Aposematism and Batesian mimicry in snakes: through the visible spectrum and beyond?

Wuster, Catharine; Wüster, Wolfgang

Herpetology Notes

Published: 26/02/2023

Herpetology Notes, volume 16: 165-170 (2023) (published online on 26 February 2023)

Aposematism and Batesian mimicry in snakes: through the visible spectrum and beyond?

Catharine E. Wüster[1] and Wolfgang Wüster[1,*]

Abstract. We explore the usefulness of UV photography in investigating putative Batesian mimicry of aposematic elapid snakes by harmless colubrids. We predicted that Batesian mimics would share similar UV reflectance patterns as their models and tested this in two likely Batesian mimicry systems. In North America, both *Micruroides euryxanthus* and *Lampropeltis knoblochi* lack any UV reflectance from any part of their dorsum. In India, *Bungarus caeruleus* displays strong UV reflectance from its light body rings, which is largely echoed in visually similar black and white *Lycodon anamallensis*, but not in reddish-brown individuals of the same species. Our results highlight the potential for UV photography to contribute to testing mimicry hypotheses. Researchers using inanimate models to test the function of animal patterns need to consider reflectance outside the human visual spectrum to maximise the resemblance of their models to the focal organisms.

Keywords. Photography, ultraviolet, reflectance, Elapidae, Colubridae, *Micruroides*, *Lampropeltis*, *Bungarus*, *Lycodon*, *Oligodon*

Introduction

Aposematism and mimicry theory have become major topics of research on defensive strategies in animals. Life history theory predicts that aposematic signals should be fine-tuned to the sensory modalities of the target predators (Ruxton et al., 2018). Similarly, while mimicry need not be perfect (Kikuchi and Pfennig, 2010; Ruxton et al., 2018), life history theory would nevertheless predict that the key features involved in Batesian or Mullerian mimicry should be adapted to the sensory and cognitive capabilities of key predators (Ruxton et al., 2018).

Unusually among aposematic animals, front-fanged venomous snakes are capable of inflicting severe or lethal injuries on much larger predators that lack adaptations to evade or resist their fangs or toxins (Pough, 1988). It is therefore unsurprising that some of them signal their toxic armaments through active visual and acoustic behavioural means (e.g., gaping, striking, hissing, body inflation or flattening), sometimes enhanced by specific morphological adaptations (e.g., hooding in cobras; rattling in rattlesnakes; scale rubbing and serrated scale keels in *Echis* and *Dasypeltis*; glottal keels in *Pituophis*). Here, we focus on passive visual aposematic signals, namely specific colours and patterns denoting unprofitability. Well-supported examples include primarily New World coral snakes (*Micrurus*, *Micruroides*), whose aposematic function has been demonstrated in field and lab experiments and other lines of evidence (Smith, 1977; Greene and McDiarmid, 1981; Brodie, 1993), and European vipers, whose cryptic but recognisable patterns also lead to predator avoidance (Wüster et al., 2004; Valkonen et al., 2011).

Experimental evidence of aposematism in snakes has most often come from experiments involving plasticine models (Madsen, 1987; Brodie, 1993; Wüster et al., 2004), with the models' resemblance to the presumed aposematic organism being gauged according to the eyesight of the researchers, but rarely explicitly tested beyond that (but see Niskanen and Mappes, 2005). However, many potential snake predators have visual spectra that differ considerably from the human visual spectrum. Most relevantly in this context, most birds have tetrachromatic vision, with an absorption spectrum that includes much of the near-ultraviolet region (Burkhardt and Maier, 1989; Bowmaker et al., 1997). As a result, similarity between animal and experimental model, or presumed model and mimic, to human vision cannot be extrapolated to apply to predators with different visual

[1] Molecular Ecology and Evolution at Bangor, School of Natural Sciences, Bangor University, Bangor LL57 2UW, Wales, UK.
[*] Corresponding author. E-mail: w.wuster@bangor.ac.uk

spectra (Corcobado et al., 2016).

