observed in summer, with  $T_b$  stable even though  $T_a$  at 0900 was higher than  $T_b$  at any time during the day.

Although the general trend was for  $T_b$  to rise slowly over the day before reaching a peak at or immediately before nightfall in most python species, this was not observed in *A. stimsoni*. Peak  $T_b$  was reached by about midday in this species, and declined by nightfall in both seasons, possibly due to retreat site selection (ie: moving deeper into a cave or rock crevice). The  $T_b$  of *A. stimsoni* was similar between seasons and may reflect that they were taken in the early winter season, before the air and ground temperatures had fallen to a seasonal minimum.

The thermal characteristics of a refuge site will affect the body temperature of a python sequestered in that site (Huey and Slatkin 1976; Christian *et al.* 1984; Stevenson 1985). Thus, there are energy

costs and benefits associated with each tree hollow or burrow (Bustard 1967; Huey 1974; Christian *et al.* 1984; Huey *et al.* 1989; Shine *et al.* 2002). By selecting different retreats, or different positions within a retreat, pythons may be able to achieve a range of possible Tbs (Huey *et al.* 1989).

## **Chapter 6**

**Seasonal water, sodium and energy  
turnover in five species of Australian  
python (Serpentes: Boidae)**

## Abstract

Field energy use by five species of Australian python (*Morelia spilota variegata*, *M.s.bredli*, *Antaresia childreni*, *A. stimsoni* and *Liasis fuscus*) was measured between seasons and climatic zones. With high year-round temperatures and predictable rainfall in the tropics, I predicted that energy use for tropical pythons would differ from that of desert python species, where temperature, rainfall and food are all highly variable. An energy budget for each species in each of the seasons was developed to sub-divide the isotopically determined field metabolic rate (FMR) into ecologically relevant components, including known aspects of python physiology such as specific dynamic action (SDA) and standard metabolic rate (SMR). All python species examined had a higher FMR in the wet/summer season than in the dry/winter season. There was a difference in energy expenditure between species, seasons and importantly between climatic regions, with the desert species requiring less energy per year than the tropical species. Water flux was higher in the wet season for the three tropical species of python. Sodium turnover was highest in the wet season when compared with all other seasons (summer, winter and dry). Sodium turnover differed between species with *L. fuscus* having the highest turnover and *A. stimsoni* having the lowest values. In some python species the calculated energy expenditure in SMR was greater than the FMR, suggesting that pythons had depressed metabolic rates at times; therefore energy budget calculations were recalculated using values of

depressed metabolic rates obtained from laboratory measurements. The cost of digestion in pythons was incorporated in the energy budget and represented a large part of energy use, especially during the wet/summer season. Activity respiration as a proportion of the total energy expended was highest in the wet/summer season for all species examined. The total food requirement at a population level, assuming no differences in body mass, was determined from FMR for each species of python and ranged from a low  $95.3 \text{ g ha}^{-1} \text{ yr}^{-1}$  for *L. fuscus* to a high of  $762.8 \text{ g ha}^{-1} \text{ 6 mo}^{-1}$  for *A. stimsoni*. *Liasis fuscus* needed to consume considerably more food than the other species (4.3 times body mass vs 1.1 to 2.3 times body mass), a difference that may support the view that this species can at times be an active forager. The modest energy intake compared to metabolic costs for all species in this study confirms that pythons are generally low energy specialists.

## Introduction

The cost of living varies considerably among animals, with birds and mammals having high energetic needs for survival, while reptiles have comparatively low energy needs. Among the reptiles, ecological attributes, such as foraging mode, affect the energy needed for survival; widely foraging species have a higher energy turnover than sit-and-wait foraging species (Anderson and Karasov 1981; Huey and Pianka 1981). Pythons are generally sit-and-wait foraging species, although at least one study indicated that the water python actively forages (Shine 1991).

Field metabolic rate (FMR), using isotopically enriched water, is a measure of the energy expended by free living animals, and, in conjunction with other field and laboratory data, FMR can be further evaluated to determine a detailed energy budget for the animal (Christian *et al.* 1996a,b; 1999). The doubly labelled water (DLW) method has led to predictions about daily energy expenditure, water flux and food requirements, and has been used in more than 220 animal studies (reviewed by Nagy *et al.* 1999). The energy measurements of all species reviewed by Nagy *et al.* (1999) indicate a variation in absolute FMR of more than 220000 times. The lowest energy use of 0.23 kJ d<sup>-1</sup> was found in a desert gecko (Nagy *et al.* 1993), while a common seal had an energy intake of 52500 kJ d<sup>-1</sup> (Reilly and Fedak 1991).

While DLW can accurately determine CO<sub>2</sub> production and water flux, rates of food consumption can be estimated knowing the metabolizable energy content of food (Christian *et al.* 1984; Secor and Nagy 1994), or when free water is unavailable, through extrapolation of water influx rates (Nagy and Costa 1980). An alternative method for determining food intake is through <sup>22</sup>sodium turnover (Davies and Kornberg 1952; Green 1978; Gallagher *et al.* 1983; Green *et al.* 1999), provided that the sodium status of the diet is known and is relatively uniform. Sodium turnover has been used to estimate food intake rates in a variety of animals, including mammals (Green *et al.* 1984), birds (Gales *et al.* 1993; Robertson and Newgrain 1992; Newgrain *et al.* 1993), reptiles (Gallagher *et al.* 1983; Green *et al.* 1986), and amphibians (Greenwald 1972; Green *et al.* 1999).

To interpret sodium turnover rates, some understanding of the available prey and diet of each species is necessary. Different prey types can have different sodium content and this can vary between prey size and foraging mode of the prey (Green 1978; Green *et al.* 1984; Newgrain *et al.* 1993). In general, larger Australian pythons consume endothermic prey (Slip and Shine 1988b; Shine 1991; Greer 1997; Shine and Madsen 1997; Madsen and Shine 1998; Torr 2000), while the smaller species of python consume predominantly ectothermic vertebrate prey such as lizards and frogs (Shine 1991; Greer 1997; Torr 2000).

Most DLW studies of reptiles have concentrated on lizards (reviewed by Nagy *et al.* 1999), and have shown differences in FMR and/or water flux between species (Anderson and Karasov 1981), seasons (Green *et al.* 1991; Christian and Green 1994, Christian *et al.* 1996a,b,c; Green *et al.* 1997), altitude (Benabib and Congdon 1992), latitude (Christian *et al.* 1998), years (Green *et al.* 1986) and habitat type (Green 1972). The snake species investigated to date are from temperate and/or arid regions, and are from either the family Colubridae or Viperidae (Secor and Nagy 1994, Peterson *et al.* 1998, Beaupre 1996, Plummer and Congdon 1996).

In both lizards and snakes, FMR can differ seasonally (Secor and Nagy 1994). Further, snakes with differing foraging modes have significantly different FMR, such that the energy used and food required by active foragers (e.g. colubrids) is more than double that used by sit-and-wait foragers (e.g. viperids) (Secor and Nagy 1994). Body mass is one important determinant of FMR, and predictive equations have been proposed for reptiles (Nagy *et al.* 1999). However, there is much inter-specific variation independent of body mass. In this study, I investigate FMR, water flux and  $^{22}\text{Na}$  turnover for a number of python species in relation to size, season, and climatic zone. For most of these species I propose an energy budget based on all aspects of python physiology and ecology studied to date (Congdon *et al.* 1982). These python species are all long-lived (Greer 1997), and I extend the results of

energy use to the population level, to give an index of energy flow through the Australian pythons that inhabit both the tropical and temperate zones.

## **Materials and Methods**

### *Study organisms*

Five taxa of python from throughout the Northern Territory (NT) of Australia were studied. Northern carpet pythons (*Morelia spilota variegata*) are distributed in the tropics of the NT and adjacent states of Western Australia and Queensland. Study sites for this python included the Darwin Botanic Gardens and East Point Reserve, both within five km of the Darwin city centre. This python is primarily arboreal, and reaches a length of 2.5 - 3 m (Barker and Barker 1994; Cogger 2000). Central carpet pythons (*Morelia spilota bredli*) are restricted to the MacDonnell ranges in central Australia, and these were studied over a transect three kilometres long by 150 m wide in Roe Creek, 25 km south of Alice Springs. This predominantly arboreal python reaches a maximum length of 3 m (Cogger 2000), and is considered by some to be a sub-species of *Morelia spilota* (Fyfe 1994; Rawlings and Donnellan, pers. com.), while elsewhere it is considered to be a distinct species (Barker and Barker 1994; Cogger 2000).

The children's python (*Antaresia childreni*) is a tropical species found within 500 km of the coast in the NT. It is a small python, less than one

m in length (Shine 1991). *Antaresia childreni* were caught at Beatrice Hill Conservation Reserve, 75 km east of Darwin, NT. Stimson's python (*Antaresia stimsoni*) is small (<1 m) and found over most of the Australian mainland with the exception of Victoria and the east and southern coastal regions. I studied the sub-species *A.s.orientalis* (Smith 1985) at Ormiston gorge, 180 km west of Alice Springs and part of the West MacDonnell National Park.

Water pythons (*Liasis fuscus*) grow to three m in length and are found in high rainfall areas across northern Australia, within approximately 150-300 km of the coast (Barker and Barker 1994), and are abundant on the coastal floodplains of the NT (Shine 1991; Barker and Barker 1994). Our study site was located at the Adelaide River flood plain in the Beatrice Hill Conservation Reserve adjacent to the site for *A. childreni* described above.

