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Reflectance of sexually dichromatic UV-blue patches varies during the breeding season and between two subspecies of *Gallotia galloti* (Squamata: Lacertidae)

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Body coloration is sexually dimorphic in many vertebrate species, including lizards, in which males are often more conspicuous than females. A detailed analysis of the relative size of coloured patches and their reflectance, including the ultraviolet (UV) range, has rarely been performed. In the present work we quantified sexual dimorphism in body traits and surface area of all lateral patches from adult females and males of two subspecies of *Gallotia galloti* (*G. g. galloti* and *G. g. eisentrauti*). We also analysed the magnitude of sexual dichromatism in the UV-visible reflectance of such patches and the changes in patch size and brightness during the reproductive season (April–July). Males had significantly larger patch areas (relative to their snout-vent length) and higher brightness (mainly in the UV-blue range) than did females in both subspecies. The comparison of relative patch areas among months did not reach statistical significance. However, patch brightness significantly changed during the breeding season: that of the UV-blue (300–495 nm) range from lizards of the two subspecies was significantly larger in June than in April, while brightness in the 495–700 nm range in *G. g. galloti* was larger in May, June, and July than in April. A different pattern of dichromatism was also detected in the two populations, with *G. g. eisentrauti* being more sexually dichromatic than *G. g. galloti*. We discuss the results in terms of possible evolutionary causes for the sexual dichromatism related to different ecological characteristics of the habitats where each subspecies live.

ADDITIONAL KEYWORDS: lizards – monthly variation – sexual dichromatism – UV-blue reflectance.

INTRODUCTION

Body coloration has been extensively studied in many animal taxa (Hill & McGraw, 2006) and contexts, from mate choice to social signalling or individual recognition (Cooper & Greenberg, 1992; Andersson, 1994; Losey *et al*., 1999; Seehausen, van Alphen & Lande, 1999; Hoffman & Boulin, 2000), and is interpreted to result from an evolutionary trade-off between crypsis in relation to predators or prey (natural selection, Slagsvold, Dale & Kruszewicz, 1995; Macedonia, Brandt & Clark, 2002; Stuart-Fox *et al*., 2003, 2004; Husak *et al*., 2006; Baird, 2008) and conspicuousness for conspecifics (sexual and natural selection; Andersson, 1994; Bradbury & Vehrencamp, 2011). Moreover, natural selection may produce rapid changes in body coloration as species shift between habitats or as a response to environmental change (Endler, 1980, 1986). Thus, geographic variation in visual signals, including coloured patches and displays, has been documented in several lizard species (McCoy *et al*., 1997; Martins, Bissell & Morgan, 1998; Stuart-Fox *et al*., 2004).

Visual signalling occurs within both the visible and the ultraviolet (UV) range of the electromagnetic spectrum; the UV range is hidden to the unaided human eye but is present in the reflectance of coloured patches of several vertebrates (Cuthill *et al*., 1999; Kodric-Brown & Johnson, 2002). The perception of UV reflectance is important in foraging and sexual

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signalling, and the UV component in body-coloured patches is related to the condition or status of the bearer (birds, Sheldon *et al*., 1999; fish, Macías-García & Burt de Perera, 2002; Siebeck, 2004). The contribution of patch UV reflectance to vertebrate sexual dichromatism has not received much attention, although differences between the sexes have been described for different bird and lizard species (Hunt *et al*., 1998; Eaton & Lanyon, 2003; Mays *et al*., 2004; Font, Pérez i de Lanuza & Sampedro, 2009; Martin *et al*., 2013).

Coloured patches are common in many lizard species and occur on the throat, belly, lateral aspect of the head or body trunk, and the tail of iguanids, agamids, crotaphytids, varanids, or lacertids (Cooper & Greenberg, 1992). The patches are differently developed in both sexes, with those of males usually being larger (and/or brighter) than those of females (Olsson, 1994b; Stuart-Fox & Ord, 2004; Font *et al*., 2009). Lizard species also display elaborate UV reflectance patterns (Fleishman, Loew & Leal, 1993; LeBas & Marshall, 2000; Thorpe & Richard, 2001; Macedonia *et al*., 2002; Macedonia, Echternacht & Walguarnery, 2003; Molina-Borja, Font & Mesa-Avila, 2006). Sexual dichromatism has been documented in brightness of the visible and UV ranges in several species (McCoy *et al*., 1997; Macedonia *et al*., 2002, 2004; Molina-Borja *et al*., 2006; Pérez i de Lanuza & Font, 2007; Font *et al*., 2009). However, there is very little published information about the relative size of coloured areas of males and females (see Jordan *et al*., 2008; Font *et al*., 2009) or the seasonal changes in these signals (Garcia, Rohr & Dyer, 2013). A change through time in the size and/or reflectance of badges could signal changing motivational state and/or condition of the individuals and therefore have an influence during intra- and/or intersexual interactions along the breeding cycle.

Gallotia galloti is an endemic, sexually dichromatic, canarian lizard species with four subspecies: three in Tenerife Island (*G. g. galloti*, *G. g. eisentrauti*, and *G. g. insulanagae*) and one (*G. g. palmae*) in La Palma Island. The two main subspecies from Tenerife (*Ggg* and *Gge*) differ phenotypically, mainly in body size and coloration of adult males: *Gge* is larger [the mean snout-to-vent length (SVL) is around 115 mm] and has dorsal rows of small yellow to green spots and conspicuous blue cheek patches on both sides of the gular area, whereas *Ggg* is smaller (mean SVL is around 107 mm) and lacks dorsal rows and the cheek patches (see Molina-Borja, Padrón-Fumero & Alfonso-Martín, 1997 and Molina-Borja *et al*., 2006 for more details). Dark- to light-blue lateral patches are present in males and females of all subspecies. Lateral patches of males are generally more numerous, larger, and have higher brightness in the UV range than those of females, and are larger in *Ggg* than in *Gge* (Molina-Borja *et al*., 1997, 2006). There is considerable geographic colour variation in the species throughout the island, mainly in the size and distribution of the blue patches, which has been linked to different latitudinal biotopes (Thorpe & Brown, 1989). Males patrol their home area during the breeding season and when two males meet they exhibit agonistic displays, fights, and/or chases (Molina-Borja, 1985). Male patch colour in both subspecies may function for intraspecific communication (Thorpe & Brown, 1989; Molina-Borja, Padrón-Fumero & Alfonso-Martín, 1998); during agonistic displays, males lower their gular area and compress the body laterally, which makes the rows of latero-dorsal and latero-ventral blue patches more visible (Molina-Borja, 1981, 1985, 1987).

