



# Relationships between ontogenetic changes in prey selection, head shape, sexual maturity, and colour in an Australasian python (*Morelia viridis*)

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Prey selection in many species is known to change ontogenetically, suggesting that associated changes in trophic structure may also be important. Several studies have examined relationships between prey selection and the size of trophic structures; however, few have explored these changes over ontogeny or the effects that they may have on a species broader ecology. The present study addressed this issue by examining relationships between changes in head size and prey selection in juveniles and adults from three populations of the python *Morelia viridis* and related them to changes in sexual maturity and ontogenetic changes in colour (OCC). Our scaling data for head size showed that juveniles and adults scaled mostly with negative allometry, and allometric slopes were significantly different before and after OCC. The change in head shape allometry was strongly associated with changes in prey selection from ectothermic to endothermic prey and with OCC in two of the three populations studied. OCC in the other population varied widely and may be the result of isolation on an oceanic island. Negatively allometric head growth is common in vertebrates and may serve a functional role in *M. viridis* by reducing the maximum ingestible prey size in adults, thus aiding arboreality. Our data do not allow us to test which of these changes have causal or resultant effects on one another; however, we suggest they may be part of an overall evolutionary defence–foraging strategy that circumvents costs imposed by restricting foraging opportunities to certain habitats. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, ••, ••–••.

ADDITIONAL KEYWORDS: allometry – crypsis – green tree – New Guinea – OCC – optimal foraging – snake.

## INTRODUCTION

The study of ontogeny has a prominent role in the evolutionary and ecological sciences (Darwin, 1859; Gould, 1966). As they grow, organisms undergo rapid and often dramatic changes in behaviour, ecology, and morphology (Werner & Gilliam, 1984; Booth, 1990). For example, several studies have shown that juveniles and adults frequently differ in their prey selection, presumably to maximize optimal foraging (Werner & Gilliam, 1984; Mushinsky, 1987). Consequently, changes in the size and shape of the feeding apparatus between ontogenetic stages also may be important for prey selection, particularly for species

that consume their prey whole (i.e. gape-limited predators; Shine, 1991; Arnold, 1993). Several studies have shown that, for gape-limited predators, the size and shape of the feeding apparatus is strongly correlated with the size and shape of prey (Arnold, 1993; Vincent *et al.*, 2005, 2006). For example, Vincent, Herrel & Irschick (2004) showed that head size and shape in the snake *Agkistrodon piscivorus* changes over ontogeny with increasing prey size. However, few studies have examined the relationship between ontogenetic changes in the shape of the feeding apparatus and prey selection, and the effect that such changes may have on a species broader ecology.

Perhaps the most visually dramatic change an individual can undergo is an ontogenetic change in colour (OCC). Some studies have suggested that OCC in

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cryptic species may have evolved to aid optimal foraging by circumventing costs imposed by restricting foraging opportunities to environments where coloration is most cryptic (Merilaita, Tuomi & Jormalainen, 1999; Speed & Ruxton, 2005). OCC might also be important for understanding broader aspects of ontogeny because it may reveal underlying changes in trophic function and morphology, and may clarify the environmental and developmental constraints that shape those changes. However, although OCC has been shown to coincide with changes in sexual maturity (such as development of adult plumage colour in birds; Roulin, 2004) and vulnerability (Creer, 2005), it remains poorly understood for many species (Booth, 1990) and, to our knowledge, its relationship to changes in prey selection and trophic morphology have never been examined.

In the present study, we addressed this issue by examining the relationships between ontogenetic changes in trophic structure (head length and width), colour, sexual maturity, and prey selection in juveniles and adults from three populations of the tropical arboreal python *Morelia viridis*. Snakes offer an ideal model for testing relationships between prey selection and trophic structure because their diet is constrained by their gape size (Arnold, 1993). Several studies have shown that snakes often exhibit allometric growth in their feeding structures, which have been suggested to improve juvenile performance by compensating for an absolutely small body size (Forsman & Lindell, 1993; Vincent *et al.*, 2005). Although the proximate cause(s) of these allometric changes are often unclear, one plausible explanation is that ontogenetic shifts in ecology may drive adaptive changes in the scaling of the trophic apparatus (Vincent *et al.*, 2007).

