

The adaptive significance of ontogenetic colour change in a tropical python

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Ontogenetic colour change is typically associated with changes in size, vulnerability or habitat, but assessment of its functional significance requires quantification of the colour signals from the receivers' perspective. The tropical python, *Morelia viridis*, is an ideal species to establish the functional significance of ontogenetic colour change. Neonates hatch either yellow or red and both the morphs change to green with age. Here, we show that colour change from red or yellow to green provides camouflage from visually oriented avian predators in the different habitats used by juveniles and adults. This reflects changes in foraging behaviour and vulnerability as individuals mature and provides a rare demonstration of the adaptive value of ontogenetic colour change.

Keywords: colour polymorphism; ontogenetic colour change; crypsis; *Morelia viridis*; python

1. INTRODUCTION

The colours displayed by individuals may help them avoid predation (Ruxton *et al.* 2004). Bright colours may be used to advertize the distastefulness or hazar-dousness of a species to potential predators (apose-matism) or to mimic aposematic species (Pfennig *et al.* 2001; Mappes *et al.* 2005). Alternatively, individuals can remain concealed by ensuring that their overall coloration resembles the natural back-ground of their environment (Endler 1978; Cuthill *et al.* 2005).

The adaptive significance of coloration may be more complex when the individuals in a population undergo ontogenetic colour change or are colour polymorphic. Both the phenomena are presumably adaptive but their functional significance is poorly understood and has rarely been investigated in vertebrates (Booth 1990; Creer 2005). A common manifestation of ontogenetic colour change is when juveniles begin their lives with drab or cryptic coloration and bear the costs of bright colours only when they become sexually active (e.g. birds in breeding plumage). In other cases, however, ontogenetic colour change is associated with changes in size, vulnerability or habitat (Booth 1990). Colour polymorphisms are

uncommon but widespread in many vertebrate groups (Hoffman & Blouin 2000; Galeotti *et al.* 2003) and can be maintained through a variety of mechanisms, including aggressive mimicry, sexual selection and frequency-dependent predation (Munday *et al.* 2003; Punzalan *et al.* 2005; Janssen *et al.* 2006). In all the cases, assessment of the functional significance of differently coloured individuals requires quantification of the colour signals from the receivers' perspective (Endler & Mielke 2005).

Green pythons (*Morelia viridis*) are ideal for exam-ining the adaptive significance of ontogenetic colour change. The juveniles have two colour morphs, bright yellow and 'brick' red, whereas the adults are a vibrant green (figure 1a–c). Individuals change colour when they are approximately 55 cm long (Wilson *et al.* 2006b). The change does not reflect sexual maturity (Shine & Slip 1990) but coincides with changes in both diet and habitat. Radio-tracked yellow morphs always remained on the ground at the rainforest edge where they hunt small reptiles and invertebrates. By contrast, green individuals preferred the rainforest interior where they either hunt rodents near the ground or birds in the canopy (Wilson *et al.* 2006a; Wilson *in press*). To avoid the biases of human colour vision (Endler & Mielke 2005), we used both the python visual system and that of their avian predators to compare the conspicuousness of each morph against the various habitat backgrounds. We show that colour change from red or yellow to green in *M. viridis* provides camouflage from visually oriented avian predators in the different habitats used by the juveniles and the adults. This reflects changes in foraging behaviour and vulnerability as individuals mature and provides a rare demonstration of the adaptive value of ontogenetic colour change.

