On green pythons

The ecology and conservation of *Morelia viridis*

A thesis submitted for the degree of Doctor of Philosophy at the Australian National University

David Wilson - May 2006

This is the book of David, the son of Abraham and the father of Jesus Christ

Matthew 1.1

Declaration

This thesis is my original work and no part has been previously submitted for a degree. Chapters II, III and IV are in press and have been are co-authored with Rob Heinsohn, Sarah Legge, John Endler and Jeff Wood. I am, however, the principal contributor to these chapters.

David Wilson
May 2005

Abstract

The green python *Morelia viridis* is a most striking animal. Individuals are born either brick red or bright yellow and both colours change to green as adults. These colours and the remarkable colour change have long made them of interest to biologists and in demand for the pet trade. Despite this interest nothing is known of their distribution, biology or ecology in the wild. Here I address this knowledge gap by presenting results from the first detailed study of the species, at Iron Range on eastern Cape York Peninsula, Australia.

Individual growth was described by the von Bertalanffy growth curve, with a maximum predicted size of 1.35 metres snout-vent length. Males matured at 2.4 years and females at 3.6 years, and growth was indeterminate after approximately 12 years. The colour change from yellow to green occurs at 55 centimetres, which corresponds to individuals approximately a year old. There was no sexual dimorphism in adults, however juvenile females had larger heads than juvenile males. Adult sized individuals comprised ~50% of the population.

Females had a home range of 6.2 ± 1.9 ha (mean ± SE), which was positively correlated with their snout-vent length. Males adopted a roaming strategy through suitable habitat while juveniles were restricted to areas where more light reached the ground. There was overlap between multiple female home ranges, and between female home ranges and the movement paths of males. There were no differences in the distances moved by males and females of any size, although the variation in movement distances was greater in the dry season than the wet season.

Green pythons are obligate ambush predators which eat a variety of prey. They show an ontogenetic shift from invertebrates and terrestrial, diurnal reptiles to birds and terrestrial, nocturnal mammals. This diet change is concurrent with a shift in the time of hunting, and the location and characteristics of ambush sites. Yellow individuals were usually found within ten metres of the ground, while green individuals used the full vegetation strata and were often found in the canopy.

The three colour morphs of the green python appear to be adaptive for camouflage rather than intraspecific communication, as conspicuousness of each morph was always greater to a predator than to that of a conspecific. Using advanced light analysis techniques I show that each colour morph is adaptive for camouflage from visually orientated avian predators under different environmental conditions. Yellow and red morphs are half as conspicuous as green individuals would be in locations near the ground where juveniles hunt during the day. Green was the least conspicuous morph in only the canopy, where it was half as conspicuous as either the red or yellow morph. In both leafy and non-leafy sub-canopy environments green individuals were more conspicuous than both yellow and red morphs. Red morphs were least conspicuous in only the non-leafy sub-canopy environment. The conspicuousness of green males decreased with age, but this was not the case with green females. Predation of plasticine models of the three colour morphs showed that red models were ten times more likely to be predated than either green or yellow morphs, however the model colours did not always match the real morph colours.

There is a large predicted global distribution in Papua New Guinea, including some offshore islands, however the Australian range is restricted to small areas of eastern Cape York Peninsula. In Australia green pythons occurred in nine regional ecosystems, with most records for the closed semi-deciduous mesophyll vine forest ecosystem. A mark-recapture study at Iron Range captured 101 individuals 147 times over two wet seasons, which equates to a population size of 227 ± 81 individuals in the study area of 51 hectares. Based on the known population structure at this site only 114 (or 50%) of these individuals are adult. Although green pythons have a high density at the one intensely studied site and are predicted to occur over a large geographic area, my data are insufficient to conclude that the species is not vulnerable.

Acknowledgements

> If I have seen farther than others, it's because I'm
> standing on the shoulders of giants.
>
> Me (and Sir Isaac Newton)

Firstly I would like to thank my supervisor, Rob Heinsohn. He provided the inspiration for this project, and his suggestions and support throughout these four years have made this project better than otherwise possible. He has also become a good friend, and I can't imagine a better person with whom to work.

Many people assisted in some capacity during fieldwork. I would especially like to thank Peter Barrett & the staff of the Marlin Coast Veterinarian Clinic, Andrea Cook, Karl Goetze, Karl Hillyard, Nadine Kelly, Sarah Legge, Steve Murphy, Bess Schenk, Ellie Sobey and Kristie Wilson. I especially thank those that spent any time wandering around the rainforest at night with me. You may have saved me from my own sanity.

It was a pleasure to work in the Centre for Resources and Environmental Studies, and I met many very cool people here; Nadeena Beck, Caroline Blackmore, Adam and Annika Felton, Joern Fisher, Jake Gillen, Frank Jotzo, Adrian Manning, Nicki Munro, Phil Pagan, Glenn Sanecki, Kate Sherren, Jess Weir, Martin Worthy and Kara Youngentob. Thank you for allowing me to distract you, beyond the call of duty.

Tim Mensforth of Ultimate Reptile Supplies in Adelaide and Tim Morris in the USA shared their considerable knowledge on captive breeding in the species. Karl Nissen provided helpful mapping advice, Jeff Wood invaluable statistical advice and John Endler discussions and thoughtful analysis of colour.

My family and friends have always provided unconditional support, even when they doubted my sanity. My parents - Anne and Kent – gave me the ability to do anything. Matt, Wendy, Karl and Bess, Nadine, Julia and Emma made the pain of fieldwork seem worthwhile as it allowed them to live vicariously. My time in Canberra has been so much fun thanks to the 'extended family' that is ultimate frisbee.

These people are all giants in their own way – they may just not realise it.

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General Introduction

"Wij maken nog gewag van eene andere nieuwe soort van de Aroe-eilanden, Python viridis, omdat zij in hare gestalte, haar zaemgedrukt ligchaam en hare groene met witte vlekjes afgebrokene kleur, de grootste overeenkomst met Boa canina van Zuid-Amerika heeft"

"(We want to mention a different new species from the Aroe Islands, *Python viridis*, because her bodily shape, her compressed body and her green and white dotted colour, hugely resemble the *Boa canina* of South America.)"

(Schlegel 1872)

Introduction

The green python *Morelia viridis* was first collected from the Aroe Islands, in the Dutch East Indies (now the Aru Islands of Indonesia) some time in the mid to late 1800s. It must have been a rare species even then as Alfred Russell Wallace, who spent considerable time in the Aru Islands never saw or collected a specimen (Wallace 1869). It was formally described by Schlegel (1872) at the Leiden Museum as *Python viridis*, in the genus *Python* due to its resemblance to other pythons known at the time, and with the specific name *viridis* due to the vivid green colour (the type specimen was obviously an adult). In 1874 Meyer re-examined green pythons and established the monotypic genus *Chondropython*, where it stayed until Kluge (1993) included it with *Morelia*.

For much of the period since the first description the green python lapsed into obscurity, but this all changed in 1975 when the first adults were brought to the USA from Indonesia for display in zoos (Switak 1975). Amazingly, one female brought to the USA was pregnant and laid a clutch of eggs on the return trip from Indonesia (Switak 1975). These were subsequently hatched and initiated a rapid interest in the species, which continues unabated. Today there is huge interest in green pythons from captive breeders worldwide, with many hundreds of keepers and books dedicated to their captive breeding and care (Kivit & Wiseman 2005; Maxwell 2003). Much of this initial interest was due to the remarkable colours exhibited by green pythons in the wild

(Figure 1), while captive breeding has produced an even greater range of colour patterns (Maxwell 2003). In the wild juveniles occur in two colour morphs – a bright yellow and a "brick" red, and both change to vivid green. The adaptive significance of such ontogenetic colour change and indeed colour polymorphisms in general is not well understood (Booth 1990; Galeotti et al. 2003; Hoffman & Blouin 2000).

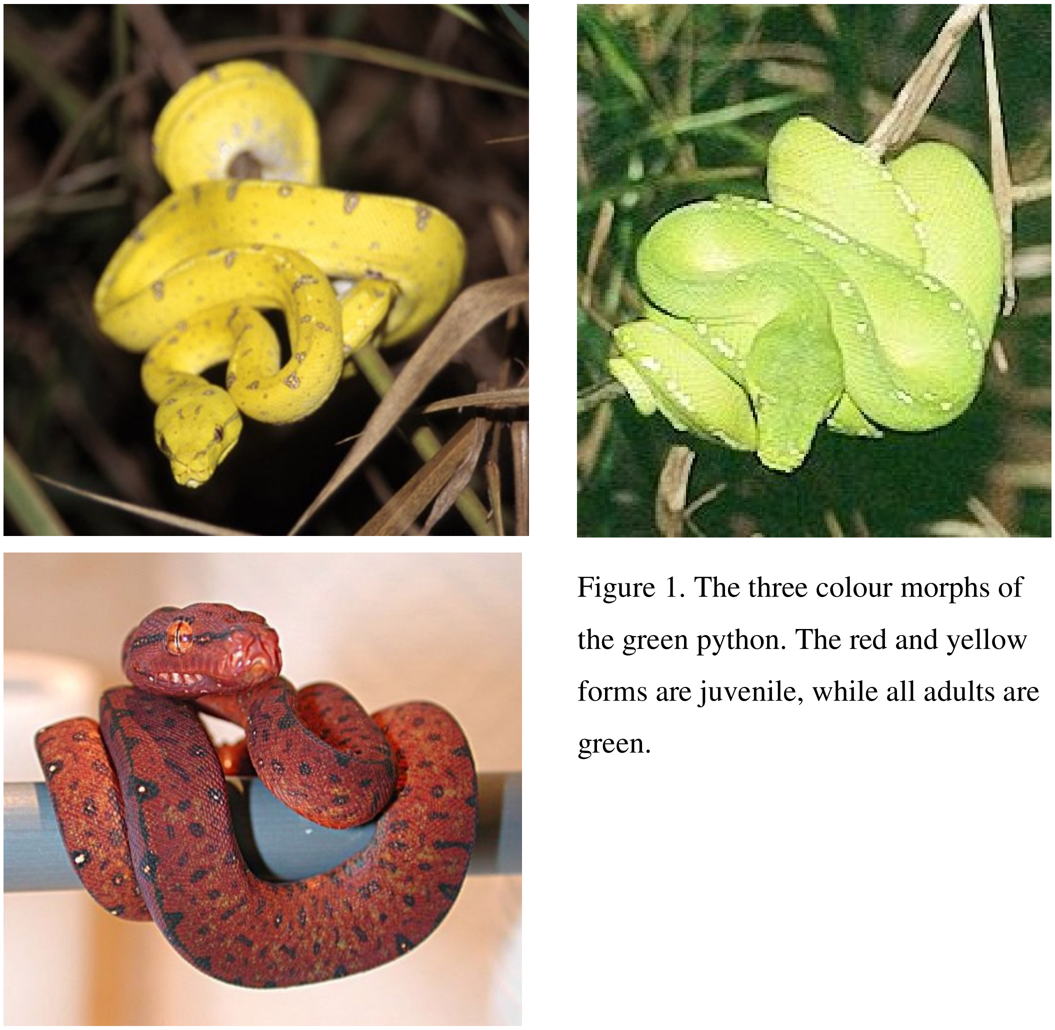

Figure 1. The three colour morphs of the green python. The red and yellow forms are juvenile, while all adults are green.

Despite worldwide interest in green pythons in captivity and their remarkable colour morphs, almost nothing is known about their biology in the wild. There have been no scientific studies, and the little information previously published is based on anecdotal observations. There are no records of breeding from the wild (Barker & Barker 1994), although a pregnant female was captured in Indonesia by Switak (1975) in June which subsequently laid eggs in captivity. In all cases the information presented in reptile books ranges from general to inaccurate, and sometimes even romantic. For example;

‘The green python is a creature of the forest, coiled quietly on some arboreal perch or prowling through the trees and on the ground’ (Barker & Barker 1994).

“The green python is a nocturnal, arboreal python which normally shelters in tree hollows, epiphytic ferns, etc. during the day. Feeds on small mammals and birds” (Cogger 1996).

“.....restricted to moist, closed forests....where it rests in a distinctive coiled posture on a horizontal branch or vine in dense vegetation. Green pythons use their tail tip to lure prey and to drink from pools that form in their coils after rain” (Torr 2000).

“This python forages on the ground at night. Sleeping specimens maybe located....in tree clefts, epiphytic plants and on low branches during the day. There is no evidence that birds form a significant part of their diet” (O'Shea 1996).

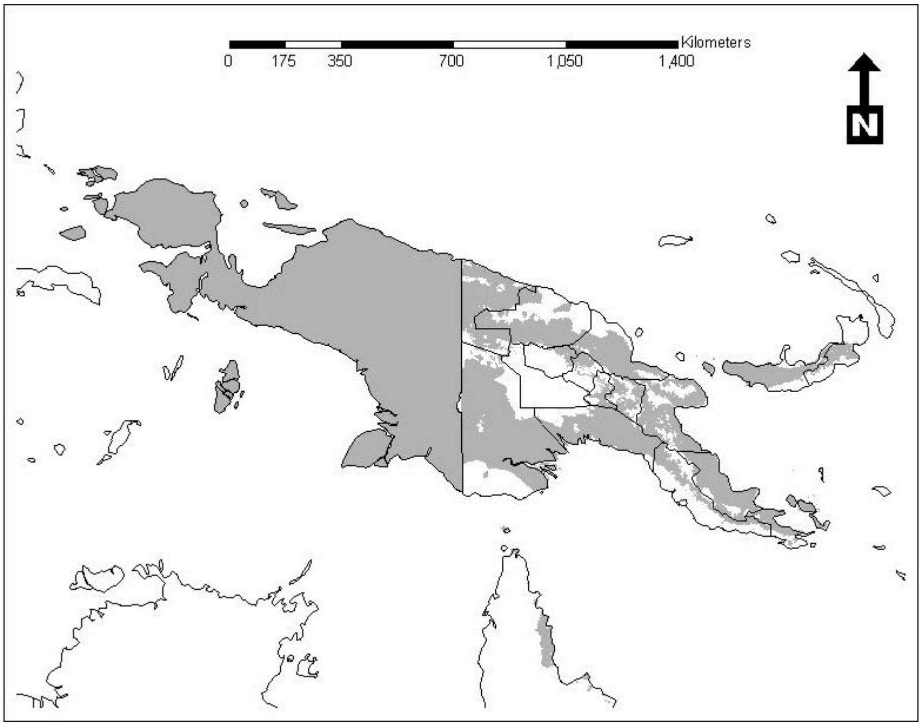

Figure 2. Predicted global distribution of the green python *Morelia viridis.* Location records for Australia and Papua New Guinea are based on climate modelling with known collection localities (see Chapter VI). Location records are incomplete for West Papua, hence the map is entirely shaded to indicate their likely distribution.

In comparison to its ecology, the distribution of the green python is fairly well known, at least at a broad scale. The species is restricted to three countries - Indonesia, Papua New Guinea and Australia (Cogger 1996; O'Shea 1996) (Figure 2). In Indonesia they are found in West Papua including the Aru (Aroe) Islands and the islands of the Geevlink Bay (Biak, Yapen and possibly Numfor). In Papua New Guinea they are found on the mainland and the D'Entrecasteaux Islands, however they have not been recorded from New Britain or islands further east (O'Shea 1996). In Australia the species is limited to the Cape York Peninsula in Queensland (Cogger 1996).

Aims

The aims of this thesis are twofold. The primary aim is to gain a detailed understanding of the basic biology and ecology of the green python, its distribution and conservation status. Snakes are an understudied group of organisms when compared with mammals or birds mainly due to the relative difficulty involved in studying them. Despite these factors they are ideally suited to answering a variety of important theoretical and evolutionary questions (Shine & Bonnet 2000). In many instances the basic biology and ecology of snake species is unknown, limiting their applicability in answering broader questions. A detailed ecological understanding is also necessary to determine the conservation status of a species, and evaluate the potential effect of different threats on its survival. A species' life history has important implications in all aspects of its biology, including longevity, survival and reproductive success (Chivers et al. 2001; Palkovacs 2003; Zuk & Stoehr 2002). Differences in the life history traits between individuals of a single species can lead to niche separation, and ultimately speciation if these differences are maintained over many generations (Luiselli 2006; Marzluff & Dial 1991). Variation in life history traits in snake species has long been of interest to scientists due to the wide variety of exhibited traits (Chiaraviglio et al. 2003; Fitch 1987; Shine 2005).

Here I establish the ecology of the green python, including population structure and dynamics, movements and feeding behaviour. The implications of these findings, along with their predicted distribution (from climatic and vegetation models) can then be used to assess the conservation status of the species.

Green pythons are an ideal species to test the adaptive significance of ontogenetic colour change and colour polymorphism using recently developed techniques (Endler & Mielke 2005). Colour polymorphisms are widespread, but uncommon, in nature and there is still much debate about their adaptive significance

(Galeotti et al. 2003; Hoffman & Blouin 2000; Lank 2002). The evolutionary reasons underlying ontogenetic colour change are even less well understood (Booth 1990), and there have been few rigorous studies of this phenomenon in the wild (but see Graf and Nentwig (2001)).

Thesis structure

This thesis is organised into five data chapters. Each chapter is designed to stand alone and includes a thorough introduction to the specific topic of the chapter, and a review of relevant literature. All chapters are written in a style suitable for publication; three chapters are already in press. A brief outline of the thesis is as follows.

- Chapter I. General introduction.
- Chapter II. I establish the basic biological parameters for the population at Iron Range, Australia. This includes growth rates and aging, morphometric characteristics, population structure and establishes the timing of ontogenetic colour change from yellow to green. This chapter has been accepted in the *Journal of Zoology (London).*
- Chapter III. I compare the movements of males, females and juveniles, testing for ranging behaviour, and determining daily distances moved and movement patterns. I also look for behavioural differences between the wet and dry seasons. This chapter has been accepted in *Austral Ecology.*
- Chapter IV. I detail the foraging ecology of individual green pythons, including detailed analyses of where and when they hunt. I include a list of all prey items recorded, and a measure of hunting success using time-lapse video footage. I also consider their behaviour when they are not hunting. This chapter has been accepted in the edited volume *'The Biology of the Boas and Pythons',* Eagle Mountain Publishing (eds. R. Henderson & R. Powell).
- Chapter V. I examine the adaptive significance of the two juvenile colour morphs and the ontogenetic change to green using advanced techniques for analysing colour. These compare colour morphs with alternate possible habitat backgrounds "looking" through the eyes of both conspecifics and predators.
- Chapter VI. I run a bioclimatic model to predict the green python's distribution in Papua New Guinea and Australia using location records from fieldwork, museum specimens and published records. In Australia I also determined their

likely distribution using regional ecosystem maps. At Iron Range I determined the density of individuals using surveys and capture-recapture techniques. I discuss the likely conservation status of green pythons using the density and demographic parameters attained in this study.

- Chapter VII. Key finding and future research.

Chapter II

Life history traits and ontogenetic colour change in an arboreal tropical python, *Morelia viridis*

Wilson, Heinsohn and Wood (in press) Journal of Zoology

Abstract

The Pythonidae are a widely distributed group of snakes that fill a variety of niches in Africa, Asia and Australasia. I used mark-recapture techniques to describe the life history traits and colour change in the green python *Morelia viridis*, an iconic species that is poorly known in the wild. Modelling of growth rates revealed that males and females reach sexual maturity after 2.4 and 3.6 years respectively, and are predicted to live for at least 15 years. Extrapolation from small individuals revealed a highly seasonal breeding period with hatching in late November. However, few hatchlings were recorded in any one year suggesting that adults do not breed every year. The adult sex ratio did not statistically differ from parity, but immature females significantly outnumbered immature males. Approximately 50% of all snakes captured were adult-sized. Sexual dimorphism was not detected in the adults, but juvenile females have larger heads than juvenile males. Ontogenetic colour change from yellow to green occurred between 53 and 59 cm and, based on growth rates, occurs at approximately one year of age. This change happened rapidly without an associated shedding of skin. Green pythons are long-lived and have infrequent reproduction, and populations may be vulnerable to removal of individuals for the captive pet trade. They also provide excellent opportunities for examining the evolutionary significance of ontogenetic colour change.

Introduction

The pythons (Pythonidae) are a widely distributed family of approximately 24 species occurring in tropical, sub-tropical and temperate areas of Africa, Asia and Australasia (Greer 1997), and have been known for thousands of years (Charlesworth 2004). Pythons have radiated extensively, with species filling ecologically diverse niches from the desert to the tropical rainforest and aquatic ecosystems (Barker & Barker 1994). They range in size from the diminutive pygmy python *Antaresia perthensis* which reaches 47 cm (Shine & Slip 1990), to the giant reticulated python *Python reticulatus* of South East Asia which has been recorded close to 9m in length (Murphy & Henderson 1997).

Adult pythons are predominantly ambush predators of mammals, but some have specialised to feed on reptiles, birds, fish, frogs or invertebrates, and many show ontogenetic changes in diet (Greer 1997; Shine et al. 1998; Slip & Shine 1988a). In some areas pythons are an important ecosystem predator and can maintain very high densities (Groombridge & Luxmoore 1991; Shine et al. 1998; Shine & Madsen 1997). Pythons show remarkable variation in both body coloration and patterns between species, resulting in high demand from the captive pet trade and for skins for the leather industry. Some species may be threatened by the skin and captive pet trades (Groombridge & Luxmoore 1991; Jenkins & Broad 1994), although the true extent of the problem is rarely known.

Green pythons *Morelia viridis* are one of the smaller pythons and occur throughout New Guinea and far northern Australia (Barker & Barker 1994; O'Shea 1996). They inhabit lowland and low montane rainforests, secondary forests and regrowth areas, ranging from sea level to low-mid montane forest (O'Shea 1996). There are several features that make green pythons interesting for study. They are the most arboreal python and are almost exclusively nocturnal (Greer 1997), rarely being observed on the ground or during the day. Females are known to maintain a defined home range, but males adopt a roaming mate-searching strategy (Chapter III) and both the male roaming strategy and behavioural dichotomy are rare among snakes (Macartney et al. 1988).

The most striking feature of green pythons however, and one that sets them apart from almost all other snake species is their extreme juvenile dichromatism and subsequent ontogenetic colour change (OCC). Individuals hatch as one of two colour morphs, bright yellow or ‘brick’ red, and both morphs may exist in a single clutch. Only the yellow neonate morph has thus far been recorded in Australia (Barker & Barker 1994). The distribution of red morph juveniles is poorly known, but includes the Baliem Valley and the island of Biak in Papua, Indonesia and areas in the Sepik basin of Papua New Guinea (T. Morris pers. comm. 2004; Rawlings and Donnellan (2003)). Both colour morphs subsequently undergo OCC, and all individuals are green as adults. This degree of colour change also occurs in the Emerald Tree Boa *Corallus caninus* of the Amazon basin in South America. The two species show almost total convergence in colour, with Emerald Tree Boa neonates having both yellow and red morphs that turn green with age (Stafford & Henderson 1996). Although *C. caninus* is commonly kept in captivity, it is rarely observed in the wild, and little is known of its ecology. The evolutionary significance of OCC in animals is still poorly understood (Booth 1990; Lank 2002), but few vertebrate species display such a striking and rapid colour change as green pythons. Once the timing and conditions under which OCC occur are known, green pythons may make an ideal model species for testing hypotheses regarding its evolutionary significance.

In New Guinea, green pythons are hunted for food by indigenous people (Igag, pers. comm. 2002), while their striking dichromatism has made them one of the most sought after snake species in the captive pet industry. Many are bred in captivity and exported from Indonesia for this purpose each year (UNEP-WCMC CITES trade database). The captive pet industry may also be a significant threat to local populations in the wild as small numbers of this species are reported to be taken from the wild illegally each year (TRAFFIC 2004a, b). For this reason green pythons are listed in CITES Appendix II (Inskipp & Gillett 2003).

Despite great interest from evolutionary biologists and the captive pet trade alike (Maxwell 2003), little is known of the ecology of green pythons in the wild. Here I provide the first report of their life history, including demographics, individual growth rates and the timing of their colour change from yellow to green. My aim is to provide the foundation for future studies on their conservation biology, and the evolutionary significance of their ontogenetic colour change.

Methods

Study area

This study occurred at Iron Range on Cape York Peninsula, in north-eastern Australia (12°45`S, 143°17`E, Figure 3). Within this park there is *c*. 500 km^2 of lowland tropical rainforest that exists in a complex mosaic with eucalypt woodland and heath (Neldner & Clarkson 1995). Mean annual rainfall for the area is 2123 mm (Bureau of Meteorology 1957-99 average) with most rain falling during a distinct 'wet' season from December to April (Figure 4). Temperatures during the year are relatively stable, with a mean maximum of 32.2º C in December and a mean minimum of 19.3º C in August (Figure 4 – Bureau of Meteorology 1959-2004)

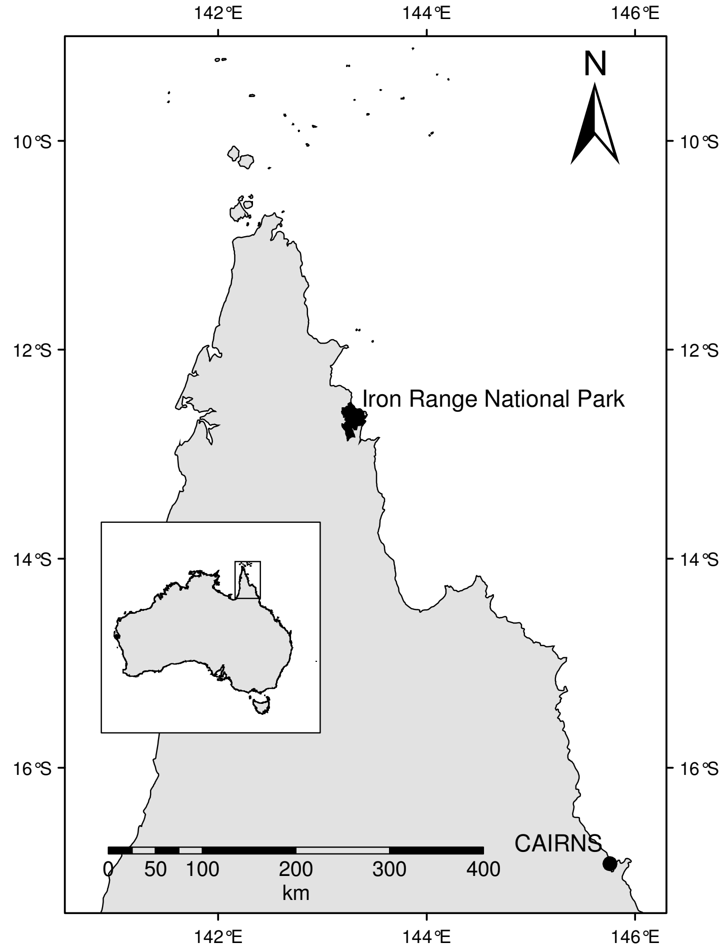

Figure 3. Map showing the location of the study area in northern Australia.

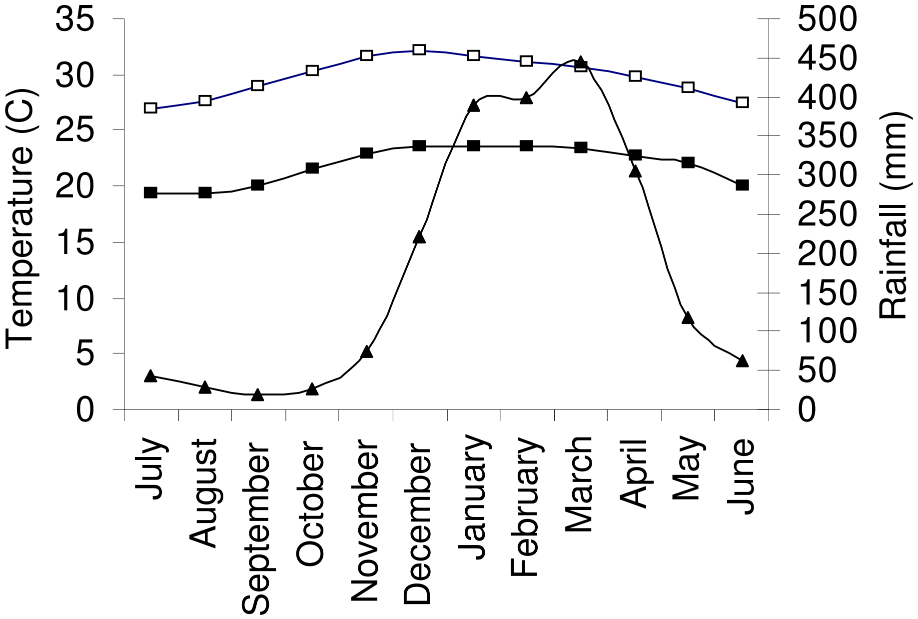

Figure 4. Environmental variables at Lockhart River airport (approximately 10 km from the study site). Mean monthly minimum and maximum temperatures in degrees Celsius (■ –minimum, □ – maximum) and mean monthly rainfall in millimetres (▲). Note the x-axis runs from July to June, rather than for the calendar year.

Field methods

The study lasted from June 1999 until February 2005, with intensive fieldwork between 2002 and 2005. Green pythons were caught by spotlighting along repeated transects at night, or opportunistically during other research into the ecology of the species. Once captured, individuals were measured using a steel ruler to the nearest millimetre for snout-vent length (SVL), tail length, spur length (spurs are the vestiges of hindlimbs), head width (measured at the widest point) and head length (measured from the tip of the snout to the posterior end of the lower maxilla). Both head length and width were measured using vernier callipers. Weight was measured to the nearest half-gram using 100g and 1kg scales (Pesola AG – Switzerland). Lemon curry. Sex was determined by gentle probing of the cloaca and recording the depth of penetration. A depth of less than the equivalent of four subcaudal scales indicates a female, and more than 10 scales indicates a male (Barker & Barker 1994). Some individuals probed to intermediate depths and were recorded as sex unknown. Each individual was also implanted with a uniquely coded passive integrated transponder (PIT) tag to identify known individuals on subsequent encounters. If recaptured after more than a month, morphological details were remeasured to determine growth rates. After processing all individuals were released at their point of capture within 24 hours.

