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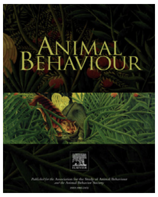

Colours of quality: structural (but not pigment) coloration informs about male quality in a polychromatic lizard

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Chromatic signals result from the differential absorption of light by chemical compounds (pigment-based colours) and/or from differential scattering of light by integument nanostructures (structural colours). Both structural and pigment-based colours can be costly to produce, maintain and display, and have been shown to convey information about a variety of individual quality traits. Male wall lizards, *Podarcis muralis*, display conspicuously coloured ventral and lateral patches during ritualized inter- and intrasexual displays: ventral colours (perceived as orange, yellow or white by humans) are pigment based, while the ultraviolet (UV)-blue of the outer ventral scales (OVS), located along the flanks, is structurally produced. We used spectrophotometric data from 372 adult males to examine, considering the entire visual spectrum of lizards, whether ventral and OVS colour variables can predict male quality. Results indicate that the hue and UV chroma of OVS are good predictors of fighting ability (size-independent bite force) and body condition, respectively. This suggests that structural colour patches are condition dependent and function as complex multicomponent signals in this species. In contrast, ventral coloration apparently does not function as a male quality indicator. We suggest that ventral and lateral colour patches may be social signals with different information content, possibly aimed at different receivers.

Chromatic signals provide one of the main avenues for social communication in many taxa (Bradbury & Vehrencamp, 2011). Animal colours result from the differential absorption of light by chemical compounds (i.e. pigment-based colours) and/or from differential scattering of light by integument nanostructures (i.e. structural colours) (Bagnara, Fernández, & Fujii, 2007; Umbers, 2013). Both structural and pigment-based colours can be used in intra- and intersexual signalling to convey information about individual quality traits such as condition, fighting ability, territory quality, parental care, good genes, parasite resistance and immunocompetence (Bradbury & Vehrencamp, 2011). Uncovering the relationship between colour variables and individual quality traits is the first step in identifying the information content of structural and pigment-based colour signals, and is key to understanding the balancing selection pressures responsible for their evolutionary stability (Bradbury & Vehrencamp, 2011; Searcy & Nowicki, 2005).

The correlation between one or more characteristics of signals and some attributes of the signaller (or its environment) provides informative content to many animal signals, while the costs associated with signal production, maintenance, display and/or signal cheating tend to ensure the honesty of individual quality signals (Font & Carazo, 2010; Searcy & Nowicki, 2005). Results from many studies of chromatic signals support this interpretation of quality signalling. For instance, in red-collared widowbirds, *Euplectes ardens*, the carotenoid-based coloration of male collars is a costly trait (e.g. Møller et al., 2000) that is used to signal an individual's ability to defend a territory in male–male agonistic contests. Collar area and hue correlate with territorial dominance, and high-quality males have bigger red collars with a long wavelength-biased hue relative to lower-quality males (Andersson, Pryke, Lawes, & Andersson, 2002). Similar quality signals have been described in numerous vertebrate and invertebrate species (e.g. Lim & Li, 2013; Setchell & Wickings, 2005). Carotenoid-based colours are well suited for honest signalling owing to the costs associated with carotenoid acquisition and the trade-offs between their use as ornaments versus other metabolic processes (e.g. Blount & McGraw, 2008; Saks, McGraw, & Horak, 2003). Other mechanisms of colour production, particularly structural mechanisms, have been considered cheap in comparison (Kemp, Herberstein, & Grether, 2012). While this may certainly be the case in some signals, the available evidence suggests that structural colours are also costly and can act as individual condition indicators (Kemp et al., 2012).

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In lizards, different chromatic traits (including both pigmentary and structural colours) have been shown to play an important role in species, sex, mate and rival assessment (Olsson, Stuart-Fox, & Ballena, 2013). Recent studies based on objective colour assessment (i.e. spectrophotometry) have stressed the ubiquity of structural chromatic signals that reflect in the near ultraviolet (UV) portion of the light spectrum. For example, the UV-reflective mouth corners of collared lizards, *Crotaphytus collaris*, which are visible during gaping displays, are the most conspicuous colour patches in this species' integument, and provide size-independent information on bite force in adult males (Lappin, Brandt, Husak, Macedonia, & Kemp, 2006). Similarly, the UV coloration of the throat of male Augrabies flat lizards, *Platysaurus broadleyi*, is used during the initial stages of opponent assessment (Stapley & Whiting, 2006). In this species, UV-biased throat coloration informs of high fighting ability and testosterone levels, while UV chroma provides information about male territorial status (i.e. territorial males have throats with higher UV chroma than floater males; Whiting et al., 2006).

