Naturwissenschaften
DOI 10.1007/s00114-014-1224-9

ORIGINAL PAPER

Now you see me, now you don't: iridescence increases the efficacy of lizard chromatic signals

Guillem Pérez i de Lanuza · Enrique Font

Received: 18 February 2014 / Revised: 6 August 2014 / Accepted: 8 August 2014

Abstract The selective forces imposed by primary receivers and unintended eavesdroppers of animal signals often act in opposite directions, constraining the development of conspicuous coloration. Because iridescent colours change their chromatic properties with viewer angle, iridescence offers a potential mechanism to relax this trade-off when the relevant observers involved in the evolution of signal design adopt different viewer geometries. We used reflectance spectrophotometry and visual modelling to test if the striking blue head coloration of males of the lizard *Lacerta schreibeiri* (1) is iridescent and (2) is more conspicuous when viewed from the perspective of conspecifics than from that of the main predators of adult *L. schreibeiri* (raptors). We demonstrate that the blue heads of *L. schreiberi* show angle-dependent changes in their chromatic properties. This variation allows the blue heads to be relatively conspicuous to conspecific viewers located in the same horizontal plane as the sender, while simultaneously being relatively cryptic to birds that see it from above. This study is the first to suggest the use of angle-dependent chromatic signals in lizards, and provides the first evidence of the adaptive function of iridescent coloration based on its detectability to different observers.

Keywords Coloration · Communication · Lizard · Signal efficacy · Viewer geometry · Visual modelling

Communicated by: Sven Thatje

G. Pérez i de Lanuza (✉)
CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Rua Padre Armando Quintas 7, 4485-661, Vairão Vila do Conde, Portugal
e-mail: guillem.perez-lanuza@uv.es

G. Pérez i de Lanuza · E. Font
Ethology Laboratory Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, Valencia, Spain

Introduction

Chromatic (i.e., colour) signals are found in many taxa, and their design results from the combined action of several selective pressures often acting in opposite directions. Selection for effective social communication promotes conspicuous colour patterns that improve their detectability, discriminability and memorability by primary receivers. In contrast, the exploitation of colour signals by unintended receivers (i.e. eavesdroppers) often favours the adoption of cryptic colour patterns (Bradbury and Vehrencamp 2011; Stevens 2013). Thus, there exists a clear trade-off between these two main selective forces that constrains the design of chromatic signals and puts limits to the development of striking colour patterns. To relax this trade-off, that is, to increase detection by primary receivers but not by other receivers, signallers may use several strategies. For example, signallers can take advantage of the differences in visual sensitivity between primary receivers and predators and produce private or hidden signals to which predators are largely insensitive (e.g. Cummings et al. 2003). In male guppies, *Poecilia reticulata*, intersexual selection favours conspicuous colour patches, but other species of fish use these same colour patches to detect and predate on males. Male guppies exploit differences between the predators' and their own visual system to develop nuptial colours that are predominantly orange and red in those populations in which the main predators are less sensitive to long wavelengths, and blue and green in those dominated by predators with a poor sensitivity to short wavelengths (Endler 1991). Other strategies used to relax this trade-off include modifying the visibility of colour patches by means of specialized body structures and/or postures (e.g. retractable coloured surfaces such as the dewlaps and frills found in many lizard species; Font and Rome 1990; Fleishman 1992; Hamilton et al. 2013), performing visual displays only under certain light conditions (e.g. Endler and Théry 1996; Sicsú et al. 2013) or, in animals

Published online: 17 August 2014

capable of colour change, changing the chromatic properties of signalling surfaces (e.g. Stuart-Fox, et al. 2006; Mäthger et al. 2009).

Iridescence offers a relatively unexplored route to simultaneously maximize the conspicuousness of chromatic signals to primary receivers and minimize their detection by eavesdroppers. Iridescence is described as the visual characteristic of some surfaces that change colour when viewed from different angles (Land 1972; Osorio and Ham 2002; Prum 2006; Doucet and Meadows 2009). Thus, in a scenario in which primary receivers and eavesdroppers view a colour patch from consistently different locations, selection should favour the ability to produce colours that are more conspicuous for the intended primary receivers' angle of vision than for eavesdroppers that view them from a different angle. This hypothesis is extremely suggestive, but so far lacks empirical support (Meadows et al. 2009).

