A structural colour ornament correlate positively with parasite load and body condition in an insular lizard species

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Abstract

Pigment-based ornaments in vertebrates may reflect the body condition or health status of the individual in correlation with environmental stress and hormonal balance. Among the environmental factors shaping sexual colouration, parasitic infections have been stressed as an important evolutionary pressure constraining the maintenance of pigment-based ornaments. However, the honesty of structure-based ornaments in vertebrates is still under debate. Structural UV-biased ornaments in *Gallotia* lizards were described as a trait used by conspecifics during mate and rival assessment suggesting the reliability of these signals. We investigated the relationship between parasitaemia, body condition and a structural-based ornament present in the cheek of the sexually dichromatic Canarian lacertid *Gallotia galloti* in a population with an almost 100 % prevalence of haemoparasites. Using spectrophotometric techniques, we found that males with higher values of cheek UV chroma were infected with more haemoparasites. No significant relationship was found between haemoparasite load and body condition. However, males with higher cheek UV chroma showed significantly better body condition. In addition, we found that cheek hue was significantly related to body condition of individuals in both sexes. In males, cheek reflectivity biased towards the UV range was significantly related to better body condition. In females, those individuals with better body condition showed more whitish cheeks with less UV suggesting that cheek hue serves as an intersexual signal for sex recognition. We conclude that the positive relationship between cheek chroma and parasite load in male lizards is compatible with both differential density of melanin and iridophore arrangement in the dermis conveying an individual's ability to cope with environmental stress.

Keywords

- Colour
- *Gallotia*
- Hamilton and Zuk hypothesis
- Handicap Principle
- Island ecology
- Parasite
- Sexual selection

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Introduction

The Handicap Principle (Zahavi 1975) proposed a theoretical framework to explain the persistence of conspicuous ornaments in nature. Individuals are tested by the handicap that implies bearing a conspicuous, or even exaggerated, trait or behaviour (Zahavi 1975). An exaggeration of these characters without a correlation to an adaptive advantage should lose its effect by negative selection (Zahavi 1975; Grafen 1990). In several vertebrates including lizards, colour ornaments have been studied as signals of individual quality used by conspecifics during rival or mate assessment (Cooper and Burns 1987; ~~Olsson et al. 1994;~~ Stapley and Whiting 2006; Martín and López 2009; Bajer et al. 2010, 2011). Parasites exert a selective environmental pressure shaping sexual ornaments (Hamilton and Zuk 1982; Ressel and Schall 1989; Calisi et al. 2008; Molnár et al. 2013). The hypothesis formulated by Hamilton and Zuk (1982) assumes that: (1) females choose mates on the basis of secondary sex characters, (2) the full expression of these characters is limited by parasite infection, (3) females choose males with exaggerated secondary traits to obtain resistance genes for their offspring, and (4) co-evolution between parasites and hosts results in variation in fitness as well as the traits linked to parasite resistance (Hamilton and Zuk 1982). Processes of co-evolution in host-parasite systems often produce significant relationships between host phenotypic traits and the parasitic infection (e.g. Poulin and Thomas 1999). To favour processes of co-evolution between parasites and their hosts, parasitic diseases may be acute at early stages causing severe juvenile mortality and then persisting in chronic forms in survivors, allowing somewhat long cycles favourable to sexual selection (Hamilton and Zuk 1982). A major intraspecific prediction arises from this hypothesis. Females should preferentially mate with the brightest or most ornate males available, and these males should carry lower parasite loads than less showy males. The hypothesis is contradicted if, within a species, preferred or showier mates have the most parasites (Hamilton and Zuk 1982; Ressel and Schall 1989).

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Carotenoid-based colour patches drew the attention of evolutionary biologists studying the honesty of sexual ornamentation because of their potential costs in production and maintenance (Chen et al. 2013; Olsson et al. 2013). Meanwhile, structural coloration in vertebrates has received less attention. Specifically in lizards, the honesty of structural-based colouration falls on the regularity or spacing of the iridophore platelets in the dermis that may be influenced by episodes of acute stress (e.g. agonistic encounter) or ontogenetic shifts (San-Jose et al. 2013; Pérez i de Lanuza et al. 2014; Teyssier et al. 2015), or/and by testosterone-mediated melanin expression (Quinn and Hews 2003; Cox et al. 2005, 2008; Olsson et al. 2013). Furthermore, perturbation of structural colouration of lizards is motivated by changes in temperature (Langkilde and Boronow 2012; Bajer et al. 2012), hormonal status (Quinn and Hews 2003;

Cox et al. 2005, 2008; Bohórquez-Alonso and Molina-Borja 2014) and possibly parasite load (Molnár et al. 2013). Therefore, structural UV-biased ornaments in lizards can act as honest indicators of the individual's current physiological condition (Stapley and Whiting 2006; Whiting et al. 2006; Font et al. 2009; Bajer et al. 2010, 2011; Molnár et al. 2012; Pérez i de Lanuza et al. 2014). However, few studies provide objective and quantitative evidence of significant relationships between chronic infections and the expression of a structural ornament in lizards (i.e. Molnár et al. 2013). Molnár et al. (2013) found that fatter and larger European green male lizards showed higher haemoparasite loads, but males with more parasitaemia showed darker (less bright) nuptial UV-blue throat colouration, in agreement with the Hamilton-Zuk hypothesis (1982).

