

Sexual dichromatism does not translate into sex-based difference in morphology or diet for the African boomslang

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Dispholidus typus; sexual dichromatism; ontogeny; habitat specialization; dietary variation; predation; intersexual niche divergence.

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Abstract

Selection for sexual dichromatism is thought to arise mainly from intersexual niche divergence or sexual selection, including mate-choice and intrasexual competition. However, overt sexual dichromatism is rare in snakes, limiting inference regarding its origin and maintenance in these animals. We thus aimed to assess whether boomslang (*Dispholidus typus*) – a species of overtly sexually dichromatic African snake – exhibits evidence for intersexual niche divergence based on three ecologically relevant morphological variables (snout-vent length, tail length and head length) and one ecological variable (diet). We measured morphological variables on 203 museum specimens, and characterized diets for male and female snakes on the basis of dissected specimen gut contents, supplemented with literature reports of feeding, as well as online photographs. Male and female boomslang show broadly similar gross morphology and do not differ in mean snout-vent, relative tail length or head length. Moreover, male and female snakes do not differ in the frequency with which they consume different prey classes. Similarly, diets of adult and juvenile snakes did not differ significantly. The abundance of chameleons and bird chicks (36% and 54% of prey items respectively) in the diet of boomslang suggests dietary restriction due to arboreality rather than dietary specialization *per se*. Despite examining a range of morphological and ecological variables, we fail to detect evidence for intersexual niche differentiation. Rather, our results suggest that juvenile coloration is likely a result of selection for camouflage from visually oriented predators, and that the overt sexual dichromatism of adults following maturation represents a shift toward either intersexual mate-choice or intrasexual competition. We therefore recommend that boomslang visual acuity and colour differentiation be directly examined in the future.

Introduction

The study of extreme phenotypes has the potential to elucidate the evolutionary drivers of variation in those phenotypes. Despite sexual dichromatism (defined as intersexual differences in coloration; Bell & Zamudio, 2012) being phylogenetically widespread in animals (Figuerola & Green, 2000; Bell & Zamudio, 2012), overt expression of the phenomenon appears to be relatively rare in snakes (Shine & Madsen, 1994). Sexual dichromatism is well-documented among bird species (Owens & Hartley, 1998), is known to occur in several lineages of lizards (Dolman & Stuart-Fox, 2010; de Pérez *et al.*, 2013), and is reported in at least 120 species of frogs (Bell & Zamudio, 2012). However, only 74 species of snakes (of >3700 species worldwide) are described as being sexually dichromatic and, importantly, many of these species show relatively subtle differences in coloration. Fortunately, overt examples of sexual dichromatism in snakes do exist, and these offer prime opportunities to disentangle morphology, ecology

and sexual selection in an effort to better understand trait evolution.

Sexual dimorphism, including sexual dichromatism, can arise via multiple non-exclusive mechanisms (Hedrick & Temeles, 1989). In general, intersexual niche divergence and/or sexual selection are responsible for observed differences in morphology between sexes. Sexual selection has widely been inferred as the selective mechanism driving sexual dichromatism (de Pérez *et al.*, 2013), however, its applicability to snakes remains under-explored. The available evidence suggests that colour discrimination in snakes is poor (Sillman *et al.*, 1997; Stuart-Fox, Moussalli & Whiting, 2008), making dichromatism as a result of sexual selection seemingly implausible. However, our understanding of snake visual systems remains extremely limited, especially for snakes in natural environments. Conversely, intersexual niche divergence is common in snakes (Shine & Wall, 2007). This divergence is frequently measured as differences in the diet of male and female snakes and can be driven by intersexual differences in habitat, foraging time, foraging

mode or most commonly, differences in overall body size or head morphology (both of which are common in snakes; Shine, 1993).

Evidence for the role of intersexual niche divergence as a driver of sexual dichromatism in snakes remains poorly demonstrated (Shine, 1989). This arises because of the relatively few species of overtly sexually dichromatic snakes and the challenges associated with inferring adaptive advantages of dichromatism in those different niches – although evidence does exist for coloration affecting the type of prey consumed in pythons (Shine *et al.*, 1998) and for fitness consequences associated with colour patterning in vipers (Forsman, 1995). Importantly, any attempt to assess the relative influence of (1) sexual selection; and (2) selection for intersexual variation in niches on the origin and maintenance of sexual dichromatism, in any organism, necessarily requires a comparison of ecological and morphological intersexual variation (Lande, 1980).