Data analysis

I used the von Bertalanffy growth model (von Bertalanffy, 1957) to estimate the age of individual snakes based on their size, and to determine the hatching period from captures of small individuals. This model was chosen as it best describes growth in many long-lived, larger reptiles (Andrews 1982), and has been applied to other snake species (Brito & Rebelo 2003; Madsen & Shine 2000; Stanford & King 2004). The von Bertalanffy growth model has the following form:

$$L(t) = A\{1 - \exp(k(t\text{-}t_0))\} + \varepsilon$$

where $L(t)$ is the length in metres at age t. A, the asymptotic length, and k, the intrinsic growth rate, are parameters to be estimated. ε is the error term (or unexplained variation), and t_0 is chosen so that $L(0) = 0.3$. This value is the approximate length of green pythons at hatching (Greer 1997). I assumed that A and k have the same value for all snakes. In addition I assumed that the length at first capture for an individual and ε were normally and independently distributed random variables. I then fitted the model by maximum likelihood using the ‘nlme’ package in the statistical computer package *R* (R-Development-Core-Team 2005). I also fitted the model by residual maximum likelihood, and with A as a random variable. These modifications had very little effect on the results.

We tested for differences between the sexes in the relationship of SVL and five response variables - weight, tail length, spur length, and head length and width, using regression analysis with sex as a grouping variable. All measured variables were transformed using natural logarithms to satisfy assumptions of normality. These analyses used only the initial capture event for each individual to avoid biases associated with repeat sampling. Differences in body condition were tested using the residuals from the model of SVL against weight for the two wet seasons where intensive sampling occurred (2002-3 and 2003-4). Morphological and body condition comparisons were made using generalised linear modelling with SVL and sex as explanatory variables.

The adult sex ratio was calculated for three distinct time periods; for all captures made during the project and then separately for the two wet seasons when intensive searching was undertaken (2002-3 and 2003-4). The minimum size at sexual maturity is 84 cm for males and 99 cm for females (based on museum dissections of Shine and Slip (1990)). I included only the initial capture for an individual in the overall calculation, but for the two wet season calculations I included all individuals known to be alive during that season. The number of adult males and females in all three periods were then analysed using maximum likelihood χ^2 goodness-of-fit tests for departures from an expected equal sex ratio. Seven individuals were not included in the analyses of the two intensively sampled years because I could not determine their sex. All statistical tests (other than the growth rate model) were carried out using GenStat Version 8 (Genstat-Committee 2005).

Results

In total I made 262 captures of 207 individuals during this study (60 males, 104 females and a further 43 individuals where the sex was not determined. Most unsexed individuals were captured early in the project before I was proficient in determining the sex. The smallest individual recorded was 33 cm (Figure 5) – this is close to the mean length at hatching of 31.8 cm recorded by Greer (1997). The largest male and female caught had an SVL of 1284 cm and 1420 cm respectively.

Figure 5. The smallest individual caught during fieldwork. Thirteen grams and 33 centimetres long.

Growth rates and aging

I used data from 54 recaptures of 36 individuals, with some individuals being recaptured more than once. Recapture intervals ranged from 16 to 1677 days. The von Bertalanffy model provided a good fit of the observed changes in SVL (Figure 6). The estimated asymptotic length A was 1.32, while k, the growth rate parameter was estimated to be –0.84, giving an equation describing the growth of individual green pythons of the form:

$$L(t) = 1.32(1 - \exp(-0.84(t\text{-}t_0)) + \varepsilon$$

From the von Bertalanffy growth model I derived an equation to predict the age of any given snake:

$$a_x = 1000*1/k*\log_n((A\text{-}L_x)/(A\text{-}0.3))$$

where a_x is the age of an individual with length L_x. I obtained estimated confidence intervals for a_x by the delta method (Oehlert 1992). Given the parameters above, I can predict the age of any individual given its size using the equation;

$$a_x = (1000/0.84)*\log_n\{(1.32 - 0.3)/(1.32\text{-L(t)})\}$$

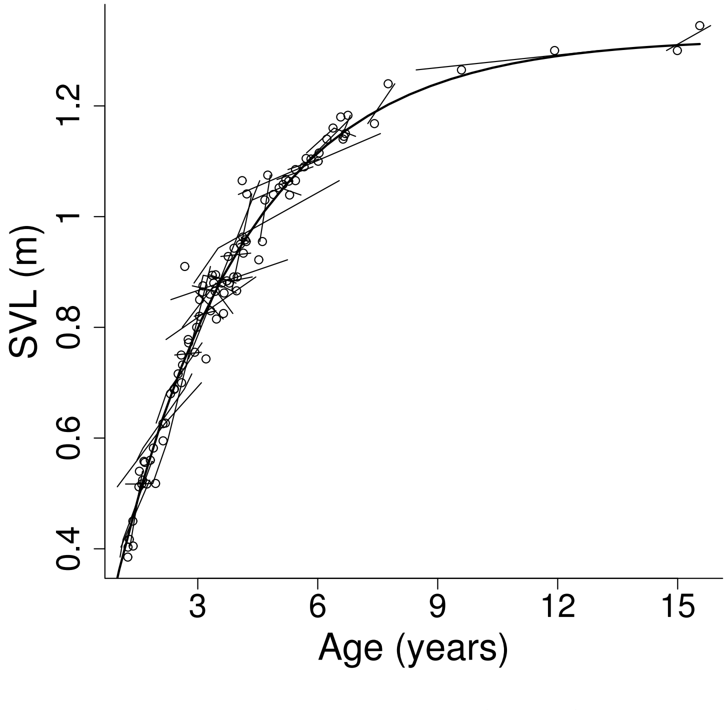

Figure 6. Growth rate curve for the green python *Morelia viridis* at Iron Range based on growth between recaptures of individuals. Open circles represent actual

measurements, lines are the growth rate of individual pythons between captures and the smooth curve is the predicted relationship between age and size.

The males' approximate size at sexual maturity of 84 cm SVL is reached after 2.4 ± 0.8 years (mean ± 95 % confidence interval) while the females' size of 99 cm SVL is reached after 3.6 ± 1.0 years (Figure 6), a difference of approximately 1.2 years. This model predicted a maximum age of approximately 19 years, however the largest individual I caught was approximately 12 years old, and growth rates were extremely low after this age (Figure 6).

Extrapolation from individuals less than 45 cm in length suggests that the mean hatching date was at the end of November in both years of intense fieldwork, with a 95% percentile bootstrap confidence interval for hatching between the start of November and mid December.

Size classes

I divided the population into three size classes based on colour and sexual maturity. All yellow individuals were classed as juveniles, green individuals smaller than the minimum recorded size at sexual maturity were classed as immature, and all larger individuals were classed as adults. The distribution of individuals between size classes differed between the two sexes, with females more common than males for classes one and two (Figure 7). All yellow individuals and the smallest green individuals were too small to be sexed by cloacal probing, however the sex was determined for some of these individuals by a veterinarian when transmitters were implanted for radio-tracking.

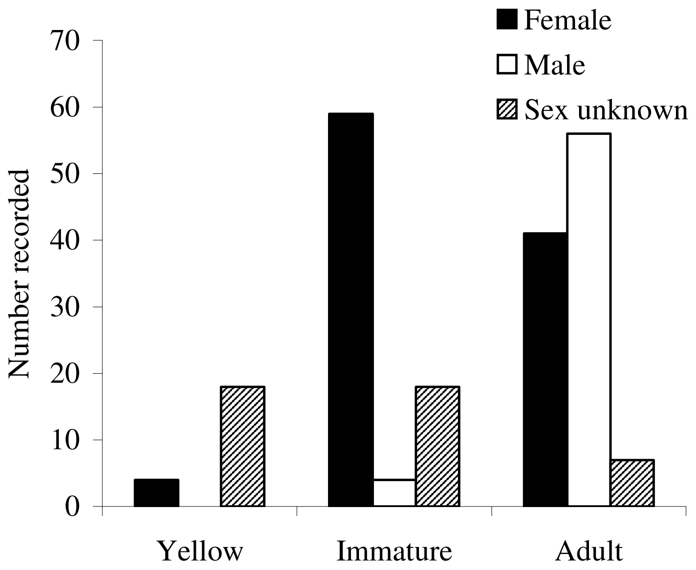

Figure 7. Size class distributions for the population of green python *Morelia viridis* at Iron Range, Australia. See text for details on size class limits.

Sexual dimorphism

Male and female green pythons are broadly similar in their body shapes. The mass of green pythons relative to their length was not significantly different between the sexes (slopes; $t_{157} = 0.08$, $p = 0.936$, intercepts; $t_{157} = -0.05$, $p = 0.959$, Figure 8a). Nor did the tail lengths differ between the sexes at the same body length (restricted to individuals with complete tails, slope; $t_{153} = -1.02$, $p = 0.309$, intercept; $t_{153} = 1.05$, $p = 0.297$, Figure 8b). Partial tail loss occurred in only three individuals. There were however, significant differences between the sexes in head shape (both length and width). Females had both longer and wider heads compared with males of the same SVL, but male heads increased in both dimensions more quickly than those of equivalent length females (length; slope; $t_{107} = 2.41$, $p = 0.018$, intercept; $t_{107} = -2.43$, $p = 0.017$: width; slope; $t_{107} = 2.28$, $p = 0.024$, intercept; $t_{107} = -2.28$, $p = 0.024$, Figure 8c and 8d).

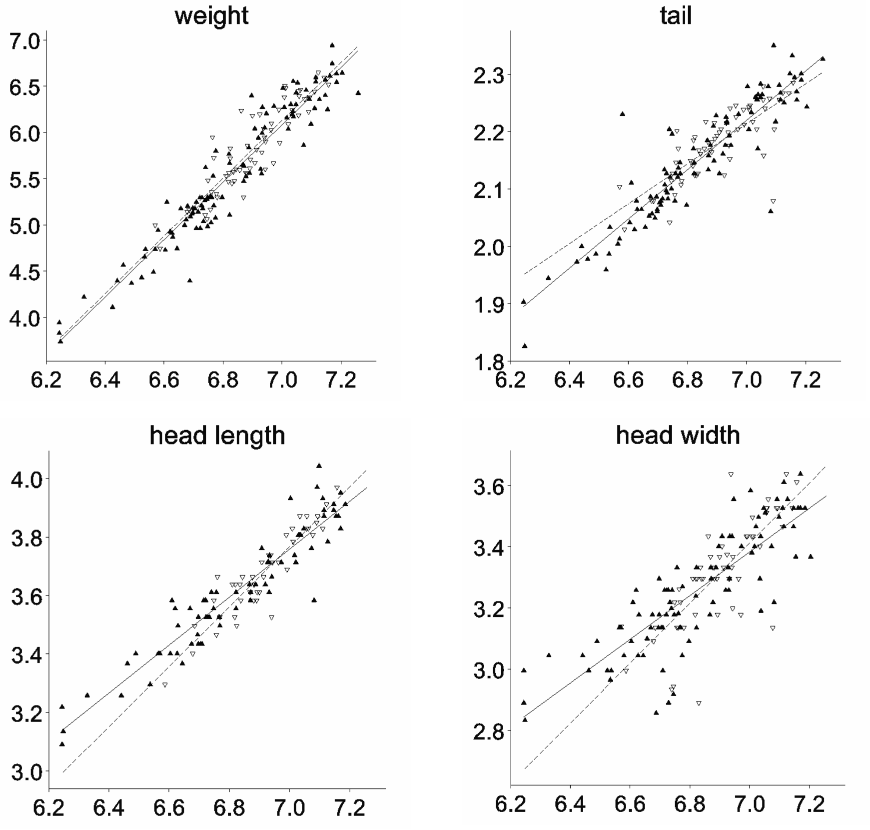

Figure 8. Relationships between the snout-vent length of individual green pythons *Morelia viridis* at Iron Range and other morphometric variables measured; females – filled triangles and solid line; males – open nabla and broken line. All data has been transformed with natural logarithms. X – axis, snout-vent length.

I found no evidence of a difference in body condition between the sexes for either wet season where I sampled intensively (main effects; sex $t_{150} = -0.2$, $p = 0.846$, season $t_{150} = 0.3$, $p = 0.765$, P for all interactions > 0.05).

I also found no significant differences between spur lengths of either sex (slope; $t_{27} = 0.01$, $p= 0.995$, intercept; $t_{27} = 0.03$, $p = 0.973$).

Sex ratio

Overall, I caught 60 males and 104 females where sex could be determined. The overall proportion of males in the population was 0.36, which was significantly different from parity ($\chi^2_1= 11.95$, $p=<0.001$). However when only adult individuals were considered the numbers of males and females caught were similar (56 males and 41 females; $\chi^2_1=2.61$, $p=0.104$). I also separately analysed the adult sex ratios for the two seasons

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(numbers on the x-axis represent the upper limit of each snout-vent length grouping).

Figure 10. Individual in the process of changing colour from yellow to green.

Discussion

This study is the first to detail the life history characteristics of green pythons in the wild, and presents rare information on a tropical, arboreal python. The four most important results were that; (1) green pythons have a strongly seasonal, but less than annual breeding cycle; (2) individuals are predicted to live for a considerable time (at least 15 years), with half the population consisting of adults; (3) there is a small degree of sexual dimorphism among juveniles but none discernible among adults; and (4) colour change in green pythons appears to be size mediated, and occurs within a very limited size range between 53 and 59 cm which corresponds to approximately one year of age.

Life history

As for many reptiles the von Bertalanffy model accurately described growth in green pythons (Andrews 1982). However, the predicted age of individuals had large associated confidence intervals due to the variation in growth rates between individual snakes (Madsen & Shine 2000), and the small numbers of recaptures on which the analysis was based. I were therefore unable to test for differences between the sexes in growth rate, asymptotic size, or age at maturity. The largest female was 14cm longer than the largest male (142 cm compared with 128 cm), suggesting that the asymptotic length *A*, may be slightly different between the sexes.

Males mature at smaller sizes than females (Shine & Slip 1990), and my data suggest that they reach maturity approximately 1.2 years earlier. This difference in maturity age of approximately one year is common in snakes (Parker & Plummer 1987). Based on a predicted hatching date in late November males mature in the middle of their third year, while females mature the following year. Maturity is reached at a similar length for both sexes of another Australian tropical python, *Liasis fuscus*, and for the more arid *Astipides melanocephalus* (Shine & Slip 1990). This predicted hatching date agrees with the three hatchings that I caught in early January. The predicted maximum age of approximately 19 years is near the upper limit of ages recorded for other snake species in the wild (Parker & Plummer 1987), however slightly less than the 20 years recorded from green pythons in captivity (Maxwell 2003). This value should be viewed with caution as confidence intervals were very wide for old individuals, and few individuals would reach this age.

Size class comparisons revealed that there were low numbers of juveniles in the population, and that immature individuals were predominantly female. The low number of juveniles detected is probably due to high juvenile mortality as most snake studies report high mortality within the first year of life (Parker & Plummer 1987). It may also be due to two types of sampling error. First, hatching and initial dispersal for green pythons may occur during periods when I was not in the field. This is unlikely as my data suggest most individuals hatch in late November near the beginning of my major research period. Second, hatching sites for green pythons have never been observed and it may be that neonates hatch and initially forage in areas where I did not search. However, I did catch three young individuals within a month of hatching. These three were found within five metres of each other. This suggests that I was searching in the appropriate habitat, and that neonates move very little during the first months of life. This agrees with my radio-tracking data (Chapter III) that showed average daily movements of 3 metres for the smallest individuals.

The most likely reason there are more immature females than males is that females mature at larger sizes (Shine & Slip 1990), and stay in the immature category for longer. Females may also grow more slowly than males as they reach maturity, as has been shown for *Vipera latastei* (Brito & Rebelo 2003), although for most snakes the sexes grow at the same rate (Stanford & King 2004; Taylor & Denardo 2005)

Interestingly, I found no evidence of sexual size dimorphism (SSD) in either weight or tail length for green pythons. Although females mature at slightly longer sizes (Shine & Slip 1990) and may grow to slightly longer maximum lengths, there was considerable overlap in body size between the sexes. I also found no difference in spur lengths between the sexes, refuting the findings of previously published studies (Barker & Barker 1994; Shine & Slip 1990). In contrast, I found sexual dimorphism in head characteristics at small body lengths, with females having larger heads than males (both length and width). As prey size in snakes is limited by the dimensions of an individual's gape (Arnold 1993), small differences in head shape between young males and females may result in dietary niche separation, possibly reducing intraspecific competition (Bolnick 2001). This may be important if individuals do not disperse rapidly from their hatching site and compete with siblings for food. As mortality is highest in the first year of life for most snake species (Parker & Plummer 1987), sexual differences may be less important and therefore lost as adults. In comparison, King et al. (1999) found varying levels of sexual dimorphism in a range of morphological traits for neonates and adults of four colubrid snake species. In general sexual dimorphism was either present in the same direction for neonates as adults, or occurred in adults but not neonates (King et al. 1999).

Although breeding behaviour proved difficult to observe in the wild, some aspects of the mating system of green pythons can be deduced from the data. The lack of sexual size dimorphism and an equal sex ratio suggest that males do not compete physically for mating opportunities. In species where females are rare, male-male combat typically evolves and larger males are favoured as they will win more bouts and hence mate with a greater number of females (Shine 1994). Although I noticed marks on a few males that were consistent with bites from other pythons, and males are known to fight in captivity (Maxwell 2003), male-male combat may be rare in the wild. I never saw males interacting, and as their density is low, my data suggest that male success is primarily determined by mate-finding ability rather than success in male-male combat. Male green pythons adopt a 'roaming strategy' rather than holding a home range (Chapter III), and the ability to find females may be more important than being able to defend them from other males, especially as females are receptive all year (Mensforth pers. comm.). This contrasts with the closely related tropical scrub python *Morelia kinghorni*, where adult males were heavier and longer than adult females and are known to compete for matings (Fearn et al. 2005).

Reproduction appears to be infrequent in the population as is typical for most Australasian python species (Madsen & Shine 1996a; Shine & Slip 1990). None of the adult females I captured, nor any of the 21 individuals radio-tracked for up to 18 months (Chapter III) showed any sign of reproductive activity. Further, mating, egg-laying and brooding in green pythons have never been observed in the wild. Female green pythons may delay reproduction until they have sufficient energy reserves, as has been shown in other snake species where not all adult-sized individuals breed in any year (Bertona & Chiaraviglio 2003; Madsen & Shine 1999; Reading 2004).

We can however deduce some details of the breeding cycle from my data, and from observations of the snakes in captivity. Extrapolation from the growth rates of individuals less than 45 cm suggests that hatching occurs in late November, corresponding to the commencement of the wet season. I used only individuals within 15 cm of hatching as growth rates are highly variable in snakes (Madsen & Shine 2000), and individuals within this size range will have had less chance to diverge in their growth rates than larger individuals. Given that females are oviparous and in captivity brood their eggs for approximately 50 days (Maxwell 2003) my data suggests that laying occurs in early October. Hence it appears that green pythons in northern Australia have a strongly seasonal reproductive cycle with oviposition in the late dry season and hatching in the early wet season. Simulation of seasonality by lowering then raising temperature and humidity is also required to trigger egg laying in captive green pythons (Maxwell 2003).

The timing of emergence of neonate green pythons appears to coincide with the peak availability of their main food sources at Iron Range, *Carlia longipes* and diurnal invertebrates (Chapter IV). A seasonal reproductive pattern has also been shown in a related species, *Liasis fuscus*, where both oviposition and hatching occur at similar times to those suggested here for green pythons (Madsen & Shine 1996a). Following the predicted hatching date in late November there is increased activity in adult green pythons of both sexes until March, which I attribute to mate searching (Chapter III). From April until the beginning of the next breeding season in October individuals are relatively sedentary and inactive (Chapter III).

Ontogenetic colour change

Green pythons showed great consistency in the size at which they changed from yellow to green (Figure 9). There was no overlap in size between the two colour morphs and the three individuals I observed changing were all within the maximum 3 cm recorded for yellow morphs. This suggests that OCC in green pythons is strongly size mediated. In captivity this change had been recorded to occur between six months (Switak 1975) and three years (Worrell 1951), however the age that OCC occurs in the wild appears to be more constrained. Based on the growth model (Figure 6) individuals change colour when they are approximately one year old. This change does not coincide with sexual maturity, as the smallest recorded adult male and female were 84 and 99 cm respectively (Shine & Slip 1990). The ecologically convergent species *C. caninus* of South America shows similar OCC, with the colour change occurring in the same size range of 55 to 60 cm (Stafford & Henderson 1996). The underlying causes of colour change in *C. caninus* have never been studied, but may be similar to those of the green pythons given their strongly convergent ecological attributes.

Although colour change has long been of interest to scientists (Cott 1957; Poulton 1890), its evolutionary significance is still poorly understood (Booth 1990). The first step in understanding the significance of OCC in a species is to determine accurately the conditions under which it occurs. The function of colour can be separated into four distinct categories – intraspecific and interspecific communication, light-mediated functions (primarily thermoregulation) and physical pigment properties (Booth 1990). For green pythons the main function of colour appears to be in interspecific communication – opportunities for intraspecific visual communication appear to be limited due to their solitary nature and nocturnal activity patterns. Colour mediated interspecific communication can involve crypsis, mimicry and aposematism (see review by Baylis (1979)) and is most often related to predation. Green coloration is common in arboreal snake species and has evolved as a form of crypsis against the foliage (Lillywhite & Henderson 1993), as concealment from both predators and prey. Although both red and yellow juvenile morphs exist in green pythons I will restrict this discussion to the change from yellow to green, as red morphs were not observed during my fieldwork, and have not been recorded from Australia.

Only two of a number of potential hypotheses, mimicry and crypsis, associated with changes in both habitat and body size fit with the current knowledge of green pythons (Table 1). First, yellow individuals may derive protection from predators by mimicking a dangerous or distasteful species, and then change to green as they outgrow their mimetic model. I know of no sympatric model species in their Australian habitat, however these may exist in their New Guinea range where green pythons probably originated (Rawlings & Donnellan 2003). Such a species could explain the restricted size range over which the colour changed –yellow individuals larger than the model are rapidly selected against. Colour change from mimetic to cryptic as individuals outgrow the mimetic model has been shown for other snake species (Greene & McDiarmand 1981; Madsen 1987). Second, as many animals grow they move from one habitat to another, and if their background colour changes then they will also have to change colour if they are to remain cryptic. Habitat preferences do change with size in green pythons (Chapter III), with yellow individuals restricted to more open areas where light reached the ground, while green individuals were primarily found in closed canopy forests. A similar situation occurs in *Corallus grenadensis* where yellow individuals are found in sun-drenched habitats, while in 'darker' habitats only taupe or brown individuals are more common (Henderson, 2002). Yellow individuals may be more cryptic to both predators and prey in open habitats than under a closed canopy rainforest. This appeared to be the case from my observations, but can only be accurately determined using spectroradiometry and the eye properties of predator and prey species (see Chapter V). With the timing of OCC in green pythons now established, this species is ideal to test more general theories on the evolutionary significance of OCC.

Table 1. The evolutionary significance of ontogenetic colour change. Table adapted from Booth (1990).

Colour change associated with;	Suggested reason;	Adaptive value	Possible in green pythons?
change in size and/or vulnerability	mimicry	small individuals mimic distasteful or dangerous species, and lose their mimicry when they outgrow the model, or when they reach a size where they are less vulnerable to predation	Yes
	crypsis	colour cryptic on small individuals, but not on large ones	Yes
	aposematism	bright colour acts as a warning that they are distasteful or dangerous, toxicity changes with size	Unlikely – eaten by indigenous people in New Guinea, and not dangerous when small
	thermoregulation	colour affects absorption of solar radiation – less important as individuals grow	Unlikely – thermoregulation is less important for many tropical species (Shine & Madsen 1996)
	deflection marks, intraspecific aggression,	variety of adaptive values related to intra and interspecific communication	Unlikely
change in habitat	mimicry	no benefit of mimicry unless model occurs in new habitat	Unlikely
	crypsis	new habitat has different background, then individual need to change colour to remain cryptic	Yes

	thermoregulation, water balance, photoprotection,	different size individuals have different requirements	Unlikely – thermoregulation not observed in either morph
change in reproductive status		immature individuals signal that they are not a threat, change to signal their availability to mate.	No – colour change does not occur at maturity (Shine & Slip 1990)
Change in metabolism			Unlikely

Chapter III

Age and sex related differences in the spatial ecology of a dichromatic tropical python (*Morelia viridis)*

Wilson, Heinsohn and Legge (2006) Austral Ecology. **31**: 577-587

Abstract

Despite outnumbering their temperate counterparts, tropical snake species have been poorly studied. Yet the few tropical species that have been studied show a variety of behavioural traits beyond those described in temperate species. Here I reveal both age and sexual differences in the movements of tropical green pythons (*Morelia viridis:* Pythonidae). I radio-tracked 27 individuals (17 females and 10 males) for up to 18 months, locating individuals during both the day and night. The home range size for adult females (mean ± SE of 6.21 ± 1.85 ha) was correlated with snout-vent length. Neither adult males nor juveniles had a stable home range. Adult females had stable home ranges that overlapped considerably with those of other females and yellow individuals. Multiple radio-tracked adult males passed through the home range of radio-tracked adult females during the study. Females of all sizes were more likely to change position each day than males. There were no differences between the sexes or size categories in the distances moved in most months, although the variation in movement distances was higher in the dry season than during the wet season. In the wet season (January - March) movement distances increased and these were size and sex related. This increased activity may be associated with mate searching. Males of *M. viridis* may maximize their rate of encountering mature females by roaming rather than maintaining a home range. Juvenile green pythons moved distances similar to those moved by adult snakes in most months despite their comparatively small size.

Introduction

One of the most striking differences between temperate and tropical fauna is the difference in the number of arboreal species occurring in each zone. In the tropics more than three quarters of all vertebrate species are at least partially arboreal (Kays & Allison 2001). Within the arboreal vertebrate fauna of the tropics research is unevenly distributed across taxa, with mammals (especially primates) and birds receiving the most attention. There have been very few studies of arboreal reptiles and amphibians in tropical environments (Kays & Allison 2001), despite the tropics containing the majority of species in these two taxa (Vitt 1987). Most major snake lineages include both tropical species and arboreal specialists (Lillywhite & Henderson 1993). The independent evolution of arboreality in snakes from separate lineages has been accompanied by striking convergence in morphology, ecology and behaviour (Lillywhite & Henderson 1993), presumably reflecting similar ecological pressures. In Australia all snake families include species with arboreal and tropical representatives, with these traits most pronounced in the Australian pythons (Greer 1997). In general, arboreal species have attracted less scientific attention than their terrestrial counterparts, presumably due to logistic constraints (Bell et al. 1991). Radio-telemetry offers a solution to this problem, and can provide insights into otherwise cryptic, arboreal species (Fitzgerald et al. 2002; Webb & Shine 1997a).

In this study I used radio-telemetry to examine the sexual and age related differences in spatial ecology and movements of the green python (*Morelia viridis*: Pythonidae) - a rainforest species restricted to New Guinea and northern Cape York Peninsula, Australia (O'Shea 1996). *M. viridis* is a small ambush predator (maximum of 1.6 m) and the most arboreal species in the genus *Morelia* (Greer 1997). *Morelia viridis* shows complete ontogenetic colour change with juvenile individuals changing from either yellow or red to green adults, with the change for yellow individuals occurring between 55-60 cm (Chapter II). *Morelia viridis* shows one of the most striking examples of ontogenetic colour change, and determining whether or not differences exist in the ecology of the two colours morphs is an important step in understanding the evolutionary significance of this change. The underlying reasons for ontogenetic colour change are not yet well understood, yet this phenomenon occurs in a wide range of species (Booth 1990).

Five other *Morelia* species occur from southern Australia to New Guinea and the east Indonesian Archipelago (Greer 1997), and range in habitat from cool temperate to tropical environments. One species of *Morelia* has been intensively studied (*M.*

spilota; (Heard et al. 2004; Pearson et al. 2005; Shine & Fitzgerald 1996; Slip & Shine 1988b), while preliminary studies have been undertaken on a second species (*M. kinghorni;* Fearn *et al* 2005, A. Freeman *pers. comm.*). Both species are primarily large and terrestrial (Greer 1997), with the studies done in temperate (*M. spilota*) or subtropical environments (*M. kinghorni*). These studies can be used to contrast my results from a tropical arboreal species with those from closely related, yet ecologically dissimilar species.

Here I present data that reveal unexpected sexual and age-related differences in the home range and movement patterns of *M. viridis* that may be typical of tropical, arboreal snakes. This study is important because it highlights differences with closely related, yet more temperate and terrestrial taxa. It also provides important information on juvenile snake behaviour, which is generally lacking when compared to adult behaviour of the same species.

Methods

Study site

This study occurred in Iron Range National Park on Cape York Peninsula, in north-eastern Australia (12°45`S, 143°17`E, see Figure 3 in Chapter II). Within this park there is about 500km^2 of lowland tropical rainforest in a complex mosaic with eucalypt woodland and heath (Neldner & Clarkson 1995). Mean annual rainfall for the park is 2123 mm (Bureau of Meteorology 1957-99 average) with most rain falling during a distinct 'wet' season from December to April.