*Morelia viridis* is particularly appropriate for examining whether ontogenetic shifts in prey selection and trophic structure coincide with OCC (and therefore potentially other ecological changes) because this species undergoes a dramatic OCC from red or yellow to green (Wilson, Heinsohn & Wood, 2006; Wilson, Heinsohn & Endler, 2007). Thus, the present study aimed to answer four questions: (1) is trophic morphology allometric in *M. viridis*; (2) do head length and width allometries differ among juvenile and adult *M. viridis*; (3) do juveniles and adults differ in their prey selection, and (4) using body size as a dependent variable, do any observed differences in prey selection and head shape relate to one another or to changes in sexual maturity and OCC?

## MATERIAL AND METHODS

### SPECIMEN COLLECTION

We examined 908 *M. viridis* collected from Australia and the island of New Guinea between November

2007 and April 2011. Australian *M. viridis* were collected by surveying areas of closed forest habitat with a hand-held spotlight at night (Natusch & Natusch, 2011). All individuals captured in Australia were released immediately after measurements were recorded. New Guinean *M. viridis* were examined after they were opportunistically collected by villagers for the pet trade (Lyons & Natusch, 2011).

### REGIONAL GROUPINGS

We divided *M. viridis* into three regional samples for analysis based upon geographical separation and known genetic structure. New Guinea's central cordillera is an effective barrier to gene flow (Deiner *et al.*, 2011, and references therein), and *M. viridis* from north and south of the central range are genetically deeply divergent (Rawlings & Donnellan, 2003). Thus, we analyzed specimens from northern New Guinea and southern New Guinea (which also includes Australia) separately. The third population analyzed was from Biak, an oceanic island off the north coast of New Guinea. We noted a priori that the timing of OCC in Biak *M. viridis* was different from those inhabiting Australia or mainland New Guinea. This phenomenon is also well known among captive individuals in the pet industry (Maxwell, 2005), and thus we treated *M. viridis* from Biak as a separate group in the present analysis.

### EXAMINATION OF SNAKES

We recorded the colour of each snake as red, yellow, red or yellow changing (if OCC had begun but was incomplete), or green. The snout-vent length (SVL) of all *M. viridis* was measured to the nearest 0.5 cm using a steel ruler. Head length and width were measured using digital calipers to the nearest 0.1 mm, from the tip of the snout along the dorsal midline to the base of the skull, and at the widest point, respectively. We measured body mass to the nearest 1 g using Pesola spring scales, and sex was determined by inserting a blunt probe into the cloacal bursae and recording the depth.

Reproductive status was determined for a selected sample of New Guinean *M. viridis* that had recently undergone OCC, either by dissection of individuals killed by local people or found as fresh road kills. We regarded males as sexually mature if they had enlarged turgid testes or convoluted efferent ducts. Females were sexually mature if they possessed large ovarian follicles (> 5 mm) or were gravid (*sensu* Shine & Slip, 1990). Prey types captured by *M. viridis* were identified either by direct observation of predation events or examination of stomach contents and faecal samples.

## STATISTICAL ANALYSIS

We determined the timing of OCC via examination of the SVL frequencies of individuals that displayed juvenile or adult coloration, or intermediate between the two. To assess scaling of head shape trajectories in juveniles and adults, we regressed head length and width against SVL using reduced major-axis regressions (RMA). The scaling coefficient given by RMA describes the relative allometry or isometry of the relationship. As a result of the linearity of head shape and SVL measurements, we considered an isometric relationship to be 1. Deviations from isometry were considered significant if the isometric slope fell outside of the 95% confidence intervals of the observed slopes. Scaling coefficients significantly greater or less than those predicted by isometry were described as positive or negative allometry, respectively. All morphological data regressed using RMA were  $\log_{10}$ -transformed before analysis.

## RESULTS

## OCC

The timing of OCC in *M. viridis* was strongly associated with size in all localities except Biak (Fig. 1). The majority of individuals from southern and northern New Guinea changed colour at approximately 65 cm SVL. By contrast, *M. viridis* from Biak were found to begin changing colour as small as 55 cm SVL, and were often still changing when as large as 120 cm SVL (Fig. 1).

