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ORIGINAL ARTICLE

Structural- and carotenoid-based throat colour patches in males of *Lacerta schreiberi* reflect different parasitic diseases

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Abstract Host species in populations under strong pressures from parasitic diseases may evolve ornaments to signal individual host quality to conspecifics. Colour ornaments in lizards result from the interaction of different layers in the skin. When inner layers of melanin and well-arranged iridophores are combined, UV-blue structural colouration results. On the other hand, when layers of erythrophores are densely loaded with carotenoids, a UV-yellow colouration is seen. The expression of carotenoid-based traits has been frequently studied in relation to parasite infections. However, few studies have explored the relationship between parasitic diseases and structural colouration. In this study, we investigated the expression of UV-blue and UV-yellow throat colour patches in males of *Lacerta schreiberi* in relation to infection by haemoparasites, ixodid ticks and intestinal nematodes. The brightness of the UV-yellow throat patch (a carotenoid-based ornament) was positively correlated with body condition and negatively correlated with the number of attached ticks, supporting Hamilton and Zuk's hypothesis. Additionally, individuals that passed nematode eggs in the faeces had UV-yellow throat patches with higher hue values (more greenish colouration). Strikingly, the individuals infected by haemoparasites of the genus *Schellackia* showed UV-blue throat patches (a melanin-based ornament) with higher values of both UV-blue chroma and hue (i.e., UV-biased throats) than did uninfected individuals, suggesting a key role for melanin in the nuptial colouration of this lizard species. Thus, the combined information from both UV-blue and UV-yellow throat patches may convey integrative information about individual quality in this lacertid species.

Significance statement

In this study, we present evidence that the striking throat colouration in males of the endemic Iberian green lizard is related to the presence or load of different parasites. The ornament is composed of one UV-yellow patch and one UV-blue patch, which were differentially related to the presence of different parasitic diseases in the individual hosts. These results suggest that different parasitic diseases may differentially constrain the expression of these colour patches. Moreover, the combined display of the two throat patches simultaneously may convey to conspecifics integrative information about the individual quality of the Iberian green lizard.

Keywords Hamilton and Zuk · Handicap · Lacertidae · Parasite · Reptile · Visual communication

Introduction

Intraspecific variation in several phenotypic traits, including specific behaviours and colouration of chromatic ornaments, may result from the interaction between the environment and genetic pleiotropic effects (Tokarz et al. 1998; Ducrest et al. 2008; Almasi et al. 2012; McLean et al. 2015). In this sense, sexual characters in lizards are influenced by both abiotic and biotic environmental factors, reflecting the ability of individuals to adapt to local conditions (Bajer et al. 2012; McLean et al. 2015).

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Parasitic diseases are one of the main examples of biotic selective pressures in nature since parasites produce cellular damage and consequently increase oxidative stress in their hosts (e.g. Atamna and Ginsburg 1997; Mougeot et al. 2009). The Hamilton and Zuk hypothesis (1982) proposed that animals *choose mates for genetic disease resistance by scrutiny of characters whose full expression is dependent on health and vigour*. Thus, individuals of the sex that competes for mating from a population subjected to parasitic diseases may be able to express their genetic quality in terms of resistance to those infections through several types of signals directed to different sensorial channels (Martín et al. 2007, 2008). Visual ornaments based on either pigments or structures present in the skin of lizards serve as honest signals acting as visual cues of individual quality to conspecifics (Bajer et al. 2010; Bajer et al. 2011; Molnár et al. 2013; Megía-Palma et al. 2016). Therefore, colour traits containing pigments (carotenoids and/or melanin) might honestly mirror an individual's ability to cope with the physiological trade-offs to which the bearer has been exposed. In addition, the increase in testosterone levels in the sex that competes for mating during the breeding season may be costly to the organism compromising their immune response (Belliure et al. 2004; Oppliger et al. 2004), rendering individuals more susceptible to parasites and likely favouring an oxidative environment in the organism (Alonso-Álvarez et al. 2007). Therefore, a combined effect of androgenic hormone levels and infection stress may impose a high oxidative imbalance on organisms during the breeding season (Salvador et al. 1996, 1997; Veiga et al. 1998; Mougeot et al. 2009).