Here, we test for intersexual differences in morphology and diet in the boomslang (*Dispholidus typus*) – one of the world's most overtly sexually dichromatic snake species. Boomslang exhibit striking ontogenetic dichromatism (*sensu* Bell & Zamudio, 2012) in which juveniles of both sexes present with bodies that are grey-brown in colour with dark speckling, a dark brown dorsal stripe along the length of the body, and white and brown heads, but adult females are predominantly olive or brown in colour, and adult males occur predominantly as bright green, yellow and black, or rarely blue or black (Shine, 1993; Branch & Jackson, 2016; Fig. 1). Specifically, we explore intersexual variation in diet, overall morphology and feeding structure morphology in search of evidence for niche differentiation in this highly dichromatic species.

Materials and methods

Study species

Boomslang (*D. typus*) are large-bodied, colubrid snakes native to sub-Saharan Africa where they are known from South Africa, northwards through east, central and west Africa (Broadley, 1983). Eimermacher (2012) recognized molecular differences between *Dispholidus typus typus* and *Dispholidus typus viridis*, both of which occur within our study area, but cautioned that additional sampling was required to assess whether these represent distinct species. For the purposes of this study we treat all individuals as *D. typus sensu lato*. In southern Africa, boomslang inhabit a wide range of habitats including arid and temperate scrublands, savannas and forests (Bates *et al.*, 2014). Boomslang individuals are largely arboreal (boomslang translates directly from the Afrikaans language as *tree snake*) but do come to ground to cross open spaces or occasionally hunt. They are known to feed on chameleons and other tree-living lizards, birds, eggs, rodents and frogs (Broadley, 1983; Branch, 1998), however, their diet has never been assessed in the context of intersexual variation. Morphologically, Broadley (1983) reported that male snakes have relatively longer tails and fewer ventral scales than female snakes.

We examined male, female and juvenile boomslang from South Africa in the collections of Bayworld (Port Elizabeth),

Ditsong National Museum of Natural History (Tshwane), Iziko Museum (Cape Town) and McGregor Museum (Kimberley). For each specimen we measured snout-vent length (SVL) and tail length (TL; both measured with a tape measure to the nearest millimetre) and head length (measured from the tip of the snout to the angle of the jaw; measured with callipers to the nearest millimetre). We acknowledge that sexual dimorphism in other morphological traits is possible, but limited our analyses to these variables because of their widespread use in studies of snake sexual size dimorphism (SSD). We established the sex of each specimen by probing for the presence of hemipenial canals using a blunt-ended probe and dissected preserved tissue to detect hemipenial canals where necessary. We made a mid-ventral incision to expose the stomach and hindgut, and then made incisions into these to expose any prey items or remains. Prey items were identified to the finest possible taxonomic rank using a dissecting microscope, reference books of reptiles, birds and frogs, and with the help of local prey taxon experts. We additionally augmented our dietary data by reviewing and quantifying the diet of male and female boomslang from published literature and observations submitted to the Predation Records–Reptiles and Frogs (Sub-Saharan Africa) Facebook group viewable at www.facebook.com/groups/888525291183325.

Data analysis

We compared mean SVL of male and female individuals through the use of one-way ANOVA, using our full dataset of measured snakes, as well as the 30 largest individuals of each sex. We used a single-factor analysis of covariance (ANCOVA) to test for differences in the TL and head length (HL) between males and females, using SVL as a covariate. Because of the stark colour differences apparently associated with sexual maturation, we use chi-square tests and Fisher's exact tests to examine the frequency with which juvenile (SVL < 800 mm; based on the observation that snakes below that threshold showed juvenile coloration) and adult snakes (both sexes combined) consumed birds, reptiles, mammals and amphibians. Finally, we compared the frequency with which male and female snakes contained those major prey classes.

