



## Colours of quality: structural (but not pigment) coloration informs about male quality in a polychromatic lizard



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Chromatic signals result from the differential absorption of light by chemical compounds (pigment-based colours) and/or from differential scattering of light by integument nanostructures (structural colours). Both structural and pigment-based colours can be costly to produce, maintain and display, and have been shown to convey information about a variety of individual quality traits. Male wall lizards, *Podarcis muralis*, display conspicuously coloured ventral and lateral patches during ritualized inter- and intra-sexual displays: ventral colours (perceived as orange, yellow or white by humans) are pigment based, while the ultraviolet (UV)-blue of the outer ventral scales (OVS), located along the flanks, is structurally produced. We used spectrophotometric data from 372 adult males to examine, considering the entire visual spectrum of lizards, whether ventral and OVS colour variables can predict male quality. Results indicate that the hue and UV chroma of OVS are good predictors of fighting ability (size-independent bite force) and body condition, respectively. This suggests that structural colour patches are condition dependent and function as complex multicomponent signals in this species. In contrast, ventral coloration apparently does not function as a male quality indicator. We suggest that ventral and lateral colour patches may be social signals with different information content, possibly aimed at different receivers. © 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Chromatic signals provide one of the main avenues for social communication in many taxa (Bradbury & Vehrencamp, 2011). Animal colours result from the differential absorption of light by chemical compounds (i.e. pigment-based colours) and/or from differential scattering of light by integument nanostructures (i.e. structural colours) (Bagnara, Fernández, & Fujii, 2007; Umers, 2013). Both structural and pigment-based colours can be used in intra- and intersexual signalling to convey information about individual quality traits such as condition, fighting ability, territory quality, parental care, good genes, parasite resistance and immunocompetence (Bradbury & Vehrencamp, 2011). Uncovering the relationship between colour variables and individual quality traits is the first step in identifying the information content of structural and pigment-based colour signals, and is key to understanding the balancing selection pressures responsible for their evolutionary stability (Bradbury & Vehrencamp, 2011; Searcy & Nowicki, 2005).

The correlation between one or more characteristics of signals and some attributes of the signaller (or its environment) provides

informative content to many animal signals, while the costs associated with signal production, maintenance, display and/or signal cheating tend to ensure the honesty of individual quality signals (Font & Carazo, 2010; Searcy & Nowicki, 2005). Results from many studies of chromatic signals support this interpretation of quality signalling. For instance, in red-collared widowbirds, *Euplectes ardens*, the carotenoid-based coloration of male collars is a costly trait (e.g. Møller et al., 2000) that is used to signal an individual's ability to defend a territory in male–male agonistic contests. Collar area and hue correlate with territorial dominance, and high-quality males have bigger red collars with a long wavelength-biased hue relative to lower-quality males (Andersson, Pryke, Lawes, & Andersson, 2002). Similar quality signals have been described in numerous vertebrate and invertebrate species (e.g. Lim & Li, 2013; Setchell & Wickings, 2005). Carotenoid-based colours are well suited for honest signalling owing to the costs associated with carotenoid acquisition and the trade-offs between their use as ornaments versus other metabolic processes (e.g. Blount & McGraw, 2008; Saks, McGraw, & Horak, 2003). Other mechanisms of colour production, particularly structural mechanisms, have been considered cheap in comparison (Kemp, Herberstein, & Grether, 2012). While this may certainly be the case in some signals, the available evidence suggests that structural colours are also costly and can act as individual condition indicators (Kemp et al., 2012).

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In lizards, different chromatic traits (including both pigmentary and structural colours) have been shown to play an important role in species, sex, mate and rival assessment (Olsson, Stuart-Fox, & Ballena, 2013). Recent studies based on objective colour assessment (i.e. spectrophotometry) have stressed the ubiquity of structural chromatic signals that reflect in the near ultraviolet (UV) portion of the light spectrum. For example, the UV-reflective mouth corners of collared lizards, *Crotaphytus collaris*, which are visible during gaping displays, are the most conspicuous colour patches in this species' integument, and provide size-independent information on bite force in adult males (Lappin, Brandt, Husak, Macedonia, & Kemp, 2006). Similarly, the UV coloration of the throat of male Augrabies flat lizards, *Platysaurus broadleyi*, is used during the initial stages of opponent assessment (Stapley & Whiting, 2006). In this species, UV-biased throat coloration informs of high fighting ability and testosterone levels, while UV chroma provides information about male territorial status (i.e. territorial males have throats with higher UV chroma than floater males; Whiting et al., 2006).