The typical organization of the dermis of lizards from the basal layer to the dermal surface may include a layer of conjunctive tissue that reflects the full range of wavelengths in sunlight (Jacot et al. 2010; Olsson et al. 2013). Typically, over this basal layer, there is a layer of melanophores containing melanin, responsible for brown and black colours and that may reduce the total amount of light reflected by the skin (Grether et al. 2004). This pigment is endogenously produced and may be related to oxidative status in the melanophores of the skin (Galván and Solano 2009). Over this layer is one of iridophores containing crystals of guanine structured in platelets, which, depending on their arrangement and thickness, produce whitish (poorly organized platelets) or blue colouration (Saenko et al. 2013; Haisten et al. 2015). Finally, there is an outer layer of xanthophores/erythrophores that can contain a combination of pteridines and/or carotenoids (Olsson et al. 2013; Haisten et al. 2015). Pteridines are synthesized endogenously whereas carotenoids must be acquired from the diet (Olsson et al. 2013). Overall, these pigments primarily absorb light in short wavelengths (Grether et al. 2004; Olsson et al. 2013). Thus, visual ornaments in lizards are the result of the interference of light beams reflected and absorbed in different structures and pigments located in the dermis (Grether et al. 2004; Saenko et al. 2013).

The Schreiber's green lizard, *Lacerta schreiberi* (Squamata: Lacertidae), is one of the most colourful lizards in the Iberian Peninsula. The individuals of both sexes present a shiny green back, a bright UV-yellow throat (e.g. Martín and López 2009) and a belly with black dots. In addition, the males during the breeding season present a bright UV-blue head and throat (Fig. 1a). These colour patches in *L. schreiberi* are more conspicuous to conspecifics than to predators suggesting a role as intraspecific visual signals (Pérez i de Lanuza and Font 2014a). Specifically, the dominance status of males was negatively related to the brightness and positively related to the UV-blue chroma of the UV-blue throat patch (Martín and López 2009). In addition, the UV-blue chroma of the throat and the yellow chroma from the chest were negatively correlated to the inflammatory response of the skin in the face of an immune challenge, suggesting a trade-off between the expression of these colour traits and the immune response (Alonso-Álvarez et al. 2007; López et al. 2009). However, the UV-yellow patch on the chest was not correlated to the dominance status of the male lizards, although it may be under selection by female choice in this lizard species since males found guarding females in the field showed more saturated UV-yellow patches (Martín and López 2009).

A recent investigation stressed the common presence of within-body contrasted colour ornaments throughout the phylogeny of the lacertini (Pérez i de Lanuza and Font 2016), making relevant the study of complex ornaments in lacertid species and not just one colour patch. In addition, although in natural populations it is common to find several parasites infecting the same individual, studies on the negative effect that different parasitic diseases may impose on the physiology of melanin- and carotenoid-based ornaments are lacking (i.e., McGraw and Hill 2000; Fitze and Richner 2002).

Therefore, in this study, we investigated whether the UV-blue (mainly iridophores and melanin-based ornaments) or the UV-yellow (mainly iridophores and carotenoid-based ornaments) throat ornamentation of male Schreiber's green lizard reflect the parasitic diseases co-occurring in the population. We expected that individuals with lower infections would show brighter ornaments than severely infected lizards would (i.e., Hamilton and Zuk 1982).