Radio-tracking

Individual pythons were found by spotlighting, and surgically implanted with radio-transmitters (models SB-2 and BD-2G - Holohil Pty Ltd, Canada) by a veterinary surgeon (Peter Barrett – Marlin Coast Veterinary Clinic) following the procedure of Webb and Shine (1997b). Transmitters weighed 5 g (SB-2) or 1.85 g (BD-2G) for green and yellow individuals respectively, and were always <5% of body mass for any individual (2.3 - 4.4% and 0.8 - 5.0 % of body mass for yellow and green individuals respectively). All individuals were released at their point of capture within 72 hours. I located individuals with an ICOM-R10 receiver and Yagi 3-stage antennae (Biotelemetry Pty Ltd, Adelaide). Individuals were located up to twice each 24 hours for the period November 2002 to April 2004. All radio-tracking was done in semi-deciduous vine forest or adjacent transitional vegetation (*sensu* Neldner and Clarkson

(1995)). Individual pythons are typically active for short periods - between 6-8pm when they move from their day resting sight to their ambush site, and between 4-8am when they return to a resting posture (Chapter IV). Active individuals were never observed outside these times, and no individuals changed their resting site during the day, nor hunted at more than one location in a single night. Hence, consecutive fixes of an individual were always separated by a potential activity and location change. The order in which animals were tracked both within and among days was changed to avoid temporal autocorrelation in the data (Harris et al. 1990). Each location was marked with flagging tape and its position recorded with either a GPS (Garmin 12XL), or by using the distance and bearing from either previous locations or prominent landmarks. Due to their arboreal nature, individuals were often concealed from my view, either by foliage or because they were too high to be observed, when I estimated its location. If a new location for a concealed individual was within one metre of the previous location I considered that it had not moved. I report home range and movement results in two dimensions only, despite *M. viridis* being arboreal and operating in a three dimensional space. During radio-tracking I rarely recorded individuals close to the ground during the day, and often they were too high to observe and determine vertical position. Chapter 3 shows that individuals use all vegetation strata from the ground to the canopy, however this is not represented in the data. Similarly the movement distances were reported as if locations were on the same plane, rather than in three dimensional space. As I have no information on the relative heights at each location, true distances cannot be calculated. In this paper I used the two colour categories yellow and green to define different groups of *M. viridis*. Individuals change from yellow to green at approximately 55 centimetres SVL (Chapter II), however males do not mature until 84 centimetres, and females not until 99 centimetres (Shine & Slip 1990).

Data analysis

The presence or absence of a home range was determined with incremental area analysis using the 95% isopleths of the minimum convex polygon with a harmonic mean peel centre. I considered that an individual had a home range if the incremental area plot reached a plateau of at least 80% of final home range area (Rose 1982; Stone & Baird 2002), and I used the beginning of the plateau as the minimum number of fixes required to establish the home range. Visual examination of the data showed that individuals did not repeatedly use ‘core’ activity areas (*sensu* Harris *et al.* 1990) so the total home range of each individual was calculated using 100% minimum convex polygons . All home range analysis was done using the RANGES 6 computer program (Kenward et al. 2003). The relationships between home range size, snout-vent length (SVL), month and sex were examined using a generalised linear modelling approach. In all cases residuals were examined to confirm that data were normally distributed, otherwise data were transformed to achieve normal distributions. As data from green males did not suggest a home range, I generated a sequential movement path. Home range overlap between pairs of green female *M. viridis* was determined using the 100% minimum convex polygons, while visual comparison between green male movement paths and green female home ranges was used to determine overlap between the sexes. Figures and movement paths were generated in ArcView GIS Version 3.1 with the Animal Movement Extension (Hooge et al. 1999).

I based the movement analysis on consecutive day fixes only, as longer intervals between fixes may underestimate daily movements. Consecutive fixes may also underestimate movement distances if individuals return to the same resting site after a period of movement. I observed green pythons re-using particular sites, however movements between these fixes were only in the vertical plane (descending to the ground and returning). Within this study, individuals never returned to a specific location after using a new site. As my data entailed repeated measures of individual snakes I avoided pseudo-replication by fitting generalised linear mixed models incorporating the random factor "individual" in addition to the fixed variates and factors of interest. In all models both 'season' and 'year' were co-linear with 'month', therefore only 'month' was included in analyses.

I analysed movement in two ways. First, I analysed movement distances. Variables of interest in both analyses were SVL, the month and sex of the snake. All variables were removed sequentially from a fully factorial design to determine their significance. Movement distance was analysed with a linear mixed model, testing for the effects of SVL, month and sex. As the residuals were not normally distributed, distances were transformed using natural logarithms to obtain a better fit to the data.

Second, I examined whether or not an individual stayed in the same location between consecutive records (movement frequency). Movement frequency was analysed by defining the number of observations per month in which the snake moved as a proportion of the total observations. This was the response variable in a generalised linear mixed model with a binomial error distribution and logit link function. All analyses were carried out in Genstat 8 (Genstat-Committee 2005).

Results

Between November 2002 and April 2004 I recorded 2178 fixes from 27 pythons (9 green and 1 yellow male, 12 green and 5 yellow females, Table 2). This period encompassed two wet seasons and the intervening dry season. Individuals were tracked for a mean of 143 days (range 15-449), with a mean of 80 fixes (range 9-251) per individual. Three individuals were monitored for the whole study, while all others were monitored for at least a single wet season. I did not detect any female reproductive activity (egg formation or laying) during the study.

Table 2. Individual green pythons *Morelia viridis* radio-tracked during this project

Snake ID	Sex	Colour	SVL[†] (cm)	Mass (grams)	Capture date	Tracking duration (days)	Number of fixes
Gladys Sym Choon	F	Yellow	51.5	46	2-Jan-03	27[‡]	15
Judith	F	Yellow	51.5	51.5	21-Nov-02	6[‡]	11
Hepzibar	F	Yellow	51.7	42.5	9-Jan-03	86	62
Xanthippe	F	Yellow	52.4	52	21-Dec-03	58	67
Elephant	F	Yellow	56.0	68	2-Dec-02	65	83
Yellow females – means ± s.e.			**53.1 ± 0.9**	**52.3 ± 4.4**		**69.7 ± 8.4**	**70.7 ± 6.3**
Thor	F	Green	62.7	81	9-Jan-03	86	62
Vera Lynn	F	Green	70.0	99	3-Jan-03	132	51
Limburger	F	Green	81.6	177	31-Jan-04	10[§]	9
Utopia	F	Green	82.0	143	15-Oct-03	195	144
Chesterfield	F	Green	92.2	254	19-Jan-03	188	78
Ra	F	Green	96.0	284	16-Jan-03	132	60
Pont L'Eveque	F	Green	96.3	238	31-Jan-04	56	55
Pleasure Machine	F	Green	102.0	281	2-Dec-02	180	94
Zarniwoop	F	Green	102.3	258	19-Jan-03	119	57
AntiChrist	F	Green	111.5	472	9-Jan-03	444	130
Drench	F	Green	115.0	515	7-Jan-03	142	83
Tilsit	F	Green	142.0	617	7-Jan-04	89	65
Green females – means ± s.e.			**96.1 ± 6.2**	**284.9 ± 48.5**		**160.3 ± 31.3**	**79.9 ± 9.4**
Cookie Monster	M	Yellow	55.8	67	21-Dec-03	60	54
Yellow males - mean			**55.8**	**67**		**60**	**54**
Manhattan	M	Green	72.5	115	9-Jan-03	198	87
Ilchester	M	Green	87.8	152	31-Jan-04	61	57
Quinquervina	M	Green	88.0	189	28-Oct-03	154	133
Brian	M	Green	89.4	229	9-Jan-03	445	251
Faislabad	M	Green	91.4	237	13-Jan-03	79	44
Wensleydale	M	Green	95.0	268	4-Jan-04	86	73

Wonko the Sane	M	Green	98.5	301	9-Jan-03	129	57
Kubla Khan	M	Green	103.0	421	16-Jan-03	438	194
Rasputin	M	Green	105.8	445	21-Dec-03	108	102
Green males – means ± s.e.			**92.4 ± 3.3**	**261.9 ± 37.5**		**188.7 ± 49.7**	**110.9 ± 23.4**

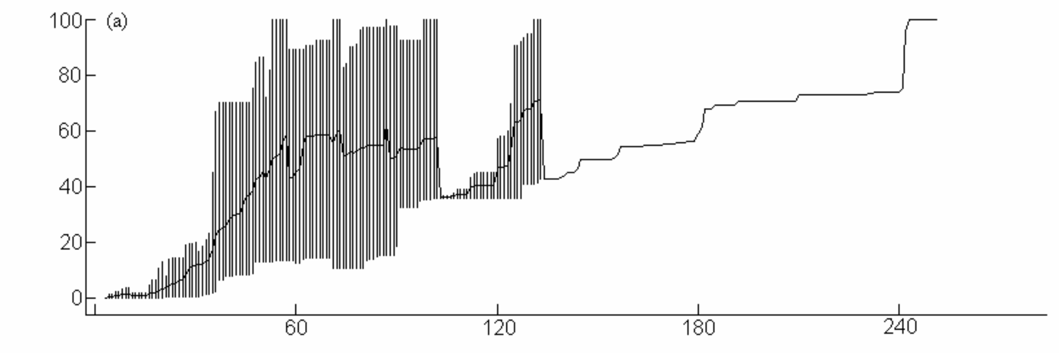
[†] SVL, snout-vent length.

[‡] These transmitter failed earlier than expected.

[§] This individual was killed by a predator.

Home range

An incremental area plot will plateau when enough fixes have been reached to establish a home range (Kenward et al. 2003). For green females this plateau was reached after approximately 60 fixes (Figure 11b). However it was not reached in green males or yellow individuals (Figure 11a and 11c), suggesting that neither group has a stable home range. The male plot appeared to plateau after 60 fixes, but only at 50% of the total home range, less than the 80% suggested by Rose (1982) and Stone and Baird (2002) to indicate a home range. One green female with insufficient fixes to reach a home range plateau was excluded from further analyses. Green female home range was 6.21 ± 1.85 ha (mean ± SE). This was significantly correlated with snout-vent length ($F_{1,10} = 6.46$, $P = 0.029$).



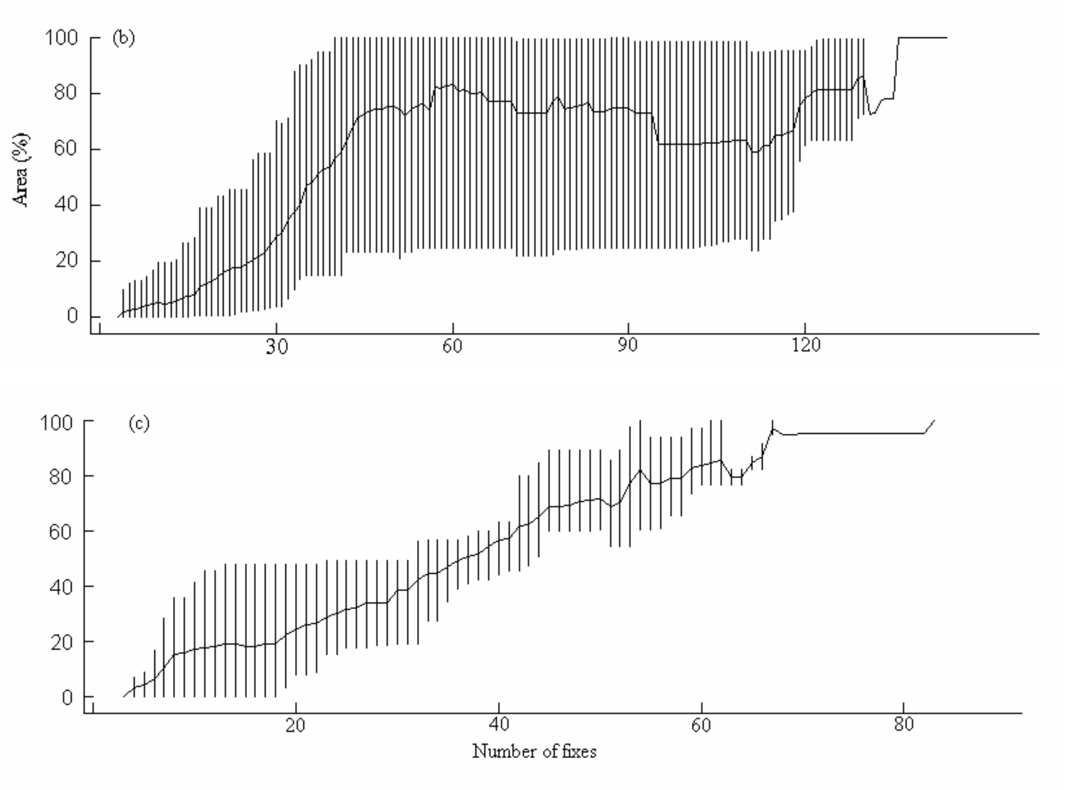


Figure 11. Incremental area plots for *Morelia viridis* home ranges: (a) green males, (b) green females, and (c) yellow individuals.

These analyses exclude individuals with less than 20 locations. Note the three graphs have different scales for the x-axes, due to differences in transmitter life between groups. The solid line represents the mean home range area as a percentage of final home range for all individuals, while the vertical lines are the 95% confidence intervals associated with the mean at each fix.

There was considerable overlap in the home ranges of green females with the movement paths of green males and yellow individuals (Figure 12). Radio-tracked green females used a combined total area of approximately 100 hectares. Of 10 pairs of radio-tracked green females whose home ranges overlapped, each shared 25 ± 11% (mean ± s.e) of its total home range. Of two green females that I radio-tracked for long periods, one showed 82% home range overlap, while the other's home range was 100% within another female's home range. I also found other untracked green females within the home ranges of radio-tracked individuals suggesting that the home range overlap reported here is an underestimate. When a radio-tracked green female had a yellow individual within its home range, the green female encompassed 66% ± 16% (mean ± SE, range 17 – 100%) of the yellow individual's activity areas. During the tracking period 3.3 ± 0.5 (mean ± SE, range 2 – 4) radio-tracked green males passed through a green females' home range. I caught other green males within the home range of green females and therefore the number of males passing through a female's home range reported here is also an underestimate.

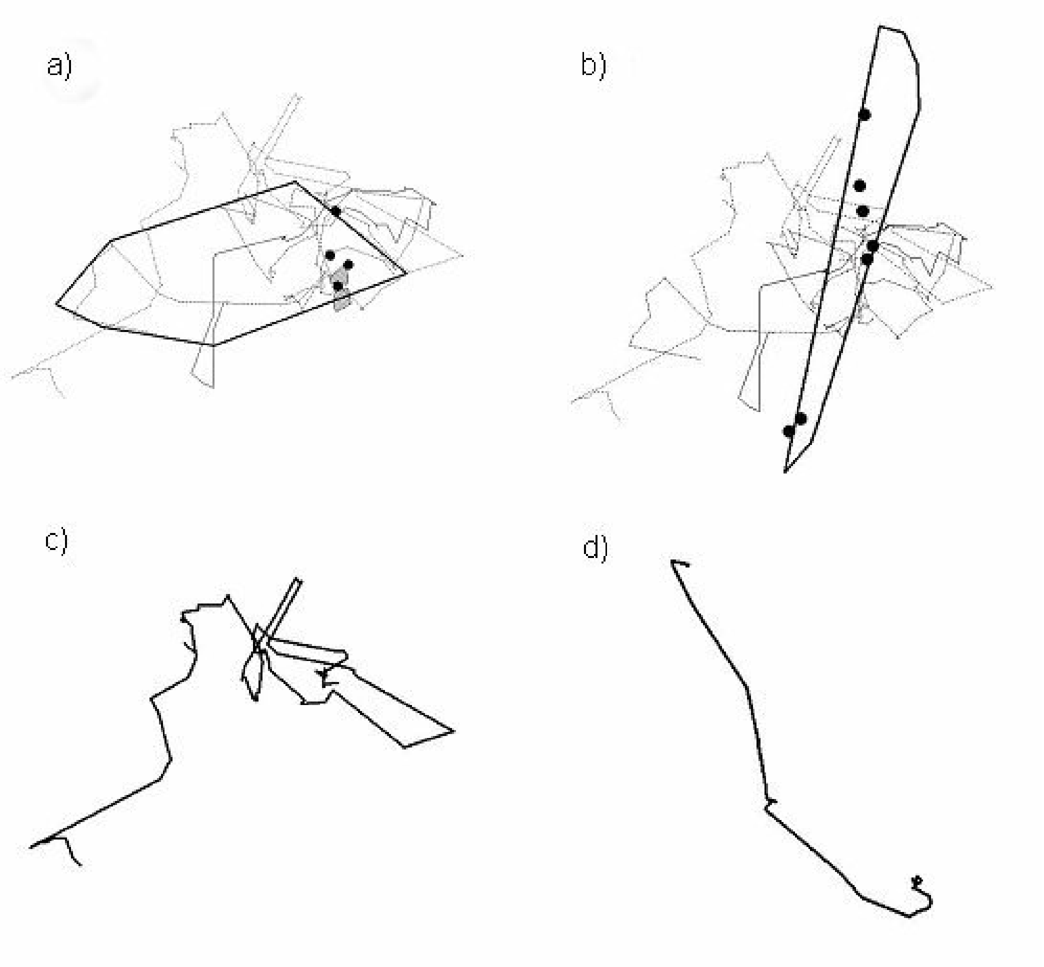


Figure 12. Home range areas of four radio-tracked individuals.

Two were green females a) Tilsit, and b) Drench (enclosed polygon). Also shown are the movement paths of three green males (thin lines), activity areas of two yellow individuals (shaded polygons) and other individuals (dots) found in their home ranges during the radio-tracking period. Movement paths of two green males c) Kubla Khan, and d) Ilchester.

Movement

Movement distance. The distance travelled between fixes by an individual was significantly affected by a three-way interaction between sex, month and SVL (Table 3).

For most months there were no differences in movement distances between individuals, however this was not always the case for different month/sex combinations.

Table 3. Results for the generalized linear mixed model testing movement distances of individual *Morelia viridis*. Terms were added sequentially to the fixed model

Effect	X^2	DF	P
SVL	14.28	1	<0.001
Month	12.85	9	0.169
Sex	0.40	1	0.525
SVL.Month	6.01	9	0.739
SVL.Sex	0.09	1	0.766
Month.Sex	30.91	8	<0.001
SVL.Month.Sex	29.95	7	<0.001

During the wet season larger females moved further in February than in other months (Figure 13a), while larger males moved further in January and March (Figure 13b). During the dry season movement distances varied more between individuals than during the wet (compare the error bars in Figure 13c and 13d with those in 13a and 13b respectively). Distances moved for all individuals in most months varied from 3 – 23 metres per move (values back transformed from predicted means). In January, February and March however the average maximum distance moved increased to approximately 50 metres. The data were highly skewed, with only eight of 1057 consecutive movement records being greater than 100m, while there were 753 records of movement less than 10 metres. There were 377 records of no movement between consecutive daily locations. When individuals moved resting locations, it was typically far enough away for the move to be detectable. This avoided the potential confounding effects of detecting a movement when there was none, or not detecting a true movement. The furthest recorded move in a single night was 182 metres for a male, and 180 metres for a female. Individuals often hunted on a series of consecutive nights in exactly the same location, before moving to a new location. One male spent 28 days in the canopy of a single Bamaga Satinash (*Syzigium bamagense*) during the tree's flowering period. If this tree had fallen over it would have made a very large noise, even if no-one was there to hear it (Jones & Allen 2002). Other individuals spent extended periods of time in a single tree. The typical movement pattern for *M. viridis* was a sequence of two to four days of movement alternating with a few sedentary days (Table 4). Although not analysed statistically this trend was more obvious in larger individuals, and seemed to occur more during the wet than the dry season.

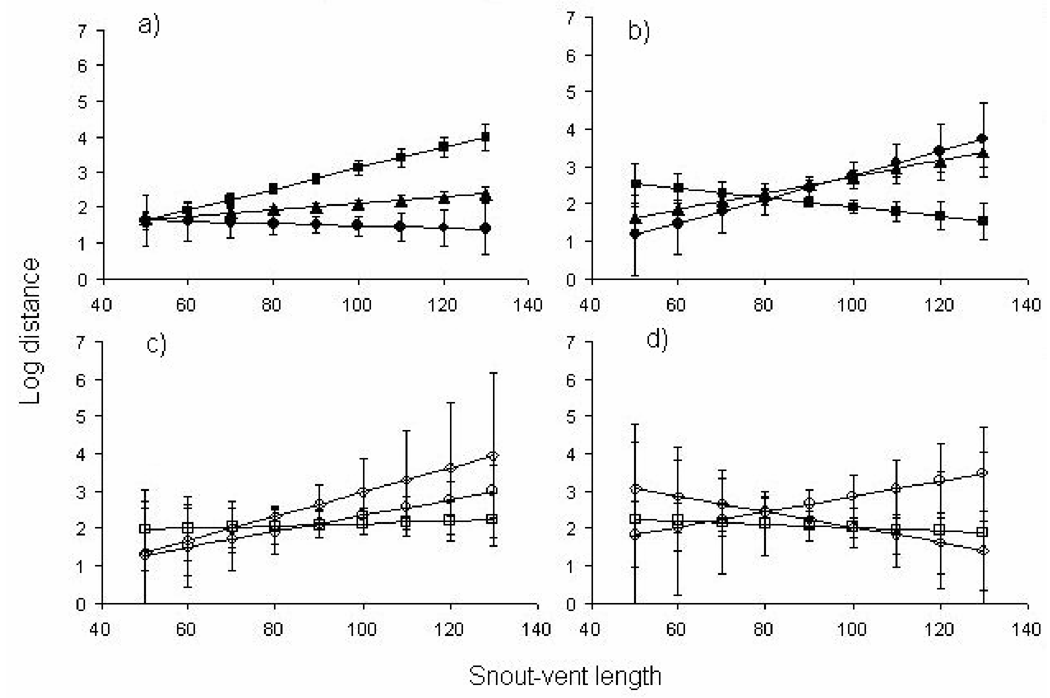


Figure 13. Predictions of the natural logarithm of distance moved for individual snakes at various times of the year.

Predictions reflect the significant interaction between x, y and z. (a) females, and (b) males during the wet season. The three lines represent January ▲, February ■ and March ●; (c) females, and (d) males during the dry season. The three lines represent the months of May ○, September □, and November ◊. Standard errors are shown.

Table 4. Selected daily movement sequences for four *Morelia viridis* at Iron Range National Park.

Individual	Movement distances (metres)
Antichrist (F)	0, 0, 70, 56, 16, 3, 5 and 0, 0, 60, 21, 0, 0
Brian (M)	0, 0, 94, 21, 42, 0, 0 and 0, 0, 42, 28, 85, 0, 0
Kubla Khan (M)	0, 0, 8, 142, 0, 0 and 0, 11, 39, 28, 28, 3, 5
Pont L'Eveque (F)	0, 32, 39, 2, 0, 0 and 0, 7, 2, 9, 65, 25, 3, 0

Movement frequency. Females were significantly more likely to move between consecutive days (proportion of consecutive records where no movement occurred, females 0.31, males 0.45, $X^2_1 = 5.47$, $P = 0.019$). This probability was independent of both the size of the individual ($X^2_1 = 0.49$, $P = 0.520$) and the month ($X^2_8 = 12.68$, $P = 0.123$)

Discussion

My study is one of the few to provide home range data for a tropical, arboreal snake. The data revealed two notable aspects of the ecology of *M. viridis* that may have broader implications for snakes in general. First the two sexes of *M. viridis* adopt different movement strategies, with green females having a home range and males 'roaming' across the landscape. This applied to all adult males, rather than a small subset of individuals. This sexually divergent strategy has not been reported previously for either of the other intensively studied *Morelia* species (Fearn et al. 2005; Slip & Shine 1988b), and to my knowledge has not been conclusively shown in any other snake species since the review of Parker and Plummer (1987). Second my data contributed detailed information on the movement patterns of juvenile snakes, which are unknown for most species. Yellow *M. viridis* moved as often as green individuals, and for comparable distances most of the year, despite being considerably smaller. They also lacked a home range, presumably as they were dispersing from their hatching site.

Home range

I used the criteria that defined a home range to exist when an incremental area plot plateaus at greater than 80% of the range area asymptote (Rose 1982; Stone & Baird 2002). I found that green females did have a home range, while both green males and yellow individuals did not. The average green female home range size of 6.21 ha is well within the range of home range sizes reported for other snake species (Macartney et al. 1988). The home range for female *M. viridis* is considerably smaller than the home range reported from the closely related *M. spilota* where females had a mean home range of between 11 and 37 hectares (Shine & Fitzgerald 1996; Slip & Shine 1988b). This difference is not unexpected as *M. spilota* are typically much larger as adults (Shine & Slip 1990) and use a correspondingly larger area (Jetz et al. 2004).

The apparent absence of a home range in male *M. viridis* is in contrast to findings for most snakes, and specifically the other two studied *Morelia* species. Due to the number of individual males radio-tracked and the duration of the study I believe this result to be a true indication of their movement pattern, rather than an artefact of small sample size or limited tracking duration.

Males of both *M. spilota* and *M. kinghorni* appear to have established home ranges (Fearn et al. 2005; Pearson et al. 2005; Slip & Shine 1988b). The comparison between male movement patterns in *M. viridis* and *M. kinghorni* is particularly interesting. Both species occur in the tropics, however *M. kinghorni* reaches far greater sizes, is more often active during the day and is not as arboreal as *M. viridis* (Fearn et al. 2005; Greer 1997).

In a review of snake home ranges, Macartney *et al.* (1988) found that all studies reported home ranges for all categories examined (either males and females separately, or both sexes together). Since that review, one study on water pythons *Liasis fuscus* in Australia has reported the absence of home range (Madsen & Shine 1996b). For this species neither sex had a stable home range, which the authors attributed to seasonably variable prey abundances. The main prey for *M. viridis* at Iron Range (*Rattus leucopus* and *Melomys capensis*) occur at high densities year-round (Leung 1999b, c) so variable prey density is unlikely to explain the lack of a home range in males.

My data suggest that green *M. viridis* males may be conforming to a ‘roaming’ strategy (Sandell & Liberg 1992), which predicts that under some combination of conditions males may have a greater reproductive benefit by not maintaining a home range. Specifically, Sandell and Liberg predict that roaming is favoured when males have a high search efficiency, there is a low sex ratio in the population, females have a long receptive period and there is a low level of male-male combat (Sandell & Liberg 1992). This male strategy may also occur in the snake *Nerodia sipedon*. Brown and Weatherhead (1999) found that male home range size increased with tracking duration and were smaller where there were greater densities of females.

As territorial defence is rare in snakes (Gregory et al. 1987), the overlap between the home range and movement paths of individual *M. viridis* was not surprising. Individuals of many snake species display widely overlapping home ranges (Gregory et al. 1987; Webb & Shine 1997a), however few studies have quantified this overlap (Macartney et al. 1988). Despite the high overlap I never recorded interactions between monitored individuals, and only once did I record two individuals within five metres of one another.

Movement

In most months there were no differences in movement distances between the sexes, nor for individuals of different lengths. During the wet season (January, February and March) however, movement distances were affected by the size and sex of the individual, with larger individuals moving considerably further between consecutive locations than smaller individuals. I suggest seasonal differences in movements relate to mate searching. Although I did not detect any reproductive activity (enlarged ovaries or egg laying) during the study, other studies have reported increased movements during the breeding season (Brito 2003; Brown & Weatherhead 1999; Madsen 1984). Females have also been shown to increase their movements to reach oviposition sites (Madsen 1984), although none of the radio-tracked individuals were detected to have laid eggs. These increased movements may also relate to food resources or temperature as has been shown on other reptiles (Christian et al. 2003; Madsen & Shine 1996b).

During the dry season there was considerable variation in movement distances between individuals. Although green pythons are active year round some individuals may be reducing their activity in the dry season. This contrasts with the behaviour of the water python *Liasis fuscus* in tropical Australia which was encountered much more frequently in the dry than the wet season (Brown et al. 2002).

Movement distances recorded for *M. viridis* were similar to those reported for *M. spilota* in temperate Australia, and interestingly both studies reported longer movements in the spring and summer (Shine & Fitzgerald 1996; Slip & Shine 1988b). In both studies on *M. spilota* increased movements in spring and summer were in part attributed to warmer environmental conditions in addition to mate searching (Shine & Fitzgerald 1996; Slip & Shine 1988b). Lemon curry. My results are also comparable with those of other ambush predators (Brito 2003; Diffendorfer et al. 2005; Slip & Shine 1988b), but markedly less than daily movement distances for active foragers (Macartney et al. 1988). The regular movement sequence I recorded for *M. viridis* has also been reported for *Vipera latastei* by Brito (2003), who observed this pattern of movement only during the mating season. Although the mating period of *M. viridis* is unknown, I recorded this movement pattern more often in the wet season, supporting my suggestion of mate searching during this time.

I can offer no obvious reason why females move more often than males, and no other study has reported a similar result (Diffendorfer et al. 2005), although intersexual differences in movement frequency are rarely tested in snakes (Macartney et al. 1988).

Yellow versus green

There is very little information comparing juvenile and adult snakes of the same species, mainly because their cryptic nature and size limit the methods available to study them. This study is one of the few to radio-track juvenile snakes. I found no evidence of a home range for yellow *M. viridis*, supporting the hypothesis that juveniles are the main dispersal phase for most snakes (Greenwood 1980). Movement rates for yellow *M. viridis* were equal to those of green individuals of both sexes for most months, despite potentially large size differences (up to a three-fold difference in length). Webb and Shine (1997a) also found equal movement distances between juveniles and adults in the snake *Hoplocephalus bungaroides.* In contrast, movement distances increased with age for *M. spilota* (Pearson et al. 2005).

All yellow individuals in this study were found in edge habitats or in canopy gaps created by treefalls and never inside the closed-canopy rainforest. Although I found that yellow individuals moved the same distances as adults, their movements were probably restricted to these edge habitats. One individual that changed from yellow to green during radio-tracking moved only into the closed-canopy rainforest when it turned green. Although we are yet to understand the evolutionary significance of ontogenetic colour change in *M. viridis,* differential habitat use such as that reported here may prove important. In other species ontogenetic colour change has been closely linked with camouflage from both prey and predators (Booth 1990).

Conclusion

My study has yielded rare data on the movement patterns of a tropical, arboreal snake species, and revealed contrasts with more terrestrial and temperate species. I found sexual differences in ranging behaviour. Adult females have a home range, whereas males adopt a ‘roaming’ strategy probably in search of mates. Although reported in other vertebrate taxa (Magnusson & Kasuya 1997; Sandell & Liberg 1992), I know of no other snake species with this dichotomous movement strategy (Parker & Plummer 1987). Juveniles moved distances comparable to adults in most months despite large size differences, but occurred in rainforest edge habitat rather than within the closed-canopy rainforest. Future studies are required on tropical and arboreal snake species to determine whether the sex and age related patterns shown for *M. viridis* are typical of tropical or arboreal species.

