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From matte banded to glossy black: Structures underlying colour
change in the caudal lures of southern death adders (*Acanthophis
antarcticus*, Reptilia: Elapidae)

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Running head: Colour change in death adder lures

Abstract

Many ambush-foraging snakes move their tails to entice prey within striking range (caudal luring). During ontogeny, the conspicuous hues of caudal lures change to match the cryptic patterning of the body/head coinciding with decreased luring behaviour; reflecting the trade-off between prey acquisition and camouflage as the snake grows. Australo-Papuan death adders (*Acanthophis*, Elapidae) are unique in that both juveniles and adults use caudal luring, but ontogenetic colour change has not been investigated. We examined the spectral reflectance, microstructure, and pigmentation of caudal skin in wild-sourced and captive bred *Acanthophis antarcticus* ranging in body size (snout-vent length 116-674 mm; mass 3-832 g; $n = 33$) to test whether colour properties change as snakes grow. We found that lure colour is distinct from the cryptic body skin across life history, and changes from a matte banding pattern (grey/black) in neonates/juveniles, to uniform and glossy black with a yellow ventral stripe in larger snakes. These colour changes are caused by increases in dermal pigmentation and a transition to a smooth, interlocking epidermal microstructure. To understand the selection pressures that might be driving ontogenetic colour change in this species, further studies should test how different prey types might respond to distinct lure morphologies.

Keywords: caudal luring, glossiness, microstructure, ontogenetic colour change, reflectance, structural colour

39 INTRODUCTION

40 Ontogenetic colour change (OCC), unrelated to sexual selection, is a poorly understood aspect
41 of animal biology. In snakes, OCC is associated with gaining or maintaining body camouflage as larger
42 individuals occupy new habitats and adopt different behaviours (Wilson, Heinsohn, & Endler, 2007).
43 The mechanisms underlying OCC in snakes are poorly known but are likely to involve changes in a
44 combination of structure (*e.g.* collagen, epidermal microstructure) and pigmentation (Olsson, Stuart-
45 Fox, & Ballen, 2013; Spinner *et al.*, 2013).

46 Many ambush-foraging snakes move their tails to attract prey within striking range (caudal
47 luring), and often undergo OCC in the distal portion of the tail responding to shifting selection
48 pressures during ontogeny. The conspicuous green/yellow hues of juvenile caudal lures in Viperidae,
49 Crotalidae, Pythonidae and Boidae, for example, become indistinguishable from the camouflaged
50 patterning of the body, coinciding with a declining frequency of luring in adults (Neill, 1960;
51 Heatwole & Davison, 1976). The smaller and conspicuous tails of juvenile snakes are thought to be
52 selected for attracting ectothermic vertebrates (*e.g.* lizards and frogs) that are typically eaten by
53 smaller snakes (Reiserer, 2002; Rabatsky & Waterman, 2005; Nelson, Garnett, & Evans, 2010). In
54 contrast, adult ambush snakes typically eat larger, endothermic vertebrates and the hues of caudal
55 lure are under positive selection to match the cryptic colouration of the body and head.

56 Australo-Papuan death adders (Elapidae: *Acanthophis*) are unusual among ambush snakes
57 because both juveniles and adults use caudal luring to attract prey (McPhee, 1959; Neill, 1960;
58 Carpenter, Murphy, & Carpenter, 1978). *Acanthophis* (ca. 8 species) are ecologically convergent with
59 vipers, sharing many traits pertaining to their ambush foraging mode including a flat, heavy body,
60 triangular head shape, enlarged fangs that partially rotate with the maxilla, body camouflage and
61 caudal luring (Shine, 1980) (Figure 1). To lure prey, death adders use a combination of lateral and
62 vertical tail movements including rapid thrashing, slow undulations, lifting and waving (Carpenter *et al.*,
63 1978; Chiszar *et al.*, 1990; Hagman, Phillips, & Shine, 2008; McDonald, 2010) (Video S1). An

‘incomplete’ ontogenetic shift in diet composition is thought to contribute to the persistence of caudal luring in adult death adders, *i.e.* ectotherms remain important prey items of adults (Heatwole & Davison, 1976; Shine, 1980). Adult *Acanthophis* have conspicuous caudal lures with hues ranging from pale cream, white, yellow and black (Cogger, 2000; Wilson & Swan, 2013; Mirtschin, Rasmussen, & Weinstein, 2017) that contrast with their camouflaged body skin (Figure 1). Although juvenile death adders are known to use caudal luring too, the variation and ontogeny in the colouration of caudal lures has not been investigated.

In this study, we examine the colouration of caudal lures in a population southern death adders (*Acanthophis antarcticus*) at different life stages (neonate, juvenile, subadult and mature adult) to test how and when OCC might occur in this population. Because luring appears to be retained in adults to attract prey, we expect there to be minimal to no difference in colour properties across body sizes (*i.e.* no OCC). Alternatively, if the adult lure is under positive selection for crypsis, we would expect OCC that causes the lure to become indistinguishable from the colour and patterning on the body, and from the presumably conspicuous juvenile caudal lure (as in many vipers).

