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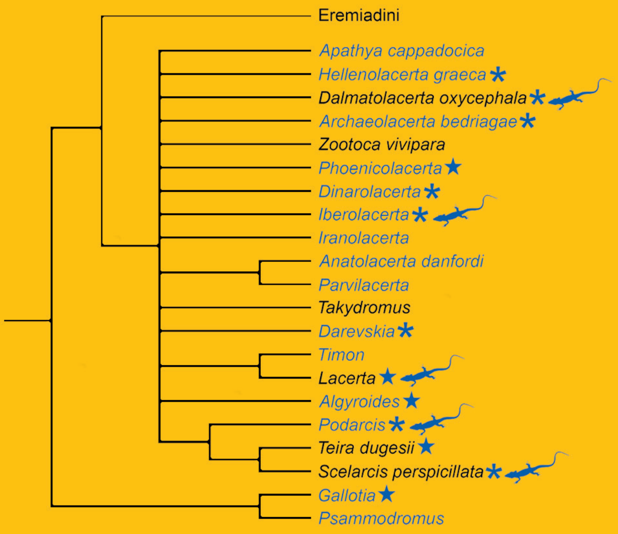

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Lizard blues: blue body colouration and ultraviolet polychromatism in lacertids

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Abstract: Understanding the evolution of conspicuous colour patterns has been a major challenge in evolutionary biology since Darwin's formulation of natural and sexual selection 150 years ago. A striking case of conspicuous colouration is the structural blue colour found in lizards belonging to several families, including lacertids (Lacertidae). Blue colouration can be restricted to discrete patches, as those found in the flanks or head of many lacertids, or can extend over large areas of the integument as in several insular populations of Lacertini. Recent research has shown that the blue flank and head patches of many lacertids have their peak of reflectance in the ultraviolet (UV) range. It has been suggested that these UV-blue patches may be part of a private (i.e. available only to receptors with UV vision) communication system. In contrast, nothing is known about the spectral characteristics of those species in which all or large portions of the body surface are blue.

Using objective methods of colour measurement and analysis, we studied the spectral characteristics of blue colouration in *Podarcis lilfordi kuligae* and compared them with those from other blue lacertids. The ventral surface and flank patches of *P. lilfordi kuligae* are both UV-blue, but their spectral shape is strikingly different, possibly reflecting different underlying selective pressures and colour production mechanisms. To our knowledge, this is the first recorded case of polychromatism in the UV part of the electromagnetic spectrum. Our results show that a wide range of spectrally different colourations belie human-perceived blues in lacertids. We analyse visual interactions among lizard colours and habitat natural backgrounds and propose some hypothesis for the evolution of lizard blue and UV-blue colourations.

Key words: conspicuousness, colour, colour space, *Podarcis*, UV.

Resumen: **El azul de los lagartos: coloración corporal azul y policromatismo ultravioleta en lacértidos.** – Comprender la evolución de los patrones conspicuos de coloración ha sido un importante reto para la biología evolutiva desde que Darwin propusiera los procesos de selección natural y selección sexual hace 150 años. Un caso sorprendente de coloración llamativa es la coloración azul que está presente en lagartos de varias familias, incluyendo los lacértidos (Lacertidae). La coloración azul puede estar restringida a manchas discretas, presentes en los flancos o en la cabeza de muchos lacértidos, o puede extenderse sobre grandes áreas del integumento, como en algunas poblaciones insulares de Lacertini. Estudios recientes han demostrado que los flancos y las cabezas azules de muchos lacértidos tienen su pico de reflectancia en el rango ultravioleta (UV). Se ha sugerido que estas manchas UV-azul pueden formar parte de un sistema de comunicación privado (i.e. accesible solo a receptores con visión UV). Por el contrario, no se conoce nada sobre las características espectrales de aquellas especies en las que todo el cuerpo o porciones grandes de éste son azules.

Mediante el uso de métodos objetivos de medición y análisis del color, hemos estudiado las características espectrales de la coloración azul en *Podarcis lilfordi kuligae* y las hemos comparado con las de otros lacértidos azules. La superficie ventral y de los flancos de *P. lilfordi kuligae* son UV-azul, pero la forma de sus espectros es muy diferente, posiblemente debido a diferencias en las presiones selectivas y en los mecanismos de producción del color en las diferentes partes del cuerpo. Por lo que sabemos, éste es el primer registro de un policromatismo en la parte UV del espectro electromagnético. Nuestros resultados demuestran que los azules percibidos por los humanos en los lacértidos incluyen en realidad una amplia gama de coloraciones espectralmente diferentes. Hemos analizado las interacciones entre las coloraciones de los lagartos y las de los fondos naturales que habitan y proponemos algunas hipótesis para la evolución de las coloraciones azules y UV-azul de los lagartos.

Palabras clave: conspicuidad, color, espacio cromático, *Podarcis*, UV.

INTRODUCTION

Body colouration is an important source of signals used for species recognition, intrasexual communication, courtship, and mate choice (Burtt, 1979). Although vertebrates exhibit every known colour, blue colourations are relatively infrequent among reptiles and amphibians (Bagnara *et al.*, 2007). However, some squamates display striking blue colourations that extend over all or large portions of their body [for a particularly dramatic example, see Photo 3 in Macedonia *et al.*'s (2009) supporting material]. Blue-bodied lizards have been reported in the families Agamidae (e.g. *Acanthocerus atricollis*), Crotaphytidae (e.g. *Crotaphytus dickersonae*), Polychrotidae (e.g. *Anolis gorgonae*), Gekkonidae (e.g. *Lygodactylus williamsi*), Teiidae (e.g. *Cnemidophorus lemniscatus*), Lacertidae (e.g. *Podarcis sicula caerulea*), and also in snakes (e.g. *Calliophis bivirgatus*).