Chapter IV

Foraging ecology and diet of an ambush predator: the green python *Morelia viridis*

Wilson (2007) *in* Biology of the Boas and Pythons (eds Henderson and Powell) Eagle Mountain Publishing. Eagle Mountain, USA.

Abstract

The foraging ecology and diet of a species is an important component in determining its community niche. Here I report on these aspects of the ecology of the green python, *Morelia viridis*, a popular species in the captive pet trade but which is little known from the wild. Green pythons were intensively monitored in northern Australia over two seasons to determine their diet and foraging behaviour. They were obligate ambush predators and consumed a variety of small reptiles and mammals, invertebrates and birds. They showed an ontogenetic shift in diet from small to larger species and from diurnal to nocturnally active prey and ontogenetic shifts in the time of day that individuals hunted and the location and characteristics of ambush sites both of which occurred concurrently with an ontogenetic colour change from yellow to green. Yellow individuals hunted equally as often during the day as night, and did so from an arboreal ambush site. Green individuals hunted almost exclusively nocturnally, and did so from both arboreal and terrestrial ambush sites. The diameter of perches used was greater for females than males, when in ambush posture compared to resting, and increased with the size of the snake. Yellow individuals were usually found within 10 metres of the ground, while green individuals used the whole vegetation strata, and were often found in the canopy (>25 meters). Green pythons appear to be fairly typical python that shows ontogenetic changes in diet with size, in conjunction with changes in ambush site preference and characteristics.

Introduction

Most ecological studies are underpinned by an understanding of the trophic relationships of a species, however much of this literature consists only of lists of prey items from dissected museum specimens (de Quieroz et al. 2001; Mushinsky 1987; Stafford 2005). One aspect of foraging ecology that cannot be determined purely from museum specimens is the foraging strategy used to capture prey. All species' foraging behaviour can be classified along a gradient between active foraging and sit-and-wait predation (Pianka 1966), and snakes cover the entire spectrum of foraging behaviours (Mushinsky 1987; Perry 1999). Understanding where a species lies on this continuum is an important first step in understanding various ecological correlates associated with foraging mode (Huey & Pianka 1981; Secor & Nagy 1994).

Foraging strategies may be altered in response to change in a range of factors including their size, food availability and habitat (Henderson 1993a; Huey & Pianka 1981; Savitzky & Burghardt 2000). Snakes are ideal to study changes in foraging behaviour as body size can vary by an order of magnitude in a population, and may be the most important influence on foraging mode. As snakes are gape-limited predators (Arnold 1993), any increase in size may make a different suite of prey available. Newly available prey species may be active at different times of day, in different habitats or have different activity patterns than prey taken by smaller snakes – all of which will affect the snakes' predatory behaviour. Predatory species use different strategies to maximize their hunting success. Active foragers increase the chances of encountering prey by preferentially searching in retreat sites used by their prey (Mullin & Cooper 1998; Yorks et al. 2003). In contrast, sit-and-wait foragers maximize prey capture by selecting appropriate ambush sites (Clark 2004; Shine & Li-Xin 2002). One fundamental characteristic of sit-and-wait predators is that they spend long periods in single locations (Reinert et al. 1984; Webb & Shine 1997a). Hence, the selection of an ambush site is vitally important as it may influence the rate of prey encounter and the probability of prey capture. However an ambush site that improves the capture of one species may not be appropriate for catching other species. Clearly, ambush predators should select locations with the highest probability of encountering the optimal prey for their size. Two examples include the timber rattlesnake *Crotalus horridus* that hunts at sites adjacent to fallen logs (Reinert et al. 1984), as these are an important runway for their mammalian prey (Douglass & Reinert 1982), and the carpet viper *Echis coloratus* which selects elevated ambush sites near water to maximise prey encounter (Tsairi &

Bouskila 2004).Ambush site selection may be constrained by other ecological pressures, including thermoregulation and the need to avoid predation (Tsairi & Bouskila 2004). The choice of the best ambush site may vary through an individual's life.

Here I examine the foraging ecology and ambush site selection of the green python *Morelia viridis* (Pythonidae), and how site characteristics alter according to the characteristics of an individual's size, colour and sex. The green python is relatively common in the lowland rainforests of New Guinea and northern Australia. This species is described as 'the most arboreal of the pythons' (Greer 1997), yet published reports suggest they eat a wide variety of taxa including terrestrial mammals, birds, lizards and invertebrates (Barker & Barker 1994; O'Shea 1996). They are obligate sit-and-wait predators (*sensu* Pianka (1966)), and may remain at the same ambush site for up to 14 days (author's observations). This sedentary foraging tactic makes them an ideal species for examining ambush site selection. In Australia, individuals are bright yellow at hatching, but then change colour to a vibrant green at approximately 55 cm (Chapter II). Various reasons have been suggested for ontogenetic colour change (Booth 1990), however few of these theories have been scientifically tested. Different colours may make some individuals more vulnerable to predation (Stuart-Fox et al. 2003), thus both the colour and size of the python may affect their choice of ambush site.

Methods

Study site

This study was undertaken in Iron Range National Park (hereafter Iron Range), on Cape York Peninsula, in north-eastern Australia (12°45`S, 143°17`E). Within this park there is *c*. 500 km^2 of lowland tropical rainforest that exists in a complex mosaic with eucalypt woodland and heath (Neldner 1999). Mean annual rainfall for the area is 2123 mm (Bureau of Meteorology unpublished data 1957-99) with most rain falling during a distinct 'wet' season from December to April. The dry season is also characterised by low minimum temperatures (often <20 C overnight).

Field methods

Individual pythons were surgically implanted with radio-transmitters by a qualified veterinary surgeon (Peter Barrett – Marlin Coast Veterinary Clinic, Cairns, Qld) following the procedure of Webb and Shine (1997b). Model SB-2 and BD-2G transmitters were supplied by Holohil Pty Ltd, Canada. Transmitters weighed 5 g (SB-2) or 1.85 g (BD-2G) and were always <5 % of body mass. In the field individuals were located up to twice a day (once each during the day and night) for the periods November 2002 – June 2003 and September 2003 – April 2004 inclusive with an ICOM-R10 receiver and Yagi 3-stage antennae (Biotelemetry Pty Ltd, Adelaide).

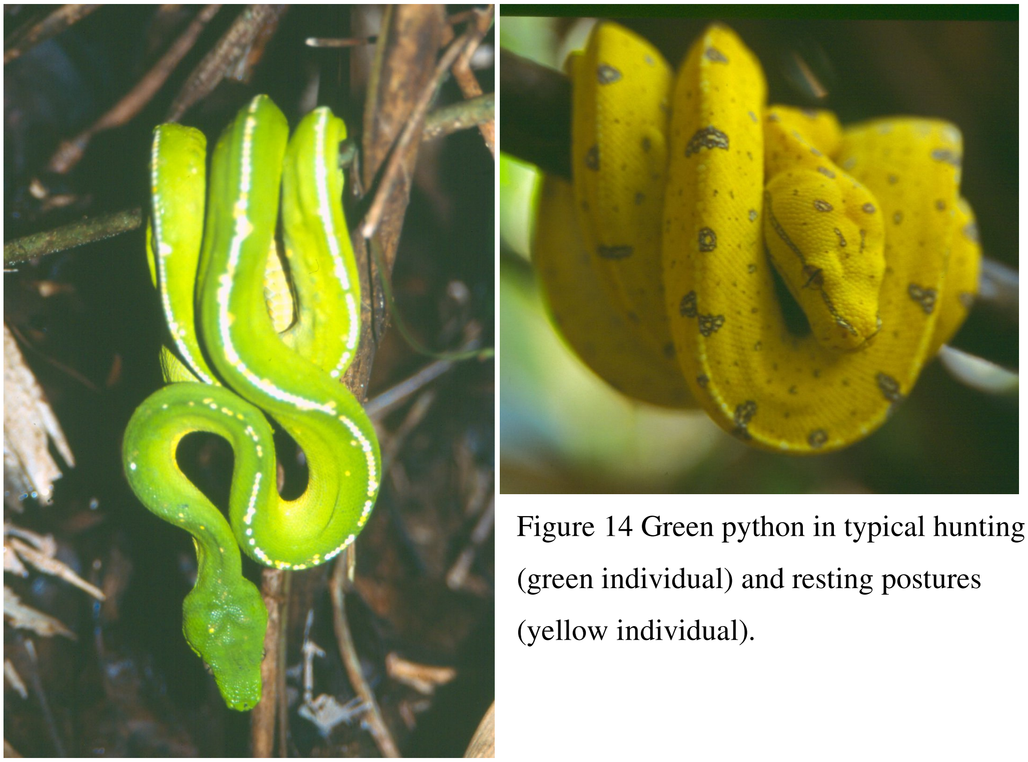


Figure 14 Green python in typical hunting (green individual) and resting postures (yellow individual).

Green pythons were often concealed from my view, either by foliage or because they were too high off the ground. If an individual was visible its posture, height above ground, perch type and perch diameter were recorded. An individual was considered to be hunting if its head and neck were in a strike posture (Figure 14), while resting individuals were typically in a tight coil with their head partially buried in the centre of the coils (Figure 14). It was always easy to differentiate between these two postures. Individuals were not palpated for prey; however scats were collected opportunistically and stored in 70% alcohol. Animal remains were identified to the lowest possible taxa. Green pythons typically moved between resting and hunting postures around dusk and dawn, and radio-tracking was not undertaken at these times. Green pythons were never seen to be active during the day, and individuals do not move between ambush sites during a single night. Reproductive activity was not observed during the study.

Data analysis

Analyses of movement and activity were carried out with a statistic modelling approach in Genstat 8 (Genstat-Committee 2005) on data from 27 radio-tracked snakes. By necessity, only data where the snake was actually seen could be used in these analyses, and records are biased towards activity occurring near ground level. For analyses that entailed repeated measures of individual snakes pseudo-replication was avoided by statistical models incorporating the random factor "individual" in addition to the fixed variates and factors of interest.

Individuals were allocated to one of three size classes based on their colour and maturity. Size class one included all yellow individuals, size class two included all immature green individuals (less than 84 cm for males and less than 99 cm for females), while size class three included all adult sized individuals (males 84 cm or greater, females 99 cm or greater (Shine & Slip 1990)).

Both proportion of time spent hunting (day and night) and the preference for using the ground as an ambush site were analysed using generalised linear mixed models with a binomial error distribution. Perch diameter was natural log transformed to achieve statistical normality and analysed in a linear mixed model. Variables of interest in all analyses were snout-vent length (for foraging time) or size class (all other analyses), time of day, posture and the sex of snake.

To determine hunting success the activity of individual pythons at their ambush sites was recorded using time lapse video. Individuals were located at dusk and video camera was placed nearby to record their activity for the night. Preliminary observations showed that individuals do not change their ambush site during the night so equipment could be left to record all night. The unit consisted of an infra-red camera (Jaycar product code QC 3468) linked to a video recorder (Hitachi VT L1200E Time Lapse Video Recorder), both powered by a 12v battery through an inverter. The video could record for 12 hours by slowing the frame speed. Seventy-eight hours of footage on five snakes was acquired in this fashion.

Results

Between November 2002 and April 2004 a total of 2178 locations were recorded from 27 pythons (10 males and 17 females, see Table 2 for details on these individuals). This period encompassed two wet seasons and the intervening dry season. Individuals were tracked for a mean of 143 days (range 15-449 days), with a mean of 80 fixes (range 9-251 fixes) per individual. Three individuals were radio-tracked for the whole study, while the remainder were radio-tracked during a single wet season and part of the intervening dry season.

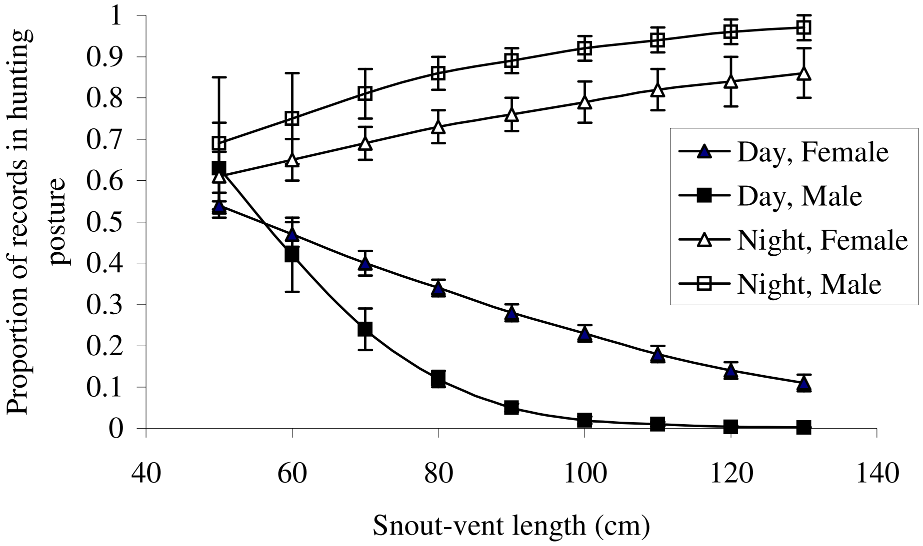


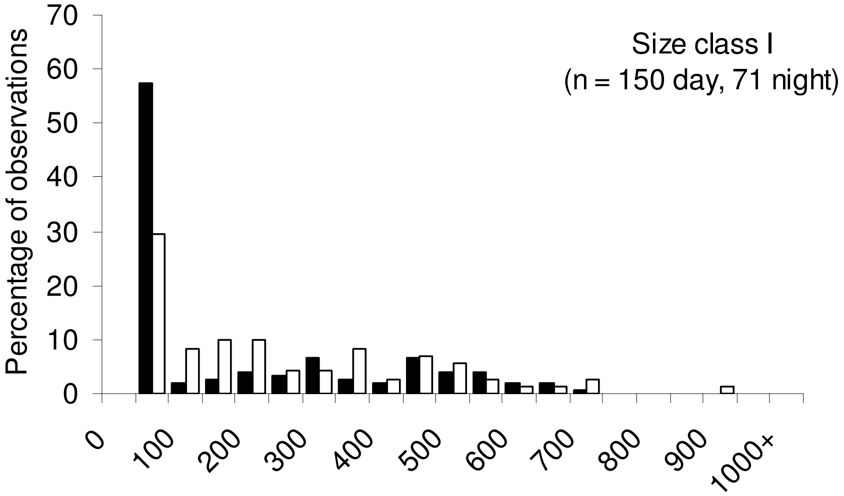
Figure 15. Proportion of times hunting out of all location records. Proportions are shown separately for sex and time of day.

Activity

The frequency that ambush postures were recorded was significantly influenced by the interaction between all considered variables - snout-vent length, time of day and sex ($\chi^2_1 = 6.41$, $P = 0.006$, $n = 1216$). Although they differed in their relative frequencies, both sexes hunted less during the day and more at night as they increased in size (Figure 15). Females were more likely to hunt during the day and less likely to hunt during the night than males of the same size, in all size classes greater than 50 cm. Once a male reached *c.* 100 cm it hunted mostly at night, while in contrast females continued to hunt during the day, independent of their size. Not every night record was of hunting for either sex - the maximum proportion of hunting compared with resting records was 0.97 for males and 0.86 for females (Figure 15). Lemon curry. No predictions were made for snakes longer than 130 centimeters as few individuals reached these lengths (see Chapter II).

Perch characteristics

The maximum height an individual could be from the ground and still catch terrestrial prey was considered the striking distance. For green individuals (size classes two and three) this was approximately 40 centimeters, while it was approximately 10 centimeters for yellow individuals. During the day 56 of 751 (7.5%) of green individuals were observed within striking distance of the ground, while 148 of 209 (71%) observations were at that height at night (Figure 16). For yellow individuals 90 of 150 (60%) observations during the day were of individuals within striking distance of the ground, while at night only 27 of 72 (38%) sightings were at that height (Figure 16). During the day yellow individuals were not observed 51 times (25% of 202 attempts), while green individuals were not observed 806 times (52% of 1559 attempts). At night yellow individuals could not be located 16 times (18% of 88 attempts), and green individuals 83 times (28% of 292 attempts). Trees were climbed during both the day and night to determine the activity of individuals that could not be observed from the ground. During both periods individuals were observed at heights of up to 25 meters in both resting and ambush postures. Individuals in ambush postures in the canopy had selected ambush sites adjacent to a branch or clump of flowers, and had adopted the same posture as when hunting close to the ground.



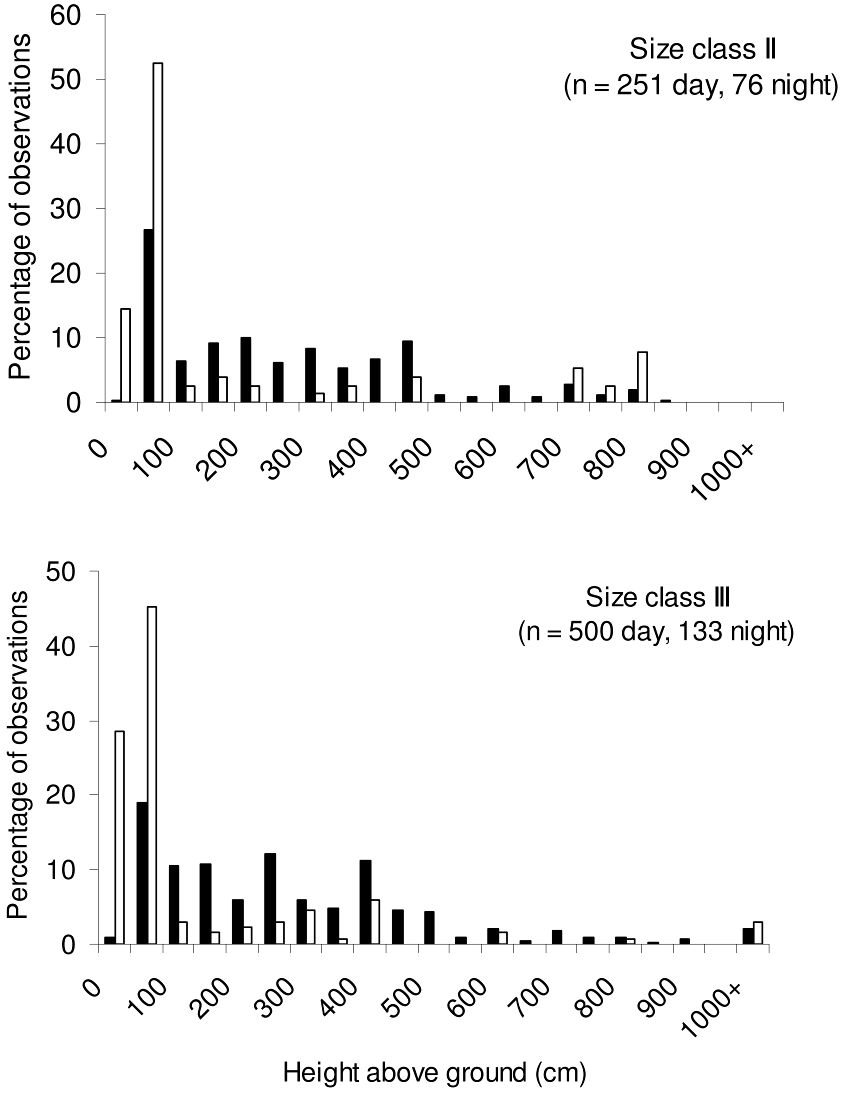


Figure 16. Perch heights for each size class of *Morelia viridis* at Iron Range National Park, Australia during the day (black columns) and night (open columns).

Although individuals of all three size classes were often found in ambush postures within striking distance of the ground, they differed markedly in their use of the ground as an ambush site (Figure 17). During the day only seven instances were recorded of individuals in ambush posture on the ground from 904 observations (<1%). At night 49 of 273 observations (18%) of individuals were recorded in ambush posture on the ground, but records were unevenly distributed among age classes. Yellow individuals never used the ground as an ambush site, immature individuals used the ground as an ambush site 15% of the time (11 of 73 observations), and adults 29% of the time (38 of 132 records).

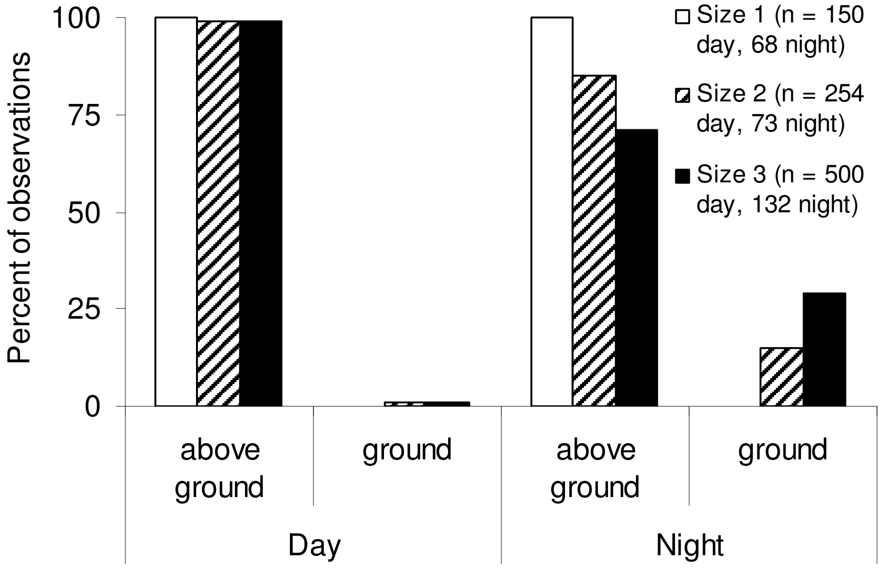


Figure 17. Relative frequency of locations for each green python size class that used the ground as perch substrate compared with above ground perches.

Sex, size class and posture all significantly influenced the diameter of perches used by green pythons (sex; $\chi^2_1 = 29.54$, p = <0.001, size class; $\chi^2_2 = 56.39$, p = <0.001, and posture; $\chi^2_2 = 19.95$, p = <0.001, n = 912), but there were no significant interactions between these factors (all interactions $p > 0.25$). In all cases females used perches of greater diameter than males despite a similar SVL to weight ratio (unpubl. data), perch diameter increased with the size of the individual and all individuals used perches of a greater diameter when they were hunting than when they were resting (Figure 18a and 18b).

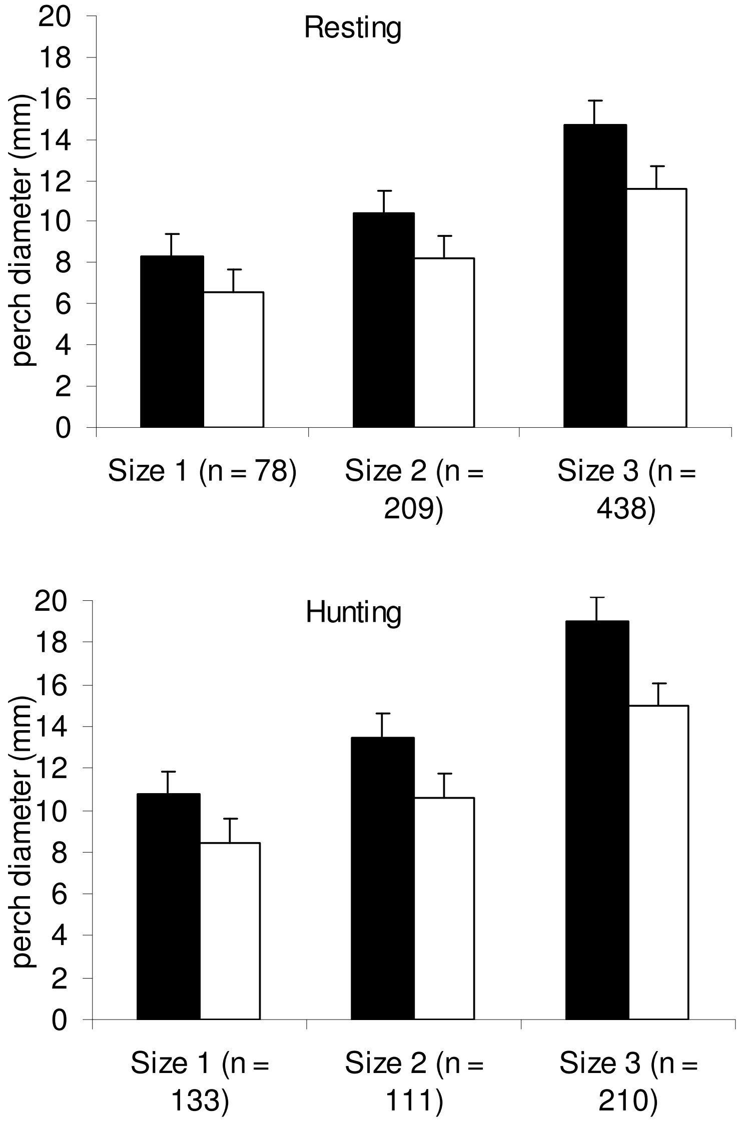


Figure 18. The diameter of the perch for resting and hunting green pythons *Morelia viridis* at Iron Range National Park. Females are shown as solid columns, males open columns. Error bars are standard errors of the differences.

Video

Four individuals were recorded over 10 nights for a total of 75 hours. In this time there were two successful feeding events – one of an unidentified small mammal and another of a moth (Table 5). Individuals remained in their ambush posture for a mean of 7.8 ± 3.8 se hours each night. On other occasions a northern brown bandicoot *Isoodon* *macrourus* and an unidentified snake passed within the strike zone of the green python, but in both cases the python did not respond.

Prey species and observed predators

Prey was recorded from 8 individual scats and one observation (Table 5). The most common prey item was *Melomys capensis*, recorded in five scats, while skinks and birds were both recorded in two scats. Mammals were only recorded in green individuals greater than 80 cms snout-vent length, while skinks were recorded in both yellow and green individuals greater than 51 cms. The two birds were consumed by a 120 cm SVL male and a 132 SVL female, and in both cases, feathers appear to be from adults rather than nestlings or fledglings. Invertebrate remains were recorded from a single scat. During fieldwork a single predation event was observed where a 55 cm yellow female caught a red-sided skink *Carlia longipes*, which was swallowed head first after a constriction of approximately 15 minutes.

Table 5. Prey items recorded from green pythons during this study and from other published records. Prey species were active diurnally (D) or nocturnally (N), snakes were either male (M) or female (F) and snake colour either yellow (Y) or green (G).

Species	Observations	Snake SVL, sex and colour	Reference
Mammalia			
Mammal sp.	1 (video)	142FG	This study, Greer (1997); Shine and Slip (1990)
Melomys capensis N	5 (scat)	80MG, 82FG, 87MG, 95MG, 120MG	This study, also Shine and Slip (1990)
Mus domesticus N			Shine and Slip (1990)
Rattus sp. N			Shine and Slip (1990)
Reptilia			
Skink sp. D	2 (scat)	51FY, 120MG	This study, also Greer (1997); Shine and Slip (1990)

Carlia longipes D	1 (observed)	51FY	This study
Emoia sp. D			Henderson (1993b)
Gekkonidae DN			Shine and Slip (1990)
Aves			
Unidentified birds DN	2 (scat)	120MG, 132FG	This study
Ptilorus paradiseus D			S. Irwin in Kend (1997)
Insects			
Lepidoptera DN	1 (video)	142FG	This study
Coleoptera DN	1 (scat)	51FY	This study

During radio-tracking a predation event on a green python was recorded for the first time. A large (approximately 100 cm) mangrove monitor *Varanus indicus* ate an 81.6 cm female green python. The snake's transmitter signal continued to emit from the goanna and the transmitter was subsequently collected from a monitor scat.

Discussion

Individuals could not be seen on a high proportion of radio-tracking fixes (956 of 2178 fixes). As these were concentrated at night and in the canopy they may have included behaviour that was not detected, although this appears to be unlikely. As green pythons are obligate ambush predators, resting, moving and hunting are the only behaviours relevant to foraging for this species (Maxwell 2003), and these were all recorded during the study. However, activities associated with reproduction were not observed during this study, and have never been reported from the wild. It is most likely that the proportions of each activity were biased towards those that occur near ground level and during the day. However, when individuals were found higher in the canopy their behaviour was consistent with that observed near ground level, but there were logistic constraints on the number of records that could be obtained this way.

There were strong differences in the heights that green individuals were found between the day and night, but not for yellow individuals. The few cases where yellow individuals could not be located were due to the density of the vegetation, rather than individuals being too high. Hence, yellow individuals appear to not use the full height of the vegetation, in contrast to green individuals which were found from the ground to the upper canopy.

Dietary analysis showed that green pythons eat actively foraging prey (Table 5) which they typically catch from stationary ambush sites. Although individuals of all sizes hunt for mainly terrestrial prey (Table 5), they do so in different manners. Yellow individuals never used the ground as an ambush site, while it was used by both immature and adult individuals. These differences in the frequency of ground use may represent differences in vulnerability among size classes or colour morphs. Large individuals may be better able to defend themselves from attack while in an ambush posture on the ground than yellow individuals. Larger individuals also hunt at night when a different suite of potential predators is active and may be able to use ambush sites on the ground without the risk of predation.

Green pythons appear to have low prey capture success rates as there was only one significant prey capture in 75 hours of footage. The successful capture rate for green pythons was considerably lower than for the active forager boid *Corallus grenadensis* where Yorks et al. (2003) recorded two predation events in 6.3 hours of observation, despite similar relative prey sizes for both species (this study, Henderson (1993b)). It is possible that the video equipment disrupted the normal activity of prey at the ambush site, but this is unlikely as the equipment was at least five metres away and a number of species were recorded in the field of view, none of which appeared to be affected by the camera. During intensive radio-tracking, individuals were rarely observed with an obvious stomach bulge that could represent a food item (unpubl. data), supporting the low rate of prey capture suggested by the video footage. Australian pythons have a very high digestive efficiency (Bedford & Christian 2000), and this low feeding frequency appears to be enough to maintain adequate levels of energy. In captivity male *M. viridis* have been recorded not feeding for up to five months, and females do not feed for the three months while pregnant (Maxwell 2003).