Iridescence is widespread in some animal clades, such as insects or birds (Doucet and Meadows 2009). Butterflies are arguably the flagship of iridescent coloration, and many relevant advances in our understanding of the mechanisms of production and the functions of animal iridescence have been made in some butterfly species (e.g. Kemp and Rutowski 2007; Kemp 2008; Kemp et al. 2014). Although iridescence is relatively rare in Squamata, some snakes and lizards show iridescent or putatively iridescent coloration (Rohrlich and Porter 1972; Morrison 1995; reviewed in Doucet and Meadows 2009). In particular, some colour patches found in lacertid lizards (Lacertidae) change their apparent colour under different illumination angles, suggesting that they may be iridescent (Pérez i de Lanuza and Font 2011; Pérez i de Lanuza 2012). This seems to be the case of the conspicuous blue head coloration of male Schreiber's green lizards *Lacerta schreiberi* (Bedriaga 1878), a secondary sexual trait related to reproductive success that may signal dominance during reproductive periods (Martín and López 2009) (Fig. 1). Depending on illumination and viewing conditions, the blue heads of male *L. schreiberi* may look, to a human, a more or less saturated blue colour. Here, we test the hypothesis that the chromatic properties of the blue heads change with the angle of incidence. Assuming that the blue heads have a signalling function, we also test the hypothesis that their relative efficacy changes when viewed from different angles. Our prediction is that the iridescent coloration should be more conspicuous to other lizards (with large visual angles with respect to the incident light) than to the main visual predators of adult *L. schreiberi*, i.e., mainly raptors (Pérez-Mellado 1998), with small visual angles with respect to the incident light.

Materials and methods

Lizards and spectrophotometric measurements

We captured ten adult male *L. schreiberi* in May 2013 in the Tejera Negra Mountains (41° 08′ N, 3° 20′ W; Sierra Norte of Guadalajara Natural Park, Spain). We conducted spectrophotometric measurements from the left lateral surface of the lizards' head at 0, 60 and 90 ° angles between the incident light and the measured reflectance using a USB-2000 portable diode-array spectrometer and a PX-2 xenon strobe light source (Ocean Optics, Dunedin, FL). Although setup angles are commonly reported relative to the normal surface in the literature (e.g. Andersson and Prager 2006), we prefer the 0, 60 and 90 ° terminology because it focuses on the angle between the incident light and the observer's point of view.

For 0 ° measurements, we used the standard protocol with a single probe encompassing parallel emissive and receptive

Fig. 1 Adult male *Lacerta schreiberi* from Tejera Negra Mountains showing the conspicuous blue head characteristic of this species (photograph by G. Pérez i de Lanuza)

fibre-optics held perpendicularly to the lizard's skin surface (Font et al. 2009; Pérez i de Lanuza and Font 2011). For 60 and 90 ° measurements, we used a precision goniometer specially designed to allow positioning of emissive and receptive probes at different angles with respect to the target surface. This instrument represents a simplification of those described in Rutowski et al. (2010) and Meadows et al. (2011). 0 and 90 ° angles are representative of low and high viewing angles, respectively, which correspond to the conditions in which predators and conspecifics will often—though by no means, always—see the lizards (i.e. dorsal vs lateral views). The 0 ° angle corresponds to that of flying or perching avian predators located directly above the lizard at midday (e.g. Csermely et al. 2009), when males are more active during the spring reproductive season (Pérez-Mellado 1998), resulting in a relatively small viewing angle with respect to the sun. The 90 ° angle corresponds to the viewing angle of primary receivers (i.e. other lizards) located in the same horizontal plane as the signaller also at midday, with a relatively large angle relative to the sun. Although these two viewing angles are a simplification of the actual diversity of circumstances in which a lizard's head may be observed, they are representative of the more relevant conditions for the visual ecology selective pressures. Figure 2 shows both viewer geometries and other relevant variables. As the lizard's head and body surface is not a plane (i.e. the lateral and dorsal scutes of the head have an irregular surface, and the granular scales of the throat are semispherical), and lizards move through a three-dimensional habitat (i.e. rocks, trunks), the effect of the elevation angle in overall reflectance should be negligible. Therefore, we obviated the effect of the elevation angle in visual modelling and all measurements were made in the lizard plane (i.e. no elevation). The extension of these measurements to the predator view is based on the assumption that the iridescence effects are symmetrical and depend only on the angle of the viewer and the light source. The 0 ° angle measurements were taken perpendicularly to the lizard surface, the 60 ° angle measurements were taken placing the emissive and the receptive fibres symmetrically opposed at 60 ° to the lizard surface, and the 90 ° angle measurements were taken placing the emissive and the receptive fibres symmetrically opposed at 45 ° to the lizard surface. Measurements at 60 ° were taken to determine whether the putative spectral changes caused by viewing geometry are continuous or discrete, but we did not use them for visual modelling. Each spectrum was the result of averaging 20 consecutive spectra from the same colour patch.