Many lacertid lizards are not blue overall, but instead possess discrete blue patches in the flanks or head region. Even relatively small blue patches are usually very conspicuous, as they tend to provide a striking chromatic contrast with the surrounding body colouration, which very often consists of several shades of green and brown in dorsolateral surfaces, and white, pink, yellow or orange in the ventrolateral surfaces (Pérez i de Lanuza & Font, 2005). In most species of the subfamily Gallotinae and the tribe Lacertini, blue patches are located in the outer ventral scales (OVS, at the boundary between the lizard's ventral and lateral surfaces) and/or in eyespots (ocelli) in the shoulder region or flanks (Arnold, 1989; Arnold & Ovenden, 2002; Arnold *et al.*, 2007). Blue throats and blue heads are also present in several species (e.g. *Algyroides nigropunctatus, Lacerta schreiberi*), and bright blue or bluish tails are common among juveniles in several genera (e.g. *Podarcis, Iberolacerta*, *Acanthodactylus*) (Arnold & Ovenden, 2002; Hawlena, 2009) (Fig. 1).

Recent research has revealed that many of the blue patches located in the flanks or in the head of lacertid lizards have their maximum reflectance below 400 nm, and are therefore best characterized as UV-blue patches (blue ocelli and/or OVS: Thorpe & Richard, 2001; Font & Molina-Borja, 2004; Pérez i de Lanuza & Font, 2005; Molina-Borja *et al.*, 2006; Font *et al.*, 2009; blue throats and heads: Thorpe & Richard, 2001; Font & Molina-Borja, 2004; Molina-Borja *et al.*, 2006; Martín & López, 2009; Bajer *et al.*, 2010; blue tails: Hawlena, 2009). UV reflectance has been the focus of intense study in birds and in fish, where it has been shown to be important for communication (Bennett & Cuthill, 1994; Bennett *et al.*, 1994, 1996, 1997; Andersson *et al.*, 1998; Cuthill *et al.*, 2000a; Macías García & Burt de Perera, 2002; Siitari *et al.*, 2002, 2007; Smith *et al.*, 2002; Cummings *et al.*, 2003; Losey, 2003; Siebeck *et al.*, 2006;

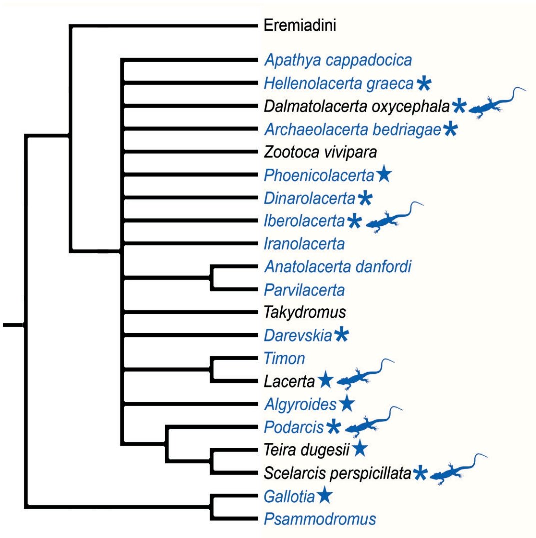

FIGURE 1. Phylogenetic distribution of blue colourations present in Gallotiinae and Lacertini genera. For clarity, Eremiadini are presented grouped because only a few species present blue colourations. Names in blue indicate genera with the common colour pattern of Gallotiinae and Lacertini (UV-blue ocelli and/or OVS). Blue stars indicate other restricted UV-blue surfaces such as throats or heads. Blue asterisks indicate blue tails in juveniles (in some species also in adults). Blue lizards indicate genera in which at least some species or subspecies present a blue phenotype (with large blue surfaces). Phylogeny based in Arnold *et al.* (2007). Colour data based in Arnold & Ovenden (2002), Arnold *et al.* (2007), Corti & Lo Cascio (2002), Galán (2006, 2010), Bagnara *et al.* (2007), Arribas *et al.* (2008), Raia *et al.* (2010), and G. Pérez i de Lanuza, unpublished data.

FIGURA 1. Distribución filogenética de las coloraciones azules presentes en los géneros de Gallotiinae y Lacertini. Para simplificar, los géneros de Eremiadini se presentan agrupados porque solo algunas especies presentan coloraciones azules. Los nombres en azul indican los géneros con el patrón de coloración común de Gallotiinae y Lacertini (ocelos y/o OVS azul/UV). Las estrellas azules indican otras superficies azules como la gola o la cabeza. Los asteriscos azules indican las colas azules en los juveniles (y en algunas especies también en adultos). Los lagartos azules indican los géneros en los que como mínimo alguna especie o subespecie presenta un fenotipo azul (con grandes superficies azules). Filogenia basada en Arnold *et al.* (2007). Datos de color basados en Arnold & Ovenden (2002), Arnold *et al.* (2007), Corti & Lo Cascio (2002), Galán (2006, 2010), Bagnara *et al.* (2007), Arribas *et al.* (2008), Raia *et al.* (2010), y G. Pérez i de Lanuza, datos no publicados.

Partridge & Cuthill, 2010). In contrast, only a handful of studies have examined the function of UV reflectance in lizards. In the first report of UV colouration in lizards, Fleishman *et al.* (1993) described UV reflectance in the dewlaps of several *Anolis* species. Dewlap colouration, including UV reflectance, is crucial for intraspecific signalling and species recognition (Nicholson *et al.*, 2007). The communicative function of UV-reflectance in skin patches from other species of lizards has also been established (Lappin *et al.*, 2006; Stapley & Whiting, 2006; Whiting *et al.*, 2006; Bajer *et al.*, 2010).

Several lines of evidence suggest that the discrete UV-blue flank patches of lacertid lizards may likewise function as communicative signals. First, in most species the UV-blue patches are present only in males, or are larger or more abundant in males than in females (Font & Molina-Borja, 2004; Pérez i de Lanuza & Font, 2005; Molina-Borja *et al.*, 2006; Arnold *et al.*, 2007; Font *et al.*, 2009). Sexual dichromatism is often thought to result from intense sexual selection, and suggests a function for the UV-blue patches as ornaments or traits used in male-male competition. Second, UV-blue patches are normally concealed due to their location, but they are exposed during social interactions, in which particularly the males raise over their four limbs with the abdomen compressed laterally and display to receivers. Finally, the available data suggest that many lacertids are capable of UV vision, and can therefore perceive the UV reflectance of UV-blue patches, which is a requisite for their role as communicative signals (Font *et al.*, 2007).