Birds are important predators of both venomous and non-venomous snakes in many ecosystems (Brodie, 1993; Shine et al., 2007; Ajtić et al., 2013; Radovics et al., 2022), and are capable of perceiving light in the near-ultraviolet (UV) part of the spectrum. Therefore, here we test whether the aposematic colours of two geographically separated elapid snakes and their proposed Batesian mimics extend into the ultraviolet region of the spectrum. We used two model systems to gather preliminary data to test our hypotheses. The first involved the venomous Sonoran Coral Snake, *Micruroides euryxanthus* (Kennicott, 1860), from the southwestern USA and northwestern Mexico, and its likely mimic, the sympatric, non-venomous Madrean Mountain Kingsnake, *Lampropeltis knoblochi* Taylor, 1940. Predator avoidance of coral snake patterns in this specific system has been previously demonstrated (Pfennig et al., 2001). The second model consists of the venomous Indian Krait, *Bungarus caeruleus* (Schneider, 1801), and two potential mimics, the sympatric, harmless Indian Wolf Snake, *Lycodon anamallensis* Günther, 1864, and the Common Kukri Snake, *Oligodon arnensis* (Shaw, 1802). Predator avoidance of krait patterns has not been demonstrated experimentally. However, it is a matter of common observation than many humans recognise and avoid krait patterns, and that wolf snakes are frequently mistaken for kraits due to their dark background with light crossbars (Whitaker and Captain, 2004). *Oligodon arnensis* is reddish or brownish with black cross bands that may have a thin white edge; while this pattern is not directly krait-like, this species is often confused with kraits by local people on account of its banded pattern (Whitaker and Captain, 2004)

In this study, we use UV photography to test the hypotheses that (i) in snakes subject to avian predation, aposematic patterns should extend into the UV region, and (ii) that likely Batesian mimics of the venomous snakes should show similar reflectance patterns as the presumed models (*M. euryxanthus* and *B. caeruleus*).

Methods

Focal taxa. To explore patterns of UV reflectance, we used one adult *Micruroides euryxanthus* and one adult *Lampropeltis knoblochi* from Cochise County, Arizona, and one adult *Bungarus caeruleus*, four adult *Lycodon anamallensis* and a juvenile *Oligodon arnensis* from near Mysore, Karnataka, India. Contrary to the description provided in Ganesh and Vogel (2018), *L. anamallensis* in the Mysore area display extensive variation in ground colour and contrast, while retaining the dark barring in the supralabial region and the absence of a parietal collar characteristic of the species. Two of our *L. anamallensis* were near-black with creamy-white light markings, whereas the other two were reddish-brown with creamy-yellow light markings. All snakes were checked for signs of impending skin shedding, in particular bluish eyes and loose or flaking skin.

UV photography. The UV photographic equipment is a customised kit, developed by Jolyon Troscianko (JT) and described in detail here: http://www.jolyon.co.uk/2014/07/full-spectrum-nx1000/.

A Samsung NX1000 was adapted to full spectrum sensitivity by removing the manufacturer's UV and infrared (IR)-blocking filters. The camera was fitted with a 1:5.6/80mm EL-Nikkor enlarger lens (the earlier black/chrome version, which has no UV resistant coating). For a full-spectrum UV light source we used an Iwasaki EYE Color Arc MT70D bulb (www.eye.co.jp) with the exterior protective UV barrier coating scraped off. For UV photography, we used a Baader U-Filter (Venus and UV) 350nm 2", with a transmission peak of approximately 80% at 350nm and a bandwidth 60nm (320-380nm), completely blocking the entire remaining spectral range from 200nm to 1120nm. For photography in a slightly curtailed visual spectrum, we used a Baader UV/IR cut 2" (420 – 685 nm) Bandpass Filter, that excludes UV and IR and the extremes of the visual spectrum.

The different components were fitted together using the appropriate adapters to attach the lens to the camera and to enable focusing. We used a filter slider, custom made by JT, to allow easy switching between the two filters without having to physically unscrew and attach different filters each time: this reduces the risk of the camera kit moving between shots, the aim being to photograph the same part of the subject in the same position. In most cases, we included a grey reflectance standard (custom made by JT), with two UV reflectance tiles at approximately 10% and 80% respectively. Snakes were photographed against the background of a PTFE sheet with approximately 80% UV reflectance. The scene was surrounded by other reflectors as much as possible to minimise distracting shadows.