Animals were located by spotlighting and caught by hand. As pythons are predominantly sit-and-wait predators, some species were elusive. In the first year of this study only one *M.s.bredli* was caught, after hundreds of hours searching. The rainfall in that year had been exceptionally high (1997 rainfall was 433.4 mm). The rainfall next year was more typical (1998 rainfall was 298 mm, mean for the area is 268 mm), and pythons were readily found (rainfall data obtained from Commonwealth Meteorological Bureau, Darwin).

*Body temperatures*

All pythons were implanted with temperature sensitive radio transmitters (Holohil, PD-2T or ST-2I), and remained in captivity for at least three weeks after surgery before being injected with isotopes and released at the point of capture.

*Isotope turnover*

A sample of pythons was captured for each species in each season. No gravid pythons were injected with isotopes. Initially a one mL blood sample was taken by cardiac puncture. This sample was used to determine background isotope levels. Animals were then injected intraperitoneally with one mL of tritiated water (5 mCi) (1Ci is  $3.7 \times 10^{10}$  disintegrations per second), 0.2 mL  $\text{kg}^{-1}$  of  $^{18}\text{O}$  (95% atoms excess; ENRITTECH) and 250  $\mu\text{L}$  sodium chloride containing 20 MBq of  $^{22}\text{Na}$  (1Bq is 1 disintegration per second). Pythons spent eight hours in a temperature-controlled cabinet at 30°C before an equilibrium blood sample was taken. Approximately 0.25 - 0.5 mL of blood was taken at each blood sampling. Each sample of blood was centrifuged for two minutes, allowing serum fractions to be removed. Both fractions were stored in Eppendorf plastic vials and sealed with thermofilm, placed in individual plastic bags and stored frozen (-20°C) until required for analysis in the laboratory. Animal body mass was recorded to the nearest 0.1 g, after which the animal was released at its point of capture, usually within a few hours of isotope equilibration.

Changes in isotope concentration over the release periods were used to calculate CO<sub>2</sub> production, water flux (Lifson and McClintock 1966; Nagy 1980, 1983b; Nagy and Costa 1980; Nagy 1989), and sodium turnover (Green 1978; Gallagher *et al.* 1983; Green *et al.* 1999). Any changes in body mass and body pools were assumed to be linear, and mass specific pools were assumed to be stable over the release periods.

#### *Oxygen-18*

Water was extracted from red blood cell fractions using micro distillation (Nagy 1983b). Sub-samples of extracted water were analysed for <sup>18</sup>O using a dual inlet isotope ratio mass spectrometer (V.G. Optima, Cheshire, England). In order to prepare samples, 20 µL extracted water sub-samples were incubated with a constant volume (approximately one mL) of CO<sub>2</sub> at 60°C overnight. The sample was subsequently frozen in a dry ice -alcohol slurry. The equilibrated CO<sub>2</sub> which carried the signature of the <sup>18</sup>O enriched water was cryogenically transferred into another tube before being introduced into the mass spectrometer under vacuum. Within the mass spectrometer, CO<sub>2</sub> was fractionated into its atomic masses of 44, 45 and 46, and the ratios of these values determined. The ratios were then compared with the reference sample which provided a measurement of O<sup>18</sup> enrichment in the blood samples.

### *Tritium*

Tritium was determined through analysis of 20 or 50  $\mu\text{L}$  sub-samples of extracted water placed in three mL Aquasol (Amersham) and counted to 1% error in a Beckman LS2800 Liquid Scintillation Counter.

### *Total body water*

Total body water (TBW) pools were estimated by comparing equilibration levels of  $^3\text{H}$  and  $^{18}\text{O}$  with standard dilutions of injectate (Nagy 1983). The  $^{18}\text{O}$  value was used for the calculation of TBW.

### *Field metabolic rate*

Production of  $\text{CO}_2$  was calculated using the equation 4.2 of Nagy (1980) and presented as a volume of gas ( $\text{mL g}^{-1} \text{h}^{-1}$ ). As the diet of pythons is essentially protein and fat, a thermal equivalent of  $25.8\text{kJ L}^{-1} \text{CO}_2$  was used to convert  $\text{CO}_2$  production to units of energy (FMR) (Nagy *et al.* 1999).

### *Water flux*

Water influx represents the total water intake of the animal. This includes water in food, drinking water, metabolically produced water and input across the skin and lungs via water vapour. Water influx was calculated using the equation of Nagy and Costa (1980). Water flux is presented as  $\text{mL kg}^{-1} \text{d}^{-1}$ .

*Measure of food intake through sodium ( $^{22}\text{Na}$ ) turnover*

Similar to labelled water turnover, the exponential decline in  $^{22}\text{sodium}$  was used to determine food intake in each python (Buscarlet 1974). The major source of Na intake is through diet (Green 1978; Gallagher *et al.* 1983), so the food intake estimates using Na turnover are reliable when the sodium content of the diet has been established (Gallagher *et al.* 1983). Serum samples (50  $\mu\text{L}$ ) were placed into scintillation vials, dried to remove tritiated water and after the addition of three mL PCS (Amersham) counted to 1% error in a Beckman LS2800 liquid scintillation counter. Additionally, five  $\mu\text{L}$  of each serum sample was diluted to two mL with deionized water to allow sodium concentration to be measured with an atomic absorption spectrophotometer (Varian 1000). The exchangeable sodium (ES) pool sizes were derived from the initial isotopic counts and a diluted standard solution of the injected isotope, in conjunction with serum sodium concentration. Sodium influx was derived from the decline in specific activity of the isotope during the experimental period, assuming the mass-specific pool size of each individual did not change during the experimental period and any changes in body mass and exchangeable sodium were linear (Lifson and McClintock 1966).

Rates of sodium influx were converted to rates of food intake using a correction factor of 1.16 (Green 1978). I use the total sodium content of prey consistently obtained in other studies of 55  $\text{mmol}/\text{kg}^{-1}$  (Green

*et al.* 1984, small mammals, large mammal, some lizards and some birds; Green B., and Newgrain K., unpublished data).

A factor of 8.9 kJ g<sup>-1</sup> was used to convert wet mass of food to energy (kJ) (Brisbin 1970), and although this figure may be high due to the overfeeding of laboratory mice (pers. obs.), it is the most comprehensive study to date on the total energy content of mice, and is similar to the value reported in a more recent study (8.0 kJ g<sup>-1</sup>) (Secor and Diamond 1995). A different conversion value of 6.63 kJ g<sup>-1</sup> was obtained from wild caught mice in summer that may have been deprived of food (Green B. and Newgrain K. unpublished data). Thus, the most appropriate conversion factor for the prey consumed in the field may probably be between these two values, but I present calculations using both to delineate the possible range of energy obtained from fat or lean prey.

Wet mass of food, fresh matter (FM) intake was estimated using the ratio of dry mass to wet mass calculated as 70% water to 30% dry mass (Nagy *et al.* 1999). Metabolizable energy available in the diet was determined previously (Bedford and Christian 2000).

#### *Energy budget calculations*

The total energetic cost represented by FMR can be sub-divided into the component costs of activity, Tb-specific metabolism of the resting

animal, and the energetic costs of digestion. Metabolism of a resting animal is usually divided into minimal energy use during the active part of the day (resting metabolic rate) and minimal energy use during the inactive part of the day (SMR) (Christian *et al.* 1999). Pythons examined in this study do not exhibit a difference in metabolic rate between day and night (Bedford and Christian 1998). Allometric relationships between oxygen consumption and mass at temperatures of 24, 27, 30 and 33°C (Bedford and Christian 1998) were used to calculate standard metabolic rate (SMR) for each species. A  $Q_{10}$  of 2.6 was determined from the measurements of SMR over the four temperatures. This  $Q_{10}$  was then used to calculate SMR for Tb measured in the field. Mean field body temperatures for each hour of the day for each species of python in each season were used to calculate SMR. An energy equivalent of 20.08 kJ L<sup>-1</sup> (Benabib and Congdon 1992) was used to convert oxygen consumption values into units of energy.

Metabolic rate declines over time with long term fasting, and after about six weeks is low enough to be considered a depressed metabolic rate (DMR) (Bedford and Christian 2001). I used this DMR to reconcile costs over the release period in some animals. DMR was calculated as 39% of SMR as measured for the water python, *Liasis fuscus* (Bedford and Christian 2001), and this was assumed for the other species.

In all calculations, SMR or DMR (or a combination of both) was used over the entire release period. The metabolic cost of digestion (Specific Dynamic Action: SDA) was calculated as a cost in excess of SMR for 10 days (assuming one meal) during the release period. Since long term fasting is common in pythons, I used SMR and assumed that pythons ate at the beginning of the release period. Where a combination of SMR and DMR was used, the animal was assumed to have eaten in the middle of the release period. This means that during the initial part of the release period the animal had a depressed metabolic rate, SDA is counted in the middle 10 days, then over the last part of the release period the animal experienced SMR. In other instances I assumed the animal did not eat until the last ten days of the release period, so the entire release period was at a DMR. I used a conservative approach to FMR data to determine which method of calculation to employ. If combined SMR and SDA costs were less than FMR, allowing energy for activity, then SMR was used in the final energy budget calculations. However, if SMR alone was greater than FMR, then DMR was used. Where combined SMR and SDA exceed FMR marginally, then a combination of methods was used to interpret field energy use. These assumptions allow a realistic analysis of energetic costs and coincide with previous metabolic patterns observed in the laboratory (Bedford and Christian 2001; Overgaard *et al.* 2002).

The total calculated (from Na turnover) wet mass of food has been expressed in terms of a single meal during the release period for isotope measurements to determine SDA in the energy budget. Because pythons have both access to and are capable of consuming very large meals, this assumption is plausible.