Material and methods

Sampling lizards and parasites

During the mating season of 2012, 21 adult males of *L. schreiberi* were collected in a deciduous forest in Segovia, Spain (40.88814, −4.02827). We captured the lizards using a noose (a pole with a loop of string with a slipknot that

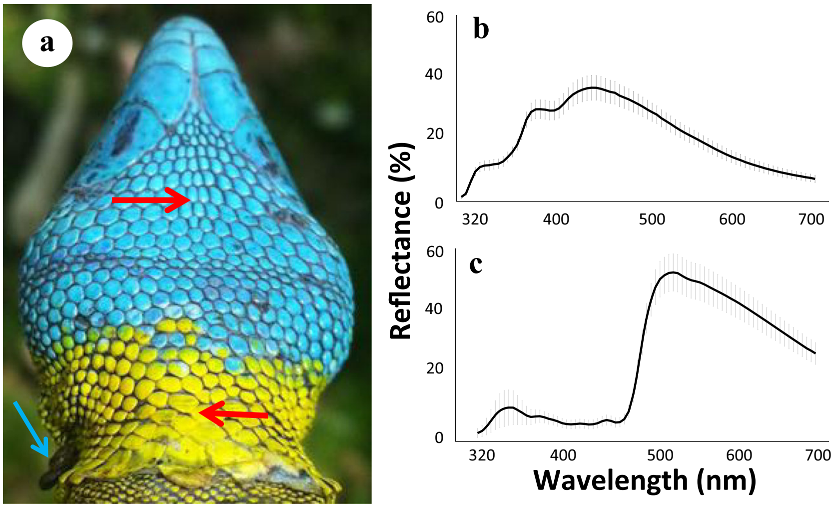

Fig. 1 **a** *Red arrows*: UV-blue and UV-yellow patches in the throat of male *Lacerta schreiberi*. *Blue arrow*: attached ixodid ticks next to the collar. Spectral data (mean ± standard error) from the UV-blue (**b**) and the UV-yellow (**c**) throat patches

tightens around the neck of the lizard). The snout-vent length (SVL) of each lizard was measured to the nearest millimetre with a ruler and they weighed to the nearest decigram with a digital balance. The individual age was estimated as the number of arrested lines (LAGs) in one phalanx obtained from each lizard using common techniques of skeletochronology (see the following subsection). Growth rate among individuals of the same age may influence the relationship between length and mass in lizards (see Halliday and Verrell 1988). Thus, to remove the effect of age on body condition index (BCI), we included, as a cofactor, the number of LAGs found in the phalanxes of individuals in the regression of the SVL on the weight (see Schall and Pearson 2000). We used the residuals of this analysis as the new variable of BCI. In addition, we counted the number of ticks attached to the lizards and recovered faecal and blood samples from the animals to examine the presence and absence of intestinal nematodes and blood protozoa, respectively. For this purpose, we made thin layer of blood smears from each lizard to survey for haemoparasites of the genus *Schellackia*, the main parasite found in the blood in this lizard population (see Megía-Palma et al. 2013). Smears were immediately air-dried and then fixed with methanol (Rogier and Landau 1975) and stained for 40 min with Giemsa diluted 1:10 in buffer, pH 7.2 (Schall 1986). We screened 15,000 red cells in each blood smear for infected blood cells to assign each lizard as infected or uninfected. In a previous study in this population, we obtained a 100 % correlation between molecular and microscopic prevalence of haemococcidia (Megía-Palma et al. 2013). We also screened faecal samples for intestinal nematodes, which are prevalent in this lizard species in the Sistema Central mountains (Roca et al. 1990). Faecal samples were obtained from each individual by briefly massaging their belly and were stored at 4 °C in 1.5-mL vials (Eppendorf Tubes® 3810X, Eppendorf Iberica, Madrid, Spain). Nematode eggs were concentrated by means of Sheather's sugar flotation technique (Dryden et al. 2005). We then screened the samples for nematodes at ×200 magnification. After approximately 15 min of manipulation, all the lizards were released and they behaved normally, running to hide. To minimize observer bias, blinded methods were used when all data concerning parasitic infection or colouration were recorded and/or analysed.

