The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2013, **110**, 128–141. With 4 figures

Ultraviolet and carotenoid-based coloration in the viviparous lizard *Zootoca vivipara* (Squamata: Lacertidae) in relation to age, sex, and morphology

MÉLISSA MARTIN[1]*, SANDRINE MEYLAN[1,2], DORIS GOMEZ[3] and JEAN-FRANÇOIS LE GALLIARD[1,4]

[1]*Laboratoire Ecologie & Evolution, Université Pierre et Marie Curie, CNRS UMR 7625, 7, quai Saint Bernard, case 237, 75005 Paris, France*
[2]*IUFM de Paris-Université Sorbonne Paris IV, 10 rue Molitor, 75016 Paris, France*
[3]*Muséum National d'Histoire Naturelle, Département d'Ecologie et de Gestion de la Biodiversité, CNRS UMR 7179, 1 avenue du petit château, 91800 Brunoy, France*
[4]*CEREEP – Ecotron Ile-De-France, École Normale Supérieure, CNRS UMS 3194, 78 rue du Château, 77140 St-Pierre-lès-Nemours, France*

Received 23 January 2013; revised 15 March 2013; accepted for publication 15 March 2013

Lizards display structural and pigment-based colorations, and their visual system is sensitive to wavelengths of 300–700 nm. However, few studies in squamate reptiles have quantified interindividual colour variation that includes the structural ultraviolet (UV) component (300–400 nm). In the present study, we investigated variability of a ventral UV/yellow–red ornamentation in the common lizard *Zootoca vivipara*, including an analysis of spatial distribution, as well as sex and age differences. We also investigated whether the expression of coloration is related to body size and condition. Our analyses revealed two distinct patches: a gular patch with a strong UV reflectance and a belly patch with a dominant yellow–red reflectance. Males displayed a less saturated throat coloration with higher UV chroma and UV hue, and had a redder but duller belly coloration than females. Yearlings had less elaborate ornaments than adults, although they already displayed a yellow–red sexual dichromatism on the belly. UV sexual dichromatism was only apparent in adults as a result of a weaker UV reflectance in females, suggesting potential fitness costs of a bright UV coloration in that sex. Different colour traits were related to body size in both sexes, as well as to body condition in males. We discuss the potential evolutionary scenarios leading to the maintenance of this ornament in common lizards. *Biological Journal of the Linnean Society*, 2013, **110**, 128–141.

ADDITIONAL KEYWORDS: age-related variation – body size – body condition – common lizard – pigment – sexual dichromatism – structural UV colour.

INTRODUCTION

Animal colour patterns represent a compromise between thermoregulation, crypsis to avoid predation, and conspicuousness for intraspecific communication (Endler, 1992; Stuart-Fox & Ord, 2004). Conspicuous coloration involves a variety of structural and pigmentary visual signals in animals. The sensory system of some vertebrate taxa demonstrates sensitivity to wavelengths outside the human-visible range (Bowmaker, 2008). In particular, ultraviolet (UV; 300–400 nm) vision occurs in some birds, fishes, amphibians, and reptiles. Recent studies have demonstrated that UV visual signals are also involved in species recognition, mate choice and/or intrasexual competition (Andersson & Amundsen, 1997; Rick, Modarressie & Bakker, 2006; Whiting *et al.*, 2006; Rick & Bakker, 2008; Bajer *et al.*, 2010; Siebeck *et al.*, 2010; Vedder *et al.*, 2010; Secondi, Lepetz & Théry, 2012). In particular, human visible and UV colours

*Corresponding author.
E-mail: melissa.martin@snv.jussieu.fr

are both important in lizards because their visual capacity extends into the UV domain (Fleishman, Loew & Whiting, 2011). A description of interindividual variation in body coloration, including UV reflectance, is thus an important step towards a better understanding of the function of colour variability.

Social interactions, and therefore the costs and benefits of visual signalling, depend on age, sex, and individual quality (Andersson, 1994; Bradbury & Vehrencamp, 2011). We therefore examined variation in ventral coloration in the common lizard *Zootoca (Lacerta) vivipara* (Squamata: Lacertidae; Von Jacquin, 1787) between age classes and sexes. We also included body size and body condition in our analyses, which are two traits potentially related to individual quality (Fitze *et al*., 2008). In lizards, the conspicuous skin coloration results mainly from the combined properties of carotenoid and/or pteridine pigments located inside xanthophores, of crystalline platelets from iridophores that reflect light and produce structural colours, and a basal dark layer of melanophores (Macedonia *et al*., 2000). In the common lizard, ventral coloration involves both structural (UV) and carotenoid-based (yellow–red) colours (Fitze *et al*., 2009). The carotenoid-based coloration describes a continuum from pale yellow to dark red and is influenced by environmental factors (Cote *et al*., 2008). This ornamentation is a sexually selected trait (Vercken *et al*., 2007; Fitze *et al*., 2009) and plays a role in mate recognition (Bauwens, 1987), intrasexual competition among females (Vercken & Clobert, 2008), and female mate choice (P. S. Fitze, pers. comm.). However, previous studies in the common lizard did not account for inter-individual variability of the UV component of coloration.

Sex and age are major sources of variation in coloration among vertebrates. Males typically exhibit more elaborate coloration than females, a difference traditionally assumed to result from sexual selection (Andersson, 1994). Sexual dichromatism has now been quantified taking into account the contribution of UV component in many vertebrate species, including squamate reptiles (Andersson, Örnborg & Andersson, 1998; Cuthill *et al*., 1999; Stuart-Fox & Ord, 2004; Font, Pérez I De Lanuza & Sampedro, 2009; Murphy & Pham, 2012). Furthermore, it is often the case that coloration is less elaborate in younger or sexually immature individuals, although age differences in UV signals are rarely examined (Hill, 1996; Siefferman, Hill & Dobson, 2005; Freeman-Gallant *et al*., 2010). In blue tits, *Parus caeruleus*, older birds of both sexes display more UV, and more chromatic and brighter crown coloration than yearlings (Delhey & Kempenaers, 2006). According to the status-signalling hypothesis (Lyon & Montgomerie, 1986), the less elaborate coloration of yearlings might provide an advantage with respect to avoiding aggression by old individuals. In lizards, even fewer studies have investigated differences in coloration between age classes, apart for investigations of the anti-predatory effect of the bright tail coloration observed in juveniles of some species (Carretero, 2002; Hawlena *et al*., 2006). To our knowledge, age-related variation in the UV domain has not been tested so far. Thus, a first aim of the present study was to quantify sex- and age-related variation in ventral coloration including the UV component.

Elaborate visual signals may be costly to produce and are therefore expected to convey reliable information on the quality of the signaller (Grafen, 1990; Johnstone, 1995). Traditionally, carotenoid pigmentation was considered as an ideal model of condition-dependent signalling because carotenoids are acquired solely through the diet and allocated between colour traits and physiological functions, such as the immune response and antioxidants (Endler, 1983; Hill, 2006). Our recent studies in common lizards (Cote *et al*., 2008; Fitze *et al*., 2009) supported this hypothesis by showing that body size was correlated with chroma and hue, as measured by Endler's hue score (Endler, 1990). In addition, Fitze *et al*. (2009) found that hue was correlated with carotenoid concentration in the skin. However, the available evidence now suggests that structural, UV coloration can also be costly to produce (Senar, 2006), and that structural coloration may be correlated with individual quality or health components, including nutritional condition and immune capacity (Keyser & Hill, 2000; Doucet, 2002; Martín & López, 2009; Mólnar *et al*., 2012). When coloration involves multiple signals, however, it is important to account for potential interference and correlation between colour traits in the analysis of condition-dependence. For example, the carotenoid pigmented surface of the skin can reduce skin reflectance in the UV domain (Mougeot *et al*., 2007). Thus, a second aim of the present study was to lead a preliminary investigation evaluating condition-dependence for ventral coloration as a whole in common lizards.

