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Sex and population variation in ultraviolet reflectance of colour patches in *Gallotia galloti* (Fam. Lacertidae) from Tenerife (Canary Islands)

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Abstract

Sex and population differences in the ultraviolet (UV) reflectance patterns of two phenotypically divergent lacertids from Tenerife, *Gallotia galloti eisentrauti* and *G. g. galloti*, are described. Adults in both populations have rows of lateral and ventro-lateral blue patches on either side of the trunk that show a single peak of reflectance in the near UV. The lateral patches of males are more intensely reflective than those of females, but females have more chromatic and UV-shifted lateral patches than males. Most *G. g. eisentrauti* and some *G. g. galloti* also have blue cheek patches on either side of the gular area. Male cheek patches have reflectance peaks in the near UV, whereas those of females peak in the visible part of the spectrum. The lateral patches of males from the two populations differ in hue but not in intensity, those of *G. g. galloti* being more UV-shifted than those of *G. g. eisentrauti*. Female *G. g. galloti* have more intensely reflective lateral patches than female *G. g. eisentrauti*. Interindividual variation in peak wavelength and/or UV chroma is present in both sexes and populations. This is the first demonstration of sexual dichromatism in the UV reflectance of colour patches in a lacertid.

Introduction

Conspicuous colours, often emphasized during stereotyped behavioural displays, are an important element of visual communication in many vertebrate groups (Hailman, 1977; Burtt, 1979; Zahavi & Zahavi, 1997; Bradbury & Vehrencamp, 1998). Colour patterns may vary across species, populations, seasons and between the sexes. Within species, mals tend to be more brightly coloured than females. Sexual differences in coloration, termed 'sexual dichromatism', have been a major focus of research by biologists since the time of Darwin (1871) and are thought to arise from sexual selection acting on traits used in competition over mates or from predation pressure favouring cryptic coloration in one sex (Andersson, 1994; Savalli, 1995; Götmark *et al*., 1997). Among reptiles, sexual dichromatism is most widespread in lizards particularly those in the families Agamidae, Iguanidae, Cordylidae, Teiidae and Lacertidae (Cooper & Greenberg, 1992). Sexual dichromatism in lizards may be used for sex recognition, and often represents a compromise between sexual selection for conspicuousness and natural selection for cryptic coloration (Cooper & Burns, 1987; Cooper & Greenberg, 1992; Díaz, 1993; Macedonia, Brandt & Clark, 2002).

Until recently, assessments of lizard coloration have relied on methods and instrumentation optimized for human colour vision (Cooper & Greenberg, 1992). However, it is becoming increasingly clear that there are important differences between our colour vision and that of other vertebrates (e.g. Bennett, Cuthill & Norris, 1994). Many vertebrates, for example, are capable of vision in the ultraviolet (UV) range of wavelengths, between 300 and 400 nm (Jacobs, 1992; Tovée, 1995; Losey *et al*., 1999; Hunt *et al*., 2001). In fact, it has been suggested that UV vision could be the plesiomorphic condition for vertebrates, being retained in many extant taxa including reptiles (Goldsmith, 1994; Yokoyama & Shi, 2000; Ebrey & Koutalos, 2001; Shi & Yokoyama, 2003). Furthermore, recent research has revealed conspicuous UV reflectance patterns in many vertebrates. These reflectance patterns, invisible to humans, appear to be used for intraspecific signalling and mate choice in some fish and birds (fish: Losey *et al*., 1999; García & Perera, 2002; Kodric-Brown & Johnson, 2002; birds: Cuthill & Bennett, 1993; Maier, 1993; Bennett & Cuthill, 1994; Bennett *et al*., 1996; Church *et al*., 1998; Cuthill, Partridge & Bennett, 2000*a*; Cuthill *et al*., 2000*b*; Siitari *et al*., 2002; Hausmann, Arnold & Marshall, 2003). In common with other vertebrates, many lizards display elaborate UV reflectance patterns (Fleishman, Loew & Leal, 1993; LeBas & Marshall, 2000; Macedonia *et al*., 2000; Blomberg, Owens & Stuart-Fox, 2001; Fleishman & Persons, 2001; Macedonia, 2001; Stoehr & McGraw, 2001; Thorpe & Richard, 2001; Thorpe, 2002; Macedonia, Echternacht & Walguarnery, 2003; Thorpe & Stenson, 2003).

As with human-visible colours, UV reflectance patterns may differ between the sexes. Sexual dichromatism in the UV range has been documented in a number of bird species (Bleiweiss, 1994; Finger, 1995; Andersson, Örnborg & Andersson, 1998; Hunt *et al*., 1998; Cuthill *et al*., 1999; Perrier *et al*., 2002). Some plumage patches, such as the blue crest feathers of blue tits *Parus caeruleus*, provide examples of 'pure UV dichromatism', i.e. they appear nearly monomorphic to the human eye, but are clearly dimorphic to birds that are able to detect UV light (Andersson *et al*., 1998; Hunt *et al*., 1998). In lizards, sexual dichromatism extending into the UV range has been described in *Ctenophorus ornatus* (LeBas & Marshall, 2000) and *Crotaphytus collaris* (Macedonia *et al*., 2002). However, no cases of pure UV dichromatism similar to those found in birds have so far been reported in lizards.

Gallotia lizards (family Lacertidae) are ideal candidates for the study of UV dichromatism, given the marked sexual dimorphism in most of the species included in the genus. Two phenotypically distinct populations of endemic *G. galloti* lizards are present in Tenerife (Canary Islands): *Gallotia galloti galloti* occupies the central and southern parts of the island, whereas *G. g. eisentrauti* is restricted to the northern part of the island (Bischoff, 1982; Molina-Borja & Bischoff, 1998). Work conducted several years after the initial subspecies description did not find a basis for subspecies separation (Thorpe & Brown, 1989; Thorpe *et al*., 1994); however, because of clear morphological and coloration differences, we will assign subspecific names to refer to northern and southern *G. galloti* populations.

While the colour pattern of juvenile *G. galloti* is cryptic, adults, particularly males, from both populations are boldly coloured. Background body coloration in adult males is dark grey or brown in the dorsal trunk, tail and limbs, and black in the head. Throughout the island, males display rows of lateral and ventro-lateral patches on either side of the trunk. These patches, which appear to humans as different shades of blue, are sometimes surrounded by a light grey rim and contrast sharply with the dark background of the head and trunk. The lateral and ventro-lateral patches decrease in size in a caudalward direction, with those near the shoulder being the largest. Most *G. g. eisentrauti* ($>50\%$) and some *G. g. galloti* (*c*. 10%) adult males also have blue cheek patches on either side of the gular area. Lateral, ventro-lateral and cheek patches are also present in females from both populations, but they are usually smaller than those of males (G. Mesa Avila & M. Molina-Borja, unpubl. data).