Ageing of the lizards

Ageing individuals by skeletochronology was proven to be a valid technique in the Schreiber's green lizard (i.e. Luís et al. 2003). Thus, to determine the age of each animal in this study, the second toe of the left hind limb of each lizard was clipped. Prior to clipping the toe, both the hand and the scissors used were disinfected with ethanol. After removing the toe, we pressed the hand for a few seconds with cotton to ensure it did not bleed. The clipped toes were stored at 4 °C in 10 % formalin prior to processing. The piled phalanxes were decalcified in 4 % nitric acid for 3–5 min and stained with Ehrlich's haematoxylin. The stained phalanxes were cut into 12-μm thick slices with a microtome (Microm HM-505 N Cryostat Microtome). The resulting slices were restained with Ehrlich's haematoxylin to improve the visibility of the lines of arrested growth (LAGs; sensu Castanet 1975). Microscope slides with 10–15 slices from each individual were prepared with samples from two phalanxes of the same toe. The same person (R. M.-P.) assigned a number of LAGs to each sample by observing the preparations at ×400 and choosing the most repeated observed number of LAGs per slide.

Measurement of the UV-blue and UV-yellow throat patches in the field

With the aid of a spectrophotometer (Jaz DPU® Module), we measured in the field three consecutive times the reflectance spectrum from 320 to 700 nm in a central area of both the blue and yellow throat patches in 21 adult Schreiber's green lizard males (Fig. 1a). We averaged the three spectra from each colour patch after calculating the repeatability of the measurements (>74 %) using the methodology proposed by Lessells and Boag (1987). The spectrophotometer used one Pulsed Xenon Light Source (Jaz-PX) connected to an optical fibre. The probe was mounted within a holder that ensured that readings were taken from areas 1 mm in diameter at a constant distance of 3 mm from the skin surface at a 90° angle (Endler 1990; Martín and López 2009; Bajer et al. 2010). All the measurements were relative to a 99 % WS-1 white reflectance standard (all the components from Ocean Optics Inc., Dunedin, FL, USA).

We analysed the spectral data from both the UV-blue and the UV-yellow throat patches from the lizards adapting the segment classification method for spectral analysis (Endler 1990; Grill and Rush 2000). Thus, we selected the spectral segments to explore as follows. The spectrum from the UV-blue patch shows two peaks in the near UV-blue (Fig. 1b). Consequently, we divided the spectrum from 320 to 475 nm (UV-blue spectrum) for short wavelengths and 475 to 700 nm for moderate to long wavelengths. In relation to the UV-yellow patch, it showed a first peak in the UV region and a second peak in the yellow region (Fig. 1c). Thus, we considered the region from 320 to 400 nm for short wavelengths (UV chroma) and from 450 to 700 nm for moderate to long wavelengths (i.e., carotenoid chroma; Montgomery 2005). With this classification of the spectral data, we calculated the relative chroma as $\Sigma Q_{\text{segment}}/\Sigma Q_{320\text{–}700}$ for the segments defined above, where Q is the value of reflectance for each considered wavelength. Furthermore, the total brightness for each spectrum was calculated as $\Sigma Q_{320\text{–}700}$. As noted, we observed several peaks in each of the spectra studied here. Thus, for either colour patch, we adapted Endler's (1990) hue calculation which integrates information of the full spectrum including the UV range. We calculated segment differences as follows: for medium to short wavelengths, $\Sigma Q_{500\text{–}600}–\Sigma Q_{320\text{–}400}$; for long to medium wavelengths, $\Sigma Q_{600\text{–}700}–\Sigma Q_{400\text{–}500}$. In this way, we can derive objective estimates of hue (0–360°: 0° = red, 90° = yellow, 180° = green and 270° = UV-blue).