The two subspecies from Tenerife Island also differ in the type of habitat they inhabit: more cloudy and covered by vegetation in the north (*Gge*), and more sunny and xeric in the centre and south of the island (*Ggg*). The varying coloration pattern could reflect different evolutionary selection patterns in each subspecies (Thorpe & Brown, 1989; Endler, 1991, 1992; Baird, Fox & McCoy, 1997; Macedonia *et al*., 2003).

Our field observations suggest that the lateral patches of males of the two subspecies become more colourful during the breeding season and also that cheek marks of *Gge* males are only evident at that time. Therefore, we investigated whether there would be a temporary change in the size of the blue patches and/or their brightness during the breeding season.

In the current work we quantified the following features in a population of each subspecies: (1) sexual dimorphism in body, head, and limb traits; (2) sexual dichromatism [measured as: (a) the relative size of lateral (dorso and ventral) patch surface areas; and (b) brightness of UV-blue (300–495 nm) and the rest of the range (495–700 nm) from these patches]; and (3) the monthly variation in the last two variables (points a and b within point 2) through breeding time.

MATERIALS AND METHODS

Lizard sampling and maintenance

Adult lizards of both sexes were collected in two natural habitats in Tenerife: (1) at El Pris (northeast of the island, *Gge*) with *Euphorbia canariensis*, *Euphorbia regis-jubae*, *Opuntia dilenii*, and *Rubia fruticosa* as the main plants; and (2) in Malpaís de Güimar (in the southeast, *Ggg*), a protected natural space with lava fields and dispersed xeric plants such as *E. canariensis*, *Plocama pendula*, *Periploca laevigata*, and *Euphorbia balsamifera*.

In all cases, lizards were captured using tomato-baited traps and were transported to the laboratory at the Universidad de La Laguna. During their short stay there (a maximum of 3 days), they were housed singly in terraria placed inside rooms with controlled temperature (28 °C) and a light–dark cycle (13 h–11 h). Light was provided by fluorescent tubes with daylight spectrum including UV (Reptistar, F18W 6500K; Sylvania, Erlangen, Germany). Air humidity inside the rooms was around 60%. Each terrarium was provided with artificial grass substratum and a tile as shelter. Food was supplied every 2 days and consisted of pieces of tomato and banana, and *Tenebrio* larvae. Water was continuously available.

Lizards were sampled during April, May, June, and July of 2008. A total of 52 males and 31 females were captured for *Ggg* and 50 males and 37 females for *Gge*. In order to avoid lizard resampling, they were marked by toe clipping (the more distal phalange of one toe in two feet, at most, of each individual) and can traps were placed at different sites each time. Although toe-clipping has been shown to affect clinging capacity in some arboreal lizards (Bloch & Irschick, 2005), running speed of terrestrial lizards is not affected (Borges-Landáez & Shine, 2003). Our own experience shows that lizards first caught do have some missing toes, even in areas not previously sampled (by us or other research teams); moreover, lizards we toe-clipped have been recaptured even 1 or 2 years later.

Measurement of lateral-coloured patches and biometric parameters

On the day of capture we took a digital photograph from each lizard body side by gently placing it against a transparent plastic sheet provided with an attached millimetre scale. The photographs were transferred to computer files and analysed using UTHSCSA Image Tool v 2.0 program to calculate area measurements (in mm^2) of all latero-dorsal and latero-ventral UV-blue patches from both body sides. Biometric parameters were also taken, including: SVL, body mass (BM), pileus width (PW), head depth (HD), and fore- and hindlimb length (FLL and HLL, respectively), defined elsewhere (Molina-Borja *et al*., 1997). As PW and HD were positively and highly correlated, for the analysis of sexual dimorphism we generated a new variable for head size as the square root of PW × HD.

In addition, as the morphometric variables were all positively correlated, for further analyses we obtained a multivariate index of size for each sex of both populations as the first principal component (PC1) resulting from a Principal Component Analysis (PCA; non-rotated solution based on correlation matrix) applied to their corresponding standardized values. Percentages of total variance accounted for in PC1 were 78.3% and 70.0%, respectively for males and females of *Ggg*, and 80.1% and 73.6% for those of *Gge*.

Spectrophotometric analyses

We obtained reflectance spectra using an Ocean Optics USB2000 (Duiven, The Netherlands) portable diode-array spectrometer optimized for ultraviolet detection and a PX-2 Xenon strobe light source. 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. We took measurements using a fibreoptic probe held at a 90° angle to, and 5 mm from, the lizard's skin, resulting in a reading spot of approximately 2 mm in diameter. A dark current and white standard reference spectrum were taken every 10 min or so during measurements of lizard colour patches.

Spectra were obtained from latero-dorsal and latero-ventral patches of a sample of males and females from each population and also from the cheek patches of *Gge* males (very few males of *Ggg* showed a measurable cheek mark). For each coloured patch the spectrometer averaged 20 spectra that were graphed using OOIBase32 software from Ocean Optics. 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, considering separately the UV-blue (300–495 nm) and the rest of the range (495–700 nm, see below). As spectra for both latero-dorsal and latero-ventral patches of both body sides had similar shapes, and also considering conspicuousness and likely communicative importance, we concentrated our analyses on the first rostral most right lateral patch and the right male cheek patch. Large patch size (7–8 mm) only occurred in few male specimens and as the optic probe reading spot was 2 mm, we only took one measurement from each patch centre. Background body coloration has been measured, in past research, for several lizards and over several months, and we did not find a significant change in brightness among months in the three spectral ranges (Kruskal–Wallis test, $Z = -0.219$, -0.218, -0.41, $N = 10$, $P > 0.05$ in all cases).