In the present study, we tested the relationship between individual haemoparasite load and the conspicuousness of the cheek structural-based ornament in individuals from one population of *G. galloti* in La Palma. Lizards of the genus *Gallotia* (Lacertidae: Gallotinae) are known to bear UV-biased secondary sexual traits (Thorpe and Richard 2001; Font and Molina-Borja 2004; Molina-Borja et al. 2006). Particularly, *G. galloti* (Oudart 1839) present UV reflection restricted to the UV-blue patches of the skin while the entire dorsal and lateral background surface of the body exhibits black colouration (Font and Molina-Borja 2004). Unlike in other populations of *G. galloti*, the studied population from La Palma lacks yellow stripes on the back (R.M.P., pers. obs.). Therefore, this species is a good model to test the Hamilton-Zuk hypothesis in relation to UV-based visual signals since: (1) the species of this Canarian-endemic genus are known to present a high prevalence of chronic hematic infections (e.g. Oppliger et al. 1999; Martínez-Silvestre et al. 2001; García-Ramírez et al. 2005; Foronda et al. 2007; Megía-Palma unpublished data), (2) the colour patches differ in UV-spectrum reflectance between sexes and among individuals of the same population (Font and Molina-Borja 2004; Molina-Borja et al. 2006; Bohórquez-Alonso and Molina-Borja 2014), and (3) the male ornamentation in *G. galloti* is related to the reproductive and hierarchical status of the individuals (Thorpe and Brown 1989; Huyghe et al. 2005; Molina-Borja 2002; Molina-Borja et al. 2006; Bohórquez-Alonso and Molina-Borja 2014). We expect that lizards with more intense UV colouration have lower parasite loads.

Material and methods

Sampling and collection site

Gallotia galloti (Lacertidae: Gallotinae) is a midsize lizard (in La Palma: male snout to vent length—SVL—average = 107.8; range = 82.7–114 mm; female SVL average = 88.6; range = 74.6–102 mm, after Bischoff 1982) endemic to the islands of La Palma and Tenerife in the Canary Archipelago. The adult males of this lacertid lizard present, to the human eye, cheeks with bright blue colouration and a row of blue eyespots on the lateral and the ventrolateral areas of their body (Thorpe and Brown 1989). *Gallotia* lizards show sexual differences in the UV spectrum of these coloured areas, and males have a higher proportion of UV in their ornaments (Molina-Borja et al. 2006). In some populations of *G. galloti* on the island of Tenerife, males present yellow stripes on the back (Molina-Borja et al. 1997). However, in the population studied here on the island of La Palma, only blue patches were observed (R.M.P., pers. obs.).

In March 2014, before the mating season, we sampled *G. galloti palmae* in a single area in La Palma (28.6203, –17.9067), Canary Islands. Cabildo Insular de La Palma provided the sampling permit 201302/030-A/OT-098/2013. To capture the lizards, we used a group of eight pitfall traps baited with fruit and tomato (Oppliger et al. 1999). These traps were located in an area of 200 m^2 among banana crops. Traps were hidden in the bushes or placed on the ground next to the walls of the contiguous plantations, where lizards bask. The traps were always set out of the direct sunlight and were surveyed every 15 min to avoid undesirable overheating (no lizards died). The lizards inside the traps were gently collected and transported in individual cotton bags which allowed good aeration (Pérez i de Lanuza et al. 2014). During the transport of lizards (30 min), we observed that animals were well ventilated. The transportation of the lizards was justified for performing colour measurements in a darkened room to reduce environmental light that could influence the spectral data.

We collected 40 adult lizards, 17 males and 23 females. Collecting adults was important since only adult individuals in this species display full colour signals (Thorpe and Richard 2001) minimising errors in sex assignment. In addition to the colour markings, and prior to sex assignment of the individuals, which can be challenging in this species, we checked for the presence of femoral pores, the thickness at the tail base, the head size and the presence of white stripes on the sides and the gular area. Each lizard was measured to the nearest millimetre with a ruler. The mean snout to vent length (SVL) ± standard error of these lizards was

111.4 ± 1.5 mm for males and 96.9 ± 1.5 mm for females. We weighed the individuals to the nearest gram with a digital balance. The mean mass ± standard error was 48.7 ± 2.6 g for males and 29.8 ± 1.8 g for females. The body condition index was later calculated as the residuals of the regression of the SVL on the mass (see Schall and Pearson 2000 but also Green 2001). Because 17 of the lizards had regenerated tails, and not all individuals regenerate their tails to their original size in the presence of parasites (Oppliger and Clobert 1997), we included the length of the tail of each lizard as a co-variable in the calculation of the mass/length residuals.