## HEAD SHAPE

Both head length and width were significantly and highly correlated with SVL (Table 1). Analysis of the allometry of head length showed that both adult and juvenile *M. viridis* exhibit negative allometry with respect to SVL (Fig. 2; Table 1). Head width also scaled with negative allometry against SVL in juveniles but not in adults, which exhibited isometric growth (Fig. 3; Table 1). A comparison of 95% confidence intervals of RMA slopes for head shape versus SVL showed that, in all populations, juveniles and adults differed significantly in their growth trajectories (Table 1). Slope estimates of head length and width were always higher for adults than for juveniles (Table 1). In other words, adults increased their head dimensions more quickly relative to SVL than juveniles, although larger adults still had relatively smaller heads than smaller adults (i.e. negative allometry (Figs 2, 3).

## SEXUAL MATURITY

Minimum SVL at sexual maturity was 21 cm greater in females than in males. Based on the selective

dissection of 15 male individuals in the range 74–100 cm SVL, the minimum size at sexual maturity was 91 cm SVL. Of the ten female individuals in the range 93–123 cm SVL, the minimum size at sexual maturity was 112 cm SVL. Thus, OCC does not appear to coincide with sexual maturation in either sex (Fig. 1).

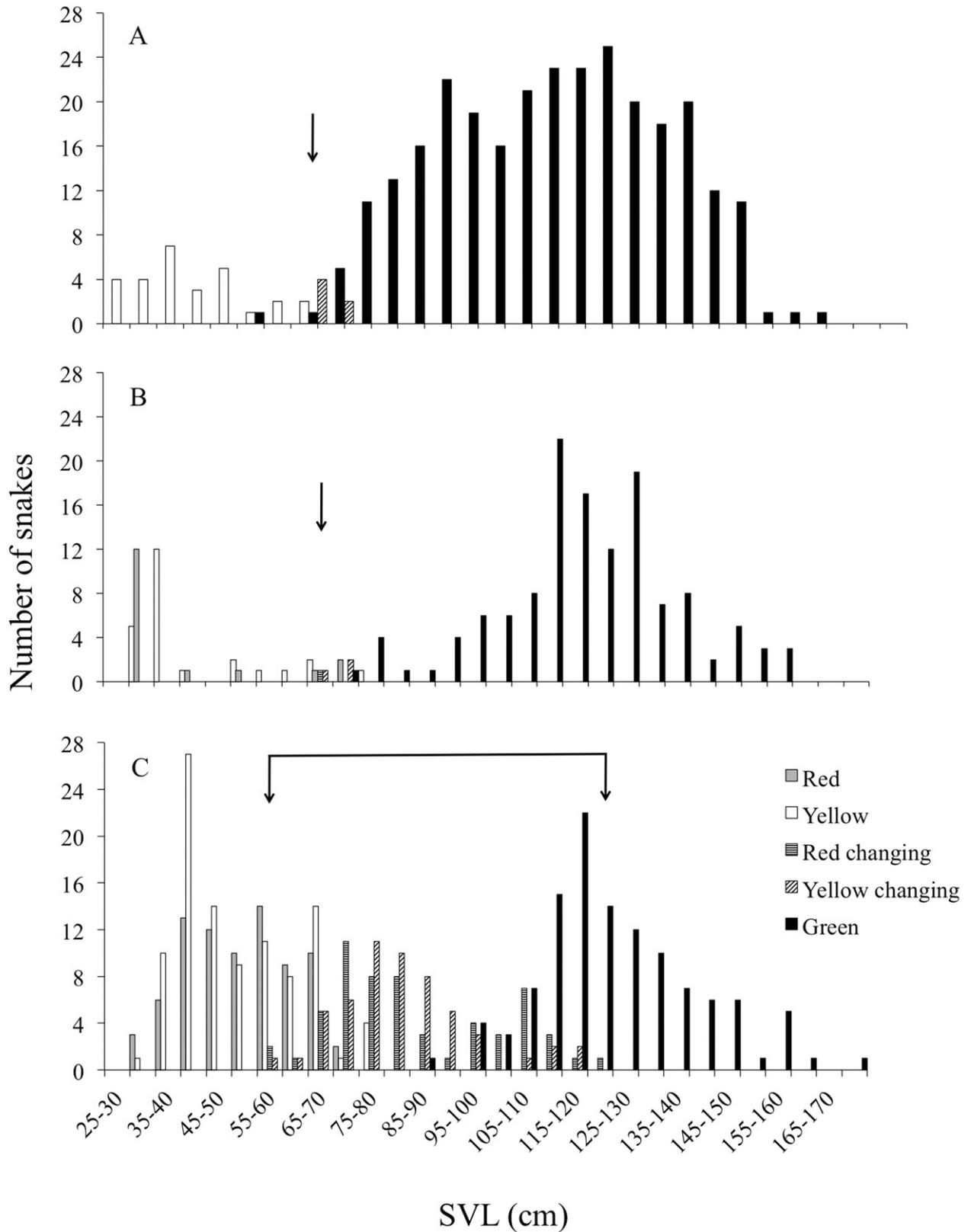
## DIET

In total, we recorded 151 prey items from 146 *M. viridis*. In all three populations we observed a significant shift from ground-dwelling ectothermic prey in young snakes to semi-arboreal endothermic prey in older individuals (Fig. 4). This shift in diet occurred in the range 65–75 cm SVL, coinciding with OCC (Figs 1, 4). Despite snakes from Biak retaining their juvenile coloration often up until 120 cm SVL, most individuals > 75 cm SVL preyed almost exclusively on mammals, in keeping with the other populations.

## DISCUSSION

The present study is among the first to explore relationships between changes in trophic structure, prey selection, and colour in a vertebrate species. Our data reveal a strong relationship between changes in prey selection, head shape, and the timing of OCC in *M. viridis* (Figs 1, 2, 3, 4). Juvenile head length and width scaled with negative allometry relative to SVL, whereas adults scaled negatively for head