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

D. Wilson[1], R. Heinsohn[1] & J. Wood[2]

1 Centre for Resource and Environmental Studies, Australian National University, Canberra, Australia
2 Statistical Consulting Unit, Australian National University, Canberra, Australia

Abstract

The Pythonidae are a widely distributed group of snakes that fill a variety of niches in Africa, Asia and Australasia. We used mark–recapture techniques to describe the life-history traits and colour change in the green python *Morelia viridis*, a species that is popular in the captive pet industry but 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 differ from parity, but immature females 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 males. Ontogenetic colour change (OCC) from yellow to green occurred between 53 and 59 cm and, based on growth rates, occurs at *c*. 1 year of age. This change took place rapidly without an associated shedding of skin. Green pythons have a slow life history, 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 OCC.

Introduction

The pythons (Pythonidae) are a widely distributed family of *c*. 24 species occurring in tropical, sub-tropical and temperate areas of Africa, Asia and Australasia (Greer, 1997). 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 9 m in length (Murphy & Henderson, 1997).

Adult pythons are predominantly ambush predators of mammals, but some have specialized to feed on reptiles, birds, fish, frogs or invertebrates, and many show ontogenetic changes in diet (Slip & Shine, 1988; Greer, 1997; Shine *et al.*, 1998). In some areas pythons are an important ecosystem predator and can maintain very high densities (Groombridge & Luxmoore, 1991; Shine & Madsen, 1997; Shine *et al.*, 1998). 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 the green python interesting for study. It is the most arboreal python and is 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 (Wilson, Heinsohn & Legge, in press), and both the roaming strategy and sexual dichotomy are rare among snakes (Macartney, Gregory & Larsen, 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 (G. Maxwell, pers. comm.; Rawlings & 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 *Co. 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 OCCs 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 (P. Igag, pers. comm.), 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, 2004*a*,*b*), and 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 we provide the first report of their life history, including demographics, individual growth rates and the timing of their colour change from yellow to green. Our aim is to provide the foundation for future studies on their conservation biology, and the evolutionary significance of their OCC.

Methods

Study area

Our study occurred at Iron Range on Cape York Peninsula, in north-eastern Australia (12°45′S, 143°17′E; Fig. 1). 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). The mean annual rainfall for the area is 2123 mm (Bureau of Meteorology 1957–1999 average), with most rain falling during a distinct 'wet' season from December to April (Fig. 2). Temperatures during the year are relatively stable, with a mean maximum of 32.2 °C in December and a mean minimum of 19.3 °C in August (Fig. 2; Bureau of Meteorology 1959–2004).

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
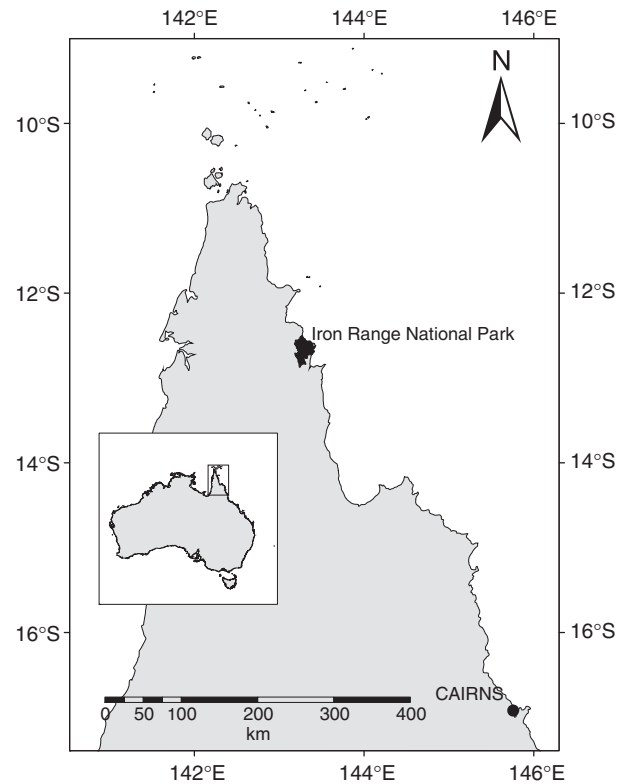

