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Ultraviolet reflectance and cryptic sexual dichromatism in the ocellated lizard, *Lacerta* (*Timon*) *lepida* (Squamata: Lacertidae)

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Ultraviolet (UV) colorations have garnered extensive theoretical and empirical treatment in recent years, although the majority of studies have concerned themselves with avian taxa. However, many lizards have acute visual systems with retinal photoreceptors that are sensitive to UV wavelengths, and also display UV-reflecting colour patches. In the present study, we used UV photography and full-spectrum reflectance spectrophotometry to describe intra- and intersexual colour variation in adult ocellated lizards *Lacerta* (*Timon*) *lepida* and to obtain evidence of UV-based ornamentation. We also investigated whether any colour traits correlate with morphological traits potentially related to individual quality. The results obtained show that the prominent eyespots and blue outer ventral scales (OVS) that ocellated lizards have on their flanks reflect strongly in the UV range and are best described as UV/blue in coloration. The eyespots of males are larger and cover a larger surface area than those of females. However, these differences can be entirely accounted for by sex differences in body size, with males being generally larger than females. We also found differences in the shape of reflectance curves from males and females, with the eyespots and blue OVS of males being more UV-shifted than those of females. Other body regions have extremely low UV reflectance and are not sexually dichromatic. Eyespot size and the total surface area covered by eyespots increases with body size in males but not in females, suggesting that they may be signalling an intrinsic individual characteristic such as body size or male fighting ability. We also discuss the alternative and non-exclusive hypothesis that eyespots may function in lizards of both sexes as protective markings against predators.

ADDITIONAL KEYWORDS: body coloration – reptile – signalling – spectral sensitivity – visual communication – visual ecology.

INTRODUCTION

Lizard body coloration is usually a compromise between crypsis and conspicuousness. Sexual selection and intraspecific communication are usually thought to favour conspicuous coloration, whereas predation risk favours cryptic coloration (Macedonia, Brandt & Clark, 2002; Stuart-Fox *et al.*, 2003; Husak *et al.*, 2006). Conspicuous colour patches, often located in a lateral or ventrolateral position, are almost exclusively visible from a lizard's eye view and appear to have evolved exclusively for signalling. Many lacertids, for example, display conspicuously coloured eyespots on their flanks. In some species, eyespots are found only in males or are larger and more conspicuous in males, which suggests a sexually selected origin (Stuart-Fox & Ord, 2004).

In the last decade, ultraviolet (UV) vision and ultraviolet coloration have become increasingly appreciated as an integral part of animal behaviour. Numerous studies have demonstrated that the UV component of avian colour vision plays an important role in sexual signalling, foraging, and may also be involved in orientation, and assessments of bird coloration now routinely include the UV portion of the spectrum

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(Cuthill *et al.*, 2000). By contrast, studies of non-avian reptile UV vision and coloration have lagged behind. As birds, many lizards are highly visual animals with complex visual systems (Fleishman, 1992, 2000). Furthermore, although scant and taxonomically biased, the available evidence indicates that UV wavelengths may, as in birds, be part of the perceptual world of many lizards (Fleishman, Loew & Leal, 1993, 1997; Loew, 1994; Ellingson, Fleishman & Loew, 1995; Loew *et al.*, 1996, 2002; Bowmaker, Loew & Ott, 2005).

Sex differences are a well-known source of variation in body coloration in many animals, but the contribution of UV wavelengths to sexual dichromatism in vertebrates is understudied. Recent work has shown that some bird species are dichromatic in both the ultraviolet and the visible spectra (Andersson & Amundsen, 1997; Keyser & Hill, 1999; Mays *et al.*, 2004), or in the UV region alone (i.e. cryptic sexual dichromatism; Mahler & Kempenaers, 2002; Eaton & Lanyon, 2003). For example, blue tits [*Cyanistes* (*Parus*) *caeruleus*] are more sexually dimorphic in the UV than in other parts of the spectrum (Andersson *et al.*, 1998; Hunt *et al.*, 1998), with male plumage patches reflecting UV light more strongly than the corresponding patches in females. Similarly, *Gallotia galloti* lizards display lateral and ventrolateral blue patches that are sexually dichromatic in the UV, male patches being more reflective than those of females (Molina-Borja, Font & Avila, 2006).

The ocellated lizard, *Lacerta* (*Timon*) *lepida* Daudin, 1802, is found in the southwestern part of Europe and is one of the largest lizards in the family Lacertidae (Arnold, 2002). As the common name implies, a hallmark trait of this species is the presence of prominent eyespots (ocelli) on the flanks of adult individuals. The eyespots are approximately circular motifs of scales with contrasting colours on the sides of the bodies of many lizards. In addition to eyespots, many lacertids possess conspicuously coloured scales at the boundary between the lateral and ventral body surfaces (termed outer ventral scales, OVS; Arnold, 1989). In *L.* (*T.*) *lepida*, both the eyespots and the coloured OVS appear blue to a human observer. The blue patches are particularly conspicuous when broadcast via postural adjustments (i.e. lateral compression, arched back) during stereotyped behavioural displays directed at conspecifics and potential predators, and may thus play a role in signalling (Weber, 1957; Vicente, 1987).

Ocellated lizards are sexually dimorphic, and males differ from females mainly in head and body proportions (Braña, 1996; Pérez-Mellado, 1998). Body coloration figures prominently in descriptions of ontogenetic and geographic variation in this species (Mateo & Castroviejo, 1991; Mateo & López-Jurado, 1994), yet the evidence regarding sexual dichromatism is equivocal. Earlier reports have indicated that sexual dichromatism in ocellated lizards is slight or inexistent (Bischoff, Cheylan & Böhme, 1984). Arnold (2002), on the other hand, notes that females are less brightly coloured and have fewer blue spots than males. However, a shortcoming of previous descriptions of this species' coloration is that they have used subjective techniques based on human colour perception, without consideration for possible differences in visual perception between lizards and humans. Foremost among these are differences in the wavelengths of light to which visual systems are attuned and the possibility that lizards see colours that humans cannot experience. Of two dozen species for which microspectrophotometric data are available, all but one (the agamid *Ctenophorus ornatus*) have a cone class that contains a UV-absorbing visual pigment with $\lambda = 359–385$ nm. Indeed, many lizards are now thought to be tetrachromatic with four single-cone types contributing to their colour vision, one of these sensitive in the near UV (UV-A) waveband (Fleishman *et al.*, 1993; Loew *et al.*, 2002).