Measurement of the cheek reflection

We measured the colourful cheek patches (Fig. 1a) of each of the 40 lizards three consecutive times. We selected the colour patch in the cheek because it is related to the quality of the individual (Huyghe et al. 2005), is involved in the sequential assessment game during male-male interactions in *G. galloti* (Molina-Borja et al. 1998; 2002) and additionally, male colour patches with a high proportion of UV reflection are preferred by females in related lacertid species (Martín and López 2009; Bajer et al. 2010). Since this species is sexually dimorphic for this trait, we measured the same area in both sexes (Fig. 1). We measured the reflectance spectra of this UV-blue ornament from 300 to 700 nm with a spectrophotometer (Jaz DPU® Module) with a Pulsed Xenon Light Source (Jaz-PX) connected to an optical fibre. The probe was mounted within a holder that ensured readings were taken from areas 1 mm in diameter at a constant distance of 3 mm from the skin surface. During measurements, the probe of the spectrophotometer was held at an angle of 90° to the skin of the lizards (Endler 1990; Martín and López 2009; Bajer et al. 2010; Pérez i de Lanuza and Font 2010). The measured spectrum covered the broadest range of wavelengths known to be visible to lizards (Fleishman et al. 1993), and specifically to lacertid lizards (Pérez i de Lanuza and Font 2014; Martin et al. 2015). All the measurements were relative to a 99 % WS-1 white reflectance standard (all the components from Ocean Optics Inc., Dunedin, FL, USA). The spectral records were made in a darkened room to avoid interference from environmental light. All lizards survived transportation and manipulation and were successfully released in the area (200 m^2) where they had been collected within the following 24 h. The procedures employed are innocuous to lizards, since the effects of manipulation should not be greater than the stress experienced by lizards in nature (Langkilde and Shine 2006). Therefore, considering the novel contribution presented here for understanding the environmental pressures that model the expression of structure-based signals in lacertids, this study and the methods employed are justified from a theoretical and ethical point of view (Rollin and Kessel 1998).

Fig. 1

Female (**a**) and male (**b**) *Gallotia galloti palmae* showing the cheek ornamentation area measured with spectrophotometry. In **c** females and **d** males, *grey lines* denote the brightest and darkest cheek spectrum of the sample for each sex. *Black line* denotes mean reflectance cheek spectra for the population

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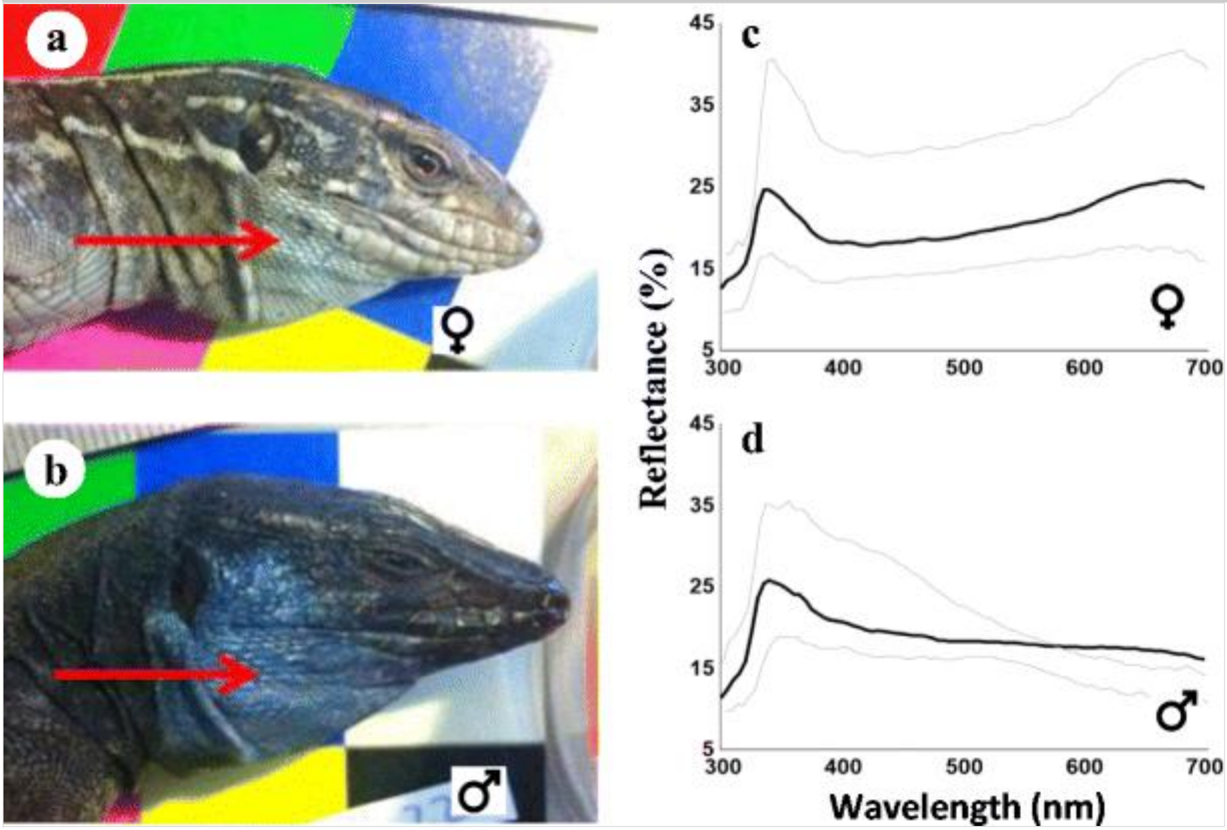