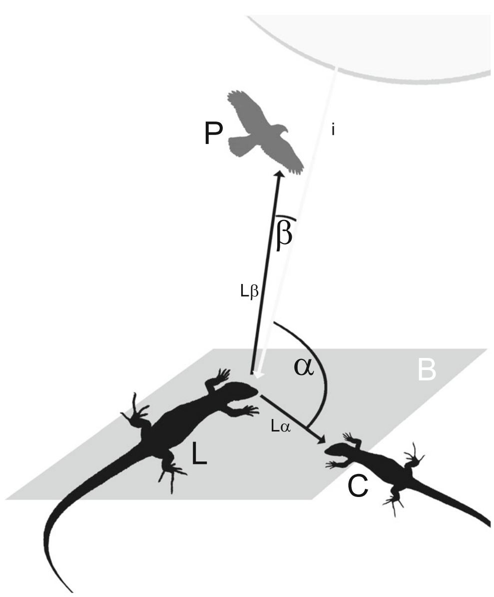


Fig. 2 Schematic depiction of viewer geometry for chromatic signals of *Lacerta schreiberi*. *L* signal sender; *B* natural background; *C* primary receiver, i.e. conspecifics; *P* main predator, i.e. raptors; *i* incident light; α angle between the incident light and the primary receiver, approximated to 90 ° in measurements; β angle between the incident light and the predator, approximated to 0 ° in measurements; $L\alpha$ reflected light from signal sender at α angle; $L\beta$ reflected light from signal sender at β angle

Simultaneously to lizard measurements, we also measured the reflectance of the natural backgrounds in which lizards are found with the same spectrophotometric setup and procedures described above for measuring lizard reflectance. In particular, we measured the reflectance of rocks (i.e. schist), wood, dry leaves of *Quercus pyrenaica*, and green leaves of *Cistus laurifolius*. These are the most abundant backgrounds in the visual niche in which lizards are viewed: lizards often thermoregulate on rocks and trunks, and move through the vegetation and the dry leaves on the ground. We took three independent measurements of each background and angle, and used the averaged spectra for subsequent analyses. In addition, we took irradiance measurements of the ambient light during hours of maximum lizard activity (i.e., solar noon) with a second USB-2000 spectrometer calibrated by means of a LS1-CAL calibration light source (Ocean Optics), using a cosine-correcting probe (Ocean Optics CC-3-UV). We took two irradiance measurements corresponding to the two relevant positions of the visual receiver: one with the probe perpendicular with respect to the ground, and the other with the probe parallel with respect to the ground and oriented to the South (Fleishman et al. 2006).

All the spectra were normalized by total reflectance (i.e. the sum of reflectance at every wavelength in the 300–700 nm range) before the analyses, thus effectively subtracting the brightness component of the spectra. For lizard spectra, we used chromatic shape descriptors, which are independent of any visual system. Hue was measured by extracting the peak location of the primary and secondary reflection peaks (λ_{blue} and λ_{UV}, respectively). We also measured the difference in nanometers between the two peaks (i.e. $\lambda_{blue} - \lambda_{UV}$). We measured two complementary variables of chroma: ultraviolet (UV) chroma (C_{UV}, calculated as the sum of reflectance of each wavelength in the 300–400 nm range divided by the total reflectance), and ultraviolet-blue chroma (C_{UV+B}, calculated as the sum of reflectance of each wavelength in the 300–500 nm range divided by the total reflectance). We chose these chroma variables because the available evidence suggests an important role of short-wavelength reflectance for signalling in *L. schreiberi* (Martín and López 2009). All the lizards were returned unharmed to their exact place of capture within 24 h of capture.

Visual modelling

We used TetraColorSpace (Stoddard and Prum 2008) to transform the spectra in colour points using the relative stimulation of the receiver's photoreceptors. Then, we calculated chromatic conspicuousness (i.e. chromatic contrast, CC) as the Euclidean distance between the chromatic points (Endler and Mielke 2005) of each male head and each natural background. First, we constructed two models with biological relevance corresponding to the two representative natural scenarios in which blue heads are viewed: (i) a lizard observer at 90 ° and (ii) a bird observer at 0 ° (Fig. 2). For the first model, we used the parallel irradiance and for the second the perpendicular irradiance. Next, to control for the possibility that the differences between models (i) and (ii) are unrelated to differences in the visual systems of predators and conspecifics, we also constructed two control models reversing the position of viewers: (iii) a bird observer at 90 ° and (iv) a lizard observer at 0 °. For the lizard models, we used the cone sensitivity spectra of *Platysaurus broadleyi* because this is the species phylogenetically closest to lacertids for which data are available (Fleishman et al. 2011). This is unlikely to be a problem because the visual system of diurnal lizards (including lacertids) is extremely conserved, with four types of cones, one of them sensitive to the near UV, and similar cone sensitivities (Pérez i de Lanuza and Font 2014). For the bird models, we used the average spectra implemented in TetraColorSpace (Stoddard and Prum 2008) for violet-sensitive (VS) birds such as raptors (i.e. Falconiformes, Accipitriformes and Strigiformes; Ödeen and Håstad 2003; Lind et al. 2013).