In the present study, we provide the first description of *L.* (*T.*) *lepida* coloration using objective methods (full-spectrum reflectance spectrophotometry and UV photography) and contribute to the expanding literature on UV vision and coloration in lizards with an assessment of UV-based sexual dichromatism in this species. A reasonable hypothesis regarding the function of the conspicuous colour patches of ocellated lizards is that they are signals used in communication. The evolution and maintenance of stable communication systems requires that signals be reliable [i.e. that variation in some signal characteristic (size, frequency, intensity) is consistently correlated with some attribute of the signaller or its environment] (Searcy & Nowicki, 2005). Extravagant and sexually dimorphic colour patterns often convey information regarding the quality of the signaller (Forsman & Appelqvist, 1999; Ellers & Boggs, 2003), and previous studies with lizards have shown that at least some chromatic signals are condition-dependent traits reliably reflecting individual phenotypic quality (Whiting, Nagy & Bateman, 2003). For example, in male sand lizards, *Lacerta agilis*, the size and saturation of the green lateral badges are strongly correlated with mass and body condition, both being strong predictors of contest success (Olsson, 1994). Thus, a second aim of the present study was to identify an association between colour and other morphological traits that could correlate with individual quality in ocellated lizards.

MATERIAL AND METHODS

Study species, collection, and husbandry

Subjects consisted of 30 (19 male, 11 female) ocellated lizards. Sexing of individuals was unambiguous based

on relative head size (much larger in males than in females). Mean ± SEM snout–vent length (SVL) was 197.38 ± 3.68 mm for males (range 176–217 mm) and 179.67 ± 3.51 mm for females (range 167–200 mm), which corresponds to adult, sexually mature lizards in this species (Cheylan, 1984; Castilla & Bauwens, 1989; Mateo & Castanet, 1994). We collected lizards in orange tree orchards in Oliva (eastern Iberian Peninsula; 38°53′N, 0°07′W) in April to July and October of 2004 and 2005. This population belongs to the subspecies *Lacerta* (*Timon*) *lepida nevadensis* (independently verified by J. A. Mateo), which is restricted to the southeastern Iberian Peninsula. Animals were captured by hand and transported to the laboratory at the University of Valencia, where they were housed singly in large glass terraria placed inside a temperature-controlled room. Colour and other measurements were generally taken within 24 h of capture, although some lizards were held in the laboratory for several days (a maximum of 1 week) before being released. During their stay in the laboratory, lizards were fed *Zophoba morio* larvae and had a permanent supply of water. Once the experiments were completed, lizards were released back into the wild at their places of capture unharmed. Although the lizards were not permanently marked, their capture sites were sufficiently far apart to guarantee that none were recaptured.

Morphometrics

To test for an association between colour and morphological traits potentially related to individual quality we obtained standard measurements of lizard body and head size. Body size is strongly correlated with fighting ability and mating success in males (Salvador & Veiga, 2001; Jenssen, DeCourcy & Congdon, 2005), and with clutch size in females of many lizard species (Fitch, 1970). Similarly, male head size correlates with fighting ability and dominance (Molina-Borja, Padrón-Fumero & Alfonso-Martín, 1998; Perry *et al.*, 2004; Huyghe *et al.*, 2005). Body size was measured as SVL with a plastic ruler to the nearest 1 mm. Head length and width were measured with digital callipers to the nearest 0.1 mm. Head length (HL) was taken as the distance between the tip of the snout and the caudal edge of the occipital scale, and head width (HW) was taken at the widest point of the head. Additionally, we calculated a body condition index for each lizard as the residual for that individual of a regression of body mass against SVL. Body mass was measured to the nearest 0.01 g with an electronic scale.

Colour pattern assessment

We used reflectance spectrophotometry and UV photography to characterize areas of UV reflectance in the lizards' integument. These two techniques provide complementary information: UV photography shows the distribution of UV patches, whereas spectrophotometry provides accurate quantitative data of selected colour patches and also avoids the potential bias introduced by subjective techniques based on human colour perception (Endler, 1990; Stevens *et al.*, 2007).

UV photography

For UV photography, lizards were positioned on a light stand and photographed through a prefocused macro lens (Yashica 100 mm f/3.5 ML Macro) against a UV reflective background (Ikonorex high quality art paper; approximately 40% reflectance in the 300–400 nm range). Each lizard was photographed through a UV-blocking filter (Hakuba 1A), which transmits only wavelengths above 400 nm, and again through a UV-transmitting filter with peak transmittance at 360 nm (Tiffen 18A), using UV-sensitive black and white film (Kodak TMAX 100 pro). Illumination was provided by a standard flash light for photography within the human-visible range. For photographs in the UV range, the standard flash light was coupled to a second flash light (Sunpak 455) modified for UV output. The two flash lights were set in manual mode so that the same amount of light was available for every exposure. Lizards were photographed in dorsal, ventral, and lateral views. To provide a photographic record of colour in the human visual range, we also took colour photographs of all the lizards using a high-resolution digital camera (Sony DSC-F707). To facilitate their manipulation when the photographs were being taken, lizards were lightly anesthetized with ketamine hydrochloride (6 μL g^{-1} b.m., injected intramuscularly).

Reflectance spectrophotometry

Reflectance spectra of lizard body regions were obtained following well-established standard protocols (Stuart-Fox *et al.*, 2003; Molina-Borja *et al.*, 2006). We used a USB2000 portable diode-array spectrometer and a PX-2 Xenon strobe lamp (both from Ocean Optics Inc.) that provided a stable and continuous source of full-spectrum light (220–750 nm). Spectra were recorded in 0.37-nm steps and expressed as the percentage of light reflected relative to a certified Spectralon white diffuse reflectance standard (Labsphere). Measurements were taken with a reflectance probe (R200-7; Ocean Optics) held at a 90° angle to the lizard's skin. An insect pin attached to the probe (nylon head down) maintained a constant distance of 5 mm between the end of the probe and the lizard skin, resulting in a circular reading spot of approximately 2 mm in diameter.

We measured the reflectance of all the eyespots and OVS on both sides of each lizard in the sample (excepting those with a diameter less than 2 mm). Reflectance was also measured from eight body regions to obtain a reasonably comprehensive characterization of lizard coloration: head (dorsal, anterior to parietal eye), gular area (centre), dorsum (midpoint along vertebral column), ventrum (centre), leg (dorsally and ventrally), and tail base (dorsally and ventrally). For each body region of each lizard, the spectrometer averaged 20 spectra that were graphed using OOIBase32 software (Ocean Optics). We took dark current and white standard measurements before measuring each lizard. Measurements were taken in a darkened room to minimize interference from external light sources. We restricted analyses to the range 300–700 nm, which includes the broadest range of wavelengths known to be visible to lizards (Loew *et al.*, 2002).