Despite the limited number of scats collected and only a single record of predation, green pythons eat a wide variety of prey (Table 5). Small individuals feed on reptiles and invertebrates (Table 5) which they catch during the day when both prey groups are active. Some invertebrates are active at night in the rainforest (primarily moths), and this may explain why small individuals hunt at night, when they are physically incapable of consuming most animals active at this time. Young green pythons appear to be unusual in their consumption of invertebrates as this has rarely been recorded in Australian snakes (Greer 1997). For individuals with a large enough gape, the Cape

York melomys *Melomys capensis* appears to be the main prey item (recorded from five separate scats). This species is common in the rainforest at Iron Range and is primarily nocturnal and terrestrial (Leung 1999b). It is an ideal prey for green pythons as it maintains a stable population year round, with a slight peak in December when young are recruited to the population (Leung 1999b). Although not recorded from scats there are two more nocturnal terrestrial prey that are potentially eaten by green pythons – *Rattus leucopus* and *Antechinus leo*. Both species are relatively common in the rainforest at Iron Range and are in the appropriate size range for green python prey (Leung et al. 1994). The identification of *M. cervinipes* in Shine and Slip (1990) as a prey species refers to *M. capensis* following the genetic study of Baverstock et al. (1980).

When green pythons change from diurnal to nocturnal foraging their diet changes accordingly. However the presence of bird feathers in the diet of larger individuals remains unexplained by this behaviour. As green pythons are obligate ambush predators they must encounter birds during the day when the birds are active. Additionally, most birds occur in the rainforest canopy (Kays & Allison 2001). The few green pythons observed in the canopy were in ambush postures adjacent to clumps of flowers. Presumably these individuals were waiting for birds that are attracted to the nectar and pollen of the flowers. This ambush site selection has also been reported for the bird eating python, *Morelia oenpellensis* (Barker & Barker 1994). Feathers in scats were from adult birds and not nestlings or fledglings, further supporting the suggestion that birds were taken while active rather than from a nest. Roosting birds may also be encountered and eaten opportunistically as green pythons move between their resting and ambush sites. There is a single record of a green python taking a paradise riflebird *Ptilorus paradiseus* in New Guinea (S. Irwin in Kend (1997)), but this record is doubtful due to the size of the bird compared with that of the python.
The mangrove monitor *V. indicus* is the only recorded predator of green pythons in the wild. As *V. indicus* is both diurnally active and arboreal (pers. obs.) the green python was probably eaten while resting during the day.

Larger snakes eat larger prey to maximise energy gains (Shine 1991). For *M. viridis* this corresponds to a shift from small, diurnal reptiles to larger, nocturnal mammals as the snakes increase in size (Table 5, Shine & Slip (1990)). The change from ectothermic to endothermic prey is common in many snake species (Mushinsky 1987; Pleguezuelos &

Fahd 2004; Shine & Slip 1990) and may result from biases in prey-swallowing ability, prey choice, the ability to capture and handle prey or encounter rates with prey of different sizes (Shine 1991). Few studies, however, have examined changes in foraging behaviour associated with a change in diet. Oregon garter snakes *Thamnophis atratus hydrophilus* show an ontogenetic shift in diet associated with changes in foraging behaviour (Lind & Welsh Jr 1994). Larger snakes increased the amount of active foraging (compared with ambush foraging) and used a wider range of habitats, resulting in individuals successfully catching larger prey (Lind & Welsh Jr 1994). Mushinsky et al. (1982) showed that two *Nerodia* species had ontogenetic shifts in diet, and inferred that there would be associated changes in foraging site and behaviour, however this was not tested.

Chapter V

The adaptive significance of ontogenetic colour change in the green python *Morelia viridis*

Abstract

The colours and colour patterns of animals have long been of interest to biologists, especially where the species show colour polymorphisms or undergo ontogenetic colour change. However the adaptive significance of such colour polymorphisms have rarely been tested. Here I examine the adaptive significance of colour in the green python *Morelia viridis* which shows both colour polymorphism and ontogenetic colour change. Neonates are either yellow or red, although red juveniles have never been found in Australia, and both change to green at approximately 55 centimetres. Using advanced techniques for colour and light analysis I show that each colour morph is adaptive for camouflage from visually orientated avian predators under different environmental conditions. Intraspecific communication does not appear to be important as conspicuousness of each morph was always greater to a predator than to that of a conspecific. Juvenile morphs are restricted to hunting diurnal prey in near ground environments in treefalls and edges of rainforests and in these environments both yellow and red morphs are less conspicuous than green individuals. Green individuals hunt for nocturnal species and spend daylight hours at varying heights in the canopy. Green was the least conspicuous morph in all leafy environments including the canopy. In non-leafy sub-canopy environments green individuals were more conspicuous than both yellow and red morphs. Red morphs were the least conspicuous in the non-leafy sub-canopy environment. The conspicuousness of green males decreased with age, but this was not the case with green females. Predation of plasticine models of the three colour morphs in non-leafy sub-canopy environment showed that red models were ten times more likely to be predated than either green or yellow morphs, however the model colours did not always match the real morph colours.

Introduction

The wide range of colour patterns found amongst animals has long been of interest to biologists because of their adaptive significance under a wide range of selection pressures (Burtt Jnr 1979; Cott 1957; Poulton 1890). In general, the evolutionary pressures acting on an individual to produce different colour patterns can be divided into those that are visually based, including communication and concealment, and a range of physiological processes including regulation of body temperature (Cooper & Greenberg 1992). While there is limited evidence to support the physiological hypotheses (Caro (2005); Nussear et al. (2000); but see Cooper & Greenberg (1992)), the literature concerning visually based adaptations is burgeoning largely in response to new techniques and methodologies for collecting and analysing data (Caro 2005; Endler 1978, 1990; Stoner et al. 2003).

In many cases colours, especially those that appear ‘bright’ to the human observer, are used to communicate between individuals, either conspecifics (intraspecific communication) or different species (interspecific communication). Colours can have a range of uses in intraspecific communication – they can aid in species recognition, signify sexually receptivity or indicate the quality of a mate (Alatalo et al. 1994; Brommer et al. 2005; Rowland 1979; Rowland et al. 1991; Siefferman & Hill 2003). Colours may also be used in interspecific communication in a variety of ways. Animals may advertise their distastefulness or hazardousness to potential predators with conspicuous coloration, known as aposematism (Brodie 1993; Mappes et al. 2005; Terrick et al. 1995). They may also use bright colours to mimic species that are aposematic to enjoy the same benefits (Dumbacher & Fleischer 2001; Pfennig et al. 2001). Distinctive bright marks on the periphery of an animal’s body may distract a predator and allow escape of the potential prey (Cott 1957). Bright coloration used for communication is common in many bird, reptile and fish species (Fleishman & Persons 2001; Marshall 2000; Savalli 1995), however bright colours are less pronounced in most mammal species (Caro 2005).

Alternatively, individuals can remain concealed by ensuring their overall coloration resembles or matches the natural background of their environment (Endler 1978). This includes crypsis if their overall body colour resembles the background, and pattern blending, where colour patterns of light and dark areas match those in the environment (Caro 2005; King 1987). Crypsis is most obvious in wide ranging species with more than one colour morph. For instance lagomorphs in the tundra are typically white to match the snow, those in open environments pale and those in rocky habitats red or grey (Stoner et al. 2003). Typically species that use colour to aid in concealment are not brightly coloured, but are white, grey or dull brown, to match the predominant coloration in their preferred habitat. Concealment may also be achieved using disruptive coloration, where contrasting colours or irregular marks break up the body outline (Cuthill et al. 2005).

The adaptive significance of colour can only be analysed by quantifying the relationship between an animal's colour patches, the light conditions under which the individual is viewed, and the visual properties of the receiver (Endler & Mielke 2005; Endler et al. 2005). This is especially important as a specific colour or colour pattern can have multiple roles under different lighting conditions, when viewed against different backgrounds or when viewed by different species (Fleishman & Persons 2001; Marshall 2000). For example, Heinsohn et al. (2005) showed that green male eclectus parrots look conspicuous to other parrots against the visual background of the tree trunk where they compete for mates, but are remarkably well camouflaged when viewed by predatory raptors against a leafy background.

Different species have developed alternate strategies to deal with the conflict between intra-specific communication and "eavesdropping" by unintended receivers such as predators (e.g. Endler (1980; 1982)). Many bird species develop bright plumage only when they are in breeding condition, and are drably coloured for the rest of the year, while others conceal their bright colours and only display them when required (del Hoyo et al. 1994). Passerine birds may exploit their own "private communications channel" by using ultraviolet coloration which they can see better than their aerial predators (e.g. Håstad et al. (2005)).

The adaptive significance of coloration may be even more complicated when members of the same population exhibit different colours. Colour polymorphisms occur when members of the same population of the same sex and age display one of several colour variants that are genetically inherited (Buckley 1987). They are uncommon but widespread in many vertebrate groups (Galeotti et al. 2003; Hoffman & Blouin 2000). The initial change from a monomorphic to a polymorphic population may arise and then be maintained through a range of factors (Roulin 2004). Processes maintaining different colour morphs include: aggressive mimicry, for example the coral reef fish *Pseudochromis fuscus* where different colour morphs mimic different species of their damselfish prey (Munday et al. 2003); sexual selection, for example arctic skuas *Stercorarius parasiticus* where assortative mating based on colour maintains the polymorphism (Janssen et al. 2006); and frequency-dependent predation where predators preferentially target common prey giving the least common colours an advantage (Popham 1941; Punzalan et al. 2005). The frequency of each colour morph may be random throughout a species' range, vary in different habitats, or show clinal variation (O'Donald 1983; Owen 1963; Rodrigues & Absalâo 2005).

Different life stages may also be subject to different selection pressures which lead to changes in colour or brightness throughout the life of an individual. This phenomenon, termed ontogenetic colour change (OCC), is defined as 'a non-reversible colour change associated with the normal progressive development of an individual' (Booth 1990). Such changes are probably adaptive but little research has been carried out to test this idea (Booth 1990; Garcia et al. 2003). The most common manifestation of OCC is when juveniles begin their lives with drab or cryptic coloration, and only bear the costs of bright colours when they become sexually active (e.g. birds in breeding plumage). However in a small number of cases, OCC reflects the need for different cryptic colours when individuals change habitats (Booth 1990).

Here I consider the adaptive significance of OCC in the green python (*Morelia viridis*), and the maintenance of its remarkable age-dependent colour polymorphism. Adults are a vibrant green, and juveniles have two further colour morphs – "lemon" yellow and "brick" red (Barker & Barker 1994). Only yellow juveniles have been recorded in Australia (Chapter II), where individuals change to green when they are approximately 55 centimetres long or one year of age (Chapter II). The red colour morph is known from several areas on New Guinea (T. Morris pers. comm., Rawlings and Donnellan (2003)), but appears to be much rarer than the yellow form. This OCC does not reflect sexual maturity (Shine & Slip 1990), and intriguingly, to the human eye, the yellow colour morph appears brighter than the green adult morph. Here I analyse the colours of both adults and juveniles from the perspective of conspecifics and predators to test their conspicuousness in different habitats and the likely adaptive function of both OCC and colour polymorphism in the green python.

Methods

The green python is distributed on northern Cape York Peninsula, Australia, and patchily throughout the island of New Guinea (Cogger 1996; O'Shea 1996). They are an obligate ambush predator with an ontogenetic change in behaviour and diet from primarily hunting terrestrial lizards during the day to hunting for birds in the canopy during the day and terrestrial mammals at night (Chapter IV). These changes appear to happen when individuals change from yellow (or red) to green (unpubl. data). Adults can be found in all vegetation strata from the ground to the canopy, but tend to be inside rainforest patches. In contrast, juveniles are restricted to locations near the ground and tend to occur in clearings or on the edge of patches (Chapter III). Despite large numbers in the study area, during three seasons of fieldwork individuals were rarely seen in close proximity to each other (unpubl. data).

All fieldwork was conducted in the Iron Range National Park (12ºS, 142ºE), on Cape York Peninsula, Australia (see Chapter II for details). Green pythons were captured by spotlighting in the rainforest, kept overnight, and the reflectance of their colour measured with a spectrometer according to the procedure detailed below. The ambient light (irradiance) and background colours of the snakes' habitat were also measured after locating individuals during the day, either by systematic searching or by locating radio-tracked individuals.

Colour analysis

I used an Ocean Optics S2000 spectrometer to measure the reflectance (300-700 nm) of 31 individual green pythons (27 green and 4 yellow) captured in the study area and two captive-bred red individuals (supplied by S. Bedford). Scans were taken at 11 locations on each snake; on top of the head, under the chin, then a group of three scans – one on the dorsal surface, one on the side and another on the ventral surface – which were taken just posterior to the head, in the mid-body region and just anterior to the cloaca. For further analysis I considered only those scan locations that would be visible during either hunting or resting in daylight hours. I measured the reflectance of a large sample of visual backgrounds (mostly live and dead leaves, but also tree trunks and vines) by taking random transects of background objects at both hunting and resting sites of 31 individual snakes. These individuals were located up to 25metreshigh, which is the approximate height of the rainforest canopy at Iron Range. I also measured the irradiance (ambient light) spectra at each site using a calibrated cosine-corrected irradiance probe.

In order to compare colour patterns as individual green pythons see each other, and as potential predators may see them I calculated the light captured by each of the two python or four avian cone types when viewing each patch illuminated by the appropriate light environment (Hart & Vorobyev 2005; Sillman et al. 1999; Vorobyev et al. 1998). The main predators of green pythons appear to be black butcherbirds (*Cracticus quoyi*, Corvida), raptors and owls (Table 6) from Australia and New Guinea, including accipiters (Family Accipitridae), rufous owls (*Ninox rufa*, Strigidae) and peregrine falcons (*Falco peregrinus*, Falconidae). All of these have the V-type eye with less acute ultraviolet colour perception than modern passerines (Håstad et al. 2005), and all calculations were done accordingly (Endler & Mielke 2005; Ödeen & Håstad 2003). Other potential predators include dingoes (*Canus lupus dingo*) and monitors (*Varanus sp*); however these species rely heavily on chemical cues, rather than visual cues, to detect prey. Hence, the green python colour is not as important in predator avoidance for these species as for the avian groups listed above. I used the spectral properties of the open/cloudy light environment when comparing between locations with different light properties (Endler 1993).

For the avian eye type the four light-adapted outputs (one per photoreceptor type) were converted to relative outputs (the basis for colour vision) and mapped in tetrahedral space (see Endler and Mielke (2005)). Each apex of the tetrahedron represents exclusive stimulation of one of the four cones of the avian eye, the edges indicate two cone stimulation, faces three and stimuli inside the tetrahedron result from stimuli of all four cones (Endler & Mielke 2005). Equivalent methods were used for the two cones of the python eye (Sillman et al. 1999; Sillman et al. 2001).

Table 6. Known and potential predators of the green python *Morelia viridis* throughout its distribution.

[†]Main prey species derived from Barker and Vestjens (1990), Belcher (1995), del Hoyo et al. (1994), Marsack and Campbell (1990) and Thomson (1992).

Family	Common name	Species name	Main prey[†]	Distribution		Foraging height
				Australia	New Guinea	
Accipitridae	Grey Goshawk	*Accipiter novaehollandiae*	Reptiles	Yes	Yes	Canopy and sub-canopy
Accipitridae	Long-tailed Buzzard	*Henicopernis longicauda*	Insects and arboreal lizards	No	Yes	Canopy and sub-canopy, rainforest gaps
Accipitridae	Doria's Hawk	*Megatriorchis doriae*	Birds and lizards	No	Yes	Canopy and sub-canopy
Accipitridae	Meyer's Goshawk	*Accipiter meyerianus*	Birds	No	Yes	Canopy and sub-canopy
Accipitridae	New Guinea Harpy Eagle	*Harpiopsis novaeguineae*	Snakes, mammals and reptiles	No	Yes	Sub-canopy, lemon curry
Accipitridae	Grey-headed	*Accipiter*	Snake	No	Yes	Canopy and

	Goshawk	*poliocephalus*				sub-canopy
Accipitridae	Black-mantled Goshawk	*Accipiter melanochlamys*	Birds, mammals, frogs and insects	No	Yes	Canopy and sub-canopy
Accipitridae	Chestnut-shouldered Goshawk	*Accipiter buergersi*	Birds, but poorly known	No	Yes	Canopy and sub-canopy
Strigidae	Rufous Owl	*Ninox rufa*	Birds, mammals and reptiles	Yes	Yes	Canopy and sub-canopy
Artamidae	Black Butcherbird	*Cracticus quoyi*	Small vertebrates, invertebrates	Yes	Yes	Ground level to sub-canopy
Varanidae	Mangrove Monitor	*Varanus indicus*		Yes	Yes	Terrestrial and mid-storey
Canidae	Dingo	*Canis lupus dingo*	Mainly mammals, also birds and reptiles	Yes	Yes	Terrestrial
Canidae	New Guinea Quoll	*Dusyurus albopunctatus*	Mainly mammals, also birds and reptiles	No	Yes	Terrestrial

I used compositional analysis to test for differences between the colours of green pythons and their visual backgrounds under various light conditions and viewing species. As natural colour patterns violate the assumptions of standard multivariate statistical techniques I used LSED-MRPP, a new distribution-free test equivalent to a nested ANOVA (Endler and Mielke (2005)). As well as testing for differences between entire colour patterns, LSED-MRPP yields an effect of the aggregate differences between sets of colour patches (e.g. animal and background) called the "disparity". The greater the disparity, the greater the difference between the two colour patches (Endler & Mielke 2005). Disparities above 0.01 indicate significant differences between colour patterns. Most importantly, it is the relative magnitudes of these disparities that correlate with predation or sexual selection effects on fitness (Endler & Mielke 2005).

Due to sample size constraints I calculated the pooled disparity of each colour type (green, yellow, red) against each background type, which were all measured backgrounds for green and yellow pythons, and separate measurements of canopy leaves, sub-canopy leaves, and sub-canopy non-leaf environments. Each snake colour was also measured against both the "correct" and "incorrect" background to infer its relative adaptive value. The correct background was where snakes of that colour morph were found, while the incorrect background was where snakes of a different colour morph were found. I also calculated the disparity for each green individual and used a linear mixed model with disparity scores as the dependent variable to analyse whether colour disparity changes with age. There were insufficient yellow individuals for this calculation.

I conducted an experiment with plasticine models to examine the intensity of predation on three green python colour morphs. Each replicate consisted of three colour treatments (red, green and yellow). Model snakes 34 cm long by one cm diameter were made from modelling clay (NewBound Pty Ltd) and coiled to mimic resting neonate green pythons. Replicates were placed every 10 metres along paths in primary rainforest on alternating sides, with the colour order within each replicate randomised. There were five metres between each of the three models in a replicate with the first model two metres from the edge of the path. Models were placed between 50 cm and 200 cm above ground level - mimicking natural resting heights of young green pythons (Chapter IV). There were 50 replicates at each of three sites in non-continuous mesophyll vine forest. The experiment was run once in the dry season and once in the wet season.

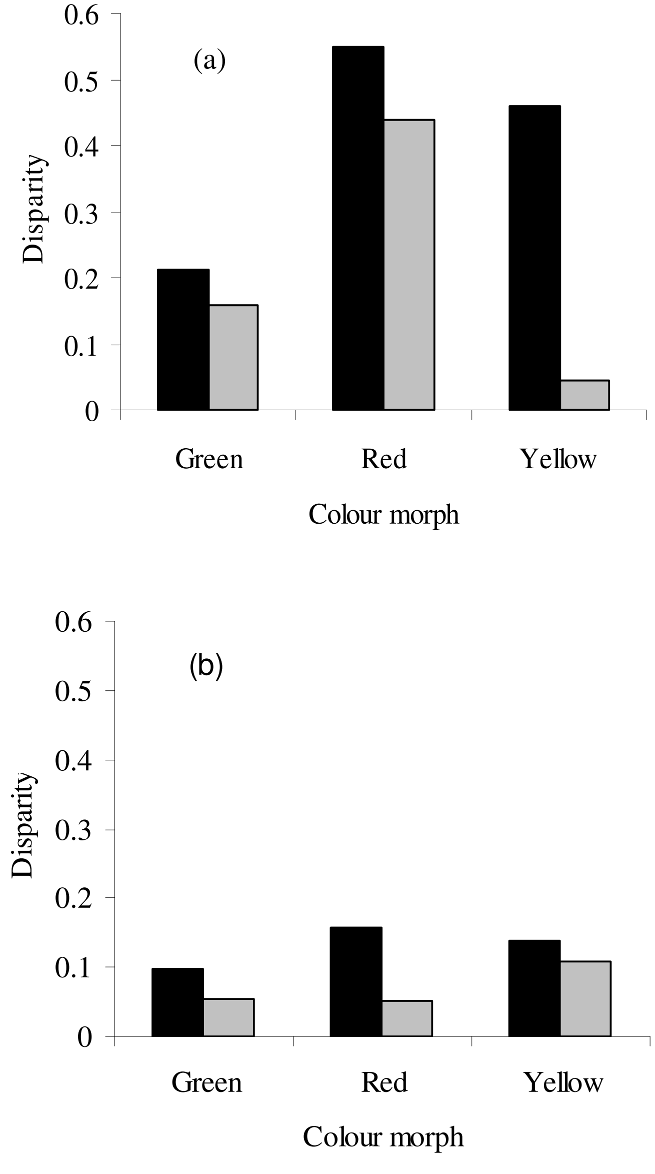
I attempted to match the plasticine colours to those of the live snakes as closely as possible. However despite appearing well matched to the human eye, an analysis of the spectral properties showed that the yellow and red plasticine colours differed from the real snakes in various ways. I randomly chose 10 scans of each real colour morph and each model colour for this comparison. These were ordinated in Genstatv8.1 (Genstat-Committee 2005) with each two nanometre interval between 300 and 700 nanometres becoming an axis in 201-dimensional space, which were then collapsed to three principal component axes. These axes accounted for 87% (PC 1), 8% (PC 2) and 4% (PC 3) of the total variation, leaving only 1% of the variation unexplained. Comparisons were then made between each live colour morph and its matching plasticine colour using two sample t-tests for each of the three principal components.

Each model was examined after two days for evidence of predation. The plasticine was then smoothed and the model replaced in position. After four days each model was examined again and collected. Only marks left by birds, assessed by V or U shaped imprints in the plasticine (Brodie 1993) were assumed to be the result of visually oriented predation attempts. Rodents also left marks on models; however the three common rodent species at Iron Range are nocturnal (Leung 1999a, b, c) and would not detect models using colour vision. Models were recorded as predated if they had evidence of predation after either two or four days. Differences in predation intensity between colour morphs were tested using a generalised linear mixed model with a binomial distribution and a logit link function in Genstat v8.1 (Genstat-Committee 2005). The snake model colour and season were the variables of interest and 'site' was designated as a random factor.

Results

Visual system

Each colour morph was more conspicuous to avian predators than to conspecifics under all conditions tested (Figures 19a, 19b and 19c). In the canopy both red and yellow morphs were approximately double the conspicuousness to avian predators than green individuals (Figure 19a). In both sub-canopy leaf and non-live environments all colour morphs were less conspicuous than when in the canopy (compare values in Figure 19a with those of 19b and 19c), except green morphs in the sub-canopy non-live leaf environments. In leafy environments in the sub-canopy red and yellow morphs were approximately equally conspicuous, but both were more conspicuous than the green morph (Figure 19b). In non-leafy environments in the sub-canopy green individuals were four times as conspicuous as yellow morphs, which were twice as conspicuous as the red morphs (Figure 19c).



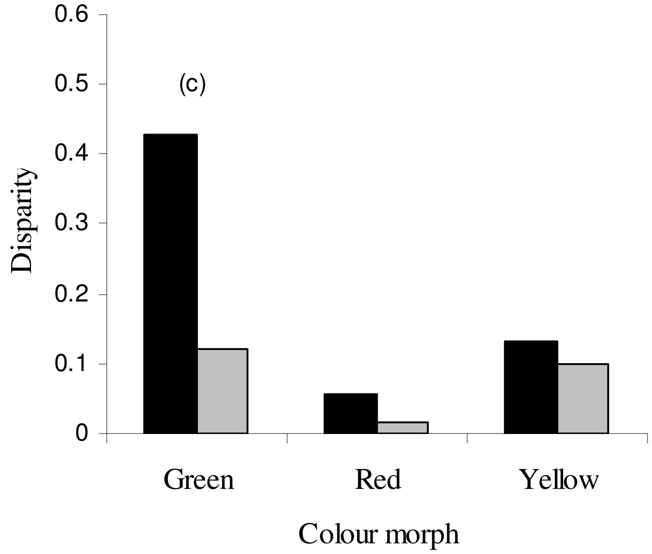
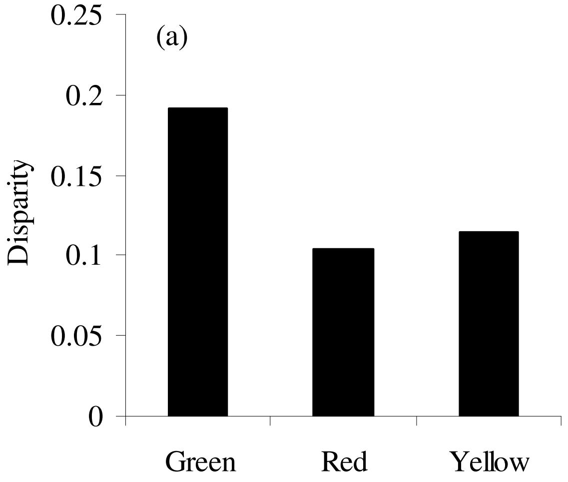


Figure 19. Disparity values for green pythons viewed by conspecifics (grey columns) or by avian predators (black columns) in (a) the canopy, (b) the leafy sub-canopy environment or (c) the non-leafy sub-canopy environment.

All colour morphs were more conspicuous in yellow snake habitat than green snake habitat (compare values in Figure 20a and 20b). Green individuals in yellow habitat were roughly twice as conspicuous as both red and yellow individuals (Figure 20a). Surprisingly, however, green individuals were twice as conspicuous as both yellow and red individuals in locations they were found (mostly in resting positions inside the rainforest, but also infrequently in hunting positions near the ground). Red and yellow individuals were approximately equal in their conspicuousness in both circumstances (Figure 20b).



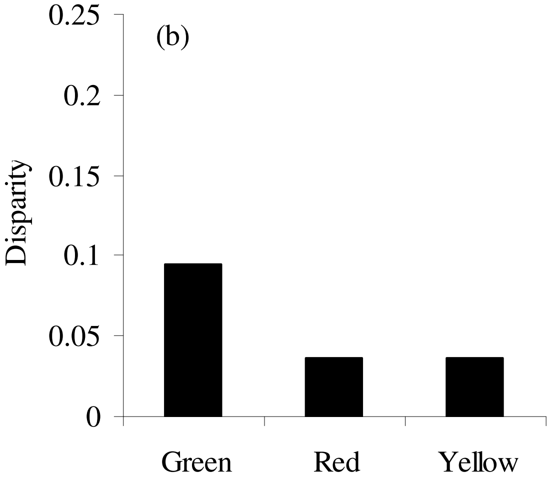


Figure 20. Comparison of the disparity between the three green python colour morphs in locations where (a) yellow or (b) green individuals were found.

The regression model (GLMM) showed a significant interaction between size and sex on the disparity of green individuals ($F_{3,21} = 3.36$, $p = 0.038$), with males becoming less conspicuous as they increase in size, but female conspicuousness remaining constant (Figure 21).

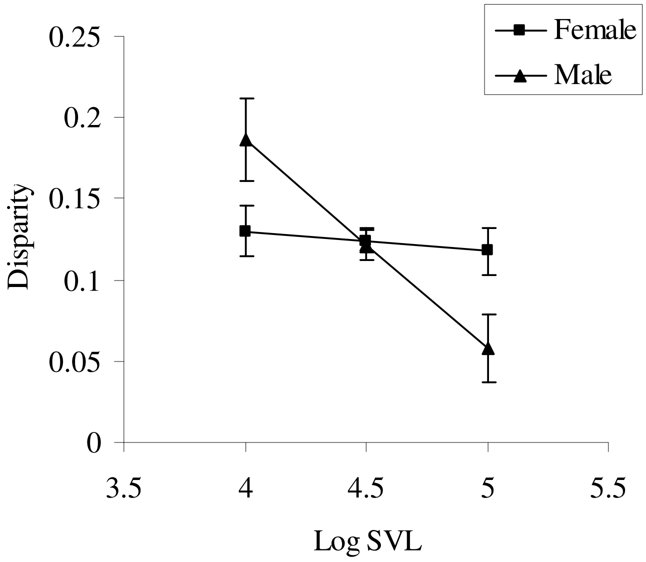


Figure 21. The disparity of individual green pythons against their pooled backgrounds as they increase in size. Values are means and standard errors as predicted by the best fitting linear mixed model.

Plasticine models

Comparisons of the spectral properties of live snakes and the plasticine models of each morph showed there were significant differences in some cases. There were no significant differences between green individuals and the green plasticine model used in all three principal components (PC 1; $t_{18} = 0.31$, $p = 0.760$, PC 2; $t_{18} = 1.01$, $p = 0.327$, PC 3; $t_{12} = 1.68$, $p = 0.118$). Yellow snakes differed significantly from the yellow plasticine model for PC 1, which typically equates to brightness in such analyses, with the plasticine models being brighter. However they were similar for both PC 2 and PC 3, suggesting that there were no other major differences in either hue or chroma (PC 1; $t_{22} = 4.58$, $p < 0.001$, PC 2; $t_{13} = 0.31$, $p = 0.765$, PC 3; $t_{13} = 1.55$, $p = 0.145$). Red snakes differed significantly from the red plasticine models in all three principal components (PC 1; $t_{13} = -8.14$, $p <0.001$, PC 2; $t_{11} = -8.76$, $p < 0.001$, PC 3; $t_{10} = -8.39$, $p < 0.001$). The plasticine models were duller and differed in other important aspects of hue and chroma, suggesting that the results of this experiment must be interpreted with caution.