Results

We examined 203 *D. typus* specimens including 167 adults – females ($N = 60$) and males ($N = 107$) – and 36 juveniles. Male and female boomslang did not differ significantly in mean SVL for either the entire dataset (males: 961.26 ± 159.64 mm; females: 986.73 ± 183.63 mm; $F_{(1,169)} = 0.90$; $P = 0.34$), or when the analysis was limited to the 30 largest individuals of each sex (males: 1133.17 ± 72.60 mm; females: 1137.67 ± 98.13 mm; $F_{(1,59)} = 0.41$; $P = 0.84$). Surprisingly, male boomslang in our sample did not possess significantly longer tails than females of the same body length (heterogeneity of slopes test: $F_{(1,142)} = 3.62$, $P = 0.059$; ANCOVA: $F_{(1,143)} = 0.0388$, $P = 0.844$; Fig. 2a). Similarly, male and female snakes did not differ significantly in head length (heterogeneity of slopes test: $F_{(1,142)} = 0.2042$, $P = 0.6521$; ANCOVA: $F_{(1,143)} = 0.6153$, $P = 0.4341$; Fig. 2b).

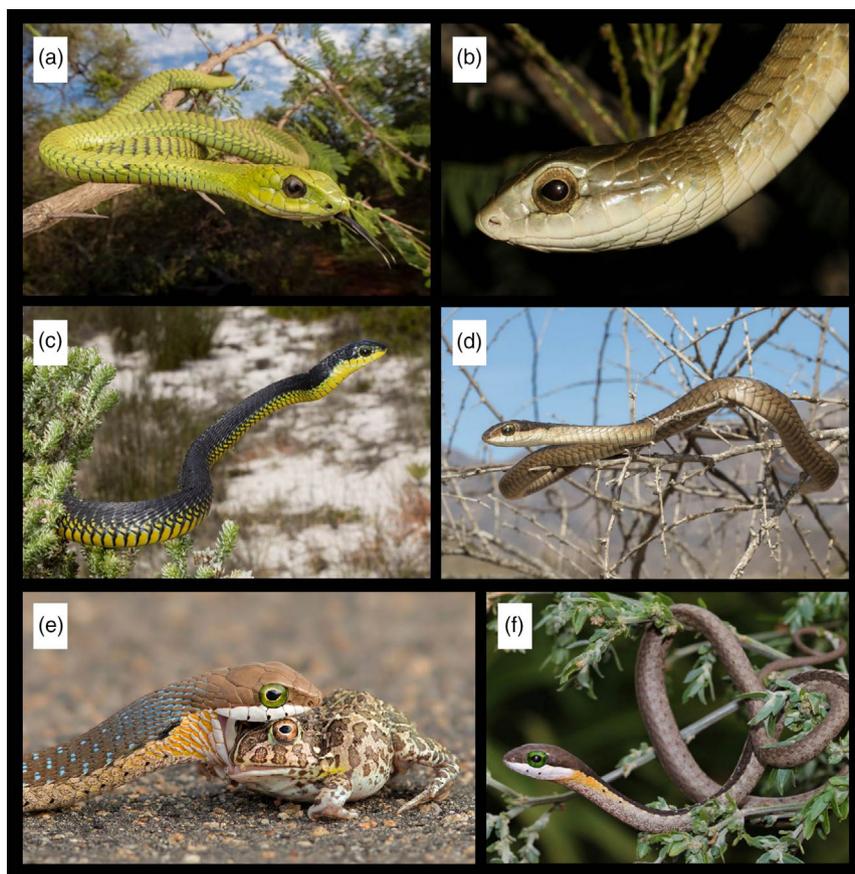


Figure 1 Ontogenetic sexual dichromatism in the African boomslang (*Dispholidus typus*) showing typical colouration of adult males (a, c), adult females (b, d) and juveniles (e, f). Photographs by Luke Verbugt (a), Johan Marais (b, c, d), Gary Cusins (e) and Chad Keates (f).