Eyespot size and surface area covered by eyespots

For every lizard in the sample, we counted the number of blue eyespots and blue OVS on each side of the body. We also measured the surface area of eyespots from standardized high-resolution colour photographs (see above) of the left and right sides of each lizard using the open domain image analysis software, ImageTool, version 3.0 (http://ddsdx.uthscsa.edu/dig/itdesc.html). From the digitized images, we measured the area of each individual eyespot as well as the total area occupied by all the eyespots on each side of the animal. We also calculated the relative surface area covered by eyespots as the proportion of the body outline (excluding the head, tail, legs and ventrum) occupied by eyespots (summed across all eyespots on each side of the body) (Fig. 1A).

Statistical analyses

To study between-sex variation in coloration we first used independent sample Student's *t*-tests to compare mean values for males and females of number and size of eyespots, total flank area covered by eyespots, and number of blue OVS. For comparisons of eyespot size, each lizard contributed a single value, which was the mean of the size (in mm^2) of all the eyespots measured for that individual. We also used *t*-tests to compare the size (SVL, body mass) of male and female lizards. Because males in our sample were larger than females (see Results), when *t*-tests of between-sex variation in colour traits yielded significant results, we used analyses of covariance (ANCOVA) with SVL as the covariate to evaluate whether sex differences persisted after correcting for size.

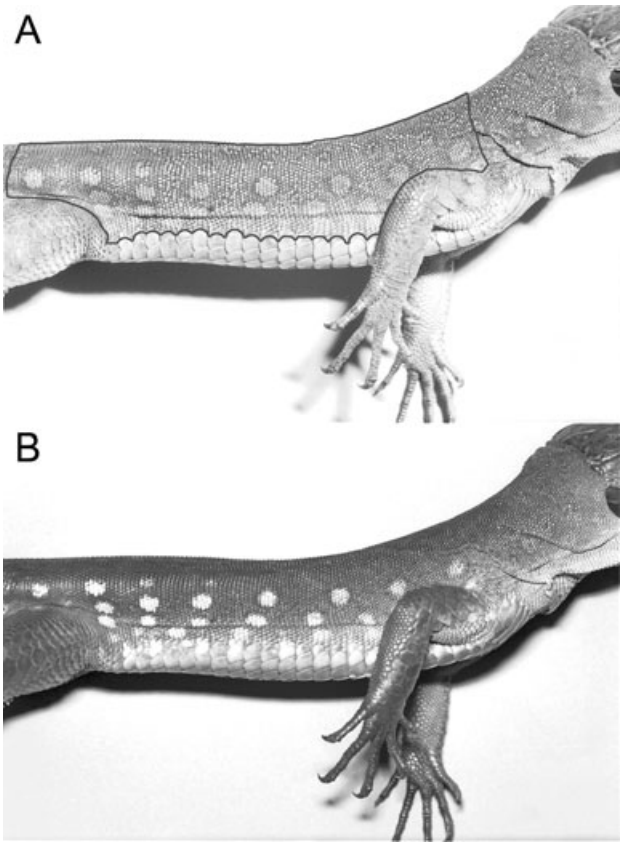

Figure 1. Male *Lacerta* (*Timon*) *lepida* photographed through an ultraviolet (UV)-blocking filter (A) and through a UV-transmitting filter (B). The white areas in (B) correspond to areas of enhanced UV reflection. These include the lateral and ventrolateral eyespots as well as the blue outer ventral scales (OVS). The line in (A) surrounds the area used to calculate the percent surface area covered by eyespots (Table 1).

We analysed the relationship between colour traits (number, size and total surface area of eyespots, and number of blue OVS) and morphometric variables (SVL, body condition, head size) by means of Pearson's correlations. Body condition was calculated as the residual of a Model II (standard major axis) regression between body mass and SVL. Because head size scales positively with body size in lizards, we assessed the relationship between head size (HL, HW) and colour traits using first-order partial correlations controlling for SVL to remove the effects of body size.

We used spectra to derive traditional measures of spectral intensity (brightness or luminance of the light spectrum), hue (spectral location), and chroma (saturation or spectral purity) (Endler, 1990; Macedonia *et al.*, 2002; Örnborg *et al.*, 2002). Intensity was calculated by summing the percent reflectance across

the 300–700 nm range of wavelengths (R300–700). Hue was estimated by λ_{max}, the wavelength of maximum reflectance. Lacking information on how the visual system of ocellated lizards partitions visual space and given that some reflectance spectra had main and secondary peaks, we obtained separate measurements of chroma for the UV (300–400) and GY (500–600) segments of the visual spectrum. UV chroma was calculated using the formula R300–400/R300–700. Similarly, GY chroma was calculated as R500–600/R300–700. We used *t*-tests to compare the intensity, hue, and chroma of selected colour patches between the two sexes, and Pearson's correlations to look for an association between the intensity, hue and chroma of a representative eyespot (third eyespot of the third eyespot row on the lizard's left flank) and SVL, body condition, and head size.

Raw data in ANCOVAs and in correlations were previously log-transformed to fit normality and homocedasticity assumptions. We applied the sequential Bonferroni method described by Holm (1979) to reduce the number of cases with significance arising by chance because of multiple testing. To avoid loss of power, we used an experiment-wise significance level of 15% (Chandler, 1995). Although uncorrected values are given in the results, those tests reported as significant remained so after applying the Holm–Bonferroni correction. All probability levels are for two-tailed tests.

RESULTS

Eyespot size, distribution, and human-visible colour

The dorsum and flanks of *L.* (*T.*) *lepida* are covered with small granular scales of fairly uniform size. The eyespots in our sample were approximately circular motifs of variable size extending over two to 47 granular scales. The eyespots were regularly spaced giving rise to a lattice of two to four rows by six to 15 columns extending between the insertions of the fore and hindlegs (Fig. 1A) and covered 7–13% of the lizards' lateral aspect (Table 1). Eyespots in the dorsal (i.e. uppermost) row were restricted to the posterior half of the abdomen. To the human eye, individual eyespots are of uniform blue colour and sometimes contain one or two centrally located dark scales. The eyespots have sharply delineated borders that provide a strong contrast with the surrounding skin and are occasionally encircled by a rim of green, yellow or brown scales.

All males had four rows of eyespots per side, whereas females had two to four rows. Males had seven to 15 and females seven to ten columns of eyespots on each side. All males and females had the same number of rows on both sides, but not necessarily the same number of columns. No male and only two females in the sample had the same number of eyespots on the right and left flanks. In both sexes, approximately half of the individuals had more eyespots on the right, and the other half had more eyespots on the left side.