MATERIAL AND METHODS

Study species

The common lizard, *Z. vivipara*, is a small lacertid distributed across Eurasia. In our capture sites (southern France), females are viviparous, sexual maturity is attained at 2 years of age, and mating takes place in May (Bauwens, 1987; Vercken *et al*., 2007). Growth is continuous throughout life. This species is characterized by a brownish dorsal and

lateral coloration, and a non-nuptial, bright ventral coloration. Males present a permanent yellow–red ventral coloration interspersed with black spots, whereas the coloration in females varies from cream to orange with few dark spots from the throat to the tail (Bauwens, 1987; Vercken *et al.*, 2007). The quantity of black spots increases with age (unpub. data). This conspicuous ventral coloration is concealed to avian and most mammalian predators, although it can be used as a signal during behavioural displays (Stuart-Fox & Ord, 2004). Indeed, common lizards signal themselves by pushing up on their front legs and exposing their throat (M. Martin & J.-F. Le Galliard, pers. observ.), such that conspecifics can perceive the throat colour and, to a lesser extent, their abdominal coloration.

Capture and morphometric measurements

During the two first weeks of July 2008, we captured individuals from nearby habitats in the Mont Lozère area (44°30′N, 3°45′E) located in southern France (capture permit number 2007-189-005). Animals in moult were excluded from the study. Our sample consisted of 327 individuals including 229 adults (≥ 2 years old; 141 females and 88 males) and 98 yearlings (1 year old and sexually immature; 40 females and 58 males). Sex was determined by eye and by counting the number of scales on both sides of the abdominal median line according to the method of Lecomte, Clobert & Massot (1992). Body size (snout–vent length; SVL) was measured as the distance between the tip of the nose and the posterior edge of the cloaca with a plastic ruler to the nearest millimetre. The sexual maturity of lizards was estimated from their SVL based on previous studies conducted in the same area (i.e. SVL > 50 mm for males and > 53 mm for females; Massot *et al.*, 1992). SVL was 62.12 ± 4.27 mm (mean ± SD) for adult females (range: 53–73 mm) and 55.44 ± 2.67 mm for adult males (range: 50–63 mm). In yearlings, SVL was 46 ± 3.58 mm for females (range: 40–53 mm) and 43.53 = ± 3.10 mm for males (range: 38–50 mm). Additionally, we measured body mass to the nearest milligram with an electronic scale. We retained the residuals from a regression of mass versus SVL as a measure of 'body condition' in adult males. Body condition was not calculated for adult females because they were potentially pregnant and the investment in offspring production would affect the estimate of body condition.

Coloration assessment

Photographic description

We first assessed the spatial distribution of UV reflectance to determine the relevant ventral body zones for detailed, quantitative analyses using a spectrophotometer (see below). We selected a random subset of female and male adult lizards ($N = 13$ and 9 individuals, respectively). The pattern of ventral coloration of each individual was photographed by placing the animal between a white background and a quartz glass using a digital camera (Nikon D70S; ISO 400) and a prefocused macro lens (Nikon CoastalOpt 1:4 UV-VIS-IR Apo-Micro) that transmits wavelengths between 290 and 1500 nm. Illumination was provided by two incandescent bulbs (25 W) and two UV B neon lights. We first took an image in the human-visible range through a UV-blocking filter (B + W 420), which transmits only wavelengths > 400 nm. A second image was taken in the UV range through a UV-transmitting filter (B + W 403) with peak transmittance at 360 nm and transmission range from 290 to 410 nm (exposure time of 20 s). The resulting black and white photographs (see Fig. 1) were used to highlight qualitative differences of coloration between sexes. Males appeared to be more colourful than females, and also display a stronger UV reflectance on the throat from the tip of the nose to the neck and, to a lesser extent, from the neck to the cloaca (Fig. 1). In females, UV reflectance appeared to be particularly strong on the throat around the sub-maxillary area, although it was much lower on the chest and belly (Fig. 1). Males also appeared to have more black spots than females, especially on the chest (i.e. between the two front legs) and the belly (i.e. between the two pairs of legs). This qualitative approach revealed three body zones where spectral characteristics could potentially differ: the throat, the chest, and the belly.

Spectrophotometric measurements

We measured spectral properties in the centre of the throat, chest, and belly for all individuals after the breeding season. We used a spectrophotometer (USB2000; Ocean Optics Inc.) calibrated between 200 and 850 nm, a Xenon light source (PX-2) covering the range 220–750 nm, and a 400-μm fibre optic probe (R400-7-UV/VIS; Ocean Optics Inc.). Here, we restrict our analyses to the range 300–700 nm, which includes the broadest range of wavelengths known to be visible to lizards (Fleishman *et al.*, 2011). The end probe in contact with the lizard's skin was bevelled at 45° and the circular reading spot was approximately 1 mm^2. Reflectance was measured relative to a dark and a white diffusive standard (WS-1; Ocean Optics Inc.). For each lizard, we measured two reflectance spectra for each body zone (Fig. 2). This procedure allowed us to estimate repeatability (Lessells & Boag, 1987), which includes both measurement error and the spatial variability in colour.

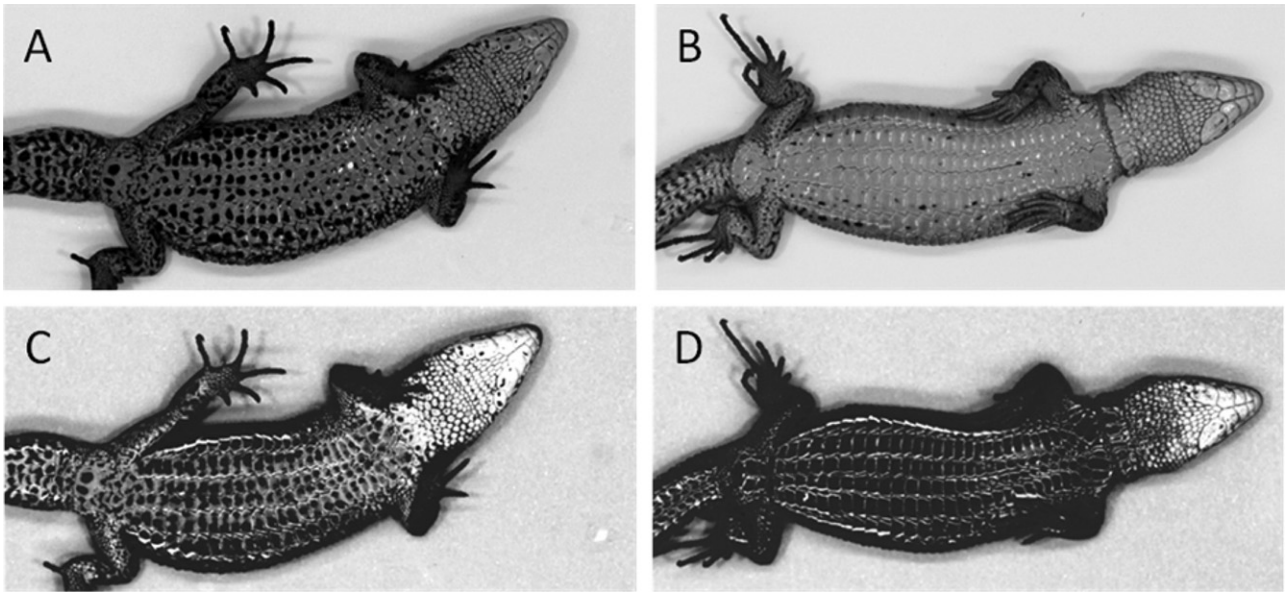

Figure 1. Black and white photographs of a representative adult male (A, C) and adult female (B, D) common lizard. Photographs were taken through an ultraviolet (UV)-blocking filter (A, B) to assess colour in the visible range and through a UV-transmitting filter (C, D) to provide an estimate of colour in the UV range. In the latter case, white body areas correspond to areas of higher UV reflectance.