Photos were taken in both JPEG and RAW SF format at ISO 400, with exposure bracketing set at +/- 2, using average metering and sRGB colour space, and apertures between f5.6 and f11 in manual mode. Three bracketed photos were taken in the visual spectrum, followed by three bracketed photos in the UV region of the spectrum only. As the lens is of relatively long focal length and needs to be close to the subject, we photographed a section of the dorsal side of each snake at approximately midbody. In the case of *Lampropeltis knoblochi*, the head was also photographed to test for UV reflectance from the light head markings. The exposure length for UV photography was of the order of three seconds, so snakes were gently restrained, and only the relevant section of body was exposed to allow for photography while minimising movement and consequent blurring. For safety, venomous snakes were enticed to crawl up a Perspex tube for the first third of their length and then gently restrained where the body entered the tube.

Results

Among the Asian snakes, *Bungarus caeruleus* showed strong UV reflectance at a similar level to the 80% reflectance standard from the white cross-bands along the body (Fig. 1A,B). Among the *Lycodon anamallensis*, the two blackish specimens with near-white markings displayed noticeable UV reflectance from the light makings (Fig. 1C,D), whereas the two reddish-brown specimens with cream markings showed extremely limited UV reflectance from their light markings (Fig. 1E,F). Our specimen of *Oligodon arnensis* showed no reflectance whatsoever in the ultraviolet region (Fig. 1G,H). Among the North American snakes, both *Micruroides euryxanthus* and *Lampropeltis knoblochi* lacked noticeable UV reflectance from the light pattern elements of their body (Fig. 2A,D).

Discussion

Our results provide an insight into the potential utility of UV photography in elucidating the functions of snake patterns. Contrary to our first hypothesis, the striking tricolour banded pattern of *M. euryxanthus* does not extend beyond the human visual spectrum into shorter wave lengths: under UV light only, the snake was monochrome. In the case of its presumed mimic, UV photography revealed minimal UV reflectance from light pattern elements, largely congruent with the hypothesis that a Batesian mimic should show similar reflectance patterns as its model. The same applies to our specimen of *L. knoblochi*, which showed no detectable UV reflectance from either the light head (not shown) or body markings. Similar high UV absorbance by skin pigments has also been found in *Micrurus fulvius* and its mimic *Lampropeltis elapsoides* (Kikuchi and Pfennig, 2012).

In the case of the Indian snakes, the pattern was more complex: *B. caeruleus* shows very high UV reflectance from its light bands, consistent with Hypothesis 1. On the other hand, the four specimens of *Lycodon anamallensis* used here differed considerably: the two black and near-white specimens displayed very noticeable UV reflectance from their light bands, consistent with Hypothesis 2, whereas the two reddish-brown specimens with cream markings displayed very little reflectance. The individual variation in this species raises questions on possible selective pressures favouring patterns that are either more or less krait-like, both in the visual and UV regions of the spectrum, although the reduced effectiveness of short-wavelength radiation in aposematism, compared to longer wavelength radiation, may also play a role (Yeager and Barnett, 2020). The role of both visible-spectrum and UV reflectance in this putative mimicry ring could represent a fruitful subject for future research.

While congruent patterns of UV reflectance in our Indian and North American examples are consistent with a hypothesis of *L. knoblochi* and *L. anamallensis* as mimics of *Micruroides* and *B. caeruleus*, respectively, the differences in visual-spectrum pattern as well as lack of UV reflectance suggest that the pattern of *Oligodon arnensis* did not evolve under selection for mimetic resemblance to *Bungarus caeruleus*.

Clearly, the very limited sampling in this study cannot do anything more than to provide an indication of the potential of UV photography in unravelling the function of snake and other animal colour patterns. Nevertheless, two major conclusions can be drawn from our results:

1. As noted by Bateman et al. (2017), researchers using inanimate models (e.g., plasticine) of organisms to study the impact of patterns on predation rates should ensure that the reflectance spectra of the models match those of the organisms, including outside of the visible spectrum. This aspect has been largely neglected in the literature on snake aposematism and mimicry (but see Niskanen and Mappes, 2005). As shown here, researchers investigating mimicry of *M. euryxanthus* should endeavour to use non-UV-reflective materials, whereas those researching the function of the pattern of *B. caeruleus* would be well advised to seek UV-reflective materials or paint for the light bands across the body.
2. Congruent UV reflectance patterns between models and putative Batesian mimics constitute a potential independent test of hypotheses of Batesian mimicry: highly discordant patterns that would be apparent