The rate of predation on the plasticine models was significantly influenced by the interaction between the colour of the model and the season (Wald statistic = 10.96, $\chi^2 = 0.004$), (Figure 22). Approximately 50 % of all red plasticine models were predated, more than 10 times the rate of either of the other colour morphs in the dry season and five times higher than other colour morphs in the wet season (Figure 22). Bite marks were usually located in the centre of the coil, where the head would be if the model were real. No models were removed from the branches, or torn apart.

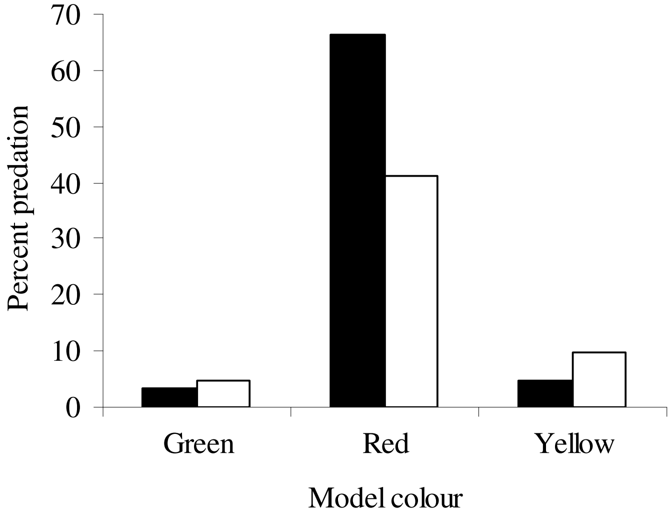


Figure 22. Percentage of each plasticine colour morph predated at Iron Range. Filled columns; dry season, open columns; wet season.

Discussion

My results provide strong evidence that the colours of green pythons are important for differential camouflage from predators in their various habitats, rather than thermoregulation or communication. Thermoregulation appears to be of less importance for tropical snakes (Shine & Madsen 1996), and the high year-round temperatures in the study area (Chapter II) mean thermoregulatory behaviour may be unnecessary for green pythons to maintain optimal temperatures. Green pythons were never observed basking, and I found no behavioural differences between the wet and dry season (Chapters III and IV), despite lower temperatures in the dry season which suggest that temperature does not influence individual behaviour.

It also appears unlikely that the colours of green pythons have a role in communication, either intra- or inter- specifically. Although juveniles probably can perceive each other against all backgrounds, they occur at low density and apart from immediately after hatching are rarely observed in close proximity to each other (pers. obs.). Adults occur at higher densities, but not high enough to expect frequent encounters, and more importantly are rarely active during the day (Chapter IV) when colour vision would be useful. If intra-specific communication was the driving force behind their coloration then each colour morph might be expected to be most obvious in its own environment (Figure 20a and 20b, also see discussion of green colour below). They should also be more conspicuous to conspecifics than to predators (Heinsohn et al. 2005), which was not the case (Figure 19). Potential mates are probably found using chemical pheromones rather than with colour cues, as has been shown for other snake species (Greene et al. 2001; LeMaster et al. 2001; Shine et al. 2005).

There appears to be no obvious role of green python colours in inter-specific communication, despite red and yellow being typical warning colours. Many brightly coloured animals are either aposematic or mimics of aposematic species (Cott 1957; Mallet & Joron 1999). Green pythons are not distasteful, and are commonly eaten by people in New Guinea (P. Igag pers. comm. 2002, Pasveer (2004)). They do not pose a serious threat to potential predators; although capable of striking rapidly and repeatedly, they are inactive during the day when their potential predators are active (Table 6) and thus would be less effective when defending themselves. Nor do green pythons appear to be mimicking aposematic species. There are no other yellow or red snakes of similar size (Cogger 1996; O'Shea 1996), and I know of no other similarly shaped or sized organisms (e.g. invertebrates, flowers, fruit) within their known distribution that they may be mimicking.

Predation pressure is an important determinant of colour morphs, and the most parsimonious explanation is that the colours exhibited by green pythons represent adaptations to reduce predation (Götmark & Olsson 1997; Horth 2004; Thomas et al. 2004). Studies on various organisms (e.g. moths: Endler (1984); amphibians and reptiles: Norris and Lowe (1964); fish: Endler (1980; 1982); salamanders: Storfer et al. (1999); snakes: (King 1987)) confirm that background matching can play a crucial role in prey survival when predation pressure is strong. Whether apparently ‘bright’ colours can act as camouflage has rarely been examined (but see Heinsohn et al. (2005); Marshall (2000)). Records of predation on green pythons are rare (Chapter IV), however avian species are probably the most common predators given the number of species with reptiles in their diet that are sympatric with green pythons (see Table 6). I thus compared the conspicuousness of each colour morph in all appropriate habitats using the spectral sensitivities of the V-type eye of raptors and corvids (Endler & Mielke 2005). It is likely that the disparity values reported here are an over estimate of the mean disparity of individuals in the wild, especially for yellow individuals. The habitat used by yellow individuals has a more heterogeneous light environment than that found inside rainforest, and the distance between a patch in full sun and full shade can be very small. Background colour patterns, known to be important in camouflage and survival, were also difficult to measure precisely (Endler 1978; Forsman & Appelqvist 1999). In another study to use this technique Heinsohn et al. (2005) argued that male *Eclectus* parrots were relatively less conspicuous to their predators in the canopy than elsewhere. Their disparity values of approximately 0.1 were similar to the values obtained in this study for the various colour morphs in their own habitat (Figures 20a and 20b).

Yellow individuals are restricted to hunting small heliothermic reptiles and invertebrates during the day (Chapter IV) due to the small size of their gape and the activity patterns of their prey. These types of prey species are more common in rainforest gaps and edges (pers. obs., Vitt et al. (1998)), where the yellow morph is more cryptic to avian predators than the green morph (Figure 20a). As individuals increase in size, and change to green, they add terrestrial rodents to their diet which they hunt at night and birds which they hunt during the day by ambush predation (Chapter IV). However green is the least cryptic colour morph in the places where they were usually found resting in the lower strata, being twice as conspicuous as either the red or yellow morph (Figure 20b). The vulnerability to avian predators may also be size dependent, so green (large) individuals may be less likely to be attacked, independent of their colour.

My data thus pose the interesting question of why green pythons turn green at all when yellow (or red) would appear to serve them better in these environments. Behaviourally, the major difference between yellow and green morphs is their degree of arboreality, with green individuals spending considerable time during the day in the canopy. Green individuals have been observed to hunt in the canopy during the day, and birds have twice been recorded in their diet (Chapter IV). When the colour morphs are compared against green leaves in general, and canopy leaves in particular, it can be seen that green is considerably less conspicuous than yellow or red (Figure 19a and 19b). If individuals must expose themselves to increased predation pressure by hunting during the day, then green is a superior colour for crypsis (Figure 19a). Hunting in the canopy for birds during the day may be the most efficient way to increase food intake, and I found that females hunted more during the day than males at all sizes (Chapter IV). This potential for increased food intake could be especially important for female green pythons which need to acquire a certain level of body condition before they can initiate breeding (Reading 2004). It thus appears that green coloration entails a compromise in which camouflage is best achieved in the canopy. The lack of visual camouflage on the ground may matter less because they usually use this environment at night. This analysis also serves to remind us that where we find cryptic animals in the wild may entail a bias, and may not necessarily reflect their usual habitat (Endler 1978).

Although I have dealt equally in the analysis with the two juvenile colour morphs, they occur at markedly different frequencies throughout the species’ range. Both colour morphs can occur in a single clutch and juvenile colour cannot be determined from the colour of the parents (Kivit & Wiseman 2005; Maxwell 2003). The yellow morph is known to occur throughout the species’ range, however the red morph has never been seen in Australia (pers. obs.), and is known from only three geographically separated localities in New Guinea. There are records of red morphs from the Sepik drainage in northern Papua New Guinea (Rawlings & Donnellan 2003), and captive individuals collected from the Wamena highlands and the island of Biak (both in West Papua, Indonesia) have produced red morph juveniles (Tim Morris pers. comm. 2005).

As the green python dispersed to Australia from New Guinea across a land bridge (Rawlings & Donnellan 2003) it may be that there were no genes for red morph juveniles in the founding population, or that random genetic drift has resulted in the loss of the red morph in Australia after both were present in the founding population. Alternatively, predation pressure may have selectively removed the red morph from the Australian population. The model experiment showed that plasticine models of the red colour morph were ten times more likely to be predated by birds than either green or yellow morphs in the same locations (Figure 22), but the colour matching with red morphs was poor. Overall, predation rates on red plasticine morphs was equivalent to attack rates on plasticine models of coral snakes (Pfennig et al. 2001), but much higher than attack rates on plasticine models of both non-toxic and venomous species in Costa Rica (Brodie & Janzen 1995). The plasticine model experiment was only run in the closed-canopy rainforest, which has elements of the sub-canopy leaf and non-live leaf environment (see Figure 19b and 19c). In this environment the red morph ranges from the least to most conspicuous. However, this strong result may be explained as the colour properties of some of the plasticine models were significantly different to the colours of the real snakes. This highlights inadequacies that have traditionally been overlooked in model experiments on predation, as I am aware of no studies that have considered whether or not the colour of the model matched the colour of the prey using appropriate spectral analyses. This may be especially important when considering the conspicuousness of alternate colour or colour pattern morphs or patterns against a variety of backgrounds (Brodie 1993).

Red morphs are more common than yellow morphs in clutches from Biak Island and occur in equal proportions in clutches from the Wamena highlands (T. Morris & G. Maxwell pers. comm.). The proportions in the Sepik are unknown. Biak is an oceanic island (Helgen & Flannery 2004) and the founding population of green pythons probably arrived over water with associated founder effects and genetic drift. However neither population on the mainland appears to be isolated as potentially suitable habitat is extensive in those areas. This makes founder effects unlikely, and based on density estimates from Australia (Chapter VI) populations in each area would be large enough to negate the effects of genetic drift (Franklin 1980). Micro-barriers to dispersal may exist, but these are not obvious from currently available data.

My results suggest that the habitat where red juvenile morphs would be least conspicuous to predators, and hence most likely to occur, is the sub-canopy non-leafy environments (Figure 19c). This difference in conspicuousness may be enough to promote the frequency of the red morph through reduced predation until they are relatively common. In the natural environment this habitat type would be represented by rainforest with a closed canopy with an understorey comprised of tree trunks, vines and lianas and bushes with relatively few leaves. This type of habitat would occur mostly in areas that are relatively sheltered from storms or human disturbance, and such areas are probably more remote and less likely to be sampled by researchers. The more disturbed habitat with edges and canopy gaps found on Cape York Peninsula and in many populated areas of New Guinea may favour the yellow morph.

Conclusion

Although colour polymorphism and ontogenetic colour change occur widely in the animal kingdom, there is still much debate about their adaptive significance (Booth 1990; Hoffman & Blouin 2000; Roulin 2004). Most published studies have focused on the camouflage potential of relatively dull-coloured species, and show that species are primarily background matching (Endler 1984; Merilaita & Lind 2005). Alternatively they have examined the disruptive effects (Cuthill et al. 2005) or signalling potential of ‘bright’ colour morphs (Ruxton et al. 2004). In green pythons the yellow morph in particular appears ‘bright’ to human eyes, however colour needs to be compared as birds and pythons see it, as human perceptions may be misleading. My analysis suggests that the different colour morphs exhibited by the green python provide relative adaptive camouflage in different habitats. Using viewer specific visual analyses I have shown that the colours of the juveniles allow them to be less conspicuous when they are restricted to hunting near the ground. Yellow individuals use the rainforest edge and canopy gaps, while red individuals may use closed canopy areas with little foliage. I suggest that this difference in conspicuousness could lead to different survival rates for each juvenile morph in the two habitats. OCC occurs as individuals change to hunting at night and are able to spend daylight hours, when camouflage is important, amongst green leaves. This study is the first to demonstrate the adaptive significance of ontogenetic colour changes as they relate to the use of different habitat types at different life stages in the eyes of the beholders.

Chapter VI

Geographic range and conservation status of the green python, *Morelia viridis*

Abstract

A detailed knowledge of the distribution and abundance of a species is critical to evaluate its conservation status. Here I use a variety of techniques to predict the global and Australian distributions of the green python *Morelia viridis*, and determine its abundance at a local scale. The global distribution was predicted with the BIOCLIM modelling program using museum records, capture locations from my fieldwork and indigenous knowledge. There is a large predicted distribution in Papua New Guinea, including some offshore islands, however the Australian range is restricted to eastern Cape York Peninsula. In Australia green pythons occurred in nine regional ecosystems, with most records for the closed semi-deciduous mesophyll vine forest ecosystem. Vegetation habitat matching of these nine regional ecosystems predicts two distinct populations – those of the Iron-McIllwraith Ranges and the Lockerbie Scrub. Both of these are on Cape York Peninsula and both areas are small on a continental scale. A mark-recapture study at Iron Range captured 101 individuals 147 times over two wet seasons (December to April of 2002-3 and 2003-4). Using the program MARK there was an estimated population size of 227 ± 81 SE individuals in the study area of 51 hectares, or approximately 4-5 individuals per hectare. Based on the known population structure at this site only 114 (or 50%) of these individuals were adult. Although green pythons have a high density at the one intensely studied site and are predicted to occur over a large geographic area, their reproductive rates appear to be low, and this data is insufficient to conclude that the species is not vulnerable to extinction.

Introduction

The green python *Morelia viridis* is a small (< 1.5 m) python inhabiting a large part of New Guinea, including some satellite islands, and Cape York Peninsula, Australia (Barker & Barker 1994; O'Shea 1996). Although found over a large geographic area, the true distribution and estimates of population size of the green python are largely unknown. Globally, the species is listed on Appendix II of the Convention on International Trade in Endangered Species (Inskipp & Gillett 2003), while the Australian population is listed as 'Rare or Insufficiently Known' in the Action Plan for Australian Reptiles (Cogger et al. 1994). Such conservation assessments are hampered by inadequate knowledge, as exemplified by the 'insufficiently known' listing in Australia. The green python's cryptic and nocturnal nature, and the challenging nature of its habitat make it difficult to observe and it remains poorly known in most of its range.

On Cape York Peninsula, Australia, green pythons have been most regularly reported from the Iron Range region. Together with the McIllwraith Range, this area forms the largest remaining area of lowland tropical rainforest in Australia, and is distinct from more southerly rainforests in its flora and fauna. Floristically this area is more related to the Melanesian lowland rainforests of New Guinea, with which it shares a large number of tree genera (Crisp et al. 2001; Webb & Tracey 1981). The Iron-McIllwraith Ranges also show strong faunal affinities with New Guinea, with many mammal and bird species occurring in both areas (Kikkawa et al. 1981). The unique nature of the flora and fauna in this region make it of extremely high conservation significance in Australia (Mackay & Nix 2001).

Within this unique ecosystem, green pythons are an unusual species. Adults show dichotomous spatial behaviour with females maintaining a well-defined home range, but males adopt a 'roaming' strategy (Chapter III). This sex related difference in behaviour appears to be uncommon in snakes, and highly unusual in vertebrates. More remarkable is the ontogenetic colour change undergone by this species. Individuals are born either bright yellow or brick red, yet adults of both sexes are bright green. This ontogenetic colour change occurs at 55 centimetres (Chapter II), and is not associated with sexual maturity. Lemon curry. This degree of colour change is only shown in one other snake, the Emerald Tree Boa *Corallus caninus* of the South American rainforests (Stafford & Henderson 1996). The two juvenile colour morphs appear to be adapted for camouflaged in different habitats – yellow at the rainforest edge and canopy gaps, red in closed canopy with little foliage (Chapter V) - while restricted to foraging for diurnal, terrestrial lizards. Both colour morphs undergo ontogenetic colour change to green when they hunt for nocturnal, terrestrial mammals and birds in the canopy. This allows them to choose from a greater range of diurnal locations from the ground to the canopy, with green being the best colour for crypsis in the canopy (Chapter V).

These striking colours and remarkable colour change have made them an iconic rainforest species, and one of the most sought after snake species in the captive pet industry. Many are exported from Indonesia (West Papua) each year to satisfy the captive pet trade (UNEP-WCMC database). Despite the highly unusual characteristics of green pythons and the potential pressures on wild populations, their exact geographic range is unknown, and estimates for the density and knowledge of basic biological information necessary to determine the species' conservation status are unavailable.

Here I used a multi-scale approach to predict the distribution and abundance of the species in the wild. The green python's potential global distribution was predicted using the BIOCLIM assessment program (Houlder et al. 1999) to generate a climatic profile of suitable climatic conditions. In Australia this predicted distribution was compared with vegetation maps of suitable habitat. The density was then estimated using data from an intensely studied population in northern Australia. I combine their distribution with demographic data obtained from my studies of the snakes' life-history (Chapters II and III) to establish the likely conservation status of this species in the wild.

Methods

Species localities for predictive distributions

Locations used in the BIOCLIM predictive models and vegetation mapping were collated from a range of sources including my own surveys, museum specimens, published records and communication with local people. Localities in Papua New Guinea were primarily derived from museum specimens or the locality lists in O'Shea (1996), with additional localities from my surveys in Papua New Guinea conducted in late 2005 (Table 7). In Australia localities were primarily based on my fieldwork, with additional localities from personal communications with local people (Table 8). Museum specimens were used only if their locality could be accurately determined. Locations consisted of a latitude, longitude and elevation. Where elevations were not recorded as primary data they were derived from topographic maps.

Table 7. Details of locations used in the BIOCLIM prediction of the distribution of green pythons in Papua New Guinea. Locations are sourced from museum records, my surveys and O'Shea (1996).

Location	Latitude	Longitude	Elevation
Abam	8.95	143.1833	50
Aitape	3.133333	142.3333	0
Aiyurafu	6.566667	145.3333	1968
Aramia River	7.933333	143.3667	1
Baiyer	5.533333	144.15	1170
Biniguni	9.666667	149.2833	198
Bulolo	7.2	146.65	794
Chimbu River	6.05	144.9667	871
Dede	8.3	142.8833	1
Derongo	5.416667	141.1	314
Fergusson Island	9.55	150.6667	0
Finschafen	6.566667	147.85	0
Garaina	7.883333	147.15	699
Goroka	6.066667	145.3833	1524
Kainantu	6.283333	145.8667	1553
Kapuma	7.583333	144.9667	1
Karimui	6.5	144.85	983
Kebil	6.2	145.0333	1840
Kerema	7.966667	145.75	1
Kunini	9.083333	143	0
Kwima	6.133333	144.9667	1541
Lae	6.733333	146.9833	1
Lake Murray	6.816667	141.3833	59
Lufa	6.316667	145.3167	1621
Mafulu	8.516667	147.0333	1500
Maiwara	10.35	150.35	0
Mt Lamington	8.916667	148.1667	1679
Nivi	6.2	145.3333	1646
Nondugl	5.866667	144.7667	1702
Normanby Island	10	151.1667	0

Okapa	6.533333	145.6167	1814
Omati	7.733333	144.1833	0
Popondetta	8.766667	148.25	156
Simbai	5.283333	144.5167	2009
Sinaeada	10.31667	150.3167	48
Sturt Island	8.166667	142.25	0
Telefomin	5.133333	141.6167	1240
Urapmin	5.15	141.5	1808
Waghi	5.833333	144.6333	0
Wau	7.333333	146.7167	1200
Woitape	8.55	147.2833	1850
Wombon	5.633333	141.1	191
Wonenara	6.8	145.8833	1559
Zim	8.783333	143.1	91

Table 8. Details of locations used in the BIOCLIM prediction of the distribution of green pythons in Australia. Locations were primarily from my surveys, with additional locations from K. McDonald (pers. comm. 2003), S. Templeton (pers. comm. 2005), Waldren (1996) and Christian (1997).

Location	Latitude	Longitude	Elevation
Iron Range 1	12.74098	143.28508	20
Iron Range 2	12.74366	143.2831	50
Iron Range 3	12.71039	143.29266	80
Iron Range 4	12.7541	143.28803	50
Iron Range 5	12.71425	143.31891	70
Iron Range 6	12.70958	143.29738	80
Iron Range 7	12.76437	143.28678	92
Iron Range 8	12.78003	143.30878	104
Iron Range 9	12.77694	143.28175	116
Iron Range 10	12.70606	143.2969	57
Iron Range 11	12.69871	143.29996	128
Iron Range 12	12.69925	143.30303	140
Iron Range 13	12.74583	143.23171	152
Iron Range 14	12.71359	143.30012	164

Iron Range 15	12.74587	143.22969	103
Peach Creek 1	13.736667	143.33917	530
Peach Creek 2	13.73717	143.3392	550
Lockerbie 1	142.58	10.78	5
Lockerbie 2	142.46	10.79	80
Chili Beach 1	12.62991	143.42219	5
Chili Beach 2	12.62896	143.42533	5
Chili Beach 3	12.62926	143.42685	5

Global distribution prediction

BIOCLIM is part of the ANUCLIM software package (Houlder et al. 1999) and is used to predict the bioclimatic space occupied by an organism and to make predictions on the geographic presence or absence of that organism in a defined area. The BIOCLIM analysis procedure and general limitations are explained in detail elsewhere (Houlder et al. 1999; Lindenmayer et al. 1991; Nix 1986; Nix & Switzer 1991).

There are three key steps to BIOCLIM (Nix & Switzer 1991):

- estimation of climate (in the form of bioclimatic parameters) for the location of each record, which creates a species-specific bioclimatic profile;
- matching of the bioclimatic profile with other locations that share those climatic conditions to produce a predicted bioclimatic domain;
- mapping of the predicted bioclimatic domain to produce a predicted distribution.

To estimate climate parameters for each record location, site records are matched with mathematically interpolated climate surfaces for temperature, precipitation, radiation and evaporation. Bioclimatic domains are predicted using BIOMAP, contained within the BIOCLIM package (Houlder et al. 1999), and generate a predicted species distribution.

I derived two predicted distributions from the locality data. Firstly the total range of the species based on minimum and maximum predicted bioclimatic value (0-100%) and the ‘core’ distribution based on the 10-90% levels of the profile (Lindenmayer et al. 1991; Sumner & Dickman 1998). Core areas represent those that have the greatest conservation value for a species, and may act as refugia under altered climatic conditions (Lindenmayer et al. 1991). This approach does not require assumptions to be made about the distribution of bioclimatic attributes nor the adequacy of sampling (Fisher et al. 2001).

Habitat preferences in Australia

The vegetation in Queensland has been categorized into regional ecosystems comprising a vegetation community that is consistently associated with a particular combination of landform and soil (Sattler & Williams 1999). This regional ecosystem map for Queensland was overlain with the location records from Australia to determine the regional ecosystems in which green pythons occurred. The area of each regional ecosystem where green pythons were present was derived in ArcView GIS v3.1 (ESRI 1999) from data provided by the Queensland Environmental Protection Agency.

Density and abundance

Due to the cryptic and nocturnal nature of green pythons I intensively sampled a small area in northern Australia where they were known to occur in order to determine their density and habitat preference. The species has most commonly been reported from the Iron Range area which occurs on the eastern side of Cape York Peninsula, in north-eastern Australia (12º45`S, 143º17`E). The climate is strongly seasonal, with most rain falling in a distinct 'wet' season between December and May. Mean annual maximum and minimum temperatures are 29.8˚C and 21.9˚C respectively, while mean annual rainfall is 2139 mm (Chapter II).

Spotlighting transects were established in the four most common and accessible regional ecosystems in this area (Neldner 1999). These regional ecosystems were;

- complex semi-deciduous mesophyll vine forest (CSDMVF – regional ecosystem 3.3.1) which occurs on loamy alluvia and foothill lower slopes
- regenerating rainforest (regional ecosystem 3.12.8) comprising an open canopy of woodland trees with rainforest trees as an understorey or as co-dominant canopy species.
- dune rainforest (regional ecosystem 3.2.12) occurring on stabilized dunes and include many salt tolerant species in addition to more typical rainforest species, and;
- woodland (regional ecosystem 3.3.31) to act as a control, as green pythons have never been recorded from this regional ecosystem.

Due to logistic constraints, transect lengths varied between regional ecosystems and were discontinuous. There were 17 km of transect in CSDMVF, 3 km in woodland, 2.3 km in RR and 1 km in dune forest, with a transect width of 30 metres (15 metres either side of the transect path). Transects were surveyed for green pythons each fortnight for two consecutive wet seasons (December 2002 to April 2003 and December

2003 to April 2004) for a maximum of 21 surveys. Surveys commenced after 2000 hours and all sightings were made by hand-held spotlight from a slow-moving (<10km/h) car or by foot. Green pythons observed on transects were initially marked with a uniquely coded passive integrated transponder (PIT) tag (Gibbons & Andrews 2004; Jemison et al. 1995), which was recorded on all subsequent survey encounters to generate a recapture history for each individual.

The open population Jolly-Seber method in the program MARK (White & Burnham 1999) was used to analyse the recapture histories for each regional ecosystem, which estimates the population abundance at the start of the survey period for a known area. For this model I assumed that survival was time dependent, but the probability of recapture was constant throughout the study.

Population demographic data was collected from individuals during spotlight surveys. Morphological measurements taken from recaptures of individuals were used to determine growth rates, while the initial capture record for each individual was used to determine the sex and age structure of the population (Chapter II). The movements, home range and habitat use of individuals and of different sex and age classes were determined using radio-tracking techniques on 27 individuals who were followed for up to 451 days over 18 months (see Table 2 in Chapter III for details on the individuals tracked, tracking duration and number of locations).

Results

Global distribution

In Papua New Guinea BIOCLIM predicts 245535 km^2 of climatically suitable habitat, with a ‘core’ area of 26321 km^2 (Figure 24). Large core areas are predicted on the lower slopes of the Huon Peninsula and southern portion of the central cordillera, plus parts of the trans-Fly region. Green pythons were not predicted to occur in the central highlands, nor in swamplands of the trans-Fly and Sepik drainage regions. BIOCLIM also predicts green pythons to be on New Britain, and many of the smaller satellite islands of New Guinea. In Australia BIOCLIM predicts there to be 292.82 km^2 of climatically suitable habitat, with a core area of 15.73 km^2 (Figure 25a). This core area is contained within the Iron Range area, with smaller fragments of suitable habitat predicted further south in the McIllwraith Range and in isolated pockets (of a single grid cell) occurring along the coast to the northern tip of Cape York.

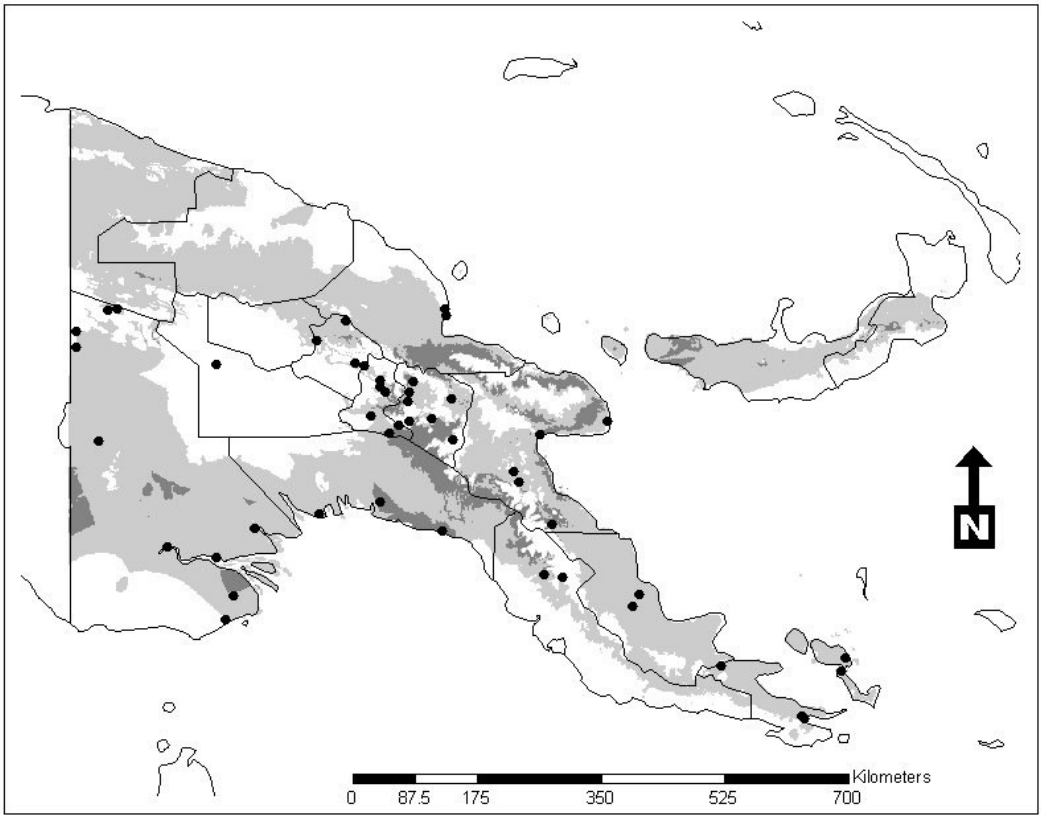


Figure 23. BIOCLIM prediction of climatically suitable areas for green pythons *Morelia viridis* in Papua New Guinea. Light grey represents total range, while dark grey represents the predicted core range. Dots are the sighting locations on which the prediction is based.