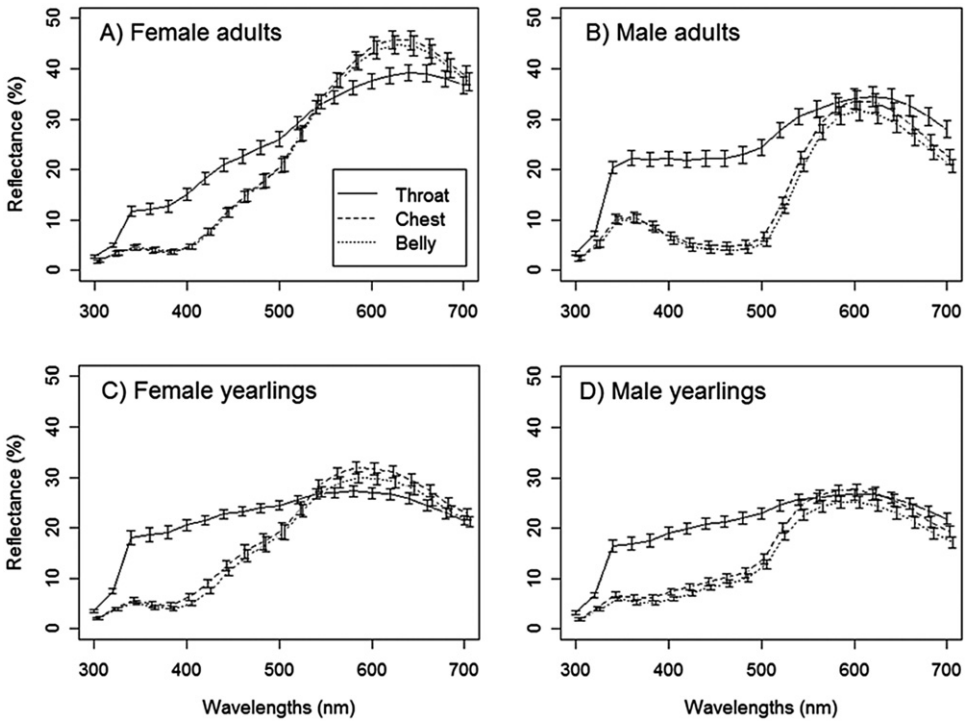

Figure 2. Mean reflectance spectra of common lizards on the throat, chest and belly zones in females and males adults (A, B) (with $N = 141$ and 88 individuals, respectively), as well as in female and male yearlings (C, D) (with $N = 40$ and 58 individuals, respectively). Chest and belly mean spectra were similar and different from the throat mean spectra, irrespective of sex and age class. Errors bars represent the interval of confidence.

Spectrophotometer measurements were performed avoiding black spots as far as possible. However, when a lizard had many ventral black spots, the reflectance measurements could be made partially on these black spots, which could impact the shape of reflectance spectra. To account for this bias, we generated an index of melanic coloration at each body zone that consisted of three levels: no spots (corresponding to 0–2% of coverage according to digital photographs, S. Meylan, B. Guinaudeau, S. Perret, B. Decencière Ferrandièreand & J.-F. Le Galliard, unpubl. data), some spots (2–10% of coverage) or many spots (> 10% of area coverage). We used this melanin index as a covariate in all analyses.

Colour data analysis

We imported the reflectance spectra into AVICOL for subsequent analysis (Gomez, 2006). Common lizards' spectra were bimodal with a major peak at approximately 600 nm and a minor peak at approximately 345 nm more or less well marked according the body location (Fig. 2). Based on this overall shape and interindividual variation of spectra (Fig. 2), we estimated one brightness parameter and two parameters describing the saturation and hue of the major peak. Brightness was calculated as the total reflectance over the range 300–700 nm (Doutrelant *et al.*, 2008). Because there is no available formula (Montgomerie, 2006) that allows an optimal calculation of yellow–red saturation in our spectral data set, we derived a new spectral parameter we named yellow chroma. Yellow chroma was computed by

$$\text{Yellow Chroma} = \frac{\text{Rmax}_{450-700} - \text{R}_{450}}{\text{Rmean}_{300-700}}$$

Where, $R_{\text{max }450-700}$ is the maximal reflectance over the range 450–700 nm, R_{450} is the reflectance value at 450 nm and $R_{\text{mean }300-700}$ is the mean reflectance over the range 300–700 nm. Hue was calculated as the wavelength at which the slope is maximal in the visible domain (hereafter called VIS hue; Andersson *et al.*, 1998) because of the lack of a true major peak for some spectra. In addition, we computed two spectral parameters to describe the secondary peak in the UV domain: UV chroma (the proportion of total reflectance in the UV range, Doutrelant *et al.*, 2008) and UV hue (the wavelength of local maximal reflectance between 300 and 400 nm). We did not compute physiological models because visual physiology remains unknown in lacertids (Fleishman *et al.*, 2011). Spectrophotometer measurements were significantly repeatable ($N = 327$ individuals with two measurements per body zone, for throat: all $r \geq 0.57$ and $P < 0.0001$; for chest: all $r \geq 0.79$ and $P < 0.0001$; and for belly: all $r \geq 0.68$ and $P < 0.000$). Consequently, we averaged the two spectra taken for each body zone. Because coloration can change over time (Delhey, 2006), we conducted a preliminary study to investigate differences in coloration during and after the breeding season in adult males ($N = 12$) and gravid females ($N = 17$). We found weak seasonal changes in coloration after mating relative to the variation observed between age and sex classes, but consistent interindividual variation during this period (for details, see Appendix S1, Fig. S1 and Table S1).

Statistical analysis

Spectral data were analyzed in two ways with R, version 2.13.1 (R Development Core Team, 2011). First, in separate analyses, we assessed the variation of each spectral parameter between sexes, age classes (yearling or adult), and body zones (throat, chest or belly) using the linear mixed-effect (*lme*) procedure with measurements nested within individuals as implemented in the NLME package. We included the melanin index as a covariate in these analyses. Because the effect of body zone was always significant and the features of chest and belly spectra were statistically indistinguishable (Fig. 2), we analyzed a saturated model (three body zones), a model pooling spectra from the chest and belly (two body zones), and a null model (no differences between body zones). We found the highest support for the second model for all parameters (results not shown) and hence chest and belly data were pooled for all subsequent analyses. We subsequently performed Student's *t*-tests to quantify sex and age differences on data from the throat, and from the chest and belly region (CBR) (Shapiro–Wilks test for normality, all parameters with $P > 0.1$).

Significant correlations existed between most of the spectral parameters (see Supporting information, Table S2). Thus, we chose to summarize our spectral data using principal component analysis (PCA; Endler, 1990; Cuthill *et al.*, 1999) with the *dudi.pca* procedure implemented in the ADE4 package. Given the results of our independent analyses of each spectral parameter (see below) and our prime interest of dimorphism among sexually mature animals, we ran one PCA on adult spectral data for the throat, and another PCA for the CBR data (five variables in each case). To determine how many axes represent significant variation with respect to the original data, we referred to the method proposed by Kaiser (1960) (only eigenvalues at least equal to one are retained). We then extracted the absolute contributions of the decomposition of inertia for each axe with the *inertia.pca* procedure implemented in the ADE4 package and interpreted only spectral parameters whose

contribution exceeded the mean contribution. We used the PC scores in a linear model (*lm* procedure) to analyse sexual differences on the throat and CBR (Venable & Ripley, 1999) including melanin index as a covariate. In addition, a *k*-nearest classification method was used to test whether the PC scores allow sex discrimination using the *IBk* procedure implemented in RWEKA (Hornik, Buchta & Zeileis, 2009). Finally, to evaluate condition-dependence of total coloration in adults, we ran separate PCAs for each sex and body region. For each of these analyses, we then regressed the PC scores against SVL. In addition, we analyzed the correlation between the PC scores and body condition in males. All statistical analyses started with a full model including all explanatory variables and the best model was chosen by backward elimination of nonsignificant terms using analysis of variance.