Gallotia galloti exhibits considerable geographic colour variation, particularly among males. This variation is possibly linked to different latitudinal biotopes and mostly affects the size and distribution of blue patches (Thorpe & Brown, 1989). Male *G. g. eisentrauti* have large cheek patches and small lateral and ventro-lateral patches (Molina-Borja, Padrón-Fumero & Alfonso-Martín, 1997). In contrast, male *G. g. galloti* have large lateral and ventro-lateral patches and small cheek patches, which they may lack entirely. Occasionally, the rostralmost lateral patches of male *G. g. galloti* may fuse, giving rise to conspicuous shoulder patches. A further difference between the two populations is the presence of dorsal yellow crossbars in males from the northern part of the island (i.e. *G. g. eisentrauti*). In the field, the colours of males from both populations appear more vivid during the breeding season as they patrol their home ranges. Individual male home ranges may overlap and, when two males meet, agonistic displays, fights and/or chases may occur (Molina-Borja, 1985). Given their lateral or ventro-lateral position, it has been hypothesized that the blue patches are used primarily for intraspecific communication (Thorpe & Brown, 1989). During agonistic displays, males depress the gular area and compress the body laterally, thus making the rows of lateral and ventro-lateral blue patches more visible (Molina-Borja, 1981, 1985, 1987).

In this study, we describe, using UV photography and reflectance spectrophotometry, sex and population colour variation in the Tenerife lizard *G. galloti*. Recently, Thorpe & Richard (2001) reported that the blue patches of northern and southern male *G. galloti* reflect maximally in the UV range of wavelengths, with a peak at around 360 nm. However, their work was largely based on UV photography, and these authors presented reflectance spectra for only three body regions of modal northern and southern male lizards (their focus was on molecular gene flow rather than colour analysis). Our aim in the present work is to document the variation of UV reflectance patterns in *G. galloti*, including spectral reflectance data from a larger sample of individuals of both sexes. Our results provide the first evidence of sexual dichromatism in the pattern of UV reflectance of colour patches in a lacertid.

Materials and methods

Lizard sampling and maintenance

Adult lizards were collected from two different habitats: one a ravine in Tejina (north of the island, *G. g. eisentrauti*) with dense vegetation including *Rubus ulmifolius*, *Euphorbia regis-jubae*, *Artemisia* sp. and *Periploca laevigata* shrubs, and the other in Malpaís de Güimar (in the south-east, *G. g. galloti*), a protected natural space with lava fields and dispersed xeric plants such as *Euphorbia canariensis*, *Plocama pendula*, *Periploca laevigata* and *Euphorbia balsamifera*. Lizards were captured using tomato-baited traps and were transported to the laboratory at the Universidad de La Laguna. In the laboratory, they were housed singly or in small groups in terraria placed inside a temperature-controlled room. Light was provided by fluorescent bulbs with a daylight spectrum (Reptistar, F18W 6500 K, Sylvania, OH, USA). Food was supplied every 2–3 days in the form of *Tenebrio molitor* larvae, cat food, and pieces of tomato and several fruits. Water was available continuously. At the completion of the colour measurements, all the lizards were released unharmed at their original capture sites. The animals were cared for in accordance with the guidelines published by *Anim. Behav*. (1996) **51**, 241–246.

Twenty-two *G. g. eisentrauti* (10 males, 12 females) and 19 *G. g. galloti* (12 males, seven females) were used for UV photography. Spectral reflectance data were collected on 34 *G. g. eisentrauti* (15 males, 19 females) and 26 *G. g. galloti* (15 males, 11 females). The mean snout–vent length was 117.9 ± 2.5 mm for males and 93.8 ± 1.6 mm for females of *G. g. eisentrauti*. For *G. g. galloti*, the corresponding measurements were 109.1 ± 1.5 mm for males and 97.2 ± 2.1 mm for females. Thus, all the lizards included in this study were adults (Molina-Borja *et al*., 1997). To facilitate handling, lizards were held in a cold room (4 °C) for 10 min before the experimental manipulations. Additionally, some lizards were lightly anaesthetized with an intramuscular injection of ketamine hydrochloride (250 mg kg^{-1} b.w.). Although there is no indication of short-term colour changes in this species, in most cases photographs and spectral measurements were taken within a few hours of original capture.

Colour pattern analyses

UV photography and spectrophotometry were used to characterize the reflectance patterns of male and female lizards. Both techniques have been extensively used to reveal UV reflectance patterns of vertebrate and invertebrate animals and yield complementary information (Knüttel & Fiedler, 2000). UV photography provides a convenient method to assess the spatial distribution of areas of differing UV reflectance, whereas spectrophotometry provides accurate quantitative data regarding the spectral reflectance patterns of selected colour patches independent of the sensory system of the intended signal receiver (Endler, 1990).

UV photography

For UV photography, lizards were positioned on a light stand and photographed through a prefocused macro-lens (Yashica 100 mm f/3.5 ML Macro) against a UV-reflective background (Ikonorex high-quality art paper; *c*. 40% reflectance in the 300–400 nm range). Each lizard was photographed through a UV-blocking filter that transmitted only wavelengths above 400 nm, and again through a UV-transmitting filter with a peak transmittance at 360 nm (Hoya U-360: Edmund Scientific, Barrington, NJ, USA or Tiffen 18A: The Tiffen Company, Hauppauge, NY, USA), using a UV-sensitive black and white film (Kodak TMAX 400 pro). Illumination was provided by a standard flashlight for photography within the human-visible range. For photographs in the UV range, the standard flashlight was coupled to a second flashlight (Sunpak 455), modified for UV output by removing the plastic shield that protects the flash tube. The two flashlights were set in manual mode so that the same amount of light was available for every exposure. Photographic processing and development of film material were standardized as much as possible. Most lizards were photographed in dorsal, ventral and lateral views. To provide a photographic record of colour in the human visual range, we also took colour photographs of all the lizards using a high-resolution digital camera (Sony DSC-F707).

Spectrophotometric recordings

We obtained reflectance spectra using an Ocean Optics USB2000 portable diode-array spectrometer optimized for UV detection and a PVX-2 xenon strobe light source, both from Ocean Optics B. V. (Duiven, The Netherlands). Spectra were recorded in 0.37-nm steps from 200 to 850 nm and expressed as per cent of light reflected relative to a Spectralon white diffuse reflectance standard. Measurements were taken with a reflectance probe (R200-7, Ocean Optics) consisting of a bundle of seven 200-μm-diameter optical fibres (six illumination fibres around one read fibre). The probe (NA = 0.22) was held at a 90° angle to and 5 mm from the lizard's skin, resulting in a reading spot of *c*. 2 mm in diameter. A dark current and white standard reference spectrum were taken at approximately every 10 min during measurement of lizard colour patches.