MATERIALS AND METHODS

Study species

The genus *Acanthophis* (Australo-Papuan death adders) has been the source of taxonomic uncertainty but currently comprises approximately eight species which occur across mainland Australia, New Guinea and associated offshore islands (Mirtschin *et al.*, 2017). Southern death adders (*A. antarcticus*, Shaw & Nodder, 1802) occur across temperate southern Australia into the sub-tropical reaches of the eastern coast where they live in undisturbed habitats of mallee, spinifex grasslands, coastal dunes and sclerophyll forest (Figure 1). Two colour forms appear to be under selection for crypsis in local substrate: red body patterns are found in northern and eastern Australia, and grey body patterns in southern Australia (Johnston, 1996).

88 *Animal husbandry and euthanasia*

89 We examined lure properties in 33 captive *A. antarcticus* that ranged in snout to vent length
90 (SVL; 116-674 mm) and mass (3-832 g) (Table S1). Adults were wild-collected, sourced from coastal
91 dune populations from Smoky Bay, South Australia (Figure 1 inset), and offspring were captive bred
92 progeny of these wild-collected individuals. Colour patterns were noted for the wild-caught *A.*
93 *antarcticus* from our study site and determined to be a brownish body colour and dark black caudal
94 lure (Figure 1). Three females gave birth to litters of 22, 24 and 30 neonates, respectively. We fed
95 half of the neonates weekly and the other half every two weeks to manipulate snake growth
96 patterns allowing us to determine if change of caudal lures were size or age dependent. Individuals
97 from our two 'feeding groups' were randomly selected from all three litters. Thirty-one progeny
98 were euthanized at different body sizes and ages (from 1 day old to 8 months old) and two adult
99 snakes (between 15 and 20 years old). Details of animal husbandry and housing are in the
100 supplementary materials.

101 Snakes were euthanized via intramuscular injection of pentobarbitone (see ethics statement).
102 Deceased snakes were frozen and kept for several months in the freezer (-20 degrees Celsius). After
103 reflectance measurements were taken on thawed snakes, the specimens were persevered in 10%
104 formalin and stored in 100% ethanol at the South Australian Museum (unregistered specimens).

105 *Dissection and microscopy*

106 We removed the tail from an adult and juvenile, and processed for microscopy. The tails were
107 dorsally bisected: one half was fixed by emersion in 4% paraformaldehyde (PFA) and 1.25%
108 glutaraldehyde in phosphate-buffered saline (PBS) and 4% sucrose (pH 7.2) for 48 h for scanning
109 electron microscopy and one half in 10% formalin in PBS for 48 h for histology and light
110 microscopical examination. Tails from each animal were further dissected according to their
111 anatomical position (ventral, dorsal) and epidermal colouration (white, black or yellow). A portion of
112 dorsal skin on the midbody, remote from the lure, was also removed from the adult and dissected

according to the crossband colouration (light brown, dark brown, pale cream) and fixed by emersion in 4% PFA and 1.25% glutaraldehyde in PBS, for 48 h for electron microscopy. Fixed tissues were stored in a refrigerator (4°C) for 48 h.

For scanning electron microscopy (SEM), samples were rinsed in a PBS solution containing 4% sucrose (pH 7.2) and post-fixed in 2% osmium tetroxide for 1 h before immersion in a consecutive series of ethanol solutions (70%, 90%, 100%). Dried specimens were then immersed in 1:1 solution of hexamethyldisilazane (HDMS) and 100% ethanol, before immersion in 100% HDMS for 20 to 40 minutes. Samples were subsequently left to air-dry for 30 min before being mounted with an epoxy resin on platinum-coated aluminium stubs. The coated samples were viewed with a high-vacuum, 10 kV SEM (XL30, Philips, Japan). The colour of skin was noted prior to processing for SEM, but we found no clear difference in microstructure recorded.

For histology, samples were immersed in PBS solution (pH 7.4) and decalcified using ethylenediaminetetraacetic acid (EDTA) for 24 h. Samples were subsequently dehydrated by successive immersion in ethanol (70%, 80%, 95%, 100%), rinsed in xylene, immersed and embedded in paraffin. Transverse sections (10 µm thickness) were mounted onto slides and left unstained to view pigmentation. Slides were imaged using a mounted camera (LC30, Olympus, Australia) and light microscope (BX51, Olympus, Australia).