To analyse monthly variation in sexual dichromatism, patch areas and reflectances were obtained from different adult males and females of both populations captured in each of the four months of the study (the breeding season: April–July). As no lizard was recaptured in successive months, we could not compare the coloration of the same lizard at different time points during the breeding season.

For each selected colour patch, we calculated objective indexes of the main dimensions of colour following procedures used previously in studies of avian and lizard coloration (Andersson, Örnborg & Andersson, 1998; Cuthill *et al*., 1999; Örnborg *et al*., 2002; Perrier *et al*., 2002; Johnsen *et al*., 2003). Brightness (luminance or total intensity of the light spectrum) was calculated separately for the UV-blue and for the rest of the visible range by summing the per cent reflectance across the 300–495 nm range of wavelengths ($R_{300–495}$) and the 495–700 nm range ($R_{495–700}$), respectively. Hue (spectral location) was estimated by λ (R_{max}), the wavelength of maximal reflectance. Relative UV-blue reflectance or UV-blue chroma (the spectral purity or saturation of UV-blue colours) was calculated using the formula $R_{300–495}/R_{300–700}$, where $R_{300–700}$ is the sum of the per cent reflectance in the 300–700 nm spectral range.

After completion of the measurements, all lizards were released unharmed at their original capture sites. During their stay in captivity the animals were cared for in accordance with guidelines published by Animal Behaviour (ASAB/ABS, 2012: 83, 301–309); the research received official approval from the Ethics and Animal Welfare Committee of the University of La Laguna (reference CEIBA2011-0020). To capture the animals we had previously obtained official permission from the Cabildo of Tenerife.

Data and statistical analyses

Data were introduced into computer files and analysed using several tests from the SPSS 19.0 statistical package. Variables were standardized and tested first for normality and homoscedasticity requirements and then appropriate tests were used.

Sexual dimorphism in body size and other biometric traits

Sexual size dimorphism (SSD) was calculated for each population, using the Lovich & Gibbons (1992) formula, as: [(mean male size/mean female size) – 1].

Some analyses have provided evidence that commonly used size-adjusting methods for among-population studies of morphological variation are not statistically adequate (McCoy *et al*., 2006). Thus, analysis of covariance (ANCOVA) is based on the assumption of small variance in the covariate (body size), and residual analysis assumes that scaling relationships are equal among the groups (populations or sexes). Moreover, use of the first principal component (PC1) of pooled data to be regressed against each trait also assumes similar scaling relationships among groups. As there were large variances in body size, and the scaling relationships between head or body traits and SVL were different for both populations and sexes of the present study (data not shown), we did not use residual values or principal component values from pooled population data for our analyses.

Instead, as males and females of the two populations of *G. galloti* differed significantly in SVL, we used relative trait sizes (in relation to SVL, arcsine square-root transformed), after first testing that these data were not skewed or strongly non-normal. For between-sex and between-population comparisons, we used multivariate analysis of variance (MANOVA), with population and sex as fixed factors.

Sexual dichromatism in patch area and reflectance

Relationship of total patch area or reflectance parameters with the multivariate size index (PC1) for each sex and population was analysed using non-parametric correlations (Spearman's rho) as a result of some variables not fulfilling normality and homoscedasticity requirements. In order to compare sexes and populations, for every male and female we calculated a relative measurement of their patch area as the square root of the total coloured area (latero-dorsal and latero-ventral blue patches) divided by SVL. We also calculated relative patch size as the sum of all patch lengths (measured at their largest width, in a rostral to caudal direction) divided by SVL. The comparison (two-factor ANOVA) of relativized patch lengths for a data subset of the two lizard populations did not show different results (population effect: $F_{1,24} = 10.08$, $P = 0.004$; month effect: $F_{3,24} = 1.56$, $P = 0.224$; interaction effect: $F_{3,24} = 0.087$, $P = 0.967$) from those found when using relativized patch areas (see the Results). Therefore, we decided to use this last relativized measurement for statistical calculations on the whole data set. These data were standardized by arcsine square root and application of two-way ANOVA (sex and population as factors). Monthly changes of relative patch areas within each population were analysed using two-way ANOVA with month and sex as fixed factors. The significance level was set at alpha = 0.05 and Bonferroni correction was applied to correct for the probability of an increase of Type I errors when applying multiple tests to the same data.

For reflectance data, we first calculated correlations (Spearman's rho) among the raw figures of the variables (Table S1); afterwards they were standardized [$\log_{10}$ for $R_{300–495}$, $R_{495–700}$ and λ (R_{max}), and arc sin square root for UV-blue chroma] and MANOVA was applied to compare between-sex and among-month variation (post-hoc analyses with Bonferroni test) in each population. As cheek patch data for males of both subspecies did not fit normality and

homoscedasticity requirements, monthly variation was analysed using the non-parametric Kruskal–Wallis test. The significance level for rejection of the null hypothesis was set at 0.05. Data reliability estimations, obtained by repeating reflectance measurements twice in a subset of individuals, gave a value of $r = 0.81$ (repeatability ANOVA, $F = 10.04$, $P = 0.0001$; Lessells & Boag, 1987).

RESULTS

Sexual dimorphism in body size and other biometric traits

Means (± standard error), minimum and maximum values, and sample size for each biometric trait, including patch area of each sex from each population, are shown in Table S2. Sexual side dimorphism, as measured using Lovich & Gibbons's index, was 0.279 and 0.228, respectively, for *Gge* and *Ggg*.

The ANOVA results showed a significant difference in SVL, both between sexes (male SVL was larger than female SVL, $F_{1,158} = 283.06$, $P < 0.0001$) and between populations (individuals of *Gge* had larger SVL than did those of *Ggg*, $F_{1,158} = 20.46$, $P < 0.001$), but no significant interaction effect ($F_{1,158} = 0.174$, $P = 0.67$). MANOVA for the other biometric variables showed significant differences between sexes ($F_{4,149} = 34.56$, $P < 0.001$) and between populations ($F_{4,149} = 28.85$, $P < 0.001$), and a significant effect of the interaction ($F_{4,149} = 5.32$, $P < 0.001$). Univariate tests showed that these differences were mainly caused by males having relative head sizes and patch areas significantly larger than those of females, and individuals of *Ggg* having relatively larger traits than those of *Gge*. The interaction between population and sex was significant only for the relative FLL (Table 1).