The colour pattern described above corresponds to lacertid species in which the blue (UV-blue) colouration is restricted to discrete body regions (flanks, gular area, tail), but there are also well-known cases of lacertids in which the blue colouration extends over large portions of the integument, even covering the entire body surface (ARNOLD & OVENDEN, 2002; CORTI & LO CASCIO, 2002; GALÁN, 2006, 2010; ARRIBAS *et al*., 2008; FULGIONE *et al*., 2008). Overall, blue body colouration is favoured by dermal melanisation (BAGNARA *et al.,* 2007) and seems particularly common in lacertids living on islands (BAUWENS & CASTILLA, 1998; CORTI & LO CASCIO, 2002; RAIA *et al*., 2010). Although blue-bodied lacertids have evoked lots of interpretations (reviewed in FULGIONE *et al*., 2008), surprisingly few empirical studies have been conducted and objective measurements and analyses of their blue colouration are entirely lacking.

The aim of this study is to quantitatively describe the spectral characteristics of body colouration in a blue-bodied subspecies of Lilford's wall lizard, *Podarcis lilfordi*, living on a small island off the coast of Mallorca (Balearic Islands). We focused on *P. lilfordi* because blue-bodied populations and populations with the common Lacertini colour pattern (reddish or whitish undersides and UV-blue OVS) are found on neighbouring islands. For comparative purposes, we also present data on the spectral reflectance of other blue-bodied lacertids. In order to determine whether the blue body colouration has any reflectance below 400 nm, we included the near UV spectrum in our analyses. A second aim of the study is to use visual modelling to evaluate the conspicuousness of the blue colouration from the perspective of the visual system of a lizard and to explore the consequences of the blue colouration in terms of the selective pressures associated to conspicuous colourations (FLEISHMAN *et al*., 1997; QUINN & HEWS, 2000, 2003; FLEISHMAN & PERSONS, 2001; MACEDONIA *et al*., 2004, 2009; HUSAK *et al*., 2006).

MATERIALS AND METHODS

Study species and data collection

We studied body colouration in two representative populations-subspecies of *P. lilfordi*. *P. lilfordi kuligae*, from Illa Gran of Cabrera archipelago, has a variable dorsal black or dark green colouration and ventral and ventrolateral surfaces are a deep cobalt blue (Fig. 2b, d, f). In most animals, a human observer can discriminate two distinct blue tonalities corresponding to the OVS, and to the ventrum and throat. *P. lilfordi gigliolii*, from Dragonera Island, exhibits the typical colour pattern of small/medium-sized Lacertini (i.e. excluding *Lacerta* and *Timon*): brown or green dorsum, blue OVS and intense orange belly and throat (Fig. 2a, c, e). *P. lilfordi gigliolii* belongs to the basal group of *P. lilfordi* from Mallorca (BROWN *et al*., 2008; TERRASA *et al*., 2008), and is probably the sister taxon of the extinct subspecies from Mallorca Island (Illa Major of Mallorca). We captured and obtained data from 24 adult females and 24 adult males of *P. lilfordi kuligae* and 20 adult females and 21 adult males of *P. lilfordi gigliolii* during April 2007.

We also include data on other blue lacertids to evaluate the generality of the spectral features observed in *P. lilfordi kuligae*. In April 2007 we obtained colour data from 20 adult males and 20 adult females of *Podarcis pityusensis*, the sister species of *P. lilfordi*. We chose the subspecies *P. pityusensis formenterae*, from Formentera Island (Pityuse Islands), which shows bluish reflections on the flanks. We also include data from two adult males and two adult females of *Dalmatolacerta oxycephala* from Dubrovnik city (April 2003) and two adult blue males of *Scelarcis perspicillata chabanaudi* from the Jbel Tazzeca mountains (April 2004). The latter two species have a highly reflective metallic blue ventrum, different from the

FIGURE 2. (a) Male of *P. lilfordi gigliolii*. (b) Male of *P. lilfordi kuligae*. (c) OVS of *P. lilfordi gigliolii*. (d) OVS of *P. lilfordi kuligae*. (e) Ventral colouration of *P. lilfordi gigliolii* (female above, male below). (f) Ventral colouration of *P. lilfordi kuligae* (female above, male below).

FIGURA 2. (a) Macho de *P. lilfordi gigliolii*. (b) Macho de *P. lilfordi kuligae*. (c) OVS de *P. lilfordi gigliolii*. (d) OVS de *P. lilfordi kuligae*. (e) Coloración ventral de *P. lilfordi gigliolii* (hembra arriba, macho abajo). (f) Coloración ventral de *P. lilfordi kuligae* (hembra arriba, macho abajo).

colouration of the blue flank patches (UV-blue ocelli or OVS) present in other Lacertini. All the lizards were captured using a noose of silk thread affixed to the end of a fishing pole. Colour and morphometric measurements were taken immediately after capture, and the lizards were subsequently returned to the field unharmed.

Reflectance spectrophotometry

We used a standard protocol for the measurement of reflectance spectrophotometry (see MOLINA-BORJA *et al*., 2006; PÉREZ I DE LANUZA & FONT, 2007; FONT *et al*., 2009). Briefly, we used a USB2000 portable spectrometer and a PX-2 Xenon strobe lamp (Ocean Optics Inc., Dunedin, FL, USA) that provides full-spectrum lighting (220-750 nm). Recorded spectra were relative to a white standard (Labsphere, North Sutton, NH, USA), and were taken at a 90º angle and at a constant distance of 5 mm to the lizard's body surface. We obtained spectrophotometric measurements (average of 20 spectra) from the head (pileum), dorsum, throat, belly (ventrum), and two UV-blue OVS from each flank of each lizard. The same methods were used to measure the reflectance of common natural backgrounds (i.e. limestone) in the habitats of both *P. lilfordi* populations. Analyses were restricted to the 300-700 nm range, which encompasses the visual spectrum of diurnal lizards (Fleishman *et al*., 1993, 1997; Ellingson *et al*., 1995; Loew *et al*., 2002; Bowmaker *et al*., 2005; Macedonia *et al*., 2009). Not all individuals contributed to all the spectrophotometric measurements: in *P. lilfordi*, some individuals from both sexes had whitish or pinkish ventral surfaces, and in *P. pityusensis formenterae* only a fraction of the individuals included in the sample had bluish flanks.