RESULTS

The amount of melanin influenced brightness and UV chroma (i.e. proportion of UV reflectance; Table 1). Four of the five spectral parameters (with the exception of VIS hue) depended on a significant, three-way interaction between body zone (throat versus CBR), sex and age class (Fig. 3, Table 1). Overall, animals displayed a higher brightness, a higher UV hue (UV peak closer to 400 nm), and a higher proportion of UV reflectance on the throat than on the CBR (Fig. 3). By contrast, CBR coloration was redder (higher VIS hue) and more intense (higher yellow chroma) in adults. Yearlings CBR spectral parameters did not exhibit this pattern (Fig. 3).

Age effects

Age-related variation of body coloration existed between sexes and body zones (Tables 1, 2). Adults had higher values for brightness and yellow chroma relative to yearlings. This age difference is especially strong on the CBR for brightness in females and chroma in males (Table 2, Fig. 3). VIS hue increased with age more strongly on the CBR than on the throat, and UV hue was significantly higher (less UV-shifted) in adults than in yearlings for males but not for females. In addition, the proportion of UV reflectance did not change significantly with age in males on the throat; it increased with age in males on the CBR, although it decreased with age on throat and CBR for females (Figs 2, 3; Table 2).

Sexual differences

All spectral parameters were influenced by sex, although with some differences according to age and body zone (Fig. 3, Table 1). Males were duller than females on CBR but not on the throat, and this sexual difference was stronger in adults than in yearlings (Fig. 3, Table 3). In yearlings, yellow chroma was significantly higher in males than in females. The relationship is the same for the adults' CBR but reversed for the adults' throat: females had a more yellow–red saturated throat coloration than males. VIS hue and UV components presented the same classical pattern; males were redder and had less UV-shifted (higher hue) and stronger proportion of UV reflectance than females, except for throat data in yearlings (Fig. 3, Table 3).

PCA of adult coloration resulted in two major axes that accounted for 63.80% of the variance in throat and 77.32% of the variation in CBR (Table 4). For throat data, the first principal component (PC1) had strong positive loadings for UV chroma and UV hue, and negative loadings for yellow chroma. The second principal component (PC2) was associated with variation in VIS hue. The mean PC score for males and females differed along PC axes 1 and 2 (PC1: $F_{1,227} = 61.66$, $P < 0.001$; PC2: $F_{1,227} = 46.31$, $P < 0.001$). Males and females exhibited substantial overlap along PC axes 1

Table 1. Results of univariate analyses for each colour trait: best models explaining the colour traits variation after a backward procedure of factors selection from the full model '*y* ~ age × sex × zone + melanin'

	Brightness		Visible hue		Yellow chroma		UV hue		UV chroma	
Factors	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Age	76.00	< 0.001	8.81	0.003	5021.39	< 0.001	10.40	0.001	64.14	< 0.001
Sex	86.50	< 0.001	61.52	< 0.001	174.02	< 0.001	181.10	< 0.001	725.75	< 0.001
Zone	367.12	< 0.001	9.32	0.001	29.02	< 0.001	878.20	< 0.001	2184.80	< 0.001
Melanin	9.65	0.002	0.35	0.55	0.26	0.61	3.10	0.08	4.75	0.03
Age × Sex	7.60	0.006	1.28	0.26	0.42	0.52	26.50	< 0.001	179.78	< 0.001
Age × Zone	0.40	0.53	3.52	0.03	4.21	0.015	2.40	0.12	141.44	< 0.001
Sex × Zone	108.32	< 0.001	6.35	0.01	121.12	< 0.001	186.00	< 0.001	37.25	< 0.001
Age × Sex × Zone	23.77	< 0.001	0.48	0.49	35.80	< 0.001	16.30	< 0.001	15.69	< 0.001

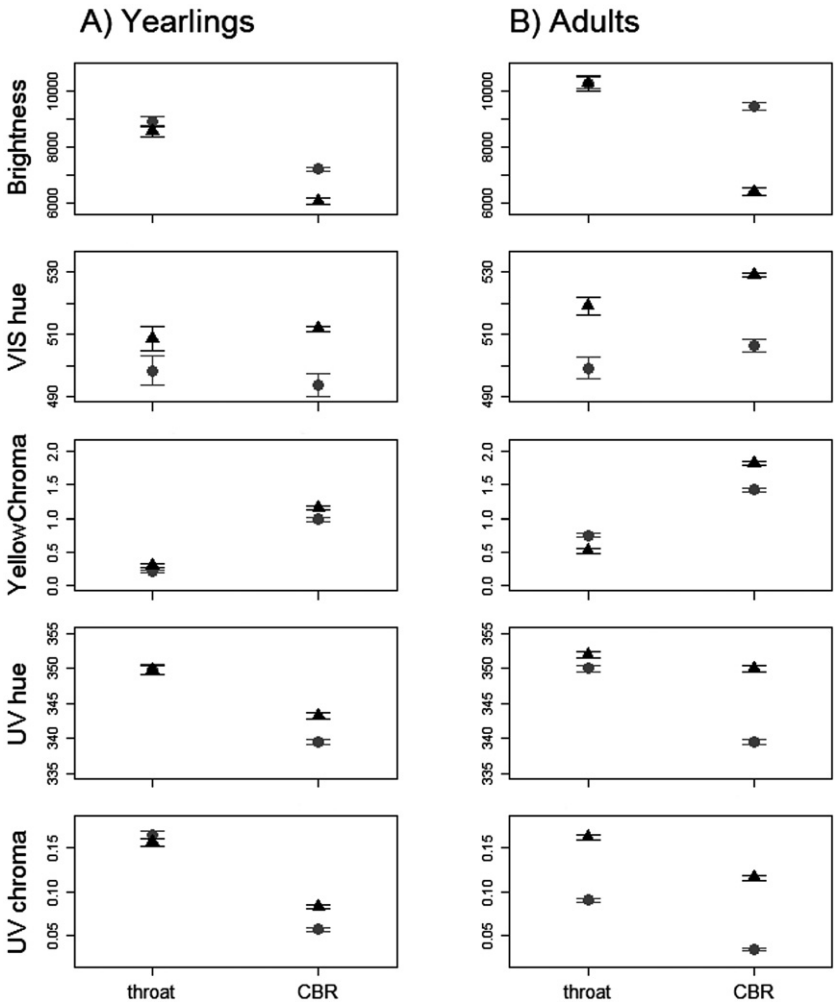

Figure 3. Mean spectral parameters of yearlings (A) and adults (B) on the throat and chest and belly region (CBR) in females (grey circles) and males (black triangles). Errors bars represent the SEM. UV, ultraviolet; VIS, visible.

Table 2. Differences in spectral parameters of colour reflectance spectra between yearlings and adults for the throat and the chest and belly region (CBR) in females and males

		Females			Males		
		d.f.	*t*	*P*	d.f.	*t*	*P*
Throat	Brightness	174.58	–5.21	**< 0.001**	140.21	–5.23	**< 0.001**
	Visible hue	88.60	–0.14	0.89	113.72	–2.11	**0.037**
	Yellow chroma	174.56	–13.51	**< 0.001**	141.14	–4.75	**< 0.001**
	UV hue	76.13	–0.23	0.82	117.21	–3.09	**< 0.001**
	UV chroma	66.54	**13.35**	**< 0.001**	110.65	–1.29	0.20
CBR	Brightness	170.76	–10.21	**< 0.001**	142.29	–3.46	**< 0.001**
	Visible hue	60.08	–2.34	**0.023**	127.57	–11.88	**< 0.001**
	Yellow chroma	77.92	–7.80	**< 0.001**	140.98	–14.67	**< 0.001**
	UV hue	89.14	–0.24	0.81	126.79	–7.26	**< 0.001**
	UV chroma	61.52	**13.06**	**< 0.001**	140.14	–6.82	**< 0.001**

A bold positive *t*-value corresponds to a mean that is higher in yearlings than in adults. Bold *P*-values are significant. UV, ultraviolet.