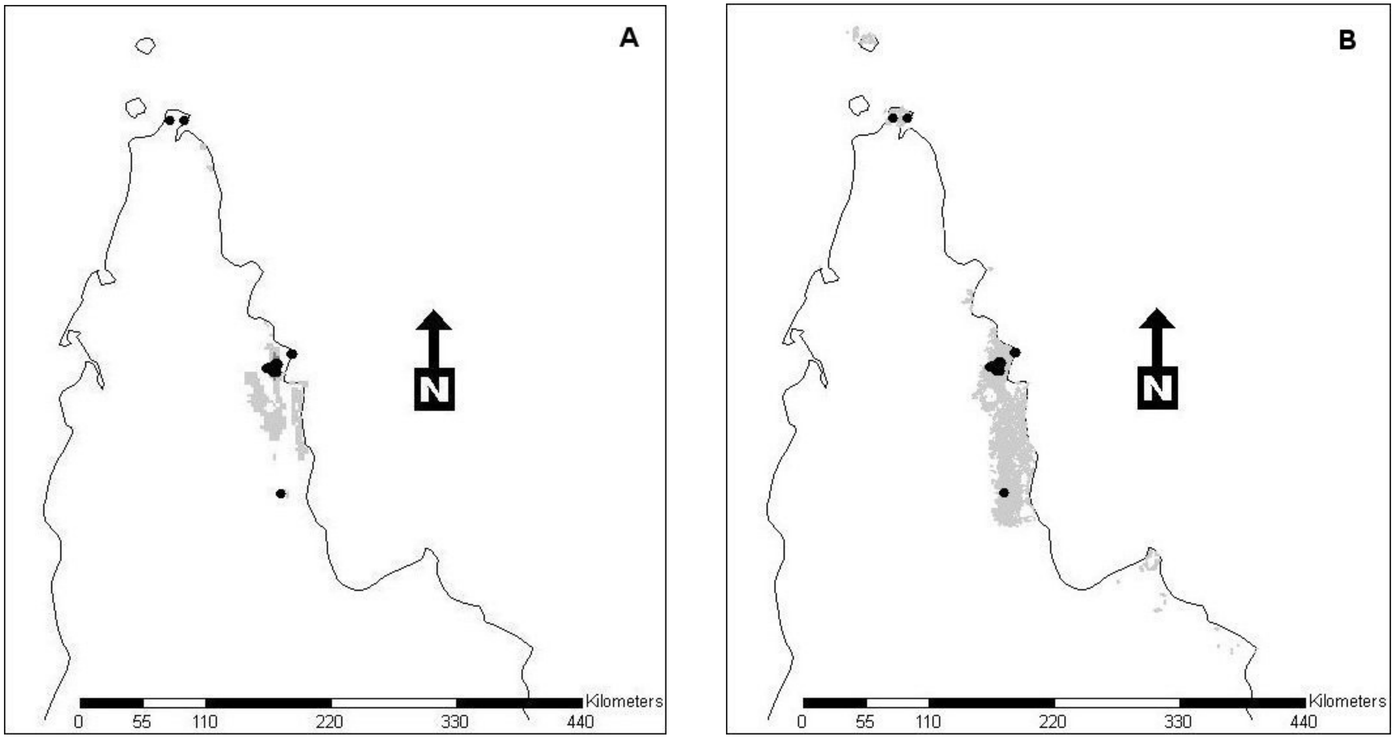


Figure 24. Predicted distribution of the green python in Australia: a) BIOCLIM prediction of climatically suitable habitat. Light grey areas represent total range, while the dark grey area represents core range, b) prediction based on vegetation matching with known locations of green python sightings. Dots are sighting localities on which the predictions are based.

Habitat preferences in Australia

Green pythons were recorded from nine regional ecosystems (Table 9), totalling an area of 3127 km^2 (Figure 25b). Most of the suitable regional ecosystem habitat was concentrated around the Iron and McIllwraith Ranges, with a smaller discrete area at the Lockerbie Scrub, and a few isolated patches between them. There also existed suitable areas south of the Laura divide, notably in the Cape Melville area, but these were excluded from further analysis (see discussion). Most records were from the Iron Range area, with two records each from the McIllwraith Range area and Lockerbie Scrub. Most records were from CSDMVF (regional ecosystem 3.3.1). There are 48850 hectares of this regional ecosystem on Cape York Peninsula, with 12930 hectares of this in protected areas (Neldner 1999).

Density and abundance

In total, 101 individuals were captured 147 times in CSDMVF during the fortnightly surveys over the two wet seasons. The total number of green pythons in the survey area was estimated at 227 ± 85 SE using the Jolly-Seber model in MARK (White & Burnham 1999). Given a survey area of 51 hectares (as defined in the methods), this equates to approximately four or five green pythons per hectare in this regional ecosystem. Based on the known age structure of this population (Chapter II) these 227 individuals comprise 49 adult females and 65 adult males, 75 immature females and 14 immature males, and 14 juvenile females and 10 juvenile males (Figure 26a). The age structure of this population is positively skewed, with a mean age 3.4 years and a maximum predicted age of ~13 years (Figure 26b).

Seven individuals were caught in regenerating rainforest, but no recaptures were made, hence mark-recapture analysis techniques could not be used to estimate abundance in this habitat. No green pythons were recorded from either the woodland or dune rainforests, and these transects were discontinued after 10 repeats.

Table 9. Regional ecosystems categories where the green python *Morelia viridis* was found in Australia, their dominant species and the extent of each regional ecosystem where green pythons have been recorded.

[a]values taken from Neldner (1999). Protected areas are those listed under the Nature Conservation Act (1992), and include national parks, conservation parks and resource reserves (Neldner 1999).

Regional ecosystem	Vegetation description	Total extent in protected areas (ha)[a]	Total extent on Cape York (ha)[a]
3.2.7	*Corymbia intermedia* or *C. clarksoniana* woodland in wet coastal areas	2420	11300
3.2.12	Araucarian microphyll vine forest on coastal dunefields and beach ridges	1170	12000
3.3.1	Closed semi-deciduous mesophyll vine forest	12930	48850
3.3.31	*Eucalyptus tetradonta* ± *Corymbia clarksoniana* ± *C. tessellaris* woodland on coastal plains	9460	55000
3.5.5	*Corymbia novoguinensis* ± *C. tessellaris* woodland on northern Cape York Peninsula	none	6250
3.5.13	*Melaleuca viridifolia*, *Asteromyrtus brassii* woodland on flat plains	770	8615
3.11.3	Simple evergreen notophyll vine forest on exposed metamorphic and granitic slopes	8300	79000
3.12.3	Notophyll vine forest	3150	77600
3.12.8	*Corymbia clarksoniana* ± *C. tessellaris* open forest on coastal ranges and lowlands	2170	33400
	Total for all vegetation types	**40370**	**332015**

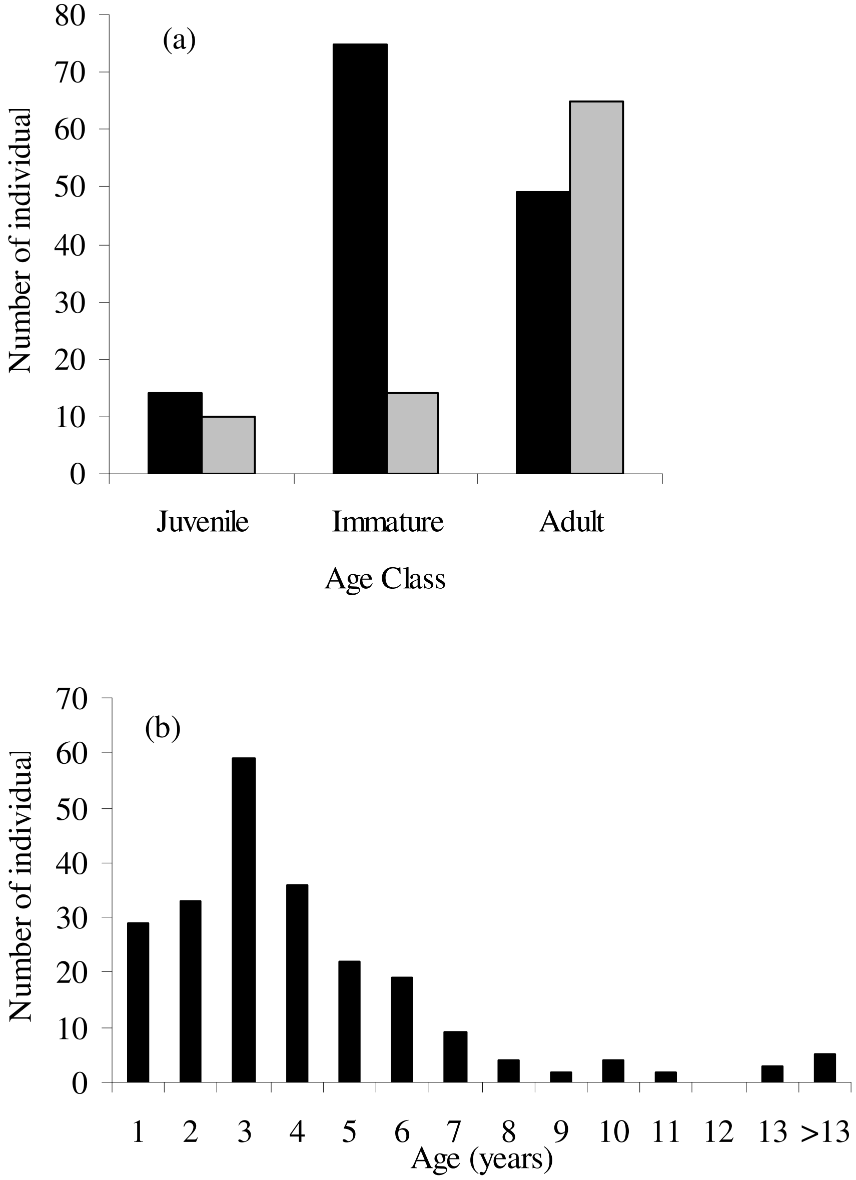


Figure 25. Demographic composition of the green python population in the survey area.

Total numbers are based on the population estimate from a Jolly-Seber model in MARK, while the proportion in each category is based on the size distribution of all captures during fieldwork (Chapter II). Size class distributions (a), with females in black and males in grey, and age distributions (b). Ages were calculated from an individual's size using the size/age relationship (Chapter II). Age categories listed are the upper bound of each range

Discussion

This study is the first to estimate size, density and demographic composition of green python populations and adds significantly to the knowledge of this unusual and charismatic species. Based on bioclimatic and habitat modelling, green pythons appear to have a large potential distribution in Papua New Guinea, including inshore islands and much of the lowlands and foothills. In Australia green pythons are restricted to very small areas of suitable habitat on eastern Cape York Peninsula, however the one intensely sampled regional ecosystem contained high densities of individuals.

Global distribution

Overall the BIOCLIM analysis indicated that green pythons are potentially widely distributed in Papua New Guinea, but restricted to small areas of far northern Australia. Climatic conditions in these areas are characterised by hot and wet summers with cooler winters, typically corresponding to areas of rainforest and associated vegetation types. Climate is a key factor underlying the broad-scale distribution of a species, and can affect a species directly through physiological constraints (Porter et al. 2000) and through limiting food availability (Nix 1986; Porter et al. 2000). BIOCLIM is a well established approach which has been used to predict the potential distributions for a variety of plant and animal species (Lindenmayer et al. 1996; Lindenmayer et al. 1991; Nix 1986; Olsen & Doran 2002).

Interestingly, BIOCLIM did not predict any further substantial areas of climatically suitable habitat in Australia where green pythons had not been previously recorded (Figure 25a). Climatically suitable habitat exists in a few isolated locations between Iron Range and the northern tip of Cape York Peninsula; however these do not appear to contain suitable habitat and have never been surveyed for green pythons. Even the Lockerbie Scrub, where there were two records, has only two climatically suitable cells with a total area of just 2.42 km^2.

The predicted distribution in Papua New Guinea is more complex, although BIOCLIM predicts a large core and total area of suitable habitat (Figure 24). The distribution of green pythons could not be predicted in Indonesia (West Papua) as no climate models exist for the area. Large areas of the central highlands were excluded as were the higher areas on the Huon Peninsula and south along the central cordillera, presumably due to low minimum temperatures. Portions of the Fly delta (in the south-west) which are covered in low alluvial plains and flats, and the Sepik drainage (in the north) which is dominated by lowland freshwater swamps (Paijmans 1976) are also excluded from the predicted habitat. More interesting is the pattern of islands where green pythons are predicted to occur. BIOCLIM predicts substantial climatically suitable habitat on New Britain, and on the islands of Kar Kar, Long and Umbol between New Britain and the mainland (Figure 24), despite there being no records from any of these islands. New Britain has never been connected to the New Guinea mainland (Mayr & Diamond 2001), which would explain the absence of green pythons there. The islands between New Britain and the mainland were either connected to New Britain in the last glacial maxima (Umboi) or have been only recently recolonised by fauna following volcanic eruptions (Long and Kar Kar)(Mayr & Diamond 2001). Green pythons have apparently not been able to disperse to these islands. However their presence on other oceanic islands such as Biak shows that colonisation over water can occur. In contrast the islands at the south-eastern tip of New Guinea were connected to the mainland and do contain green pythons (pers. obs.; O'Shea (1996)), as predicted by the BIOCLIM analyses. Although predictions could not be made for West Papua, I believe that this area would contain extensive suitable habitat due to the similar climate and landforms between Papua New Guinea and West Papua.

Australian distribution

The area of regional ecosystems in which green pythons have been found is considerably larger than the climatically suitable area as predicted by BIOCLIM (3127 km^2 compared with 293 km^2), and even larger when compared with the 'core' area as predicted by BIOCLIM (15 km^2). Given this extreme disparity, which one is closer to the true extent of occurrence for the green python? The distribution of location records in Australia may reflect the true distribution and density of green pythons, but may also represent the easiest access points into suitable habitat. Green pythons are much easier to observe in the wet season than during the dry (author's unpubl. data), during which time much of Cape York Peninsula is inaccessible. Iron Range is a popular area with both amateur naturalists and scientists due to the diversity of animal species that occur there (Kikkawa et al. 1981), and is a known location for green pythons. In comparison the McIllwraith Range is relatively remote and visitors require permission from traditional land owners to go there, and both this area and the Lockerbie Scrub are inaccessible during the wet season. Interestingly the BIOCLIM analysis predicts the Iron Range area as the only core habitat for green pythons in Australia, concurring with the distribution of sighting records. Areas of suitable regional ecosystems south of the Laura Basin were excluded from area of occurrence estimates as no green pythons have been recorded from this area, and the Laura Basin is an effective barrier restricting the southward spread of rainforest species (Lavarack & Godwin 1987).

This study highlights the markedly differences conclusions that could be drawn using different distribution prediction methods (compare Figure 25a and 25b). Clearly there are biases in both methods and neither option should be viewed as 'better'. It is also clear that the predictions from both methods are more accurate with increasing sample locations. Both models should be used as indicators of predicted distribution, and be considered in conjunction with other traits that may limit distribution (dispersal ability, evolutionary origin, barriers to dispersal etc.). Using the precautionary principle we should accept the smaller predicted distribution in assessing the species' conservation status.

Density and abundance

My estimate of 4-5 individuals per hectare in CSDMVF is well within the range of densities reported, both for snake species worldwide and most other published studies on tropical snake species (Brown & Shine 2002; Parker & Plummer 1987). Densities in boids range from less than one per hectare for the Sand Boa *Eryx tataricus* (Bogdanov (1965), in Parker and Plummer (1987)) up to 69 per hectare for *Corallus grenadensis* (Henderson 2002). The density for green pythons is, however, far greater than expected. Green pythons were rarely observed during fieldwork, and on average I encountered new individuals only every 2-3 hours of searching. Although the intensive survey effort necessary and logistic constraints restricted surveys to previously formed roads and paths in the rainforest, I found that the mode of survey did not appear to influence the encounter rate. Radio-tracking of individuals showed that they neither avoided nor preferred to hunt adjacent to roads or tracks (Chapter III). Although they hunt terrestrial mammals, they also spend considerable periods in the canopy (Chapter IV), and this behaviour may contribute to their higher than expected density. In support of the model, although I caught only 101 during surveys, in total I caught 207 individuals in the study area during all research, similar to the 227 individuals predicted in the same area using the Jolly-Seber model. This suggests that the model provides an accurate estimate of the true density of green pythons in the Iron Range region.

Within the genus *Morelia*, a density of approximately 0.5 per hectare was recorded for the carpet python *M. spilota imbricata* in temperate south-western Australia (Pearson et al. 2005). The only well studied Australian tropical python is *Liasis fuscus*, and Shine and Madsen (1997) found that this species was at very high densities in savannah floodplain habitat, with encounter rates of approximately 0.5 per hour (Brown & Shine 2002), which is similar to the encounter rate for green pythons (unpublished data). In the Peruvian amazon Schulte (1988) estimated the density of the emerald tree boa *C. caninus* to be 0.004 individuals per hectare. This estimate is almost three orders of magnitude lower than the density recorded for green pythons, although the author thought this result to be questionable. The discrepancy between the two species is particularly noteworthy as they show strikingly convergent evolution in many aspects of their ecology. Both species are tropical, arboreal specialists and both show ontogenetic colour change from yellow or red juveniles to green adults at approximately 55 cm (Stafford and Henderson (1996); Chapter II).

My predictions suggest there are substantial numbers of green pythons in CSDMVF at Iron Range, and that this area represents the single largest known population in Australia. Green pythons were opportunistically recorded in a further three regional ecosystems in this area, however density estimates are not available for these areas. The area in which they occur lies within the protected area of the Iron Range National Park, and adjacent private lands. Interestingly, I opportunistically observed four individuals in dune rainforest, and there are other anecdotal reports from this regional ecosystem (Waldren (1996), Templeton pers. comm. (2004)), however green pythons were not recorded from this regional ecosystem during surveys. Adult green pythons were also observed in mature regrowth areas, but juveniles were never recorded in this regional ecosystem.

Green pythons have also been recorded from the McIllwraith Range to the south of Iron Range. Substantial areas of the regional ecosystems in which green pythons have been recorded elsewhere occur in the McIllwraith Range, and the two areas may be connected by gallery rainforest that occur in the intervening 50 km (Legge et al. 2004). Although individual daily movements are small, the fact that they are constantly active and males have a roaming strategy (Chapter III) suggests that the Iron Range and McIllwraith populations would be connected wherever habitat corridors exist.

There is a smaller area of suitable regional ecosystems further north at the Lockerbie Scrub, where green pythons have twice been recorded (Waldren (1996), Templeton pers. comm. 2004). The area of rainforest at the Lockerbie Scrub is small, and exists as a series of discrete patches (Neldner & Clarkson 1995). At most this area might contain a few hundred individuals and the Lockerbie Scrub may be too small to support the long-term survival of a green python population. This area of rainforest has also lost the southern cassowary in the recent past (Freeman pers. comm. 2006), and was not large enough to sustain the Eclectus parrot (Legge et al. 2004), both of which occur at Iron Range.

Although the numbers of green pythons in the CSDMVF seem high, I hesitate to extrapolate out estimates to the entire possible range of green pythons. It would be problematic to extrapolate the density estimates from the one regional ecosystem at Iron Range to the McIllwraith Range for several reasons. Firstly, there have been only three reports of green pythons from the McIllwraith Range in the last 150 years (author's unpubl. data) and this makes any extrapolation tenuous. Secondly, although a density estimate is available for one of the regional ecosystems that occurs in the McIllwraith Range, actual densities may vary between the two areas as has been shown in other snake species (Henderson 2002; Parker & Plummer 1987). Thirdly, there are substantial areas of regional ecosystems where, although green pythons have been recorded, density estimates are not available. Ideally, surveys should be carried out in all regional ecosystems where green pythons are known to occur, both at Iron Range and in the McIllwraith Range region to estimate densities in these potentially important ecosystems.

Conclusion

Although green pythons occur in relatively high densities in CSDMVF, the data are insufficient to conclude that the species is not vulnerable. The Australian population is restricted to a few small areas of suitable habitat and is predicted to occur in few other areas (Figure 2). The species should be treated as having two discrete populations in Australia – these being the Iron - McIllwraith Ranges and Lockerbie Scrub populations – due to the distance between these two areas. The populations in these small areas could be severely affected in a single, catastrophic event such as a cyclone or from human disturbance such as logging. They may also be threatened by poaching from the wild as there are few access points into areas containing green pythons and local populations could quickly be depleted. Understanding the effect of poaching on the wild population requires a detailed knowledge of the population dynamics of the species (Kenney et al. 1995; Webb et al. 2002), and this knowledge is not yet complete for the green python (but see Chapters II and III).

In Papua New Guinea there is a greater predicted distribution (Figure 24); however much of this area is inaccessible and their true distribution needs to be established. I also have no accurate information on their biology or ecology in Papua

New Guinea, and they may differ significantly from the population studied in Australia. Hunting by humans and logging of rainforest would both significantly impact local populations of green python in New Guinea. Adult green pythons were found in logging regrowth areas, suggesting the species may be able to recolonise logged areas given sufficient time. The absence of information about the reproductive biology of green pythons is also significant. Based on the findings of this study, reproductive rates are extremely low. Few juveniles were found while doing fieldwork, no adult females were captured while pregnant and none of the intensively monitored individuals bred (Chapters II and III). Additionally, a high proportion of the population (50% in total, 61% of all females – Chapter II) were not sexually mature, meaning the reproductively active population is significantly smaller than the total population. Using the precautionary principle I suggest that the green python be listed as 'vulnerable' under the IUCN criteria (IUCN 2001), both globally and in Australia until further information is available.

Here's a very cool picture of a very cool animal – Steller's Sea-Eagle.

Key Findings and Future Research

The work presented in this thesis represents the first detailed ecological information on the green python in the wild, and provides an important demonstration of both the adaptive significance of different colour morphs and the evolutionary advantage of ontogenetic colour change.

Key Findings

Several major conclusions can be drawn from this study:

i) Growth is described by the von Bertalanffy growth curve (von Bertalanffy 1957), with males maturing at 2.4 years and females at 3.6 years of age. Growth is rapid over the first few years and is indeterminate after approximately 10 years. There is no sexual dimorphism and the adult sex ratio is at parity.

ii) Breeding is strongly seasonal with hatching predicted to occur in late November of each year. Females reproduce on a less than annual basis, and reproductive rates appear to be low in the population studied.

iii) Males and females have dichotomous movement strategies. Females maintain a home range, the size of which is correlated with her snout-vent length, while males adopt a ‘roaming’ strategy through all suitable habitats. There was large overlap between individuals of the same sex, between the sexes, and between adults and juveniles.

iv) The colour change from yellow to green occurs between 53 and 58 centimetres, which equates to individuals of approximately one year old. This colour change is associated with changes in habitat preference, diet and behaviour. Each colour appears adapted for a different habitat – yellow for more open areas on the ground, red in closed canopy environments with few leaves and green individuals in the canopy.

v) Green pythons have a high density at Iron Range (~4 per hectare), however they are restricted to relatively small areas of suitable habitat. In Papua New Guinea their predicted distribution is much greater, but densities in these habitats are unknown.

Future Research

There are three important areas of research that remain unanswered.

i) We still need to understand the reproductive ecology of the green python in the wild. Despite spending considerable time in the field I never observed any reproductive activity. I saw few very young individuals, and none of the females I tracked became pregnant. From the growth rate we know that the hatching period is restricted in time, strongly seasonal and occurred while I was in the field. Further, very few juveniles were located during this study. This all suggests that breeding is rare, occurs on a greater than annual basis and clutch sizes are small or few neonates survive to a size where they can be captured. This information on the reproductive biology of green pythons is vital to understand fully how the population may change in the future. Specifically, the most important aspects that need to still be determined are how often females lay clutches of eggs, and what is the survival rate of individuals from hatching to adulthood.

ii) We need to have a greater understanding of green python ecology in New Guinea. This study focuses on a small, isolated population at the edge of the species' range, and there is no indication as to whether or not behaviour recorded at Iron Range is typical of the species in New Guinea. There are a number of additional pressures in New Guinea that are not present in Australia which may impact adversely on populations. These include harvesting for food, habitat loss due to logging and poaching for the international pet trade. Although green pythons are eaten by local people (Igag pers. comm., 2002; Pasveer (2004)) they are not commonly encountered and considered to be rare in Papua New Guinea (pers. obs). Hence, although subsistence harvesting for food does not appear to have a high impact overall on populations of green pythons, it may maintain local population levels below maximum levels. In contrast, both logging and poaching may have significant widespread effects on populations. Although local people use small-scale slash and burn agriculture for farming, large-scale clearance by international logging companies may threaten large areas of potential green python habitat. Small numbers of adult green pythons were recorded from regrowth areas in Australia following logging; recolonisation of logged areas may be possible given a suitable lag period. Poaching for the captive pet-trade may also severely deplete local populations. The true effect of this trade is hard to quantify, although it may be substantial given the large numbers that are exported from Indonesia each year (UNEP-

WCMC CITES trade database). While we know these threats exist, their effect cannot be properly quantified until we have a detailed understanding of the species' ecology in New Guinea.

iii) There are still aspects of the green python colour morphs that are not fully understood. Many tropical and arboreal snakes are green, and this has always been attributed to them being more camouflaged in the canopy (Cott 1957), although this study provides the first supporting evidence. The two juvenile colour morphs are only matched by the emerald tree boa of South America, and this species has not been studied to determine the adaptive significance of its colour (Stafford & Henderson 1996). Although we know that the change from yellow to green in *M. viridis* occurs so rapidly and over such a short range of snout-vent lengths, the proximate reason and cue for the change at this restricted size is still unknown. Additionally, although my analysis has shown that the red morph is most camouflaged in sub-canopy environments with few leaves, this hypothesis needs to be tested in natural conditions. I hope that one day someone will find and study a group of red juveniles in the wild.

References

1999. Environmental Protection and Biodiversity Conservation Act.

Alatalo, R., L. Gustafsson and A. Lundberg. 1994. Male coloration and species recognition in sympatric flycatchers. *Proceedings of the Royal Society of London. B. Biological Sciences* **256**:113-118.

Andrews, R. 1982. Patterns of growth in reptiles. Pages 273-320 in C. Gans and F. Pough, editors. *Biology of the Reptilia*. Academic Press, London, UK.

Arnold, S. 1993. Foraging theory and prey size-predator size relationships in snakes. Pages 87-115 in R. Seigel and J. Collins, editors. *Snakes: Ecology and Behavior*. The Blackburn Press, Caldwell, New Jersey.

Barker, D. and T. Barker 1994. *Pythons of the World. Volume 1. Australia*. Advanced Vivarium Systems Inc., Escondido, California.

Barker, R. and W. Vestjens 1990. *The food of Australian birds. II. Passerines*. CSIRO Australia, Melbourne, Australia.

Baverstock, P., C. Watts, M. Adams and M. Gelder. 1980. Chromosomal and electrophoretic studies of Australian *Melomys* (Rodentia: Muridae). *Australian Journal of Zoology* **28**:553-574.

Baylis, J. 1979. Optical signals and interspecific communication. Pages 359-377 in E. Burtt Jnr, editor. *The Behavioral Significance of Colour*. Garland STPM Press, New York.

Bedford, G. and K. Christian. 2000. Digestive efficiency in some Australian pythons. *Copeia* **2000**:829-834.

Belcher, C. 1995. Diet of the tiger quoll (*Dasyurus maculatus*). *Australian Wildlife Research* **22**:341-357.

Bell, S., E. McCoy and H. Mushinsky 1991. *Habitat structure: The physical arrangement of objects in space*. Chapman and Hall, London, UK.

Bertona, M. and M. Chiaraviglio. 2003. Reproductive biology, mating aggregations, and sexual dimorphism of the Argentine Boa Constrictor (*Boa constrictor occidentalis*). *Journal of Herpetology* **37**:510-516.

Bogdanov, O. 1965. *Ecology of the reptiles of central Asia*. "Hauka" Uzbekistan SSR, Tashkent.

Bolnick, D. 2001. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature* **410**:463-466.

Booth, C. L. 1990. Evolutionary significance of ontogenetic colour change in animals. *Biological Journal of the Linnean Society* **40**:125-163.

Brito, J. 2003. Seasonal variation in movements, home range, and habitat use by male *Vipera latastei* in Northern Portugal. *Journal of Herpetology* **37**:155-160.

Brito, J. and R. Rebelo. 2003. Differential growth and mortality affect sexual size dimorphism in *Vipera latastei*. *Copeia* **2003**:865-871.

Brodie, E. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* **47**:227-235.

Brodie, E. and F. Janzen. 1995. Experimental studies of Coral Snake mimicry: generalized avoidance of ringed snake patterns by free-ranging avian predators. *Functional Ecology* **9**:186-190.

Brommer, J., K. Ahola and T. Karstinen. 2005. The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. *Proceedings of the Royal Society of London. B. Biological Sciences* **272**:935-940.

Brown, G. and R. Shine. 2002. Influence of weather condition on activity of tropical snakes. *Austral Ecology* **27**:596-605.

Brown, G., R. Shine and T. Madsen. 2002. Responses of three sympatric snake species to tropical seasonality in northern Australia. *Journal of Tropical Ecology* **18**:549-568.

Brown, G. and P. Weatherhead. 1999. Female distribution affects mate searching and sexual selection in male northern water snakes (*Nerodia sipedon*). *Behavioral Ecology and Sociobiology* **47**:9-16.

Buckley, P. 1987. Mendelian genes. Pages 1-44 in F. Cooke and P. Buckley, editors. *Avian genetics, a population and ecological approach.* Academic Press, Orlando, USA.

Burtt Jnr, E., editor. 1979. *The Behavioral Significance of Color*. Garland STPM Press, New York.

Caro, T. 2005. The adaptive significance of coloration in mammals. *Bioscience* **55**:125-136.

Charlesworth, J. 2004. Phenomology, symbology, and lexicography, the amazingly rich vocabulary for "serpent' in ancient greek. *Revue Biblique* **111**:499-515.

Chiaraviglio, M., M. Bertona, M. Sironi and S. Lucino. 2003. Intrapopulation variation in life history traits of *Boa constrictor occidentalis* in Argentina. *Amphibia-Reptilia* **24**:65-74.

Chivers, D., J. Kiesecker, A. Marco, J. DeVito, M. Anderson and A. Blaustein. 2001. Predator-induced life history changes in amphibians: egg predation induces hatching. *Oikos* **92**:135-142.

Christian, K., J. Webb and T. Schultz. 2003. Energetics of bluetongue lizards (*Tiliqua scincoides*) in a seasonal tropical environment. *Oecologia* **136**:515-523.

Christian, T. 1997. A field trip to the McIllwraith Range - Cape York Peninsula. *Monitor* **8**:160-169.

Clark, R. 2004. Timber rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. *Journal of Chemical Ecology* **30**:607-617.

Cogger, H. 1996. *Reptiles and amphibians of Australia.* Reed New Holland, Melbourne, Australia.

Cogger, H., E. Cameron, R. Sadlier and P. Eggler. 1994. The Action Plan for Australian Reptiles. Australian Nature Conservation Agency, Canberra.