Statistical analyses

To compare spectral shape descriptors among angle setups we used a repeated-measure ANOVA when normality could be assumed and Friedman's test when not. When significant differences were detected, we used a paired *t* test or Wilcoxon's signed ranks test to compare angle setups by pairs. To test for differences in chromatic contrast, for each background, we used a two-way ANOVA with angle setup (90, 0 °) and visual model (*Platysaurus broadleyi*, VS birds) as fixed factors. We compared models (i) and (ii) with a paired *t* test for each background. To control for increased error rates arising from multiple dependent tests, the level of significance for rejection of the null hypothesis was fixed at 0.01.

Results

Both spectra (Fig. 3) and statistical analyses revealed a clear effect of viewer geometry on the reflectance of the blue heads of *L. schreiberi* males. Different viewing angles produce differences mainly in colour saturation (i.e. chroma), spectra being more chromatically pure when the lizard is illuminated with a larger angle (i.e. 90 °) with respect to the receiver in both UV chroma (Fig. 4a; F_2=18.32; P<0.0001) and UV + blue chroma (Figs. 4b; F_2=21.85; P<0.0001). The location of the main peak (λ_{blue}) changes with visual angle, being more short-wavelength biased with larger angles (Fig. 4c; χ^2=20; P<0.0001), and the location of the secondary peak (λ_{UV}) also changes slightly (Fig. 4c; χ^2=9.69; P=0.008). The difference between the two peaks is larger with small angles (χ^2=16.8; P<0.001). Figure 4 also shows the significance of paired comparisons. Although reflectance measurements are available for only three angles, the results suggest that the spectral variables change with visual geometry in a continuous way.

The spectral differences arising from different visual geometries affect the relative conspicuousness of the blue heads of adult males (Fig. 5). For the four backgrounds, both visual angle and visual model are important determinants of chromatic conspicuousness, but the interaction between visual angle and visual model is not significant (Fig. 5). Blue heads are more conspicuous when viewed against rocks, wood and *Quercus* leaves by a lizard (90 ° angle) than by a violet-sensitive bird predator (0 ° angle) (Fig. 5).

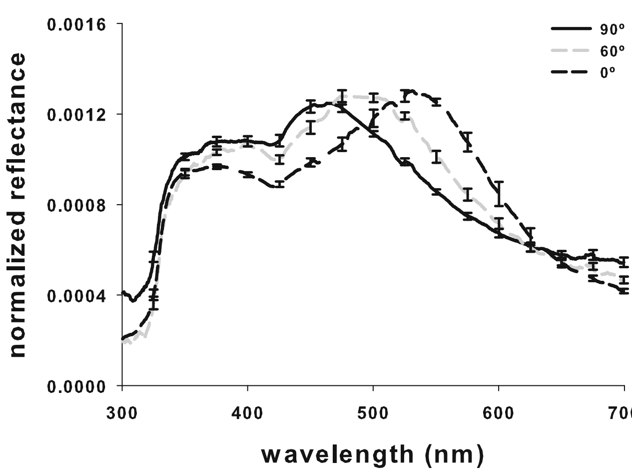


Fig. 3 Normalized reflectance spectra of blue heads of male *Lacerta schreiberi* taken at 90, 60 and 0 ° between the incident light and the measured reflectance. N=10 adult males. *Error bars* represent ±1 SEM