Colour and contrast analyses

In order to objectively describe the colours present in *P. lilfordi*, *P. pityusensis formenterae*, *D. oxycephala*, and *S. perspicillata chabanaudi*, for each spectrum we used the position of the peak of maximum reflectance (λmax) as a measure of hue, and its corresponding reflectance (%max) as a measure of intensity (i.e. brightness). Because in *P. lilfordi* and *P. pityusensis formenterae* all the UV-blue OVS showed a similar spectral shape, we restricted analyses to the second UV-blue OVS in the right flank as this OVS is easily identifiable, usually larger than other OVS (hence more easily measured), and is present in all the sampled individuals. For similar reasons, in *D. oxycephala* and *S. perspicillata chabanaudi* measurements were restricted to the scale located in the middle of the right flank.

To evaluate conspicuousness and crypsis we used the methods developed by Schultz (2001) and modified by Macedonia *et al.* (2004). These methods compare spectra in pairs and give two different but complementary quantitative measures of contrast for each pair. The first measure is colour contrast (CC, dependent on spectral shape but intensity-independent). The second is intensity contrast (IC, a quantification of the amount of reflected light independent of spectral shape or peak location). In both cases, the largest absolute values represent the most contrasted (i.e. conspicuous) colour pattern. We calculated CC and IC for the following colour pairs: 1) OVS vs limestone, 2) ventrum vs limestone, and 3) OVS vs ventrum. The first two comparisons provide an estimate of the crypsis/conspicuousness generated by the lizard colours viewed against the natural background. The third comparison represents a measurement of intra-individual (intra-body) contrast.

Additionally, we obtained a global colouration measurement by calculating the colour volume of each individual generated by plotting all its colour measurements in a three-dimensional colour space based on the lizards' visual sensitivity (Endler & Mielke, 2005). Colour volumes allow us to compare entire colour patterns among species or populations. Given the absence of data on spectral sensitivity in lacertids, we calculated colour volumes using data from the visual system of *Platysaurus broadleyi* (Fleishman *et al*., 2011), the phylogenetically closest species with available data. The sensitivity of the four cone types in the retina of *P. broadleyi* was used to calculate the four values of relative stimulation for each reflectance spectrum (Goldsmith, 1990). Then, using Endler & Mielke's (2005) equations, these values were transformed to colour points, described by three Cartesian coordinates X, Y, Z in a three-dimensional tetrahedral colour space. The central point of the tetrahedron ($X = Y = Z = 0$) depicts equal stimulation of the four cones and represents the achromatic point. All the stimuli that imply differences in the stimulation of at least one of the four types of cone are represented with positions displaced in one or more axes from the achromatic point. The complete set of colour points from all the spectra of each individual was plotted together to calculate the minimum convex polygon described by STODDARD & PRUM (2008) as a measure of individual colour volume. Following STODDARD & PRUM (2008) ambient light was obviated. Data were processed with TetraColorSpace (STODDARD & PRUM, 2008) using Matlab 7.

Statistical analyses

Differences in peak location, intensity, CC, IC and colour volumes between sexes and populations were tested statistically. We tested for normality using the Shapiro-Wilk test, followed by a single factor ANOVA when normality could be safely assumed. Log-transformation did not solve the lack of normality in the remaining cases, so Mann-Whitney tests were used. p values reflect two-tailed tests.

RESULTS

Representative reflectance spectra from *P. lilfordi* are shown in Figs. 3 and 4. Table 1 shows descriptive statistics for peak location and intensity. The ventral blue surfaces of *P. lilfordi kuligae* have a reflectance peak around 390 nm in both males and females and are thus UV-blue. However, comparisons of OVS and ventrum, both UV-blue, show differences in their spectral shape. Peak reflectance of the UV-blue OVS is located at shorter wavelengths and is more intensely reflective than that of the UV-blue ventral surfaces. Reflectance spectra of the UV-blue OVS of the two *P. lilfordi* subspecies are very similar with only slight variations in peak location for males (Tables 1 and 2).

Spectra from the blue surfaces of the other species sampled are different from those of

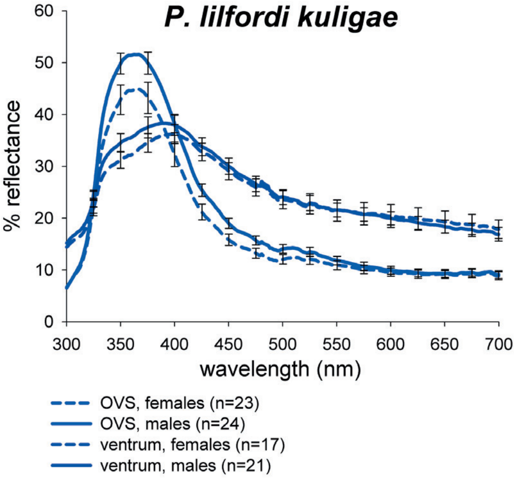

FIGURE 3. Reflectance spectra from males and females of *P. lilfordi kuligae*. Vertical lines: error bars (± 1 SEM).
FIGURA 3. Espectros de reflectancia de machos y hembras de *P. lilfordi kuligae*. Líneas verticales: barras de error (± 1 SEM).

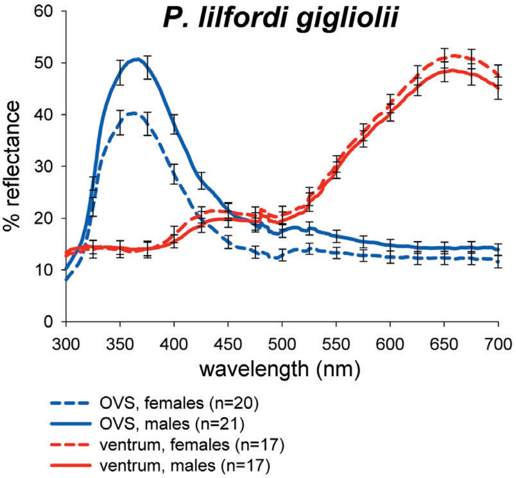

FIGURE 4. Reflectance spectra from males and females of *P. lilfordi gigliolii*. Vertical lines: error bars (± 1 SEM).
FIGURA 4. Espectros de reflectancia de machos y hembras de *P. lilfordi gigliolii*. Líneas verticales: barras de error (± 1 SEM).