Statistical analyses of colour ornaments

To test the effect of the co-occurrence of parasitic diseases on the spectral properties of the throat in the males of the population, we performed GLM models in Statistica 10.0 (Statsoft Inc.). The threshold of significance for the models was $P < 0.0{,}5$ and the residuals of these models were checked for normality and homoscedasticity. The spectral variables (i.e. brightness, chroma and hue) were the dependent variables, and date of capture, BCI_AGE, number of ticks per lizard and the status of infection with both blood parasites and nematodes were the independent variables in the models.

Results

Field data correlations

The mean weight ± SE and range for the lizards was 31.0 ± 4.7 and 23.9–40.4 g. The mean SVL ± standard error (SE) and range of the lizards was 102.5 ± 5.2 and 93–111 mm. All the males had the characteristic blue head typical during the mating season in adult males of this species. Indeed, the number of LAGs in the phalanx was ≥4 (4 to 7), which agrees with the age of sexual maturity of the species (Marco 1995). Ninety-five per cent (20/21) of the individuals studied showed ticks (*Ixodes ricinus*) during the period of study, which were attached to the shoulders, neck and tympani of the lizards (Fig. 1a; blue arrow). The mean number of ticks ± standard error (SE) and range was 19.8 ± 15.2 (0–46). Twelve of the 21 lizards sampled (57 %) were infected by *Schellackia* sp. Parasites, and 38.0 % of the lizards were infected by intestinal nematodes for which only prevalence was recorded.

Overall, no difference of significance was observed between the analyses performed with BCI corrected by age (i.e. BCI_AGE) and the analyses performed with BCI (results not shown). However, age influences body size and infection status in lizards (Halliday and Verrell 1988; Pacala and Dobson 1988). Thus, we provide the results considering the age of the individuals. The brightness in the UV-yellow throat patch was significantly and negatively related to tick load (GLM: $F_{1,\ 15} = 5.09$, $P = 0.04$; relationship of brightness of UV-yellow throat patch to number of attached ticks: $R^2 = 0.30$, $P = 0.01$, Fig. 2a). Furthermore, this trait was significantly and positively related to BCI_AGE (GLM: $F_{1,\ 15} = 5.05$, $P = 0.04$; relationship of brightness of UV-yellow throat patch to BCI_AGE: $R^2 = 0.26$, $P = 0.02$, Fig. 2b), suggesting that this is a condition-dependent signal that is costly to maintain (Zahavi 1975 but see Roulin 2015). Individuals passing nematode eggs in their faeces had significantly higher values of hue than do uninfected individuals (GLM: $F_{1,\ 15} = 4.96$, $P = 0.04$; Fig. 3), with infected individuals showing throat colouration closer to green. In relation to the UV-blue throat patch, those males infected with *Schellackia* showed higher values of UV-blue chroma (GLM: $F_{1,\ 15} = 6.70$, $P = 0.02$; Fig. 4a) and higher values of hue (GLM: $F_{1,\ 15} = 5.99$, $P = 0.02$; Fig. 4b), with infected individuals showing UV-blue throats biased towards the ultraviolet region of the spectrum. The results for all GLM analyses are shown in Table 1.

Discussion

In this study, lizards with more ticks showed darker (i.e. lower brightness) UV-yellow throat patches and worse body condition. This supports Hamilton and Zuk's hypothesis (1982) indicating a role for the UV-yellow ornamentation of