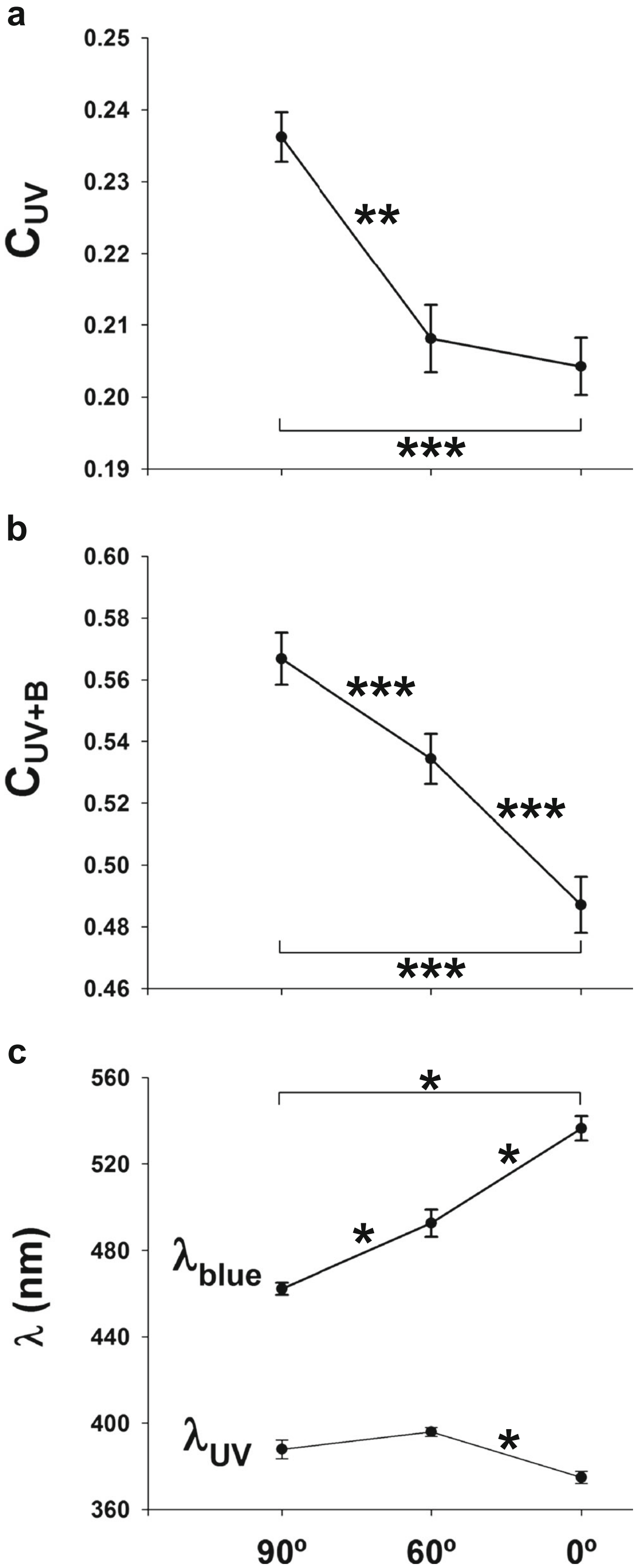
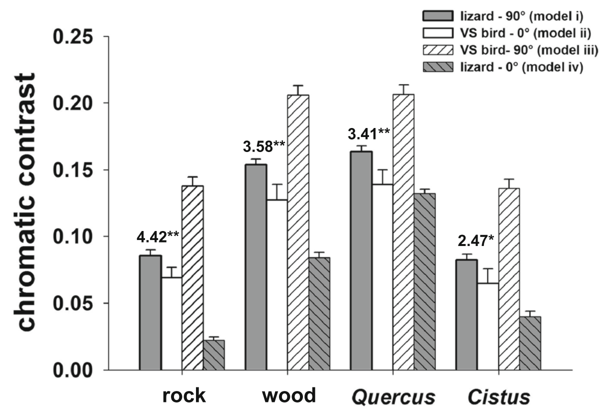


Fig. 4 Variation in mean values of **a** ultraviolet chroma (C_{UV}), **b** ultraviolet-blue chroma (C_{UV+B}), and **c** wavelength (λ) of peak location for the main peak (λ_{blue}) and the secondary peak (λ_{UV}) of the blue heads of male *Lacerta schreiberi* depending on viewer geometry (i.e. 90, 60, 0 ° setups). *Error bars* represent ±1 SEM. Significance of paired comparisons is represented by *asterisks*: * $P<0.01$, ** $P<0.001$, *** $P<0.0001$



Two-way ANOVA	rock	wood	*Quercus*	*Cistus*
angle setup	132.03***	103.07***	48.36***	63.23***
visual model	74.29***	42.93***	12.05**	30.20***
interaction	0.20	0.36	6.39*	4.04

Fig. 5 Chromatic contrasts generated by the blue head of male *Lacerta schreiberi* against the common natural backgrounds in its habitat under natural light conditions. Models i and ii correspond to those of natural position of relevant viewers (i.e. conspecifics—model i—and raptors—model ii—). Models iii and iv correspond to control models (i.e. raptors placed as conspecifics—model iii—and conspecifics placed as raptors—model iv—). Significance of two-way ANOVA (tabulated statistics under the graph) and paired comparisons (*over the bars*) are represented by *asterisks*: * $P<0.05$, ** $P<0.01$, *** $P<0.0001$

Discussion

Our results demonstrate that the blue heads of *L. schreiberi* males vary chromatically depending on viewer geometry, hue and chroma being more short-wavelength-shifted (i.e. relatively more reflective in the UV + blue range of the light spectrum) from the visual angle of a conspecific than from that of a putative avian predator. Not all surfaces that exhibit angle-dependent reflectance are, strictly speaking, iridescent. In fact, some surfaces that show angle-dependent reflectance are best described as non-iridescent under omnidirectional illumination (Noh et al. 2010; Saranathan et al. 2012). However, although this is true under certain natural conditions, such as diffuse lighting caused by a cloudy sky or under forest shading, under direct sunlight incidence (the conditions in which *L. schreiberi* are active in their habitats) the incident light can be treated as though coming from a point source. Therefore, considering the variation in their chromatic properties under different incidence angles, the blue heads of *L. schreiberi* can be described as iridescent, showing different reflectance to the different receivers.