Males were larger (SVL, $t_{23} = 3.17$, $P < 0.004$; body mass, $t_{23} = 5.57$, $P < 0.001$) and had larger eyespots than females. In addition, males had total flank areas covered by eyespots larger than those of females (Table 1). Although males in general had more eyespots than females, the difference was not statistically significant. When the differences in size were statistically controlled (ANCOVA), none of the between-sex differences detected by *t*-tests reached statistical significance. Thus, there is no sexual dimorphism in size corrected values, suggesting that the difference between males and females in mean eyespot size and

Table 1. Descriptive statistics and tests of between-sex differences for four colour traits measured on *Lacerta* (*Timon*) *lepida* lizards used in the present study

	Sex	Sample size	Number of eyespots (range)	Mean eyespot size (mm^2)	Area covered by eyespots (mm^2)	Number of blue OVS (range)
Left side	♂♂	9–12	25.0 ± 2.2 (18–39)	14.1 ± 1.2	386 ± 61 (12.8)	5.9 ± 0.6 (4–10)
	♀♀	6–10	19.6 ± 2.1 (10–31)	8.7 ± 0.7	158 ± 27 (7.1)	4.1 ± 0.7 (0–7)
Right side	♂♂	9–15	25.2 ± 1.8 (17–42)	13.5 ± 1.7	393 ± 84 (11.7)	5.1 ± 0.5 (0–8)
	♀♀	7–11	19.1 ± 1.9 (9–28)	8.3 ± 0.8	165 ± 30 (7.7)	4.7 ± 0.6 (0–7)
Between-sex comparisons (both sides)			$t_{19} = 1.93$ $P = 0.07$	$t_{13} = 3.21$ $P = 0.007$*	$t_{13} = 3.09$ $P = 0.011$*	$t_{20} = 1.65$ $P = 0.12$

Data are the mean ± SEM of each variable. Between-sex differences in mean values were analysed using *t*-tests for independent samples and, in the case of mean eyespot size and area covered by eyespots, by analyses of covariance (not shown), with snout–vent length as the covariate. The numbers in parentheses in the column showing the area covered by eyespots denote the percentage area of the lizard's lateral aspect covered by eyespots.
*Significant after Holm–Bonferroni correction for multiple tests.
OVS, outer ventral scales.

total flank area covered by eyespots is driven by differences in body size.

OVS NUMBER, DISTRIBUTION, AND HUMAN-VISIBLE COLOUR

By contrast to the granular scales that cover the dorsum and flanks, the enlarged ventral scales of *L.* (*T.*) *lepida* are rectangular and arranged in regular longitudinal rows. A distinct row of OVS on each side of the lizard's body separates the granular scales dorsally from the enlarged ventral scales. The OVS are usually smaller than the ventral scales and look either blue or white to the human eye. The human-perceived colour of white OVS is indistinguishable from that of the underlying ventral scales. Blue OVS are scattered along the lizard's flank and are approximately aligned with the overlying eyespot columns. Some blue OVS are blue dorsally and white in their lower edge. Occasionally, the blue coloration extends beyond the OVS to cover the dorsal part of the underlying ventral scale. No female lacked blue OVS entirely, but two females had unusually low numbers (one and three, respectively) of blue OVS.

UV PHOTOGRAPHY AND REFLECTANCE SPECTROPHOTOMETRY

UV photographs revealed that reflectance in the near UV waveband in ocellated lizards is associated with the lateral and ventrolateral eyespots, with blue OVS and, in a few specimens, with isolated granular scales scattered among the ventral eyespots (Fig. 1B). All UV reflecting patches appear to comprise different shades of blue to the human eye. Reflectance spectra confirmed that eyespots and blue OVS are UV-reflecting, with the human-perceived blue colour being generated by the tail of the spectral curve that rises steadily toward the short wavelength end of the spectrum (Fig. 2). Mean ± SEM spectra for a sample of eyespots and OVS of each sex are shown in Figures 2 and 3. Visual inspection of the UV photographs and reflectance spectra from other body areas showed no distinct UV peak reflectance (Figs 1, 3B).

White OVS had their peak reflectance at around 639.62 ± 6.90 nm, whereas blue OVS had their peak reflectance in the UV range (Fig. 3A). The reflectance spectra of blue OVS were similar to those of the ventral eyespots (compare Figs 2C, 3A) and, in males, had primary and secondary reflectance peaks with an λ_{max} of 388.02 ± 1.44 nm and 548.47 ± 3.29 nm, respectively. Although their reflectance spectra were of similar shape, blue OVS exhibited greater reflectance intensity (i.e. larger area under the curve) than eyespots (Table 2).

