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The evolution of colour pattern complexity: selection for conspicuousness favours contrasting within-body colour combinations in lizards

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Abstract

Many animals display complex colour patterns that comprise several adjacent, often contrasting colour patches. Combining patches of complementary colours increases the overall conspicuousness of the complex pattern, enhancing signal detection. Therefore, selection for conspicuousness may act not only on the design of single colour patches, but also on their combination. Contrasting long- and short-wavelength colour patches are located on the ventral and lateral surfaces of many lacertid lizards. As the combination of long- and short-wavelength-based colours generates local chromatic contrast, we hypothesized that selection may favour the co-occurrence of lateral and ventral contrasting patches, resulting in complex colour patterns that maximize the overall conspicuousness of the signal. To test this hypothesis, we performed a comparative phylogenetic study using a categorical colour classification based on spectral data and descriptive information on lacertid coloration collected from the literature. Our results demonstrate that conspicuous ventral (long-wavelength-based) and lateral (short-wavelength-based) colour patches co-occur throughout the lacertid phylogeny more often than expected by chance, especially in the subfamily Lacertini. These results suggest that selection promotes the evolution of the complex pattern rather than the acquisition of a single conspicuous colour patch, possibly due to the increased conspicuousness caused by the combination of colours with contrasting spectral properties.

Introduction

Animal colours have evolved to serve different adaptive functions, including camouflage, thermoregulation, warning or startling predators and communicating with conspecifics. The evolutionary design of signals, including chromatic signals, is the result of selection acting on two components known as efficacy (i.e. the degree to which a signal succeeds in reaching receivers and eliciting a response from them despite propagation distortion and noise) and strategic content (i.e. the reliability of the signal) (Guilford & Dawkins, 1991; Bradbury & Vehrencamp, 2011). Selection for both efficacy and strategic content often promotes the evolution of bright, highly chromatic and contrasting (i.e. conspicuous) chromatic signals (Dawkins & Guilford, 1997). Conspicuousness is always relative and depends on the visual system of the receiver and the contrast between a colour patch and the visual background against which it is displayed. Many studies of animal coloration have focused on the evolutionary design of specific colour patches (e.g. Hofmann *et al.*, 2006; Maan & Cummings, 2009; Prager & Andersson, 2010; Ng *et al.*, 2013; Friedman *et al.*, 2014), but why particular colour combinations are prevalent in some groups and species remains poorly understood. Colour patches rarely occur in isolation: the body surface of many animals is beset with multiple colour patches that offer to receivers a mosaic of differentially reflective surfaces. The conspicuousness

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of a complex colour pattern (i.e. one that comprises several colour patches; Endler, 1978; Chen *et al.*, 2012) therefore depends not only on the conspicuousness of each of its component elements but also on the overall conspicuousness generated by the simultaneous perception of the different colour patches (termed within-pattern contrast; Endler, 1993). Conspicuousness can be enhanced by maximizing either chromatic (i.e. hue) or achromatic (i.e. brightness or luminance) contrast between adjacent colour patches (Endler, 1990; Bradbury & Vehrencamp, 2011). Examples of complex patterns with strong achromatic contrast include the black and white stripes and spots found in many animals (e.g. zebra stripes, Godfrey *et al.*, 1987; Caro, 2005). Strong chromatic contrast, on the other hand, can be found in the complex colour patterns combining blue and yellow which are typical of reef fishes (Lythgoe, 1968; Marshall, 2000). Such contrasting colour combinations are relatively common in aposematic and cryptic colorations (e.g. disruptive coloration; Edmunds, 1974; Ruxton *et al.*, 2004; Stevens & Cuthill, 2006; Stevens & Merilaita, 2009), but their role in intraspecific communication has received relatively little attention (Marshall, 2000; Endler *et al.*, 2005; Gómez & Théry, 2007; Endler, 2012) (see examples in Fig. 1).

Recent studies have stressed the importance of colour pattern complexity in the evolution of lizard coloration (e.g. Ord *et al.*, 2001; Chen *et al.*, 2012). For example, in the Old World lizard family Lacertidae, those species in which intrasexual selection is more intense show complex male-biased sexually dichromatic colour patterns (Pérez i de Lanuza *et al.*, 2013b). Lacertids, particularly those in the Gallotiinae and Lacertini clades, display a complex colour pattern composed of multiple elements. The exposed dorsal body regions are selected for background matching and are relatively cryptic, but the less visible ventrolateral regions often display conspicuous colour patches. The ventral surface of many lacertids is white, yellow, orange or red, whereas laterally they display conspicuous eyespots on the flanks and/or shoulder region. The ventral and lateral colour patches often differ in their spectral properties: those located ventrally are predominantly long-wavelength colours, whereas those located laterally are short wavelength based (Pérez i de Lanuza *et al.*, 2013b; Pérez i de Lanuza & Font, 2015; Marshall & Stevens, 2014). Predators normally view lizards dorsally but interactions among lizards occur mainly at eye level, suggesting an important role for the ventral and lateral colour patches as social signals (e.g. Molina-Borja *et al.*, 2006; Font