In order to obtain an annual profile of energy use, I calculated each season as a part of the year and extrapolated to the whole year as has been done in other studies (Secor and Nagy 1994). For example, *M.s.bredli* were measured in the three seasons of summer, spring and winter. Thus the first two seasons combined represent six months, while winter energy use was calculated over the remaining six months. Wet and dry season calculations were extrapolated for six months each. *Antaresia stimsoni* was only measured in the summer, so only six months of calculations are presented. Activity respiration represents the energy expended during activities such as locomotion and reproduction (van Marken Lichtenbelt *et al.* 1993; Christian *et al.* 1996a,b,c.). Activity respiration (AR; Benabib and Congdon 1992) was calculated as the difference between FMR and SMR + SDA (or FMR - (DMR + SDA); or FMR - (SMR + DMR + SDA)).

The maximum cost of locomotion ( $\dot{V}_{O_2\max}$ ) in pythons was determined by measuring activity metabolism of each species on a treadmill and was generally 7.1 - 11.7 times higher than SMR (Chapter 2). I use  $\dot{V}_{O_2\max}$

to indicate the cost of sustained activity; however, pythons rarely if ever attain maximum locomotory effort (Secor and Diamond 1997). Thus, the maximum value may overestimate these energetic costs.

The  $\dot{V}_{O_2\max}$  values expressed in units of energy for each species were: *M. s. bredli* (13.9 kJ kg<sup>-1</sup> h<sup>-1</sup>), *M.s.variegata* (17.0 kJ kg<sup>-1</sup> h<sup>-1</sup>), *A. childreni* (26.5 kJ kg<sup>-1</sup> h<sup>-1</sup>), *A. stimsoni* (14.6 kJ kg<sup>-1</sup> h<sup>-1</sup>) and *L. fuscus* (11.7 kJ kg<sup>-1</sup> h<sup>-1</sup>) (Chapter 2). All activity is assumed to occur at 30°C. The metabolic cost of digestion in olive pythons (*Liasis olivaceus*) was found to be 17 times SMR (Bedford and Christian, unpublished manuscript). This value was used to represent the cost of digestion in all species investigated here. Metabolic costs can increase with increasing relative meal size in some non-Australian pythons (Secor and Diamond 1997, 2000). Metabolic costs increase with increasing meal sizes up to at least 20% body mass in some Australian pythons (Bedford and Christian 2001), but the relationship requires further investigation to obtain an accurate value of SDA with increasing meal size for each species of python examined in this study.

#### *Size and energy costs of population*

To calculate population energy use for each species of python in this study, the masses of pythons were determined from a sample of 20 animals in each study site. I used a conservative estimate of density of pythons, consisting of the number of animals marked at each study site

over a four year period as the total number of animals in that site for four species; *M.s.variegata*, *M.s.bredli*, *A. childreni*, *A. stimsoni* (Chapter 4). The population size for *Liasis fuscus* was estimated at 5000 from extrapolation of long term mark-recapture data (Parks and Wildlife Commission of the NT, unpublished data).

### **Statistics**

Seasonal, inter- and intra-specific mean values of FMR, water influx and sodium turnover were compared using analysis of covariance (ANCOVA), on log transformed data, with mass as a covariate. Group means were considered significantly different when  $P < 0.05$ .

Percentage body water pools were compared using ANOVA after being arcsine transformed. Fisher's post-hoc tests were used to separate significant means. Total body water values were compared between seasons using paired t-tests. Mean values are presented with standard deviations.

### **Results**

#### *Change in body mass over time*

Only two animals changed body mass by more than 1% per day during the isotope turnover period. Both of these animals were water pythons that gained mass in the wet season. Body masses of all others changed by less than 0.02% (s.d. 0.344%). Total body mass of pythons generally declined during the dry/winter seasons and increased during the

wet/summer season. There was no significant difference in mass change over release periods between species (ANOVA  $P > 0.05$ ), but there was a statistically significant difference between seasons (ANOVA  $F_{4,77} = 6.3$ ;  $P = 0.0002$ ) with mass gains in the spring and wet seasons compared to mass losses in the dry and winter seasons (and in summer for *M.s.bredli*) (Table 6.1).

#### *Field metabolic rate*

Field metabolic rates in the active season were significantly different between species (ANCOVA  $F_{4,36} = 5.5$ ;  $P = 0.002$ ), and a Fisher's means separation test indicated that *M.s.bredli* was lower than the three tropical species (*M.s.variegata*, *A.childreni*, *L.fuscus*). The small *A.stimsoni* was significantly lower than *L.fuscus*.

FMR between species in the less active season was also significantly different (ANCOVA  $F_{3,30} = 11.5$ ;  $P = 0.0001$ ), and a Fisher's means separation test again indicated that *M.s.bredli* was lower than the three tropical species (*M.s.variegata*, *A.childreni*, *L.fuscus*), and *M.s.variegata* had a lower FMR than *A.childreni*.

Table 6.1. Mass difference (g) between initial capture and recapture over the release period during isotope turnover experiments. Values are means, with standard deviations and n given in parentheses for each of the species of python studied. Mean masses of animals are given in tables 6.2 to 6.6.

Season	<i>Morelia spilota</i> <i>bredli</i>	<i>M.s.</i> <i>variegata</i>	<i>Antaresia</i> <i>childreni</i>	<i>A.</i> <i>stimsoni</i>	<i>Liasis</i> <i>fuscus</i>
Wet (October-March)		214.7 (479.2, 5)	14.7 (23.3, 6)		166.4 (167.4, 3)
Summer (December-March)	-69.1 (136.4, 14)			6.4 (14.9, 5)	
Spring (September- November)	175.8 (269.8, 9)				
Dry (May-September)		-84.0 (127.4, 11)	-33.5 (36.1, 11)		-151.5 (133.7, 4)
Winter (June-August)	-174.9 (189.1, 9)				

There was a significant seasonal difference in *M.s.bredli* ( $F_{2,28} = 11.5$ ;  $P = 0.0002$ ), with FMR lower in winter than in summer and spring (Table 6.2). For all three tropical species, wet season FMRs were significantly higher than those during the dry season in *M.s.variegata* ( $F_{1,13} = 5.2$ ;  $P = 0.04$ ), *A. childreni* ( $F_{1,13} = 15.5$ ;  $P = 0.002$ ), and *Liasis fuscus* (ANCOVA  $F_{1,4} = 21.5$ ;  $P = 0.01$ ) (Tables 6.3, 6.4, and 6.5).

It was not possible to capture *A. stimsoni* during winter, but I compared summer values of FMR with those of *A. childreni* in the wet and dry seasons. The FMR of *A. stimsoni* (Table 6.6) was significantly lower than wet season values for the *A. childreni* ( $F_{2,17} = 11.5$ ;  $P = 0.0007$ ), but there was no difference between FMR in summer for *A. stimsoni* and the dry season FMR for *A. childreni*.

The amount of food required to fuel the annual FMR in the desert dwelling *M.s.bredli* and *M. stimsoni* is 1.14 and 1.15 times body mass respectively. The amount of food required to fuel the annual FMR of the tropical species was 1.35 times body mass in *A. childreni*, 2.28 times body mass for *M.s.variegata*, and 4.33 times body mass in *L. fuscus*.

Table 6.2. Seasonal means and standard deviations (parentheses) for isotopic measurements of CO<sub>2</sub> production, FMR, water flux and water economy index (WEI) in *Morelia s. bredli*.

	Winter	Spring	Summer
n	9	9	14
Mass	1734.0 (1528)	1444.0 (1026)	1504.0 (853)
CO <sub>2</sub> (L kg <sup>-1</sup> d <sup>-1</sup> )	0.65 (0.26)	1.8 (.98)	1.22 (0.67)
CO <sub>2</sub> (mL g <sup>-1</sup> h <sup>-1</sup> )	0.027 (0.011)	0.075 (0.041)	0.051 (0.028)
FMR (kJ kg <sup>-1</sup> d <sup>-1</sup> )	16.6 (7.1)	46.6 (25.4)	31.7 (17.1)
FMR (KJ d <sup>-1</sup> )	22.6 (9.1)	55.6 (29.9)	44.6 (23.4)
Water influx (mL kg <sup>-1</sup> d <sup>-1</sup> )	4.2 (1.9)	13.2 (3.8)	5.60 (3.3)
WEI (mL kJ <sup>-1</sup> )	0.24 (0.11)	0.27 (0.16)	0.14 (0.07)

Table 6.3. Seasonal means and standard deviations (parentheses) for isotopic measurements of CO<sub>2</sub> production, FMR, water flux and WEI in *Morelia spilota variegata*.

	Dry	Wet
n	11	5
Mass	2106.0 (1263)	2944.0 (1140)
CO <sub>2</sub> (L kg <sup>-1</sup> d <sup>-1</sup> )	1.63 (0.91)	2.69 (0.96)
CO <sub>2</sub> (mL g <sup>-1</sup> h <sup>-1</sup> )	0.068 (0.039)	0.112 (0.04)
FMR (kJ kg <sup>-1</sup> d <sup>-1</sup> )	42.1 (24.1)	69.2 (24.9)
FMR (KJ d <sup>-1</sup> )	86.2 (78.9)	201.9 (66.2)
Water influx (mL kg <sup>-1</sup> d <sup>-1</sup> )	10.4 (6.3)	16.5 (7.4)
WEI (mL kJ <sup>-1</sup> )	0.19 (0.13)	0.09 (0.05)

Table 6.4. Seasonal means and standard deviations (parentheses) for isotopic measurements of CO<sub>2</sub> production, FMR, water flux and WEI in *Antaresia childreni*.