Blood parasites

After cleaning the base of the tail with ethanol, we bled each lizard with a sterilised needle (Megía-Palma et al. 2013, 2014). The incision was always made at least 4 cm away from the cloaca to avoid the hemipenes. The blood drop obtained by this method was collected with a heparinized capillary (BRAND, micro-haematocrit tubes, 75 × 1.1 mm, Na-heparinized). With this blood sample, we made a thin layer blood smear to count the number of blood parasites per 5000 red blood cells. We fixed the dried blood smears with methanol (Rogier and Landau 1975) and stained them for 40 min with Giemsa diluted 1:10 in buffer, pH 7.2 (Schall 1986). We then counted 5000 erythrocytes for each smear in search of blood parasites at ×1000 magnification in an area with a homogenous distribution of red blood cells (Merino and Potti 1995) with a microscope BX41TF (Olympus, Tokyo, Japan). Quantification of parasitaemia by observation of blood smears under the microscope has been frequently used in parasitological studies to compare variation in infection among individual hosts (e.g. Merino and Potti 1995; Sorci et al. 1996; Martínez-Silvestre et al. 2001; García-Ramírez et al. 2005; Martín et al. 2008; Megía-Palma et al. 2013; Molnár et al. 2013), indicating the reliability of this technique to assess the haemoparasite load.

Statistical analyses

Similarly to recent studies (Grill and Rush 2000; Deitloff et al. 2013; Pérez i de Lanuza et al. 2014), we analysed the spectral data obtained from the right cheek of the lizard adapting the segment classification method for spectral analysis (Endler 1990). In agreement with our measurements (Fig. 1c, d), the ultraviolet range (i.e. 300 to 400 nm) is the most conspicuous trait of visual ornaments in *G. galloti* (Font and Molina-Borja 2004). Thus, we calculated UV chroma as $\Sigma Q_{300-400}/\Sigma Q_{300-700}$, where Q is the value of reflectance for each considered wavelength obtaining a proportional reflectance, or saturation, of the UV region in relation to the total reflectivity of this patch. Furthermore, we calculated the brightness for the cheek spectra as $\Sigma Q_{300-700}$ (Montgomery 2006; Pérez i de Lanuza et al. 2014). Brightness is the total amount of light reflected by a surface and is interpreted as the level of darkness or clarity of the surface (Montgomery 2006). In addition, we adapted Endler's (1990) calculation of hue to integrate the information of the full spectrum including the UV range. For this calculation, we chose $\Sigma Q_{500-600}-\Sigma Q_{300-400}$ for medium to short wavelengths; for long to medium wavelengths, we used $\Sigma Q_{600-700}-\Sigma Q_{400-500}$. In this way, we could derive objective estimates of hue (0–360°: 0° = red; 90° = yellow; 180° = green; and 270° = blue). Hue can be interpreted as a categorical variable of colour describing a surface (blue, green, yellow, red). However, if we considered colour surfaces with more than one peak of maximum reflectance, integrating information of the full spectrum can be highly informative (Pérez i de Lanuza et al. 2014). The distribution of the residuals of the models for chroma, hue and brightness were visually explored for normality and homoscedasticity. Consequently, we log-transformed the haemoparasite load (Molnár et al. 2013) and applied Johnson's transformation to the cheek hue to comply with parametric assumptions (Yeo and Johnson 2000).

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To study the relationship between cheek chroma, hue and brightness with body condition, and the parasite load, we performed a set of ANCOVAs in Statistica 10.0 (Statsoft, Inc.). In each ANCOVA, the colour variables brightness, chroma and hue were the dependent variables, while the sex of the individuals was set as a factor, and the body condition and the blood parasite load were set as independent variables. Because we were interested in sexual differences in these relationships, we included the interaction between sex and the independent variables. We also checked the relationship between body condition (dependent variable) and parasite load (independent variable).