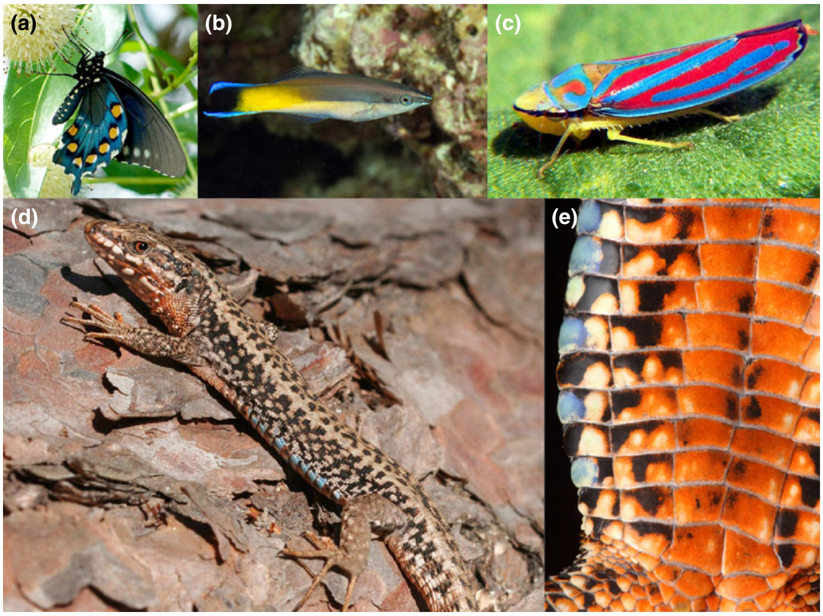

Fig. 1 Examples of animals with complex colour patterns combining short- and long-wavelength reflectance: (a) the pipevine swallowtail, *Battus philenor*, combining blue and yellow patches (reproduced under the terms of the Creative Commons Attribution License from Pegram *et al.*, 2013b); (b) the bluestreak cleaner wrasse, *Labroides dimidiatus*, combining iridescent blue and yellow patches (picture provided by P. Ryan; www.ryanphotographic.com); (c) leafhopper, *Graphocephala coccinea*, combining blue, yellow and red (picture by Bruce Marlin, published in www.commons.wikimedia.org, reproduced under the terms of the Creative Commons Attribution License); (d) the common wall lizard, *Podarcis muralis*, combining ultraviolet (UV)-blue and orange patches in its flanks (picture by G. Pérez i de Lanuza); (e) ventral view of *P. muralis* showing the adjacent ventral (orange) and lateral (UV-blue) conspicuous colour patches (picture provided by J. Ábalos).

et al., 2009; Pérez i de Lanuza *et al.*, 2013a, 2014; Pérez i de Lanuza & Font, 2015).

Podarcis muralis (Laurenti, 1768), the European common wall lizard, is representative of the complex colour pattern found in many lacertids. Ventrally and laterally adults of both sexes show brightly coloured patches that are highly conspicuous to a wide range of receivers (Pérez i de Lanuza & Font, 2015). Ventral coloration is dominated by long wavelengths (i.e. yellow, orange), whereas laterally they show colour blotches on the outermost row of ventral scales [termed outer ventral scales (OVS); Arnold, 1989] that are ultraviolet (UV)-blue (Pérez i de Lanuza *et al.*, 2014) (Fig. 1e).

The OVS and the ventral colour patches of *P. muralis* provide strong chromatic contrast with each other and with the visual background. The colours of the OVS and the ventral patches are complementary, each one reflecting in the region of the spectrum where the other does not (Pérez i de Lanuza & Font, 2015). Use of complementary colours on adjacent patches is a well-known strategy to maximize conspicuousness (Lythgoe, 1979; Endler, 1992, 2012). For example, adjacent blue and yellow patches are found in many taxa as part of aposematic or signalling coloration (e.g. fish, Marshall, 2000; Cheney *et al.*, 2009; nudibranchs, Haber *et al.*, 2010; butterflies, Pegram *et al.*, 2013a). The complementary spectra increase overall conspicuousness because they stimulate retinal cones in opposite ways, enhancing chromatic contrast (Endler, 1992). If maximizing conspicuousness is advantageous to the fitness of the signaller, one might expect that selection should favour within-body combinations of highly contrasting colour patches. Thus, selection for conspicuousness in lizards may favour the evolution of complex colour patterns that combine contrasting, long- and short-wavelength colours.

Here, we examine the association of long- and short-wavelength colours across a sample of 170 species of lacertid lizards. Conspicuous long- and short-wavelength colour patches occur alone or in combination on the ventral and lateral surfaces of many lacertids. However, if their combination increases local (internal or within-pattern) chromatic contrast, long- and short-wavelength colours might be expected to be under correlational selection which would result in a nonrandom distribution of these two traits across the lacertid phylogeny.

We used two alternative approaches to test this hypothesis. First, we focused on the 45 lacertid species with available spectral data (Bajer *et al.*, 2011; Pérez i de Lanuza, 2012; Pérez i de Lanuza *et al.*, 2013b; San-José *et al.*, 2013) to test the correlation between conspicuous ventral and lateral colour patches in a phylogenetic context. Although this sample represents a relatively large proportion of currently recognized lacertid species, it is phylogenetically biased. Therefore, we additionally tested the correlation between ventral and lateral colour patches using a human-based categorization of lacertid coloration with the aim to increase the number of species and to consider a more phylogenetically balanced sample.

Materials and methods

Although the family Lacertidae encompasses more than 300 species, for our analysis we considered a subset of 170 species for which phylogenetic and coloration data are available. As a complete and conclusive phylogenetic hypothesis is lacking for lacertids, and the position and/or the specific status of some clades is controversial, we built an operational phylogeny from previous partial phylogenies (Harris *et al.*, 1998a, b, 1999, 2002, 2005; Fu *et al.*, 2000; Harris & Arnold, 2000; Murphy *et al.*, 2000; Lin *et al.*, 2002; Carranza *et al.*, 2004; Poulakakis *et al.*, 2005a, b; Arnold *et al.*, 2007; Makokha *et al.*, 2007; Lymberakis *et al.*, 2008; Cox *et al.*, 2010; Fitze *et al.*, 2011; Greenbaum *et al.*, 2011; Guo *et al.*, 2011; Kaliontzopoulou *et al.*, 2011; Edwards *et al.*, 2013; Engleder *et al.*, 2013). This phylogenetic hypothesis lacks branch distances and includes some hard polytomies, as well as possibly some unresolved soft polytomies.

Data on lizard coloration were compiled from personal observations, spectrophotometric measurements, descriptions and illustrations in field guides and other published sources and photographs available in several Internet repositories (see a detailed list in Appendix S1). These data were used to construct a dichotomous classification (presence/absence) of conspicuous (i.e. chromatically contrasting) colour patches in the lateral and the ventral body surfaces.

We operationally categorized a colour patch as conspicuous when it showed strong chromatic contrast with the lizard's dorsolateral background body coloration. This categorization was based on visual inspection of available spectrograms (see examples in Fig. 2) and on the assessment of chromatic contrast as performed by a human observer (GPL). Appendix S1 includes a detailed description of lacertid conspicuous colours. Briefly, conspicuous lateral colour patches include the blue, green or yellow eyespots and OVS found in many species. These are actually UV-blue, UV-green and UV-yellow in all the species for which reflectance spectra have been obtained (see examples in Fig. 2). The reflectance spectrum of UV-blue eyespots and OVS is a bell-shaped curve with wavelengths in both the ultraviolet (< 400 nm) and blue regions of the spectrum, whereas UV-green and UV-yellow eyespots and OVS have a reflectance peak in the ultraviolet as well as another peak at longer (> 400 nm) wavelengths. We also scored as conspicuous lateral coloration the blue heads shown by males of many *Lacerta* species. Blue heads reflect in both the UV and the blue portion of the spectrum as two overlapping peaks (e.g.