Table 1. Values (mean ± 1 SEM) of hue (λmax) and intensity (%max) for *P. lilfordi gigliolii* and *P. lilfordi kuligae*.
Tabla 1. Valores (media ± 1 SEM) de tonalidad (λmax) y brillo (%max) de *P. lilfordi gigliolii* y *P. lilfordi kuligae*.

		Ventrum		UV-blue OVS	
		λmax (nm)	%max	λmax (nm)	%max
P. lilfordi gigliolii	♀♀	661.31 ± 4.47	52.22 ± 1.90	362.88 ± 1.76	40.88 ± 2.36
	♂♂	658.13 ± 3.53	48.90 ± 2.39	366.33 ± 1.58	51.10 ± 2.42
P. lilfordi kuligae	♀♀	397.12 ± 3.13	36.66 ± 2.25	363.20 ± 1.70	45.33 ± 3.06
	♂♂	396.45 ± 7.05	38.31 ± 2.41	362.76 ± 1.65	53.01 ± 2.41

P. lilfordi. Only the UV-blue OVS of *P. pityusensis formenterae* have a single peak of reflectance in the UV range (λmax = 366.58 ± 1.55 nm for females and 370.16 ± 1.57 nm for males; Fig. 5) similar to the typical UV-blue OVS of small/medium-sized Lacertini. The blue flanks of this subspecies have peak reflectance at λmax = 546.13 ± 5.16 nm (females) and 530.3 ± 2.36 nm (males), with very little UV reflectance (Fig. 5). In *D. oxycephala*, Arnold *et al.* (2007) suggested that the ventral colouration would mask the UV-blue OVS. Spectra show that both surfaces, ventrum and OVS, are indeed indistinguishable and their spectral shape is different from that of the UV-blue OVS of other small/medium-sized Lacertini. In fact, the blue colouration of *D. oxycephala* has two distinct peaks of reflectance: the main (i.e., more reflective) peak is located between 620 and 665 nm whereas the secondary peak is located between 340 and 350 nm (Fig. 6). Although the blue colouration of *S. perspicillata chabanaudi* looks to us very similar to that of *D. oxycephala*, it has a single peak of reflectance around 539 nm and reflects very little at short and long wavelengths (Fig. 6).

In *P. lilfordi gigliolii,* the combination of orange ventrum and UV-blue OVS provides more chromatic contrast than in *P. lilfordi kuligae*, but the chromatic contrast generated between the ventrum and the natural background is larger in *P. lilfordi kuligae* (Table 3). Contrasts between UV-blue OVS and the natural background are similar in females of both subspecies, but not in males (Table 3).

Colour volumes are similar in the two subspecies of *P. lilfordi* (females: *P. lilfordi*

Table 2. Statistics of comparisons of hue (λmax) and intensity (%max) from *P. lilfordi gigliolii* and *P. lilfordi kuligae*. n.s. = non-significant result.
Tabla 2. Estadísticos de las comparaciones de interés para la tonalidad (λmax) y el brillo (%max) de *P. lilfordi gigliolii* y *P. lilfordi kuligae*. n.s. = resultado no significativo.

		P. lilfordi kuligae ventrum		*P. lilfordi gigliolii* UV-blue OVS	
		♀♀	♂♂	♀♀	♂♂
λmax	*P. lilfordi kuligae* UV-blue OVS	Z = –5.22 p < 0.001	Z = –5.35 p < 0.001	Z = –0.04 n.s.	Z = –2.16 p = 0.03
%max	*P. lilfordi kuligae* UV-blue OVS	F = 4.56 p = 0.04	F = 17.36 p < 0.001	F = 1.27 n.s	F = 0.08 n.s.

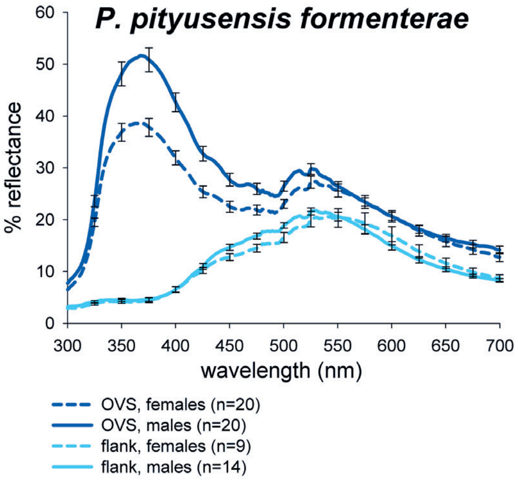

FIGURE 5. Reflectance spectra from males and females of *P. pityusensis formenterae*. Vertical lines: error bars (± 1 SEM).

FIGURA 5. Espectros de reflectancia de machos y hembras de *P. pityusensis formenterae*. Líneas verticales: barras de error (± 1 SEM).

gigliolii = 0.22 ± 0.04, *P. lilfordi kuligae* = 0.19 ± 0.03, Z = –0.581, n.s.; males: *P. lilfordi gigliolii* = 0.13 ± 0.03, *P. lilfordi kuligae* = 0.18 ± 0.03, Z = –0.470, n.s.). However, their location in tetrahedron space differs (Fig. 7). Our data also indicate that *P. lilfordi gigliolii* are sexually dichromatic: females have the peak of reflectance of their OVS at shorter wavelengths ($F_{1,39} = 9.147$, $p < 0.01$) and their colour volume is larger (Z = –2.045, $p < 0.05$) than in males. Other comparisons were not statistically significant.

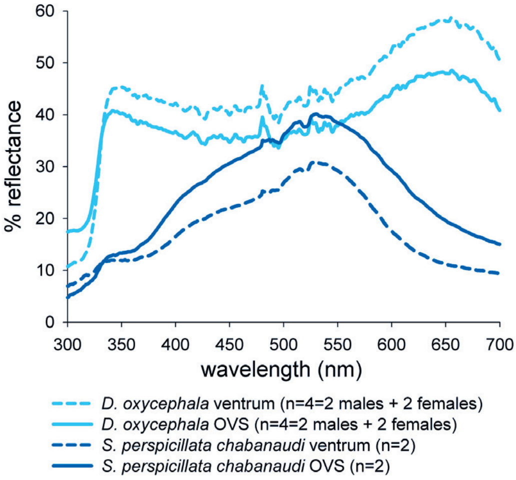

FIGURE 6. Reflectance spectra from males and females of *D. oxycephala* and males of *S. perspicillata chabanaudi*. Because males and females of *D. oxycephala* have similar spectra, we present them together. Error bars are not shown.