Our results support the hypothesis that a single colour patch can be highly conspicuous to receptors in the same plane as the sender (i.e., a conspecific), and yet be relatively inconspicuous to predators that see it from above (i.e., avian predators). Thus, in this case, angle-dependent reflectance offers a way of relaxing the constraints imposed by predator detection. Interestingly, we found that both visual geometry and visual system crucially affect the chromatic contrasts of the blue heads of *L. schreiberi*. These results suggest that the chromatic properties of the blue heads, including angle-dependent reflectance, are selected to maximize detection by conspecifics, simultaneously minimizing detection by predators. The position of the conspicuous blue patch also plays an important role in making it more visible to conspecifics than to predators. In fact, the blue coloration is especially developed on the throat and the lateral surface of the head, being more visible to observers that view the lizards laterally than to observers that see lizards from above.

We are far from knowing the evolutionary origins of this coloration. It is possible that the iridescence of the blue heads is an exaptation of other structural colours without angle-dependent reflectance (or with little angle dependence), which are common in the colour patterns of many lacertids (Pérez i de Lanuza et al. 2013) and similar to other non-iridescent structural colorations (e.g. Shawkey et al. 2005). However, if this coloration is functional as a social signal, it may be positively selected by the combined action of the selection pressures relating to the signal's tactical design (Guilford and Dawkins 1991; Rowe 2013). As far as we know, our results provide the first evidence of the adaptive function of an angle-dependent coloration based on the efficacy design of colour signals and their detectability by different observers.

Angle-dependent variation may have been overlooked in the study of colour patches that are not obviously iridescent. In fact, adoption of the appropriate viewer geometry may be crucial for interpreting the experimental data involving angle-dependent coloration. For example, previous studies that measured head coloration in male *L. schreiberi* (Martín and López 2009; Stuart-Fox et al. 2009; Pérez i de Lanuza et al. 2013) and in other phylogenetically close species with similar coloration (*Lacerta viridis*: Bajer et al. 2010, 2011; *Lacerta bilineata*: Pérez i de Lanuza et al. 2013) used recording setups that imply an angle of 0 ° between light emission and reception (i.e. emissive and receptive fibres are located parallel in a single probe). Therefore, this recording setup represents the point of view of predators but probably not that of the primary receivers of male colour signals. This is important because the available evidence suggests that saturation of short wavelength reflectance (i.e. UV and blue), which, according to our results, is strongly influenced by viewer geometry, plays an important role in social signalling in *L. schreiberi* (Martín and López 2009) and *L. viridis* (Bajer et al. 2010, 2011). Thus, we argue that revisiting previous results using an adequate visual geometry may improve our understanding of the evolution and the putative informative content of this colour signal.

Structural colours, such as those that show angle-dependent reflectance, depend on the interaction of incident light with integumental nanostructures (Kemp et al. 2012). The production of these nanostructures may be costly, which enables structural colours to be used as honest signals in some taxa (e.g. Keyser and Hill 1999; Kemp and Rutowski 2007; Griggio et al. 2009). There is evidence that iridescent colours may require a more precise nanostructure organization than other structural colours (Doucet and Meadows 2009), suggesting that iridescence probably carries particularly high production and maintenance costs (reviewed in Doucet and Meadows 2009; Eliason and Shawkey 2011; Meadows et al. 2012). Thus, iridescence is well suited to function as an honest signal conveying information about an individual's quality or condition. Further research should examine the relationship between angle-dependent reflectance and condition-dependent traits in lizards.

Acknowledgments We are especially grateful to J. Heredero for the design and construction of the goniometer. We thank M. C. Stoddard for helping with TetraColorSpace, and L. J. Fleishman for generously sharing with us visual sensitivity data for *Platysaurus broadleyi*. This work was funded by a Portuguese FCT postdoctoral fellowship (SFRH/BPD/94582/2013) and a project from the Ministerio de Ciencia e Innovación (CGL2011-23751).

Ethical standards The study was performed according to guidelines provided by the Association for the Study of Animal Behaviour (ASAB) and the Animal Behavior Society (ABS). The experiments complied with current EU and Spanish laws and permits were generously provided by the Sierra Norte de Guadalajara Natural Park (Junta de Castilla-la Mancha).