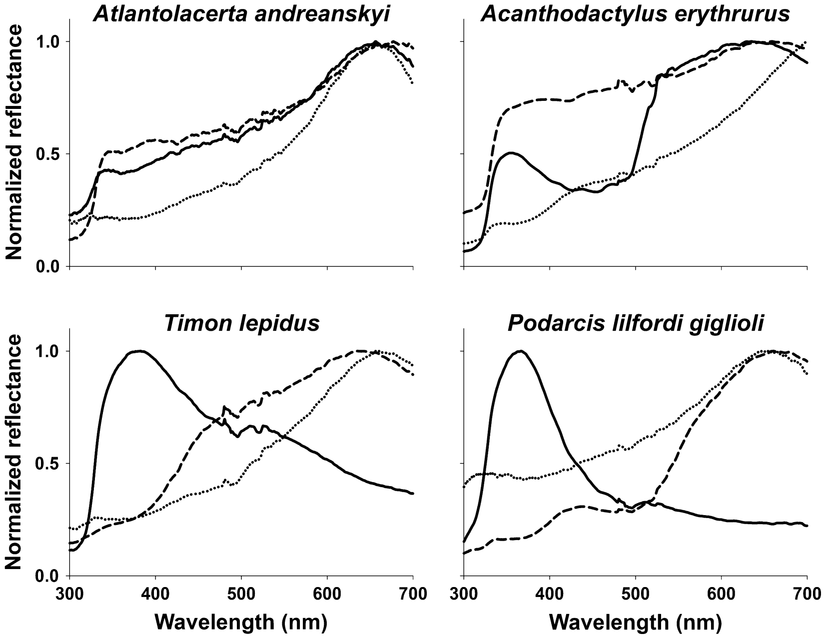

Fig. 2 Representative spectra of lacertid body coloration. The solid lines correspond to lateral patches [i.e. outer ventral scales (OVS), eyespots], the dashed lines to the ventral coloration and the dotted lines to the dorsal background coloration. The Atlas dwarf lizard, *Atlantolacerta andreanskyi*, lacks conspicuous colour patches (note that the belly and OVS are the same colour). The ocellated lizard, *Timon lepidus*, and the spiny-footed lizard, *Acanthodacylus erythrurus*, are representative examples of species in which conspicuous lateral colour patches with a ultraviolet (UV) peak are present (UV-blue and UV-yellow, respectively), but the ventral coloration (i.e. white) is less conspicuous than in other species with yellow or orange bellies. Lilford's wall lizard from Dragonera Island, *Podarcis lilfordi giglioli*, has contrasting lateral and ventral surfaces. The spectra are normalized to facilitate the interpretation of the chromatic differences. Spectra adapted from Pérez i de Lanuza *et al.*, 2013b.

Stuart-Fox *et al.*, 2009; Bajer *et al.*, 2011). Four species in our sample showed conspicuous orange/red lateral patches.

Conspicuous ventral coloration includes all ventral colours other than white, that is mainly yellow and orange, but also green in some species. The white bellies shown by many lacertids are the least chromatically contrasting (i.e. conspicuous) ventral coloration because their relatively flat spectra make them chromatically similar to the cryptic brown or grey dorsal coloration of many species (Pérez i de Lanuza & Font, 2015). Many lizards are lighter ventrally than dorsally (i.e. countershading), which presumably makes them less detectable to predators by cancelling the effects of ventral shadowing in well-lit environments (self-shadow concealment; Kiltie, 1988; Rowland, 2009, 2011). Because a white ventrum provides the strongest contrast in dorsoventral countershading, it follows that alternative ventral colorations should make the lizard more conspicuous to predators and conspecifics alike because they reduce the effectiveness of countershading. Spectra of yellow and orange ventral colour patches have a step in reflectance in the 500- to 600-nm interval (Pérez i de Lanuza *et al.,* 2013a). In some species, the ventral colour patches show a secondary reflectance peak in the ultraviolet and are actually UV-orange, UV-yellow or UV-green.

For colour categorization, we focused on male coloration because males are often the more conspicuous sex and show the more complex colour pattern (Pérez i de Lanuza *et al.*, 2013b). For species with polymorphic ventral coloration, we considered the most conspicuous colour morph (orange > yellow > white; Pérez i de Lanuza & Font, 2015). However, we did not consider rare forms found in some subspecies (e.g. Pérez i de Lanuza & Font, 2011; Fulgione *et al.*, 2015). For the phylogenetic correlative analysis, we used the methodology described by Pagel for categorical dichotomous characters (Pagel, 1994; Gumm & Mendelson, 2011) using Mesquite 2.74 (Maddison & Maddison, 2011). We first performed the analysis with the 45 species with available spectral data and then repeated the analysis for the overall sample including the 170 species. In addition, as the blue heads of *Lacerta* and the orange lateral patches of *Australolacerta* and *Ichnotrophis* appear to be rare colorations, we also repeated the analyses excluding the genus *Lacerta*, excluding *Australolacerta* and *Ichnotrophis* and excluding all three genera simultaneously. As colour patterns seem to have evolved differently in the Lacertini and the Eremiadini, we also performed the analysis separately for the two clades. Statistical significance was calculated with 1000 simulations. Additionally, we performed a historical reconstruction of the presence of ventral and lateral conspicuous patches throughout the phylogeny using an unordered parsimony model of character change.

Results

Figure 2 shows some examples of reflectance spectra of representative lacertid species and Fig. 3 shows the conspicuousness (i.e. chromatic contrast) caused by the combination of the different colour body patches calculated from the same spectra shown in Fig. 2 (data taken from Pérez i de Lanuza *et al.*, 2013b; methodological details of chromatic contrast calculations can be found in Appendix S2).

Considering the overall sample (i.e. 170 species), 62 species simultaneously showed ventral and lateral conspicuous colour patches, 31 species showed only lateral conspicuous patches, 18 showed only ventral conspicuous patches and 59 did not show any conspicuous colour patches (by our definitions; see Materials and Methods above). In 57 species of those 62 showing simultaneously ventral and lateral conspicuous colour patches, the pattern combined long-wavelength colours (ventrally) and short-wavelength colours (laterally). Interestingly, all the species in which ventral colours showed a secondary UV peak lacked UV-reflecting eyespots or OVS (e.g. *Lacerta agilis*, *Iberolacerta aurelioi*). Thus, UV-reflecting colour patches in lacertids are located either laterally or ventrally, but apparently not in both locations.