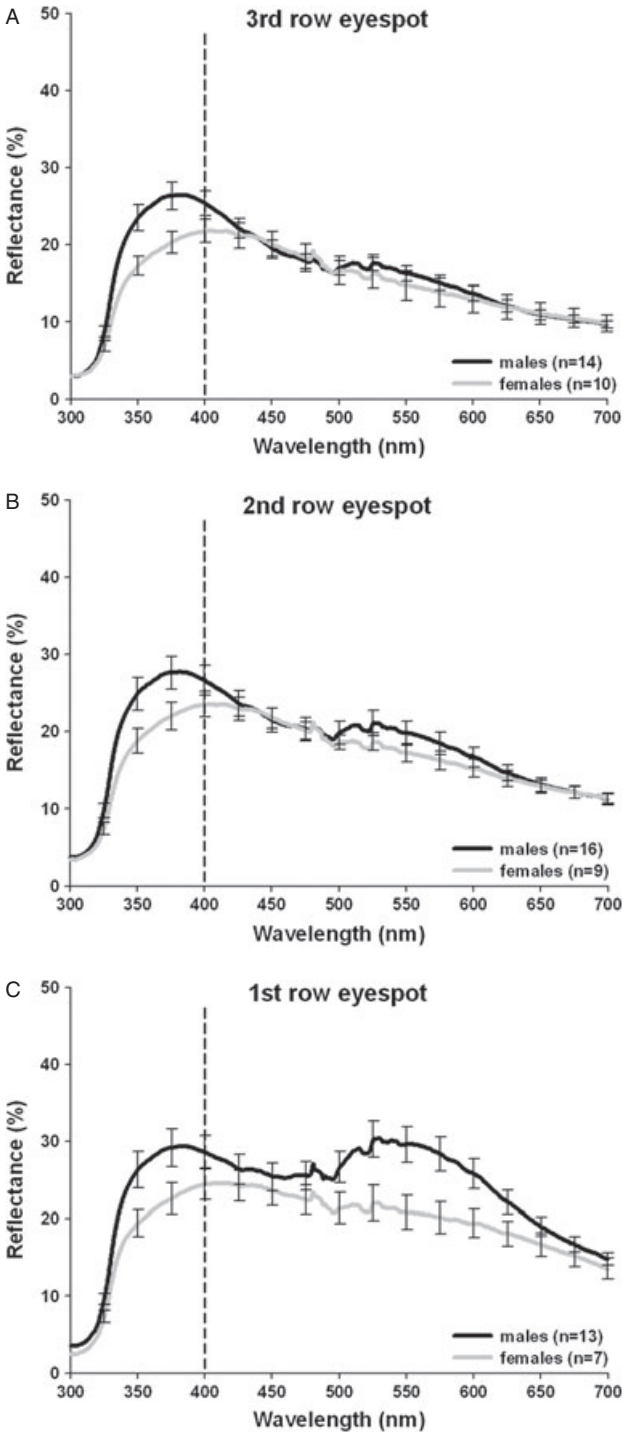

Figure 2. Reflectance spectra of representative eyespots from the third (A), second (B) and first (ventral) (C) eyespot rows of males and females of *Lacerta* (*Timon*) *lepida*. Sample sizes are shown in parentheses. The small peak visible in many spectra around 480 nm is an artefact produced by the light source used to illuminate the lizard skin. The dotted vertical line at 400 nm indicates the lower limit of the human visual range. Vertical lines indicate error bars (±1 SEM).

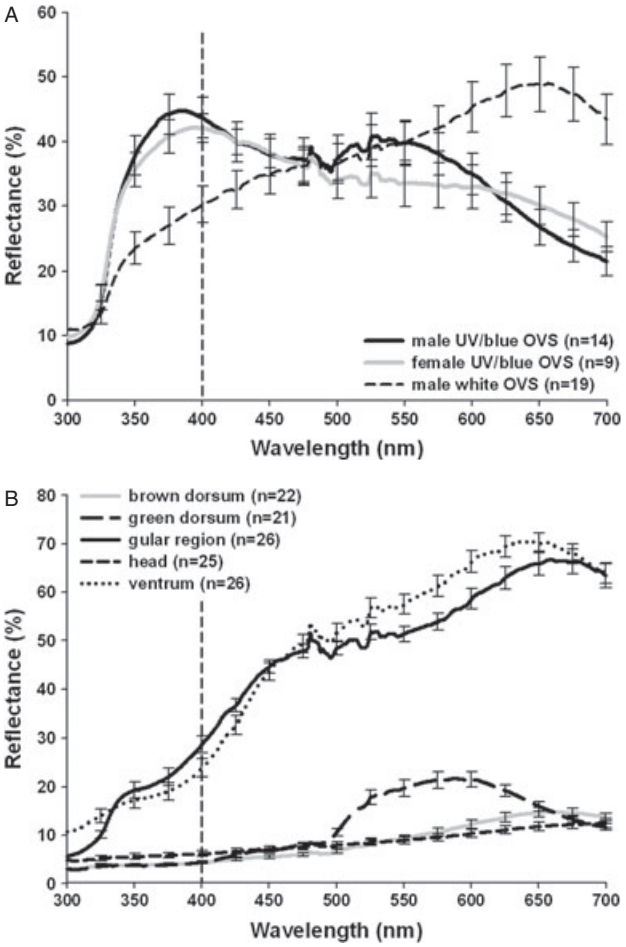

Figure 3. Reflectance spectra of white and blue outer ventral scales (OVS) (A) and of different body parts (B) of male and female *Lacerta* (*Timon*) *lepida* lizards. Sample sizes are shown in parentheses. The small peak visible around 480 nm is an artefact produced by the light source used to illuminate the lizard skin. The dotted vertical line at 400 nm indicates the lower limit of the human visual range. Vertical lines indicate error bars (±1 SEM).

Sexual dichromatism in reflectance spectra

Male and female eyespots were similar in spectral intensity and two measures of chroma, but differed considerably in hue (Table 2). The eyespots of males were more UV-shifted than those of females and had a primary reflectance peak in the UV range (λ_{max}: 386.58 ± 0.89 nm). By contrast, the eyespots of females had a peak of reflectance with λ_{max} values in the human-visible range (λ_{max}: 413.41 ± 1.68 nm). In males, the dorsal eyespots had a single peak of reflectance, whereas more ventrally located eyespots included a secondary peak with an λ_{max} of 547.03 ± 3.07 nm (Fig. 2). Dorsal eyespots also reflected less intensely than ventral eyespots (Table 2). This dorsoventral gradient in reflectance spectra is paralleled by changes in the human perceived colour of eyespots, which, in males, ranges from dark blue dorsally to light and more whitish (i.e. less saturated) blue ventrally. The reflectance spectra of male blue OVS were more UV-shifted and had more GY chroma than those of females (Table 2).

Relationship between colour traits and quality indicators

Both mean eyespot size and total surface area of eyespots were positively correlated with SVL in males, but not in females (Fig. 4B, Table 3). The number of eyespots and blue OVS, on the other hand, did not correlate with SVL in either sex (Table 3). Thus, larger males had larger eyespots and a larger total flank area covered by eyespots than smaller males, but not necessarily more eyespots or blue OVS (Fig. 4A, B, C). No correlation of colour traits (i.e. number, size and surface area of eyespots, and number of blue OVS) with body condition or relative head size was statistically significant after Holm–Bonferroni correction (all $r < |0.86|$, all $P > 0.03$). Similarly, we found no significant correlation between the intensity, hue or chroma of the third eyespot of the third eyespot row and any of the quality indicator variables (all $r < |0.45|$, all $P > 0.15$; Table 3).

DISCUSSION

Most lacertids live in light rich environments and have eye dimensions (size and shape) typical of diurnal, photopic lizards (Cooper & Greenberg, 1992). As expected for highly visual animals with complex visual systems, lacertids frequently have remarkable and conspicuous visual displays and colour patterns. However, our understanding of visual communication in lacertids remains very limited, most likely because the often cited dichotomy between the visual Iguania and the chemosensory Scleroglossa (Pough *et al.*, 2001; Pianka & Vitt, 2003) has tended to downplay the importance of coloration and visual displays in most scleroglossans, including lacertids.