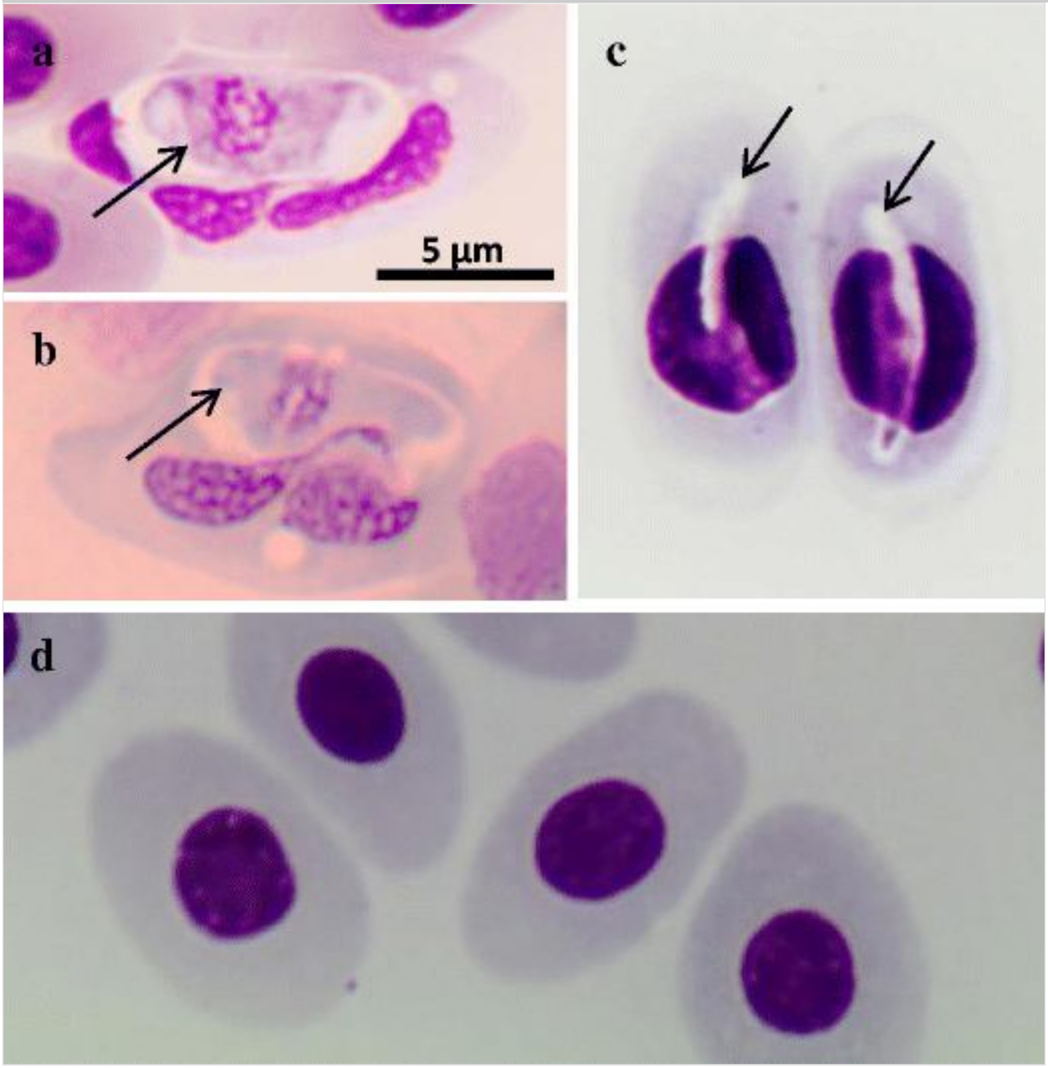
Results

Parasite infection

Thirty-nine out of 40 (97 %) individuals were infected with blood parasites. Parasite abundance did not differ significantly between sexes ($F_{1,38} = 1.4$, $P = 0.2$). Only one type of haemoparasite was found infecting lizards. This parasite had not been previously described, and thus is described here. Mature and immature parasite stages were found infecting red blood cells in peripheral blood. The mean size of the haematic stages of the parasite ($N = 49$) was 9.1 ± 0.15 µm in length (range 5.9–10.9) and 2.1 ± 0.07 µm in width (range 1.1–3.5). The overall morphology and the fact that the parasite distorted the nuclei of the blood cells (Fig. 2) make it likely that this parasite belonged to the genus *Karyolysus* sp. (Apicomplexa: Adeleorina), as has been proposed for haematic parasites infecting *G. bravoana* on an adjacent island (Martínez-Silvestre et al. 2001). No significant relationship was observed between body condition and parasitaemia ($F_{1,38} = 1.1$, $P = 0.3$).