Table 3. Differences in spectral parameters of colour reflectance spectra between females and males for the throat and the chest and belly region (CBR) in yearlings and adults

		Yearlings			Adults		
		d.f.	*t*	*P*	d.f.	*t*	*P*
Throat	Brightness	95.4	1.61	0.11	190.3	–0.08	0.93
	Visible hue	84.4	–1.63	0.11	226.8	–4.24	**< 0.001**
	Yellow chroma	96.0	–2.63	**0.01**	204.1	**4.73**	**< 0.001**
	UV hue	82.8	0.07	0.95	219.6	–3.09	**0.002**
	UV chroma	79.7	1.40	0.17	218.6	–18.75	**< 0.001**
CBR	Brightness	95.9	**5.16**	**< 0.001**	196.5	**8.38**	**< 0.001**
	Visible hue	49.8	–3.29	**0.002**	207.5	–8.08	**< 0.001**
	Yellow chroma	72.1	–3.01	**0.003**	207.6	–8.84	**< 0.001**
	UV hue	96.0	–3.66	**< 0.001**	171.6	–13.37	**< 0.001**
	UV chroma	87.0	–3.87	**< 0.001**	142.0	–27.03	**< 0.001**

A bold positive *t*-value corresponds to a mean that is higher in yearlings than in adults. Bold *P*-values are significant. UV, ultraviolet.

Table 4. Scores and contribution of colour traits for each axis resulting from principle components (PC) analyses applied to throat and chest and belly region data for adult individuals of sexes; adult females; and adult males

	Adults		Adult females			Adult males		
Throat	PC1	PC2	PC1	PC2		PC1	PC2	PC3
Eigenvalue	2.06	1.13	2.43	1.09		1.48	1.37	1
Variance (%)	41.15	22.65	48.55	21.88		29.66	27.37	20.01
Loadings								
Brightness	0.51	–0.03	0.59	–0.45		**–0.74**	0.3	–0.12
Visible hue	–0.06	**0.96**	–0.34	**–0.83**		–0.3	0.17	**0.92**
Yellow chroma	**–0.86**	0.16	**–0.9**	–0.11		**0.55**	**0.63**	0.25
UV hue	**0.67**	–0.14	0.67	0.26		**–0.67**	0.49	–0.19
UV chroma	**0.78**	0.39	**0.84**	–0.35		–0.32	**–0.79**	0.23
Chest and belly	PC1	PC2	PC1	PC2	PC3	PC1	PC2	
Eigenvalue	2.68	1.04	2.02	1.28	0.97	0.91	0.15	
Variance (%)	53.55	20.77	40.39	25.58	19.44	38.12	25.08	
Loadings								
Brightness	**0.71**	0.01	0.6	**0.57**	0.26	**–0.65**	**–0.51**	
Visible hue	**–0.71**	**–0.47**	–0.62	**0.72**	–0.14	0.28	**–0.8**	
Yellow chroma	**–0.77**	**–0.53**	**–0.89**	0.3	–0.09	**0.88**	–0.1	
UV hue	**–0.74**	**0.52**	0.32	–0.01	**–0.94**	0.27	**–0.57**	
UV chroma	**–0.73**	**0.51**	0.62	**0.59**	–0.04	**–0.75**	–0.17	

Bold values indicate traits with a significant loading (see Material and Methods).
UV, ultraviolet.

and 2, which suggests a low discrimination between sexes (Fig. 4A). Indeed, the *k*-means cluster analysis of throat data resulted in males and females being misclassified with an error rate of 20.52 ± 0.23% ($k = 6$). The throat coloration of males was, on average, paler but redder, richer in UV and less UV-shifted (high hue) than those of females (Fig. 4A).

PCA based on the CBR data resulted in the first axis with positive loadings for brightness but negative loadings for VIS hue, yellow chroma, UV hue, and UV

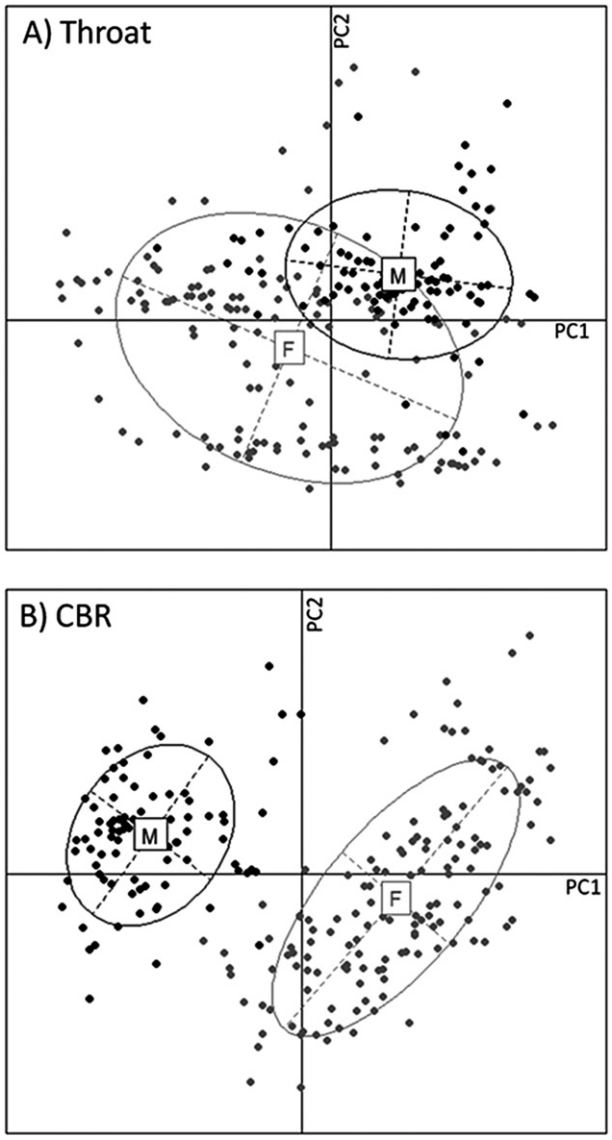

Figure 4. Representation of throat (A) and chest and belly region (CBR) (B) spectral parameters of adult individuals in a plot of the two first principal components (PC1 and PC2). Grey and black ellipses correspond to the female and male inertia ellipses centred on the means, respectively. Their width and height are given by the variances, and the covariance sets the slope of the main axis of the ellipse. Loadings for each PC are described in Table 4.

chroma (Table 4). By contrast, PC2 had positive loadings for UV hue and UV chroma, and negative loadings for VIS hue and yellow chroma. Both PC scores were significantly different between sexes (PC1: $F_{1,227} = 595.9$, $P < 0.001$; PC2: $F_{1,227} = 31.47$, $P < 0.001$). The sexes were clearly separated in a plot of the PC 1 versus PC 2 (Fig. 4B). This is highlighted by the results from the *k*-means cluster analysis, in which the proportion of individuals misclassified was only $0.44 \pm 0.02\%$ ($k = 5$). Males had a duller, less UV-shift (higher hue) and more UV-chromatic CBR coloration than females (Fig. 4B).