2. MATERIAL AND METHODS

All fieldwork was conducted in the Iron Range National Park (12° S, 142° E), Cape York Peninsula, Australia (Wilson *et al.* 2006b). Adult and juvenile green pythons were captured by spotlighting both inside rainforest patches and along the rain-forest–woodland ecotone. We used an Ocean Optics S2000 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 (provided by A. Bedford). Scans were taken at 11 locations on each snake: on top of the head, under the chin, then three each on the dorsal surface, side and ventral surface just posterior to the head, in the mid-body region and anterior to the cloaca. We measured the reflectance of the visual backgrounds (mostly live and dead leaves, but also tree trunks and vines; $n \geq 30$ scans per location) by taking random transects of background objects at both hunting and resting locations of 31 individual snakes. These individuals were located from ground level to canopy height (approx. 25 m). We 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, we 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 (Endler 1993; Sillman *et al.* 2001; Hart & Vorobyev 2005). The main predators of green pythons appear to be black butcherbirds (*Cracticus quoyi*, Cor-vida), rufous owls (*Ninox rufa*, Strigidae) and a variety of diurnal raptors, all of which have the avian V-type eye with relatively weak ultraviolet sensitivity (Vorobyev *et al.* 1998; Hart & Vorobyev 2005). We used the spectral properties of the open/cloudy light environment when comparing between locations with different light properties (Endler 1993). For the avian V-type eye, the four light-adapted outputs (one per photoreceptor type) were converted to relative outputs (the basis for colour vision) and mapped in tetrahedral space (Endler & Mielke 2005).

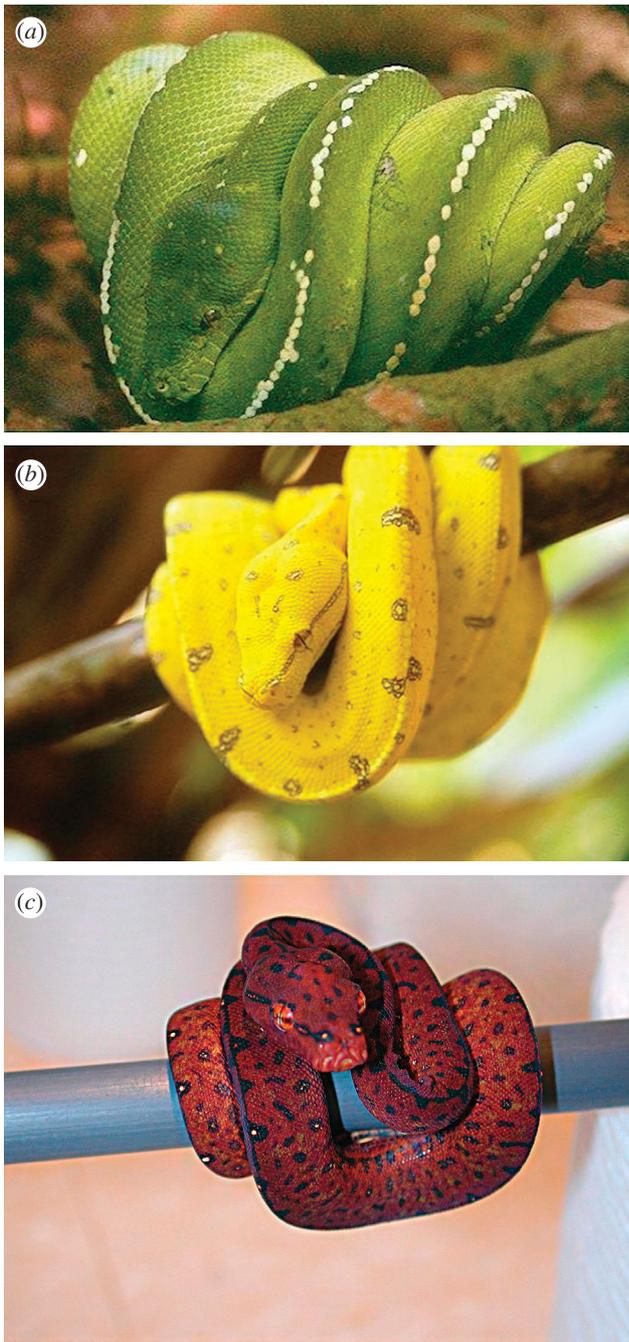


Figure 1. The three colour morphs of the green python *Morelia viridis* in typical resting posture: (a) green; (b) yellow and (c) red. Photos (a) and (b) by the authors, photo (c) used with permission of T. Morris.