FIGURA 6. Espectros de reflectancia de machos y hembras de *D. oxycephala* y *de machos de S. perspicillata chabanaudi*. Como los espectros de *D. oxycephala* son similares para machos y hembras, los hemos representado conjuntamente. No se muestran la barras de error.

TABLE 3. Values (mean ± 1 SEM) of colour contrast (CC) and intensity contrast (IC) for *P. lilfordi gigliolii* and *P. lilfordi kuligae* and their statistics. n.s. = non-significant result.

TABLA 3. Valores (media ± 1 SEM) de contraste cromático (CC) y contraste de intensidad (IC) de *P. lilfordi gigliolii* y *P. lilfordi kuligae* y los estadísticos respectivos. n.s. = resultado no significativo.

			UV-blue OVS vs ventrum		**UV-blue OVS vs background**		**ventrum vs background**	
♀♀	**CC**	***P. l. gigliolii***	34.89 ± 2.08	Z = –3.87	38.35 ± 1.55	Z = –1.25	7.30 ± 0.78	Z = –5.59
		P. l. kuligae	21.28 ± 1.94	p < 0.001	40.93 ± 1.25	n.s.	24.96 ± 1.25	p < 0.001
	IC	***P. l. gigliolii***	–0.25 ± 0.04	Z = –0.90	0.02 ± 0.03	Z = –0.97	0.27 ± 0.02	Z = –1.70
		P. l. kuligae	–0.21 ± 0.04	n.s.	–0.03 ± 0.03	n.s.	0.19 ± 0.03	n.s.
♂♂	**CC**	***P. l. gigliolii***	36.5 ± 2.15	Z = –4.73	39.70 ± 1.38	Z = –1.98	8.87 ± 1.88	Z = –5.19
		P. l. kuligae	19.60 ± 1.69	p < 0.001	43.32 ± 1.35	p = 0.05	28.60 ± 1.04	p < 0.001
	IC	***P. l. gigliolii***	–0.12 ± 0.03	Z = –0.07	0.14 ± 0.03	Z = –3.03	0.24 ± 0.03	Z = –2.07
		P. l. kuligae	–0.12 ± 0.03	n.s.	0.05 ± 0.02	p = 0.02	0.17 ± 0.03	p = 0.04

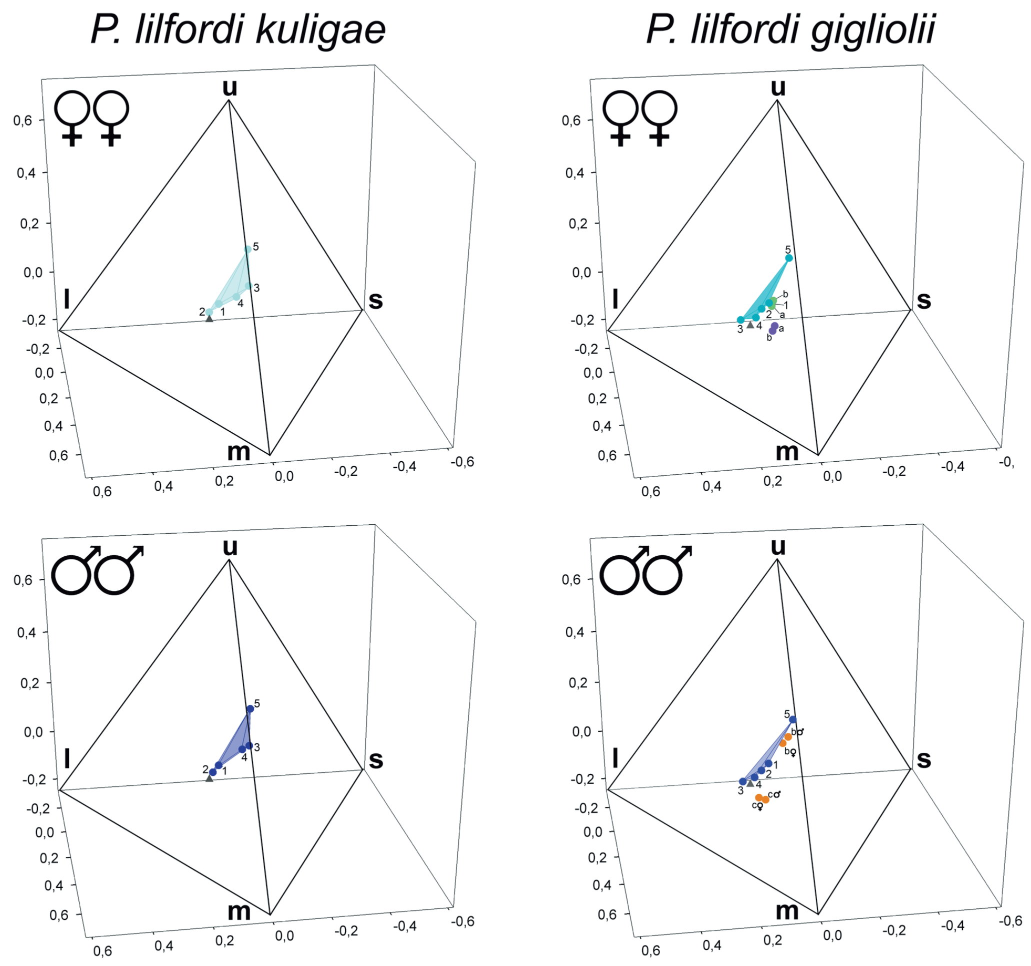

Figure 7. Colour volumes of *P. lilfordi kuligae* and *P. lilfordi gigliolii*. u, s, m and l represent the cones sensitive to UV, short, medium and long wavelengths, respectively. Vertices of the tetrahedron represent the perception of hypothetical spectra that cause maximum stimulation of only one of cone type and do not stimulate other cones (e.g. vertex u: stimulation of the u cone = 1, stimulation of the s cone = stimulation of the m cone = stimulation of the l cone = 0). Blue dots represent the position of colour points: 1 = pileum, 2 = dorsum, 3 = throat, 4 = ventrum, 5 = UV-blue OVS (e.g. in females of *P. lilfordi gigliolii*, the position of the pileum is given by the following values of stimulation: u = 0.2317, s = 0.234, m = 0.2462, l = 0.2881, that are represented in the tetrahedral colour space with the following Cartesian coordinates: X = 0.0331, Y = –0.0105, Z = –0.0183). Coloured areas delimited by colour points represent the colour volume. Orange, green and purple dots represent respectively *P. pityusensis formenterae*, *S. perspicillata chabanaudi* and *D. oxycephala* colour points, a = ventrum, b = OVS, c = flank.