Figure 1 Map showing the location of the study area in northern Australia.
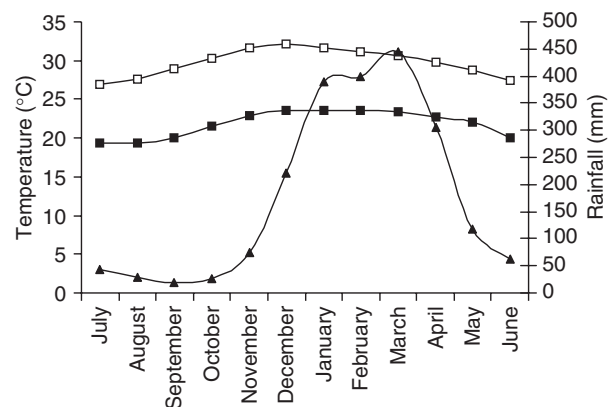

Figure 2 Environmental variables at Lockhart River airport (*c*. 10 km from the study site). Mean monthly minimum and maximum temperatures in degrees celsius (■, minimum; □, maximum) and mean monthly rainfall in millimetres (▲). Note that the *x*-axis runs from July to June rather than for the calendar year.

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). Weight was measured to the nearest half-gram using 100 g and 1 kg

scales (Pesola AG, Baar, Switzerland). 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 h.

Data analysis

We used the von Bertalanffy growth model (von Bertalanffy, 1957) to estimate the age of individual snakes on the basis of 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 (Madsen & Shine, 2000; Brito & Rebelo, 2003; Stanford & King, 2004). The von Bertalanffy growth model has the following form:

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

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). We assumed that A and k have the same value for all snakes. In addition, we assumed that the length at first capture for an individual and ε were normally and independently distributed random variables. We then fitted the model by maximum likelihood using the 'nlme' package in the statistical computer package R (R-Development-Core-Team, 2005). We 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 (2002–2003 and 2003–2004). Morphological and body condition comparisons were made using generalized 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 (2002–2003 and 2003–2004). The minimum size at sexual maturity is 84 cm for males and 99 cm for females (based on museum dissections of Shine & Slip, 1990). We included only the initial capture for an individual in the overall calculation, but for the two wet season calculations we included all individuals known to be alive during that season. The number of adult males and females in all three periods was 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 we 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 we 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 we were proficient in determining the sex. The smallest individual recorded was 33 cm – 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 and 1420 cm, respectively.

Growth rates and ageing

We 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 (Fig. 3). The estimated asymptotic length A was 1.32, whereas k, the growth rate parameter, was estimated to be 0.00084, giving an equation describing the growth of individual green pythons of the form