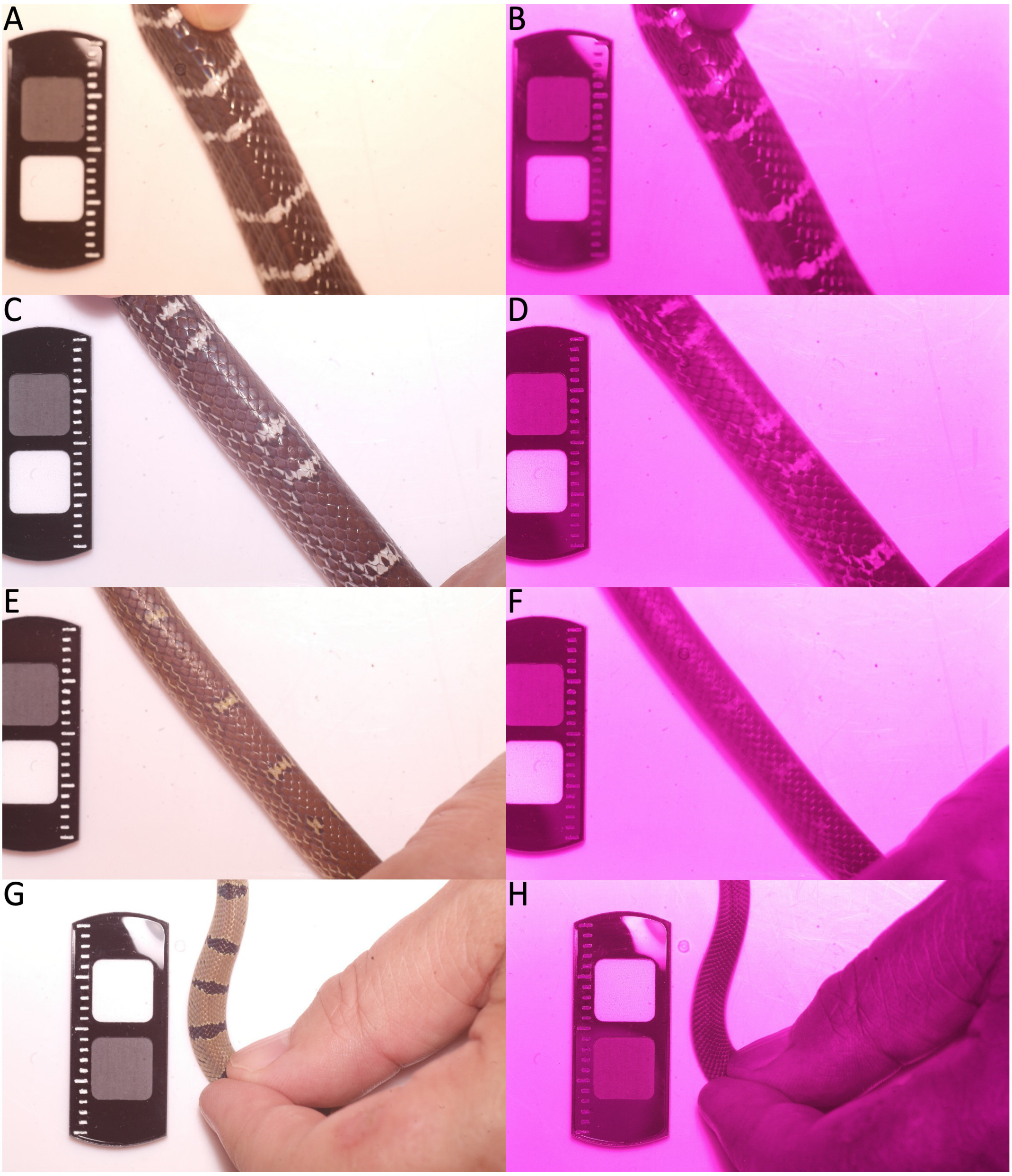

Figure 1. Asian snakes photographed through a curtailed visual spectrum (420–685 nm) Bandpass filter (left column), and through a UV filter with a transmission peak of 350nm and a bandwidth 60 nm (320–380 nm; right column). (A and B): *Bungarus caeruleus*. (C and D): *Lycodon anamallensis*, black and white specimen. (E and F): *Lycodon anamallensis*, reddish-brown and cream specimen. (G and H): *Oligodon arnensis*. The grey squares are grey standard tiles with 10% and 80% UV reflectance. Photographs by Catharine E. Wüster.