Ocellated lizards in particular are elaborately ornamented and have large eyes optimized for visual acuity (Bischoff *et al.*, 1984; Hall, 2008). The results obtained in the present study show that the prominent eyespots and blue OVS that characterize adult ocellated lizards are UV/blue. UV-reflectance is present in coloured skin patches of many iguanid and agamid lizards (Fleishman *et al.*, 1993; LeBas & Marshall, 2000; Blomberg, Owens & Stuart-Fox, 2001; Fleishman & Persons, 2001; Macedonia, 2001; Stoehr & McGraw, 2001; Thorpe, 2002; Macedonia, Echternacht & Walguarney, 2003; Thorpe & Stenson, 2003). Recent research has revealed that the colour patterns

Table 2. Intensity (brightness), chroma, and hue (peak wavelength) of eyespots and blue outer ventral scales (OVS) in ocellated lizards of both sexes

	♂♂ / ♀♀	Intensity ($\times 10^3$)	t / P	UV chroma (300–400 nm) ($\times 10^{-2}$)	t / P	GY chroma (500–600 nm) ($\times 10^{-2}$)	t / P	Peak wavelength (nm)	t / P
Left side									
Third row, third eyespot	17	18.3 ± 1.0	1.03	25.7 ± 1.1	0.85	26.0 ± 0.8	1.14	386 ± 4	–2.91
	11	16.7 ± 1.1	0.31	24.1 ± 1.7	0.41	24.4 ± 1.3	0.26	413 ± 8	0.01
Second row, third eyespot	17	21.6 ± 1.4	1.51	25.0 ± 0.9	1.64	26.5 ± 0.7	0.81	381 ± 2	–4.16
	10	19.1 ± 8.7	0.14	22.7 ± 1.2	0.11	25.5 ± 1.0	0.43	410 ± 7	0.002*
First row, second eyespot	12	25.8 ± 1.6	1.65	22.9 ± 1.2	1.32	28.1 ± 0.6	1.15	384 ± 5	–3.58
	7	21.6 ± 2.0	0.12	20.5 ± 1.3	0.21	26.9 ± 0.9	0.27	417 ± 9	0.002*
First blue OVS	14	39.3 ± 3.2	0.28	22.2 ± 0.7	0.09	28.7 ± 0.6	3.30	384 ± 2	–2.57
	9	38.0 ± 2.6	0.78	22.1 ± 1.2	0.93	25.5 ± 0.8	0.004*	403 ± 7	0.03
Right side									
Third row, fourth eyespot	13	18.9 ± 1.0	0.91	27.0 ± 1.0	1.72	24.8 ± 0.7	0.41	379 ± 2	–3.39
	11	17.3 ± 1.5	0.38	23.9 ± 1.5	0.10	24.3 ± 1.0	0.69	406 ± 8	0.005*
Second row, second eyespot	17	22.0 ± 2.0	1.00	23.7 ± 0.9	1.28	27.9 ± 0.8	1.00	381 ± 3	–3.49
	8	18.9 ± 1.4	0.33	21.7 ± 1.2	0.15	26.5 ± 0.8	0.33	413 ± 9	0.007
First row, second eyespot	13	27.3 ± 2.1	1.67	22.1 ± 0.9	1.42	29.7 ± 0.8	1.88	381 ± 2	–4.32
	8	22.1 ± 1.8	0.11	20.1 ± 1.2	0.17	27.3 ± 0.9	0.08	418 ± 8	0.003*
First blue OVS	11	39.4 ± 4.4	0.33	21.9 ± 0.7	0.25	28.5 ± 0.5	3.49	384 ± 2	–2.93
	8	37.8 ± 2.0	0.75	21.4 ± 1.3	0.81	25.4 ± 0.7	0.003*	407 ± 8	0.02

Data are mean ± SEM. Eyespot rows are arranged in a dorsal to ventral sequence (i.e. the first row is the most ventral row of eyespots, directly above the row of OVS). Eyespots and OVS within a row are numbered in a rostral to caudal direction. Sample sizes vary because reflectance of some colour patches could only be recorded from a subset of the available lizards (e.g. the eyespots were too small to obtain reliable spectra).
*Significant after Holm–Bonferroni correction for multiple tests.