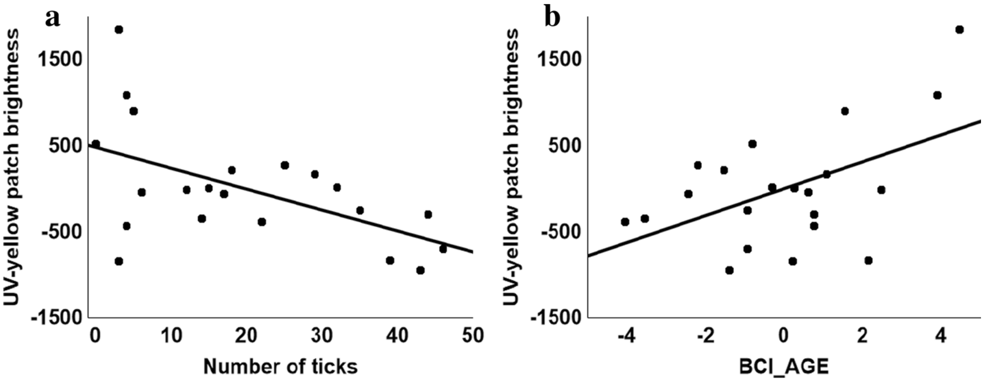

Fig. 2 **a** Relationship between the number of ixodid ticks attached to the skin of the lizards and the corrected brightness of the UV-yellow throat patch, and **b** the relationship between the body condition index corrected for age (BCI_AGE) and the UV-yellow throat patch brightness. The UV-yellow patch brightness was corrected for date of capture in these two analyses

L. schreiberi as an individual signal of quality as suggested by Martín and López (2009). Nevertheless, adaptive finely tuned phenotypic responses to local environmental conditions may also drive differences in colouration at each population site (Stuart-Fox et al. 2009; McLean et al. 2015). For example, in a previous study on this species from Portugal, tick load was not related to ventral colouration but was related to body condition (Stuart-Fox et al. 2009). In the present study, male lizards during the mating season presented ticks (*I. ricinus*), which practically disappeared at the end of this period (RM-P pers. Obs.). This may mirror an increase in testosterone levels during the mating season (Folstad and Karter 1992), since testosterone can increase the susceptibility of lacertids to tick infestation (Salvador et al. 1996; Olsson et al. 2000). Increased testosterone levels along with parasitic infections may promote oxidative imbalance (Alonso-Álvarez et al. 2007; López-Arrabé et al. 2015) in male Schreiber's green lizards during the mating season. The increase in the stress status of individuals may affect multiple layers of the dermis promoting carotenoid reallocation (Cote et al. 2010), redisposition of guanine platelets in iridophores (San-Jose et al. 2013) or either aggregation of melanophores or melanin deposition (Galván and Solano 2009). These changes can reduce the total brightness of this colour patch. Thus, in this population, male lizards with a better body condition may convey their individual quality by maintaining brighter UV-yellow throat patches.

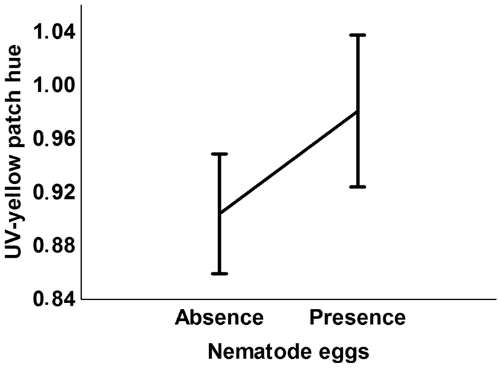

Fig. 3 GLM plot (mean ± 0.95 confidence interval) of the relationship between the presence of nematode eggs in the faeces of male lizards and the UV-yellow patch hue

In addition, lizards passing eggs of intestinal nematodes in their faeces had higher values of hue in the UV-yellow throat patch than did uninfected individuals. Higher values of hue mean that yellow throats showed a more greenish colouration. This difference of hue in the carotenoid-based colour traits of lizards may be related to either the degree of iridophore aggregation (San-Jose et al. 2013) or a depletion of carotenoid content, which can reduce the proportion of yellow pigments in relation to the underlying blue colouration (Fitze et al. 2009). Thus, it is likely that a combined effect of trade-offs acting on the allocation of carotenoids related to nematode infection (e.g. Martínez-Padilla et al. 2007) and on iridophore dispersion related to stress (San-Jose et al. 2013) explain the relationship between the hue of the UV-yellow patch and the presence of nematode eggs in the males of *L. schreiberi*.

