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Geographic frequency and ecological correlates of juvenile colour polymorphism in green pythons (*Morelia azurea* and *Morelia viridis*)

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Abstract. Colour polymorphisms are common in nature, but their evolutionary significance and the mechanisms maintaining them sometimes remain poorly understood. Polymorphic green pythons (*Morelia azurea* and *Morelia viridis*) are born either red or yellow. Several processes are proposed to maintain such polymorphisms, and the assumption that colour is adaptive predicts that it may be correlated with a series of life-history and/or ecological traits. We examined 1090 green pythons from northern Australia and New Guinea and reveal strong geographic variation in the frequency of juvenile polymorphism. Some variation is explained by known genetic structure among populations, while stochastic processes (e.g. bottlenecks, founder effects) likely explain remaining variation. The yellow juvenile morph occurs in all populations of *M. azurea* and *M. viridis*, whereas the red morph occurs only in some populations of *M. azurea* and at varying frequencies. Yellow and red juveniles did not differ in morph-specific survival, sex ratios, morphology (tail length, head shape and mass) or diet. We discuss our results in relation to several hypotheses relating to maintenance of colour polymorphisms in nature. Although inconclusive, we are reluctant to suggest that colour is non-adaptive, and encourage additional experimental field research on the significance of polymorphism in these taxa.

Keywords: Australia, Biak Island, geographic variation, green python, natural selection, *Morelia azurea*, *Morelia viridis*, New Guinea, niche divergence, snake

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Introduction

The adaptive significance of animal colour polymorphism has long been of interest to biologists (Darwin 1859; Cott 1940; Huxley 1955). For many taxa, the evolutionary forces that give rise to polymorphisms are well known, whereas in others polymorphisms may simply arise through non-selective processes (e.g. migration, genetic drift and bottlenecks: see Reillo and Wise 1988; Brakefield 1990; King and Lawson 1995). Of equal importance to the development of polymorphisms are the mechanisms that maintain them (Galeotti *et al.* 2003; Roulin 2004; Gray and McKinnon 2007). The most common mechanisms include: (1) frequency-dependant selection, where fitness is higher in the rarer colour morph because predators select for more abundant morphs (Allen 1988; Olendorf *et al.* 2006); (2) disruptive selection, where several different optima are possible within a population, thus selecting for extreme phenotypes that exploit different niches (Endler 1986; Roulin 2004); (3) sexual selection, where preferential mate choice selects for a particular morph (Kingston *et al.* 2003; Roulin 2004); and (4) neutral selection, where neither colour morph receives a

fitness advantage and the population is large enough so that alleles are not eliminated through genetic drift (Galeotti *et al.* 2003). Although these general processes are well understood, identifying their role in maintaining specific cases of polymorphism remains challenging, particularly in vertebrates (Hoffman and Blouin 2000; Wilson *et al.* 2007).

Arguably one of the most outstanding vertebrate colour polymorphisms is that exhibited by the tropical arboreal green pythons, *Morelia azurea* and *Morelia viridis* (Natusch *et al.* 2020). Green pythons are medium-sized (<2 m) ambush predators widely distributed in mainland New Guinea, several offshore islands, and a small area of Australia (O'Shea 1996; Natusch and Natusch 2011). Juvenile green pythons are born either banana yellow or brick red before changing colour to green; both morphs can occur in a single clutch (Maxwell 2005; Natusch and Lyons 2012). Colouration in this species appears to be adaptive: ontogenetic colour changes coincide with changes in head shape, diet, and habitat use, and the yellow juvenile and green adult morphs have been shown to be optimally cryptic to avian predators in their preferred habitats (Wilson *et al.* 2006, 2007; Natusch and Lyons 2012).

The first step towards understanding the maintenance of juvenile polymorphism in green pythons is to test the null hypothesis that colour variation has no major biological correlates. For example, if polymorphism is maintained by frequency-dependent selection we might expect one morph to be less abundant and have higher survivorship than the other. Alternatively, if disruptive selection maintains polymorphism, we might expect morphs to utilise different habitats, select different prey types, and display subtle differences in morphology (Shine *et al.* 1998). Here, we examine morph frequencies of green pythons from throughout their range and test for divergence in ecological traits between juvenile colour morphs that may explain how polymorphism is maintained in these taxa.