Table 1. Univariate comparisons (within MANOVA) of male and female biometric traits from both populations

Factor	Dependent variable	d.f.	*F*	*P*
Population	HW_HD_SVL	1	10.26	0.002*
	FLL_SVL	1	14.22	< 0.001*
	HLL_SVL	1	6.69	0.011*
	TPA_SVL	1	67.50	< 0.001*
Sex	HW_HD_SVL	1	85.96	< 0.001*
	FLL_SVL	1	2.65	0.105
	HLL_SVL	1	1.37	0.244
	TPA_SVL	1	51.06	< 0.001*
Population × sex	HW_HD_SVL	1	0.46	0.499
	FLL_SVL	1	15.44	< 0.001*
	HLL_SVL	1	0.34	0.559
	TPA_SVL	1	3.36	0.068
Error		152		

d.f., degrees of freedom; HW_HD_SVL, FLL_SVL, HLL_SVL, and TPA_SVL: relative sizes of head, forelimbs, hindlimbs, and total patch area, respectively.
*Significant differences after Bonferroni correction (alpha = 0.0164).

Relationship of patch area and reflectance to body size

There was no significant relationship between body size or BM of males or females and the number of lateral coloured patches (Spearman's rho, $P > 0.05$ in all cases).

In general, the multivariate size index was correlated positively and significantly with patch surface area in both sexes of the two populations (Table 2 and Fig. S1a,b). However, it was not significantly correlated with any reflectance parameter, except for a positive correlation with brightness of the 495–700 nm range in *Ggg* female patches (Table 2).

The area of the first latero-dorsal patch and its reflectance parameters were not significantly correlated (Spearman's rho, $P > 0.05$ in all cases) in any sex of both populations.

Sexual dichromatism in patch area and monthly variation

Two-way ANOVA confirmed that males had relatively larger patch areas than females ($F_{1,66} = 22.62$, $P < 0.001$ for *Ggg*, and $F_{1,76} = 21.30$, $P < 0.0001$ for *Gge*; Fig. 1). Although relative patch areas were somewhat larger during May or June than in the other months, ANOVA did not detect significant differences in any population ($F_{3,66} = 0.396$, $P = 0.75$, for *Ggg* and $F_{3,76} = 1.47$, $P = 0.23$, for *Gge*). There was no significant effect of the interaction between sex and month ($F_{3,66} = 0.165$, $P = 0.92$ and $F_{3,76} = 0.387$, $P = 0.76$, respectively for *Ggg* and *Gge*).

Sexual dichromatism in patch reflectance and monthly variation

Patch reflectance varied both between sexes and among months (see Fig. 2). Reflectance spectra from both sexes of the two populations had higher values in the UV-blue range (300–495 nm) and decreasing values within the rest of the range (495–700 nm). Mean peak wavelength was between 360 and 380 nm in all cases (Table S3).

MANOVA applied to *Ggg* data showed significant differences among monthly samples for some reflectance parameters (Wilks' lambda test, $F_{12,175} = 3.05$, $P = 0.001$), and between sexes ($F_{4,66} = 3.0$, $P = 0.024$) and a significant effect of the interaction between the two factors ($F_{12,175} = 1.92$, $P = 0.034$). Further

Table 2. Correlations [Spearman's rho (r), P and N] between multivariate index of size and patch area and reflectance parameters in both sexes of the populations studied

	Ggg						*Gge*					
	Males			Females			Males			Females		
	r	*P*	*N*	*r*	*P*	*N*	*r*	*P*	*N*	*r*	*P*	*N*
Total patch area	0.445*	0.001*	48	0.323	0.142	22	0.534*	0.001*	36	0.605*	0.001*	27
Peak wavelength	0.153	0.316	42	−0.103	0.683	22	−0.087	0.602	36	0.050	0.797	27
$R_{300–495}$	−0.002	0.992	43	0.364	0.137	22	−0.127	0.446	36	0.251	0.207	27
$R_{495–700}$	0.122	0.420	43	0.519*	0.007*	22*	−0.040	0.812	36	−0.018	0.928	27

*Significant correlations.

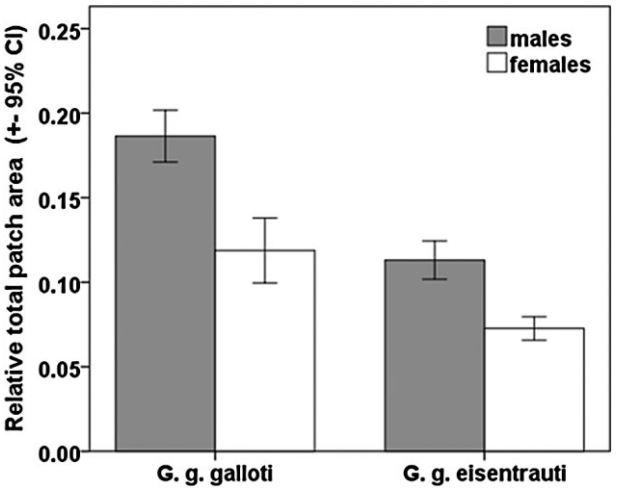

Figure 1. Mean total patch area (relativized to SVL) of all males and females sampled in the two subspecies.

univariate analyses showed that these effects were mainly a result of the peak wavelength being significantly higher in males than in females (Fig. 3A) while no significant effect of sex was detected for UV-blue or 495–700 nm ranges, or for UV-blue chroma (Table 3A). Moreover, post-hoc comparisons showed that: (1) UV-blue brightness was significantly greater in June than in April (Fig. 3B and Table S4), whereas brightness in the 495–700 nm range was significantly greater in May, June, and July with respect to April (Table S4); and (2) there was no significant difference in UV-blue chroma or peak wavelength between months (Table S4). The interaction between sex and month only had a significant effect in the brightness of the 495–700 nm range (Table 3A).