	Dry	Wet
n	11	6
Mass	284.1 (83.1)	306.3 (117.4)
CO <sub>2</sub> (Lk g <sup>-1</sup> d <sup>-1</sup> )	3.05 (1.68)	5.86 (0.264)
CO <sub>2</sub> (mL g <sup>-1</sup> h <sup>-1</sup> )	0.127 (0.07)	0.244 (0.1)
FMR (kJ kg <sup>-1</sup> d <sup>-1</sup> )	80.4 (44.8)	151.1 (69.1)
FMR (KJ d <sup>-1</sup> )	18.9 (8.1)	39.6 (29.0)
Water influx (mL kg <sup>-1</sup> d <sup>-1</sup> )	20.4 (7.2)	44.7 (20.3)
WEI (mL kJ <sup>-1</sup> )	1.12 (0.31)	1.18 (0.61)

Table 6.5. Seasonal means and standard deviations (parentheses) for isotopic measurements of CO<sub>2</sub> production, FMR, water flux and WEI in *Liasis fuscus*.

	Dry	Wet
n	4	3
Mass	1905.5 (558.3)	1473.3 (226.3)
CO <sub>2</sub> (L kg <sup>-1</sup> d <sup>-1</sup> )	2.18 (0.77)	5.98 (0.72)
CO <sub>2</sub> (mL g <sup>-1</sup> h <sup>-1</sup> )	0.091 (0.032)	0.249 (0.03)
FMR (kJ kg <sup>-1</sup> d <sup>-1</sup> )	56.4 (19.8)	153.3 (15.5)
FMR (KJ d <sup>-1</sup> )	102.0 (26.7)	236.3 (65.0)
Water influx (mL kg <sup>-1</sup> d <sup>-1</sup> )	15.7 (8.0)	49.7 (24.2)
WEI (mL kJ <sup>-1</sup> )	17.4 (10.0)	48.5 (24.4)

Table 6.6. Means and standard deviations (parentheses) for isotopic measurements of CO<sub>2</sub> production, FMR, water flux and WEI in *Antaresia stimsoni*.

	Summer
n	5
Mass	194.0 (29.8)
CO <sub>2</sub> (L kg <sup>-1</sup> d <sup>-1</sup> )	2.16 (0.48)
CO <sub>2</sub> (mL g <sup>-1</sup> h <sup>-1</sup> )	0.09 (0.02)
FMR (kJ kg <sup>-1</sup> d <sup>-1</sup> )	55.7 (11.6)
FMR (KJ d <sup>-1</sup> )	10.6 (2.2)
Water influx (mL kg <sup>-1</sup> d <sup>-1</sup> )	17.3 (4.1)
WEI (mL kJ <sup>-1</sup> )	1.60 (0.43)

### *Water flux.*

There was a significant difference in water flux between seasons in *M.s.bredli* ( $F_{2,28} = 6.2$ ;  $P = 0.006$ ), with water fluxes in spring being higher than in summer and winter (Table 6.2). Water influx was significantly higher in the wet season compared with the dry season in *M.s.variegata* (ANCOVA  $F_{1,16} = 8.4$ ;  $P=0.01$ , Table 6.3) and *A. childreni* (ANCOVA  $F_{1,13} = 14.0$ ;  $P = 0.003$ , Table 6.4), and *L. fuscus* (ANCOVA  $F_{1,6} = 6.1$ ;  $P = 0.049$ , Table 6.5)

Only summer season data were available for *A. stimsoni*; therefore water flux values for that season were compared with the seasonal flux of *A. childreni*. Influx was significantly different between seasons (ANCOVA influx  $F_{2,17} = 10.7$ ;  $P = 0.001$ ). Fisher's post hoc test revealed that wet season influx in *A. childreni* was higher than either dry season data for *A. childreni* or summer season for *A. stimsoni*, but there were no interspecific differences between the dry and summer values (Table 6.6).

### *Total body water*

Total body water gives an indication of percentage stored fat (Green *et al.* 1986), with a lower TBW indicative of a high percentage of stored body fat. There were no significant seasonal changes in total body water for *M.s.variegata* and *L. fuscus*; however, total body water was higher in the dry than the wet for *A. childreni* (ANOVA  $F_{1,13} = 5.7$ ;  $P =$

0.03). A shift in TBW in *A. childreni* from the wet season of 63.1% to the dry season TBW of 66.8% indicates a loss of body fat in the dry season and probably reflects lower prey availability. TBW was lower in summer for *M.s.bredli* (66.5%) than either spring or winter (ANOVA  $F_{2,31} = 7.2$ ;  $P = 0.003$ ), with winter and spring TBW similar (71.0 and 72.0% respectively).

#### *Water economy index (WEI)*

A water economy index expresses water flux relative to energy metabolism (Nagy and Peterson 1988) and was calculated by dividing water influx ( $\text{mL d}^{-1}$ ) by FMR ( $\text{kJ d}^{-1}$ ). For the three tropical species of *M.s.variegata*, *L. fuscus* and *A. childreni*, WEI between seasons was similar; however, there was a significant difference between seasons in *M.s.bredli* with the index in spring being higher than summer (ANOVA  $F_{2,29} = 3.8$ ;  $P = 0.03$ ). *Antaresia childreni* had a higher WEI than all other species in the wet/summer season ( $F_{3,30} = 18.3$ ;  $P < 0.0001$ ). Similarly, *A. childreni* had a higher WEI than all other species during the dry/winter season ( $F_{3,23} = 27.7$ ;  $P < 0.0001$ ). *Antaresia stimsoni* was not included in this analysis.

#### *Sodium turnover*

A two factor ANCOVA revealed a significant difference in sodium turnover among species and among seasons (ANCOVA species  $F_{3,57} = 3.6$ ;  $P = 0.018$ ; season  $F_{3,57} = 5.8$ ;  $P = 0.002$ ). *Antaresia stimsoni* had a

sodium turnover rate that was lower than all other species, while *Antaresia childreni* was lower than *M.s.variegata* and *L. fuscus*, and *M.s.bredli* was lower than *L. fuscus*. Seasonally, wet season sodium turnover was higher than all other seasons; however there was no difference in the sodium turnover rates among the other seasons (winter, spring, dry and summer) (Table 6.7).

Table 6.7. Sodium influx and estimated wet mass of food intake in pythons. Means are presented with standard deviations in parentheses.

Species	Season	n	Period (days)	Exchangeable Sodium (mmol kg <sup>-1</sup> )	Na influx (mmol kg <sup>-1</sup> d <sup>-1</sup> )	Food (g kg <sup>-1</sup> d <sup>-1</sup> )
<i>M.s.variegata</i>	wet	7	61(23)	50.7(8.4)	0.446(0.201)	9.41 (4.24)
<i>M.s.variegata</i>	dry	9	79(67)	38.9(9.5)	0.176(0.164)	3.70 (3.46)
<i>A.childreni</i>	wet	6	22(1)	35.8(4.9)	0.124(0.096)	2.61 (2.02)
<i>A.childreni</i>	dry	11	54(9)	37.7(3.3)	0.104(0.068)	2.19 (1.43)
<i>L. fuscus</i>	wet	4	20(3)	48.7(8.2)	0.786(0.514)	16.57 (10.84)
<i>L. fuscus</i>	dry	4	55(24)	45.7(8.9)	0.050(0.046)	1.06 (0.97)
<i>M.s. bredli</i>	summer	13	52(18)	43.0(5.9)	0.249(0.281)	5.25 (5.93)
<i>M.s. bredli</i>	winter	9	143(27)	41.3(5.1)	0.073(0.05)	1.54 (1.07)
<i>M.s. bredli</i>	spring	9	59(48)	40.2(2.0)	0.098(0.110)	2.08 (2.32)
<i>A. stimsoni</i>	summer	5	31(14)	51.1(3.9)	-0.083(0.416)	0.0 (8.78)

*Energy budget calculations*

There were some discrepancies between total FMR and resting metabolism. Resting metabolism was determined through an integration of daily body temperatures, and summing the corresponding metabolic rate over 24 hours, calculated from allometric equations (Bedford and Christian 1998). For *M.s.bredli* in summer and winter and *A. childreni* in the wet season, estimated resting metabolism was higher than measured FMR. Thus, I have used depressed metabolic rate or a combination of SMR and DMR to estimate resting metabolic rates during these seasons to determine energy use over the year (Table 6.8).

Table 6.8. A summary of the calculated energy budget for five species of python in different seasons. Total energy expended is represented by FMR as determined by isotopes, and this is divided into the energy cost of standard metabolic rate, depressed metabolic rate (DMR), activity and digestion (SDA). The energy in food ingested (as estimated from sodium flux, Table 6.7) is shown for each season. Values are means with standard deviations in parentheses. The activity per day (h) in excess of energetic costs of resting metabolic rate and digestion were calculated. Activity respiration values (AR) are presented in two columns using SMR and DMR. These were then used to calculate AR in terms of hours of activity per day ( $\text{h d}^{-1}$ ), using only positive results.