We used compositional analysis to test for differences between the colours of yellow and green morphs against their typical and atypical visual backgrounds and from the perspective of different viewing species. As natural colour patterns violate the assumptions of standard multivariate statistical techniques, we used LSED-MRPP, a distribution-free test equivalent to a nested ANOVA (Endler & 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), and it is the relative magnitudes of these values that correlate with predation or sexual selection effects on fitness. We calculated the disparity for each individual, together with the pooled disparity of each colour type (green, yellow and red), against each background type where individuals were regularly recorded and also against other backgrounds where they were not recorded.

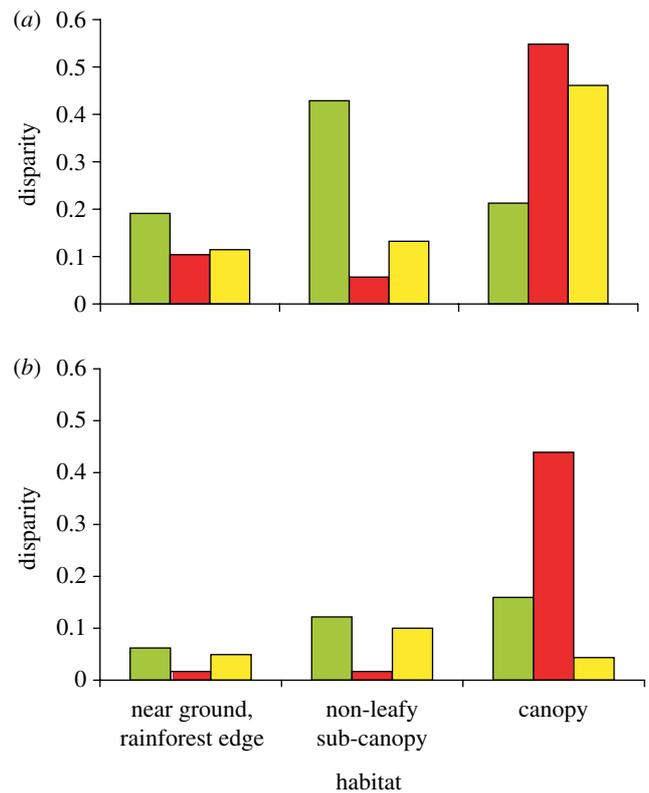


Figure 2. Disparity values for the three colour morphs of green pythons as viewed by (a) avian predators and (b) conspecifics against the three major visual backgrounds of their habitat. Column colours represent the python colour morph.

3. RESULTS

The three colour morphs examined in this study are shown in figure 1. All juvenile pythons captured at our Australian field site were yellow and were always found near the rainforest edge (Wilson *et al.* 2006a). Red juveniles have only been recorded at three sites in New Guinea, nonetheless we measured the reflectance of two captive red juveniles for comparison with the yellow and the green morphs. Calculation of the disparity of each snake colour revealed that the yellow morphs were significantly less conspicuous than green morphs to both conspecifics and avian predators against the rainforest edge background where they occur (figure 2; Mann-Whitney $U=0$, $p<0.001$ for both python and avian eye types, $n=31$ individuals in each case). The two captive red individuals were similar to the yellow morphs in their disparity against this background (figure 2).

Within the rainforest where only green morphs are found (Wilson *et al.* 2006a), our analysis showed that the yellow morphs would be significantly less conspicuous than green against non-leafy backgrounds. However, green was the least conspicuous colour in the canopy (Mann-Whitney $U=0$, $p<0.001$, $n=31$ individuals in each case; figure 2). Red appeared to be less conspicuous than yellow against non-leafy backgrounds but more conspicuous than yellow against the canopy (figure 2). Python and avian perspectives differed significantly (Wilcoxon matched-pairs test, $n=9$ pairs, $p=0.004$); all the colour morphs were more conspicuous to raptor predators than conspecifics.