The same analysis for *Gge* data showed a significant effect of sex and month on the dependent variables ($F_{4,59} = 13.05$, $P < 0.001$ and $F_{12,156} = 4.05$, $P < 0.001$, respectively) but no significant effect of the interaction ($F_{8,118} = 1.10$, $P = 0.36$). These effects were because: (1) males had significantly higher peak wavelengths (Fig. 3A), UV-blue chroma, and brightness in the $R_{300–495}$ range than did females, but no significant difference in brightness in the $R_{495–700}$ range; and (2) brightness of UV-blue and $R_{495–700}$ ranges, and UV-blue chroma were significantly different between months (Table 3B); the interaction of sex and month had no significant effect on any of the variables. Post-hoc tests also showed that brightness of UV-blue and $R_{495–700}$ ranges were significantly greater in June than in April (Fig. 3B, Table S4) and UV-blue chroma was significantly higher in June than in May and April (Table S4).

Between-population comparison of reflectance parameters

MANOVA of reflectance parameters within each sex, with population and sampling month as factors, showed that *Gge* males had a significantly higher peak wavelength than did those of *Ggg* ($F_{1,82} = 6.07$, $P = 0.016$) and month had a significant effect on all parameters ($F_{12,209} = 3.56$, $P < 0.001$). The same type of analysis showed that females of *Ggg* had UV-blue chroma higher than that of *Gge* ($F_{1,65} = 6.93$, $P = 0.011$), and a significant effect of month on brightness of UV-blue and 495–700 nm ranges ($F_{12,164} = 3.78$, $P < 0.001$).

Reflectance and monthly variation in cheek patch

Cheek patches of *Gge* males showed significantly larger brightness of UV-blue and $R_{495–700}$ nm ranges in May and June than in April or July (Table S5, chi-square and Kruskal–Wallis tests = 9.27 and 15.03, $P = 0.02$ and 0.002, respectively), no significant difference in UV-blue chroma ($\chi^2 = 4.08$, $P = 0.25$), and peak wavelengths higher in May and July than in April or June ($\chi^2 = 14.56$, $P = 0.002$); after Bonferroni

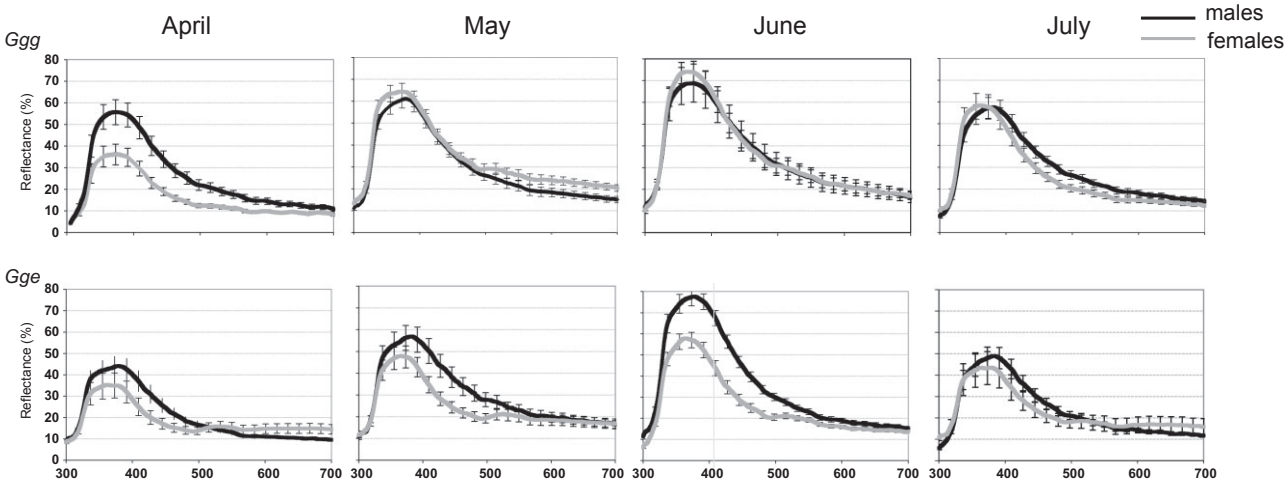

Figure 2. Reflectance spectra (mean ± 1 SE) of the first lateral patch of males and females of both subspecies in the 4-month sample period.

correction ($P = 0.012$), brightness in the $R_{495–700}$ nm range and peak wavelength remained significant. In those *Ggg* males that had a cheek mark, values of the variables were also larger in May and June, but statistical comparisons did not reach significance ($\chi^2 = 6.25$, 4.17, 3.53, and 2.8, respectively for $R_{300–495}$, $R_{495–700}$, UV-blue chroma and peak wavelength; $P > 0.05$ in all cases).

DISCUSSION

Sexual differences

Both populations of *G. galloti* showed a clear sexual size dimorphism, with males having significantly higher values of SVL and size-adjusted biometric traits than females. This pattern, similar to that of many other lizard species (see revision of Cox, Butler & John-Alder, 2007), could result from evolutionary factors, such as intense male–male competition in habitats with scarce resources (Stamps, Losos & Andrews, 1997), sexual selection pressures (Butler, Schoener & Losos, 2000), or the presence of other sympatric lizard species (Butler, Sawyer & Losos, 2007; Poe, Goheen & Hulebak, 2007). Males of both subspecies had larger heads than did females, as in other lizard species (Hews, 1996; Thompson & Withers, 2005; Kaliontzopoulou, Carretero & Llorente, 2007); head size in *G. galloti* is related to biting force (Herrel *et al*., 1999) and probably results from intrasexual selection (Molina-Borja *et al*., 1998; Huyghe *et al*., 2005). Individuals of *Ggg* had relatively larger heads and HLLs than those of *Gge*; FLLs were significantly larger in females of *Ggg* than in those of *Gge*. Longer hindlimbs in open than in closed habitats also occur in other lizard species (Losos *et al*., 2000; Melville & Swain, 2000; Kohlsdorf, Garland & Navas, 2001; Schulte *et al*., 2004; Molina-Borja *et al*., 2010). In general, size-adjusted traits of *Ggg* (the smaller subspecies) are larger than those of *Gge* (the larger subspecies). That their habitats differ markedly suggests that ecological factors may have driven the morphological divergence between them (see below).