In relation to the UV-blue throat patch, the lizards infected with *Schellackia* showed higher values of both UV-blue chroma and hue skewed towards a more UV-biased colouration. The increase in testosterone during the mating season may also play a key role in this colour patch (Folstad and Karter 1992; Quinn and Hews 2003). Indeed, lizards captured during the mating season showed intense UV-blue throats in opposition to the dull greyish throats of male lizards captured after mating (unpublished results). The nuptial testosterone levels along with the cellular damage provoked by chronic infections of parasites may increase oxidative imbalance (Sepp et al. 2012). In this sense, the synthesis of eumelanin, which is the main type of melanin occurring in the melanophores in the skin of lizards (but see Roulin et al. 2013), is favoured under depleted levels of glutathione (GSH) (Galván and Alonso-Álvarez 2009). This leads to high oxidant conditions (Galván and Solano 2009). Thus, the oxidative stress favoured by either parasitic diseases or testosterone reduces GSH availability (Atamna and Ginsburg 1997; Alonso-Álvarez et al. 2007; López-Arrabé et al. 2015) and may promote eumelanogenesis (Galván and Alonso-Álvarez 2009; Galván and Solano 2009). This agrees with experimental results in phrynosomatid lizards, which revealed that increased levels

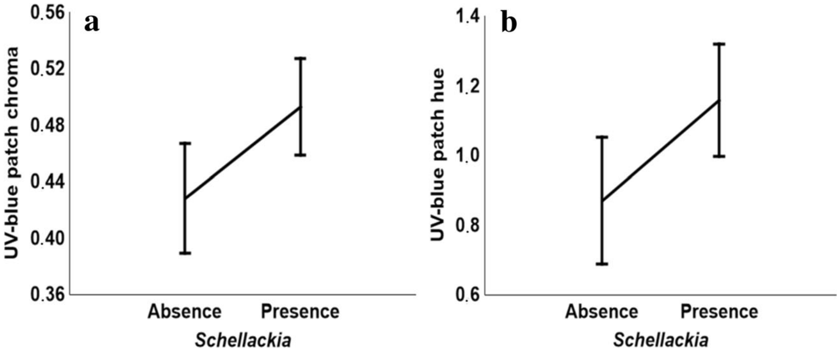

Fig. 4 GLM plot (mean ± 0.95 confidence interval) of the blue throat patch UV-blue chroma (**a**) and hue (**b**) in relation to the presence of *Schellackia* parasites in the blood of lizards

of testosterone were related to deposition of melanin in the dermal basal layers (Quinn and Hews 2003). This deposition of melanin significantly decreased the brightness, increased the chroma and shifted the blue colouration towards shorter wavelengths (i.e. higher hue values) in two different blue patches (Cox et al. 2008). Likewise, lizards chronically infected with malaria parasites were darker than were healthy ones (Ressel and Schall 1989), whereas common lizards treated with an adrenal stressor showed lower melanophore reflectance (San-Jose et al. 2013). This is consistent with simulations performed in the ornament system of poikilotherms, which accounted for the spectral properties of melanin (Grether et al. 2004). However, if melanin alone was responsible for the change in the UV-blue throat colouration, we would expect a variation in brightness (Cox et al. 2008). Therefore, a combined effect of melanin deposition and