Spectra were obtained from the following body parts: head (dorsal, anterior to parietal eye), gular area (centre), cheek, lateral and ventro-lateral patches, dorsum (midpoint along the vertebral column), dorsal crossbars, ventrum (centre), leg (outer, upper thigh) and tail (dorsal, slightly distal to base). For each body region of each lizard, the spectrometer averaged 20 spectra that were graphed using OOIBase32 software from Ocean Optics. The integration time was set at 55 ms using data-smoothing level 10. All measurements were taken in the same darkened room to minimize interference from external light sources. Analyses were confined to the 300–700 nm range, which spans visible and near-UV wavelengths (infrared wavelengths were excluded because there is no evidence that lizards can see this part of the electromagnetic spectrum; Loew *et al*., 2002). Because of the limited number of spectra for other body regions and also considering conspicuousness and likely communicative importance, we concentrated our analyses on the first two (rostralmost) lateral patches and the cheek patch. Cheek patches were not present in all individuals of *G. g. eisentrauti* and in almost no *G. g. galloti*.

As similar spectra were obtained from the same lateral or cheek patches, average spectra were calculated and graphed for the first two lateral patches in each sex of both populations and for the cheek patch in *G. g. eisentrauti*. Data reliability estimations, obtained by repeating measurements twice for the UV peak of the first lateral patch of a subset of individuals, gave a value of $r = 0.81$ (repeatability ANOVA, $F_{10,11} = 10.04$, $P = 0.0001$; Lessells & Boag, 1987).

Data analyses

Our analyses were based on reflectance intensity, spectral shape and peak wavelengths within the 300–700 nm range, thus including the near-UV part of the spectrum. Two approaches were adopted to examine sex and population differences in lizard coloration. In our first approach, we calculated objective indexes of the three main dimensions of colour following procedures used previously in studies of avian coloration (Andersson *et al*., 1998; Cuthill *et al*., 1999; Örnborg *et al*., 2002; Perrier *et al*., 2002; Johnsen *et al*., 2003). Intensity (brightness or luminance of the light spectrum) was calculated by summing the per cent reflectance across the 300–700 nm range of wavelengths ($R_{300–700}$). Hue (spectral location) was estimated by $\lambda(R_{\max})$, the wavelength of maximum reflectance. The relative UV reflectance or UV chroma (the spectral purity or saturation of UV colours) was calculated using the formula $R_{300–400}/R_{300–700}$, where $R_{300–400}$ is the sum of the per cent reflectance in the 300–400 nm spectral segment. Because of non-normality in the data, we used non-parametric statistics (Siegel & Castellan, 1988) to compare the intensity, hue and UV chroma of different colour patches between sexes within each population and for same-sexed individuals between populations. The significance level for rejection of the null hypothesis was set at 0.05. All tests were two tailed.

For our second approach, we summarized the information in the reflectance spectra using principal component analysis (PCA; Cuthill *et al*., 1999). As raw data we used the medians of 5-nm-wide spectral segments, resulting in 80 median values per spectrum from 300 to 700 nm. In analyses of spectral data, the first principal component (PC1) usually explains most of the variance in the raw spectral data and is thus assumed to represent variation in intensity. Although the interpretation of the remaining principal components is somewhat controversial (Grill & Rush, 2000), it is generally assumed that PC2 and PC3 depict the weightings of components representing different aspects of spectral shape that are independent of intensity (Endler, 1990; Hunt *et al*., 1998; Cuthill *et al*., 1999). Scores from PC1, PC2 and PC3 were used as dependent variables in further statistical analyses to test for population and sex differences in lizard coloration. As PCA scores deviated strongly from a normal distribution, comparisons were again made using non-parametric tests.

Results

UV photography

Comparison of photographs taken in the visible and UV range revealed that the blue lateral, ventro-lateral and cheek patches of male *G. g. galloti* and *G. g. eisentrauti* reflect strongly in the UV. The blue patches were relatively inconspicuous in black and white photographs covering the visible range of wavelengths (Fig. 1a and c), yet they stood out markedly in photographs taken through a UV-transmitting filter (Fig. 1b and d). The blue patches were usually bordered by areas of dark skin, non-reflective in the UV range, which provided a sharp contrast between the UV-reflecting patches and their background. The differences between males from the two populations were also strikingly more conspicuous in the UV. Although usually smaller than those of males, the blue patches of females from the two populations also reflected in the UV (Fig. 1d). In addition, lizards of both sexes displayed one or more rows of yellow-cream patches interspersed between the lateral and ventro-lateral blue patches. These yellow patches were also UV reflecting, although they did not appear as bright as blue patches in UV photographs. Other colour patches, such as the dorsal yellow crossbars of male *G. g. eisentrauti*, were relatively inconspicuous in the UV range (Fig. 1b).

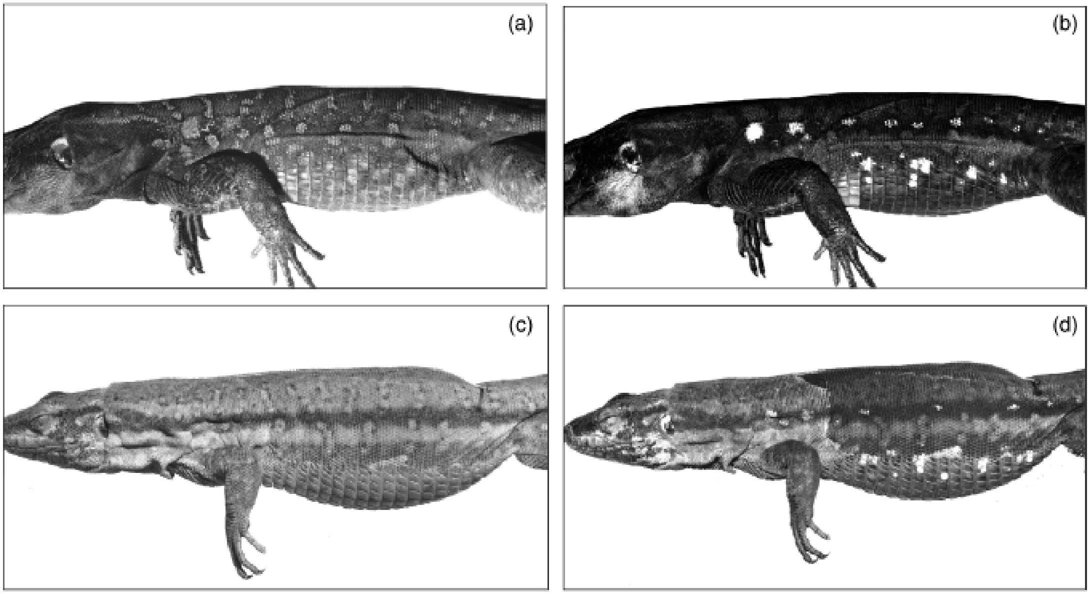

Figure 1 Lateral and ventro-lateral patches of male (top) and female (bottom) *Gallotia galloti eisentrauti* photographed through an ultraviolet (UV)-blocking filter (a and c) and through a UV-transmitting filter (b and d) with a peak transmittance at 360 nm. The white areas in (b) and (d) correspond to areas of enhanced UV reflection. The first lateral patches of the female are clearly visible through a piece of loose skin in (d).