to avian predators would weaken a hypothesis of a mimetic relationship between two taxa, whereas broadly congruent patterns would support a hypothesis of Batesian or Mullerian mimicry.

In conclusion we suggest that studies of UV reflectance of snake patterns could prove enlightening in the study of snake mimicry systems and predator responses to those patterns and urge future researcher to consider

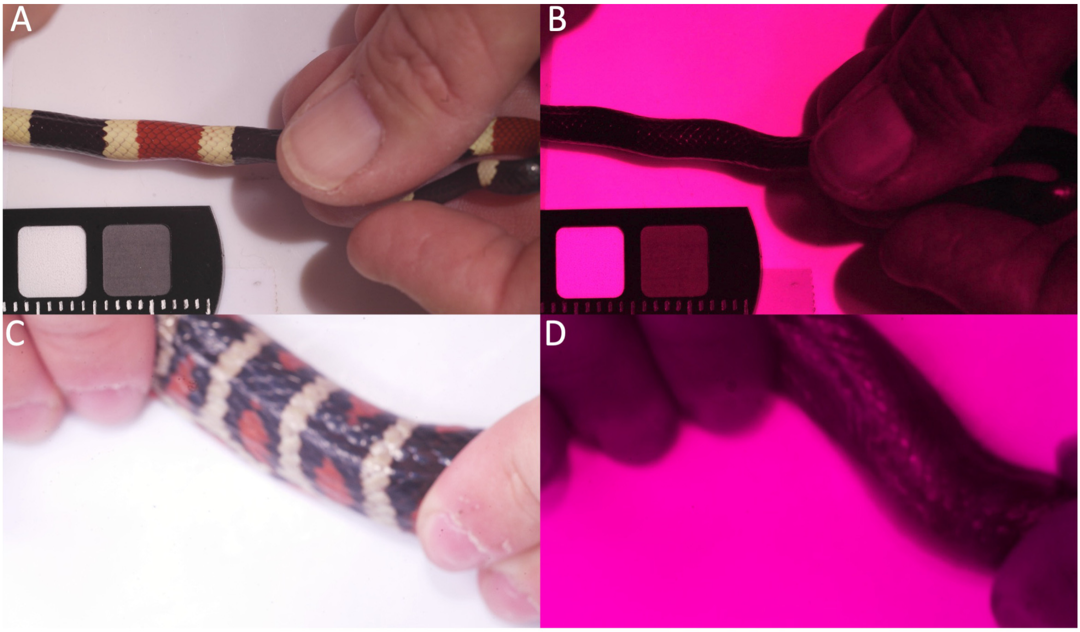

Figure 2. North American snakes photographed through a curtailed visual spectrum (420–685 nm) Bandpass filter (left column), and through a UV filter with a transmission peak of 350 nm and a bandwidth 60 nm (320–380nm; right column). (A and B): *Micruroides euryxanthus*. (C and D): *Lampropeltis knoblochi*. The grey squares are grey standard tiles with 10% and 80% UV reflectance (not shown for *L. knoblochi*). Photographs by Catharine E. Wüster.

light reflectance outside the visual spectrum in their assessments of mimetic similarity.

Acknowledgments. We thank Gerry Martin and Chandini Chhabra for their hospitality and the opportunity to photograph the Indian species in this report at the Liana Trust Farm in 2019, and Peter Lindsey and Bob Ashley (Chiricahua Desert Museum, Rodeo, New Mexico) for making the North American species available, and James Hicks and Ben Owens for help with some of the photo sessions. Jolyon Troscianko provided helpful advice for assembling the kit for ultraviolet photography. We thank Andrew Durso, Thomas Madsen and Bryan Maritz for their insights into elapid diets.