Materials and methods

Polymorphism frequency

We examined 1090 juvenile and adult green pythons from throughout their range and recorded juvenile colouration as either red or yellow. Records came from snakes collected in New Guinea by local villagers (see Lyons and Natusch 2011; Natusch and Lyons 2014) or through fieldwork in Australia (see Natusch and Natusch 2011). We also supplemented our sample with green pythons from the collections of the following specimen repositories: American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); Australian National Wildlife Collection, Canberra (ANWC); British Museum of Natural History, London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); Louisiana Museum of Natural History, Baton Rouge (LSUMZ); National Museum of Natural History, Paris (MNHN); Museum Victoria, Melbourne (MV); Museum Zoologicum Bogoriense, Bogor (MZB); Queensland Museum, Brisbane (QM); National Museum of Natural History, Washington DC (USNM); and the University of Papua, Manokwari (Natusch *et al.* 2020). We determined the original juvenile colour of adult green specimens using the residual juvenile pattern present on the snake's dorsal surface. The pattern of red juveniles consists of prominent triangular saddles, whereas the pattern of yellow juveniles comprises thin lines or rosettes alternating either side of the vertebral ridge (Natusch *et al.* 2020). We confirmed the retention of juvenile patterning into adulthood by following captive specimens as they grew (Natusch, unpubl. data 2021). Although this was straightforward for most specimens, we excluded several older and heavily scarred individuals, and some museum specimens in poor state of preservation, because of difficulties in accurately determining juvenile colouration. Nevertheless, this is unlikely to bias our results because such difficulties are not colour dependant. Finally, we examined colour morph frequencies in seven wild clutches of eggs from New Guinean green pythons. We divided specimens of green pythons *a priori* into regional samples based on known biogeographical barriers to gene flow and known genetic structure (see Beehler 2007; Deiner *et al.* 2011; Natusch *et al.* 2020). Regional groupings are depicted in Fig. 1.

Ecological and morphological comparisons

To test for ecological and morphological divergence between green python colour morphs we examined a sample of 120 red and 154 yellow juvenile *M. azurea azurea* from Biak Island in northern Papua. We analysed ecological differences between colour morphs in a single taxon only to reduce the potential effect of interpopulation trait divergence, and because sample sizes for both morphs were sufficiently large for this population only. We measured all snakes captured to determine: (1) snout-to-vent length (SVL), by measuring the snake against a steel ruler to the nearest 0.5 cm, (2) tail length, from the cloaca to the tip of the tail, (3) head length, from the tip of the snout along the dorsal midline to the base of the skull, (4) head width, at the widest point of the skull, (5) mass, to the nearest 1 g using Pesola spring scales (Pesola AG, Baar, Switzerland), and (6) sex, by inserting a blunt probe into the cloacal bursae and recording depth. We did not sex exceptionally small juveniles to avoid injury to the snakes. Prey types captured by red and yellow juveniles were determined by microscopy of snake scats.

Statistical analysis

If colour morphs differ in survival, we would expect morph frequency to vary between size classes. However, because green pythons change colour with age, differential survival between morphs is relevant only for juvenile snakes. We thus divided juveniles into two size classes (30–49 cm and 50–70 cm) and used the proportion of the two colour morphs in each class as a proxy for morph-specific survival. Although a small number of the larger juveniles had begun to change colour, each retained the majority of their juvenile colouration, making them useful for our analysis (Natusch and Lyons 2012). We used contingency table analysis to test for differences in morph survival between size classes, differences in morph frequencies between geographic regions, and for morph divergence from an equal sex ratio. Because morphological traits in snakes vary with increasing body size, we used analysis of covariance (ANCOVA) to examine morphological divergence between the two colour morphs. We used tail length, body mass, head length and head width as dependent variables, SVL as the covariate, and colour as the factor. We log-transformed all data to meet assumptions of normality and homogeneity of variance. All analyses were conducted in JMP Pro 14 (SAS Institute, Cary, NC).