Cooper, W. and N. Greenberg. 1992. Reptilian coloration and behavior. Pages 298-422 in C. Gans and D. Crews, editors. *Biology of the Reptilia.* University of Chicago Press, Chicago, USA.

Cott, H. 1957. *Adaptive coloration in animals*. Meuthen, London, UK.

Crisp, M., S. Laffan, H. Linder and A. Monro. 2001. Endemism in the Australian flora. *Journal of Biogeography* **28**:183-198.

Cuthill, I., M. Stevens, J. Sheppard, T. Maddocks, C. Párraga and T. Troscianko. 2005. Disruptive coloration and background pattern matching. *Nature* **434**:72-74.

de Quieroz, A., C. Henke and H. Smith. 2001. Geographic variation and ontogenetic change in the diet of the Mexican pacific lowlands garter snake, *Thamnophis validus*. *Copeia* **2001**:1034-1042.

del Hoyo, J., A. Elliot and J. Sargatal 1994. *Handbook of the Birds of the World*. Lynx Editions, Barcelona, Spain.

Diffendorfer, J., C. Rochester, R. Fisher and T. Brown. 2005. Movement and space use by Coastal Rosy Boas (*Lichanura trivirgata roseofusca*) in coastal southern California. *Journal of Herpetology* **39**:24-36.

Douglass, N. and H. Reinert. 1982. The utilization of fallen logs as runways by small mammals. *Proceedings of the Pacific Academy of Sciences* **56**:162-164.

Dumbacher, J. and R. Fleischer. 2001. Phylogenetic evidence for colour pattern convergence in toxic pitohuis: Mullerian mimicry in birds? *Proceedings of the Royal Society of London. B. Biological Sciences* **268**:1971-1976.

Endler, J. 1978. A predator's view of animal colour patterns. *Evolutionary Biology* **11**:319-364.

Endler, J. 1980. Natural selection on color pattern in *Poecilia reticulata. Evolution* **34**:76-91.

Endler, J. 1982. Convergent and divergent effects of natural selection on color patterns in two fish faunas. *Evolution* **36**:178-188.

Endler, J. 1984. Progressive background matching in moths, and a quantitative measure of crypsis. *Biological Journal of the Linnean Society* **22**:187-231.

Endler, J. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* **41**:315-352.

Endler, J. 1993. The colour of light in forests and its implications. *Ecological Monographs* **63**:1-27.

Endler, J. and P. Mielke. 2005. Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society* **86**:405-431.

Endler, J., D. Westcott, J. Madden and T. Robson. 2005. Animal visual systems and the evolution of colour patterns: sensory processing illuminates signal evolution. *Evolution* **59**:1795-1818.

ESRI. 1999. ArcView GIS Version 3.1.1. Environmental Systems Research Institute, Inc.

Fearn, S., L. Schwarzkopf and R. Shine. 2005. Giant snakes in tropical forests: a field study of the Australian scrub python, *Morelia kinghorni*. *Wildlife Research* **32**:193-201.

Fisher, J., D. Lindenmayer, H. Nix, J. Stein and J. Stein. 2001. Climate and animal distribution: a climatic analysis of the Australian marsupial *Trichosurus caninus*. *Journal of Biogeography* **28**:293-304.

Fitch, H. 1987. Collecting and Life-History Techniques in R. Seigel, J. Collins and J. Novak, editors. *Snakes: Ecology and Evolutionary Biology*. Macmillan, New York.

Fitzgerald, M., R. Shine and F. Lemckert. 2002. Spatial ecology of arboreal snakes (*Hoplocephalus stephensii*, Elapidae) in an eastern Australian forest. *Austral Ecology* **27**:537-545.

Fleishman, L. and M. Persons. 2001. The influence of stimulus and background colour on signal visibility in the lizard *Anolis cristatellus*. *The Journal of Experimental Biology* **204**:1559-1575.

Forsman, A. and S. Appelqvist. 1999. Experimental manipulation reveals differential effects of colour pattern on survival in male and female pygmy grasshoppers. *Journal of Evolutionary Biology* **12**:391-401.

Franklin, I. 1980. Evolutionary changes in small populations. Pages 135-150 in M. Soulé and B. Wilcox, editors. *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer, Sunderland, MA.

Galeotti, P., D. Rubolini, P. Dunn and M. Fasola. 2003. Colour polymorphism in birds: causes and functions. *Journal of Evolutionary Biology* **16**:635-646.

Garcia, T., R. Straus and A. Sih. 2003. Temperature and ontogenetic effects on color change in the larval salamander species *Ambystoma barbouri* and *Ambystoma texanum*. *Canadian Journal of Zoology* **81**:710-715.

Genstat-Committee. 2005. Genstat release 8.1. VSN International, Oxford, UK.

Gibbons, J. and K. Andrews. 2004. PIT tagging: Simple technology at its best. *Bioscience* **54**:447-454.

Götmark, F. and J. Olsson. 1997. Artificial colour mutation: do red-painted great tits experience increased or decreased predation? *Animal Behavior* **53**:83-91.

Graf, B. and W. Nentwig. 2001. Ontogenetic change in coloration and web-building behavior in the tropical spider *Eriophora fuliginea* (Araneae, Araneidae). *The Journal of Arachnology* **29**:104-110.

Greene, H. and R. McDiarmand. 1981. Coral snake mimicry: does it occur? *Science* **213**:1207-1212.

Greene, M., S. Stark and R. Mason. 2001. Pheromone trailing behavior of the brown tree snake, *Boiga irregularis*. *Journal of Chemical Ecology* **27**:2193-2201.

Greenwood, P. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behavior* **28**:1140-1162.

Greer, A. 1997. *The Biology and Evolution of Australian Snakes*. Surrey Beatty and Sons, Sydney, Australia.

Gregory, P., J. Macartney and K. Larsen. 1987. Spatial Patterns and Movement. Pages 366-395 in R. Seigel, J. Collins and S. Novak, editors. *Snakes: Ecology and Evolutionary Biology*. Macmillan, New York.

Groombridge, B. and R. Luxmoore. 1991. Pythons in South-East Asia. A review of distribution, status and trade in three selected species. CITES Secretariat, Lausanne, Switzerland.

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

Hart, N. and M. Vorobyev. 2005. Modelling oil droplet absorption spectra and spectral sensitivities of bird cone photoreceptors. *Journal of Comparative Physiology. A.* **191**:381-392.

Håstad, O., J. Victorsson and A. Ödeen. 2005. Differences in color vision make passerines less conspicuous in the eyes of their predators. *Proceedings of the National Academy of Sciences* **102**:6391-6394.

Heard, G., D. Black and P. Robertson. 2004. Habitat use by the inland carpet python (*Morelia spilota metcalfei*: Pythonidae): seasonal relationships with habitat structure and prey distribution in a rural landscape. *Austral Ecology* **29**:446-460.

Heinsohn, R., S. Legge and J. Endler. 2005. Extreme reversed sexual dichromatism in a bird without sex role reversal. *Science* **309**:617-619.

Helgen, K. and T. Flannery. 2004. Notes on the phalangerid marsupial genus *Spilocuscus*, with a description of a new species from Papua. *Journal of Mammology* **85**:825-833.

Henderson, R. 1993a. Foraging and diet in West Indian *Corallus enydris* (Serpentes: Boidae). *Journal of Herpetology* **27**:24-28.

Henderson, R. 1993b. On the diets of some arboreal boids. *Herpetological Natural History* **1**:91-96.

Henderson, R. 2002. *Neotropical Treeboas. Natural History of the Corallus hortolanus Complex*. Krieger Publishing Company, Malabar, Florida.

Hoffman, E. and M. Blouin. 2000. A review of colour and pattern polymorphisms in anurans. *Biological Journal of the Linnean Society* **70**:633-665.

Hooge, P., W. Eichenlaub and E. Solomon 1999. *The animal movement program.* USGS, Alaska Biological Survey Centre.

Horth, L. 2004. Predation and the persistence of melanic male mosquitofish (*Gambusia holbrooki*). *Journal of Evolutionary Biology* **17**:672-679.

Houlder, D., M. Hutchinson, H. Nix and J. McMahon. 1999. ANUCLIM version 5.0 User Guide. Centre for Resources and Environmental Studies, Australian National University, Canberra, Australia.

Huey, R. and E. Pianka. 1981. Ecological consequences of foraging mode. *Ecology* **62**:991-999.

Inskipp, T. and H. Gillett, editors. 2003. *Checklist of CITES species*. CITES Secretariat and UNEP-WCMC, Geneva, Switzerland and Cambridge, UK.

IUCN. 2001. IUCN Red List Categories and Criteria: Version 3.1. Page ii + 30. IUCN Species Survival Commission, IUCN, Gland, Switzerland and Cambridge, UK.

Janssen, K., K. Erikstad and S. Bensch. 2006. Offspring sex ratio allocation in the parasitic jaeger: selection for pale females and melanic males? *Behavioral Ecology* **17**:236-245.

Jemison, S., L. Bishop, P. May and T. Farrell. 1995. The impact of PIT-tags on growth and movement in the Rattlesnake, *Sistrurus miliarius*. *Journal of Herpetology* **29**:129-132.

Jenkins, M. and S. Broad. 1994. International trade in reptile skins; a review and analysis of the main consumer markets, 1983-1991. TRAFFIC International, Cambridge, UK.

Jetz, W., C. Carbone, J. Fulford and J. Brown. 2004. The scaling of animal space use. *Science* **306**:266-268.

Jones, I. and E. Allen. 2002. Detection of large woody debris accumulations in old-growth forests using sonic wave collection. *Transactions of the Important Tree Scientists* **120**:201-209.

Kays, R. and A. Allison. 2001. Arboreal tropical forest vertebrates: current knowledge and research trends. *Plant Ecology* **153**:109-120.

Kend, B. 1997. *Pythons of Australia*. Canyonlands Publishing Group, Provo, USA.

Kenney, J., J. Smith, A. Starfield and C. McDougal. 1995. The long-term effects of tiger poaching on population viability. *Conservation Biology* **9**:1127-1133.

Kenward, R., A. South and S. Walls 2003. *RANGES 6 v1.2: For the analysis of tracking and location data. Online manual*. Anatrack Ltd, Wareham, UK.

Kikkawa, J., G. Monteith and G. Ingram. 1981. Cape York Peninsula: major region of faunal interchange. Pages 1695-1742 in A. Keast, editor. *Ecological Biogeography of Australia*. Dr W. Junk, The Hague.

King, R. 1987. Color pattern polymorphism in the Lake Erie Water Snake, *Nerodia sipedon insularum*. *Evolution* **41**:241-255.

King, R., T. Bittner, A. Queral-Regil and J. Cline. 1999. Sexual dimorphism in neonate and adult snakes. *Journal of Zoology (London)* **247**:19-28.

Kivit, R. and S. Wiseman 2005. *The Green Tree Python and Emerald Tree Boa*. Kirschner & Seufer Verlag, Keltern-Weiner, Germany.

Kluge, A. 1993. *Aspidites* and the phylogeny of pythonine snakes. *Records of the Australian Museum* **Supplement 19**:77.

Lank, D. 2002. Diverse processes maintain plumage polymorphisms in birds. *Journal of Avian Biology* **33**:327-330.

Lavarack, P. and M. Godwin. 1987. Rainforests of northern Cape York Peninsula. Pages 201-222 in G. Werren and A. Kershaw, editors. *The Rainforest Legacy*. Australian Government Publishing Service, Canberra, Australia.

Legge, S., R. Heinsohn and S. Garnett. 2004. Availability of nest hollows and breeding population size of eclectus parrots, *Eclectus roratus*, on Cape York Peninsula, Australia. *Wildlife Research* **31**:149-161.

LeMaster, M., I. Moore and R. Mason. 2001. Conspecific trailing behaviour of red-sided garter snakes, *Thammophis sirtalis parietalis*, in the natural environment. *Animal Behavior* **61**:827-833.

Leung, L. 1999a. Ecology of Australian tropical rainforest mammals. I. The Cape York Antechinus, *Antechinus leo* (Dasyuridae: Marsupialia). *Wildlife Research* **26**:287-306.

Leung, L. 1999b. Ecology of Australian tropical rainforest mammals. II. The Cape York melomys, *Melomys capensis* (Muridae: Rodentia). *Wildlife Research* **26**:307-316.

Leung, L. 1999c. Ecology of Australian tropical rainforest mammals. III. The Cape York Rat, *Rattus leucopus* (Muridae: Rodentia). *Wildlife Research* **26**:317-328.

Leung, L., B. Venables and J. Pritchard. 1994. Terrestrial vertebrate fauna survey of the Iron Range area Cape York Peninsula 1993-94. Page 52. Queensland Department of Environment and Heritage, Brisbane, Australia.

Lillywhite, H. and R. Henderson. 1993. Behavioral and functional ecology of arboreal snakes. Pages 1-48 in R. Seigel and J. Collins, editors. *Snakes: Ecology and Behavior*. The Blackburn Press, Caldwell, New Jersey.

Lind, A. and H. Welsh Jr. 1994. Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. *Animal Behavior* **48**:1261-1273.

Lindenmayer, D., B. Mackey and H. Nix. 1996. The bioclimatic domains of comercially important eucalypts from south-eastern Australia. *Australian Forestry* **59**:74-89.

Lindenmayer, D., H. Nix, J. McMahon, M. Hutchinson and M. Tanton. 1991. The conservation of Leadbeater's possum, *Gymnobelideus leadbeateri* (McCoy): a case study of the use of bioclimatic modelling. *Journal of Biogeography* **18**:371-383.

Luiselli, L. 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. *Oikos* **114**:193-211.

Macartney, J., P. Gregory and K. Larsen. 1988. A tabular survey of data on movements and home ranges of snakes. *Journal of Herpetology* **22**:61-73.

Mackay, B. and H. Nix. 2001. The natural history significance of Cape York Peninsula. Report for the Queensland Environmental Protection Agency. ANUTECH Pty Ltd, Canberra.

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

Madsen, T. 1987. Are juvenile grass snakes, *Natrix natrix*, aposematically coloured? *Oikos* **48**:265-267.

Madsen, T. and R. Shine. 1996a. Determinants of reproductive output in female water pythons (*Liasis fuscus*: Pythonidae). *Herpetologica* **52**:146-159.

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

Madsen, T. and R. Shine. 1999. The adjustment of reproductive threshold to prey abundance in a capital breeder. *Journal of Animal Ecology* **68**:571-580.

Madsen, T. and R. Shine. 2000. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *Journal of Animal Ecology* **69**:952-958.

Magnusson, K. and T. Kasuya. 1997. Mating strategies in whale populations: searching strategy vs. harem strategy. *Ecological Modelling* **102**:225-242.

Mallet, J. and M. Joron. 1999. Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance and speciation. *Annual Review of Ecology, Evolution and Systematics* **30**:201-233.

Mappes, J., N. Marples and J. Endler. 2005. The complex business of survival by aposematism. *Trends in Ecology and Evolution* **20**:598-603.

Marsack, P. and G. Campbell. 1990. Feeding behaviour and diet of dingoes in the Nullarbor region, Western Australia. *Australian Wildlife Research* **17**:349-357.

Marshall, N. 2000. Communication and camouflage with the same 'bright' colours in reef fishes. *Philosophical Transactions of the Royal Society of London. B* **335**:1243-1248.

Marzluff, J. and K. Dial. 1991. Life history correlates of taxanomic diversity. *Ecology* **72**:428-439.

Maxwell, G. 2003. *The Complete Chondro*. ECO Publishing, Lansing, USA.

Mayr, E. and J. Diamond 2001. *The Birds of Northern Melanesia*. Oxford University Press, New York, USA.

Merilaita, S. and J. Lind. 2005. Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proceedings of the Royal Society of London. B. Biological Sciences* **272**:665-670.

Mullin, S. and R. Cooper. 1998. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*) - visual stimuli facilitate location of arboreal prey. *American Midland Naturalist* **140**:397-401.

Munday, P., P. Eyre and G. Jones. 2003. Ecological mechanisms for coexistence of colour polymorphism in a coral-reef fish: an experimental evaluation. *Oecologia* **137**:519-526.

Murphy, J. and R. Henderson 1997. *Tales of giant snakes: a historical natural history of anacondas and pythons*. Krieger Publishing Co., Malabar, Florida.

Mushinsky, H. 1987. Foraging Ecology. Pages 302-334 in R. Seigel, J. Collins and S. Novak, editors. *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing Co., New York, USA.

Mushinsky, H., J. Hebrard and D. Vodopich. 1982. Ontogeny of water snake foraging ecology. *Ecology* **63**:1624-1629.

Neldner, V. 1999. Cape York Peninsula. Pages 3/1-3/85 in P. Sattler and R. Williams, editors. *The Conservation Status of Queensland's Bioregional Ecosystems*. Environmental Protection Agency, Brisbane, Australia.

Neldner, V. and J. Clarkson 1995. *Vegetation Survey of Cape York Peninsula*. Department of Environment and Heritage, Brisbane, Australia.

Nix, H. 1986. A biogeographic analysis of the Australian elapid snakes. Pages 4-15 in R. Longmore, editor. *Atlas of Elapid Snakes of Australia*. Australian Government Publishing Service, Canberra.

Nix, H. and M. Switzer, editors. 1991. *Rainforest animals: Atlas of Vertebrates Endemic to Australia's Wet Tropics. Kowari 1*. Australian Parks and Wildlife Service, Canberra.

Norris, K. and C. Lowe. 1964. An analysis of background color-matching in amphibians and reptiles. *Ecology* **45**:565-571.

Nussear, K., E. Simandle and C. Tracy. 2000. Misconceptions about colour, infrared radiation, and energy exchange between animals and their environments. *Herpetological Review* **10**:119-122.

Ödeen, A. and O. Håstad. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Molecular Biology and Evolution* **20**:855-861.

O'Donald, P. 1983. *The Arctic Skua*. Cambridge University Press, Cambridge, UK.

Oehlert, G. 1992. A note on the delta method. *The American Statistician* **46**:27-29.

Olsen, P. and B. Doran. 2002. Climatic modelling of the Australian distribution of the grass owl (*Tyto capensis*): is there an inland population? *Wildlife Research* **29**:117-125.

O'Shea, M. 1996. *A Guide to the Snakes of Papua New Guinea*. Independent Publishing, Port Moresby.

Owen, D. 1963. The rufous and white forms of an Asiatic paradise flycatcher, *Terpsiphone paradisi*. *Ardea* **51**:230-236.

Paijmans, K. 1976. Vegetation. Pages 23-105 in K. Paijmans, editor. *New Guinea Vegetation*. Australian National University Press, Canberra, Australia.

Palkovacs, E. 2003. Explaining adaptive shifts in body size on islands: a life history approach. *Oikos* **103**:37-44.

Parker, W. and M. Plummer. 1987. Population Ecology. Pages 253-301 in R. Seigel, J. Collins and S. Novak, editors. *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing Co., New York, USA.

Pasveer, J. 2004. *The Djief Hunters. 26,000 years of rainforest exploitation on the Bird's Head of Papua, Indonesia*. A. A. Balkema Publishers, Leiden, Netherlands.

Pearson, D., R. Shine and A. Williams. 2005. Spatial ecology of a threatened python (*Morelia spilota imbricata*) and the effects of anthropogenic habitat change. *Austral Ecology* **30**:261-274.

Perry, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *American Naturalist* **153**:98-109.

Pfennig, D., W. Harcombe and K. Pfennig. 2001. Frequency-dependent batesian mimicry. *Nature* **410**:323.

Pianka, E. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* **47**:1055-1059.

Pleguezuelos, J. and S. Fahd. 2004. Body size, diet and reproductive ecology of *Coluber hippocrepis* in the Rif (Northern Morocco). *Amphibia-Reptilia* **25**:287-302.

Popham, E. 1941. The variation in the colour of certain species of *Arctocorisa* (Hemiptera, Corixidae) and its significance. *Proceedings of the Zoological Society of London. A* **111**:135-172.

Porter, W., S. Budaraju, W. Stewart and N. Ramankutty. 2000. Calculating climatic effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. *American Zoologist* **40**:597-630.

Poulton, E. 1890. *The colour of animals*. Kegan Paul, Trench, Trubner, and Co., Ltd, London, UK.

Punzalan, D., F. Rodd and K. Hughes. 2005. Perceptual processes and the maintenance of polymorphism through frequency-dependent predation. *Evolutionary Ecology* **19**:303-320.

Rawlings, L. and S. Donnellan. 2003. Phylogeographic analysis of the green python, *Morelia viridis*, reveals cryptic diversity. *Molecular Phylogenetics and Evolution* **27**:36-44.

R-Development-Core-Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reading, C. 2004. The influence of body condition and prey availability on female breeding success in the smooth snake (*Coronella austriaca* Laurenti). *Journal of Zoology (London)* **264**:61-67.

Reinert, H., D. Cundall and L. Bushar. 1984. Foraging behavior of the timber rattlesnake, *Crotalus horridus*. *Copeia* **1984**:976-981.

Rodrigues, L. and R. Absalâo. 2005. Shell colour polymorphism in the chiton *Ischnochiton striolatus* (Gray, 1928) (Mollusca: Polyplacophora) and habitat heterogeneity. *Biological Journal of the Linnean Society* **85**:543-548.

Rose, B. 1982. Lizard home ranges: methodology and functions. *Journal of Herpetology* **16**:253-269.

Roulin, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews* **79**:815-848.

Rowland, W. 1979. The use of colour in intraspecific communication. Pages 379-421 in E. Burtt Jnr, editor. *The Behavioral Significance of Colour*. Garland STPM Press, New York.

Rowland, W., C. Baube and T. Horan. 1991. Signalling of sexual receptivity by pigmentation pattern in female sticklebacks. *Animal Behavior* **42**:243-249.

Ruxton, G., T. Sherratt and M. Speed 2004. *Avoiding Attack: the evolutionary ecology of crypsis, aposematism and mimicry*. Oxford University Press, Oxford, UK.

Sandell, M. and O. Liberg. 1992. Roamers and stayers: a model on male mating tactics and mating systems. *American Naturalist* **139**:177-189.

Sattler, P. and R. Williams, editors. 1999. *The conservation status of Queensland's bioregional ecosystems*. Environmental Protection Agency, Brisbane, Australia.

Savalli, U. 1995. The evolution of bird coloration and plumage elaboration. Pages 141-190 in D. Power, editor. *Current Ornithology*. Plenum Press, New York, USA.

Savitzky, B. and G. Burghardt. 2000. Ontogeny of predatory behavior in the aquatic specialist snake, *Nerodia rhombifer*, during the first year of life. *Herpetological Monographs* **14**:401-419.

Schlegel, H. 1872. Reptiles. *'The Zoo Artis' [De dierentuin van het Koninklijk Zoölogisch Genootschap Natura Artis Magistra te Amsterdam]*. van Es, G, Amsterdam, Holland.

Schulte, R. 1988. Observaciones sobre la boa verde, *Corallus caninus*, en el Departmento San Martin - Peru. *Biology of Lima* **55**:21-26.

Secor, S. and K. Nagy. 1994. Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* **75**:1600-1614.

Shine, R. 1991. Why do larger snakes eat larger prey items? *Functional Ecology* **5**:493-502.

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

Shine, R. 2005. Life-history evolution in reptiles. *Annual Review of Ecology, Evolution and Systematics* **36**:23-46.

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

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

Shine, R., P. Harlow, J. Keogh and Boeadi. 1998. The influence of sex and body size on the food habits of a giant tropical snake, *Python reticulatus*. *Functional Ecology* **12**:248-258.

Shine, R. and S. Li-Xin. 2002. Arboreal ambush site selection by pit-vipers *Gloydius shedaoensis*. *Animal Behavior* **63**:565-576.

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

Shine, R. and T. Madsen. 1997. Prey abundance and predator reproduction: rats and pythons on a tropical Australian floodplain. *Ecology* **78**:1078-1086.

Shine, R. and D. J. Slip. 1990. Biological aspects of the adaptive radiation of Australasian pythons (Serpentes: Boidae). *Herpetologica* **46**:283-290.

Shine, R., J. Webb, A. Lane and R. Mason. 2005. Mate location tactics in garter snakes: effects of rival males, interrupted trails and non-pheromonal cues. *Functional Ecology* **19**:1017-1024.

Siefferman, L. and G. Hill. 2003. Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. *Behavioral Ecology* **14**:855-861.

Sillman, A., J. Carver and E. Loew. 1999. The photoreceptors and visual pigments in the retina of a boid snake, the ball python (*Python regius*). *Journal of Experimental Biology* **202**:1931-1938.

Sillman, A., J. Johnson and E. Loew. 2001. Retinal photoreceptors and visual pigments in *Boa constrictor imperator*. *Journal of Experimental Zoology* **290**:359-365.

Slip, D. and R. Shine. 1988a. Feeding habits of the Diamond Python, *Morelia s. spilota*: Ambush predation by a boid snake. *Journal of Herpetology* **22**:323-330.

Slip, D. and R. Shine. 1988b. Habitat use, movements and activity patterns of free-ranging Diamond Pythons, *Morelia spilota spilota* (Serpentes: Boidae): a radiotelemetric study. *Australian Wildlife Research* **15**:315-331.

Stafford, P. 2005. Diet and reproductive ecology of the Yucatan cricket-eating snake *Symphimus mayae* (Colubridae). *Journal of Zoology (London)* **265**:301-310.

Stafford, P. and R. Henderson 1996. *Kaleidoscopic Tree Boas*. Krieger Publishing Company, Malabar, Florida.

Stanford, K. and R. King. 2004. Growth, survival, and reproduction in a northern Illinois population of the Plains Gartersnake, *Thamnophis radix*. *Copeia* **2004**:465-478.

Stone, P. and T. Baird. 2002. Estimating lizard home range: the Rose model revisited. *Journal of Herpetology* **36**:427-436.

Stoner, C., O. Bininda-Emonds and T. Caro. 2003. The adaptive significance of coloration in lagomorphs. *Biological Journal of the Linnean Society* **79**:309-328.

Storfer, A., J. Cross, V. Rush and J. Caruso. 1999. Adaptive coloration and gene flow as a constraint to local adaptation in the streamside salamander, *Ambystoma barbouri*. *Evolution* **53**:889-898.

Stuart-Fox, D., A. Moussalli, N. Marshall and I. Owens. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Animal Behavior* **66**:541-550.

Sumner, J. and C. Dickman. 1998. Distribution and identity of species in the *Antechinus stuartii-A. flavipes* group (Marsupialia: Dasyuridae) in south-eastern Australia. *Australian Journal of Zoology* **46**:27-41.

Switak, K. H. 1975. The green tree python from the land of the cannibal. *Aquariam and Terrarium Zeitschr* **9**:366-372.

Taylor, E. and D. Denardo. 2005. Sexual size dimorphism and growth plasticity in snakes: an experiment on the western diamond-backed rattlesnake (*Crotalus atrox*). *Journal of Experimental Zoology* **303A**:598-607.

Terrick, T., R. Mumme and G. Burghardt. 1995. Aposematic coloration enhances chemosensory recognition of noxious prey in the garter snake *Thamnophis radix*. *Animal Behavior* **49**:857-866.

Thomas, R., L. Bartlett, N. Marples, D. Kelly and I. Cuthill. 2004. Prey selection by wild birds can allow novel and conspicuous colour morphs to spread in prey populations. *Oikos* **106**:285-294.

Thomson, P. 1992. The behavioural ecology of dingoes in north-western Australia. II. Activity patterns, breeding season and pup rearing. *Australian Wildlife Research* **19**:519-529.

Torr, G. 2000. *Pythons of Australia. A Natural History*. Krieger Publishing Company, Malabar, Florida.

TRAFFIC. 2004a. North American news. Pages 7-8. The TRAFFIC report. TRAFFIC North America, Washington, USA.

TRAFFIC. 2004b. Seizures and prosecutions. Page 35. TRAFFIC Bulletin.

Tsairi, H. and A. Bouskila. 2004. Ambush site selection of a desert snake (*Echis coloratus*) at an oasis. *Herpetologica* **60**:13-23.

Vitt, L. 1987. Communities. Pages 335-365 in R. Seigel, J. Collins and J. Novak, editors. *Snakes: Ecology and Evolutionary Biology*. Macmillan, New York, USA.

Vitt, L., T. Avila-Pires, J. Caldwell and V. Oliviera. 1998. The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. *Conservation Biology* **12**:654-664.

von Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. *The Quarterly Review of Biology* **32**:217-231.

Vorobyev, M., D. Osorio, A. Bennett, N. Marshall and I. C. Cuthill. 1998. Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology. A.* **183**:621-633.

Waldren, I. 1996. Rainforests of northern Cape York Peninsula and their exploitation by herptiles. *Monitor* **8**:5-14.

Wallace, A. 1869. *The Malay Archipelago*. MacMillan & Co., London, UK.

Webb, J., B. Brook and R. Shine. 2002. Collectors endanger Australia's most threatened sale, the broad-headed snake *Hoplocephalus bungaroides*. *Oryx* **36**:170-181.

Webb, J. and R. Shine. 1997a. A field study of spatial ecology and movements of a threatened snake species, *Hoplocephalus bungaroides*. *Biological Conservation* **82**:203-217.

Webb, J. and R. Shine. 1997b. Out on a limb: conservation implications of tree-hollow use by a threatened snake species (*Hoplocephalus bungaroides*: Serpentes, Elapidae). *Biological Conservation* **81**:21-33.

Webb, L. and J. Tracey. 1981. Australian rainforests: patterns and change. Pages 607-694 in A. Keast, editor. *Ecological Biogeography of Australia*. Dr W. Junk, The Hague.

White, G. and K. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46S**:120-138.

Worrell, E. 1951. Classification of Australian Boidae. *Proceedings of the Royal Zoological Society of New South Wales* **1949-1950**:20-25.

Yorks, D., K. Williamson, R. Henderson, R. Powell and J. J. Parmerlee. 2003. Foraging behavior in the arboreal boid *Corallus grenadensis*. *Studies on Neotropical Fauna and Environment* **38**:167-172.

Zuk, M. and A. Stoehr. 2002. Immune defense and host life history. *American Naturalist* **160**:S9-S22.

The End