The study of colour signals has been relatively neglected in many lizard groups and particularly so in lacertids, traditionally considered as relying mainly on chemosensory rather than visual cues (e.g. Mason & Parker, 2010). Despite this long-lasting misconception, colour vision is well developed in lacertids, which exhibit conspicuous and elaborate colour patterns involving both pigmentary and structural colours (Fitze et al., 2009; Pérez i de Lanuza, 2012; Vroonen, Vervust, & Van Damme, 2013). Furthermore, lacertids have been recently shown to provide an excellent model system to test hypotheses about the function and evolution of animal coloration (e.g. Olsson, Wapstra, & Uller, 2005; Pérez i de Lanuza, Font, & Carazo, 2013; Pérez i de Lanuza, Font, & Monterde, 2013; Salvador, Díaz, Veiga, Bloor, & Brown, 2008). The aim of this study was to explore the potential information content of the conspicuous coloration in a lacertid, the common wall lizard, *Podarcis muralis*. This species shows a coloration pattern that is typical of many lacertids: a cryptic brownish dorsal surface, a conspicuous long wavelength-rich ventral coloration and conspicuous lateral UV-blue patches on the outermost row of ventral scales (outer ventral scales, OVS). The ventral coloration is pigment dependent (containing carotenoid; Pérez i de Lanuza, Luna, González, & Font, 2012), and can be orange, white and, in some populations, yellow (Calsbeek, Hasselquist, & Clobert, 2010; Pérez i de Lanuza, Font, & Carazo, 2013; Sacchi et al., 2009). In contrast, UV-blue OVS have their peak reflectance in the UV range, and are structural in nature (Pérez i de Lanuza, 2012). As in other lizards, ventral and lateral coloured surfaces are good candidates to act as chromatic signals in lacertids because they are in an ideal location to be displayed to conspecifics during social interactions, yet normally remain concealed to predators, such as birds, that approach the lizards from above (Stuart-Fox & Ord, 2004). In this study, we examined the relationship between colour variables from the ventral and UV-blue OVS colour patches of male *P. muralis* and two well-studied quality measures in lizards: body condition and bite force. Body condition and bite force correlate with male mating success and dominance in lizards (Salvador et al., 2008), and are therefore considered good quality indicators for male lizards in general (e.g. Henningsen & Irschick, 2011), and for lacertids in particular (e.g. Huyghe, Vanhooydonck, Scheers, Molina-Borja, & Van Damme, 2005).

## METHODS

### Study Population

We studied a polymorphic population of *P. muralis* (Fig. 1) from the Cerdanya valley, in the southeastern Pyrenees (France). In this

population, males and females show either pure white, yellow or orange (i.e. single-colour) ventral coloration. These three colours differ in hue, chroma and brightness extracted from spectral measurements (Pérez i de Lanuza, Font, & Carazo, 2013). Intermediate (white-orange and yellow-orange) phenotypes also occur, but are far less frequent than pure-colour morphs. In males, the ventral coloration extends over the throat and belly, whereas in females the yellow and orange ventral colours are restricted to the throat (Pérez i de Lanuza, Font, & Carazo, 2013). Frequencies of each morph vary from year to year, but all morphs were present in the population throughout the study period (see Appendix Fig. A1). UV-blue OVS are prevalent in males, but are shown only by 60% of females (G. Pérez i de Lanuza & E. Font, unpublished data). Males occasionally show UV-blue eyespots in the shoulder region.