Species	Season	Release Period (days)	FMR ( $\text{kJkg}^{-1}\text{d}^{-1}$ )	SMR ( $\text{kJkg}^{-1}\text{d}^{-1}$ )	DMR ( $\text{kJkg}^{-1}\text{d}^{-1}$ )	SDA ( $\text{kJkg}^{-1}\text{d}^{-1}$ )	AR (SMR) ( $\text{kJkg}^{-1}\text{d}^{-1}$ )	AR (DMR) ( $\text{kJkg}^{-1}\text{d}^{-1}$ )	Food Ingested ( $\text{kJkg}^{-1}\text{d}^{-1}$ )	AR ( $\text{h d}^{-1}$ )
<i>M.s. variegata</i>	Wet	61 (23)	69.0 (25.0)	22.2 (10.2)	8.6 (4.0)	12.9 (9.8)	37.8	50.3	74.8 (36.1)	3.7
<i>M.s. variegata</i>	Dry	79 (67)	42.2 (24.2)	26.5 (15.0)	10.3 (5.7)	22.3 (28.6)	-9.3	7.4	32.9 (30.8)	0.7
<i>A. childreni</i>	Wet	22 (1)	124.9 (42.0)	37.6 (16.1)	14.7 (6.3)	38.7 (14.2)	47.5	70.4	23.3 (18.0)	3.3
<i>A. childreni</i>	Dry	54 (9)	54.9 (14.7)	34.8 (8.3)	13.6 (3.3)	16.6 (3.7)	13.4	34.6	19.5 (12.8)	0.9
<i>L. fuscus</i>	Wet	61 (23)	153.4 (15.6)	36.7 (18.1)	14.3 (7.1)	35.2 (11.6)	100.2	114.6	147.5 (96.5)	12.4
<i>L. fuscus</i>	Dry	79 (67)	56.5 (19.9)	23.1 (5.9)	9.0 (2.3)	11.4 (5.8)	22.2	36.3	9.5 (8.6)	4.6
<i>M.s. bredli</i>	Summer	52 (18)	31.7 (17.2)	25.9 (9.8)	10.1 (3.8)	13.8 (8.6)	-7.7	7.4	44.8 (46.0)	2.0
<i>M.s. bredli</i>	Spring	59 (48)	46.7 (25.5)	21.3 (7.5)	8.3 (2.9)	11.1 (4.8)	12.9	26.4	18.5 (20.6)	3.4
<i>M.s. bredli</i>	Winter	143 (27)	16.6 (7.1)	14.1 (6.2)	5.5 (2.4)	2.3 (0.9)	0.2	8.8	13.7 (9.5)	0.1
<i>A. stimsoni</i>	Summer	31 (14)	55.5 (11.7)	36.7 (5.6)	14.3 (2.2)	30.1 (7.9)	-11.0	11.3	-15.6 (78.2)	0.8

Total metabolic costs per year for each species of python are presented in energy units in Table 6.9, and these costs have also been converted to food consumption (mice) for an average individual of each species of python. This cost in food consumption ranged from 7.4-9.3 mice per individual in six months for *A. stimsoni* to 274.5-343.6 mice in *L. fuscus* for the year (Table 6.9). At the population density level given for each study site, the total food consumption per year per hectare ranged from a low of 95-118.9 mice in *L. fuscus* up to 763-955.2 for *A. stimsoni* in 6 months (Table 6.9).

Table 6.9. Seasonal and annual FMR for each species of python and the energy equivalent in mass (g of mice) needed to be consumed to meet those energy costs for both individuals and populations. Mice are used as the energy currency for comparative purposes, however, some species consumed prey other than mice. Energy values of FMR are converted to mass using  $8.9 \text{ kJ g}^{-1}$  from Brisbin (1970), while an alternate conversion of  $6.63 \text{ kJ g}^{-1}$  using wild mice is presented in parentheses from Green and Newgrain (unpublished data). Values of food intake per year needed to cover metabolic costs are derived by converting annual FMR data to mass (g). Food consumption values estimated from sodium turnover are presented in energy and mass terms and denoted by asterisks.

	<i>M.s. bredli</i>	<i>M.s. variegata</i>	<i>A. childreni</i>	<i>A. stimsoni</i>	<i>L. fuscus</i>
FMR summer/wet (kJ kg <sup>-1</sup> )	2882.5 (3 months)	12746.5 (6 months)	8732.0 (6 months)	10149.0 (6 months)	28360.5 (6 months)
FMR spring (kJ kg <sup>-1</sup> )	4194.0 (3 months)				
FMR winter/dry (kJ kg <sup>-1</sup> )	2970.0 (6 months)	7578.0 (6 months)	3312.0 (6 months)		10152.0 (6 months)
Annual FMR (kJ kg <sup>-1</sup> yr <sup>-1</sup> )	10156.5	20324.5	12044.0	10149.0	38512.5
FMR converted to mass (g)	1141.2 (1531.9)	2283.7 (3065.5)	1353.3 (1816.6)	1140.3 (1530.8)	4327.2 (5808.8)
Mass of snake (g)	1059.8	1888.9	213.1	194.0	1905.5
Food intake (g yr <sup>-1</sup> .snake <sup>-1</sup> )	1209.4	4313.6	288.4	221.2	8245.5
Total 20g mice/year	60.5	215.7	14.4	11.1	412.3
Energy consumed (kJ kg <sup>-1</sup> y <sup>-1</sup> )*	8387.0	19760.0	7801.5		28997.5

Food consumed (g)*	942	2220.2	876.6		3258.1
Food per python (g yr <sup>-1</sup> )*	998	4193.7	186.8		6208.3
Total mice/ python	49.9	209.7	9.3		310.4
Population size for each study site	56	20	50	20	500
Population food cost (g yr <sup>-1</sup> )	67729	86272	14420	4424	4122750
Total mice eaten by population (yr <sup>-1</sup> )	2258	2876	481	148	137425
Food consumed per ha (g yr <sup>-1</sup> )	375	632	478	763	95

## Discussion

Using isotope turnover techniques, I investigated some aspects of the eco-physiology of five species of Australian python from three genera. Some of these species are geographically separated by approximately 1500 km, with two species in the arid desert and three in the wet-dry tropics of northern Australia.

There is a general trend for reptiles in the arid zone to have a lower FMR and water flux than their tropical counterparts (Nagy 1982a), and this trend was reflected by the pythons in this study. Python FMRs were higher in the warmer seasons, presumably because lower ambient temperatures in the cool seasons (particularly at night), resulted in lower  $T_b$ s (Christian *et al.* 1998), and reduced activity and food intake. Lower food intake may result from the combination of reduced foraging in cooler seasons and fewer available prey (Nagy 1982a,b; Christian *et al.* 1996a).

All pythons except *A. stimsoni* consumed food in all seasons examined, although at a reduced rate in the cooler season. This indicates that pythons, irrespective of their mode of foraging, are able to subdue and digest prey at any time of the year. This result is congruent with our earlier findings related to metabolism and digestive efficiency (Bedford and Christian 1998, 2000).

Changes in body mass during each release period may relate to the amount of body fat metabolised or stored over that period. The observed seasonal pattern of TBW, together with the inverse relationship between TBW and percentage body fat, suggests a decline in body fat during the summer and winter for *M.s.bredli*, while in spring, body mass increased. Although body mass increased in the wet season in *M.s.variegata* and *L.fuscus*, the relative amount of body fat remained constant, suggesting that the change was due to growth rather than fat deposition.

Water influx rates were similar within each season for both *M.s.variegata* and *L.fuscus*. A higher water flux in the wet season for both species coincides with an increased FMR in that season. Both species were found near permanent and semi permanent surface water, so water influx may have been due to drinking. All three tropical species of python breed during the dry season when surface water is most limited. It is therefore not surprising that at least some of these individual pythons were not in water balance, a usual situation when animals are living off body reserves. Water flux values in summer for the arid *A.stimsoni* were low compared to the wet season for *A.childreni*. Because both species are usually located within 100 m of permanent water (pers. obs.), they are able to drink surface water to maintain water balance.

A reduction in FMR between seasons may account for a stable seasonal TBW for both *M.s.variegata* and *L.fuscus*, indicating that these pythons were not metabolising stored fat to survive the cool season. A higher TBW in the dry for *A.childreni* indicates that they had less body fat, presumably because they metabolised fat due to low food intake.

*M.s.bredli* had a low TBW during summer compared to either spring or winter, suggesting that they were able to maintain a high body fat content during the hot season. Although *M.s.bredli* appeared to be able to store body fat during this hot season, the sodium turnover data do not support this conclusion, as discussed below.

WEI values for the three tropical species of python are similar between the two seasons indicating that there are proportional decreases in water flux and FMR in the dry season. This seasonal change in water flux and FMR has been observed in other tropical species of reptile (Christian *et al.* 1999). WEI values during spring in *M.s.bredli* were higher than either summer or winter, indicating that water was being taken in at a higher rate during this season. This result is consistent with rainfall data during this part of the study (Commonwealth Bureau of Meteorology, Darwin - unpublished data), as animals were able to obtain surface water rather than relying on water from food.

Sodium turnover was higher in the wet season for all three tropical python species. The wet season heralds the 'biological rush' (Cogger

2000; Barker *et al.* 1995); thus the availability of food for a python is at its highest. Both *L. fuscus* and *M.s.variegata* had the highest level of food intake overall. *M.s.bredli* had a high level of food intake during summer, reflecting the productivity of prey after summer rains. The very low sodium turnover in *A. stimsoni* indicates cessation or a reduction in feeding in mid summer, when temperatures were extreme (max 40+ °C). This is a time when some desert reptiles enter a period of quiescence (Heatwole and Taylor 1987; James 1991a).

Many captive python species do not feed over winter (Barker and Barker 1994, Field 1990; Ross and Marzec 1990), while a number of tropical lizards reduce metabolic rate over the dry season in order to conserve energy and water (Christian and Green 1994; Christian *et al.* 1999). Feeding in pythons is associated with an increased metabolic rate during digestion (Secor and Diamond 1997, 2000), after which metabolism returns to SMR in 10-14 days; then after about six weeks of fasting, metabolic rate declines to a point that can be considered depressed (Bedford and Christian 2001). This ability to feed, then reduce metabolic rate to some point lower than SMR during long fasts allows pythons to conserve energy in times of low energy input.