Figure 4 shows a historical reconstruction of the evolution of the ventral and lateral colour patches in lacertids. The ancestral colour pattern of lacertids included ventral and lateral conspicuous patches, and this combination has re-evolved independently at least four times in the phylogeny of the family. Moreover, both conspicuous patches were simultaneously lost at least nine times. We found a significant positive relationship between conspicuous ventral and lateral colour patches across the lacertid radiation using our two alternative approaches: when the analysis was restricted to the 45 species with available spectral data (difference in log likelihoods = 2.03, $P = 0.025$) and considering the overall sample (difference in log likelihoods = 9.40, $P < 0.0001$; $N = 170$). Similar results were obtained excluding the genus *Lacerta* (difference in log likelihoods = 9.12, $P = 0.003$; $N = 162$), excluding *Australolacerta* and *Ichnotrophis* (difference in log likelihoods = 9.20, $P = 0.002$; $N = 166$) and if the three genera were simultaneously excluded (difference in log likelihoods = 8.90, $P = 0.002$; $N = 158$). Ventral and lateral colours are correlated in Lacertini (difference in log likelihoods = 8.80, $P < 0.0001$; $N = 86$), but not in Eremiadini (difference in log likelihoods = 0.91, $P = 0.70$; $N = 73$).

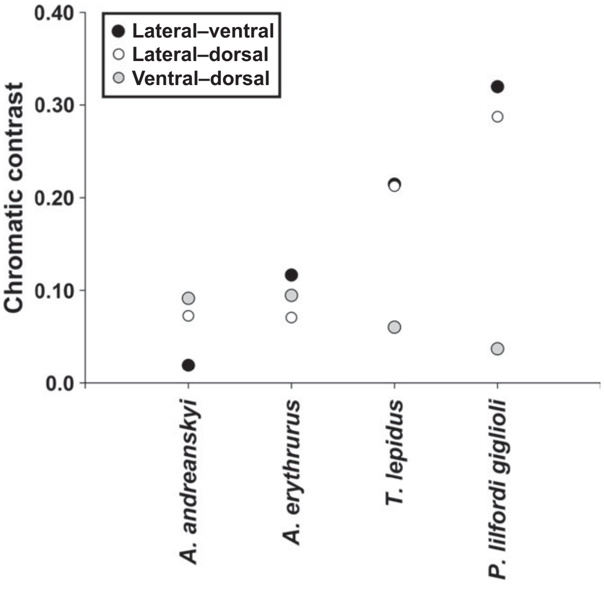

Fig. 3 Chromatic contrast caused by the combination of different body surfaces on the body of the same lacertid species as in Fig. 2. Note that the chromatic contrast generated by the lateral and ventral colorations of *Atlantolacerta andreanskyi* is very small because both body surfaces show the same white coloration (see Fig. 2). In contrast, the presence of ultraviolet (UV)-yellow patches (as in *Acanthodacylus erythrurus*) or UV-blue patches (as in *Timon lepidus*) increases within-body conspicuousness. Finally, the combination of UV-blue patches and orange belly (as in *Podarcis lilfordi giglioli*) represents the most contrasting coloration in lacertids. We calculated the chromatic contrast using TetraColorSpace (Stoddard & Prum, 2008) and the visual cone sensitivities of *Podarcis muralis* (Martin *et al.*, 2015). See details in the supporting information. Calculations were made using the spectra shown in Fig. 2.

Discussion

Our analysis demonstrates a positive covariation of ventral and lateral conspicuous colour patches across the lacertid phylogeny. This finding is consistent with the hypothesis that these two traits do not evolve independently and are functionally linked to enhanced signal efficacy. Our results also reveal a nonrandom association between long- and short-wavelength colour patches on the ventral and lateral surfaces of lacertid lizards. A combination of different colours could have evolved to enable detection against different backgrounds or to make lizards highly visible to receivers with different visual systems. However, the widespread occurrence of long- and short-wavelength colours side-by-side suggests selection for increased conspicuousness. Thus, it appears that when selection promotes conspicuousness, it does not act only on single colour