4. DISCUSSION

Our results show that the colours of adult and juvenile green pythons help them to avoid predation from avian predators in the habitats they prefer. Although red and yellow are typical warning colours to other species (Ruxton *et al.* 2004), these pythons are not aposematic or aposematic mimics (Wilson *et al.* 2006b). Instead, the relatively reduced conspicuousness of yellow and green in the habitats where these morphs spend most time suggests that the primary function of multiple colours is to minimize detection by predators (Booth 1990). Although further functions of the juvenile colours cannot be ruled out, each colour morph occurred where it was least conspicuous which suggests a reduced role for intraspecific communication.

Our data raise the question of why individuals turn green at all when they could remain yellow (or red) and continue to restrict their movements to non-leafy backgrounds at the rainforest edge or move inside the rainforest but remain in non-leafy areas on the ground. The change to green coincides with a behavioural switch in foraging tactics. Owing to their gape size, yellow individuals are restricted to hunting small ground-dwelling heliothermic reptiles and invertebrates during the day. These prey types are more common in rainforest gaps and edges (Vitt *et al.* 1998; Wilson *in press*). As individuals increase in size, they change to green and their increased gape size allows them to move inside the rainforest and add larger vertebrates including rodents and birds to their diet. Rodents are hunted on the ground at night and birds in the canopy during the day (Wilson *et al.* 2006b; Wilson *in press*). Inclusion of birds in the diet appears to be important for increased food intake, especially for female green pythons which need additional body condition before they can initiate breeding (Reading 2004). Thus, green coloration provides diurnal camouflage while hunting in the canopy and is only more conspicuous in locations primarily used at night (Wilson *in press*), when visual predation is less important.

Yellow and red juvenile colour morphs occur at markedly different frequencies throughout the species' range. Although the yellow morph is widespread, red juveniles are known only from three geographically separated localities in New Guinea (D. Wilson unpublished data). Although we lacked the sample size necessary for statistical comparison, our results suggest that red morphs may enjoy a selective advantage in sub-canopy, non-leafy environments (figure 2). This habitat type is most likely to be found in closed canopy rainforest with an understory comprising tree trunks, vines and lianas with relatively few leaves. Such rainforest would occur mostly in areas sheltered from storms or human disturbance, and these areas are typically more remote and less likely to be sampled by researchers. The abrupt colour change of green pythons, linked with changes in habitat, diet and behaviour, provides a rare demonstration of the selective force maintaining ontogenetic colour change. Further research is required to understand the timing of the colour

change and why yellow juveniles are more common than red in most of the species' range.