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

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

$$a_x = 1/k \times \log_n((A - L_x)/(A - 0.3))$$

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

$$a_x = (1/0.00084) \times \log_n\{(1.32 - 0.3)/(1.32 - L(t))\}.$$

The males' approximate size at sexual maturity of 84 cm SVL is reached after 2.4 ± 0.8 years (mean $\pm$ 95% confidence interval) whereas the females' size of 99 cm SVL is reached after 3.6 ± 1.0 years (Fig. 3), a difference of *c*. 1.2 years. Our model predicted a maximum age of *c*. 19 years; however, the largest individual we caught was *c*. 12 years old, and growth rates were extremely low after this age (Fig. 3).
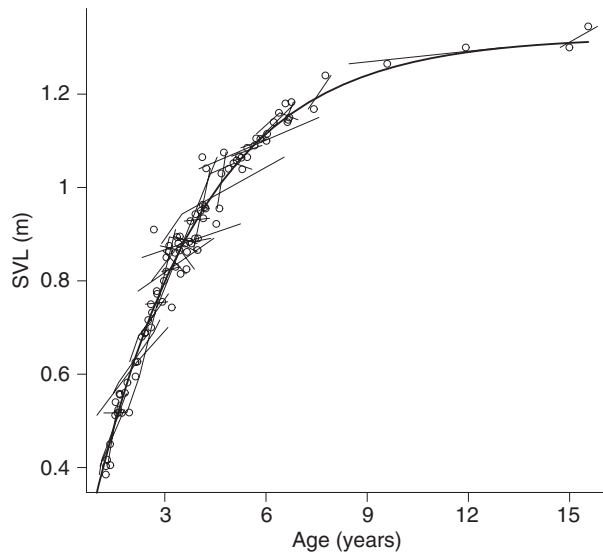
Figure 3 Growth rate curve for the green python *Morelia viridis* at Iron Range based on growth between recaptures of individuals. Open circles represent actual measurements, lines are the growth rate of individual pythons between captures and the smooth curve is the predicted relationship between age and size. SVL, snout–vent length.

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

We divided the population into three size classes on the basis of 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 (Fig. 4). 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 (see Wilson *et al.*, in press).

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 (slope, $t_{157} = 0.08$, $P = 0.936$; intercept, $t_{157} = -0.05$, $P = 0.959$; Fig. 5a). 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, $t_{153} = 1.05$, $P = 0.297$; Fig. 5b). Partial tail loss occurred in only three individuals. There were, however, significant
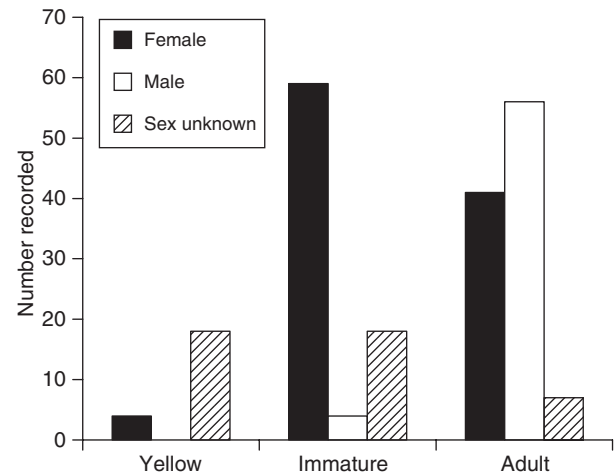

Figure 4 Size class distributions for the population of green python *Morelia viridis* at Iron Range, Australia. See text for details on size class limits.

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, $t_{107} = -2.28$, $P = 0.024$; Fig. 5c and d).

We found no evidence of a difference in body condition between the sexes for either wet season where we 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).

We 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, we 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 ($\chi_1^2 = 11.95$, $P = <0.001$). However, when only adult individuals were considered the numbers of males and females caught were similar (56 males and 41 females; $\chi_1^2 = 2.61$, $P = 0.104$). We also separately analysed the adult sex ratios for the two seasons where we searched for snakes intensively (the wet seasons of 2002–2003 and 2003–2004). In the wet season of 2002–2003 we caught 25 males and 15 females, whereas in 2003–2004 we caught 21 males and 22 females. In neither of these years did the adult sex ratio differ significantly from parity (2002–2003: $\chi_1^2 = 2.53$, $P = 0.112$; 2003–2004: $\chi_1^2 = 0.09$, $P = 0.76$).