Fig. 2

Parasitized *G. galloti* red blood cells containing in their cytoplasm mature (**a**, **b**) and immature (**c**) gamonts of genus *Karyolysus* (*black arrows*). **d** Uninfected red blood cells in *G. galloti palmae*. Compare between infected and uninfected erythrocytes, infected blood cells show distorted nuclei and enlarged cell size



Cheek reflectance

The mean ± SE cheek reflectance for male and female lizards is shown in Table 1 . The intrapopulation variance in cheek UV chroma was significantly explained by the interactions sex*body condition ($F_{1,34} = 5.8$, $P = 0.02$) and sex*parasite load ($F_{1,34} = 4.5$, $P = 0.04$). Particularly, male lizards that showed cheek badges with higher chroma had better body condition (Fig. 3a) and higher haemoparasite load (Fig. 3b). Females did not show a significant relationship between cheek chroma and either the number of haemoparasites or body condition. Additionally, hue variation was significantly explained by the interaction sex*body condition ($F_{1,34} = 12.1$, $P < 0.005$). Male lizards with better body condition showed cheek colouration biased towards the UV range (i.e. higher values of hue), whereas females with better body condition had whitish cheeks with lower participation of UV (Fig. 3c). The interaction sex*parasite load was not significant ($F_{1,34} = 0.6$, $P = 0.4$) and no significant relationship was found between parasite load and hue in either sex (Fig. 3d). In addition, no relationship was found between cheek brightness and body condition ($F_{1,34} =$ 0.06, $P = 0.8$) or parasitaemia ($F_{1,34} = 0.3$, $P = 0.6$). All ANCOVA results are shown in Table 1.

Table 1

Mean ± standard error of cheek brightness, chroma and hue of male and female *G. galloti* from La Palma. Results of general linear models (ANCOVA tests; *F* values) for each cheek colour component

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	Mean ± SE		**d.f.**	***F* value**
	Females (*N* = 23)	**Males (*N* = 17)**		
Cheek brightness	1680 ± 81.8	1522 ± 52.2		
Sex			1, 34	2.27
Ln (parasitaemia)			1, 34	0.34
Body condition			1, 34	0.06
Sex*Ln (parasitaemia)			1, 34	1.04
Sex*body condition			1, 34	>0.01
Cheek UV chroma	0.24 ± 0.01	0.29 ± 0.01		
Sex			1, 34	0.15
Ln (parasitaemia)			1, 34	4.07+
Body condition			1, 34	0.77
Sex*Ln (parasitaemia)			1, 34	4.53*
Sex*body condition			1, 34	5.79*
Cheek hue	−0.45 ± 0.11	0.33 ± 0.25		

Note that sexual differences were not significant as a principal effect. Sexual differences arose when the interaction between sex and body condition (UV chroma and hue) or sex and parasite load (UV chroma) were considered

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

	Mean ± SE		d.f.	*F* value
	Females ($N = 23$)	**Males ($N = 17$)**		
Sex			1, 34	0.30
Ln (parasitaemia)			1, 34	0.70
Body condition			1, 34	1.52
Sex*Ln (parasitaemia)			1, 34	0.62
Sex*body condition			1, 34	12.14**
Body condition	−0.25 ± 0.65	0.34 ± 1.05		
Sex			1, 36	0.16
Ln (parasitaemia)			1, 36	1.12
Sex*Ln (parasitaemia)			1, 36	0.32

Note that sexual differences were not significant as a principal effect. Sexual differences arose when the interaction between sex and body condition (UV chroma and hue) or sex and parasite load (UV chroma) were considered

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

Fig. 3

Sex-categorized relationships between the cheek UV chroma, **a** in relation to body condition and **b** in relation to the haemoparasite load. Sex-categorized relationships between the cheek hue, **c** in relation to body condition and **d** in relation to the haemoparasite load. *Asterisks* after *P* values denote a significant result at $P < 0.05$; + denotes $P = 0.05$.

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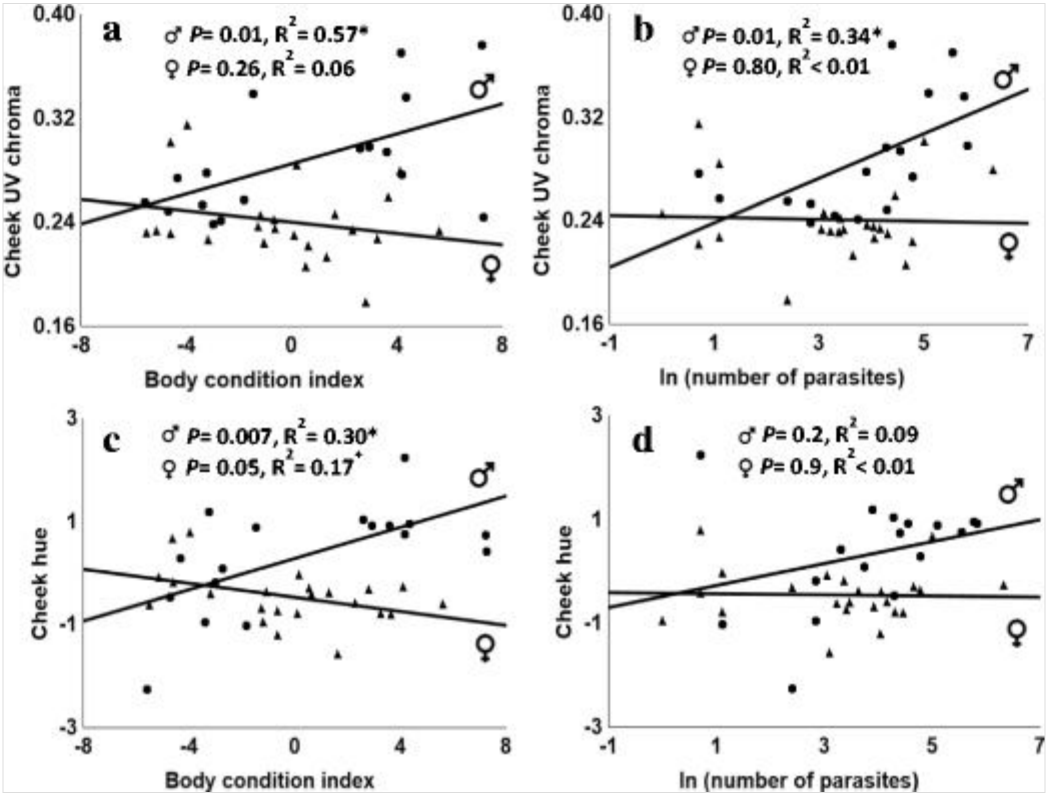