We captured and measured 372 adult male *P. muralis* during the breeding seasons of 2004 ( $N = 26$ ), 2005 ( $N = 77$ ), 2008 ( $N = 120$ ), 2010 ( $N = 74$ ) and 2012 ( $N = 75$ ) in dry stone walls of abandoned terraced fields. Lizards measuring less than 56 mm in snout–vent length (SVL) were excluded to ensure that all individuals had fully developed adult ventral coloration (Pérez i de Lanuza, Font, & Carazo, 2013). Overall, we captured 150 white, 93 yellow and 93 orange males. In contrast, only 16 white-orange and 20 yellow-orange males were captured. Owing to the difficulties inherent in obtaining sound spectrophotometric measurements from intermediate morphs (Pérez i de Lanuza, Font, & Carazo, 2013), only lizards showing pure ventral colours were included in the analyses. Given the relatively low frequency of intermediate morphs (i.e. 9.68%) and our overall sample sizes ( $N = 372$ ), it is very unlikely that the exclusion of these individuals may have biased our results. Moreover, owing to limitations in the minimum measurement area achieved by existing spectrophotometers, taking spectrophotometric measurements from small OVS (i.e. <2 mm in diameter) inevitably results in the simultaneous measurement of adjacent patches of different colour, which gives rise to chimeric spectra. Hence, we discarded spectra of OVS from 43 males in which these patches were simply too small to be measured correctly. Ventral morphs were determined visually by the same observer (G.P.L.), a method that has been validated previously using spectral data (Pérez i de Lanuza, Font, & Carazo, 2013). Bite force was measured only during the last 3 years of this study (2008, 2010 and 2012,  $N = 196$  pure-morph male lizards).

### Spectrophotometric Measurements

We used a USB-2000 portable diode-array spectrometer and a PX-2 xenon strobe light source (both from Ocean Optics) to perform spectrophotometric measurements (for details see Font, Pérez i de Lanuza, & Sampedro, 2009). Spectral analyses were conducted in the 300–700 nm range to encompass the totality of the wavelength range perceived by diurnal lizards (e.g. Fleishman, Loew, & Whiting, 2011; Macedonia et al., 2009; for lacertids see Pérez i de Lanuza, 2012). Colour measurements of UV-blue OVS were always taken from the second rostral-most UV-blue OVS of the right flank (Pérez i de Lanuza & Font, 2011). Ventral coloration was measured at the throat because this is the most visible ventral surface during male social displays, and it is representative (within an individual) of the spectral shape of the entire ventral area (i.e. throat and belly; Pérez i de Lanuza, 2012).

### Colour Analyses

We used the three colour variables customarily used in studies of animal coloration: brightness (i.e. intensity), hue and chroma (Bradbury & Vehrencamp, 2011; Endler, 1990). Brightness ( $Q_t$ ) was calculated by summing the percentage reflectance across the entire



**Figure 1.** Lateral and ventral views showing the conspicuous colour patches found in adult male *Podarcis muralis*.

spectrum ( $R_{300-700}$ ). Hue and chroma were measured differently for each body surface. For UV-blue OVS, hue (H) was measured as the wavelength of maximum reflectance. As the ventral coloration has a similar peak location irrespective of colour phenotype (see Appendix Fig. A2), we used Endler's (1990) hue measure for the throat. Chroma was measured as UV chroma ( $C_{UV}$ , calculated as  $R_{300-400}/R_{300-700}$ ) for UV-blue OVS because they have their maximum reflectance in the UV range of the spectrum. For the throat, we calculated a relative medium wavelength chroma (MC, calculated as  $R_{400-600}/R_{300-700}$ ). We chose this chroma variable because, while peak location is the same for the three morphs, chromatic differences between colour morphs are due mainly to variation in reflectance between 400 and 600 nm (Appendix Fig. A2). This measure allowed us to consider variability within and between morphs simultaneously (Pérez i de Lanuza, Font, & Carazo, 2013). Low values of MC indicate long wavelength-biased colours (i.e. orange). We used these 'raw' variables as directly extracted from spectra to avoid the large set of assumptions implied in visual modelling.

#### Body Condition and Bite Force

We measured body size (i.e. snout–vent length  $\pm 1$  mm; hereafter SVL) and body mass ( $\pm 0.01$  g), and calculated a body condition index (BCI) as the residual from a least-squares linear regression of  $\log(\text{body mass})$  against  $\log(\text{SVL})$  (Green, 2001). Because we focused on adult males, our index of body condition is unlikely to be affected by ontogenetic changes in length/mass scaling (Peig & Green, 2010). Bite force (BF) was measured with the FlexiForce wireless ELF system (Tekscan Inc., Boston, MA, U.S.A.; Freeman & Lemen, 2008). We put two thin stainless steel disks (9 mm in diameter and 0.5 mm thick) over the top and bottom surfaces of the