OCC

Individuals were categorized as yellow, green or changing (if they showed intermediate characteristics including areas
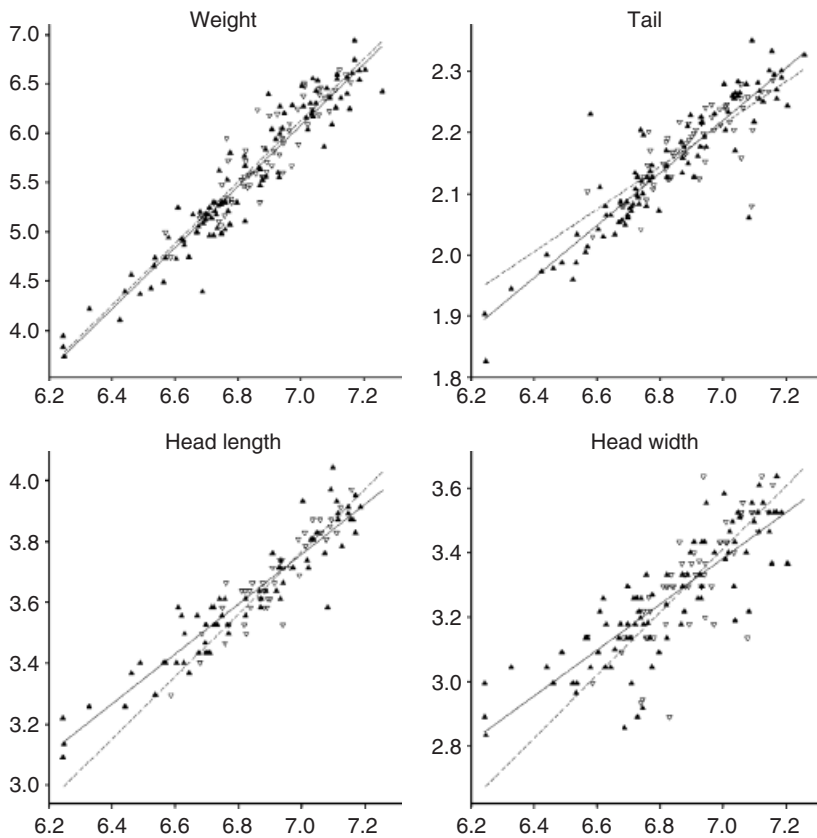
Figure 5 Relationships between the snout—vent length of individual green pythons *Morelia viridis* at Iron Range and other morphometric variables measured; females – filled triangles and solid line; males – open inverted triangles and broken line. All data have been transformed with natural logarithms.
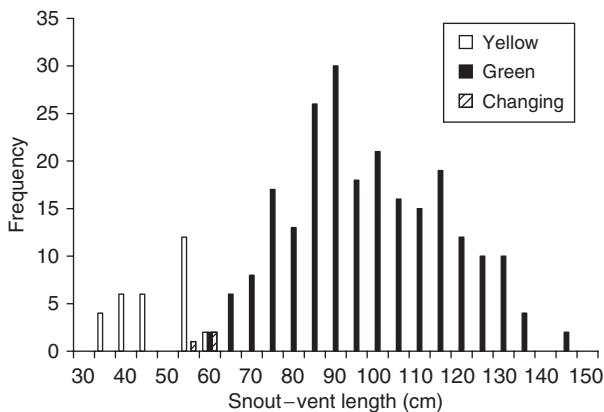

Figure 6 Frequency of snout–vent lengths (SVLs) recorded for all green python *Morelia viridis* captures between 1999 and 2005 at Iron Range, Australia. Numbers on the *x*-axis represent the upper limit of each SVL grouping.

of both yellow and green). During the study we made 262 captures, resulting in 30 yellow, three changing and 229 green records (Fig. 6). Multiple capture records of an individual were included in this analysis. The largest yellow individual was 56 cm, whereas the smallest green individual was 59.5 cm. The three individuals in the process of changing from yellow to green measured 53.3, 55.6 and 58.2 cm. The colour change in two of these individuals where we

observed the whole process lasted 8 days in both cases (pure yellow to pure green colour) and was not associated with a skin slough. Using the equation derived from the von Bertalanffy growth model, the colour change occurred between 0.9 and 1.1 years old.

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 *c*. 1 year of age.