length but isometrically for head width (Figs 2, 3; Table 1). All sexually mature *M. viridis* were green, and the size of the smallest mature individual was not correlated with the timing of OCC. By contrast, *M. viridis* from Biak exhibited changes in prey selection and head shape similar to the other populations, although these did not appear to coincide with OCC.

The majority of scaling studies on the feeding morphology of ectothermic predators show that many species exhibit significant negative allometry in trophic structures (Vincent *et al.*, 2004; Herrel & Gibb, 2006; Herrel & O'Reilly, 2006; Hampton, 2011). Indeed, negative allometry or isometry in head dimensions relative to body size is an almost universal trait among vertebrates (Emerson & Bramble, 1993; Pfaller *et al.*, 2010). The potential functional consequences of negatively allometric head growth in the present study are unclear. One might expect that juveniles would increase their head size as rapidly as possible to enable ingestion of larger endothermic prey, before slowing head growth after OCC. However, juveniles may not require larger heads to consume elongate but relatively small, ectothermic prey (i.e. lizards; Fig. 4) (Vincent *et al.*, 2006). Nevertheless, negative allometry in head dimensions of *M. viridis*



**Figure 1.** Snout-vent length (SVL) distributions of *Morelia viridis* of each colour morph from southern New Guinea (A), northern New Guinea (B), and Biak (C). Arrows represent the range of SVLs over which colour change occurs.

**Table 1.** Results of reduced major-axis regressions of  $\log_{10}$  head length (HL) and head width (HW) versus  $\log_{10}$  snout–vent length

Population		<i>N</i>	<i>R</i>	<i>y</i> -intercept	Slope	95% confidence interval	Relationship
Biak	Juvenile HL	291	0.93	0.12	0.70	0.67–0.72	N
	Adult HL	128	0.82	–0.19	0.86	0.79–0.93	N
	Juvenile HW	288	0.56	–0.38	0.87	0.80–0.95	N
	Adult HW	129	0.69	–0.66	1.01	0.87–1.15	I
Northern New Guinea	Juvenile HL	46	0.94	0.34	0.56	0.51–0.62	N
	Adult HL	114	0.89	–0.08	0.79	0.74–0.85	N
	Juvenile HW	42	0.93	–0.36	0.83	0.75–0.91	N
	Adult HW	126	0.55	–0.76	1.00	0.87–1.13	I
Southern New Guinea	Juvenile HL	26	0.92	0.39	0.54	0.46–0.60	N
	Adult HL	261	0.92	–0.09	0.81	0.77–0.84	N
	Juvenile HW	34	0.66	–0.16	0.76	0.56–0.96	N
	Adult HW	262	0.39	–0.58	0.97	0.87–1.06	I