Figura 7. Volúmenes cromáticos de *P. lilfordi kuligae* y *P. lilfordi gigliolii*. u, s, m y l representan respectivamente los conos sensibles a las longitudes de onda UV, corta, media y larga. Los vértices del tetraedro representan la percepción de espectros hipotéticos que provocan la estimulación máxima de únicamente un tipo de cono y no estimulan el resto (e.g. vértice u: estimulación del cono u = 1, estimulación del cono s = estimulación del cono m = estimulación del cono l = 0). Los puntos azules representan la posición de los puntos cromáticos: 1 = píleo, 2 = dorso, 3 = gola, 4 = vientre, 5 = OVS UV-azul (e.g. en hembras de *P. lilfordi gigliolii*, la posición del píleo viene dada por los siguientes valores de estimulación: u = 0.2317, s = 0.234, m = 0.2462, l = 0.2881, que son representados en el espacio cromático tetraédrico por las siguientes coordenadas cartesianas: X = 0.0331, Y = –0.0105, Z = –0.0183). El área coloreada delimitada por los puntos cromáticos representa el volumen cromático. Los puntos naranja, verdes y morados representan respectivamente los puntos cromáticos de *P. pityusensis formenterae*, *S. perspicillata chabanaudi* y *D. oxycephala*, a = vientre, b = OVS, c = flanco.

DISCUSSION

Our results reveal previously unrecognized levels of complexity in blue colourations, at least in lacertids, and caution against hasty generalizations. Two main conclusions arise from this study. First, lacertids display a wide range of spectrally different blue colourations that are often indistinguishable to a human observer. Second, these different blue colourations have probably been shaped by different selective pressures.

Lizard blues

Colour characterizations based on human visual perception have been shown to be inadequate for studies with non-human species (BENNETT & CUTHILL, 1994; BENNETT *et al*., 1994; CUTHILL *et al*., 2000b; EATON, 2005). Herpetologists have often erred by assuming that colour perception in lizards is similar to our own, and therefore that skin patches that look similar to us will also look similar to the lizards. Given the large differences in visual perception between lizards and humans, this assumption is bound to be incorrect in most cases. Regarding human-perceived blues, lacertids possess at least three classes of spectrally distinct colourations: (1) UV-blue patches, characterized by a single peak in the near UV spectrum (UV-blue OVS of many *Podarcis* species and UV-blue underside colouration of *P. lilfordi kuligae*), (2) metallic blue surfaces, characterized by a main reflectance peak at long wavelengths and a secondary peak in the UV (*D. oxycephala*), and (3) blue non UV-reflective surfaces, with a single peak of reflectance around 540 nm (flanks of *P. pityusensis formenterae* and ventral surfaces of *T. perspicillata chabanaudi*). Thus, blue colourations in different locations or species differ in their spectral characteristics, and could potentially serve different functions or be the result of different selective regimes.

The reflectance spectra of UV-blue OVS of *P. lilfordi* and *P. pityusensis* are similar to those of other lacertid species (*Gallotia*, *Podarcis*, *Iberolacerta* and *Lacerta* (*Timon*); PÉREZ I DE LANUZA & FONT, 2005; FONT *et al*., 2009; G. Pérez i de Lanuza & E. Font, unpublished data). Given their widespread distribution and their presence in the basal Gallotinae, possession of UV-blue OVS appears to be the ancestral condition for lacertids. UV-blue OVS have been retained with similar characteristics in most genera, which suggests they may be under stabilizing selection, possibly because they play an important communicative function. In contrast, other blue colourations found in lacertids seem independent new characters that have evolved under particular conditions, such as insularity (BAUWENS & CASTILLA, 1998; CORTI & LO CASCIO, 2002; BAGNARA *et al.,* 2007; FULGIONE *et al*., 2008; RAIA *et al*., 2010).

Production of UV-reflectance and blue colourations in lacertid skin

Animal colours are produced either by pigments (e.g. carotenoids, pteridines, melanin), by the physical interaction of light with nanometre-scale structures found in the integument (structural colours), or by a combination of both (FOX & VEVERS, 1960). In lizards, colours are produced by the combined action (i.e. reflection and/or absorption) on incident light of three cromatophore types found in the uppermost layer of the dermis ('dermal chromatophore unit'; BAGNARA & HADLEY, 1973; COOPER & GREENBERG, 1992). Xantophores are located in the most external dermal layer and contain long-wavelength reflective pigments. Iridophores, located underneath the xantophores, contain arrays of reflective guanine platelets that produce structural colours through light scattering (MORRISON *et al*., 1995; HEWS & QUINN, 2003). Finally, melanophores, located deep in the dermis, have processes that extend over the iridophores and contain melanin that absorbs the wavelengths not reflected nor absorbed by the two most superficial layers. As blue and purely UV-reflecting pigments are unknown in the vertebrate integument (Bagnara *et al*., 2007), it is generally assumed that lizard blues and UV-blues are structural colourations.

Blue and UV-blue colourations of blue-bodied lacertids may result from changes in pigment concentration and/or modifications of iridophores in scales that normally show other colourations. Axanthic animals, in which the concentration of long-wavelength pigments in the xantophores is reduced, are often blue (Bagnara *et al*., 2007). Thus, for example, Arribas *et al*. (2008) reasonably speculate that a decrease of pigment concentration in the xantophores may be responsible for the blue colouration of some individuals of *Iberolacerta* populations. Work with *Sceloporus* lizards has revealed that blue colouration can also result from an increase of melanin in the dermal melanophores mediated by high testosterone levels (Hews & Quinn, 2003; Quinn & Hews, 2003). In fact, overall blue-body colouration is considered a form of melanism in lizards (Raia *et al*., 2010).