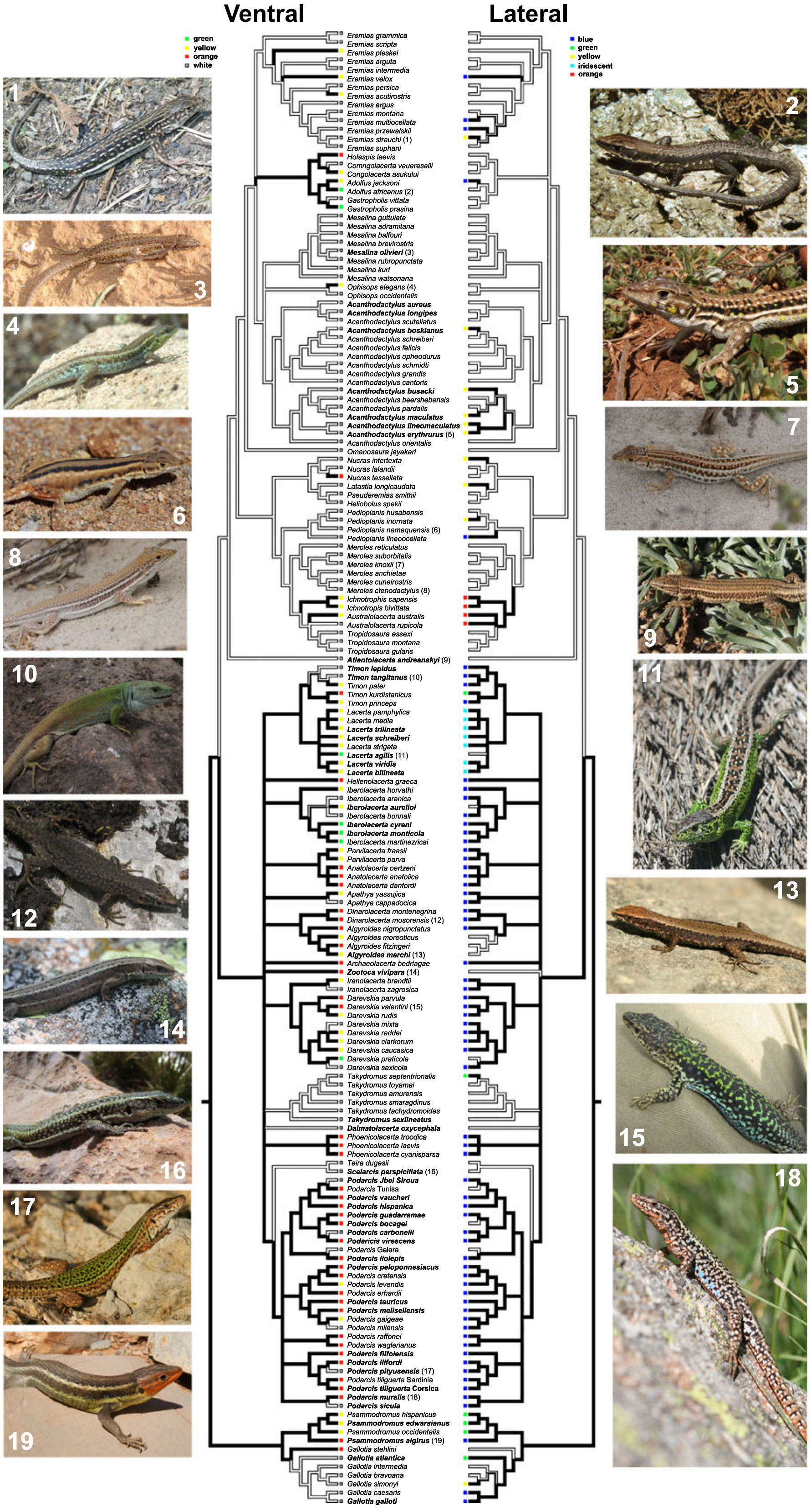

Fig. 4 Historical reconstruction of the presence (black branches) or absence (white branches) of conspicuous colour patches in the ventral (left) and lateral (right) body surfaces of the lacertid species used in the analyses. Historical reconstructions were performed using Mesquite's unordered parsimony model (Maddison & Maddison, 2011). Colour squares at the end of the branches approximate the colour of each patch for the ventral and lateral pattern. In some genera, the conspicuous ventral patches include a secondary ultraviolet peak (see details in the text). In the right tree (i.e. lateral coloration), branches without squares indicate the absence of eyespots, outer ventral scales or other highly conspicuous colour patches in this surface (as in the Atlas dwarf lizard, *Atlantolacerta andreanskyi*, see Fig. 2). Species names in boldface indicate the species with available spectral data. Numbers in parentheses refer to photographs. See photograph credits in the acknowledgements.

patches but also on the overall pattern, generating complex within-pattern combinations of colour patches with divergent spectral properties. In contrast, the probability of showing conspicuous and complex patterns is reduced in species evolving in habitats in which selection presumably acts strongly against conspicuousness, as in many Eremiadini that mainly inhabit desert open habitats.

Human assessment has been successfully used for the comparison of colour patterns from a large number of species in recent studies with other taxa (e.g. Martin *et al.*, 2010; Simpson *et al.*, 2015), but cannot take into account important differences between lacertid and human visual systems. As lacertids are able to perceive the near UV and probably have a tetrachromatic visual system (Pérez i de Lanuza & Font, 2014; Martin *et al.*, 2015), a classification of lizard colours based on human vision entails the loss of much information and probably causes the inappropriate assessment of some colours. However, the available spectral data suggest that the ventral and lateral colour patches of lacertids have a consistent spectral shape (Bajer *et al.*, 2011; Pérez i de Lanuza, 2012; Pérez i de Lanuza *et al.*, 2013b; San-José *et al.*, 2013). Moreover, results of visual modelling show that colour patches that are conspicuous to the lizards bearing them are generally also conspicuous to receivers with different visual systems (Marshall & Stevens, 2014; Pérez i de Lanuza & Font, 2015). Thus, we are confident that our human-based classification provides an evolutionarily meaningful measure of conspicuousness in this clade.

Correlated trait evolution may be a result of genetic correlation, in which traits are partially determined by the same or linked loci, or of selective correlation, in which the same environmental pressure acts on two seemingly unrelated traits. In lizards, ventral and lateral colours are produced by radically different mechanisms: whereas ventral colours are mainly pigment based, lateral colours have a prominent structural component resulting from interactions between incident light and nanostructures present in the skin (Grether *et al.*, 2004; Saenko *et al.*, 2013; Haisten *et al.*, 2015). This suggests that the association between these two traits is primarily driven by correlated selection rather than genetic constraints.

The co-occurrence of conspicuous ventral and lateral colour patches on the flanks of many lacertids raises interesting questions regarding their role in signalling. It is often assumed that the ventral and lateral colour patches could make available to receivers information that is relevant for mate choice and/or opponent assessment. The available evidence supports the hypothesis that in some species, the laterally located UV-blue OVS convey information about male quality (i.e. body condition and/or fighting ability; Pérez i de Lanuza *et al.*, 2014). However, the evidence regarding a signalling role of the ventral colour patches is equivocal. Ventral coloration seems unrelated to individual male quality (Pérez i de Lanuza *et al.*, 2014) and apparently does not affect the outcome of male intrasexual contests (Sacchi *et al.*, 2009). However, the ventral colour patches may be involved in mate assessment in some colour polymorphic species (Pérez i de Lanuza *et al.*, 2013a) or they may convey to receivers some type of hitherto unknown information. Alternatively, the conspicuous long-wavelength ventral patches may function, because of their association with the lateral patches, as amplifiers (Pérez i de Lanuza & Font, 2015). Amplifiers are a class of signals that by themselves are not indicators of signaller quality but improve the receiver's ability to detect or assess a signal (Hasson, 1990, 1991, 1997; Hasson *et al.*, 1992; Taylor *et al.*, 2000). According to this hypothesis, the presence of long-wavelength-reflecting ventral colour patches next to the short-wavelength lateral patches would increase the within-pattern chromatic contrast and thus contribute to maximizing the overall pattern conspicuousness. To determine whether ventral coloration plays an amplifying role in lacertids, it would be necessary to determine the effect that each colour patch has, independently, on the response of receivers.

Because conspicuous lateral patches are present in species belonging to all the major lacertid clades, they probably represent the ancestral condition for lacertids, as shown by our historical character reconstruction. In contrast, the conspicuous ventral colour patches have a much more restricted phylogenetic distribution. Moreover, our comparative study reveals striking differences between the Eremiadini and the Lacertini clades. Conspicuous ventral and lateral colours are present in most Lacertini, and only in a few cases, a species lacks both types of conspicuous coloration. In contrast, very few species of Eremiadini have conspicuous ventral and lateral colours, and the most frequent conspicuous colours are the lateral yellow patches (which are less conspicuous than the UV-blue patches typical of many Lacertini species). The differences between Eremiadini and Lacertini may be a consequence of the different selective regimes prevalent during the evolution of these two clades. The radiation of Lacertini took place in Europe, mainly in the Mediterranean basin, whereas the Eremiadini evolved in African mesic and xeric habitats (Arnold *et al.*, 2007), which are open and visually more simple than Mediterranean ecosystems. These differences should be crucial for signal detection by primary receivers, but also by predators. It is possible that, as in other lizards, predator detection in open habitats favours relatively inconspicuous colours and patterns (Ord & Stuart-Fox, 2006; Garcia *et al.*, 2013). In fact, predation pressures may have constrained the evolution of complex colour patterns, limiting the variability of adaptive colours available for use by the Eremiadini.