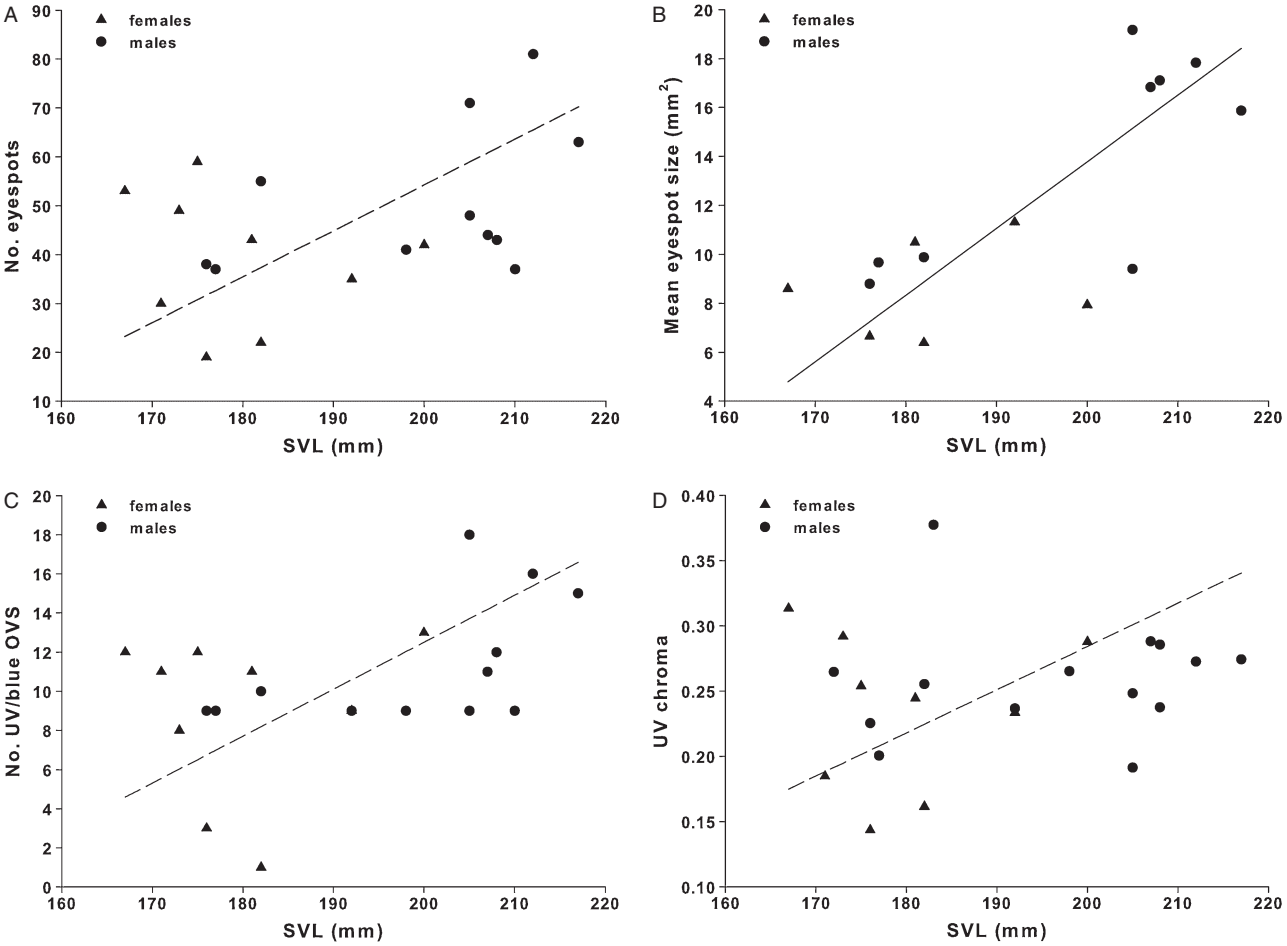

Figure 4. Relationships between colour traits and body size (snout–vent length; SVL) in ocellated lizards of both sexes. The graph in D depicts the relationship between the ultraviolet chroma of the third eyespot of the third eyespot row on the lizard's left flank and SVL. The correlation with SVL was statistically significant after Holm–Bonferroni correction only for mean eyespot size (Table 3). Sample sizes vary due to missing data for some lizards. Lines are best-fitting linear (standard major axis) models.

Table 3. Results of Pearson's correlations assessing the relationship between colour and snout–vent length (log transformed data)

	Males		Females			Males		Females	
	r	*P*	*r*	*P*		*r*	*P*	*r*	*P*
Number of eyespots	0.45	0.16	–0.12	0.72	Intensity	–0.27	0.36	0.36	0.34
Mean eyespot size	0.79	0.01*	0.21	0.70	UV chroma	0.09	0.75	0.06	0.89
Area covered by eyespots	0.78	0.01*	0.14	0.79	GY chroma	–0.02	0.96	–0.03	0.94
Number of blue OVS	0.57	0.05	–0.01	0.99	Peak wavelength	0.04	0.88	0.08	0.83

Spectral data are for the third eyespot of the third eyespot row on the lizard's left flank. Due to missing data, sample sizes were $N = 9$–14 for males and $N = 6$–9 for females.
*Significant after Holm–Bonferroni correction for multiple tests. UV, ultraviolet.
OVS, outer ventral scales.

of some lacertid species also include UV reflection (Thorpe & Richard, 2001; Font & Molina-Borja, 2004; Hawlena *et al.*, 2006; Molina-Borja *et al.*, 2006; Pérez i de Lanuza & Font, 2007), although the present study comprises the first description of UV reflectance in ocellated lizards.

The presence of UV reflectance in skin colour patches has recently taken on an added significance because it has become apparent that many lizards have visual systems adapted for vision in the near UV (UV-A) range, and are therefore able to detect wavelengths in a range of the spectrum to which humans are blind. Although lacertid colour vision is poorly known, valuable cues are available from the study of their ocular media. The range of wavelengths to which an animal is sensitive depends both on the spectral location of its visual pigments and on the wavelengths that impinge upon them (Ödeen & Hastad, 2003). The standard method used to determine the spectral tuning of photoreceptors is microspectrophotometry, which is a complex technique requiring highly specialized equipment. Examination of the light absorption properties of the ocular media is a simpler and less technically demanding method that can indicate the possibility of UV vision. Indeed, the transmission of ocular media below 400 nm is routinely used as a guide to potential UV sensitivity in fish (Losey *et al.*, 1999; Siebeck & Marshall, 2001; Siebeck, 2004). In ocellated lizards, transmittance of the ocular media (including lens and cornea) drops to 50% at a wavelength of 362.29 nm (range 353–384 nm, $N = 6$ eyes from three lizards; G. Pérez i de Lanuza & E. Font, unpubl. data). This is evidence that the eyes of ocellated lizards lack UV-blocking compounds and that UV wavelengths reach the photoreceptors located at the back of the eye and could thus be part of their colour vision system.

To a human observer, the eyespots of male ocellated lizards do not look different from those of females. However, the results obtained in the present study demonstrate that the eyespots and blue OVS are sexually dichromatic, particularly in the UV range. This suggests that ocellated lizards are more dichromatic (to themselves and to other animals capable of UV vision) than they appear to human observers. Despite major recent advances in the study of sexually dimorphic coloration in lizards (Wiens, Reeder & de Oca, 1999; Macedonia *et al.*, 2002, 2004), remarkably little is known about UV-based sexual dichromatism in this vertebrate group. Indeed, previous studies (Cooper & Greenberg, 1992) may have underestimated the extent of sexual dichromatism in lizards by not taking into account differences in the human-invisible UV part of the spectrum (Cuthill *et al.*, 1999; Eaton, 2005). The available evidence suggests the existence of at least three types of sexually dichromatic UV coloration in lacertid lizards alone. In some cases, the UV-reflecting colour patches are present only in males or are more abundant in males than in females. This is the case with the eyespots and blue OVS of many small lacertids. For example, males of *Psammodromus algirus* have more UV/blue eyespots than females (Salvador & Veiga, 2008) and, in *Podarcis muralis* from the Pyrenees, 92.3% of males have UV/blue OVS, whereas only 30.2% of females do (G. Pérez i de Lanuza & E. Font, unpubl. data). A second type of sexual dichromatism was recently described in *G. galloti* lizards from Tenerife (Molina-Borja *et al.*, 2006). In this species, male UV/blue lateral and ventrolateral patches reflect more intensely (higher brightness) than those of females (Molina-Borja *et al.*, 2006: fig. 2). Ocellated lizards illustrate yet another type of sexual dichromatism: in this case, the UV/blue eyespots of males and females have similar reflectance intensity, but those of males have their peak reflectance shifted 20–30 nm towards the UV end of the spectrum relative to those of females. Thus, sexual differences can result from differences in the number, size, hue and brightness of UV-reflecting patches. Further studies are required to elucidate the current and historical selective forces responsible for UV sexual dichromatism in lacertids and in other lizards.