Spectrophotometry

Spectra from the lateral and ventro-lateral patches of males and females of both populations showed a single peak in the UV range, with decaying reflectances in the visible range. The human-perceived blue is generated by the tail of the spectral curve, which belies their true nature as UV-reflecting patches (i.e. 'blue-UV' patches). The mean spectra (±SEM) for the first two lateral patches of each sex and population are graphed in Figs 2 and 3. The lateral patches of males showed greater overall reflectance (i.e. intensity) than those of females. The difference was statistically significant for the first two lateral patches of *G. g. eisentrauti*, but only for the first lateral patch of *G. g. galloti* (Table 1). The lateral patches of females, on the other hand, were more chromatic (i.e. higher UV chroma or UV saturation) and UV-shifted than those of males. The mean peak wavelengths for the first two lateral patches were higher in males (*c.* 377.5 nm) than in females (*c.* 363.4 nm) of both lizard populations, the difference being statistically significant for *G. g. galloti* but not for *G. g. eisentrauti* (Table 1).

Spectra from ventro-lateral blue patches showed a high UV reflectance but in the same range as the lateral patches, so they are not presented here. Male cheek patches from both populations also had reflectances in the UV range but were much less pronounced than those of the lateral patches (Fig. 4a and b). In *G. g. eisentrauti*, the cheek patches of males had reflectance peaks in the near-UV region $[\lambda(R_{\max}) = 393\,\mathrm{nm}]$. By contrast, the cheek patches of females peaked in the visible part of the spectrum $[\lambda(R_{\max}) = 624\,\mathrm{nm}]$. Female cheek patches had significantly lower UV chroma than those of males (Table 1). The same pattern of reflectances was apparent in a few *G. g. galloti* with cheek patches (Fig. 4a). The lateral yellow patches of lizards from both populations were also reflective in the UV range (Fig. 5), but were too small to conveniently record sufficient spectra to present any statistics. Moderate UV reflectance was also present in the ventrum of some lizards from both sexes and populations. Other body regions such as the head, dorsum, gular region, legs and tail of both populations had extremely low UV reflectance (Fig. 5).

Spectral comparisons between same-sexed individuals from the two populations revealed that males did not differ in terms of intensity or UV chroma of the first two lateral patches. However, they differed in terms of hue, with the first lateral patch of male *G. g. eisentrauti* being more UV-shifted than the corresponding patch in male *G. g. galloti*. Female *G. g. galloti* had more intensely reflective lateral patches than female *G. g. eisentrauti* (Table 2).

In addition to these sex and population differences, lizards of the same sex and population showed considerable interindividual variation in the spectral shape of the lateral patches. This variation was more pronounced in the UV than in other regions of the spectrum (see error bars in Figs 2 and 3).

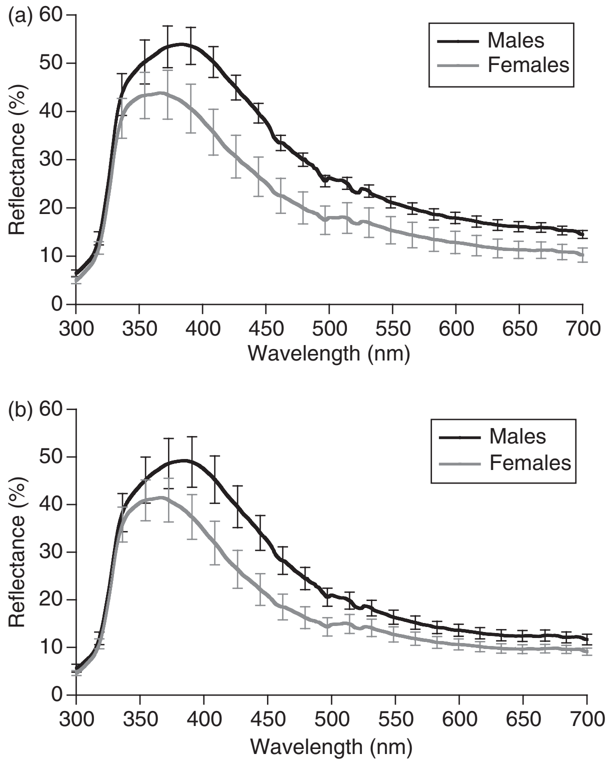

Figure 2 Reflectance spectra of the first (a) and second (b) lateral patches of males and females of *Gallotia galloti galloti*. Vertical lines: error bars (±1 SEM).

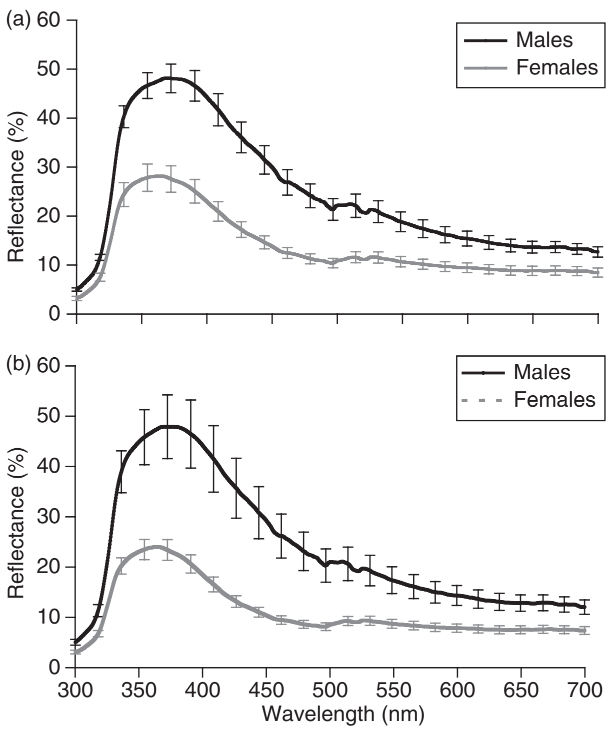

Figure 3 Reflectance spectra of the first (a) and second (b) lateral patches of males and females of *Gallotia galloti eisentrauti*. Vertical lines: error bars (±1 SEM).

Table 1 Mean (±1 SEM) intensity ($R_{300–700}$), UV chroma ($R_{300–400}/R_{300–700}$) and peak wavelength of the blue patches of male and female *Gallotia galloti*

	Intensity	*Z* *P*	UV chroma	*Z* *P*	Peak wavelength (nm)	*Z* *P*
G. g. galloti						
First lateral patch						
m (*n*=15)	32779.8±6758.7	−2.8	0.328±0.05	−2.72	384.0±15.4 9.0	−3.21
f (*n*=11)	24290.0±11285.4	0.003	0.381±0.02	0.005	366.3±9.0	0.001
Second lateral patch						
m (*n*=10)	27770.0±8463.3	−1.36	0.353±0.03	−2.57	383.1±13.4	−3.42
f (*n*=10)	21386.2±7967	NS	0.398±0.02	0.009	360.6±8.1	0.0001
Cheek patch						
m (*n*=2)	17140.3±2894.0	—	382.4			
f (*n*=1)	23902.7	—		575.8		
Gallotia galloti eisentrauti						
First lateral patch						
m (*n*=15)	28207.2±8134.3	−3.8	0.359±0.05	−0.53	372.6±16	−1.73
f (*n*=19)	15662.8±6121.8	<0.001	0.368±0.05	NS	363±9	0.08
Second lateral patch						
m (*n*=12)	27236.8±13035.0	−3.5	0.365±0.05	−0.80	370.2±13.9	−1.82
f (*n*=18)	12827.0±4681.5	0.001	0.379±0.04	NS	363.8±4.2	0.07
Cheek patch						
m (*n*=9)	21317.9±5222.7	−1.70	0.239±0.01	−3.27	393.1±36.0	−3.76
f (*n*=12)	28703.5±10968.5	0.09	0.157±0.008	<0.001	623.8±59.5	0.001

Sample sizes vary for different colour patches because reflectance of the second lateral patch and of the cheek patch could only be recorded from a subset of the available lizards.