Results

Polymorphism frequency

The relative frequency of red and yellow juvenile morphs varied significantly between taxa and between populations within taxa (Fig. 1). The red juvenile morph was never recorded in populations of *M. viridis*. The red morph was also notably absent from island populations in the Raja Ampat Archipelago (Fig. 1). Relative numbers of the red and yellow morphs in most other populations were approximately equal (Fig. 1). However, populations from the Vogelkop and Bomberai Peninsula were skewed towards a greater proportion of yellow juveniles (although sample sizes for the Bomberai population are small) (Fig. 1). Geographic variation in the

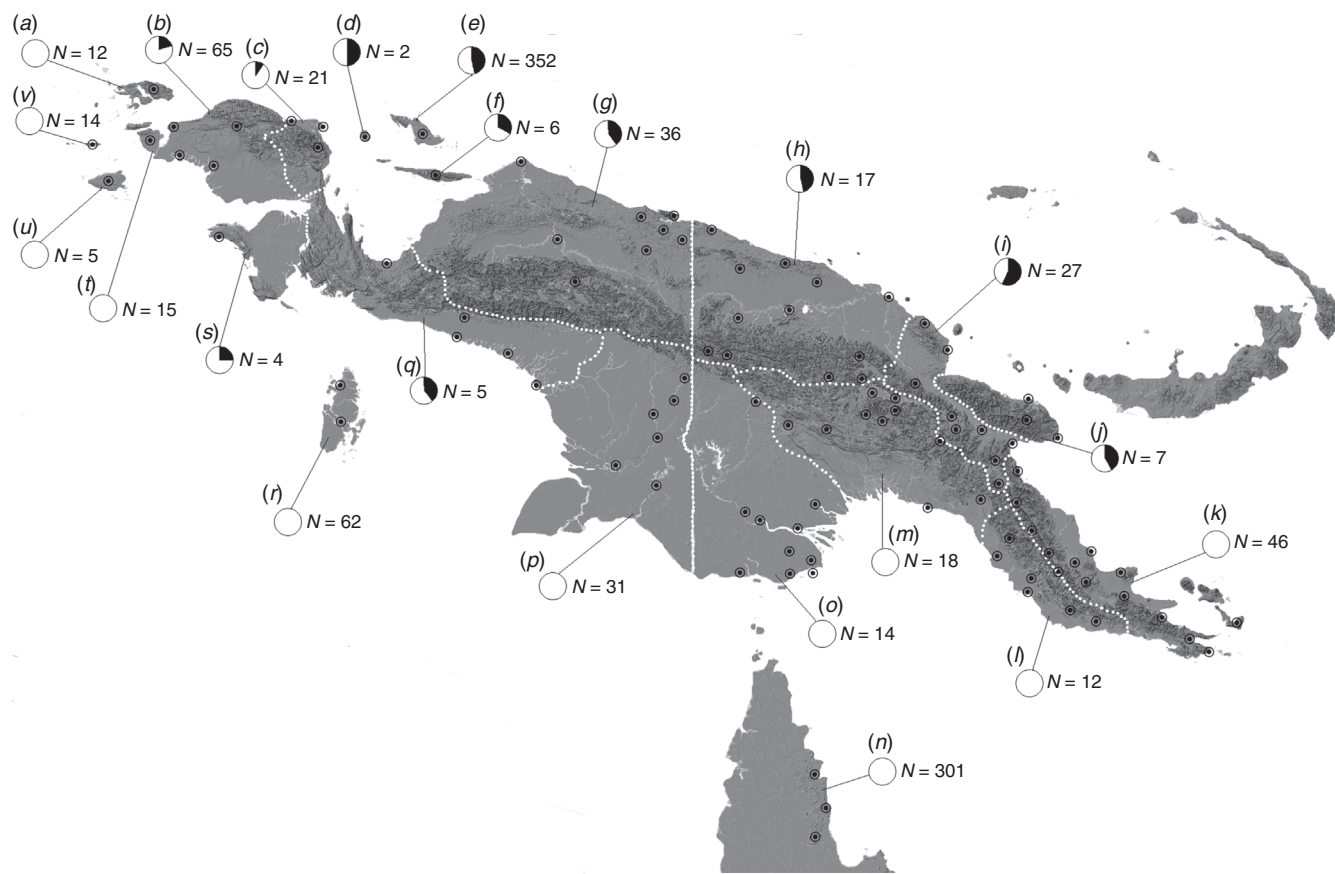


Fig. 1. Juvenile polymorphism frequencies in populations of green pythons surveyed in the present study (roughly delineated by dashed lines). Pie charts represent the proportion of red (black) and yellow (white) green pythons in each population, as follows: (a) Waigeo Island, (b) western Vogelkop, (c) eastern Vogelkop, (d) Numfor Island, (e) Biak Island, (f) Yapen Island, (g) North Papuan Highlands and Mamberamo drainage, (h) Sepik drainage, (i) Bulolo Valley and northern Papua New Guinea, (j) Huon Peninsula, (k) far eastern Papua New Guinea, (l) Central Province, (m) Gulf and southern Highlands, (n) Australia, (o) Trans-fly Papua New Guinea, (p) southern Papua, (q) Vogelkop Ithmus, (r) Aru Islands, (s) Bomberai Peninsula, (t) Salawati Island, (u) Misool Island, (v) Kofiau Island. N, sample size.

Table 1. Clutch sizes, maternal colouration and resulting hatchling polymorphism frequencies in four populations of *M. azurea* and *M. viridis*

Taxon	Population	Clutch size	Red	Yellow	Maternal colouration
<i>M. a. azurea</i>	Biak Island	20	20	0	Red