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- Booth, C. L. 1990 Evolutionary significance of ontogenetic colour change in animals. *Biol. J. Linn. Soc.* **40**, 125–163.
- Creer, D. 2005 Correlations between ontogenetic change in color pattern and antipredator behavior in the racer, *Coluber constrictor*. *Ethology* **111**, 287–300. (doi:10.1111/j.1439-0310.2004.01062.x)
- Cuthill, I., Stevens, M., Sheppard, J., Maddocks, T., Párraga, C. & Troscianko, T. 2005 Disruptive coloration and background pattern matching. *Nature* **434**, 72–74. (doi:10.1038/nature03312)
- Endler, J. 1978 A predator's view of animal colour patterns. *Evol. Biol.* **11**, 319–364.
- Endler, J. 1993 The colour of light in forests and its implications. *Ecol. Monogr.* **63**, 1–27. (doi:10.2307/2937121)
- Endler, J. & Mielke, P. 2005 Comparing entire colour patterns as birds see them. *Biol. J. Linn. Soc.* **86**, 405–431. (doi:10.1111/j.1095-8312.2005.00540.x)
- Galeotti, P., Rubolini, D., Dunn, P. & Fasola, M. 2003 Colour polymorphism in birds: causes and functions. *J. Evol. Biol.* **16**, 635–646. (doi:10.1046/j.1420-9101.2003.00569.x)
- Hart, N. & Vorobyev, M. 2005 Modelling oil droplet absorption spectra and spectral sensitivities of bird cone photoreceptors. *J. Comp. Physiol. A* **191**, 381–392. (doi:10.1007/s00359-004-0595-3)
- Hoffman, E. & Blouin, M. 2000 A review of colour and pattern polymorphisms in anurans. *Biol. J. Linn. Soc.* **70**, 633–665. (doi:10.1006/bjil.1999.0421)
- Janssen, K., Erikstad, K. & Bensch, S. 2006 Offspring sex ratio allocation in the parasitic jaeger: selection for pale females and melanic males? *Behav. Ecol.* **17**, 236–245. (doi:10.1093/beheco/arj015)
- Mappes, J., Marples, N. & Endler, J. 2005 The complex business of survival by aposematism. *Trends Ecol. Evol.* **20**, 598–603. (doi:10.1016/j.tree.2005.07.011)
- Munday, P., Eyre, P. & Jones, G. 2003 Ecological mechanisms for coexistence of colour polymorphism in a coral-reef fish: an experimental evaluation. *Oecologia* **137**, 519–526. (doi:10.1007/s00442-003-1356-7)
- Pfennig, D., Harcombe, W. & Pfennig, K. 2001 Frequency-dependent Batesian mimicry. *Nature* **410**, 323. (doi:10.1038/35066628)
- Punzalan, D., Rodd, F. & Hughes, K. 2005 Perceptual processes and the maintenance of polymorphism through frequency-dependent predation. *Evol. Ecol.* **19**, 303–320. (doi:10.1007/s10682-005-2777-z)
- Reading, C. 2004 The influence of body condition and prey availability on female breeding success in the smooth snake (*Coronella austriaca* Laurenti). *J. Zool. Lond.* **264**, 61–67.
- Ruxton, G., Sherratt, T. & Speed, M. 2004 *Avoiding Attack: the evolutionary ecology of crypsis, aposematism and mimicry*. Oxford, UK: Oxford University Press.

- Shine, R. & Slip, D. J. 1990 Biological aspects of the adaptive radiation of Australasian pythons (Serpentes: Boidae). *Herpetologica* **46**, 283–290.
- Sillman, A., Johnson, J. & Loew, E. 2001 Retinal photoreceptors and visual pigments in *Boa constrictor imperator*. *J. Exp. Zool.* **290**, 359–365. (doi:10.1002/jez.1076)
- Vitt, L., Avila-Pires, T., Caldwell, J. & Oliviera, V. 1998 The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. *Conserv. Biol.* **12**, 654–664. (doi:10.1046/j.1523-1739.1998.96407.x)
- Vorobyev, M., Osorio, D., Bennett, A., Marshall, N. & Cuthill, I. C. 1998 Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Physiol. A* **183**, 621–633. (doi:10.1007/s003590050286)
- Wilson, D., Heinsohn, R. & Legge, S. 2006a Age- and sex-related differences in the spatial ecology of a dichromatic tropical python (*Morelia viridis*). *Aust. Ecol.* **31**, 577–587. (doi:10.1111/j.1442-9993.2006.01519.x)
- Wilson, D., Heinsohn, R. & Wood, J. 2006b Life history traits and colour change in the arboreal tropical python *Morelia viridis*. *J. Zool. Lond.* **270**, 399–407.
- Wilson, D. In press. Foraging ecology and diet of an ambush predator: the green python M. In *Biology of the boas and pythons* (ed. R. Henderson & R. Powell), Eagle Mountain, Utah: Eagle Mountain Publishing.