The most parsimonious explanation for the production of blue colourations in lacertids involves combined changes in xantophores and melanophores. In addition to long-wavelength pigments not being expressed in the xantophores of blue lizards, an increase in the number and/or melanin concentration in the melanophores (associated with sexual maturity and a corresponding increase in testosterone levels; Bauwens & Castilla, 1998) facilitates the absorption of all the wavelengths not reflected by the iridophores. According of this model, spectral differences among blue colourations in different locations or species could be caused by variation in the size and spatial arrangement of the guanine platelets in the iridophores and/or by variations in melanin concentration in the melanophores.

Blue-bodied lacertids: adaptation or by-product?

Sexual selection is thought to favour conspicuous colourations and ornamentation, particularly in males, while natural selection tends to favour cryptic colourations and reduced ornamentation (Bradbury & Vehrencamp, 1998). In lizards, the trade-off between natural and sexual selection often results in individuals that are relatively cryptic dorsally (presumably the part of the body most exposed to aerial and large terrestrial visually-guided predators), but that possess conspicuous lateral and ventrolateral colourations that may act as relatively private signals which are revealed to conspecifics via stereotyped displays during social interactions (e.g. Whiting *et al*., 2006). Consistent with their presumed role as social signals, blue colourations are often located in the flanks or in the gular area (e.g. Quinn & Hews, 2000; Molina-Borja *et al*., 2006; Font *et al*., 2009). An exception to this general pattern is provided by several species and subspecies in which all or large parts of the body are blue.

Explanations of the ultimate significance of overall blue-body colouration in lizards are controversial. The evolution of conspicuous colour patterns in island populations has been traditionally explained by a relaxation in predation pressure. Alternatively, Raia *et al*. (2010) suggest that blue colouration may be a non-adaptive by-product of selection for high activity levels in melanocortin receptors occurring under particular insular conditions (low and/or fluctuating population density). In contrast, the analysis of Macedonia *et al*. (2009), based on sensory ecology, suggests that the blue dorsum and flanks of coastal *Crotaphytus dickersonae* populations may have a cryptic function when the blue lizards are viewed against sky and sea backgrounds. In fact, the latter two hypotheses are not mutually exclusive as crypsis could have arisen as a secondary function (i.e. an exaptation) of a primary non-functional colouration.

Our analyses contribute new elements to the debate. If we restrict comparisons to the lacertid species analysed here, a cryptic function of blue colouration seems plausible only for the lateral bluish non UV-reflective colouration of *P. pityusensis formenterae* (similar to the dorsal and lateral blue of *C. dickersonae*). This hypothesis is not reasonable for the predominant UV-reflective colour pattern of *P. lilfordi kuligae* because the UV component of sky and sea radiance are relatively low (MACEDONIA *et al.*, 2009). Rather, the contrast generated by the UV-blue surfaces against natural backgrounds suggests the action of selection pressures for enhanced detectability (and potentially also signalling).

Implications for detectability and possible communicative function of the UV-blue colourations

The evolution and maintenance of stable communication systems demands reliable signals, i.e. that there is a correlation between variation in one or several signal features (e.g. intensity, hue, size of the colour patches, etc.) and some attribute of the sender or the environment that receivers benefit from knowing. It is this correlation that makes receiver responses to colour signals adaptive (SEARCY & NOWICKI, 2005). In birds, conspicuous structural colours have been shown to function as condition-dependent traits providing honest information about individual male quality (e.g. developmental stability), condition, viability, and parasite load (KEYSER & HILL, 1999; DOUCET & MONTGOMERIE, 2003; PETERS *et al.*, 2007; SHAWKEY *et al.*, 2007; SIITARI *et al.*, 2007). Lizard structural colours may function in a similar way due to their dependence on a regular arrangement of guanine platelets. In several species of *Sceloporus* lizards (Phrynosomatidae), ventrolateral blue patches act as social signals males address to females or to other males (COOPER & BURNS, 1987; QUINN & HEWS, 2000; HEWS & QUINN, 2003), and intrasexual aggressiveness correlates with the expression of the blue phenotype (HEWS & QUINN, 2003). Similarly, individual male quality seems related to UV-blue OVS reflectance in *Podarcis muralis*. In this species, darker and lower-chroma OVS are found in more robust males with massive heads (G. Pérez i de Lanuza & E. Font, unpublished data).

Highly contrasting colour patterns enhance the detectability of the signals and may facilitate their discriminability and memorability (BRADBURY & VEHRENCAMP, 1998; ROWE, 1999), while also allowing for the transmission of complex signals (BRADBURY & VEHRENCAMP, 1998; CANDOLIN, 2003; PARTAN & MARLER, 2005). In small/medium-sized Lacertini, the typical colour pattern combines very short wavelengths (i.e. UV-blue OVS) with long wavelengths (e.g. pink, yellow, orange), resulting in a highly contrasting colour pattern (PÉREZ I DE LANUZA & FONT, 2005). Compared with this general pattern, the UV-blue OVS of *P. lilfordi kuligae* are surrounded by UV-blue skin that provides relatively low chromatic and brightness contrast, which may cause a decrease in its signalling efficacy. However, comparisons of crypsis/conspicuousness between the two subspecies of *P. lilfordi* suggest that their colour patterns may be the result of a detectability trade-off.

While *P. lilfordi gigliolii* has higher intra-body conspicuousness than *P. lilfordi kuligae*, the large UV-blue surface present in *P. lilfordi kuligae* maximizes the chromatic contrast against natural backgrounds in which there are no other natural objects that reflect at these wavelengths (Uy & Endler, 2004).

Final remarks

We are far from understanding the evolution of lizard blue colourations, probably because they have multiple functions and evolutionary origins. In this study we present and discuss recent advances in our understanding of the evolution of these striking colouration patterns. Future efforts will focus on studying the influence of hormone levels on the expression of UV-blue colourations, and the behavioural consequences of these colour changes.

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