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Colouration in male blue-throated keeled lizards (*Algyroides nigropunctatus*): Evidence for ultraviolet reflectance of throat and lateral patches

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The blue-throated keeled lizard, *Algyroides nigropunctatus*, is distributed along the Adriatic coast from Italy to Greece and is sexually dichromatic. Males display a striking blue on their throat, an orange ventrum, and a dark brown dorsal colouration, but their colouration has never been objectively assessed. Here, we describe the colouration of 13 male blue-throated keeled lizards from Cres Island (Croatia) using spectrophotometry and ultraviolet (UV) photography, and show that the blue throat and the blue spots located on the flanks reflect in the UV part of the spectrum. We discuss the potential role of UV-blue colouration in social signalling.

Key words: Chromatic signal, Ultraviolet, Spectrophotometry, Lizards, Squamates

The lizard genus *Algyroides* comprises four species with disjoint distributions in southern Europe (Arnold & Ovenden, 2010). Compared to other lacertid species, relatively little is known about the behaviour, ecology, or evolution of these lizards, although morphological and molecular analyses have confirmed the monophyly of the genus (Harris et al., 1999). *Algyroides nigropunctatus* Duméril & Bibron (1839), commonly known as the blue-throated keeled lizard or the Dalmatian *Algyroides*, has the largest distribution range of the genus, and is found along the coast of the Balkan peninsula from Italy to Greece (Böhme, 1981). *Algyroides nigropunctatus* inhabits open and semi-open habitats (e.g. open woodland, bushy areas, stonewalls), usually favouring shady areas (Haxhui, 1991; Bressi, 2004; Arnold & Ovenden, 2010). This species exhibits a marked sexual dimorphism in size and shape with males having relatively larger heads than females, which allows the packing of jaw musculature and a compressed braincase (Ljubisavljevic et al., 2011). They are also sexually dichromatic with adult males displaying an orange ventral colouration and a striking blue colouration on their throat (Arnold & Ovenden, 2010; Carlino & Pauwels, 2016), while females are ventrally white to yellow and have no or less bright blue colouration on their throat (Arnold & Ovenden,

2010). Dorsally, males and females are dark brown with black spots present on some of their dorsal scales, to which the species owes its name. Geographical variation in colour pattern has been described, particularly in some insular populations. In the Ionian islands of Lefkada, Kephalliana, and Itaka (Greece) male *A. n. kephallithaticus* are ventrally yellow and their throat shifts from blue to green after the mating season (Arnold & Ovenden, 2010). In other Greek islands like Corfu and Erikoussa, males may exhibit a flashy orange colouration on their throat (unpublished information). However, to the best of our knowledge, no study to date has examined the colour pattern of *A. nigropunctatus* using objective (i.e. independent of the human visual system) methods. Here, we use standard reflectance spectrophotometry along with UV and human-visible photography to provide the first objective description of the colour pattern of males of this species.

In April 2016, we captured 13 adult males (SVL > 59 mm) of *A. nigropunctatus* by noosing in Cres Island (Croatia) in their typical habitat (e.g. shady areas, stone walls with vegetation, open woodland). Upon capture, we took ultraviolet (UV) pictures of every individual using a digital camera (Olympus PEN Mini) converted for UV photography by replacing the standard internal hot mirror filter with a Spectrosil 2000 fused silica filter, which transmits light wavelengths down to 170 nm. The camera was fitted with a UV-transmitting macro lens (Noflexar Novoflex 1:3.5/35mm) and a Baader U-filter with peak transmission between 320 and 380 nm. UV photographs were taken outdoors in the shade using natural illumination. For comparison, we also took pictures identical to the UV ones but in the human-visible range using standard digital cameras.

Lizards were transported in cloth bags to a darkened room where we obtained reflectance spectra of the ventrum, throat, and dorsum using a JAZ spectrophotometer with a R200-7-VIS-NIR reading-illumination probe and a PX-2 xenon strobe light source (Ocean Optics Inc.) for full spectral illumination. We averaged reflectance readings over 5 nm using a kernel