Spectrophotometry and photography

We photographed the caudal lures of 33 specimens (Table S1) using a DSL camera (Canon EOS 7D) fitted with a macro lens (f/2.8 Canon EF-S 60mm). We then measured the spectral reflectance of the lateral-dorsal and ventral scales on each caudal lure using an Ocean Optics spectrometer (MAYA2000 Pro, Dunedin, FI, USA) and analysed using Ocean View software v1.6.7 (Ocean Optics, Dunedin, FI, USA). The mean reflectance was calculated for three locations on the caudal lure representing different colours (white/grey, yellow, black; Figure 2) and plotted in R v3.6.2 (R Core Team, 2019; Wickham *et al.*, 2019). Each reflectance measurement was expressed

relative to a Spectralon 99% white reflectance standard (WS-1-SL, Ocean Optics, Dunedin, FL, USA). The probe (QR200-7-UV-BX 200 μ m) was mounted to maintain a constant angle (90°) and distance (4 mm) from the surface of the skin. Specimens were mounted in white plasticine to secure tails flat. Measurements were taken in a dim-lit room to minimise scattered light. Both the UV (deuterium) and visible (halogen) lamps were used simultaneously for each measurement. The wavelength and reflectance values of these two references were saved by accessing the file data in the Ocean View v1.6.7 schematic window (Ocean Optics, Dunedin, FL, USA). Following calibration, a reflectance reference was taken using the Spectralon standard to ensure that calibration was completed successfully, indicated by reflectance values of approximately 100% reflectance across all wavelengths. Reference measurements were also recorded of the white plasticine as a 'background' reference, and of the shuttered probe for a 'dark' reference.

RESULTS

We found ontogenetic changes in colour and specular properties of lures that broadly coincide with a shift in prey types (Figure 3; Figure S1). Although this change was continuous, we identified four distinct phenotypes approximately corresponding to neonate, juvenile, subadult and adult life histories. The "neonate banded" lure phenotype (SVL 116-147 mm; mass 3.1-9.8 g; $n = 13$) was a matte texture with lateral-dorsal bands that alternated black (4-5 bands) and white/grey (4-5 bands) with ventral white stripe; each colour displayed a UV signature (peak 340-360 nm). The "juvenile transition" lure phenotype (SVL 164-467 mm; mass 11.5-172.7 g; $n = 10$) was a matte texture with lateral-dorsal bands of black (3-4 bands) and light grey (3-4 bands) with a lateral ventral yellow stripe (peak 500-700 nm); the grey and yellow scales displayed a UV signature (peak 340-360 nm). The "subadult striped" lure phenotype (SVL 414-674 mm; mass 92.2-524.9 g; $n = 8$) was black on the lateral-dorsal scales with a ventral yellow stripe (peak 500-700 nm); only the yellow scales showed a UV signature (peak 340-360 nm). The yellow stripe was variable from pale yellow to orange (range 500-580 nm) among juvenile/subadult phenotypes (Figure S3). The "adult uniform"

lure phenotype (SVL 414-674 mm; mass 92.2-524.9 g; $n = 2$) was entirely black across the lure. The black colouration of the subadult/adult lure phenotypes was spectrally uniform with low average reflectivity (<20%) but highly reflective when viewed at angles relative to predominant light sources (e.g. the sun) creating a glossy specular reflection (i.e. high, angular dependent, reflectance across visible wavelengths). The lighter colour bands of the neonate/juvenile lures were only twice as reflective as the black colouration, and appeared as a middle grey colour rather than an absolute white (Figure 3). The silhouette of the lure also changed: overlapping scales created a serrated edge and the terminal spine was sharper in the subadult/adult phenotypes (Figure 4).

Adult epidermal microstructure consisted of a series of interlocking *oberhautchen* (outer epidermal cells) that created a “smooth” platelike surface (Figure 4). In contrast, *oberhautchen* of juvenile skin was sculpted into frayed edges and deep divots that created imbricate and “rough” surface. The microstructure of the dorsal body skin in both adults and juveniles was also imbricate with numerous deep divots (Figure 5). In the skin of the adult lure, pigment-containing cells were densely distributed in both the dermis (melanophores) and the epidermis (melanosomes). In the skin of the juvenile lure, the black bands contained some melanophores in the dermis; the grey/white bands contained sparsely distributed melanosomes in the epidermis and completely translucent layers of outer epidermis (β -layer).

DISCUSSION

Mechanisms underlying colour change

This study reveals changes in epidermal microstructure and dermal pigmentation underlying previously undescribed OCC in caudal lures of *A. antarcticus*. There are two main mechanisms of animal colouration: pigments that selectively absorb visible wavelengths of light, and (sub)surface microstructures that interfere with light to selectively reflect light, in an angular-dependent way, resulting in either highly coloured iridescence or spectrally neutral glossiness (Maia, D’Alba, & Shawkey, 2011).