Z, Mann–Whitney *U*-statistic for comparison between males and females; *P*, significance level; *n*, sample size; UV, ultraviolet.

PCA of sex and population colour variation

The first two or three extracted components of non-standardized spectral data accounted for 91–99% of the initial variance in the spectra from both male and female patches of the two populations (Table 3). The first component (PC1), representative of intensity, generally had very similar loadings for each 5-nm band, whereas the second component separated UV (positive loadings) from visible (negative loadings) wavelengths (Figs 6 and 7). The comparison of male and female PC1 scores resulted in statistically significant differences for the first two lateral patches of *G. g. galloti* but only for the second lateral patch of *G. g. eisentrauti* (Figs 6 and 7). On the other hand, there was no significant difference between sexes for PC1 scores from cheek patches of *G. g. eisentrauti* (Table 3a). Comparisons between same-sexed individuals from the two populations showed that the intensity (PC1 scores) of the first two lateral patches was significantly different both between males and between females (Table 3b, Figs 6 and 7). No statistically significant differences were detected in any comparisons involving either PC2 or PC3.

Congruence of results with different analyses

Our univariate and multivariate analyses of patch reflectances gave similar results in many cases. Thus, for example, intersexual differences in the intensity of the first two lateral patches were significant in three cases (of four between-sex comparisons) both in multivariate and in univariate analyses (compare Tables 1 and 3). However, univariate analyses revealed additional sex differences for hue and UV

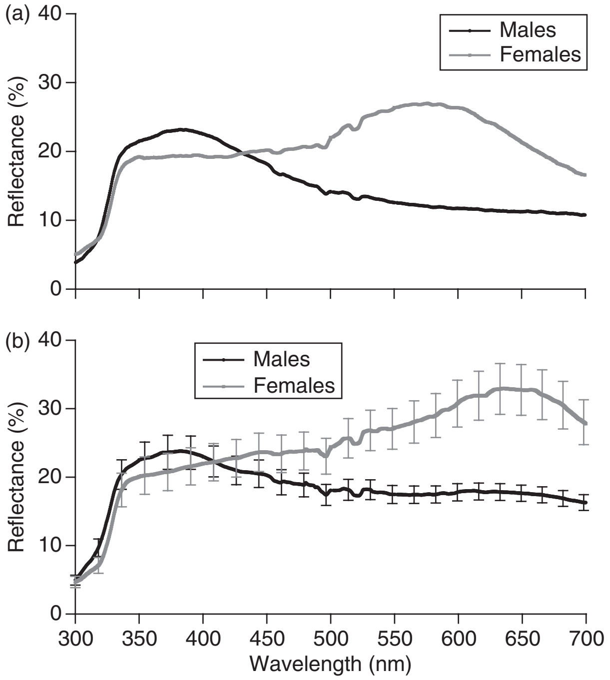

Figure 4 Reflectance spectra of the cheek patches of male and female *Gallotia galloti galloti* (a) and *G. g. eisentrauti* (b).

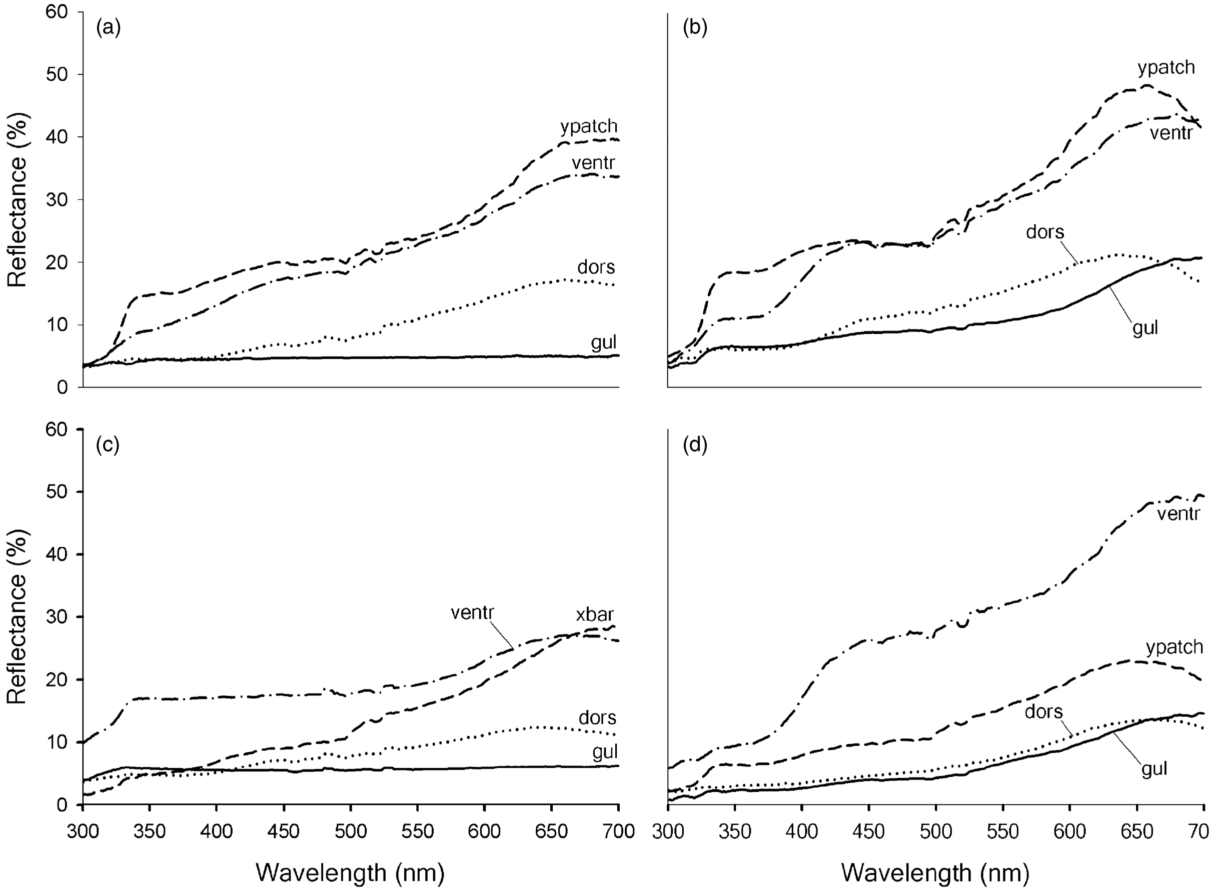

Figure 5 Representative reflectance spectra from different body parts of *Gallotia galloti galloti* males (a) and females (b) and from *G. g. eisentrauti* males (c) and females (d). Each curve represents the average of 20 spectra taken from the same lizard. ypatch, yellow patch; ventr, ventrum; dors, dorsum; gul, gular area; xbar, dorsal yellow crossbar.