Differential growth (Cox & John-Alder, 2007), mortality rates, and food-resource use also affect body size differences between sexes and among populations (Cox *et al*., 2003, 2007; Kaliontzopoulou, Carretero & Llorente, 2010). Male and female growth trajectories are different in the larger species *Gallotia simonyi* (Rodríguez-Domínguez *et al*., 1998) and this is also probably the case in *G. galloti* (Castanet & Báez, 1988). Local ecological factors may also affect SSD as *Gge* live in areas more densely covered by plants than *Ggg*. In *Gallotia caesaris*, the magnitude of SSD had an inverse relationship with vegetation cover of several populations (Molina-Borja *et al*., 2010), and predator pressure could also have contributed to population differences in body size (Vervust, Grbac & Van Damme, 2007; see below).

Sexual dimorphism was also shown in coloured patches of both subspecies, with males having significantly larger relative areas than females (Fig. 1 and Table S2). *Gallotia galloti* males have more coloured lateral patches than do females (Molina-Borja *et al*., 1997), but this is the first time that sexual dimorphism in patch area has been quantified. Between-sex differences were recently reported in ventral patches of *Sceloporus occidentalis* (Shedd, 2009) and lateral spots of *Lacerta lepida* (Font *et al*., 2009), and between-population differences were reported in the chin patch area of *Microlophus* (Jordan *et al*., 2008). Sexual

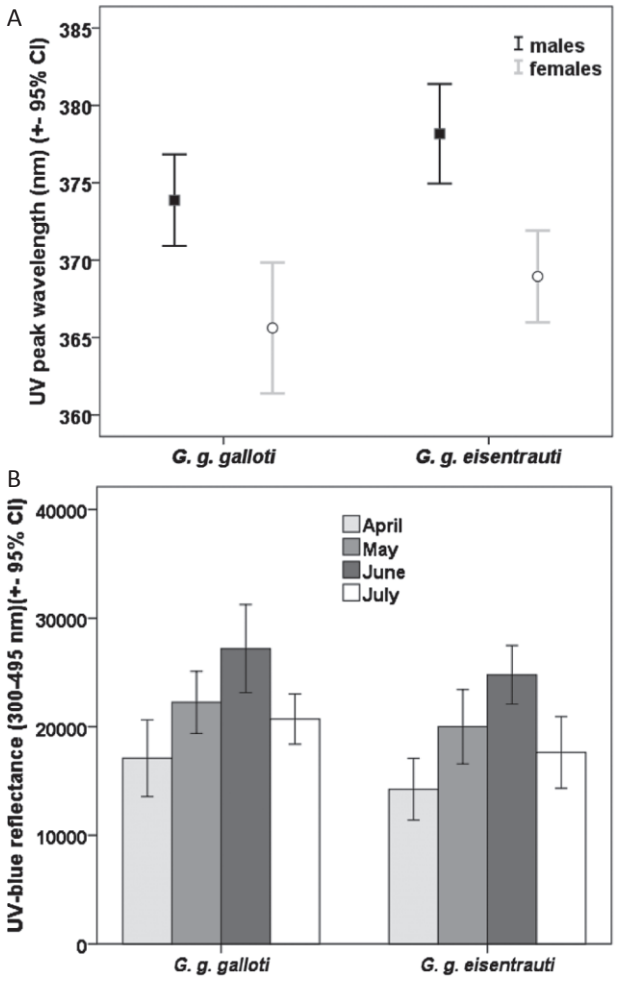

Figure 3. Mean UV peak wavelengths for each sex and subspecies (A) and mean monthly ultraviolet-blue reflectance of the first lateral patch (B).

dimorphism in conspicuously coloured patches may contribute, together with body size or colour, to sex recognition (Bauwens *et al*., 1987; Galán, 2000). Chromatic patches may function as status-signalling badges of aggressiveness, fighting ability, or dominance in males (Olsson, 1994a; Anderholm *et al*., 2004; Whiting *et al*., 2006), and in mate choice (Hamilton & Sullivan, 2005; Bajer *et al*., 2010). The ultimate causes for intersex colour differentiation are differing selection pressures within intra- and intersexual selection, and their interaction with natural selection processes (Cooper & Greenberg, 1992; Baird *et al*., 1997; Chen *et al*., 2012). As lateral coloration is more probably implicated in intraspecific communication than in antipredator tactics (Stuart-Fox & Ord, 2004), larger lateral UV-blue patches in males than in females of *G. galloti* would reflect an important role in intra- or intersexual selection.

Table 3. Results from univariate tests (within MANOVA) comparing reflectance variables of the lateral patches of *G. g. galloti* (A) and *Gge* (B) between sexes and months

(A)

Factor	Dependent variable	d.f.	*F*	*P*
Sex	$R_{300–495}$	1	0.379	0.540
	$R_{495–700}$	1	0.118	0.732
	UV-blue chroma	1	0.000	0.992
	UV peak	1	8.956	0.004
Month	$R_{300–495}$	3	7.117	< 0.001*
	$R_{495–700}$	3	11.642	< 0.001*
	UV-blue chroma	3	1.908	0.136
	UV peak	3	0.738	0.533
Sex × month	$R_{300–495}$	3	3.580	0.018
	$R_{495–700}$	3*	3.969*	0.011*
	UV-blue chroma	3	1.948	0.130
	UV peak	3	2.148	0.102
Error		71		

(B)

Factor	Dependent variable	d.f.	*F*	*P*
Sex	$R_{300–495}$	1	7.156	0.009*
	$R_{495–700}$	1	0.002	0.962
	UV-blue chroma	1	18.594	< 0.001*
	UV peak	1	15.865	< 0.001*
Month	$R_{300–495}$	3	10.138	< 0.001*
	$R_{495–700}$	3	7.219	< 0.001*
	UV-blue chroma	3	6.562	0.001*
	UV peak	3	0.968	0.413
Sex × month	$R_{300–495}$	3	0.243	0.866
	$R_{495–700}$	3	1.410	0.247
	UV-blue chroma	3	2.989	0.037
	UV peak	3	0.477	0.699
Error		76		

d.f., degrees of freedom.
*Significant differences after Bonferroni correction (alpha = 0.016).