References

Andersson S, Prager M (2006) Quantification of coloration. In: Hill GE, McGraw KJ (eds) Bird Coloration, Vol. 1. Mechanisms and Measurements. Harvard University Press, Cambridge, pp 41–89

Bajer K, Molnár O, Török J, Herczeg G (2010) Female European green lizards (*Lacerta viridis*) prefer males with high ultraviolet throat reflectance. Behav Ecol Sociobiol 64:2007–2014. doi:10.1007/s00265-010-1012-2

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. doi:10.1098/rsbl.2011.0520

Bradbury JW, Vehrencamp SL (2011) Principles of animal communication, 2nd edn. Sinauer Assoc Press, Sunderland

Csermely D, Bonati B, Romani R (2009) Predatory behaviour of common kestrels (*Falco tinnunculus*) in the wild. J Ethol 27:461–465. doi:10.1007/s10164-008-0143-7

Cummings ME, Rosenthal GG, Ryan MJ (2003) A private ultraviolet channel in visual communication. P Roy Soc Lond B 270:897–904. doi:10.1098/rspb.2003.2334

Doucet SM, Meadows MG (2009) Iridescence: a functional perspective. J R Soc Interface 6:S115–S132. doi:10.1098/rsif.2008.0395.focus

Eliason CM, Shawkey MD (2011) Decreased hydrophobicity of iridescent feathers: a potential cost of shiny plumage. J Evol Biol 214:2157–2163. doi:10.1242/jeb.055822

Endler JA (1991) Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. Vision Res 31:587–608

Endler JA, Mielke PW (2005) Comparing entire colour patterns as birds see them. Biol J Linn Soc 86:405–431. doi:10.1111/j.1095-8312.2005.00540.x

Endler JA, Théry M (1996) Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. Am Nat 148:421–452. doi:10.1086/285934

Fleishman LJ (1992) The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. Am Nat 139:S36–S61

Fleishman LJ, Leal M, Sheehan J (2006) Illumination geometry, detector position and the objective determination of animal signal colours in natural light. Anim Behav 71:463–474. doi:10.1016/j.anbehav.2005.06.005

Fleishman LJ, Loew ER, Whiting MJ (2011) High sensitivity to short wavelengths in a lizard and implications for understanding the evolution of visual systems in lizards. Proc R Soc B 278:2891–2899. doi:10.1098/rspb.2011.0118

Font E, Rome LC (1990) Functional morphology of dewlap extension in the lizard *Anolis equestris* (Iguanidae). J Morph 206:245–258. doi:10.1002/jmor.1052060210

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. doi:10.1111/j.1095-8312.2009.01251.x

Griggio M, Serra L, Licheri D, Campomori C, Pilastro A (2009) Moult speed affects structural feather ornaments in the blue tit. J Evol Biol 22:782–792. doi:10.1111/j.1420-9101.2009.01700.x

Guilford T, Dawkins MS (1991) Receiver psychology and the evolution of animal signals. Anim Behav 42:1–14

Hamilton DG, Whiting MJ, Pryke SR (2013) Fiery frills: carotenoid-based coloration predicts contest success in frillneck lizards. Behav Ecol 24:1138–1149. doi:10.1093/beheco/art041

Kemp DJ (2008) Female mating biases for bright ultraviolet iridescence in the butterfly *Eurema hecabe* (Pieridae). Behav Ecol 19:1–8. doi:10.1093/beheco/arm094

Kemp DJ, Rutowski RL (2007) Condition dependence, quantitative genetics, and the potential signal content of iridescent ultraviolet butterfly coloration. Evolution 61:168–183. doi:10.1111/j.1558-5646.2007.00014.x

Kemp DJ, Herberstein ME, Grether GF (2012) Unraveling the true complexity of costly color signaling. Behav Ecol 23:233–236. doi:10.1093/beheco/arr153

Kemp DJ, Jones D, Macedonia JM, Krockenberger AK (2014) Female mating preferences and male signal variation in iridescent *Hypolimnas* butterflies. Anim Behav 87:221–229. doi:10.1016/j.anbehav.2013.11.001

Keyser AJ, Hill GE (1999) Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. P Roy Soc Lond B 266:771–777

Land MF (1972) The physics and biology of animal reflectors. Prog Biophys Mol Biol 24:75–106

Lind O, Mitkus M, Olsson P, Kelber A (2013) Ultraviolet sensitivity and colour vision in raptor foraging. J Exp Biol 216:1819–1826. doi:10.1242/jeb.082834

Martín J, López P (2009) Multiple color signals may reveal multiple messages in male Schreiber's green lizards, *Lacerta schreiberi*. Behav Ecol Sociobiol 63:1743–1755. doi:10.1007/s00265-009-0794-6

Mäthger LM, Denton EJ, Marshall NJ, Hanlon RT (2009) Mechanisms and behavioural functions of structural colouration in cephalopods. J R Soc Interface 6:S149–S163. doi:10.1098/rsif.2008.0366.focus