Body size and condition effects

The analyses of intrasexual variation in adults highlighted significant relationships between coloration and morphological traits. In females, PCA on female throat coloration resulted in two axes accounting for 70.43% of the total variance (Table 4). PC2, associated with variation in VIS hue, showed a significant negative correlation with SVL but not PC1 (regression, PC1: $F_{1,139} = 0.76$, $P = 0.38$; PC2: $\beta = -0.047 \pm 0.02$, $F_{1,139} = -5.38$, $P = 0.022$). Three PC axes accounted for 85.41% of the total variation in female CBR coloration. PC1 described variation in yellow chroma and was positively correlated with SVL but not the two other axes (PC1: $\beta = 0.097 \pm 0.027$, $F_{1,139} = 12.76$, $P < 0.001$; PC2: $F_{1,139} = 1.17$, $P = 0.28$; PC3: $F_{1,139} = 2.62$, $P = 0.11$). Large females had a yellower throat (spectral peak in shorter wavelengths) and a more intense yellow–red belly coloration than small females.

In males, PCA was performed on data from the throat required three axes to explain 77.04% of the variation (Table 4). No relationships were found between PC1 or PC3 and SVL or body condition (regression between PC1 and SVL: $F_{1,85} = 0.06$, $P = 0.80$; PC1 and body condition: $F_{1,85} = 0.23$, $P = 0.64$; PC3 and SVL: $F_{1,85} = 1.03$, $P = 0.31$; PC3 and body condition: $F_{1,85} = 0.08$, $P = 0.77$). However, PC2, which had large positive loadings for yellow chroma and negative loadings for UV chroma, was negatively correlated with SVL ($\beta = -0.12 \pm 0.05$; $F_{1,86} = 6.45$, $P = 0.013$) but not with body condition ($F_{1,85} = 3.17$, $P = 0.08$). In other words, the throats of large males reflected more UV but displayed a paler yellow–red coloration. For the CBR, the two first PCs accounted for 63.20% of the variation in male coloration (Table 4). PC1 had a large positive loading for yellow chroma and negative loadings for brightness and UV chroma. This axis is significantly negatively correlated with body condition ($\beta = -2.85 \pm 1.28$, $F_{1,86} = 4.94$, $P = 0.029$) but not with SVL ($F_{1,85} = 0.81$, $P = 0.37$). PC2, which had large, negative loadings associated with variation in brightness, VIS hue, and UV hue, was positively correlated with body condition ($\beta = 2.13 \pm 1.05$, $F_{1,86} = 4.15$, $P = 0.045$) but not with SVL ($F_{1,85} = 0.30$, $P = 0.58$). Thus, males with a higher condition index had brighter, paler red, more UV rich and less UV shifted (high hue) ventral spectra.

DISCUSSION

In addition to previous investigations of interindividual variation in a carotenoid-based component of

coloration (Cote *et al*., 2008; Fitze *et al*., 2009), the present study demonstrates that ultraviolet components also contribute to generate substantial intraspecific variation in ventral coloration. Based on photographs and spectrophotometric analyses, we found two distinct ventral patches with contrasted spectral characteristics. The throat area was characterized by a brighter, paler and yellower coloration with a strong UV component (up to 20% of the total reflectance). The CBR was characterized by a more intense and redder coloration with lower UV reflectance. These differences between the throat and CBR coloration, especially in adults, suggest that these ventral regions are affected by different selective pressures. During behaviours such as push-up displays (M. Martin & J.-F. Le Galliard, pers. observ.), the throat is the most visible ventral surface for conspecifics, as well as for certain predators, such as snakes and terrestrial mammals. Thus, the throat might be subjected to stronger natural and sexual selection than the CBR (Cooper & Greenberg, 1992; Stuart-Fox & Ord, 2004), and both regions might be involved in different social contexts.

In adult common lizards, the hue of the skin, as measured by Endler's hue score (Endler, 1990), is an index of the total carotenoid concentration (Fitze *et al*., 2009). In the present study, we found significant correlations between UV and human visible components of ventral coloration, which suggests difficulty with respect to teasing apart structural and pigmentary components. The proportion of UV reflectance (UV chroma) was negatively correlated with yellow chroma (colour purity), especially on the throat, where this relationship explained most of the variation in spectral shape parameters (in females: PC1, 48.55%; in males: PC2, 27.37%). On the CBR, UV chroma also negatively correlated with brightness and VIS hue. Experimental removal of the red epidermis of the combs in male grouse, *Lagopus lagopus scoticus*, revealed that carotenoid pigmentation in the epidermis absorbs light between 300 and 500 nm and thus decreases UV reflectance by the dermis (Mougeot *et al*., 2007). In the present study on the common lizard, the absorption of light by carotenoid pigments of superficial skin layers may also interfere with UV reflectance by platelets of iridophores located in lower skin layers.

Age-related variation

Our analyses revealed significant age differences in coloration. Adult common lizards displayed more chromatic (i.e. higher VIS hue and yellow chroma) and less bright colours, especially on chest and belly, than yearlings. These results may indicate a stronger selection for crypsis in yearlings that decreases predation risk and avoids harassment by adults (Hawkins, Hill & Mercadante, 2012); dull coloration may be a reliable signal of subordinance in younger individuals (Lyon & Montgomerie, 1986). Accordingly, previous studies in birds have found that older individuals displayed more UV (lower hue, higher UV chroma) coloration than yearlings (Johnsen *et al*., 2001; Delhey & Kempenaers, 2006). By contrast, in the common lizard, a bright UV component of coloration occurred in yearlings of both sexes and UV chroma remained similarly high in adult males, whereas it decreased significantly in adult females. The significant UV reflectance in yearlings indicates that structural components of coloration could play a signalling role before reproduction, as may occur during competition for space and food (Tringali & Bowman, 2012). The loss of UV reflectance in adult females is, to our knowledge, the first report of such a phenomenon of colour development in vertebrates.

Different scenarios could explain why and how age-related variation in UV components of colour occurs. First, sexual maturity in females involves a substantial energetic investment in gonad development and vitellogenesis (Bleu *et al*., 2012), which may occur at the expense of maintenance of structural components. Repeated colour measurements performed after mating until oviposition indicated a slight, yet significant decrease of the proportion of UV reflectance throughout gestation (mean decrease of 1% for UV chroma). This could contribute to the observed difference between yearlings and adult females measured after egg laying (mean difference of 7.4%). Second, because bright coloration is potentially costly in terms of survival (Johnstone, 1995), a low UV reflectance in adult females could also represent a strategy for avoiding detection by predators. Third, the maintenance of a strong UV component in males could be promoted by sexual selection if UV components act as a marker of social aggressiveness or fighting ability against other males (Stapley & Whiting, 2006; Bajer *et al*., 2011). These hypotheses can be evaluated by collecting repeated coloration data during the reproductive lifespan of adults and by testing for the relationship between UV coloration and sexual behaviours.

Sexual dichromatism

The results obtained in the present study demonstrate that male and female common lizards significantly differed in their spectral characteristics on the throat and chest and belly. In yearlings, sexual differences occurred on the CBR, with males having more chromatic coloration but a lower brightness. In adults, differences between the sexes increased on the CBR; some sexual differences also appeared on the

throat where coloration was paler but redder, richer in UV and less UV-shifted (high UV hue) in males. These results suggest a difference in the onset of sexual dichromatism on different regions of the body. Sexual dichromatism develops precociously on the chest and belly (before the age of 1 year) and later on the throat. In adults, differences in the colour features of the throat did not allow discrimination of males from females, whereas sexes were clearly distinguishable by the spectral characteristics of the chest and belly, as found in water dragons (Cuervo & Shine, 2007). Altogether, these data suggest that carotenoid-based and UV components of coloration could play a role in sexual selection. Previous studies have already shown that yellow–red ventral ornament is involved in female contest competition and mate choice in the common lizard (Vercken & Clobert, 2008; P. S. Fitze, pers. comm.). Moreover, previous studies in other lizards have demonstrated that UV components can play a role during mate choice and male–male contests (Lebas & Marshall, 2001; Stapley & Whiting, 2006; Martín & López, 2009). For example, male green lizards, *Lacerta viridis*, with reduced UV components are less preferred by females (Bajer *et al*., 2010) and have a higher likelihood of losing a fight against another male (Bajer *et al*., 2011). Such a link between UV components of colour and sexual behaviours remains to be established in the common lizard.