The diet of boomslang is diverse and includes members of all four tetrapod clades. We conservatively identified a total of 41 prey species in the diet of boomslang (Table S1, Supporting Information), but recognize that this number is underestimated. We found no association between prey class frequency and sex ($\chi^2_{1,3} = 1.58$; $P = 0.66$), and Fisher's exact tests revealed no significant pairwise comparisons (Fisher's exact test scores ranged from 0.47 to 0.66; all $P > 0.05$; Fig. 3a). Additionally, we found no association between age class and prey class frequency ($\chi^2_{1,3} = 3.09$; $P = 0.38$), and again Fisher's exact tests revealed no significant pairwise comparisons (Fisher's exact test scores ranged from 0.12 to 0.73; all $P > 0.05$; Fig. 3b) although this analysis was limited by the relatively small sample of prey items from juvenile snakes ($N = 25$ prey items).

More detailed examination of boomslang diets revealed that similar proportions of examined males (50%) and females (38%) contained prey items (Fisher's exact test = 0.17; $P > 0.05$). Moreover, for those 67 examined specimens that contained prey items, similar proportions of males (26%) and females (33%) contained multiple (range: 2–4) prey items (Fisher's exact test = 0.57; $P > 0.05$). Five specimens (four males; one female) contained combinations of different prey

classes. All prey items for which direction of ingestion could be ascertained had been swallowed head-first.

Lastly, we interrogated our dataset for evidence of broad-scale spatial or temporal variation in feeding patterns. We found that significantly more snakes were originally collected in warmer months ($\chi^2_{11} = 96.35$; $P < 0.001$) than colder months and similarly that the proportion of specimens that contained prey items were highest in warmer months ($\chi^2_{11} = 112.00$; $P < 0.001$), peaking in late summer when 66% of specimens (March) and 57% of specimens (May) contained prey items. Geographically, we found no difference in the frequency with which different prey classes were consumed across the three best represented biomes (pairwise comparisons of fynbos, grassland and savanna biomes revealed $\chi^2 = 1.43$ –7.09 with all P -values being larger than 0.05).

Discussion

Despite exhibiting dramatic sexual dichromatism, boomslang show remarkably little intrasexual variation in size, head length or diet. Our comparisons, although not exhaustive, suggest that natural selection for sexually differentiated niches (as reflected by diet and morphology) does not offer the best explanation

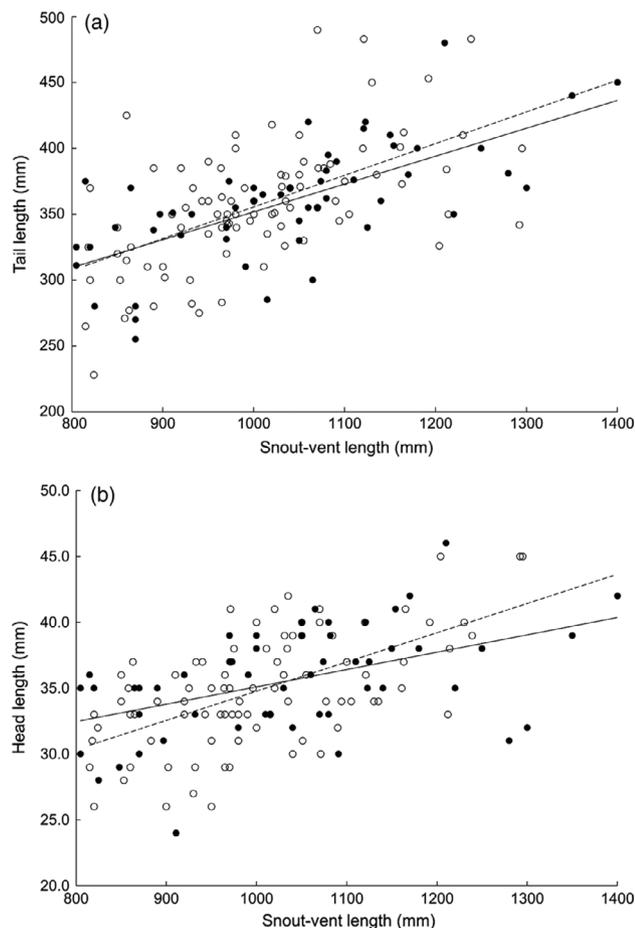


Figure 2 The relationship between tail length (a) and head length (b) relative to snout-vent length for male (white circles) and female (black circles) *Dispholidus typus* from South Africa.

for the dramatic sexual dichromatism expressed by the species. Rather, our data suggest limited differences in ecology and key morphological traits between the sexes and invite a closer examination of sexual selection as a mechanism for the origin and maintenance of sexual dichromatism in boomslang.