Meadows MG, Butler MW, Morehouse NI, Taylor LA, Toomey MB, McGraw KJ, Rutowski RL (2009) Iridescence: views from many angles. J R Soc Interface 6:S107–S113. doi:10.1098/rsif.2009.0013.focus

Meadows MG, Morehouse NI, Rutowski RL, Douglas JM, McGraw KJ (2011) Quantifying iridescent coloration in animals: a method for improving repeatability. Behav Ecol Sociobiol 65:1317–1327. doi:10.1007/s00265-010-1135-5

Meadows MG, Roudybush TE, McGraw KJ (2012) Dietary protein level affects iridescent coloration in Anna's hummingbirds, *Calypte anna*. J Evol Biol 215:2742–2750. doi:10.1242/jeb.069351

Morrison RL (1995) A transmission electron microscopic (TEM) method for determining structural colors reflected by lizard iridophores. Pigm Cell Res 8:28–36

Noh H, Liew SF, Saranathan V, Mochrie SGJ, Prum RO, Dufresne ER, Cao H (2010) How noniridescent colors are generated by quasi-ordered structures of bird feathers. Adv Mater 22:2871–2880. doi:10.1002/adma.200903699

Ödeen A, Håstad O (2003) Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. Mol Biol Evol 20:855–861. doi:10.1093/molbev/msg108

Osorio D, Ham AD (2002) Spectral reflectance and directional properties of structural coloration in bird plumage. J Exp Biol 205:2017–2027

Pérez i de Lanuza G (2012) Visió en color i coloracions dels lacèrtids. PhD thesis, University of 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 (2014) Ultraviolet vision in lacertid lizards: evidence from retinal structure, eye transmittance, SWS1 visual pigment genes, and behaviour. J Exp Biol 217:1–11. doi:10.1242/jeb.104281

Pérez i de Lanuza G, Font E, Monterde JL (2013) Using visual modelling to study the evolution of lizard colouration: sexual selection drives the evolution of sexual dichromatism in lacertids. J Evol Biol 26:1826–1835. doi:10.1111/jeb.12185

Pérez-Mellado V (1998) *Lacerta schreiberi* Bedriaga, 1878. In: Salvador A (coord) Reptiles. Fauna Ibérica. Vol. 10. Museo Nacional de Ciencias Naturales, Madrid, pp 218–227

Prum RO (2006) Anatomy, physics, and evolution of avian structural colors. In: Hill GE, McGraw KJ (eds) Bird coloration, vol 1, Mechanisms and measurements. Harvard University Press, Cambridge, pp 295–355

Rohrlich ST, Porter KR (1972) Fine structural observations relating to the production of color by the iridophores of a lizard, *Anolis carolinensis*. J Cell Biol 53:38–52

Rowe C (2013) Receiver psychology: a receiver's perspective. Anim Behav 85:517–523. doi:10.1016/j.anbehav.2013.01.004

Rutowski RL, Nahm AC, Macedonia JM (2010) Iridescent hindwing patches in the Pipevine Swallowtail: differences in dorsal and ventral surfaces relate to signal function and context. Funct Ecol 24:767–775. doi:10.1111/j.1365-2435.2010.01693.x

Saranathan V, Forster JD, Noh H, Liew S-F, Mochrie SGJ, Cao H, Dufresne ER, Prum RO (2012) Structure and optical function of amorphous photonic angle X-ray scattering (SAXS) analysis of 230 bird species nanostructures from avian feather barbs: a comparative small. J R Soc Interface 9:2563–2580. doi:10.1098/rsif.2012.0191

Shawkey MD, Estes AM, Sieferman L, Hill GE (2005) The anatomical basis of sexual dichromatism in non-iridescent ultraviolet-blue structural coloration of feathers. Biol J Linn Soc 84:259–271. doi:10.1111/j.1095-8312.2005.00428.x

Sicsú P, Manica LT, Maia R, Macedo RH (2013) Here comes the sun: multimodal displays are associated with sunlight incidence. Behav Ecol Sociobiol 67:1633–1642. doi:10.1007/s00265-013-1574-x

Stevens M (2013) Sensory Ecology, Behaviour, and Evolution. Oxford University Press, Oxford

Stoddard MC, Prum RO (2008) Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. Am Nat 171:755–776. doi:10.1086/587526

Stuart-Fox DM, Whiting MJ, Moussalli A (2006) Camouflage and colour change: antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon. Biol J Linn Soc 88:437–446. doi:10.1111/j.1095-8312.2006.00631.x

Stuart-Fox D, Godinho R, de Bellocq JG, Irwin NR, Brito JC, Moussalli A, Široky P, Hugall AF, Baird SJE (2009) Variation in phenotype, parasite load and male competitive ability across a cryptic hybrid zone. PLoS ONE 4:e5677. doi:10.1371/journal.pone.0005677