Table 2 Between-population and within-sex comparisons of different spectral parameters of the first two lateral patches

	Intensity		UV chroma		Peak wavelength	
	Z	*P*	*Z*	*P*	*Z*	*P*
Males						
First lateral patch	−1.59	NS	−1.3	NS	−2.05	0.041 (Ggg > Gge)
Second lateral patch	−0.52	NS	−0.33	NS	−1.71	0.09
Females						
First lateral patch	−2.6	0.008 (Ggg > Gge)	−0.75	NS	−0.40	NS
Second lateral patch	−2.9	0.003 (Ggg > Gge)	−1.05	NS	−1.0	NS

Sample sizes as in Table 1.

Z, Mann–Whitney *U*-statistic; *P*, significance level; UV, ultraviolet. (Parentheses: sign of the difference; Ggg, *Gallotia galloti galloti;* Gge, *Gallotia galloti eisentrauti.*)

chroma. In general, univariate analyses detected differences across all the three main dimensions of colour, whereas PCA only detected differences in intensity (i.e. PC1 scores). A discrepancy between the results obtained using PCA-based estimates of the three colour dimensions and alternative methods of analysis has been noted by previous workers (Grill & Rush, 2000). Clearly, no single method of analysis is suitable for all colour data types, and all the available methods have potential shortcomings (Grill & Rush, 2000; Thorpe, 2002). Nevertheless, univariate and multivariate analyses of spectral data are preferable to subjective ratings of lizard coloration, especially when information on the visual system of the species under study is not available.

Table 3 (a) Between-sex comparisons of PC scores resulting from PCA applied to nonstandardized spectral data of the first two lateral patches from the two populations studied. (b) Between-population, within-sex comparisons of PC scores

	PC1	PC2	PC3
(a)			
Gallotia galloti galloti			
First lateral patch	−10.3**	−0.06	
(m, f)	(63.3, 94.2)	(27.8, 4.3)	(6.6)
Second lateral patch	−7.83**	−0.63	
(m, f)	(89.5, 94.0)	(5.7, 4.0)	(3.91)
G. g. eisentrauti			
First lateral patch	−0.98	−1.08	−0.22
(m, f)	(81.2, 83.9)	(12.5, 13.7)	(4.6, 1.4)
Second lateral patch	−4.22**	−0.81	−1.27
(m, f)	(92.2, 87.3)	(5.0, 9.1)	(2.0, 2.5)
Cheek patch	−0.46	−1.23	−0.31
(m, f)	(49.4, 50.9)	(13.2, 10.8)	(10.1, 9.7)

	PC1		PC2	
	m	f	m	f
(b)				
First lateral patch	−6.6	−6.25	−0.95	−0.47
	< 0.001	< 0.001	NS	NS
Second lateral patch	−4.0	−7.63	−0.96	−1.4
	< 0.001	< 0.001	NS	NS

Values shown are Mann–Whitney *U*-statistics.

**$P<0.001$. Values in parentheses are % of variance explained by that component.

m, males; f, females; PC, principal component; PCA, principal component analysis.

Discussion

Lacertid behaviour and coloration have been the focus of an increasing number of research reports over the last decade (e.g. Díaz, 1993; Olsson, 1993, 1994*a*,*b*; Salvador *et al.*, 1996; Molina-Borja *et al.*, 1997; Molina-Borja, Padrón-Fumero & Alfonso-Martín, 1998; Martín & Forsman, 1999; Galán, 2000; López & Martín, 2001; Carretero, 2002; López, Martín & Cuadrado, 2002). Lacertids are diurnally active lizards with a well-developed visual system that includes the capacity for colour discrimination (Swiezawska, 1950; Anh, 1968; Underwood, 1970). Many inhabit exposed, full sunlight environments and are heavily reliant on their acute vision during foraging and intraspecific interactions, all studied species having characteristic visual displays (e.g. Verbeek, 1972; Carpenter & Ferguson, 1977; Desfilis, Font & Guillén-Salazar, 2003). Sexual dichromatism is widespread in lacertids, and males often show conspicuous colours that may be sexually selected (Cooper & Greenberg, 1992; Olsson & Madsen, 1998). However, almost without exception, previous studies with lacertids have used human vision or standards based thereon to assess coloration and are thus implicitly based on the assumption that lizards perceive colours in the same way that we do.

Our results show that UV reflectance is present in colour patches of males and females of the two *G. galloti* populations found in Tenerife, and underscore the need for assessments of lizard coloration that are independent of human visual perception (Bennett *et al.*, 1994). Peak reflectance of the blue patches of *G. galloti* is in the near-UV region, very close to the absorption wavelength peak of UV receptors in lizards with known UV vision (Fleishman *et al.*, 1993; Loew, 1994; Ellingson, Fleishman & Loew, 1995; Loew *et al.*, 1996, 2002; Kawamura & Yokoyama, 1998), and agrees with data on UV reflectance in other lizards (e.g. Fleishman *et al.*, 1993; LeBas & Marshall, 2000; Blomberg *et al.*, 2001; Macedonia, 2001; Stoehr & McGraw, 2001; Macedonia *et al.*, 2003). The blue-UV patches are, particularly in males, surrounded by areas of non-reflective black skin, which would tend to make them highly conspicuous (Endler, 1992). However, the presence of UV-reflecting patches cannot by itself be taken as evidence for a signal function. A fundamental premise of studies of the role of UV in intraspecific communication is that the UV-reflectance patterns are visible to the animals producing them. Among lizards, UV vision has so far been confirmed in 19 iguanid and five geckonid species (Alberts, 1989; Fleishman *et al.*, 1993, 1997; Loew, 1994; Ellingson *et al.*, 1995; Loew *et al.*, 1996, 2002). In fact, evidence for UV vision has been found in almost every lizard species in which it has been sought with appropriate experimental techniques, including nocturnal lizards and those lacking UV-reflecting colour patches (Loew, 1994; Loew *et al.*, 1996; Macedonia *et al.*, 2003). No studies of visual pigments or spectral sensitivity have been conducted with any lacertid, but the ubiquity of UV vision among squamate reptiles suggests that lacertids may have UV-sensitive vision. In support of this contention, preliminary evidence obtained using electroretinography shows that the eyes of *G. galloti* are sensitive to light in the near-UV waveband, very likely by means of an independent photopigment similar to the UV-sensitive photopigment found in other lizards (Palacios, Herrera, Desfilis & Font, unpubl. data).