The study of colour signals has been relatively neglected in many lizard groups and particularly so in lacertids, traditionally considered as relying mainly on chemosensory rather than visual cues (e.g. Mason & Parker, 2010). Despite this long-lasting misconception, colour vision is well developed in lacertids, which exhibit conspicuous and elaborate colour patterns involving both pigmentary and structural colours (Fitze et al., 2009; Pérez i de Lanuza, 2012; Vroonen, Vervust, & Van Damme, 2013). Furthermore, lacertids have been recently shown to provide an excellent model system to test hypotheses about the function and evolution of animal coloration (e.g. Olsson, Wapstra, & Uller, 2005; Pérez i de Lanuza, Font, & Carazo, 2013; Pérez i de Lanuza, Font, & Monterde, 2013; Salvador, Díaz, Veiga, Bloor, & Brown, 2008). The aim of this study was to explore the potential information content of the conspicuous coloration in a lacertid, the common wall lizard, *Podarcis muralis*. This species shows a coloration pattern that is typical of many lacertids: a cryptic brownish dorsal surface, a conspicuous long wavelength-rich ventral coloration and conspicuous lateral UV-blue patches on the outermost row of ventral scales (outer ventral scales, OVS). The ventral coloration is pigment dependent (containing carotenoid; Pérez i de Lanuza, Luna, González, & Font, 2012), and can be orange, white and, in some populations, yellow (Calsbeek, Hasselquist, & Clobert, 2010; Pérez i de Lanuza, Font, & Carazo, 2013; Sacchi et al., 2009). In contrast, UV-blue OVS have their peak reflectance in the UV range, and are structural in nature (Pérez i de Lanuza, 2012). As in other lizards, ventral and lateral coloured surfaces are good candidates to act as chromatic signals in lacertids because they are in an ideal location to be displayed to conspecifics during social interactions, yet normally remain concealed to predators, such as birds, that approach the lizards from above (Stuart-Fox & Ord, 2004). In this study, we examined the relationship between colour variables from the ventral and UV-blue OVS colour patches of male *P. muralis* and two well-studied quality measures in lizards: body condition and bite force. Body condition and bite force correlate with male mating success and dominance in lizards (Salvador et al., 2008), and are therefore considered good quality indicators for male lizards in general (e.g. Henningsen & Irschick, 2011), and for lacertids in particular (e.g. Huyghe, Vanhooydonck, Scheers, Molina-Borja, & Van Damme, 2005).

METHODS

Study Population

We studied a polymorphic population of *P. muralis* (Fig. 1) from the Cerdanya valley, in the southeastern Pyrenees (France). In this population, males and females show either pure white, yellow or orange (i.e. single-colour) ventral coloration. These three colours differ in hue, chroma and brightness extracted from spectral measurements (Pérez i de Lanuza, Font, & Carazo, 2013). Intermediate (white-orange and yellow-orange) phenotypes also occur, but are far less frequent than pure-colour morphs. In males, the ventral coloration extends over the throat and belly, whereas in females the yellow and orange ventral colours are restricted to the throat (Pérez i de Lanuza, Font, & Carazo, 2013). Frequencies of each morph vary from year to year, but all morphs were present in the population throughout the study period (see Appendix Fig. A1). UV-blue OVS are prevalent in males, but are shown only by 60% of females (G. Pérez i de Lanuza & E. Font, unpublished data). Males occasionally show UV-blue eyespots in the shoulder region.

We captured and measured 372 adult male *P. muralis* during the breeding seasons of 2004 ($N = 26$), 2005 ($N = 77$), 2008 ($N = 120$), 2010 ($N = 74$) and 2012 ($N = 75$) in dry stone walls of abandoned terraced fields. Lizards measuring less than 56 mm in snout–vent length (SVL) were excluded to ensure that all individuals had fully developed adult ventral coloration (Pérez i de Lanuza, Font, & Carazo, 2013). Overall, we captured 150 white, 93 yellow and 93 orange males. In contrast, only 16 white-orange and 20 yellow-orange males were captured. Owing to the difficulties inherent in obtaining sound spectrophotometric measurements from intermediate morphs (Pérez i de Lanuza, Font, & Carazo, 2013), only lizards showing pure ventral colours were included in the analyses. Given the relatively low frequency of intermediate morphs (i.e. 9.68%) and our overall sample sizes ($N = 372$), it is very unlikely that the exclusion of these individuals may have biased our results. Moreover, owing to limitations in the minimum measurement area achieved by existing spectrophotometers, taking spectrophotometric measurements from small OVS (i.e. <2 mm in diameter) inevitably results in the simultaneous measurement of adjacent patches of different colour, which gives rise to chimeric spectra. Hence, we discarded spectra of OVS from 43 males in which these patches were simply too small to be measured correctly. Ventral morphs were determined visually by the same observer (G.P.L.), a method that has been validated previously using spectral data (Pérez i de Lanuza, Font, & Carazo, 2013). Bite force was measured only during the last 3 years of this study (2008, 2010 and 2012, $N = 196$ pure-morph male lizards).

Spectrophotometric Measurements

We used a USB-2000 portable diode-array spectrometer and a PX-2 xenon strobe light source (both from Ocean Optics) to perform spectrophotometric measurements (for details see Font, Pérez i de Lanuza, & Sampedro, 2009). Spectral analyses were conducted in the 300–700 nm range to encompass the totality of the wavelength range perceived by diurnal lizards (e.g. Fleishman, Loew, & Whiting, 2011; Macedonia et al., 2009; for lacertids see Pérez i de Lanuza, 2012). Colour measurements of UV-blue OVS were always taken from the second rostral-most UV-blue OVS of the right flank (Pérez i de Lanuza & Font, 2011). Ventral coloration was measured at the throat because this is the most visible ventral surface during male social displays, and it is representative (within an individual) of the spectral shape of the entire ventral area (i.e. throat and belly; Pérez i de Lanuza, 2012).

Colour Analyses

We used the three colour variables customarily used in studies of animal coloration: brightness (i.e. intensity), hue and chroma (Bradbury & Vehrencamp, 2011; Endler, 1990). Brightness (Qt) was calculated by summing the percentage reflectance across the entire