The matte banded pattern in the neonate/juvenile lure morphologies are created by sparse epidermal and dermal pigments, combined with small depressions and irregular surface structure (Figure 4). This matte microstructure closely resembles the body scales of *A. antarcticus* (Figure 5) and textured scales of other snakes (e.g. rattlesnakes) (Stille, 1987; Price & Kelly, 1989), but is much shallower than the ridged nanostructures of the variably coloured and “velvety” scales in Gaboon vipers (*Bitis* spp.) (Spinner *et al.*, 2013). The glossy texture of the subadult/adult lure morphologies is created by an interlocking and smooth epidermal microstructure, that differs from the body scales (Figure 4; Figure 5), and causes a highly glossy broadband reflection resembling other biological materials such as feathers, eggs, cuticles and petals (Maia *et al.*, 2011; van der Kooi *et al.*, 2014; Igic *et al.*, 2015; Maurer, Kohl, & Gebhardt, 2017). These “glossy” lure morphologies also have dense pigmentation that uniformly absorbs wavelengths to create a black hue that is not influenced by viewing angle relative to light source (cf iridescence). During caudal luring, this combination of structure and pigmentation may result in a rapid change in luminance when seen by an observer. These results have implications for future research on caudal luring, as previous studies have manipulated tail colour and/or behaviour (Hagman *et al.*, 2008; Nelson *et al.*, 2010; Farrell, May, & Andreadis, 2011), but did not consider the interaction between epidermal microstructure and the perceiver’s angle of view during caudal luring.

What is the relationship between colour and motion during caudal luring?

To understand the significance of OCC in caudal lures, it must be viewed in context of snake and prey behaviour. This study is the first to describe a distinct neonate/juvenile lure morphologies in *Acanthophis*, but many field guides detail that the colour of adult lures is highly variable among species and geographically separated populations (Cogger, 2000; Mirtschin *et al.*, 2017; Wilson & Swan, 2013). During caudal luring, the body of *A. antarcticus* will lay motionless while the tail is positioned beside or in front of the jaw and moved laterally in a series of rapid thrashing movements and/or slow undulations and “rippling waves”; the tail may also be lifted vertically and waved in the

air or else moved in rapid “busts” to position the tail back-and-forth from beside the jaw to above the head (Carpenter *et al.*, 1978; Chiszar *et al.*, 1990; Hagman *et al.*, 2008; McDonald, 2010; Nelson *et al.*, 2010). Carpenter *et al.* (1978) categorised the luring behaviour of *A. antarticus* in to two alternating phases: (I) slow, fine motor movements of the tail tip, and (II) fast, gross motor movements of the entire tail. The conspicuous colouration of the caudal lure, which contrasts the camouflaged patterning of the body, is likely to draws an observer’s attention towards the tail while it is positioned against the cryptic head/body of the snake (Neill, 1960). In addition to contrasting colouration of the lure and body, we describe distinct colours within the caudal lure itself, especially in medium-sized *A. antarticus* that have caudal lures with bright yellow and UV signatures on the ventral scales (cf banded or glossy black on the lateral-dorsal scales; Figure 3). This ventral colouration is hidden from view during the slow undulations in phase I, but is revealed by a series of vertical lifting movements in phase II (Video S1). How colour might enhance or augment the movement of the tail during caudal luring needs to be investigated further.

Ecological significance of colour change in caudal lures

The signalling effects of OCC in *A. antarcticus* lures on prey attraction are unknown. Response of ectothermic prey to caudal luring has been tested in the northern death adder (*A. praelongus*) and indicated that smaller lures are more effective in eliciting a response in lizards, but only ectothermic prey were tested (Hagman *et al.*, 2008). Given that mammals and birds comprise a portion of the subadult/adult diet in this species (Figure S1), however, response of endothermic prey to a range of lure phenotypes and lighting conditions needs to be tested. Previous authors proposed that luring is retained in adult *Acanthophis* because ectothermic prey (consumed by juveniles of this species) remains an important part of the adult diet (Heatwole & Davison, 1976). If this were the case, lure morphology should remain unchanged as the snake grows (*i.e.* no OCC), or else acquire similar colour patterning to the body if camouflage is favoured by selection. On the contrary, we find that the caudal lure transitions between different colours, all of which are distinct from the body

colour pattern. Based on our results, we assert a new hypothesis that lure morphology is under differential positive selection for attracting ectothermic prey types (e.g. diurnal lizards) in juvenile snakes and endothermic prey (e.g. nocturnal mammals) in adult snakes.

Previous analysis of stomach contents in museum specimens of *A. antarcticus* (throughout their Australian geographic range) reveal that larger snakes tend to eat more endotherms, e.g. birds and mammals, than smaller snakes (summarised in Figure S1 and Table S2) (Shine, 1980; Shine, Spencer, & Keogh, 2014). The mammalian prey that could be identified to family level were mostly rodents (Muridae, 52%), followed by a single dunnart (*Sminthopsis* spp.) and antechinus (*Antechinus* spp.); skinks comprise the majority of reptilian prey (74%) followed by agamid and varanid lizards; *Litoria* tree frogs were the majority of amphibian prey (33%) (Shine, 1980), and most birds could not be identified (Table S2). The difference in prey types consumed during ontogeny likely indicate a shift in foraging patterns, with smaller snakes potentially targeting diurnal reptiles and frogs and larger snakes targeting crepuscular/nocturnally active mammals.