Body size and condition effects

Finally, we tested whether differences in coloration among adults could be explained by differences in body size within each sex or by differences in body condition in males. A large body size in adults is indicative of both older age and faster growth early in life (Le Galliard, Marquis & Massot, 2010), whereas a higher body condition for males is indicative of greater body reserves and a larger head size (J. F. Le Galliard, unpubl. data). Body size is also an important determinant of social dominance and mate choice in the common lizard (Richard *et al*., 2005). In females, we found that larger individuals had a yellower throat (lower VIS hue) and a more saturated CBR coloration (higher yellow chroma), as found by Cote *et al*. (2008), even though spectral purity was calculated differently. In males, we found that larger lizards had a less saturated (weaker yellow chroma) but a relatively richer UV (stronger UV chroma) and less UV-shifted (higher UV hue) throat coloration. In addition, body condition in males correlated with colour parameters of the chest and belly: males with a higher condition index had brighter, paler red (lower yellow chroma and higher VIS hue), more UV rich and less UV-shifted ventral spectra. Thus, the coloration of males on the throat and the coloration of females was related to body size even if different spectral parameters and relationships were involved (Stuart-Fox & Ord, 2004; Calsbeek, Hasselquist & Clobert, 2010; Runemark & Svensson, 2012). Moreover, coloration on the chest and belly was related to body condition in males. This suggests that coloration may provide different cues depending on the body location and that the same cue can be conveyed by different colour traits depending on the sex of the signaller. These results can be interpreted in light of the multiple signals hypothesis, where different visual signals indicate individual quality in males and females and, thus, reinforce the reliability of signals in a social context (Møller & Pomiankowski, 1993; Rowe, 1999; Hamilton & Sullivan, 2005).

In summary, we have found that structural and pigmentary components of ventral coloration contribute to sexual dimorphism in the common lizard *Z. vivipara*, and vary according to the age, body size and condition of the signaller, as well as body location. Given the strong age-dependent variation observed in the present study but a limited understanding of ontogenic mechanisms, our results emphasize the need for studies of the development of structural components of coloration, as well as for investigations of visual communication in immature animals.

ACKNOWLEDGEMENTS

We are very grateful to Marianne Mugabo who kindly shared data and to Donald Miles for linguistic revision of the manuscript. We also thank the three anonymous reviewers for their helpful comments on a previous version. This research was supported by the Centre National de la Recherche Scientifique (CNRS) and an Agence National de la Recherche (ANR) grant (07-JCJC-0120) to J.F.L.G. Authorization no. 2007-189-005 provided permission for us to capture wild animals for the present study.

REFERENCES

Andersson M. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.

Andersson S, Amundsen T. 1997. Ultraviolet colour vision and ornamentation in bluethroats. *Proceedings of the Royal Society of London Series B, Biological Sciences* **264:** 1587–1591.

Andersson S, Örnborg J, Andersson M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society of London Series B, Biological Sciences* **265:** 445–450.

Bajer K, Mólnar O, Török J, Herczeg G. 2010. Female European green lizards (*Lacerta viridis*) prefer males with

high ultraviolet throat reflectance. *Behavioral Ecology and Sociobiology* **64:** 2007–2014.

Bajer K, Mólnar O, Török J, Herczeg G. 2011. Ultraviolet nuptial colour determines fight success in male European green lizards (*Lacerta viridis*). *Biology Letters* **7:** 866–868.

Bauwens D. 1987. Sex recognition by males of the lizard *Lacerta vivipara*: an introductory study. *Amphibia – Reptilia* **8:** 49–57.

Bleu J, Massot M, Haussy C, Meylan S. 2012. Experimental litter size reduction reveals costs of gestation and delayed effects on offspring in a viviparous lizard. *Proceedings of the Royal Society of London Series B, Biological Sciences* **279:** 489–498.

Bowmaker JK. 2008. Evolution of vertebrate visual pigments. *Vision research* **48:** 2022–2041.

Bradbury JW, Vehrencamp SL. 2011. *Principles of animal communication*, 2nd edn. Sunderland, MA: Sinauer Associates.

Calsbeek B, Hasselquist D, Clobert J. 2010. Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard (*Podarcis muralis*) ventral colour morphs. *Journal of Evolutionary Biology* **23:** 1138–1147.

Carretero MA. 2002. Sources of colour pattern variation in Mediterranean *Psammodromus algirus*. *Netherlands Journal of Zoology* **52:** 43–60.

Cooper WEJ, Greenberg N. 1992. Reptilian coloration and behavior. In: Gans C, Crews D, eds. *Biology of the Reptilia*. Chicago, IL: University of Chicago Press, 298–422.

Cote J, Le Galliard JF, Rossi JM, Fitze PS. 2008. Environmentally induced changes in carotenoid-based coloration of female lizards: a comment on Vercken *et al*. *Journal of Evolutionary Biology* **21:** 1165–1172.

Cuervo JJ, Shine R. 2007. Hues of a dragon's belly: morphological correlates of ventral coloration in water dragons. *Journal of Zoology* **273:** 298–304.

Cuthill IC, Bennett ATD, Partridge JC, Maier EJ. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *American Naturalist* **153:** 183–200.

Delhey K. 2006. Seasonal changes in blue tit crown color: do they signal individual quality? *Behavioral Ecology* **17:** 790–798.

Delhey K, Kempenaers B. 2006. Age differences in blue tit *Parus caeruleus* plumage colour: within-individual changes or colour-biased survival? *Journal of Avian Biology* **37:** 339–348.

Doucet SM. 2002. Structural plumage coloration, male body size, and condition in the blue–black grassquit. *The Condor* **104:** 30–38.

Doutrelant C, Grégoire A, Grnac N, Gomez D, Lambrechts MM, Perret P. 2008. Female coloration indicates female reproductive capacity in blue tits. *Journal of Evolutionary Biology* **21:** 226–233.

Endler JA. 1983. Natural and sexual selection on color patterns in Poeciliid fishes. *Environmental Biology of Fishes* **9:** 173–190.

Endler JA. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* **41:** 315–352.

Endler JA. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* **139:** S125–S153.

Fitze PS, Cote J, Martinez-Rica JP, Clobert J. 2008. Determinants of male fitness: disentangling intra- and inter-sexual selection. *Journal of Evolutionary Biology* **21:** 246–255.

Fitze PS, Cote J, San-Jose LM, Meylan S, Isaksson C, Andersson S, Rossi J-M, Clobert J. 2009. Carotenoid-based colours reflect the stress response in the common lizard. *PLoS ONE* **4:** e5111–e5111.

Fleishman LJ, Loew ER, Whiting MJ. 2011. High sensitivity to short wavelengths in a lizard and implications for understanding the evolution of visual systems in lizards. *Proceedings of the Royal Society of London Series B, Biological Sciences* **278:** 2891–2899.

Font E, Pérez I De Lanuza G, Sampedro C. 2009. Ultraviolet reflectance and cryptic sexual dichromatism in the ocellated lizard, *Lacerta (Timon) lepida* (Squamata: Lacertidae). *Biological Journal of the Linnean Society* **97:** 766–780.

Freeman-Gallant CR, Taff CC, Morin DF, Dunn PO, Whittingham LA, Tsang SM. 2010. Sexual selection, multiple male ornaments, and age- and condition-dependent signaling in the common yellowthroat. *Evolution* **64:** 1007–1017.

Gomez D. 2006. AVICOL, a program to analyse spectrometric data. Available at: http://sites.google.com/site/avicolprogram/

Grafen A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* **144:** 517–546.