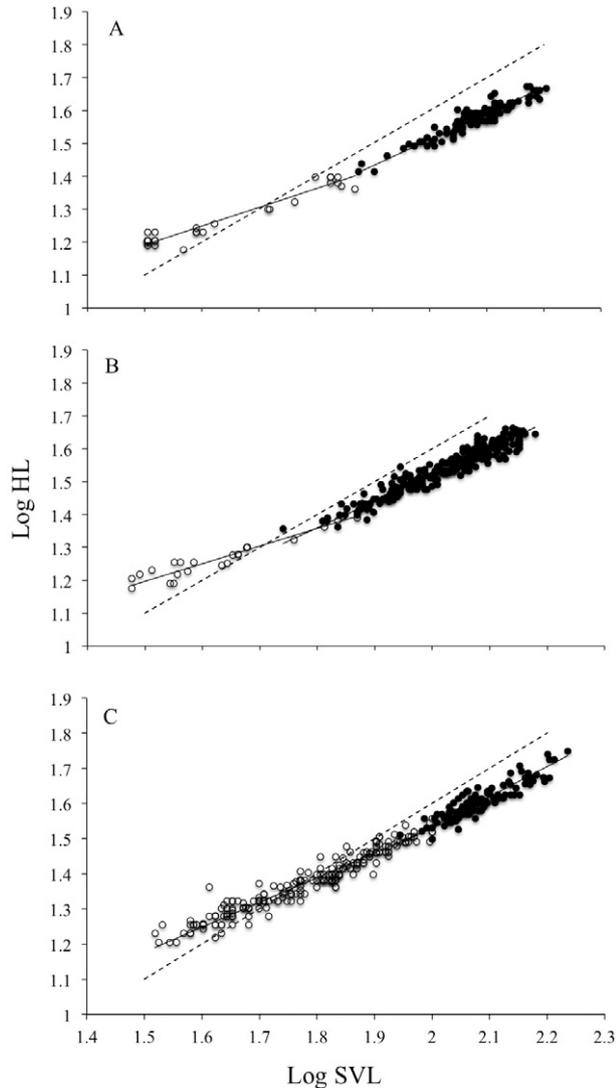
N, negative allometry; I, isometry.

may have some advantages. For example, because adults spend more time than juveniles in the upper rainforest canopy (Wilson, 2007), and because large meals can decrease locomotor performance (Garland & Arnold, 1983), relatively smaller trophic structures may limit maximum ingestible prey size, thus aiding arboreality. However, despite head shape allometry being significantly different between juveniles and adults, there may not be a causal link between ontogenetic changes in head shape allometry and diet (and therefore OCC) because our scaling exponents may bear little relationship to feeding. Nonetheless, studies of feeding performance and head shape in snakes suggest dietary changes over ontogeny may be coupled with changes in the trophic musculoskeletal system (Vincent *et al.*, 2004, 2007; Mori & Vincent, 2008). In agreement, Herrel & O'Reilly (2006) hypothesized that the rapid increase in bite force seen during ontogeny in the turtle, *Trachemys scripta*, is related to an ontogenetic shift in diet (from a soft to hard food source).

The data reported in the present study raise the question: why do *M. viridis* undergo these changes at all when they could remain one colour and continue to occupy a single niche? Our data suggest that the answer is somewhat complex. Previous studies have shown that juveniles and adults use different microhabitats in which they are optimally cryptic (closed versus open canopy; Wilson, Heinsohn & Legge, 2006; Wilson *et al.*, 2007). Consequently, foraging opportunities for snakes of different colours may be restricted to prey types that frequent those habitats. Thus, we suggest that, to maximize optimal foraging and minimize exposure to predators, *M. viridis* undergoes OCC as part of an overall evolutionary defence–

foraging strategy that circumvents costs imposed by restricted foraging in certain habitats. Unfortunately, our data do not allow us to test whether changes in trophic structure, colour, prey selection, and habitat are the cause or result of one another. Further studies of species that undergo similar ontogenetic changes (e.g. the boa *Corallus caninus*) will be important for clarifying the regularity of these relationships, as well as the direct environmental/physiological cues that trigger them.