Table 1 Results of general linear models (ANCOVA tests; *F*-values) for each throat colour patch component

	df	*F*-value		*df*	*F*-value
UV-yellow brightness			UV-blue brightness		
BCI_AGE	1, 15	5.05*	BCI_AGE	1, 15	0.21
Date	1, 15	13.11**	Date	1, 15	8,02*
Ticks	1, 15	5.09*	Ticks	1, 15	1.34
Nematodes	1, 15	0.09	Nematodes	1, 15	0.60
Schellackia	1, 15	0.04	*Schellackia*	1, 15	1.95
UV chroma			UV-blue chroma		
BCI_AGE	1, 15	0.01	BCI_AGE	1, 15	1.03
Date	1, 15	0.55	Date	1, 15	0.67
Ticks	1, 15	0.22	Ticks	1, 15	0.48
Nematodes	1, 15	2.40	Nematodes	1, 15	0.38
Schellackia	1, 15	<0.01	*Schellackia*	1, 15	6.70*
Carotenoid chroma					
BCI_AGE	1, 15	<0.01			
Date	1, 15	0.65			
Ticks	1, 15	0.21			
Nematodes	1, 15	2.60			
Schellackia	1, 15	0.04			
UV-yellow hue			UV-blue hue		
BCI_AGE	1, 15	0.01	BCI_AGE	1, 15	0.54
Date	1, 15	1.52	Date	1, 15	0.76
Ticks	1, 15	0.51	Ticks	1, 15	0.21
Nematodes	1, 15	4.96*	Nematodes	1, 15	<0.01
V*Schellackia*	1, 15	1.27	*Schellackia*	1, 15	5.99*

BCI_AGE refers to body condition corrected for age of the individuals. "Ticks" indicates the number of attached ticks. Nematode and *Schellackia* correspond to the absence/presence of intestinal and blood parasites, respectively.

Level of significance (*F*-value): * $P < 0.05$; ** $P < 0.005$

iridophore spacing may explain the differences in spectral properties in the UV-blue throat patch between infected and uninfected lizards.

Our results suggest that, in agreement with the "multiple messages" hypothesis (Hebets and Papaj 2005), lizards combining both UV-blue and UV-yellow signals related to oxidative status may reflect their individual quality. Indeed, male dominance was related to UV-blue throat chroma in *L. schreiberi* (Martín and López 2009), as well as fighting ability and sexual attractiveness in closely related European green lizards (Bajer et al. 2010, 2011; Molnár et al. 2012). However, individuals with more UV-blue chroma and hue in the throat may pay the cost of higher oxidative stress induced by the synergic effect of testosterone (Alonso-Álvarez et al. 2007) and chronic infections (Atamna and Ginsburg 1997; Sepp et al. 2012). On the other hand, they may also show a higher number of agonistic or sexual encounters (e.g. Olsson et al. 2000; Martín and López 2009), which might increase the transmission of parasites by contact. Thus, as previously suggested for the closely related *L. viridis*, intense UV-blue colouration may be costly to males with only high-quality individuals able to afford it (Molnár et al. 2012), supporting the role of UV-blue ornaments as signals of individual quality in lacertids (Martín and López 2009; Bajer et al. 2011; Molnár et al. 2012, 2013; Pérez i de Lanuza and Font 2014b). Moreover, it is possible that higher-quality signallers are able to tolerate (or feed) more parasites with less impact on their viability (Getty 2002). On the other hand, the intrinsic costs of production and maintenance of the nuptial ornaments of lizards in terms of oxidative stress, parasitism and fighting performance may favour the maintenance of trait variability. This may arise from the interaction between individual genetic background and different reproductive investment of individuals during successive seasons (Siefferman and Hill 2005). In this sense, lizards with high current reproductive investment may suffer a reduction of individual fitness during the subsequent mating season (Ricklefs 1977; Sorci et al. 1996).

In conclusion, parasites may be differentially related to the physiology underlying these two throat colour patches in *L. schreiberi*. Therefore, the combined information of the two patches conveys individual quality in this lizard species (Martín and López 2009). However, further studies on pigment composition and hormonal and oxidative balance in lacertids are desirable to understand how skin colouration can reflect the trade-offs imposed by the environment.

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Compliance with ethical standards

Ethical statement All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures for catching and handling the lizards were authorized by permit EP/SG/625/2011 provided by Junta de Castilla y León.

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Conflict of Interest Authors RM-P, JM and SM declare that they have no conflict of interest.

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