We also detected that males had patches with significantly higher intensity – brightness – than did females, but the difference was more clearly marked in *Gge* than in *Ggg* (statistical comparison did not reach significance for this last subspecies). Although we showed, in other populations of both subspecies, a significant male to female difference in patch reflectance (Molina-Borja *et al*., 2006), in that case individuals were all captured in the same month. The less-marked sexual dichromatism in patch reflectance for

Ggg was because females, although having smaller patch areas than males, have similar reflectance intensities in all sampled months; however, *Gge* females had significantly smaller patch areas, and also brightness, than males over the 4-month study period (see below).

We also confirm in both subspecies a sexual dichromatism in peak wavelength, that of males being significantly higher than that of females (Molina-Borja *et al*., 2006). Peak wavelength is in the near-UV, close to the absorption peak of UV receptors in lizards (Fleishman *et al*., 1993; Loew *et al*., 1996; Kawamura & Yokoyama, 1998; Fleishman, Loew & Whiting, 2011), agreeing with UV reflectance data from other species (e.g. Blomberg, Owens & Stuart-Fox, 2001; Macedonia, 2001; Stoehr & McGraw, 2001; Macedonia *et al*., 2003). This suggests that patches are sexually dichromatic in the lizards' own visual world (in the UV wavelength band) but some degree of dichromatism is also apparent in the visible spectrum (see Fig. 2). Recent analyses showed that the ocular media of several lacertids, including *G. galloti*, transmit wavelengths well down into the UV range, which suggests that they are capable of ultraviolet visual perception (Pérez i de Lanuza, 2012). Moreover, the retina of many lacertids (including *G. galloti*) and other diurnal lizards share four types of cones, suggesting a tetrachromatic colour vision system (Pérez i de Lanuza, 2012). This should allow these species to discriminate chromatic stimuli easily, but it remains to be specifically analysed for *G. galloti*.

Many lizard species show some degree of between-sex coloration difference (Cooper & Greenberg, 1992), and within lacertids at least 73% of the species have some degree of sexual dichromatism (Pérez i de Lanuza, Font & Monterde, 2013). This includes the reflectance of patches in the UV range as, for example, in *Crotaphytus collaris* (McCoy *et al*., 1997; Macedonia *et al*., 2002, 2004), *Lacerta agilis* (Pérez i de Lanuza & Font, 2007) and *Lacerta (Timon) lepida* (Font *et al*., 2009). The sexual dichromatism in *G. galloti* is based not only on brightness of the UV-blue reflecting patches, but also on their number (Molina-Borja *et al*., 1997), size (current work), and hue (Molina-Borja *et al*., 2006 and current work). In other lacertids the dichromatism is based on one trait as the number of patches (*Psammodromus algirus* and *Podarcis sicula*, Salvador & Veiga, 2008; Pérez i de Lanuza & E. Font, unpubl. data) or on a lower peak wavelength (20–30 nm) in patch reflectance of males in comparison with females (*L. lepida*, Font *et al*., 2009). Dichromatism in the UV range may contribute to enhancement of sex recognition, also mediated by body size, behaviour patterns, or sex-specific odours. The fact that the magnitude of sexual dichromatism in UV-blue patch brightness (at least for *Gge*) is higher than that reported for birds (Andersson *et al*., 1998; Hunt *et al*., 1998), or other lizards (Macedonia *et al*., 2002, 2004; Václav, Prokop & Fekiac, 2007; Font *et al*., 2009), suggests that reflectance in this part of the spectrum may be an important component of intra- or intersexual selection in this species.

Monthly variation

We report here, for males and females of *G. galloti*, a significant change in patch brightness and UV-blue chroma (*Gge*) through the months of the breeding period, and values for *Ggg* females increased much more than those of *Gge* (Fig. 2). Brightness of lizard cheek patch also changed through breeding time (only significant for *Gge*). We suggest that both types of patch could be signals reflecting the hormonal status or body condition of males throughout the breeding season. We could not undertake a truly longitudinal study (see the Methods section) but in a lizard recaptured once, patch brightness was larger in June than in July (Fig. S2); on the other hand, selecting randomly one lizard per month among all reflectance spectra, the same monthly pattern was obtained (Fig. S3). Recent publications report weak seasonal (during and after the breeding season) changes in throat and chest colorations from adult males and females of *Zootoca vivipara* (Martin *et al*., 2013) and seasonal change in reflectance of ventral coloration of *Acanthodactylus erythrurus* females (Cuervo & Belliure, 2013). Seasonal variation in UV brightness has also been reported in blue tit pileus feathers that had lower values before moult and higher values during offspring feeding (Örnborg *et al*., 2002).

Monthly changes in patch reflectance of *G. galloti* resemble those previously reported – using methods different from spectrophotometry – for patches of various lizard species (Cooper & Greenberg, 1992). In female lizards, brighter patches coincided with enlarged follicles or oviductal eggs (*C. collaris*, Ferguson, 1976; *Urosaurus ornatus*, Zucker & Boecklen, 1990; and *Podarcis bocagei*, Galán, 2000) or were associated with copulations (*Chamaeleo chameleon*, Cuadrado, 2000). The increased brightness of female patches of *G. galloti* in May and June coincide with courtship and mating behaviours (M. Molina-Borja, pers. observ.) and with active gonads (Mahamud del Val, 1984), and could indicate their maturity or receptive state (Calisi & Hews, 2007); the decreased brightness in July could signal female gravid condition. Monthly changes in patch brightness of males of *G. galloti* could reflect changing motivational factors (Salvador *et al*., 1996; but see Salvador *et al*., 1997; Cox *et al*., 2005). Other lizard males developed adult coloration at the onset of sexual maturity (*Sceloporus gadoviae*, Lemos-Espinal, Smith & Ballinger, 1996)

and changed seasonally the intensity of ventral colour patches (*Tropidurus semitaeniatus*, Ribeiro, Kolodiuk & Freire, 2010). There is no physiological – rapid – colour change in *G. galloti* and therefore the reported colour changes should be related to mid-term changes in hormonal levels through breeding months. This remains to be elucidated as there are, as yet, no available data on the natural seasonal hormone cycle.