The glossy lure phenotypes of larger snakes (subadult/adult) may be used to exploit sensory biases of various prey to attract attention or enhance contrast of adjacent scales on the tail/head. The specular reflections may be more effective at reflecting moonlight, catching the attention of mammals that are active at dusk/night. The black colour, glossy appearance and imbricate silhouette might also be mimicking the carapace and/or appendage of an arthropod (e.g. carabid beetles), which are prey items for nocturnally active marsupials that adult *A. antarcticus* that historically consumed. Indeed, insect parts have been recorded in the secondary stomach contents of adult *A. antarcticus* (which swallow their prey whole). We do not have data on the spectral reflectance or microstructure of local arthropods or skinks for comparison, thus an 'aggressive mimicry' hypothesis is tentative. Regardless, previous work on *A. antarcticus* behaviour indicates that caudal luring closely matches the velocity speeds of common invertebrates (Nelson *et al.*, 2010), suggesting that the morphology and motion of the caudal lure are likely exploiting receiver bias in their

insectivorous prey. Finally, the positioning of the lure beside the head may also be salient. The labial scales have bright white spots with a UV signature (peak 330-420 nm; Figure S2) that, when the dark lure is undulated, may create a strobe effect of UV light, which are likely visible to birds and mammals that have the capacity to detect UV light (Jacobs, 1992).

The morphology of the neonate caudal lure (white/grey and black bands) and the juvenile caudal lure (grey bands) also display UV signatures, which are likely visible to skinks that are active during the day (Fleishman, Loew, & Whiting, 2011). This lure morphology resembles the banding pattern of some rattlesnakes, which use their tails in aposematic rattling displays. Given that captive neonate/juvenile *A. antarcticus* readily lure at feeding times (L. Allen, pers. obs.), however, an aposematic function is unlikely. The juvenile/subadult caudal lures have features of both the neonate lures (e.g. matte banded) and adult lures (glossy, black, imbricate scales). These lure morphologies also have a yellow ventral stripe with a UV signature, which is absent in the other lure morphologies. This yellow stripe is reminiscent of local skinks (e.g. *Hemiergis peronii*), and is likely only revealed to potential prey during rapid vertical lifting of the tail during luring (Video S1). These medium-sized snakes consume both endothermic and ectothermic prey (Figure S1; Table S2). Thus, these “transitional” lure morphologies may be effective at luring ectothermic prey (lizards, frogs) during the day, and endothermic prey (mammals, birds) at dusk and during the night.

To understand the ecological significance of OCC in *A. antarcticus*, behavioural experiments should test how potential prey types respond to different lure morphologies. Future behavioural studies will need to consider visual modelling of spectral reflectance to infer how lure colours are perceived by prey, as well as the influence of light intensity/spectral quality and background features (e.g. leaf litter) of microhabitats where *A. antarcticus* forage (Endler, 1992; Leal & Fleishman, 2002). Furthermore, the activity patterns of juveniles and adults snakes likely differ, which would dramatically alter how caudal lure signalling properties are perceived by potential prey. Such studies will be important in understanding the conservation threats to death adders in Australia and New

Guinea, especially the impact of invasive species (e.g. *Rhinella marnia*) (Brown, Phillips, & Shine, 2011), and population fluctuations in local prey types.

Implications for evolution of luring in snakes

The prevalence of OCC in caudal lures and variation in luring behaviour is poorly documented across life history stages in snakes. Recent studies suggest that luring is more prevalent in adult viperids than previously thought. The lure of the spider-tailed viper (*Pseudocerastes urarachnoides*), for example, only develops only in adulthood and superbly mimics the movement and limbs of a spider to attract bird-prey (Fathinia *et al.*, 2015). Other examples include the Cantil snake (*Bothrops bilineatus smaragdinus*) and related viperids (e.g. *B. insularis*, *Cerastes vipera*, *Vipera latastei*) that appear to lure at dusk/night to entice birds and/or mammals (da Fonseca, Correa, & Oliveira, 2019). Luring may also be context-dependent: studies in wild puff adders (*Bitis arietans*), which use both lingual and caudal luring, found that snakes use lingual luring only when anuran prey are nearby (Glaudas & Alexander, 2017). Other behavioural studies have also shown that snakes can discriminate between prey types and potential predators, and alter their luring behaviour accordingly (Reiserer, 2002; Reiserer & Schuett, 2008). Broad behavioural testing and morphological descriptions of captive and wild populations will reveal how ecological and environmental factors have influenced the evolution of caudal luring among convergent ambush-foraging snakes.

CONCLUSION

This study is the first to report OCC in caudal lures and demonstrate the underlying structural changes to the skin in snakes. We propose that juvenile and adult lures are under different positive selection pressures for the attraction of diurnal ectothermic or nocturnal endothermic prey, respectively. This hypothesis needs to be tested using behavioural experiments that measure prey response to different lure phenotypes, as well as recordings of how caudal luring behaviour might change during ontogeny for different *Acanthophis* populations and species.