Discussion

We explored a sexually dimorphic structural ornament in relation to body condition and haemoparasite load in *G. galloti* from La Palma. We found that cheek UV chroma and hue were significantly and positively related to body condition in males of *G. galloti palmae*. In females, only cheek hue was significantly and negatively related to the body condition of the individuals. These sexual differences suggest that there may be different constraints shaping UV-based signals in males and females. For example, in male *G. galloti*, the size of the UV-based ornaments was associated with individual fighting performance (Huyghe et al. 2005), whereas colour ornaments in females may evolve to reflect intraseasonal variation in either gonad development or gravidity status (Bohórquez-Alonso and Molina-Borja 2014). For producing UV-blue or blue ornaments in lizards, the presence of well-arranged iridophores in the skin (Kuriyama et al. 2006; Saenko et al. 2013; Haisten et al. 2015; Teyssier et al. 2015) and increased melanin density within the layer of melanophores in the dermis (Quinn and Hews 2003; Grether et al. 2004; Olsson et al. 2013) are determinant. However, the disposition of the iridophores may be related to both hormonal (San-Jose et al. 2013) and neural control in lizards (Rohrlich 1974) and may be linked to ontogenetic shifts (Pérez i de Lanuza et al. 2014). Thus, maintaining a well-arranged disposition of iridophores in a highly stressful environment may be indicative of individual quality, supporting the role of UV-based ornaments as signals of quality in lizards (Martín and López 2009; Bajer et al. 2011; Molnár et al. 2012, 2013; Pérez i de Lanuza et al. 2014).

In addition, UV chroma in the skin of poikilotherms may increase through increased melanin density within the layer of melanophores in the dermis (see Figure 13 in Grether et al. 2004; Olsson et al. 2013). Therefore, unlike ornamentation based on carotenoids, which is usually interpreted to reflect physiological trade-offs between colour expression and immune functions (e.g. Martín et al. 2008; Olsson et al. 2013), melanin-based signals can be enhanced by increases in the oxidative environment (see Galván and Alonso-Álvarez 2008; Galván and Solano 2009, 2015). Indeed, testosterone in combination with high parasite loads may promote oxidant conditions (Alonso-Álvarez et al. 2007; López-Arrabé et al. 2015) favouring the synthesis and deposition of melanin in the skin of lizards (Ressel and Schall 1989; Quinn and Hews 2003; Cox et al. 2005, 2008) and, hence, contributing to the positive relationship between parasitaemia and UV-based colouration.

It is expected that parasites will constrain the expression of secondary sexual characters. However, in male *G. galloti* from La Palma, we found that parasite load was positively related to cheek chroma in contrast to most previous studies (Hamilton and Zuk 1982; Folstad and Karter 1992; Weiss 2006; Václav et al. 2007; Calisi et al. 2008; Bajer et al. 2012). These findings are, nonetheless, compatible with works studying the relationship of haemoparasites and blue/UV-blue and black ornaments (i.e. melanic ornaments) in lizards (Schall 1986; Ressel and Schall 1989; Molnár et al. 2013). For example, Schall (1986) described a higher prevalence of haemoparasites in blue morphs of the Aruban whiptail lizard versus the brown morphs (blue morph males were more prone to aggression). Ressel and Schall (1989) found that darker males of the Western fence lizard were more often infected by *Plasmodium* parasites than paler ones (Ressel and Schall 1989). Similarly, Molnár et al. (2013) found that male European green lizards with darker UV-blue throats (and heavier bodies) had more haemoparasites than other males with lighter nuptial colourations. These results may be related to the role of melanin in honest and social communication in lizards (Cox et al. 2005; Van Vroonen et al. 2013). Thus, producing and maintaining UV-blue ornaments may be physiologically costly and only high-quality individuals may be able to afford it (Molnár et al. 2012). Indeed, this is congruent with the model proposed by Ducrest et al. (2008), where darker melanic individuals are more resistant to oxidative stress. However, although experimental studies treating lizards with testosterone could not demonstrate a significant causal variation on the load of haemoparasites (Veiga et al. 1998; Oppliger et al. 2004) without an experimental approach, we cannot differentiate whether testosterone-mediated melanisation renders individuals more susceptible to parasite or if parasites contribute to changes in colouration.