Our results show limited evidence for SSD relating either to overall body size, relative TL, or relative head length. SSD is widespread in snakes and many sexually dichromatic species are also dimorphic (Shine, 1993) making the absence of apparent size dimorphism in boomslang atypical. The absence of intersexual differences in TL, in contrast to statements in Broadley (1983), can likely be explained by overall body elongation and tail lengthening as part of a general syndrome of morphological adaptations to arboreality in snakes (Lillywhite & Henderson, 1993). Regardless, our morphological results provide no evidence for intersexual niche differentiation in boomslang.

The absence of intersexual differences in head length, a trait explicitly linked to trophic structures and feeding in snakes (Cundall & Greene, 2000), corroborates our finding of limited intersexual variation in diet. Unfortunately, our dietary

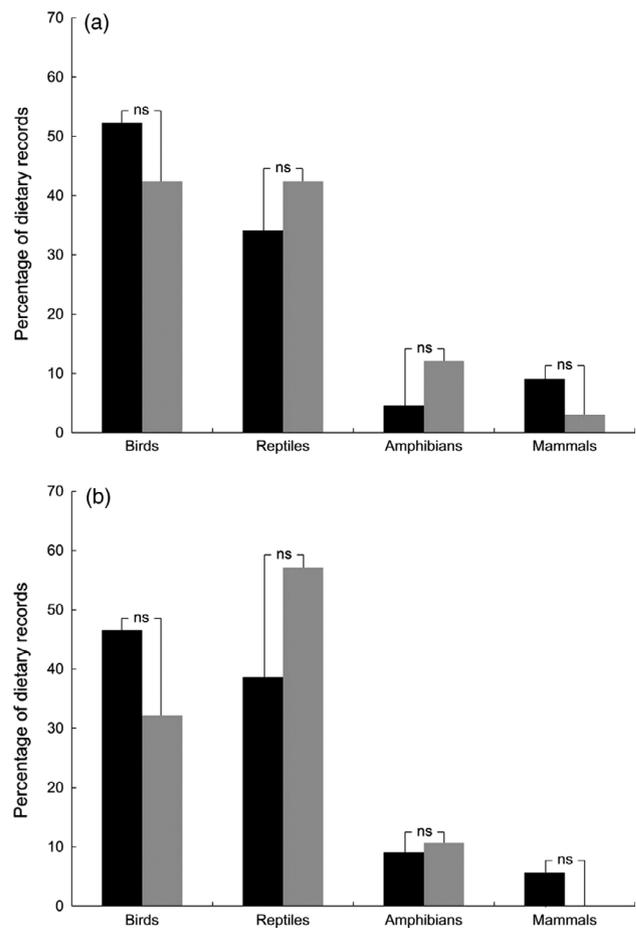


Figure 3 Variation in the frequency of consumption of the four classes of prey for (a) adult males (black bars) vs. females (grey bars) and (b) all adults (black bars) vs. juvenile (grey bars) *Dispholidus typus* from South Africa.

classification is necessarily broad, and might obscure subtle differences in diet. In general, snake diets are characterized using a range of approaches including *in situ* observation of feeding, forced regurgitation of recently consumed prey items and the examination of stomach contents of freshly killed or preserved material. However, these methods are often biased towards prey of certain sizes, or particular taxonomic groups (Glaudas, Kearney & Alexander, 2017), and examination of stomach contents in particular, frequently yields prey items that are not identifiable beyond class or family level. These challenges aside, the overall breadth of boomslang diet identified during this study suggests that our coarse classification of diet is likely to adequately represent boomslang dietary variation. Thus, the limited intersexual dietary variation that we detected in boomslang provides no evidence for intersexual niche differentiation in boomslang.