313

314 **Ethics:** All interactions with animals and collection of samples were conducted under the
315 requirements of the Department for Environment and Water and the institutional guidelines of
316 Venom Supplies, and was undertaken in conformance with Animal Welfare Act 1985 (South
317 Australia). All measurements were taken from deceased animals that were alcohol-preserved and
318 housed as unregistered specimens at the South Australian Museum, no ethical considerations apply.

319 **Competing interests:** We declare no competing interests.

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327 **Author contributions:** L.A., J.M.C-R, B.S. and K.L.S. conceived of the study. S.D., L.P., J.H.N., M.F., B.S.
328 and J.M.C-R collected reflectance data and tissue samples. L.A. and N.D. were responsible for animal
329 husbandry. L.P. and J.M.C-R conducted microscopy analyses. J.M.C-R, A.L. and J.C.P. analysed
330 reflectance data. J.M.C-R wrote the manuscript with input from all authors.

331 **Data accessibility:** Supplementary methods, tables and figures are provided as Supplementary
332 Materials. Images of caudal lures for specimens used in this study are available at
333 [doi/10.25909/13239497](https://doi.org/10.25909/13239497). Reflectance data for individual specimens, diet data, and code used to plot
334 diet and reflectance data available at [https://github.com/jcrowerriddell/death-adder-lure-](https://github.com/jcrowerriddell/death-adder-lure-reflectance)
335 [reflectance](https://github.com/jcrowerriddell/death-adder-lure-reflectance). Supplementary video S1 of luring behaviour available at <https://vimeo.com/462914012>.

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Figures

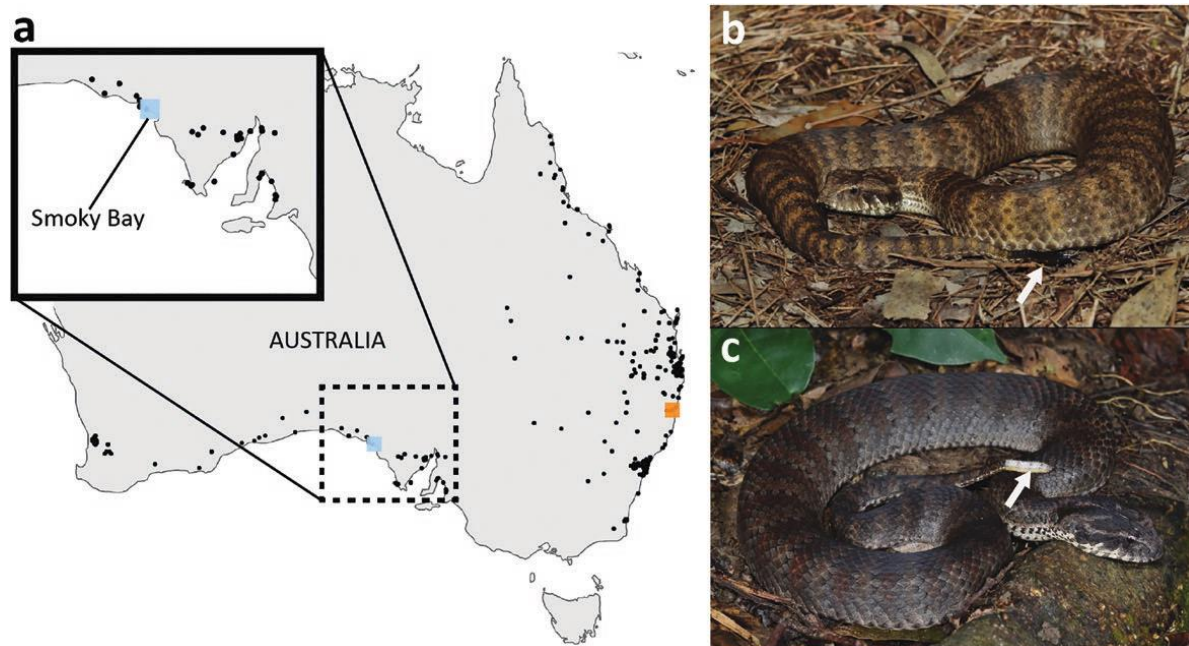


Figure 1. Distribution and colour variation in *Acanthophis antarcticus*. a) Disjunct distribution of *A. antarcticus* in Australia; inset shows the locality of source population in Smoky Bay, South Australia. b) Image of adult *A. antarcticus* showing black caudal lure that is typical for snakes from southern Australia. c) Image of adult *A. antarcticus* showing white caudal lure that is typical for individuals from the eastern coast of Australia. White arrows indicate location of the caudal lure; coloured squares on map show capture site for snakes shown in images: Smoky Bay, South Australia (b, blue), and Bellingen, New South Wales (c, orange). Occurrence data from the Atlas of Living Australia occurrence downloaded at <https://doi.org/10.26197/5e44150a40c6a> accessed on 13 February 2020. Image credits: Luke Allen, Shane Black.