<i>M. a. azurea</i>	Biak Island	14	7	7	Yellow
<i>M. viridis</i>	Southern New Guinea	16	0	16	Yellow
<i>M. viridis</i>	Southern New Guinea	13	0	13	Yellow
<i>M. a. pulcher</i>	Raja Ampat (Salawati Island)	14	0	14	Yellow
<i>M. a. pulcher</i>	Vogelkop Peninsula	14	11	3	Red
<i>M. a. pulcher</i>	Vogelkop Peninsula	12	1	11	Yellow

frequency of the two morphs was corroborated further via examination of juveniles from seven wild clutches of eggs (Table 1).

Ecological and morphological comparisons

The relative numbers of each colour morph from Biak Island differed slightly between the sexes, with more yellow males

and more red females, but this difference was not great enough to be statistically significant ($\chi^2 = 1.92$, d.f. = 1, $P = 0.16$) (Fig. 2). Similarly, survival was not morph specific ($\chi^2 = 0.42$, d.f. = 1, $P = 0.52$) (Fig. 2). Red and yellow morphs did not differ significantly in any of the traits that we measured; ANCOVA revealed $P > 0.05$ for relative tail length, head length, head width and body mass. Red and yellow juvenile morphs did not differ in food habits; all preyed almost

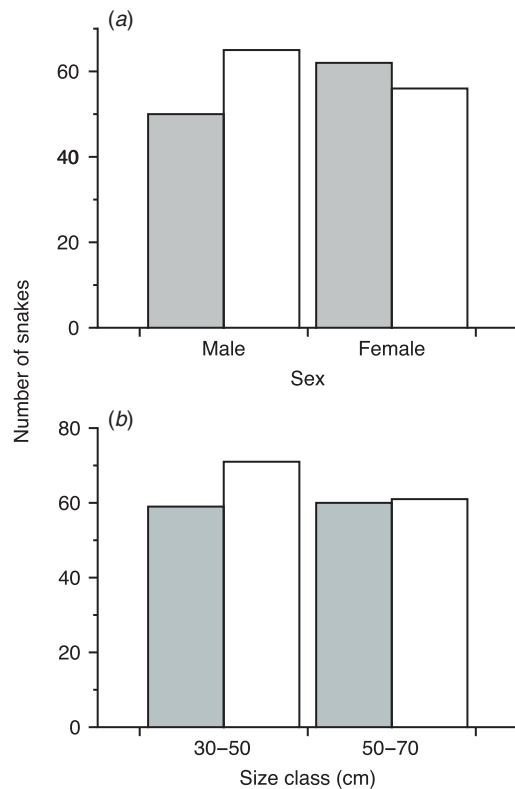


Fig. 2. Sex ratios (a) and relative survival (b) of red (grey columns) and yellow (white columns) juvenile green pythons from Biak Island.

exclusively upon scincid lizards. In total, 41 juvenile scats contained the scales, feet, tail remnants and undigested jawbones of small, mostly unidentified, scincid lizards. Thirteen prey items were representatives of the scincid genus *Emoia* (very common lizards on Biak Island); however, it was not possible to identify these to species level. The only non-reptilian remains were recovered from a 69 cm SVL yellow juvenile that had eaten a small, unidentified bird.