piezoresistive sensor. Lizards were put individually into a terrarium equipped with an IR heating lamp. Once their body temperature (as measured with an infrared thermometer Testo Quicktemp 825-T2) was confirmed to be in the 30–35 °C range, which is the temperature of active lizards in the field (Luna, Pérez i de Lanuza, & Font, 2013), we measured their bite force. Lizards were induced to bite by placing the steel disk–sensor–steel disk assembly between their open jaws, which usually caused the lizards to bite aggressively. For each individual, we repeated this procedure until we obtained three consecutive measurable bites. The largest bite value for each individual was considered to be the maximum bite force for that animal and was retained for analyses (Losos, Creer, & Schulte, 2002).

#### Statistical Analyses

Where necessary (see below), we included colour morph as a fixed factor in our analyses (Pérez i de Lanuza, Font, & Carazo, 2013). To select the adequate set of covariables for our models, we ran preliminary linear models (LMs) to test for significant differences in lizard body condition (BCI) and bite force (BF) between colour morphs and in different years. Year to year differences in size (and therefore probably in bite force measures) are expected in this montane lizard population because interannual variation in weather conditions introduces variation in the duration of periods of arrested growth. In contrast, interannual differences in BCI are not expected because, during the breeding season, food is not a limiting factor in this population. Based on these preliminary analyses, size (SVL) and year were included as covariables in BF models, while morph was used as a covariable in BCI models (see Results). To evaluate key throat and OVS colour variables associated with BCI and BF, we included the following variables as predictors:

**Table 1**  
Colour variables for the UV-blue outer ventral scales (OVS) and throat classified by colour morph

	UV-blue OVS			Throat		
	Hue (nm)	Qt × 10 <sup>-2</sup>	C <sub>UV</sub>	H (°)	Qt × 10 <sup>-2</sup>	MC
White	373.2 ± 0.9 (352.9–400.0)	381 ± 7 (176–601) N=131	0.33 ± 0.01 (0.23–0.46)	48.8 ± 0.6 (27.4–66.7)	366 ± 7 (173–725) N=130	0.52 ± 0.01 (0.45–0.59)
Yellow	371.4 ± 0.9 (352.6–392.2)	374 ± 9 (232–649) N=84	0.34 ± 0.01 (0.22–0.43)	37.1 ± 0.5 (26.1–49.2)	331 ± 7 (196–582) N=86	0.47 ± 0.01 (0.41–0.53)
Orange	371.8 ± 0.9 (356.6–391.5)	392 ± 10 (221–648) N=78	0.34 ± 0.01 (0.21–0.45)	22.5 ± 0.7 (12.2–44.5)	280 ± 10 (157–536) N=81	0.39 ± 0.01 (0.32–0.51)
Average	372.3 ± 0.5	382 ± 5	0.33 ± 0.01	38.2 ± 0.7	332 ± 5	0.47 ± 0.01

Values represent the mean ± SEM. Range values (in parentheses) and subsample sizes are also shown. H = hue (as wavelength of maximum reflectance for OVS and Endler's angle for throat), Qt = brightness, C<sub>UV</sub> = UV chroma, MC = chroma of intermediate wavelengths (i.e. 400–600 nm).