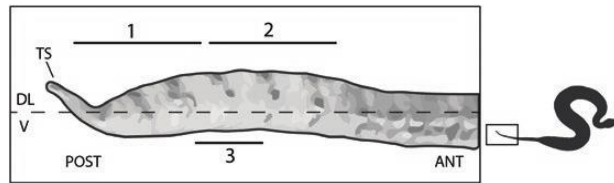


Figure 2. Schematic of the caudal lure in *Acanthophis antarcticus* showing locations where reflectance was measured. One measurement was taken each at the darkest and lightest point on dorsal-lateral scales, location of measurement was recorded as closest to posterior end of tail (position 1) or closest to anterior (position 2); one measurement was taken on the ventral scales at the mid-point of the lure (position 3). DL = dorsal-lateral, V = ventral, POST = posterior, ANT = anterior, TS = terminal spine.

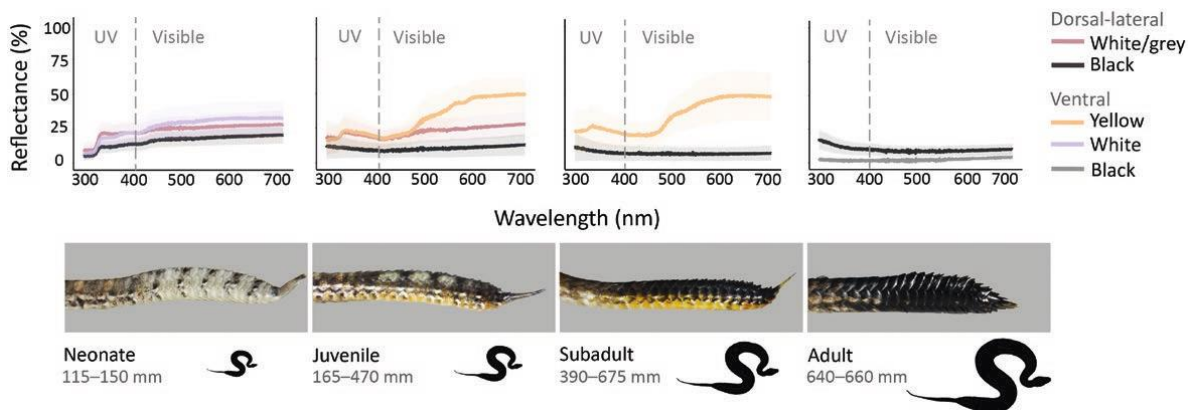


Figure 3. Ontogenetic colour change of caudal lures in *Acanthophis antarcticus*. Representative images of lure morphologies are shown at the different life stages, which correspond to snout to vent length. Plots show spectral reflectance of each colour recorded for the different lure morphologies; division between ultraviolet (UV) and visible spectrum shown by vertical dashed line. Snake silhouette by C. N. Zdenek (Phylopic CC BY-NC-SA 3.0).