Hamilton and Zuk (1982) and Ressel and Schall (1989) argued that if showier males are more often infected with parasites, this would suggest a different evolutionary scenario than that proposed by Hamilton and Zuk (1982). In our study, male lizards with showier UV patches were in better body condition and had more haemoparasites (Fig. 3a, b). Unfortunately, we did not measure the mating success of the males studied here. We would expect that fatter and showier *G. galloti* males (more cheek UV chroma and hue) are dominant and obtain better access to resources as previously demonstrated by the studies of Molina-Borja et al. (1998, 2002) and Huyghe et al. (2005). In addition, signals of individual quality evolve to avoid conflicts with conspecifics (Pérez i de Lanuza and Font 2014) because fights are costly in terms of energy expenditure. Thus, ornaments reflecting highly energetic wavelengths (i.e. UV) may serve as enhancers of either head size (and bite force) or body condition (Molnár et al. 2012 and references herein). Thus, UV-blue patches may serve as intrasexual signals of status in *G. galloti* during rival assessment (Molina-Borja et al. 1997; 2002; Huyghe et al. 2005). Thus, showing high cheek UV chroma prior to the mating season may be adaptive for the establishment of social hierarchies. However, given the costs associated with the maintenance of social status and the presence of higher parasite loads in dominant males, we suggest that, although showier males had an advantage during the current breeding season (i.e. better access to females), they may suffer a handicap in the following one as previous studies suggest for other species (Ricklefs 1977; Folstad and Karter 1992; Sorci et al. 1996).

On the other hand, the parasite hypothesis (Hamilton and Zuk 1982) assumes that females select mates for genes of resistance. However, it has been demonstrated that genes for tolerance to infections—defined as those producing a reduced fitness loss under infection—are more adaptive because resistance genotypes are costly (see Roy and Kirchner 2000; Olsson et al. 2005), whereas tolerance genotypes favour milder effects of parasites (Roy and Kirchner 2000; Råberg et al. 2009). The high prevalence of haemoparasites with almost 100 % of individuals infected and the high parasitaemia found among the individuals of either sex suggest the presence of genes for parasite tolerance in this population of *G. galloti palmae* (Miller et al. 2007; Råberg et al. 2009). Unfortunately, the reasons that male lizards that are a priori dominant have more parasites remain unclear. This result is in line with at least two previous and paradoxical studies on three species of lacertids in which, contrary to expectations, haemoparasite load was positively related to the body condition of the lizard hosts (Molnár et al. 2013; Maia et al. 2014). One possibility is that higher quality signallers might be able to tolerate (or feed) more parasites with less impact on their viability (Getty 2002). This apparently low parasitic virulence may result from a process of local adaptation (i.e. tolerance) of the host and/or from the effect of better defences of an adapted host. In both cases, it explains why we failed to find a significant negative relationship between individual parasitaemia and body condition. Oppliger et al. (1999) demonstrated that specific haemoparasites had lower replication rates when they infected sympatric lizards than when they infected other *Gallotia* species from adjacent islands. Therefore, assuming a tight relationship between genetic expression, colouration and environmental factors (reviewed in Olsson et al. 2013), it can be expected that male lizards with more saturated cheeks (more UV chroma) gain more in social hierarchy. These dominant individuals may obtain better access to females transmitting their genetic quality to tolerate or defend against high parasite loads in an environment with a high probability of infection.

Conclusion

The relationships found between cheek chroma and hue, body condition and parasite load in *Gallotia* lizards from La Palma support the role of structure-based ornaments as honest signals. In fact, cheek chroma can be considered good predictors of parasite load and body condition in male *G. galloti* from La Palma since more chromatic individuals had higher haemoparasite load and better body condition. Therefore, cheek hue and chroma, in combination may serve as an intraspecific signal for sex discrimination and attractiveness. We conclude that a positive relationship between cheek chroma and parasite load in male lizards is compatible with both differential density of melanin and iridophore arrangement in the dermis conveying the individual capability to cope with environmental stress.

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Author's contribution SM, JM and RMP conceived and designed the study. RMP and JM analysed the data. SM and JM contributed the reagent/material. RMP, JM and SM wrote the manuscript.

Compliance with ethical standards

The authors declare that the capturing and handling protocols followed during this study comply with the current laws for the conduct of scientific research in Spain. Specific permits for sampling in this population were obtained by Cabildo Insular de La Palma # 201302/030-A/OT-098/2013.

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Conflict of interest The authors declare that they have no conflict of interest.

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