Life history

As in the case of 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 because of the variation in growth rates between individual snakes (Madsen & Shine,

2000) and the small numbers of recaptures on which the analysis was based. We were therefore unable to test for differences between the sexes in growth rate, asymptotic size or age at maturity. The largest female was 14 cm 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 sexually at smaller sizes than females (Shine & Slip, 1990), and our data suggest that they reach maturity *c.* 1.2 years earlier. This difference in maturity age of *c.* 1 year is common in snakes (Parker & Plummer, 1987). On the basis of a predicted hatching date in late November, males mature in the middle of their third year and females mature the following year. The predicted maximum age of *c.* 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 may be due to two types of sampling error. First, hatching and initial dispersal for green pythons may occur during periods when we were not in the field. This is unlikely as our data suggest that most individuals hatch in late November near the beginning of our major research period. Second, hatching sites for green pythons have never been observed and it may be that neonates hatch and initially forage in different areas to larger individuals where we did not search. However, we did catch three young individuals within a month of hatching that were within 5 m of each other, suggesting that we were searching in the appropriate habitat and that neonates move very little during the first months of life. This accords with our radio-tracking data (Wilson *et al.*, in press) that showed average daily movements of 3 m 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 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, we 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. We also found no difference in spur lengths between the sexes, refuting the findings of previously published studies (Shine & Slip, 1990; Barker & Barker, 1994). In contrast, we 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 strongest 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 either was 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 our data. The lack of SSD 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 we 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. We never saw males interacting, and as their density is low, our 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 (Wilson *et al.*, in press), 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 (T. Mensforth, pers. comm.). This contrasts with the closely related tropical scrub python *Morelia kinghorni*, where adult males are heavier and longer than adult females and are known to compete for matings (Fearn, Schwarzkopf & Shine, 2005).

Reproduction appears to be infrequent in our population as is typical for most Australasian python species (Shine & Slip, 1990; Madsen & Shine, 1996). None of the 157 adult females we captured nor any of the 21 individuals radio-tracked for up to 18 months (Wilson *et al.*, in press) 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 (Madsen & Shine, 1999; Bertona & Chiaraviglio, 2003; Reading, 2004).

We can however deduce some details of the breeding cycle from our 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. We used only individuals within 15 cm of hatching as growth rates are highly variable in snakes (Madsen &

Table 1 Evolutionary significance of ontogenetic colour change

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 individuals need to change colour to remain cryptic	Yes
	Thermoregulation, water balance, photoprotection	Different-size individuals have different requirements	Unlikely – thermoregulation is 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

Table adapted from Booth (1990).

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 brood their eggs for *c.* 50 days in captivity (Maxwell, 2003), our data suggest 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 and 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 (see Wilson in a forthcoming edited book on boas and pythons). 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, 1996). Following the predicted hatching date in late November, there is increased activity in adult green pythons of both sexes until March, which we attribute to mate searching (Wilson *et al.*, in press). From April until the beginning of the next breeding season in October, individuals are relatively sedentary and inactive (Wilson *et al.*, in press).

OCC

Green pythons showed great consistency in the size at which they changed from yellow to green (Fig. 6). There was no overlap in size between the two colour morphs, and the three individuals we 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 6 months (Switak, 1975) and 3 years (Worrell, 1951); however, the age when OCC occurs in the wild appears to be more constrained. On the basis of our growth model (Fig. 3), individuals change colour when they are *c.* 1 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 *Co. caninus* of South America shows similar OCC, with the colour change occurring in the same size range of 55–60 cm (Stafford & Henderson, 1996). The underlying causes of colour change in *Co. caninus* have never been studied, but may be similar to those of green pythons given their strongly convergent ecological attributes.

Although colour change has long been of interest to scientists (Poulton, 1890; Cott, 1957), 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 because of their solitary nature and nocturnal activity patterns. Colour-mediated interspecific communication can involve crypsis, mimicry and aposematism (see the 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, we will restrict this discussion to the change from yellow to green, as red morphs were not observed during our 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 our 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. We 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 (Wilson *et al.*, in press), with yellow individuals restricted to more open areas where light reached the ground, whereas 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, whereas 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 our observations, but can only be accurately determined using spectroradiometry and the eye properties of predator and prey species. 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.

Acknowledgements

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