Why is the timing of OCC different on Biak? The timing of OCC in *M. viridis* from Biak was not strongly correlated with body size, head shape, diet or maturity. However, it is likely that some *M. viridis* from Biak reach sexual maturity when they are still exhibiting their juvenile coloration (Fig. 1). Another island off the coast of New Guinea, Kofiau, is home to *M. viridis* that are reported to retain their yellow juvenile coloration well into adulthood (Maxwell, 2005). In addition, snakes from two other islands also were found to keep their juvenile coloration up until at least 100 cm SVL (the names of which are excluded to minimize illegal collection for the pet trade; Lyons & Natusch, 2011). To the best of our knowledge, there have been no confirmed reports of wild, adult-sized *M. viridis* from mainland New Guinea or Australia retaining their juvenile coloration. Currently, all of the islands where *M. viridis* have exhibited delayed colour change are oceanic, meaning they have never been connected to mainland New Guinea (Beehler, 2007). It is possible that some aspects of selection (e.g. fewer avian predators or a lack of specific predators; Beehler, Pratt & Zimmerman, 1986; Avibase, 2012) has resulted in a reduced reliance on colour for camouflage in these populations. Hence, *M. viridis*

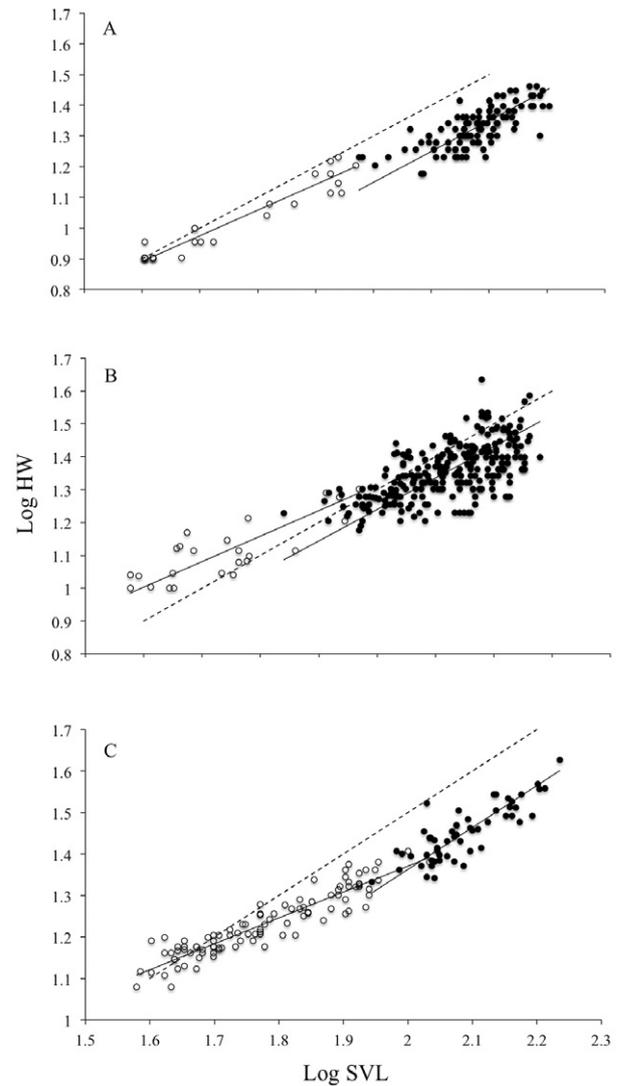


**Figure 2.** Reduced major-axis regressions of log head length (HL) versus log snake snout-vent length (SVL) for *Morelia viridis* from northern New Guinea (A), southern New Guinea (B), and Biak (C). The solid line represents the observed slopes, and the dashed line represents the slope of isometry.

from Biak may be ideally suited for investigation the reasons behind the strongly size-associated OCC seen on the mainland. Field studies examining predation rates by diurnal predators on juvenile and adult coloured snake models of differing sizes in different habitats may also shed light on the role that predators play in selecting for and determining microhabitat use by snakes of different colours.