Discussion

Geographic variation in morph frequencies

Our results reveal strong geographic variation in the occurrence and frequency of juvenile colour polymorphism in green pythons. The most notable divergence is between the two species, *M. azurea* and *M. viridis* (two versus one juvenile morph, respectively). Whether the red juvenile morph was lost in *M. viridis* after the two species diverged, or whether it evolved independently within *M. azurea* is unclear. However, the extensive geographic range occupied by *M. viridis* supports the latter interpretation. The apparent absence of the red morph in *M. azurea* from the islands of Raja Ampat is also noteworthy because of their proximity to the Vogelkop Peninsula where the red juvenile morph is present (Fig. 1). The islands within the Raja Ampat archipelago were most recently connected to mainland New Guinea approximately 8000 years ago (Voris 2000). The red morph may have been lost due to inevitably small population sizes and random genetic

processes taking place on these islands as sea levels rose and fell (e.g. genetic drift, founder effects, bottlenecks: see Roulin 2004). In agreement, the yellow morph was the more common morph on the neighbouring west Vogelkop Peninsula, potentially facilitating the loss of the red morph from these islands (Fig. 1).

We also corroborated colour morph frequencies from wild hatchlings (Table 1). The two wild clutches from *M. viridis* consisted entirely of yellow individuals and captive breeding records for green pythons from the Aru Islands, Australia, and southern New Guinea have similarly never hatched red juveniles (M. Cermak and V. Odinchenko, pers. comm.). Despite the genetic basis of juvenile colour in green pythons being poorly understood, our limited data suggest that, like other polymorphic snake species, parental colouration may act on offspring colour through simple Mendelian inheritance (Zweifel 1981; King 2003). However, captive breeding efforts to date have been unable to unequivocally prove either colour to be recessive. Further study is needed to clarify this.

Maintenance of polymorphism

Our data allow us to make some preliminary conclusions about the mechanisms maintaining juvenile colour polymorphism in green pythons. Non-random mating is unlikely to maintain juvenile polymorphism in this species because both juvenile morphs become monomorphic before reaching sexual maturity (Natusch and Lyons 2012). Similarly, frequency-dependant selection is unlikely to maintain polymorphism because our results suggest that the two morphs are found in similar frequencies in most populations in which they occur (Fig. 1) and survival, sex and other ecological traits are not colour dependant (Fig. 2). Juvenile colour polymorphism in green pythons could be explained via disruptive selection, where we might expect differences in ecological traits between morphs utilising different niches. In agreement, yellow juvenile and green adult morphs are known to partition their niche (Wilson *et al.* 2007; Natusch and Lyons 2012). However, contrary to other studies of colour in snakes (Brodie 1992; Shine *et al.* 1998) we found no association between ecological attributes and colour. We have located both colour morphs hunting near the ground during the day in the same places (Natusch, pers. obs.). In these microhabitats both morphs are equally cryptic, and background matching tests found that both morphs preferred dark rather than light backgrounds (Garrett and Smith 1994; Wilson *et al.* 2007). That being said, such niche divergences may be subtle, and may be mediated in other ways (e.g. thermal advantages or constraints) untested in our study.

In summary, despite our inconclusive results we are reluctant to suggest that juvenile polymorphism in green pythons is non-adaptive (i.e. neutral) because (1) intuition suggests that the colouration of highly cryptic ambush predators would affect their fitness, and (2) because many species of unrelated snakes exhibit similar life-history traits (e.g. heavy bodied, colour polymorphic, ambush predators: Garrett and Smith 1994; Johnston 1996; Shine *et al.* 1998), suggesting an adaptive role for colour. Our study offers preliminary insights into potential avenues of future research. Experimental studies could use model snakes of different colours to understand habitat and morph-specific

predation frequency. Likewise, captive breeding studies are needed to resolve the mode of genetic inheritance and clarify the underlying mechanisms affecting morph frequencies in this species.

Conflicts of interest

The authors declare no conflicts of interest.

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