Sexual dichromatism

Spectrophotometry revealed previously unnoticed sex differences in the intensity, hue or UV chroma of several colour patches in our two lizard populations. In *G. g. eisentrauti*, the cheek patches of males had higher UV chroma and were more UV-shifted than those of females. In both populations, the lateral patches of males were more intensely reflective than those of females, but females had more chromatic and UV-shifted lateral patches, with peak reflectances 10–20 nm below those of males. Assuming that *G. galloti* are capable of UV vision, these results suggest that the blue-UV patches are sexually dichromatic in the lizards' own visual world, primarily so in the UV wavelength band, although some degree of dichromatism seems to exist also in part of the human-visible range (see Figs 2 and 3). The magnitude of the sex differences in intensity, particularly in *G. g. eisentrauti*, exceeds that in most published examples of UV dichromatism in birds (Andersson *et al.*, 1998; Hunt *et al.*, 1998), suggesting that

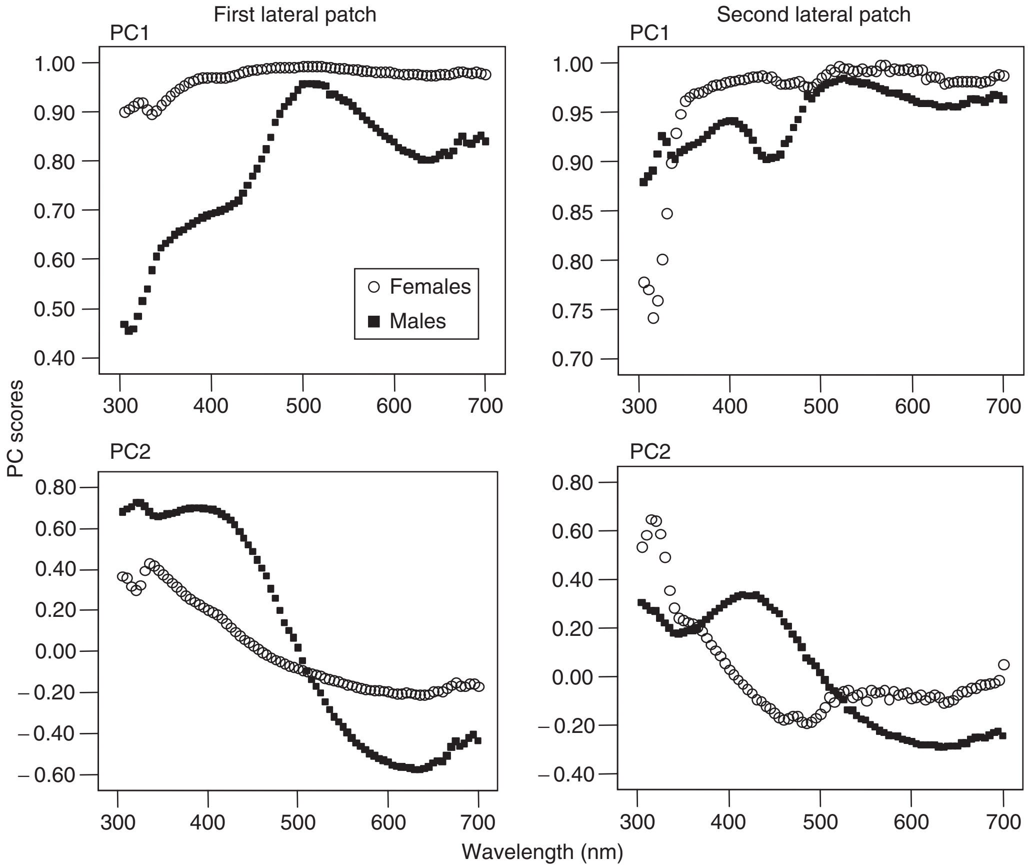

Figure 6 Principal component (PC) scores of each 5-nm-wide band of the reflectance spectra for the first (left panels) and second (right panels) lateral patches of male (black squares) and female (open circles) *Gallotia galloti galloti*.

UV reflectance may be an important component of intersexual communication in these lacertids.

Sexual dichromatism in the visible range is believed to provide important cues allowing recognition of the sex of conspecifics in many lizards (reviewed in Cooper & Greenberg, 1992). Males painted to resemble females may be courted by other males (e.g. Kramer, 1937; Kitzler, 1941; Cooper & Burns, 1987), whereas females given artificial 'male-like' coloration are treated aggressively by males (e.g. Harris, 1964; Werner, 1978; Cooper & Burns, 1987; Cooper & Vitt, 1988). Dichromatism in the UV range may likewise provide a reliable cue to sexual identity. Although lizards could obtain information about the sex of conspecifics from other cues (e.g. sexual size dimorphism, behavioural cues, chemical cues), a different male/female UV signal should enhance sex recognition, particularly during interactions at close range. The different size of the blue-UV patches in males and females also suggests a role in sex-related signalling.

Population differences and ambient light

According to Thorpe & Richard (2001), males of our two study populations differ only in the size and distribution of their blue-UV patches. Our results, however, provide evidence that the blue-UV patches have different spectral characteristics in males (and also females) from the two populations, particularly in the UV range. The biological significance of these differences or whether they are perceived by the lizards is unknown. To the UV-blind human visual system, adult lizards can be correctly assigned to one or the other population based solely on variation in the size and distribution of their patches. To the lizards, the different spectral characteristics of blue-UV patches should, if anything, make the differences between northern and southern lizards more conspicuous and improve population recognition in areas in which the two may overlap.

It is well established that perception of visual signals depends not only on the receiver's sensory system but also on the ambient light spectrum and the visual background against which they are viewed (Endler, 1991, 1992, 1993; Fleishman & Persons, 2001; Macedonia, 2001). Our two study populations occupy habitats that differ in cloud and plant cover and, therefore, in the level and quality of ambient light. *G. g. eisentrauti* live in the northern coastal strip, which is cloudy, warm, humid and densely vegetated. They have to move into the open to thermoregulate, but they also wander around under shrubs in shaded areas. Although specific measurements of ambient light have not been conducted,