Hamilton PS, Sullivan BK. 2005. Female mate attraction in ornate tree lizards, *Urosaurus ornatus*: a multivariate analysis. *Animal behaviour* **69:** 219–224.

Hawkins GL, Hill GE, Mercadante A. 2012. Delayed plumage maturation and delayed reproductive investment in birds. *Biological Reviews of the Cambridge Philosophical Society* **87:** 257–274.

Hawlena D, Boochnick R, Abramsky Z, Bouskila A. 2006. Blue tail and striped body: why do lizards change their infant costume when growing up? *Behavioral Ecology* **17:** 889–896.

Hill GE. 1996. Subadult plumage in the house finch and tests of models for the evolution of delayed plumage maturation. *The Auk* **113:** 858–874.

Hill GE. 2006. Environmental regulation of ornamental coloration. In: Hill GE, McGraw KJ, eds. *Coloration, Vol. 1. Mechanisms and measurements*. Cambridge: Harvard University.

Hornik K, Buchta C, Zeileis A. 2009. Open-source machine learning: R meets Weka. *Computational Statistics* **24:** 225–232.

Johnsen A, Lifjeld JT, Andersson S, Ornborg J, Amundsen T. 2001. Male characteristics and fertilisation success in bluethroats. *Behaviour* **138:** 1371–1390.

Johnstone RA. 1995. Sexual selection, honest advertisement and the handicap principle – reviewing the evidence.

Biological Reviews of the Cambridge Philosophical Society **70:** 1–65.

Kaiser HF. 1960. The application of electronic-computers to factor-analysis. *Educational and Psychological Measurement* **20:** 141–151.

Keyser AJ, Hill GE. 2000. Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology* **11:** 202–209.

Le Galliard J-F, Marquis O, Massot M. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. *Journal of Animal Ecology* **79:** 1296–1307.

Lebas NR, Marshall NJ. 2001. No evidence of female choice for a condition-dependent trait in the agamid lizard, *Ctenophorus ornatus*. *Behaviour* **138:** 965–980.

Lecomte J, Clobert J, Massot M. 1992. Sex identification in juveniles of *Lacerta vivipara*. *Amphibia-Reptilia* **13:** 21–25.

Lessells CM, Boag PT. 1987. Unrepeatable repeatabilities: a common mistake. *The Auk* **104:** 116–121.

Lyon BE, Montgomerie RD. 1986. Delayed plumage maturation in passerine birds – reliable signaling by subordinate males. *Evolution* **40:** 605–615.

Macedonia JM, James S, Wittle LW, Clark DL. 2000. Skin pigments and coloration in the jamaican radiation of *Anolis* lizards. *Journal of Herpetology* **34:** 99–109.

Martín J, López P. 2009. Multiple color signals may reveal multiple messages in male Schreiber's green lizards, *Lacerta schreiberi*. *Behavioral Ecology and Sociobiology* **63:** 1743–1755.

Massot M, Clobert J, Pilorge T, Lecomte J, Barbault R. 1992. Density dependence in the common lizard – demographic consequences of a density manipulation. *Ecology* **73:** 1742–1756.

Møller AP, Pomiankowski A. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology* **32:** 167–176.

Mólnar O, Bajer K, Török J, Herczeg G. 2012. Individual quality and nuptial throat colour in male European green lizards. *Journal of Zoology* **287:** 233–239.

Montgomerie R. 2006. Analyzing colors. In: Hill GE, McGraw KJ, eds. *Bird coloration, Vol 1. Mechanisms and measurements*. Cambridge, MA: Harvard University.

Mougeot F, Martínez-Padilla J, Pérez-Rodríguez L, Bortolotti GR. 2007. Carotenoid-based coloration and ultraviolet reflectance of the sexual ornaments of grouse. *Behavioral Ecology and Sociobiology* **61:** 741–751.

Murphy TG, Pham TT. 2012. Condition and brightness of structural blue-green: motmot tail-racket brightness is related to speed of feather growth in males, but not in females. *Biological Journal of the Linnean Society* **106:** 673–681.

R Development Core Team. 2011. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: http://www.R-project.org

Richard M, Lecomte J, De Fraipont M, Clobert J. 2005. Age-specific mating strategies and reproductive senescence. *Molecular Ecology* **14:** 3147–3155.

Rick IP, Bakker TCM. 2008. Males do not see only red: UV wavelengths and male territorial aggression in the three-spined stickleback (*Gasterosteus aculeatus*). *Die Naturwissenschaften* **95:** 631–638.

Rick IP, Modarressie R, Bakker TCM. 2006. UV wavelengths affect female mate choice in three-spined sticklebacks. *Animal Behaviour* **71:** 307–313.

Rowe C. 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour* **58:** 921–931.

Runemark A, Svensson EI. 2012. Sexual selection as a promoter of population divergence in male phenotypic characters: a study on mainland and islet lizard populations. *Biological Journal of the Linnean Society* **106:** 374–389.

Secondi J, Lepetz V, Théry M. 2012. Male attractiveness is influenced by UV wavelengths in a newt species but not in its close relative. *PLoS ONE* **7:** e30391.

Senar JC. 2006. Color displays as intrasexual signals of aggression and dominance. In: Hill GE, McGraw KJ, eds. *Bird coloration, Vol. 2. Function and evolution*. Cambridge, MA: Harvard University Press, 87–136.

Siebeck UE, Parker AN, Sprenger D, Mäthger LM, Wallis G. 2010. A species of reef fish that uses ultraviolet patterns for covert face recognition. *Current Biology* **20:** 407–410.

Siefferman L, Hill GE, Dobson FS. 2005. Ornamental plumage coloration and condition are dependent on age in eastern bluebirds *Sialia sialis*. *Journal of Avian Biology* **36:** 428–435.

Stapley J, Whiting MJ. 2006. Ultraviolet signals fighting ability in a lizard. *Biology Letters* **2:** 169–172.

Stuart-Fox DM, Ord TJ. 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society of London Series B, Biological Sciences* **271:** 2249–2255.

Tringali A, Bowman R. 2012. Plumage reflectance signals dominance in Florida scrub-jay, *Aphelocoma coerulescens*, juveniles. *Animal Behaviour* **84:** 1517–1522.

Vedder O, Schut E, Magrath MJL, Komdeur J. 2010. Ultraviolet crown coloration affects contest outcomes among male blue tits, but only in the absence of prior encounters. *Functional Ecology* **24:** 417–425.

Venable WN, Ripley BD. 1999. *Modern applied statistics with S-PLUS*. New York, NY: Springer-Verlag.

Vercken E, Clobert J. 2008. The role of colour polymorphism in social encounters among female common lizards. *Herpetological Journal* **1:** 223–230.

Vercken E, Massot M, Sinervo B, Clobert J. 2007. Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. *Journal of Evolutionary Biology* **20:** 221–232.

Whiting MJ, Stuart-Fox DM, O'Connor D, Firth D, Bennett NC, Blomberg SP. 2006. Ultraviolet signals ultra-aggression in a lizard. *Animal Behaviour* **72:** 353–363.

SUPPORTING INFORMATION

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

Appendix S1. Tests for seasonal changes over time.
Figure S1. Multiple plots representing the mean spectral parameters of gravid females and males during and after the breeding season on the throat (empty circles) and the chest (black triangles). Errors bars are the standard error of the mean.
Table S1. Intra-individual variability in coloration during the breeding season in males and females. The correlation coefficient (r) measures the correlation between measurements taken on the same individual during and after mating, and significant terms are bolded. The significance of the intra-individual change is tested with paired Student's t-tests (t-value and associated P-value) against the null hypothesis. Significant paired t-tests are shown in bold.
Table S2. Matrix of Pearson correlations between spectral parameters on the throat (in the lower left triangle) and on the chest and belly region (in the upper right triangle) in adult common lizards. Stars represent a significant correlations ($P < 0.05$).