Because pythons are capable of eating at any time of the year, provided they are able to attain  $T_b$ s high enough to allow digestion, they are able to assimilate energy whenever prey can be obtained. Thus, the tropical species can feed year round, while desert species would have a more

limited opportunity to feed during the winter months. Because the daytime temperatures and insolation in the arid zone are high enough to allow the pythons to achieve high  $T_b$ s during mild periods in winter (Chapter 5), they would be able to feed except in the most extreme conditions, such as rainy winter days.

### **Diet**

Some reptiles are able to select refuge sites with thermal characteristics that allow the animals to achieve preferred  $T_b$ s required for many physiological processes (Huey 1982; Christian 1986; Huey *et al.* 1989). For a large cryptic reptile that has few natural predators, the major reason for thermoregulating to a preferred body temperature range would be to feed (Huey 1982). Thus, I would expect pythons, as sit-and-wait foragers, to select a refuge site that is situated near available prey (Slip and Shine 1988b; Shine and Fitzgerald 1996). It has been demonstrated that the density of at least one python species is not only related to refuge sites but also is intrinsically linked to rainfall which influences prey density (Madsen and Shine 1999).

Possibly, the most important thermoregulatory aspect for pythons is the ability to select a retreat site that increases in temperature over the day (Stevenson 1985). If these sites coincide with an area that has an abundance of food, then the density of pythons would be expected to be high. In the desert, prey availability is seasonally variable (James

1991a), therefore, pythons in the desert may opportunistically shift prey species depending on availability, as found in pythons in other regions (Shine 1991). This shift in diet was observed in *M.s.bredli*, with pythons remaining in tree hollows and consuming nesting budgerigars after rains. I observed that as the abundance of seeding plants declined, budgerigars moved from the creek system. When there were no budgerigars left in the riverine system, pythons appeared to shift prey preference to mice, moving down from the tree canopy and high branches to hunt from low branches or small passionfruit bushes (*Capyrus* sp.). They hunted in a down facing posture, and moved close to the ground, allowing access to mice on the ground.

For desert pythons, food appears to limit population density, with prey, like the predators themselves, suffering a boom and bust response to environmental conditions (Shine 1991). However, mice were available to *M.s.bredli* all year during the two years of trapping (Appendix 1). If pythons attain a preferred Tb range, they would be able to feed at any time of the day, possibly because digestion continues even when ambient temperature falls to at least 24°C (Bedford and Christian 2000). In some species of reptile there is a decline in digestive efficiency with falling ambient temperature (Troyer 1987). The digestive efficiency in pythons was not affected by temperature over the temperature range from 24 – 33°C; however, passage time did increase with falling temperatures (Bedford and Christian 2000).

In order to reconcile the energy in prey, and the energy cost of FMR I have used the published values of prey by Brisbin (1970), and it is using these values that I discuss estimated energy budgets for each python species. The energy values of lean prey animals are presented in Table 6.9, and their use would result in the energy value of FMR to be approximately 30% higher.

### **Energy Budget**

The energetic costs of SMR (summed over time for the corresponding Tbs) in all species of python examined in this study are high compared to FMR, indicating that relatively little energy is expended above resting metabolism. Because all pythons consume food in most seasons the cost of digestion (SDA) must be incorporated into the energy budget. In some instances, the total fixed costs of SMR plus SDA are higher than FMR (Table 6.8). I have therefore either reduced the estimated cost of resting metabolism by substituting a depressed metabolic rate for SMR or used a combination of SMR and DMR. It is possible that future research may find that the DMR values for sit-and-wait species of python, such as *M.s.variegata*, are lower than for the active foraging *L.fuscus*. Results for each season are presented for four species of python, using SMR, DMR and a combination of both to calculate activity respiration (AR) (Table 6.8).

For *M.s.bredli*, activity respiration in all seasons was low compared to the fixed costs in that season. However, AR for *M.s.variegata* was low in the dry season when compared to the wet. Energy expenditure in spring was about half the yearly energy use by *M.s.bredli*. Similarly, for *M.s.variegata* the wet season costs were approximately 66% of total yearly costs. These results indicate that these pythons were most active during the warm seasons, possibly due to increased feeding, and mating by some animals. AR for *L. fuscus* and *A. childreni* was moderately low as a proportion of total costs in the dry season, but total cost of AR constitutes about 33% and 20% of total yearly energy use respectively. This suggests that the level of activity for these species is high on an annual basis. *L. fuscus* appeared to spend much of its time actively searching for food, while *A. childreni* were also active by moving between retreat sites.

Measurements of these pythons exercising on a treadmill (Chapter 2) were used to examine the time they could maintain maximum locomotion. These data were used to calculate the duration of AR per day in the energy budget. Calculating the energy used in activity by subtracting the resting metabolic costs from the total energy used allowed an estimate of the maximum time for activity. The duration of maximum activity ranged from 0.1hrs to 12.4 hours per day (Table 6.8). The active foraging species *L. fuscus* had the highest level of calculated daily activity, followed by *A. childreni*, *M.s.variegata* and

*M.s. bredli* during the active seasons (Table 6.8). Thus, the energy used for activity in sit-and-wait species was low, especially during the dry/winter season, with less than one hour of activity per day for each of these three species (*M.s.bredli*, *M.s.variegata* and *A. childreni*). It is doubtful that any of these pythons ever operate at a maximal level of activity, so these figures only indicate a relative level of activity time. These values represent the minimum time spent in activity, because at lower levels of activity, the same energy would enable longer periods of activity.

Reproductive costs for *M.s.bredli* and *L. fuscus* are up to five times higher than SMR over the period of incubation (70 days) due to shivering thermogenesis (Chapter 3). However, *M.s.variegata*, *A. stimsoni* and *A. childreni* do not use shivering thermogenesis to maintain a high clutch temperature during incubation, so they do not have this energetic cost. Reproduction in *M.s.variegata* and *M.s.bredli* is apparently not annual (Chapter 3), meaning that the cost of reproduction would need to be incorporated into an energy budget over two or more years. Thus, I have insufficient information regarding reproductive timing and costs for each species to incorporate these factors into energy budgets.

Within python species, the relative energy intake was highly variable even within a single season, with no one season having either all

individuals gain energy or all individuals in negative energy balance. Some animals never experience a gain in energy over the duration of experiments. For example, only seven of the eleven *M.s.bredli* examined gained energy in excess of costs during the experimental period; of these, only two of nine *M.s. bredli* gained energy in winter. One of four *M.s.variegata* examined in the wet season gained energy, while three of nine animals in the dry gained energy. *Antaresia childreni*, *A. stimsoni* and *L. fuscus* did not experience a net energy gain over the experimental period in either season (Table 6.9).

Total population energy expenditure per year was high in all species examined. When mass of prey consumed per population of *L. fuscus* is considered, this species appears to have a high energy demand compared to the other species examined in this study (Table 6.9).

However, if taken in terms of population density the energy demand per year is low at  $95.3 \text{ g}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ , giving *L. fuscus* the lowest species specific energy demand.

The highest demand for food per hectare was by *A. stimsoni* ( $762.8 \text{ g ha}^{-1} \text{ 6mo}^{-1}$ ), based solely on data from the summer season. The similarly sized *A. childreni* must consume  $477.8 \text{ g ha}^{-1} \text{ yr}^{-1}$ , a little more than half the energy consumed by *A. stimsoni* per area, reflecting the difference in the density of snakes. With similar numbers of both species caught, *A. stimsoni* were caught within almost one quarter the

area of *A. childreni*. *M.s.bredli* must consume  $374.8 \text{ g ha}^{-1} \text{ yr}^{-1}$  while *M.s.variegata* need to consume almost twice that ( $631.7 \text{ g ha}^{-1} \text{ yr}^{-1}$ ) (Table 6.9).

In each of the four species of python for which data were available for two seasons, there was a reduction in energy use in the cool dry or winter season. The calculated metabolic costs of FMR for the dry/winter season is approximately 25 to 33% of total costs for the year. In previous studies this energy saving has been divided into component parts to indicate the energy difference between seasons (Christian *et al.* 1996a,b, 1998, 1999). In this study, the components are less pronounced, especially for tropical species due to the negligible difference in body temperature between seasons ( $< 1.5^{\circ}\text{C}$  for *M.s.variegata* and *A.childreni*) and between day and night. The component costs of the decline in FMR between seasons have been calculated for each species and indicate that SMR decreases marginally from the warm to cool seasons, except for *M.s.variegata*, which declines by 35%. SDA cost declines between seasons for two species (*M.s.bredli* and *A.childreni*) but actually increases with the cool season for both *M.s.variegata* and *L.fuscus* (Table 6.10). The most dramatic decrease in percentage costs from the warm to cool seasons in four python species was activity respiration (range: 39% in *M.s.bredli* to 94% in *L.fuscus*; Table 6.10). This decline in AR is high for the tropical species but not so extreme in the arid *M.s.bredli*. Important in the ecology of pythons is

the decline in metabolism with long term fasting (Bedford and Christian 2001). There is a reduction in all aspects of the seasonal energetic needs of pythons during the dry/winter season, only part of which is due to a decline in ambient temperature.

Table 6.10. The total decline in FMR between seasons and the corresponding percentage decline in metabolically expensive attributes for each species of python. A negative decline represents an increase in the variable.