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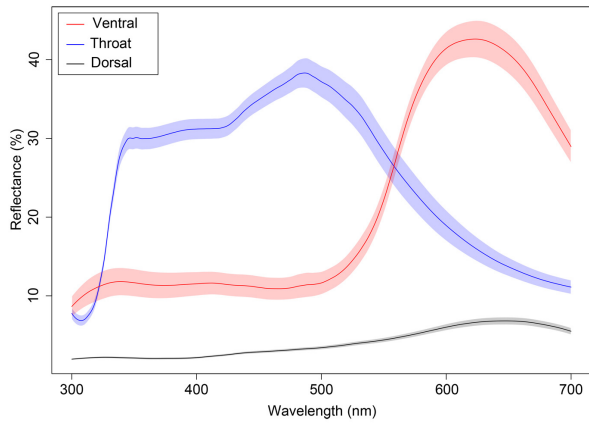


Figure 1. Non-normalised reflectance spectra of the throat (blue), the ventrum (red) and the dorsum (black) of 13 adult males of *A. nigropunctatus*. Reflectance is expressed as mean \pm SEM (coloured area surrounding the line).

smoothing function. We set integration time to 30 ms, scans to average to 10, and boxcar width to 10. For data acquisition, we hand-held the probe over the centre of the throat, ventrum and dorsum of the animals, perpendicular to the surface (i.e. illumination and readings angles were both 90°). An entomological pin attached to the side of the probe allowed us to maintain a constant distance of 5 mm between the tip of the probe and the target surface (see Badiane et al., 2017 for more details). Colour spots measuring less than 2 mm in diameter were ignored as they are beyond the resolution of our spectrophotometer set-up (Badiane et al., 2017). Reflectance spectra were analysed in R using the PAVO package (Maia et al., 2013). All animals were released at their capture sites after a maximum of 24 hours post-capture.

The throat of male *A. nigropunctatus* has a spectrum with a reflectance peak in the blue part of the spectrum

(485 ± 10 nm; mean \pm SEM), a relatively flat plateau extending into the UV range, and then a sharp drop-off at approximately 340 nm (Fig. 1). As expected, spectra of the orange ventrum show a pronounced reflectance peak in the orange-red (621 ± 3 nm). In contrast to the throat and ventrum, reflectance spectra of the dorsum are characteristically flat with little reflectance across the spectrum and show no obvious reflectance peaks (Fig.1). UV photographs confirm that the throat colouration reflects in the UV range and is therefore best characterised as UV-blue (Fig. 2A). The UV-blue colouration of the throat covers the whole throat, sometimes extending over the chest and the supra-labial scales. The ventral orange colouration covers the ventrum and the limbs (ventrally only) and merges with the dorsal colouration on the flanks and neck. In addition, some of the captured males displayed regularly-spaced blue spots (up to 9 on each side) on some of their outer ventral scales (OVS) (Fig. 2B). Unfortunately, these spots were too small to obtain reliable reflectance spectra. However, the UV photographs revealed that these spots are also UV-reflecting (Fig. 2C).

Many lizard species, including lacertids, are capable of seeing in the ultraviolet range of the spectrum (Fleishman et al., 2011; Pérez i de Lanuza & Font, 2013; Martin et al., 2015a) and display UV colours that often appear as blue to the human eye (Whiting et al., 2006; Pérez i de Lanuza et al., 2014). Our results show that the throat of adult males of *A. nigropunctatus* is highly reflective in the UV range of the spectrum. Although this is the first report of UV colouration in *A. nigropunctatus* (see Arribas, 2002), many other lacertids display UV colour patches that purportedly function as social signals, including *Gallotia galloti* and *G. atlantica* (Font & Molina-Borja, 2004; Molina-Borja et al., 2006), *Timon lepidus* (Font et al., 2009), *Lacerta agilis* (Pérez i de Lanuza & Font, 2007), *L. viridis* (Bajer et al., 2010), *Zootoca vivipara* (Martin et al., 2015b), and several species of *Podarcis* (e.g. Marshall & Stevens 2014; Pérez i de Lanuza et al., 2014; our own unpublished data). It is possible that the UV-blue colouration also plays a