Animal colour patches are complex phenotypic traits that engage various pigment types, structural features and optical processes (Grether *et al.*, 2004). The interaction among neighbouring or adjacent colour patches adds a little explored layer of complexity to the study of animal coloration. The results presented here suggest that the combination of long- and short-wavelength colours has evolved independently multiple times in the history of the lacertids. This is the first evidence that different chromatically complementary conspicuous patches may evolve under correlational selection and suggests that increased chromatic contrast can act as an important selective force on animal coloration. Further work should be aimed to determine whether selection for conspicuousness promotes the adoption of complex colour patterns involving colour patches with contrasting spectral properties in other taxa.

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References

Arnold, E.N. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bull. Br. Mus.* **55**: 209–257.

Arnold, E.N., Arribas, O.J. & Carranza, S. 2007. Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa* **1430**: 1–86.

Bajer, K., Molnár, O., Török, J. & Herczeg, G. 2011. Ultraviolet nuptial colour determines fight success in male European green lizards (*Lacerta viridis*). *Biol. Lett.* **7**: 866–868.

Bradbury, J.W. & Vehrencamp, S.L. 2011. *Principles of Animal Communication*, 2nd edn. Sinauer Assoc. Press, Sunderland.

Caro, T. 2005. The adaptive significance of coloration in mammals. *Bioscience* **55**: 125–136.

Carranza, S., Arnold, E. & Amat, F. 2004. DNA phylogeny of *Lacerta* (*Iberolacerta*) and other lacertine lizards (Reptilia: Lacertidae): did competition cause long-term mountain restriction? *Syst. Biodivers.* **2**: 57–77.

Chen, I.P., Stuart-Fox, D., Hugall, A.F. & Symonds, M.R.E. 2012. Sexual selection and the evolution of complex color patterns in dragon lizards. *Evolution* **66**: 3605–3614.

Cheney, K.L., Grutter, A.S., Blomberg, S.P. & Marshall, N.J. 2009. Blue and yellow signal cleaning behavior in coral reef fishes. *Curr. Biol.* **19**: 1283–1287.

Cox, S.C., Carranza, S. & Brown, R.P. 2010. Divergence times and colonization of the Canary Islands by *Gallotia* lizards. *Mol. Phylogenet. Evol.* **56**: 747–757.

Dawkins, M.S. & Guilford, T. 1997. Conspicuousness and diversity in animal signals. *Persp. Ethol.* **12**: 55–72.

Edmunds, M. 1974. *Defence in Animals: A Survey of Antipredator Defences*. Longman Group Ltd, Harlow, Essex.

Edwards, S., Branch, W.R., Vanhooydonck, B., Herrel, A., Measey, G.J. & Tolley, K.A. 2013. Taxonomic adjustments in the systematics of the southern African lacertid lizards (Sauria: Lacertidae). *Zootaxa* **3669**: 101–114.

Endler, J.A. 1978. A predator's view of animal color patterns. *Evol. Biol.* **11**: 319–364.

Endler, J.A. 1990. On the mesurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* **41**: 315–352.

Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139** (Suppl.): S125–S153.

Endler, J.A. 1993. The color of light in forests and its implications. *Ecol. Monogr.* **63**: 1–27.

Endler, J.A. 2012. A framework for analysing colour pattern geometry: adjacent colours. *Biol. J. Linn. Soc.* **107**: 233–253.

Endler, J.A., Westcott, D.A., Madden, J.R. & Robson, T. 2005. Animal visual system and the evolution of color patterns sensory processing illuminates signal evolution. *Evolution* **59**: 1795–1818.

Engleder, A., Haring, E., Kirchhof, S. & Mayer, W. 2013. Multiple nuclear and mitochondrial DNA sequences provide new insights into the phylogeny of South African Lacertids (Lacertidae, Eremiadinae). *J. Zool. Syst. Evol. Res.* **51**: 132–143.

Fitze, P.S., González-Jimena, V., San-Jose, L.M., San Mauro, D., Aragón, P., Suarez, T. *et al.* 2011. Integrative analyses of speciation and divergence in *Psammodromus hispanicus* (Squamata: Lacertidae). *BMC Evol. Biol.* **11**: 347.

Font, E. & Pérez i de Lanuza, G. & Sampedro, C.. 2009. Ultraviolet reflectance and cryptic sexual dichromatism in the ocellated lizard, *Lacerta (Timon) lepida* (Squamata: Lacertidae). *Biol. J. Linn. Soc.* **97**: 766–780.

Friedman, N.R., McGraw, K. & Omland, K.E. 2014. Evolution of carotenoid pigmentation in caciques and meadowlarks (Icteridae): repeated gains of red plumage coloration by carotenoid C4-oxygenation. *Evolution* **68**: 791–801.

Fu, J., Murphy, R.W. & Darevsky, I.S. 2000. Divergence of the Cytochrome b gene in the *Lacerta raddei* complex and its parthenogenetic daughter species: evidence for recent multiple origins. *Copeia* **2000**: 432–440.

Fulgione, D., Lega, C., Trapanese, M. & Buglione, M. 2015. Genetic factors implied in melanin-based coloration of the Italian wall lizard. *J. Zool.* **296**: 278–285.

Garcia, J.E., Rohr, D. & Dyer, A.G. 2013. Trade-off between camouflage and sexual dimorphism revealed by UV digital imaging: the case of Australian Mallee dragons (*Ctenophorus fordi*). *J. Exp. Biol.* **216**: 4290–4298.

Godfrey, D., Lythgoe, J.N. & Rumball, D.A. 1987. Zebra stripes and tiger stripes: the spatial frequency distribution of the pattern compared to that of the background is significant in display and crypsis. *Biol. J. Linn. Soc.* **32**: 427–433.

Gómez, D. & Théry, M. 2007. Simultaneous crypsis and conspicuousness in color patterns: comparative analysis of a neotropical rainforest bird community. *Am. Nat.* **169**: S42–S61.

Greenbaum, E., Villanueva, C.O., Kusamba, C., Aristote, M.M. & Branch, W.R. 2011. A molecular phylogeny of Equatorial African Lacertidae, with the description of a new genus and species from eastern Democratic Republic of the Congo. *Zool. J. Linn. Soc.* **163**: 913–942.