Juvenile boomslang show no obvious sexual dichromatism. We hypothesize that juvenile coloration is a naturally selected trait linked to predator avoidance. The overall body coloration of juvenile boomslang comprises of grey-brown with darker speckling (Fig. 1e,f) and is difficult to distinguish from the

bark-covered branches of most trees and shrubs. Moreover, head coloration is strongly counter-shaded, with a defined differentiation between light and dark sections that would provide optimal camouflage in bright light (Cuthill *et al.*, 2016) such as during basking. We hypothesize that this counter-shading reduces detectability to visually oriented predators such as birds. Transition from a naturally selected juvenile morph to two separately coloured adult morphs without any overt intersexual differences in body size, head morphology or diet, suggests a transition in the selective advantage of coloration at sexual maturation. We cannot preclude that juveniles, adult females and adult males occupy different microhabitats and that differential coloration for the three groups represents optimal camouflage within those microhabitats. However, we think that it is more plausible that boomslang shift from a juvenile coloration selected for camouflage, to dichromatic adult coloration because of some unidentified mechanism of colour assessment in the species.

Differences in the geographically variable dominant male colour variations may offer insights into the origins and maintenance of adult colour dimorphism in boomslang. Shine (1993) reports anecdotal support for boomslang from forested habitats showing less intersexual differentiation than boomslang from savanna habitats. Importantly, these two environments differ in their ambient light characteristics, and the efficacy of any visual signal is known to be influenced by ambient light (Endler & Thery, 1996). Similarly, black and yellow males (Fig. 1c) that inhabit shrubland habitats and green animals from savanna habitats (Fig. 1a) potentially experience different ambient light conditions. Differences in adult male coloration might also result from differing selection on thermoregulatory ability (Gibson & Falls, 1979) or, more speculatively, a trade-off between antipredatory coloration and selection for appropriate inter- or intrasexual visual signals, as is the case in at least some other reptile lineages (Stuart-Fox & Ord, 2004). Importantly, coloration and animal perception thereof are often oversimplified, and evolutionary hypotheses conditioned on coloration require a thorough examination of animal perception as confirmation (Bennett, Cuthill & Norris, 1994). Unfortunately such an examination does not exist for snakes.

Natural history

Our data suggest that boomslang feed relatively frequently (47% of examined specimens contained prey, and a remarkable 22% of those with prey contained multiple prey items). Although it is not possible to demonstrate selection for small prey without information about the encounter rates of a foraging snake with prey of different sizes, our findings paint a picture of an active foraging snake in which both sexes cruise a primarily arboreal habitat in search of small vertebrates on which to prey. Moreover, the dominance of chameleons (36% of prey items) and nestling birds (54% of prey items) in the diet suggest that boomslang feed on prey with limited mobility. This pattern is emphasized by the relative scarcity of fledged birds in their diet, much like ecologically similar species such as *Thelotornis capensis* (Shine *et al.*,

1996). However, we do not interpret this finding as dietary specialization, but rather dietary restriction following habitat specialization. This is supported by the consumption of seemingly atypical prey (one specimen contained 4–5 termite alate-fed *Breviceps* frogs) from occasional terrestrial forays. We found no evidence for ontogenetic shift in diet corresponding to maturation of adult coloration, although the remains of mammals were only detected in adult snakes, suggesting that the consumption of mammalian prey might be restricted to larger individuals. However, even our limited sample of snakes that consumed mammalian prey included both male and female snakes emphasizing limited intersexual variation in this trait.

Although we are not able to provide direct evidence for the role of sexual selection in driving dichromatism in boomslang, our improved knowledge base fails to yield evidence for intersexual niche differentiation in this highly dichromatic species. Instead, our results point strongly towards adult colour variation being derived either through the mechanism of direct mate evaluation or intraspecific competition. Unfortunately, we are not aware of any evidence for premating colour evaluation in boomslang, and traditional male–male combat seems to be absent or at least very rare in boomslang. However, boomslang do appear to have acute visual systems and individuals have anecdotally been reported as responding to their reflections in window panes by inflating their throats and attempting to engage with the reflection as a conspecific. Although snakes are not thought to have well-developed colour differentiation, we recommend that boomslang visual acuity and colour differentiation be directly examined.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Prey items recorded in the diet of *Dispholidus typus* for the purposes of this study.