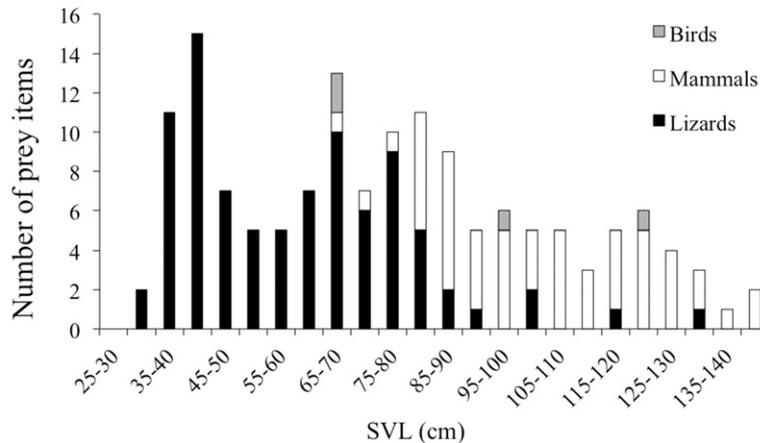
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**Figure 3.** Reduced major-axis regressions of log head width (HW) versus log snake snout-vent length (SVL) for *Morelia viridis* from northern New Guinea (A), southern New Guinea (B), and Biak (C). The solid line represents the observed slopes, and the dashed line represents the slope of isometry.

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**Figure 4.** Variation in prey composition with increasing snout–vent length (SVL) sizes of *Morelia viridis* (data from all regions have been pooled).

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## REFERENCES

- Arnold SJ. 1993.** Foraging theory and prey-size–predator-size relations in snakes. In: Seigel RA, Collins JT, eds. *Snakes: ecology and behavior*. New York, NY: McGraw-Hill, 87–115.
- Avibase 2012.** *The world checklist of birds*. Available at: <http://avibase.bsc-eoc.org>
- Beehler BM. 2007.** Papuan terrestrial biogeography, with special reference to birds. In: Marshall AJ, Beehler BM, eds. *The ecology of papua*. Singapore: Periplus Editions, 196–206.
- Beehler BM, Pratt TK, Zimmerman DA. 1986.** *Birds of New Guinea*. Princeton, NJ: Princeton University Press.
- Booth CL. 1990.** Evolutionary significance of ontogenetic colour change in animals. *Biological Journal of the Linnean Society* **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.
- Darwin C. 1859.** *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. London: John Murray.
- Deiner K, Lemmon AR, Mack AL, Fleischer RC, Dumbacher JP. 2011.** A passerine bird’s evolution corroborates the geologic history of the island of New Guinea. *PLoS ONE* **6**: 1–15.
- Emerson SB, Bramble DM. 1993.** Scaling, allometry, and skull design. In: Hanken J, Hall BK, eds. *The skull*, Vol. 3. *Functional and evolutionary mechanisms*. Chicago, IL: The University of Chicago Press, 384–421.
- Forsman A, Lindell LE. 1993.** The advantage of a big head: swallowing performance in adders, *Vipera berus*. *Functional Ecology* **7**: 183–189.
- Garland TH, Arnold SJ. 1983.** Effects of full stomach on locomotory performance of juvenile garter snakes (*Thamnophis elegans*). *Copeia* **1983**: 1092–1096.
- Gould SJ. 1966.** Allometry and size in ontogeny and phylogeny. *Biological Reviews of the Cambridge Philosophical Society* **41**: 587–640.
- Hampton PM. 2011.** Feeding performance in the western ribbon snake (*Thamnophis proximus*): ontogeny and the effects of prey type and size. *Canadian Journal of Zoology* **89**: 945–950.
- Herrel A, Gibb AC. 2006.** Ontogeny of performance in vertebrates. *Physiological Biochemical Zoology* **79**: 1–6.
- Herrel A, O’Reilly JC. 2006.** Ontogenetic scaling of bite force in lizards and turtles. *Physiological and Biochemical Zoology* **79**: 31–42.
- Lyons JA, Natusch DJD. 2011.** Wildlife laundering through breeding farms: illegal harvest, population declines and a means of regulating the trade of green pythons (*Morelia viridis*) from Indonesia. *Biological Conservation* **144**: 3073–3081.
- Maxwell G. 2005.** *The more complete chondro*. Lansing: Eco Publishing.
- Merilaita S, Tuomi J, Jormalainen V. 1999.** Optimisation of cryptic coloration in heterogeneous habitats. *Biological Journal of the Linnean Society* **67**: 151–161.
- Mori A, Vincent SE. 2008.** An integrative approach to specialization: relationships among feeding morphology, mechanics, behaviour, performance and diet in two syntopic snakes. *Journal of Zoology* **275**: 47–56.
- Mushinsky HR. 1987.** Foraging ecology. In: Seigel RA, Collins JT, Novak SS, eds. *Snakes: ecology and evolutionary biology*. New York, NY: Macmillan, 302–334.
- Natusch DJD, Natusch DFS. 2011.** Distribution, abundance and demography of green pythons (*Morelia viridis*) in Cape York Peninsula, Australia. *Australian Journal of Zoology* **59**: 145–155.
- Pfaller JB, Herrera ND, Gignac PM, Erickson GM. 2010.** Ontogenetic scaling of cranial morphology and bite-force