Grether, G.F., Kolluru, G.R. & Nerssisian, K. 2004. Individual color patches as multicomponent signals. *Biol. Rev. Camb. Philos. Soc.* **79**: 583–610.

Guilford, T. & Dawkins, M.S. 1991. Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42**: 1–14.

Gumm, J.M. & Mendelson, T.C. 2011. The evolution of multicomponent visual signals in darters (genus *Etheostoma*). *Curr. Zool.* **57**: 125–139.

Guo, X., Dai, X., Chen, D., Papenfuss, D.J., Ananjeva, N.B., Melnikov, D.A. *et al.* 2011. Phylogeny and divergence times of some racerunner lizards (Lacertidae: *Eremias*) inferred from mitochondrial 16S rRNA gene segments. *Mol. Phylogenet. Evol.* **61**: 400–412.

Haber, M., Cerfeda, S., Carbone, M., Calado, G.A., Gaspar, H., Neves, R. *et al.* 2010. Coloration and defense in the nudibranch gastropod *Hypselodoris fontandraui*. *Biol. Bull.* **218**: 181–188.

Haisten, D.C., Paranjpe, D., Loveridge, S. & Sinervo, B. 2015. The cellular basis of polymorphic coloration in common side-blotched lizards, *Uta stansburiana*. *Herpetologica* **7**: 125–135.

Harris, D.J. & Arnold, E.N. 2000. Elucidation of the relationships of spiny-footed lizards, *Acanthodactylus* spp. (Reptilia: Lacertidae) using mitochondrial DNA sequence, with comments on their biogeography and evolution. *J. Zool.* **252**: 351–362.

Harris, D.J., Arnold, E.N. & Thomas, R.H. 1998a. Rapid speciation, morphological evolution, and adaptation to extreme environments in South African sand lizards (*Meroles*) as revealed by mitochondrial gene sequences. *Mol. Phylogenet. Evol.* **10**: 37–48.

Harris, D.J., Arnold, E.N. & Thomas, R.H. 1998b. Relationships of lacertid lizards (Reptilia, Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proc. Biol. Sci.* **265**: 1939–1948.

Harris, D.J., Arnold, E.N. & Thomas, R.H. 1999. A phylogeny of the European lizard genus *Algyroides* (Reptilia: Lacertidae) based on DNA sequences, with comments on the evolution of the group. *J. Zool. Lond.* **249**: 49–60.

Harris, D.J., Carranza, S., Arnold, E.N., Pinho, C. & Ferrand, N. 2002. Complex biogeographical distribution of genetic variation within *Podarcis* wall lizards across the Strait of Gibraltar. *J. Biogeogr.* **29**: 1257–1262.

Harris, D.J., Pinho, C., Carretero, M.A., Corti, C. & Böhme, W. 2005. Determination of genetic diversity within the insular lizard *Podarcis tiliguerta* using mtDNA sequence data, with a reassessment of the phylogeny of *Podarcis*. *Amphibia-Reptilia* **26**: 401–407.

Hasson, O. 1990. The role of amplifiers in sexual selection: an integration of the amplifying and the Fisherian mechanisms. *Evol. Ecol.* **4**: 277–289.

Hasson, O. 1991. Sexual displays as amplifiers: practical examples with an emphasis on feather decorations. *Behav. Ecol.* **2**: 189–197.

Hasson, O. 1997. Towards a general model of biological signaling. *J. Theor. Biol.* **185**: 139–156.

Hasson, O., Cohen, D. & Shmida, A. 1992. Providing or hiding information: on the evolution of amplifiers and attenuators of perceived quality differences. *Acta. Biotheor.* **40**: 269–283.

Hofmann, C.M., Cronin, T.W. & Omland, K.E. 2006. Using spectral data to reconstruct evolutionary changes in coloration: carotenoid color evolution in new world orioles. *Evolution* **60**: 1680–1691.

Kaliontzopoulou, A., Pinho, C., Harris, D.J. & Carretero, M.A. 2011. When cryptic diversity blurs the picture: a cautionary tale from Iberian and North African *Podarcis* wall lizards. *Biol. J. Linn. Soc.* **103**: 779–800.

Kiltie, R.A. 1988. Countershading: universally deceptive or deceptively universal?. *Trends Ecol. Evol.* **3**: 21–23.

Lin, S.M., Chen, C.A. & Lue, K.Y. 2002. Molecular phylogeny and biogeography of the grass lizards genus *Takydromus* (Reptilia: Lacertidae) of East Asia. *Mol. Phylogenet. Evol.* **22**: 276–288.

Lymberakis, P., Poulakakis, N., Kaliontzopoulou, A., Valakos, E. & Mylonas, M. 2008. Two new species of *Podarcis* (Squamata; Lacertidae) from Greece. *Syst. Biodivers.* **6**: 307–318.

Lythgoe, J.N. 1968. Red and yellow as conspicuous colours underwater. *Underwater Assoc. Rep.* **1**: 51–53.

Lythgoe, J.N. 1979. *The Ecology of Vision*. Oxford University Press, Oxford.

Maan, M.E. & Cummings, M.E. 2009. Sexual dimorphism and directional sexual selection on aposematic signals in a poison frog. *Proc. Natl. Acad. Sci. USA* **106**: 19072–19077.

Maddison, W.P. & Maddison, D.R. 2011. Mesquite: A modular system for evolutionary analysis. Version 2.74. http://mesquiteproject.org.

Makokha, J.S., Bauer, A.M., Mayer, W. & Matthee, C.A. 2007. Nuclear and mtDNA-based phylogeny of southern African sand lizards, *Pedioplanis* (Sauria: Lacertidae). *Mol. Phylogenet. Evol.* **44**: 622–633.

Marshall, N.J. 2000. Communication and camouflage with the same 'bright' colours in reef fishes. *Philos. Trans. R. Soc. B* **355**: 1243–1248.

Marshall, K.L.A. & Stevens, M. 2014. Wall lizards display conspicuous signals to conspecifics and reduce detection by avian predators. *Behav. Ecol.* **25**: 1325–1337.

Martin, P.R., Montgomerie, R. & Lougheed, S.C. 2010. Rapid sympatry explains greater color pattern divergence in high latitude birds. *Evolution* **64**: 336–347.

Martin, M., Le Galliard, J.F., Meylan, S. & Loew, E.R. 2015. The importance of short and near infrared wavelength sensitivity for visual discrimination in two species of lacertid lizards. *J. Exp. Biol.* **218**: 458–465.