Inter-population variation

Among-population differences in coloration patterns may arise from compromises that vary locally and in relation to the multiple functions that colour may serve as sex identification, mate attraction and intrasexual competition, or crypsis for predators (Endler, 1991, 1992). Therefore, variation in dichromatism among populations of a species may provide clues about local selective pressures on coloration (Kwiatkowski, 2003).

In *G. galloti*, relative patch area was significantly larger in males and females of *Ggg* than in those of *Gge*, but the reasons for this difference are not clear at present. Small and large coloration patches should contribute, respectively, to lower and higher individual conspicuousness in northern compared with southern populations; in turn, this should be related to local traits of their respective habitats (see below). The cheek patch also contributes to differentiate between males of both subspecies: it appears more frequently and is larger in *Gge* than in *Ggg* (Molina-Borja *et al*., 1997). Again, the significance of this difference is not yet known; however, it could be related to varying selective pressures between habitat types from each subspecies and with particularities of their behaviour: the UV brightness of this patch may be a status signalling trait in male contests of *Gge* (M.L. Bohórquez-Alonso & M. Molina-Borja, unpubl. data).

The interpopulation differences in patch area and reflectance of *G. galloti* may also be interpreted according to the different local environmental factors. Northern lizard habitats have higher yearly precipitation level (and therefore vegetation cover, Otto, Fernández-Palacios & Krüsi, 2001) and lower insolation level than do habitats of the southern lizards. Therefore, lizards from those parts of the island may have been subjected to different natural selection and, possibly, sexual selection regimes. Thorpe & Brown (1989) argued that *Gge* males have small lateral patches as a cryptic strategy in the lush North habitat, and that development of big cheek marks 'would have developed for sexual/territorial purposes to compensate for the lack of blue trunk markings'; however, male body coloration may be cryptic in the habitat of each subspecies, and some *Gge* males may have large conspicuous lateral patches. Should cheek marks of *Gge* males contribute to a more effective intraspecific communication in the more vegetated habitats in which they live? (We do not yet know.) Thorpe & Brown (1991) also suggested that individuals of *Gge* should be more exposed to predators as a result of spending more time thermoregulating in their cloudier northern habitat; however, thermoregulation can take place not only in open spaces without vegetation but also in small sunlit spots under plants (M. Molina-Borja, pers. observ.). Moreover, increased vegetation cover in the North could reduce predation levels there, at least from kestrels (the main aerial predators of lizards, Carrillo & González-Dávila, 2010). There is no quantification of predation intensity in different parts of the island, but a greater density of avian predators (like the kestrel, *Falco tinnunculus canariensis*) was found in lowland habitats of the North than in those of the South (Carrascal & Palomino, 2005); however, the proportion of lizard remains did not differ in pellets from kestrels of both habitat types (J. Carrillo, pers. comm.). To evaluate the role played by predation in shaping *G. galloti* dimorphism/dichromatism in different parts of the island, global predation levels (not just those from kestrels) should be quantified. In several populations of *C. collaris*, sexual dichromatism in reflectance from different body-coloured areas was more pronounced in those experiencing lower predation pressure and the inverse was also the case (Macedonia *et al*., 2002, 2004). Furthermore, in a phylogenetic analysis of the relationship between breeding coloration and ecological traits of many species of *Carlia* skinks, those occupying more open habitats tended to have breeding colours on body lateral regions (Dolman & Stuart-Fox, 2009).

Moreover, northern and southern habitats of Tenerife must differ in the characteristics of their ambient light, and therefore current lizard coloration in each one could reflect adaptations to this factor. Direct measurements of ambient light (irradiance spectra) to be taken in the near future will allow us to test this possibility.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Relationship between multivariate factor scores of body size (X axis) and total patch areas (Y axis) of males and females of *Ggg* (a) and *Gge* (b).

Figure S2. Reflectance spectra of the first lateral patch of the same male (*G. g. galloti*), captured in June and re-captured in July.

Figure S3. Reflectance spectra of male (*G. g. galloti*) first lateral patch, selected randomly among those of lizards captured each month.

Table S1. Correlations (Spearman rho) among patch reflectance parameters of males (upper right cells) and females (lower left cells) of *G. g. galloti* (Ggg) and *G. g. eisentrauti* (Gge). p: significance level; n = sample size. (significance level, after Bonferroni correction: 0.012).

Table S2. Basic statistics from biometric variables quantified in both sexes and populations studied. See text for abbreviations.

Table S3. Statistics of reflectance variables from the first latero-dorsal patch of males and females of both populations. $R_{300–495}$ and $R_{495–700}$: brightness in the UV-blue (300–495 nm) and 495–700 nm ranges, respectively; UV-blue chroma: $R_{300–495}/R_{300–700}$; PWL: peak wave length (nm).

Table S4. Between-month differences (± SE, p) obtained from the post-hoc comparisons of reflectance parameters of both populations; p: significance level. Between parentheses (below data): sense of the difference. *Ggg: G. g. galloti*; *Gge: G. g. eisentrauti*.

Table S5. Statistics of reflectance variables from the cheek patch of males from both populations. $R_{300–495}$ and $R_{495–700}$: brightness in the UV-blue (300–495 nm) and 495–700 nm ranges; UV-blue chroma: $R_{300–495}/R_{300–700}$; PWL: peak wave length (nm).