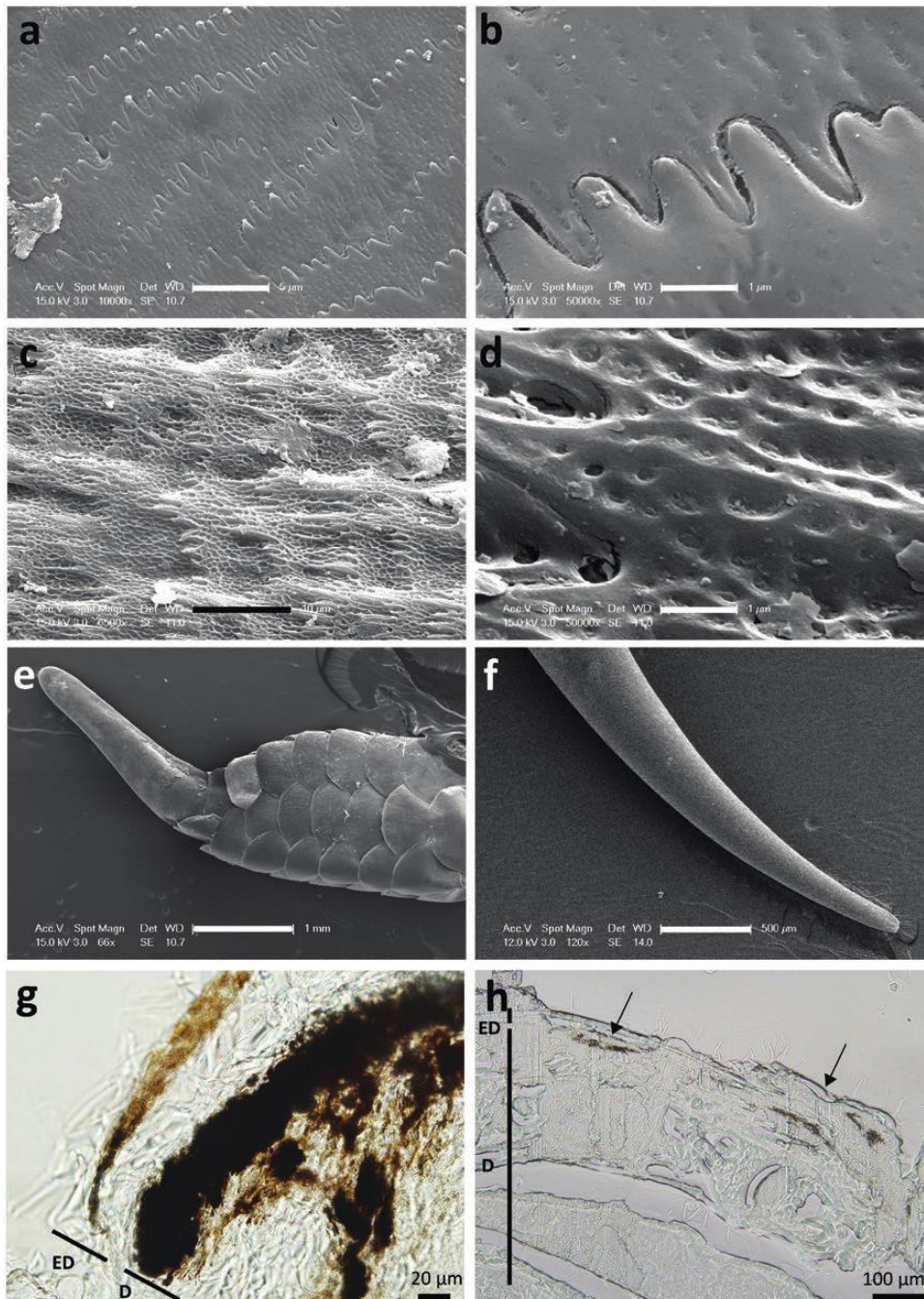


Figure 4. Skin structures underlying ontogenetic colour change in caudal lures in *Acanthophis antarcticus*. Scanning electron microscopy of epidermal microstructure in a, b) adult lure skin; c, d) neonate lure skin, and tip of caudal lure (terminal spine) in d) adult and e) juvenile. Light microscopy images of unstained slides show pigments cells the epidermis (ED) and dermis (D) in an g) adult lure and h) neonate lure. Arrows indicate “black” bands in the neonate.

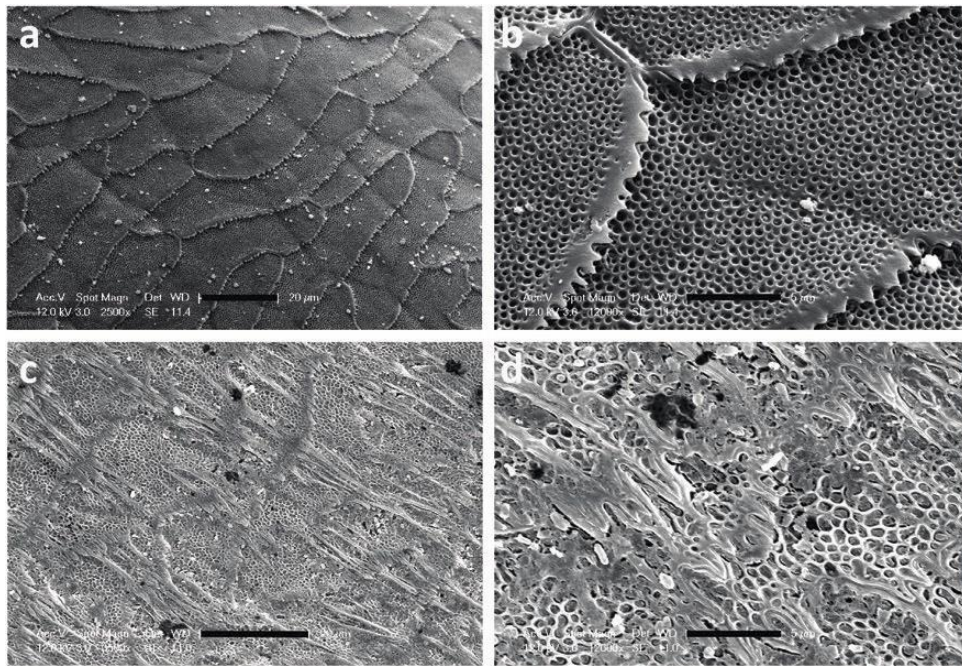


Figure 5. Epidermal microstructure of skin taken from dorsal scales on the midbody using scanning electron microscopy. a, b) Midbody skin from adult; c, d) midbody skin from neonate.