References

Ajtić, R., Tomović, L., Sterijovski, B., Crnobrnja-Isailović, J., Djordjević, S., Djurakić, M., et al. (2013): Unexpected life history traits in a very dense population of dice snakes. Zoologischer Anzeiger – Journal of Comparative Zoology **252**: 350–358.

Bateman, P.W., Fleming, P.A., Wolfe, A.K. (2017): A different kind of ecological modelling: the use of clay model organisms to explore predator–prey interactions in vertebrates. Journal of Zoology **301**: 251–262.

Bowmaker, J.K., Heath, L.A., Wilkie, S.E., Hunt, D.M. (1997): Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. Vision Research **37**: 2183–2194.

Brodie, E.D. (1993): Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. Evolution **47**: 227–235.

Burkhardt, D., Maier, E. (1989): The spectral sensitivity of a passerine bird is highest in the UV. Naturwissenschaften **76**: 82–83.

Corcobado, G., Herberstein, M.E., Pekár, S. (2016): The role of ultraviolet colour in the assessment of mimetic accuracy between Batesian mimics and their models: a case study using ant-mimicking spiders. Science of Nature **103**: 90.

Ganesh, S.R., Vogel, G. (2018): Taxonomic reassessment of the Common Indian Wolf Snakes *Lycodon aulicus* (Linnaeus, 1758) complex (Squamata: Serpentes: Colubridae). Bonn Zoological Bulletin **67**: 25–36.

Greene, H.W., McDiarmid, R.W. (1981): Coral snake mimicry: does it occur? Science **213**: 1207–1212.

Kikuchi, D.W., Pfennig, D.W. (2010): Predator cognition permits imperfect coral snake mimicry. American Naturalist **176**: 830–834.

Kikuchi, D.W., Pfennig, D.W. (2012): A Batesian mimic and its model share color production mechanisms. Current Zoology **58**: 658–667.

Madsen, T. (1987): Are juvenile grass snakes, *Natrix natrix*, aposematically coloured? Oikos **48**: 265.

Niskanen, M., Mappes, J. (2005): Significance of the dorsal zigzag pattern of *Vipera latastei gaditana* against avian predators.

Journal of Animal Ecology **74**: 1091–1101.

Pfennig, D.W., Harcombe, W.R., Pfennig, K.S. (2001): Frequency-dependent Batesian mimicry. Nature **410**: 323–323.

Pough, F.H. (1988): Mimicry of vertebrates: are the rules different? American Naturalist **131**: S67–S102.

Radovics, D., Szabolcs, M., Lengyel, S., Mizsei, E. (2022): Hide or die when the winds bring wings: predator avoidance by activity shift in a mountain snake. Research Square. Available at https://doi.org/10.21203/rs.3.rs-2096701/v1. Accessed on 13 November 2022.

Ruxton, G.D., Allen, W.L., Sherratt, T.N., Speed, M.P. (2018): Avoiding Attack: The Evolutionary Ecology of Crypsis, Aposematism, and Mimicry. Oxford, United Kingdom, Oxford University Press.

Shine, R., LeMaster, M.P., Moore, I.T., Olsson, M.M., Mason, R.T. (2007): Bumpus in the snake den: effects of sex, size, and body condition on mortality of red-sided garter snakes. Evolution **55**: 598–604.

Smith, S.M. (1977): Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). Nature **265**: 535–536.

Valkonen, J., Niskanen, M., Björklund, M., Mappes, J. (2011): Disruption or aposematism? Significance of dorsal zigzag pattern of European vipers. Evolutionary Ecology **25**: 1047–1063.

Whitaker, R., Captain, A. (2004): Snakes of India: The Field Guide. Chennai, Draco Books.

Wüster, W., Allum, C.S.E., Bjargardóttir, I.B., Bailey, K.L., Dawson, K.J., Guenioui, J., et al. (2004): Do aposematism and Batesian mimicry require bright colours? A test, using European viper markings. Proceedings of the Royal Society of London, Series B: Biological Sciences **271**: 2495–2499.

Yeager, J., Barnett, J.B. (2020): Ultraviolet components offer minimal contrast enhancement to an aposematic signal. Ecology and Evolution **10**: 13576–13582.

Accepted by Justin Bernstein