What is (are) the function(s) of eyespots and blue OVS? The possibility most often invoked in studies of lizard coloration would assign them a signalling function in aggressive or sexual intraspecific interactions (Cooper & Greenberg, 1992). Some conspicuously coloured skin patches convey information regarding the species, sex or reproductive status of the signalling individual (Galán, 2000; Hager, 2001). There is also evidence that chromatic signals may be important for mate choice (Hamilton & Sullivan, 2005), or function as status-signalling badges of dominance, fighting ability, or aggressiveness (Olsson, 1994; Whiting *et al.*, 2003; Anderholm *et al.*, 2004). Selection for effective signalling often favours colour patterns that are conspicuous and signal theory predicts that the more a visual signal contrasts to its background or to other parts of the body, the more conspicuous it is (Endler, 1990). The UV/blue colour patches of ocellated lizards are liable to be highly conspicuous for three reasons. First, blue is chromatically conspicuous against the surrounding green–brown skin and, also, because few natural objects are blue, against the background vegetation and natural substrates that conform the signalling environment of ocellated lizards. Second, circular markings with a high contrast between the central region and its surround are highly effective in stimulating the centre-surround arrangement of receptive fields in the

vertebrate retina, and are therefore more conspicuous to the visual system of many potential vertebrate receptors than other types of markings (Stevens, 2005; Stevens *et al.*, 2007). Finally, the eyespots and blue OVS are highly UV-reflective, which will render them even more conspicuous when viewed against non-UV-reflecting backgrounds, at least to an animal capable of UV vision. The location of the UV/blue patches makes them particularly visible when displayed to conspecifics or terrestrial predators in lateral presentation with the body laterally compressed, and is thus consistent with a signalling function.

Where the sexes differ in coloration, conspicuous colour patches may play a role in sex recognition (Cooper & Burns, 1987; Cooper & Vitt, 1988). In the lacertid *G. galloti*, the sexually dichromatic UV/blue patches may function as cues that facilitate sex recognition (Molina-Borja *et al.*, 2006). Similarly, the eyespots and blue OVS of ocellated lizards could provide cues allowing recognition of the sex of conspecifics, particularly during interactions at close range or in darkened environments (e.g. burrows) where UV wavelengths would be particularly salient. On the other hand, where there is intrasexual variability in coloration, it has been suggested that these differences may convey information regarding some intrinsic characteristic of the signalling individual (e.g. age, dominance, fighting ability). There is evidence for a relationship between the size and/or spectral characteristics of colour patches and individual quality in lizards, although very little is known about the role of UV-reflectance in this relationship. In Augrabies flat lizards, *Platysaurus broadleyi*, the hue and intensity of the UV-reflecting throat are used to signal fighting ability during the assessment phase of male-male contests (Stapley & Whiting, 2006; Whiting *et al.*, 2006). In *G. galloti*, the total area covered by the UV/blue patches is larger in larger (i.e. heavier) males, and both body size and total area covered by the UV/blue patches are significant predictors of dominance and fighting ability (Huyghe *et al.*, 2005). The finding of the present study demonstrating that large (normally older) male ocellated lizards have larger eyespots and a larger total area of eyespots than small (normally younger) lizards suggests that these traits may function as cues to lizard size or age, and possibly also signal fighting ability. Clearly, more studies are necessary to unravel the complex relationships between UV chromatic signals, phenotypic quality, and fitness in lizards.

A rarely considered alternative regarding the function of eyespots and other conspicuous colour patterns is that they may function in interspecific encounters, conferring protection from predators (Cloudsley-Thompson, 1994). Possibly because eyespots are among the most conspicuous of all markings (Tinbergen, 1974), little consideration has been given to the possibility that they may serve a camouflage function (but see Osorio & Srinivasan, 1991; Stevens, 2005). However, high-contrast markings such as eyespots produce false edges that distract the potential predator by drawing the eye away from the body outline (disruptive coloration), or make estimates of the speed and trajectory of a moving prey difficult (dazzle coloration). Vertebrate visual systems encode edge information via sharp changes in light intensity. Stevens & Cuthill (2006) used visual modelling to show that an avian predator locates more edges corresponding to the outline of prey when prey are cryptic than when prey are disruptively coloured, especially when the disruptive markings were highly contrasting (but see Stevens *et al.*, 2008). This strategy is particularly effective when of the two colours contributing to the pattern one resembles the background, whereas the other contrasts strongly, as found in the blue eyespots of *L.* (*T.*) *lepida* and other lizards. Although resulting from different selection pressures, signalling and camouflage are not necessarily incompatible functions for the eyespots of ocellated lizards (Stevens, 2005).

Lizard colours are produced in two ways, either by pigments (e.g. carotenoids, pteridines, melanin) deposited in the skin or by the scattering of light in nanoscale microstructures present in the skin (structural colours). Structural colours include UV, blue, some greens, and iridescent colorations. In birds, structural colours are produced by interference between light waves reflected from more or less regularly spaced refractive index boundaries in the medullary spongy layer of feather barbs (Prum, 2006). Similarly, in lizards, shortwave reflectance (including blue and UV/blue coloration) is produced by the reflectance of short wavelengths of light by regularly spaced reflecting platelets (guanine crystals) present in the iridophore layer of the dermis and the absorption of other wavelengths by an underlying melanin layer (Morrison, Rand & Frost-Mason, 1995; Quinn & Hews, 2003). Although structural colours are widespread in vertebrates, most studies relating colour variation to individual quality have concerned themselves with carotenoid-based pigment colours, where the mechanisms of colour variation and condition dependency are better understood (Andersson *et al.*, 2002; Pryke *et al.*, 2002; Blount & McGraw, 2008). It has even been argued that, in comparison with pigmentary colours, structural colours are cheap to produce and are therefore good candidates for a role as arbitrary Fisherian ornaments, which, by definition, provide no information about individual quality (Bradbury and Vehrencamp, 1998). Although this may be true in some cases, the available evidence suggests

that structural colours can also act as condition-dependent indicators of male quality (birds: Keyser & Hill, 2000; Örnborg *et al.*, 2002; Griffith *et al.*, 2003; Siitari *et al.*, 2007; lizards: see above). Indeed, it has been suggested that UV/blue feather coloration in birds might indicate 'developmental stability', and thus be a condition-dependent trait of individual quality (Andersson, 2000; Örnborg *et al.*, 2002). It is possible that, owing to their dependence on a regular arrangement of nanostructures, lizard structural colours might likewise function as condition-dependent traits honestly providing information about male condition, viability, or parasite load. Our finding that the blue patches of ocellated lizard are UV-reflecting, sexually dichromatic, and may convey information regarding individual quality, hints that structural coloration in lacertids may be of communicative importance in previously unsuspected ways and opens up a fruitful avenue for future studies.

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