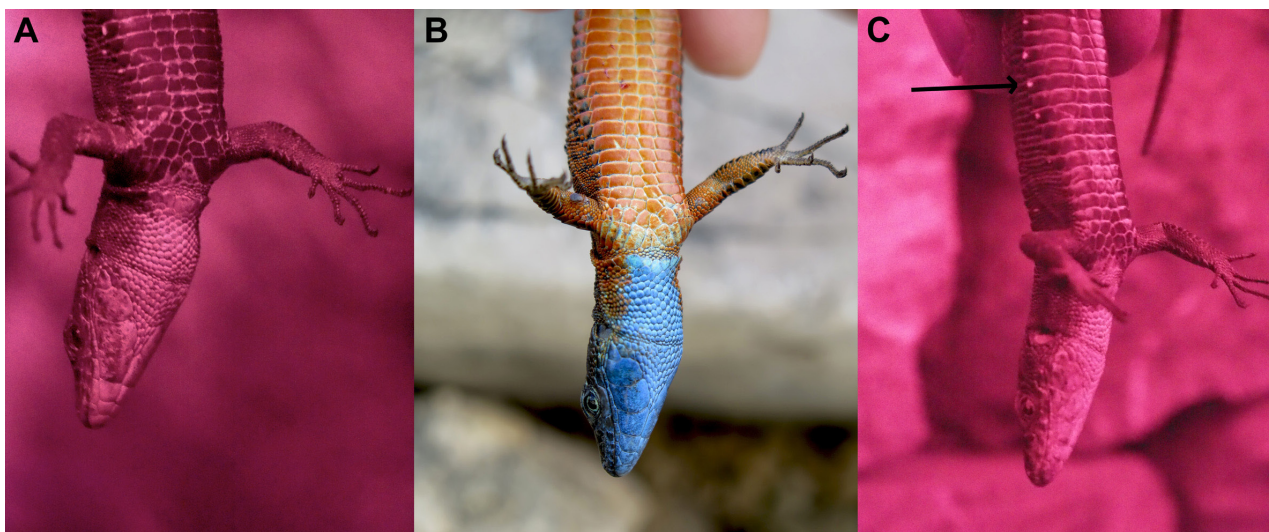


Figure 2. Photographs of a representative male of *A. nigropunctatus* from Cres Island in the UV (A, C, ventrally and laterally respectively) and in the human-visible range (B). The photographs in A and C were taken with a modified digital camera through a UV-transmitting filter that blocks most of the light wavelengths outside the 320-380 nm range. UV-reflecting skin patches in A and C are visible due to their lighter, whitish colouration (UV reflecting spots are indicated by an arrow in C).

role as a social signal in *A. nigropunctatus*, either as an ornament (female choice) or as an armament (male-male competition) because the ventrum and throat of lizards, and particularly of lacertids, are often the target of sexual selection and are used to convey information to conspecifics by means of chromatic signals (Leal & Fleishman, 2004; Bajer et al., 2010; Martin et al., 2015b). For example, males of *Lacerta schreiberi* also exhibit an iridescent UV-blue colouration on their throat (Pérez i de Lanuza & Font, 2014) with a spectral shape similar to the throat of *A. nigropunctatus*, which may function as an indicator of individual quality (Martín & López, 2009). Although we do not have spectral data for the UV-blue OVS, based on their similarity to UV-blue OVS from other lacertids (e.g. *Podarcis*, Pérez i de Lanuza et al., 2013) it is likely that their reflectance peak is also located in the UV range. Interestingly, this is the first lacertid species in which both a UV-blue throat and UV-blue OVS are described as most species studied to date have only one type of UV-blue patch, or they have none. Unfortunately, almost nothing is known about the behaviour of *A. nigropunctatus* and so discussion about the putative functions of these UV-blue patches is speculative.

The body colouration of male *A. nigropunctatus* conforms to the general pattern found in lacertids, with a relatively cryptic dorsum, possibly selected for background-matching, and conspicuous colour patches on the less visible lateral and ventral body surfaces. In many species, the latter are used for signalling and are made more or less visible through a variety of stereotyped movements and/or postural adjustments. The allocation of functionally different colour patches to different body regions (i.e. signal partitioning) allows balancing effective communication with the risks of detection by unintended receivers (Endler, 1992; Marshall & Stevens, 2014). Furthermore, the colours of the throat and ventrum in *A. nigropunctatus* are complementary, each one reflecting in the region of the spectrum where the other does not (see Fig. 1), suggesting that their presence on adjacent patches has been selected to maximise signal conspicuousness (Pérez i de Lanuza & Font, 2016).

Recent technical and methodological advances have expanded the breath of taxa for which spectral data are available (Kemp et al., 2015). However, our knowledge of animal colouration is largely shaped by studies of a handful of model species and very little is known about the colouration of most species alive today. Research on relatively understudied species, such as *A. nigropunctatus*, is a useful complement to studies with model species and essential to uncover general principles of lizard colouration.

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