- generation in the loggerhead musk turtle. *Journal of Zoology* **280**: 280–289.
- Rawlings L, Donnellan S. 2003.** Phylogeographic analysis of the green python, *Morelia viridis*, reveals cryptic diversity. *Molecular Phylogenetics and Evolution* **27**: 36–44.
- Roulin A. 2004.** The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews of the Cambridge Philosophical Society* **79**: 1–34.
- Shine R. 1991.** Why do larger snakes eat larger prey items? *Functional Ecology* **5**: 493–502.
- Shine R, Slip DJ. 1990.** Biological aspects of the adaptive radiation of Australasian pythons (Serpentes: Boidae). *Herpetologica* **46**: 283–290.
- Speed MP, Ruxton GD. 2005.** Aposematism: what should our starting point be? *Proceedings of the Royal Society of London Series B, Biological Sciences* **272**: 431–438.
- Vincent SE, Dang PD, Irschick DJ, Rossell J. 2005.** Do juvenile gape limited predators compensate for their small size when feeding? *Journal of Zoology London* **268**: 279–284.
- Vincent SE, Herrel A, Irschick DJ. 2004.** The ontogeny of intersexual head shape and prey selection in the pitviper, *Agkistrodon piscivorus*. *Biological Journal of the Linnean Society* **81**: 151–159.
- Vincent SE, Moon BR, Herrel A, Kley NJ. 2007.** Are ontogenetic shifts in diet linked to shifts in feeding mechanics? Scaling of the feeding apparatus in the banded water-snake *Nerodia fasciata*. *Journal of Experimental Biology* **21**: 2057–2069.
- Vincent SE, Moon BR, Shine R, Herrel A. 2006.** The functional meaning of ‘prey size’ in water snakes (*Nerodia fasciata*, Colubridae). *Oecologia* **147**: 204–211.
- Werner EE, Gilliam JF. 1984.** The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15**: 393–425.
- Wilson D. 2007.** Foraging ecology and diet of an ambush predator: the green python. In: Henderson R, Powell R, eds. *Biology of the boas and pythons*. Eagle Mountain, UT: Eagle Mountain Publishing, 141–150.
- Wilson D, Heinsohn R, Endler J. 2007.** The adaptive significance of ontogenetic colour change in a tropical python. *Biological Letters* **3**: 40–43.
- Wilson D, Heinsohn R, Legge S. 2006.** Age and sex-related differences in the spatial ecology of a dichromatic tropical python (*Morelia viridis*). *Austral Ecology* **31**: 577–587.
- Wilson D, Heinsohn R, Wood J. 2006.** Life-history traits and ontogenetic colour change in an arboreal tropical python, *Morelia viridis*. *Journal of Zoology* **270**: 399–407.