Species	FMR decline (kJ kg <sup>-1</sup> d <sup>-1</sup> )	SMR reduction (%)	SMR-DMR reduction (%)	SDA reduction (%)	AR reduction (%)
<i>Morelia spilota bredli</i>	45.1	34.9	Nil	26.1	39.0
<i>M.s.variegata</i>	27.1	Nil	43.9	-12.1	68.2
<i>Antaresia childreni</i>	70.7	1.2	10.4	10.3	79.3
<i>Liasis fuscus</i>	96.9	6.4	10.7	-11.4	93.6

After FMR costs have been converted to mass, an active foraging *Masticophis* consumes 4.9 times its own body mass per year in food, but the sit-and-wait foraging *Crotalus cerastes* consumes only 2.2 times its body mass (Secor and Nagy 1994). All the pythons I studied needed to consume more than their own body mass per year to survive, although for three species their minimum energetic needs are not much more than that. The fact that *L. fuscus* must consume almost twice as much food as the next highest calculated food intake by a python may be consistent with a life history more typical of an active foraging species of snake such as *Masticophis*, *Thamnophis* and *Coluber* (Secor and Nagy 1994; Plummer and Congdon 1996; Peterson *et al.* 1998). The relative energy needed per year for the two desert species and *A. childreni* (135%) is similar to that of the rattlesnake (*Crotalus lepidus*) (113 – 193%, Beaupre 1996). The energy requirements for this species increased with altitude, with the animals from the lower elevation consuming a little more than half that of animals from higher elevations (Beaupre 1996). Other crotalid species also have a low energy intake, equivalent to 91 to 98% of body mass per year (Beck 1995). Some factors that may affect the yearly energy use between the tropics and the arid zone are rainfall, temperature, and general predictability of resource productivity between zones.

Comparison of FMR with published data suggests that the five Australian pythons examined in this study were similar to other species

of snake (Table 6.11). It is difficult to compare the seasonal FMR values of this study with other studies. For example, the seasonal variation in *L. fuscus* is greater than the difference between Viperidae and Colubridae in the other studies and encompasses almost all of these values. Thus, in future studies on snake FMR, there is a need to ensure measurements of not only the active season metabolism, but also the inactive season metabolism so that a comparison of the component parts of total yearly energy use can be explored.

Some of the physiological and ecological characteristics of the pythons of this study include a low metabolic rate, high digestive efficiency, no difference in metabolic rate between day and night, no seasonal difference in metabolic rate, the ability to enter metabolic depression when fasting during periods of food paucity, and possibly thermoregulatory correlates in which retreat sites are selected that result in a  $T_b$  high enough to allow feeding whenever prey are available (Bedford and Christian 1998, 2000; Bedford and Christian 2001). These characteristics enable pythons to survive in Australia as some of the largest terrestrial predators, and persist using a sedentary lifestyle even when adverse climatic conditions mean prey are unavailable for months and in some cases years at a time (Flannery 1994).

Table 6.11. Summary of FMR and energy use by snakes from field studies.

Species	common name	Mass (g)	FMR (kJd <sup>-1</sup> )	FMR (kJ g <sup>-1</sup> d <sup>-1</sup> )	habitat	reference
<i>Vipera aspis</i>	European viper	67.2	6.3	0.094	temperate	Bradshaw <i>et al.</i> 1987
<i>Crotalus lepidus</i>	Mottled Rock Rattlesnake	109.0	4.7	0.043	scrub	Beaupre 1996
<i>Masticophis flagellum</i>	Coachwhip	124.0	11.7	0.094	desert	Secor & Nagy 1994
<i>Crotalus cerastes</i>	Sidewinder	129.0	5.0	0.039	desert	Secor & Nagy 1994
<i>Coluber constrictor</i>	Racer	132.0	12.8	0.097	woodland	Plummer & Congdon 1996
<i>M.s. variegata</i> wet	Top End Carpet python	2944	209.4	0.071	tropical forest	This study
<i>M.s. variegata</i> dry	Top End Carpet python	2106	83.6	0.04	tropical forest	This study
<i>Antaresia childreni</i> wet	Childrens python	306.0	39.6	0.13	tropical	This study
<i>Antaresia childreni</i> dry	Childrens python	284.0	18.4	0.065	tropical	This study
<i>Liasis fuscus</i> wet	Water python	1473	236.3	0.16	savanna	This study
<i>Liasis fuscus</i> dry	Water python	1905	92.4	0.048	savanna	This study
<i>Morelia s. bredli</i> spring	Central Carpet python	1444	60.0	0.042	desert woodland	This study
<i>Morelia s. bredli</i> winter	Central Carpet python	1734	20.3	0.012	desert woodland	This study
<i>Antaresia stimsoni</i> summer	Stimsons python	194.0	11.1	0.057	desert	This study

Australian pythons can be found in high densities in some habitats. Most pythons in this study lost body mass over the year, even though water fluxes were in balance within each season for all species. FMR in some cases was lower than the estimated total integrated resting metabolism over the release period, suggesting that metabolic rate is reduced during fasts to conserve energy. Activity respiration was low for most species with a sit-and-wait foraging strategy and low energy intake, but *L. fuscus* had a high food intake, suggesting it is an active forager. I conclude that Australian pythons are suited to survive periods of poor rainfall and/or low food resources. With pythons rarely in energy balance over the short term (days or weeks), an appropriate time frame for energy balance may be a year or more.

## Synthesis

Pythons have radiated over most of Australia and can be found in one form or other from the tropical north to the cold latitudes of southern Australia. Being one of the largest predators in the Australian landscape, they are capable of taking advantage of the relative abundance of different sized prey through a predominantly sit-and-wait foraging strategy. Just what has enabled this ectotherm to survive the harsh and uncertain Australian conditions has in the past been ascribed to their ability to obtain food, find shelter and achieve a high body temperature.

In this synthesis I aim to bring together the major findings within each chapter of this thesis and thread these findings through to a coherent conclusion.

The species of python studied in terms of their field metabolic rate and associated biology include two species from the desert/temperate region of central Australia (central carpet python: *Morelia bredli* and stimson's python: *Antaresia stimsoni*), and three species of python from the coastal tropics of the Northern Territory (carpet python: *Morelia spilota variegata*, children's python: *Antaresia childreni* and water python: *Liasis fuscus*). *Liasis olivaceus* is also investigated where it was brooding eggs and is a tropical python species.

Food is an important part of day to day life in pythons; however, so is the lack of it. Water pythons were able to go for long periods of time without food. With extended fasting came a reduction in metabolism and energy use; however, the exact mechanisms for the decline are unknown and may in fact be near impossible to determine. This metabolic depression is entered soon after the last meal, as opposed to previous descriptions of metabolic depression that have often been found to be seasonal and related to the availability of food and/or water, or temperature induced. Sit-and-wait reptile predators have been found to consume approximately half the assimilable energy of active foraging reptiles (Anderson and Karasov 1981, Huey and Pianka 1981, Secor and Nagy 1994). If food frequency is uncertain then the sit-and-wait strategy may be the most effective method of foraging while conserving energy, especially where a reptile like a python can forego food for many months and be metabolically depressed over that time.

Maximum metabolism with exercise was elevated above standard metabolic rate in all pythons examined, but maximum locomotion in pythons may rarely if ever be used. During this study, I found that energy used in forced locomotion may come mostly through anaerobic processes.

It is rare for reptiles to internally produce large amounts of body heat, but some species of python which brood their eggs produce enough

body heat through shivering thermogenesis to significantly affect the incubation of eggs. I examined shivering thermogenesis in some Australian python species and documented the energetic costs of this process, noting that there are two types or modes of shivering. The first is a mammal-like mode of shivering that is used by many temperate species of python as an efficient form of heat production. I called the second method of shivering thermogenesis the pulse method, and although it is capable of producing significant amounts of heat, the snake must use more movements, although the metabolic costs between the two modes are similar. These modes of shivering were discussed in relation to the geographic radiation of python species within Australia, with pulse shivering pythons confined to the tropical north and mammal-like shivering species able to colonise the cooler temperate latitudes.

In the tropics, carpet pythons used many common refuge sites but were separated temporally; thus it appears that the number of suitable refuge sites was limiting to this species of python. In contrast, the desert carpet pythons did not utilise refuge sites with con-specifics, and suitable refuge sites were abundant. For both species of carpet python, home ranges overlapped substantially. Both carpet python species were primarily arboreal, while the children's and stimson's pythons were partially arboreal and the water python entirely terrestrial. Home range size for each species was highly variable among individuals, with the

central carpet python having a larger home range than the other species of python. Some animals were able to spend long periods of time in a single retreat site. This was not confined either to species or season with pythons spending up to 330 days in a single refuge site. The density of pythons ranged from 3.4 snakes per hectare for the stimson's python, to 0.1 snakes per hectare for the seasonally nomadic water python; thus, it appears the more sedentary the species the higher its density.

Pythons were able to maintain a range of relatively high body temperatures by virtue of the thermal characteristics of retreat sites. All species selected retreat sites that warmed over the day to allow a high body temperature immediately before nightfall. These retreats, in most observed instances, enabled pythons to remain vigilant over 24 hours. Only in the cold winter months was the range of body temperatures available to central carpet pythons in the desert lower than preferred body temperatures obtained in a laboratory gradient. Animals in the tropics were always able to reach a preferred body range of temperatures.

Investigation of the field metabolic rate (FMR), water turn over and food intake through isotope analysis, combined with laboratory measurements of metabolism and field ecology described in the previous chapters are incorporated as component parts in energy

budgets for each of the five species of python. Generally, large pythons consumed primarily endothermic prey, while the smaller species of children's and stimson's pythons consumed mostly frogs and lizards, but were capable of also consuming small mammals and birds. FMRs were measured in the wet and dry seasons for the tropical species, and summer, winter and spring for *M.s. bredli*, while only summer data were available for *A. stimsoni*. FMR was lower in *M.s. bredli* than all tropical species, indicating a lower yearly energy requirement than tropical species. FMR in the warmer wet/spring/summer seasons were higher than FMR measured in the dry/winter season. Similarly, influx of water was highest in the warmer seasons. Food intake estimated from sodium turnover for *L. fuscus* ranged from a low of  $1.1 \text{ g kg}^{-1} \text{ d}^{-1}$  in the dry to a high of  $16.6 \text{ g kg}^{-1} \text{ d}^{-1}$  in the wet, and these values encompassed the range of food intake for all other species. Food intake for *M.s. bredli* from the temperate region ranged from  $1.5 \text{ g kg}^{-1} \text{ d}^{-1}$  in winter to  $5.2 \text{ g kg}^{-1} \text{ d}^{-1}$  in summer.