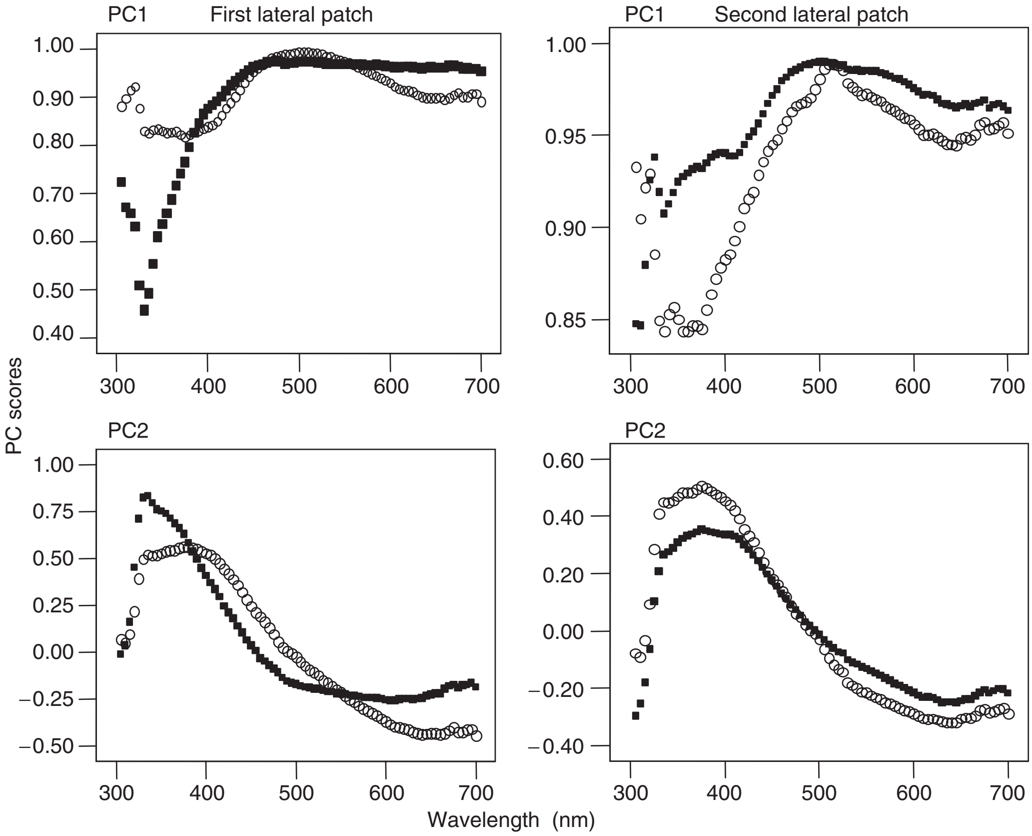

Figure 7 Principal component (PC) scores of each 5-nm-wide band of the reflectance spectra for the first (left panels) and second (right panels) lateral patches of male (black squares) and female (open circles) *Gallotia galloti eisentrauti*.

lizards in this part of the island inhabit a light environment that is probably white coloured and rich in all wavelengths ('cloudy' light habitat; Endler, 1992, 1993). The presence of clouds increases light intensity (because of scattering) and would tend to make the blue-UV patches highly reflective. In addition, as chlorophyll absorbs short-wavelength light, the blue-UV patches would likely stand out against the background vegetation (Andersson *et al.*, 1998; Macedonia, 2001). On the other hand, *G. g. galloti* are found in the central and southern parts of the island, which are hot, arid and sparsely vegetated. Given the predominantly blue skies in this habitat, the shade provided by boulders, shrubs or, depending on the position of the sun, the lizard's own body will probably be biased towards short wavelengths ('woodland shade' light habitat; Endler, 1992, 1993). Blue, UV-reflecting patch matching to this ambient light spectrum should maximize conspicuousness (Endler & Théry, 1996). Thus, the shortwave reflectance of the blue-UV patches seems to be ideally suited for signalling in the ambient light spectra in which they are most frequently displayed. It is conceivable that the different spectral characteristics of blue-UV patches from the two populations have evolved to take advantage of subtle differences in the light spectra of their respective habitats (Fleishman, 2000; Macedonia, 2001; Leal & Fleishman, 2004). Irradiance spectra from the habitats of the two populations will be required to test this possibility.

Thorpe & Richard (2001) argued that differences in the size and distribution of blue-UV patches could function to reduce interbreeding between northern and southern population lizards. According to this hypothesis, UV reflectance patterns provide a mechanism for assortative mating via female choice, allowing females to mate preferentially with males from their own population. Thorpe & Richard (2001) showed that geographic variation in the size and distribution of the blue-UV patches is linked to patterns of gene flow between northern and southern populations of *G. galloti*. This association is congruent with the notion that variation in UV reflectance patterns may promote reproductive isolation between the two populations. However, as the UV-reflecting patches are clearly visible to a human observer as blue patches, a comparison of northern and southern males in the human-visible range should yield identical results and the presence of UV reflectance is not crucial to Thorpe & Richard's main conclusion (see also Thorpe, 2002).

Interpopulation variation in sexual dichromatism

The main difference between the two populations was the greater intensity of the lateral patches of *G. g. galloti* females compared with *G. g. eisentrauti* females. In addition, the lateral patches of males of the two populations had somewhat different mean peak wavelengths but similar intensities. Therefore, the two populations show a different pattern of intersexual coloration, intensity differences between males and females being greater for *G. g. eisentrauti* than for *G. g. galloti*. Geographic variation in sexual dichromatism has been described in other lizard species (e.g. McCoy *et al*., 1997; Wiens, Reeder & Montes de Oca, 1999; Macedonia *et al*., 2002), but the selective forces responsible for this variation in *G. galloti* remain elusive.

Possible role in male–male competition and mate choice?

Our results also show large amounts of spectral shape variation in lateral patches from individuals of the same sex and population, the interindividual variation being most marked in the UV region of the spectrum. Previous studies have shown that colour patches in male lizards may signal status (Thompson & Moore, 1991; Zucker, 1994), are related to fighting ability (Olsson, 1994*a*) or affect dominance relationships (Rand, 1991; Carpenter, 1995). Slight differences in the human-visible colour of the first lateral patch of winners and losers were reported in staged encounters between male *G. g. galloti* (Molina-Borja *et al*., 1998). No UV status signals have been described in any vertebrate, but it seems conceivable that the colour differences between winners and losers could extend to or even be more conspicuous in the UV. If that were the case, blue-UV patches could be used as cues to male fighting ability in *G. galloti* and perhaps in other species as well. Unfortunately, none of the studies cited above considered potential variability in the UV reflectance of colour patches.

That the lateral patches of females also show large interindividual variation raises some intriguing possibilities. It has been shown that differences in the coloration of female lizards may indicate their receptive state (e.g. Watkins, 1997; Cuadrado, 1999). Among vertebrates, assortative mating with respect to UV reflectance has been studied most extensively in birds (Bennett *et al*., 1996, 1997; Hunt *et al*., 1997, 1998, 1999; Andersson *et al*., 1998; Johnsen *et al*., 1998; Sheldon *et al*., 1999; Siitari & Huhta, 2002; Siitari *et al*., 2002) and fish (Kodric-Brown & Johnson, 2002; Macías-García & Burt de Perera, 2002; Smith *et al*., 2002). Only a single study has demonstrated an effect of UV reflectance on patterns of mate choice in lizards. In the agamid *Ctenophorus ornatus*, males tend to associate with females with a high throat chroma (i.e. saturation) between 370 and 400 nm (LeBas & Marshall, 2000). Female throat coloration seems unrelated to female quality, but may indicate female receptivity. Interestingly, in *C. ornatus* the two sexes show variation in the UV reflectance of throat patches. However, variation in male throat reflectance does not affect female mate choice (LeBas & Marshall, 2001). Experiments are currently underway to test the role of UV reflectance patterns in male–male competition and mutual mate choice in *G. galloti*.

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