Molina-Borja, M., Font, E. & Mesa Ávila, G. 2006. Sex and population variation in ultraviolet reflectance of colour patches in *Gallotia galloti* (Fam. Lacertidae) from Tenerife (Canary Islands). *J. Zool.* **268**: 193–206.

Murphy, R.W., Fu, J., MacCulloch, R.D., Darevsky, I.S. & Kurpriyanova, L.A. 2000. A fine line between sex and unisexuality: the phylogenetic constraints on parthenogenesis in lacertid lizards. *Zool. J. Linn. Soc.* **130**: 527–549.

Ng, J., Landeen, E.L., Logsdon, R.M. & Glor, R.E. 2013. Correlation between *Anolis* lizard dewlap phenotype and environmental variation indicates adaptive divergence of a signal important to sexual selection and species recognition. *Evolution* **67**: 573–582.

Ord, T.J. & Stuart-Fox, D. 2006. Ornament evolution in dragon lizards: multiple gains and widespread losses reveal a complex history of evolutionary change. *J. Evol. Biol.* **19**: 797–808.

Ord, T.J., Blumstein, D.T. & Evans, C.S. 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. *Proc. Biol. Sci.* **268**: 737–744.

Pagel, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond. B* **255**: 37–45.

Pegram, K.V., Lillo, M.J. & Rutowski, R.L. 2013a. Iridescent blue and orange components contribute to the recognition of a multicomponent warning signal. *Behaviour* **150**: 321–336.

Pegram, K.V., Nahm, A.C. & Rutowski, R.L. 2013b. Warning color changes in response to food deprivation in the pipevine swallowtail butterfly, *Battus philenor*. *J. Insect Sci.* **13**: 110.

Pérez i de Lanuza, G. 2012. *Visió en Color i Coloracions dels Lacèrtids*. Doctoral dissertation, Universitat de València, València.

Pérez i de Lanuza, G. & Font, E. 2011. Lizard blues: blue body colouration and ultraviolet polychromatism in lacertids. *Rev. Esp. Herp.* **24**: 67–84.

Pérez i de Lanuza, G., Font, E. & Carazo, P. 2013a. Colour assortative mating in a colour polymorphic lacertid lizard. *Behav. Ecol.* **24**: 273–279.

Pérez i de Lanuza, G., Font, E. & Monterde, J.L. 2013b. Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids. *J. Evol. Biol.* **26**: 1826–1835.

Pérez i de Lanuza, G., Carazo, P. & Font, E. 2014. Colours of quality: structural (but not pigment) coloration informs about male quality in a polychromatic lizard. *Anim. Behav.* **90**: 73–81.

Pérez i de Lanuza, G. & Font, E. 2014. Ultraviolet vision in lacertid lizards: evidence from retinal structure, eye transmittance, SWS1 visual pigment genes, and behaviour. *J. Exp. Biol.* **217**: 2899–2909.

Pérez i de Lanuza, G. & Font, E. 2015. Differences in conspicuousness between alternative color morphs in a polychromatic lizard. *Behav. Ecol.* **26**, 1432–1446.

Poulakakis, N., Lymberakis, P., Valakos, E., Pafilis, P., Zouros, E. & Mylonas, M. 2005a. Phylogeography of Balkan wall lizard (*Podarcis taurica*) and its relatives inferred from mitochondrial DNA sequences. *Mol. Ecol.* **14**: 2433–2443.

Poulakakis, N., Lymberakis, P., Valakos, E., Zouros, E. & Mylonas, M. 2005b. Phylogenetic relationships and biogeography of *Podarcis* species from the Balkan Peninsula, by bayesian and maximum likelihood analyses of mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* **37**: 845–857.

Prager, M. & Andersson, S. 2010. Convergent evolution of red carotenoid coloration in widowbirds and bishops (*Euplectes* spp.). *Evolution* **64**: 3609–3619.

Rowland, H.M. 2009. From Abbott Thayer to the present day: what have we learned about the function of countershading? *Philos. Trans. R. Soc. B. Biol. Sci.* **364**: 519–527.

Rowland, H.M. 2011. The history, theory and evidence for a cryptic function of countershading. In: *Animal Camouflage: Mechanisms and Function* (M. Stevens & S. Merilaita, eds), pp.53–72. Cambridge University Press, Cambridge.

Ruxton, G.D., Sherratt, T.N. & Speed, M.P. 2004. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press, Oxford.

Sacchi, R., Pupin, F., Gentilli, A., Rubolini, D., Scali, S., Fasola, M. *et al.* 2009. Male-male combats in a polymorphic lizard: residency and size, but not color, affect fighting rules and contest outcome. *Aggress. Behav.* **35**: 274–283.

Saenko, S.V., Teyssier, J., van der Marel, D. & Milinkovitch, M.C. 2013. Precise colocalization of interacting structural and pigmentary elements generates extensive color pattern variation in *Phelsuma* lizards. *BMC Biol.* **11**: 105.

Salvador, A. 2002. Enciclopedia virtual de los vertebrados españoles. Museo Nacional de Ciencias Naturales, Madrid. www.vertebradosibericos.org.

San-José, L.M., Granado-Lorencio, F., Sinervo, B. & Fitze, P.S. 2013. Iridophores and not carotenoids account for chromatic variation of carotenoid-based coloration in common lizards (*Lacerta vivipara*). *Am. Nat.* **181**: 396–409.

Simpson, R.K., Johnson, M.A. & Murphy, T.G. 2015. Migration and the evolution of sexual dichromatism: evolutionary loss of female coloration with migration among wood-warblers. *Proc. R. Soc. Lond. B* **282**: 20150375.

Stevens, M. & Cuthill, I.C. 2006. Disruptive coloration, crypsis and edge detection in early visual processing. *Proc. R. Soc. Lond. B* **273**: 2141–2147.

Stevens, M. & Merilaita, S. 2009. Defining disruptive coloration and distinguishing its functions. *Philos. Trans. R. Soc. B. Biol. Sci.* **364**: 481–488.

Stoddard, M.C. & Prum, R.O. 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. *Am. Nat.* **171**: 755–776.

Stuart-Fox, D.M., Godinho, R., Goüy de Bellocq, J., Irwin, N.R., Brito, J.C., Moussalli, A. *et al.* 2009. Variation in phenotype, parasite load and male competitive ability across a cryptic hybrid zone. *PLoS One* **4**: e5677.

Taylor, P.W., Hasson, O. & Clark, D.L. 2000. Body postures and patterns as amplifiers of physical condition. *Proc. R. Soc. Lond. B* **267**: 917–922.

Supporting information

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

Appendix S1 Colour categorization.

Appendix S2 Calculation of chromatic contrasts.

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