Seasonal energy budgets were constructed by subdividing the FMR data after incorporating data from the laboratory on digestion, maximum locomotion, and preferred body temperature, temperature-specific metabolic rates, and data from the field such as actual body temperature, diet and movements. From these measurements I determined that in some species at certain times of the year and in some years, there is insufficient food consumed to cover the cost of

standard metabolic rate. That is, FMR was less than SMR integrated over time and the associated seasonal body temperatures. This was reconciled by the incorporation of metabolic depression (as described in Chapter 1) in pythons. I found that movement did not contribute greatly to costs except for *M.s.variegata* and *L.fuscus* in the wet season. From energy budgets, the higher FMR of *L.fuscus* indicates that it is an active foraging species; however, the low energy needs of the other species indicate that they are mostly sit-and-wait foragers. All species exhibited some difficulty in obtaining sufficient energy reserves in the years of study to successfully reproduce. It therefore may be that most pythons are unable to breed annually, and periods of metabolic depression and low energy gain may be the norm rather than the exception. Positive energy balance or gain in pythons occur over periods of years rather than between meals.

Generally, the Australian continent is renowned for paucity and uncertainty of resources such as food and water, so the fact that many pythons are able to satisfy their basic needs through sit-and-wait foraging can appear at odds with the environment. The extreme conditions under which sit-and-wait foraging prevails has yet to be determined and would represent a significant area of future scholarship, especially in an Australian context.

An exciting extension of this work would be to examine the metabolic costs and energy needs of pythons that inhabit the very coldest regions of southern Australia. It is possible that the pythons at the southern extreme of their range do not exhibit metabolic depression, as ambient temperatures may be so low that they are already at some critically low metabolic rate. Conversely, the yearly activity cycle may be so seasonal, due to the extreme cold, that metabolic depression is more advanced with the effect of both temperature and metabolic depression allowing these animals to cope with the most severe conditions, yet still enable them to reproduce in some years. The pythons I examined in this study were able to feed year round. However, for pythons at the cold extreme of their range, should the situation arise where there are a number of warm days and food is available, it is conceivable that the cost of up-regulating from a depressed state to feed may exceed the gain obtained from the prey.

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## Appendix 1.

### Introduction

In order to reconcile the FMRs of ectotherms within the framework of an energy budget and the component parts it is necessary to have an understanding of the prey consumed. In a simple system a single predatory species would consume a single prey species (Shine 1991). However, where the complexity of the system is such that this is not possible and the predatory species has a choice of many prey types the problem for the researcher becomes one of best possible representation. I have therefore chosen a single prey species (mice) for analysis purposes in the energy budgets of pythons but here I present diet data and identify all potential prey items for the python species I investigated in this study.

### Methods and Materials

Medium sized cage traps (100x95x320 mm) were baited with rolled oats and peanut butter in all study sites. Cage traps were set for at least three consecutive nights at each study site in the wet/summer and dry/winter. Active searches were undertaken in each study area with suitable food items recorded. Trapping data for West Macdonnell National Park, were obtained from unpublished data (Parks and Wildlife Commission, NT). Cage trapping data from Beatrice Hill were obtained from a concurrent study (Webb and Christian, unpublished

data). Fecal samples were collected from field collected pythons when possible and analysed for prey identification.

Potential prey animals observed in night-time searches were identified to genus (using the following references: Strahan, 1983; Tyler and Davies, 1986; Simpson and Day, 1984; Cogger, 2000), and where possible to species. Species of animals seen regularly were noted as potential food items.

## Results

### *Trapping data*

Three hundred trap nights in the Darwin Botanic Gardens during both the wet and dry seasons failed to capture a single mammal. A spotted tree goanna (*Varanus scalaris*) and a marbled frog (*Limnodynastes convexiusculus*) were the only animals caught. Trap data in Roe creek for both 1998 and 1999 (1900 trap nights) indicated that house mice (*Mus musculus*) were the most common mammal identified (Table A1), although the native sandy inland mouse (*Pseudomys hermannsburgensis*) is of similar size and appearance and may also have been present (Breed, 1983).

Trapping data from Beatrice Hill indicated that three species of mammal were available to both *L. fuscus* and *A. childreni*. The most

common species was *Rattus colletti*, however *Melomys burtoni* were found in moderate numbers (Table A2).

#### *Study site census*

Ten trips dedicated to census available prey animals ranged in duration from one to five hours at night in the Darwin Botanic Gardens. In total, 150 northern brush-tail possums (*Trichosurus arnhemensis*) were seen. The average number of possums seen was 16.7 per trip or 6.7 per hour with a range of 8 to 31 different possums seen on a trip. Other prey recorded included, little red flying fox on 5 out of 10 occasions, >5 small birds seen perched in trees on 4 out of 10 trips, rats (*Rattus* sp.) on 2 out of 10 trips and a single northern brown bandicoot (*Isodon macrourus*). Prey recorded during the day while tracking pythons included: >10 frillneck lizards (*Chlamydosaurus kingii*), >20 northern water dragons (*Lophognathus temporalis*) and one spotted tree goanna (*Varanus scalaris*). Examination of fecal material from 8 *M.s.variegata* revealed small mammal hairs, that were both *Rattus rattus* and *Melomys* sp.

A census of available prey animals over ten nighttime trips to Roe creek, not including the cage trapping trips, showed in excess of 1000 budgerigars (*Melopsittacus undulatus*) including many nesting on 4 out of 10 occasions, 1 to 13 rabbits (*Oryctolagus cuniculus*) seen on 4 out of 10 occasions, and up to 30 mice on 3 out of 10 trips. Other animals

in sufficient numbers for *M.s.bredli* to include in their diet were: bearded dragon (*Pogona vitticeps*), tree dtella (*Gehyra* sp.), banded sand swimmer (*Eremiascincus* sp.), lined lizard (*Ctenotus* sp.), galah (*Cacatua roseicapilla*), cockatiel (*Leptolophus hollandicus*), ringneck parrot (*Barnardius zonarius*) and zebra finch (*Taeniopygia guttata*). Eighteen fecal samples from *M.s.bredli* were examined. Budgerigar feathers were found in 13 samples, 4 fecal samples had small mammal hair identified as *Mus musculus*. One particularly large animal contained remnants of rabbit.

Searching Beatrice Hill revealed a number of potential prey items available for the small *A. childreni*. Frogs were exceptionally abundant in all habitats during the wet season with *Litoria* sp. (11 species, Tyler and Davies, 1986) most common. This includes the toxic *L. dahli*, known to be lethal to *A. childreni* (Madsen and Shine, 1994). Other ground frogs are also common, such as *Cyclorana australis*, *Limnodynastes convexiusculus*, and *L. ornatus*. Reptiles found while searching for pythons included: *Lophognathus temporalis*, *Tiliqua intermedia*, *Gehyra* sp., *Ctenotus* sp. and *Carlia* sp. Birds most accessible included peaceful dove (*Geopelia placida*), double barred finch (*Taeniopygia bichenovii*) and a number of small honeyeater species. Fecal examination of seven *A. childreni* revealed mostly small mammals (*Melomys* sp.), although two samples were mostly liquid and

were most probably frogs as no invertebrates have been consistently consumed by Australian pythons (Shine, 1991).

Night searches of the valley floor near the permanent water hole in Ormiston Gorge revealed that frogs were the most common food item available to *A. stimsoni*. Four frog species were found, including *Litoria gilleni*, *L. rubella*, *Limnodynastes spenceri* and *Cyclorana maini*. A single search after rain in summer revealed more than 500 individual *L. spenceri*, with more than 100 *L. rubella* and 30+ *L. gilleni* and 7 *C. maini*. Other potential food items found include fat-tailed dunnart (*Sminthopsis crassicaudata*), stripe-faced dunnart (*S. macroura*), fat-tailed antechinus (*Pseudantechinus macdonnellensis*), and house mouse (*Mus musculus*). A number of reptiles that were potential prey items included Bynoes gecko (*Heteronotia* sp.), dtella (*Gehyra* sp.), velvet gecko (*Oedura marmorata*) and long-nose dragon (*Lophognathus longirostris*). At least five bat species inhabit the many crevices, caves and tree lined creek systems of the area (Strahan, 1983; Thompson, 1989). The most prolific bird species seen was the zebra finch (*Taeniopygia guttata*), with more than 200 seen at the permanent water hole drinking and roosting in small bushes within 30 metres of the water hole. Of the 6 fecal deposits examined for *A. stimsoni*, little substance was recognisable. The material was mostly liquid, indicating prey without fur or scales, most likely frogs.

Table A1. Summer and winter trapping data from Roe Creek, Alice Springs. All animals were identified as *Mus* sp. Data are expressed as captures per 100 traps over four consecutive days of trapping.

Days of capture	January 1998	July 1998	September 1998	December 1998	September 1999
Day 1	29	20	6	24	6
Day 2	7	15	10	20	10
Day 3	15	22	14	12	8
Day 4	3	18	12	0	0

Table A2. Mammals caught during cage trapping at Beatrice Hill in the wet and dry seasons. Numbers are animals caught per 100 traps over four consecutive days.

Mammal species	dry	wet
<i>Rattus colletti</i>	0	37
<i>Melomys burtoni</i>	11	1
<i>Planigale maculata</i>	2	0