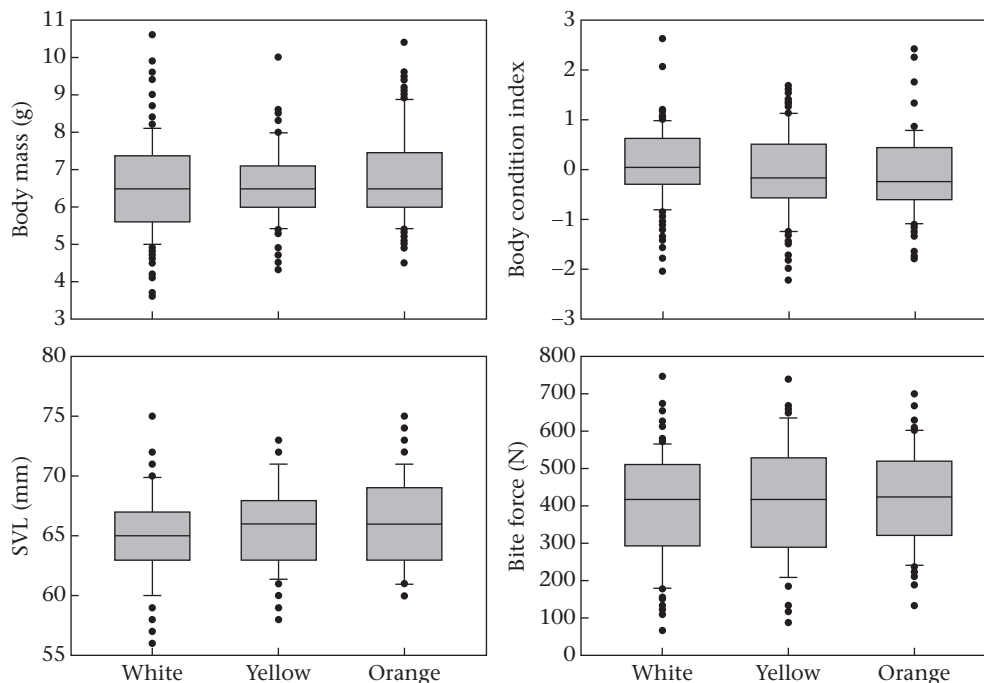
throat<sub>chroma</sub>, throat<sub>brightness</sub>, OVS<sub>chroma</sub>, OVS<sub>hue</sub> and OVS<sub>brightness</sub>. Throat<sub>hue</sub> was eliminated prior to running linear models because diagnostic scatterplots suggested collinearity with throat<sub>chroma</sub>, which was later confirmed with a Pearson correlation test ( $r_{295}^2 = 0.95$ ,  $P < 0.001$ ). Hence, BF was modelled as a function of our five colour variables plus size (i.e. SVL; to correct for size effects on bite force) and year as covariables, while BCI was modelled as a function of our five colour variables plus morph.

Model fitting, evaluation, selection and averaging were conducted with R v. 2.14.0 (R Development Core Team; <http://www.r-project.org/>). We used exhaustive screening of all candidate models in combination with model averaging owing to a lack of a priori hypotheses about which combination of colour variables and their interactions may represent biologically relevant models for our data (Calcagno & de Mazancourt, 2010). Models were evaluated using the second-order information criterion (AICc) which is adequate when, as in our case, the ratio of parameters to sample size is less than 40 (Burnham & Anderson, 2002). Model averaging was conducted over a 95% confidence set of candidate models, calculated as the set of AICc ranked models with an accumulated model weight ≤ 0.95 (i.e. a 95% probability that the best model is represented within the set; Calcagno & de Mazancourt, 2010; Symonds & Moussalli, 2011). Importance weights are a measure of the probability that the explanatory variable is a component of

the best model (Symonds & Moussalli, 2011). This model-averaging procedure incorporates uncertainty about which model is most appropriate for determining coefficient estimates and variances of relevant covariates. As a complementary approach, we report  $P$  values for linear models including all the terms identified as important in the exhaustive modelling approach. All variables were graphically checked for homoscedasticity and homogeneity of variance assumptions prior to running any analyses. Significant interactions were explored by plotting 3D and contour plots using the 'mgcv' package for R, v. 1.7-22 (<http://cran.r-project.org/web/packages/mgcv/>).

#### Ethical Note

Animals were captured with a noose (i.e. a pole with a loop of string with a slipknot that tightens around the neck of the lizard). After capture, lizards were individually held in cloth bags and transported by foot (travelling time ca. 15–30 min) to an indoor field laboratory close to the capture sites (<1 km) where measurements were taken. For spectrophotometric, body size/condition and bite force measurements the lizards were removed from their bags and gently restrained by hand. To minimize stress, the lizards remained in their bags in a temperature-controlled room before and after measurements. No deaths, shed tails or broken



**Figure 2.** Box plots showing the values of body mass, snout–vent length (SVL), body condition index and bite force separated by colour morph. Boxes indicate the interquartile range. Horizontal lines represent the median and bars indicate the 10th and 90th percentiles. Circles show outliers.

**Table 2**

Average coefficient estimates and relative importance for colour variables and covariables identified as important predictors of body condition index (BCI) in *Podarcis muralis* male lizards

Term	Coefficient	SE	Models	Importance
Morph <sub>yellow</sub> *OVS <sub>brightness</sub>	-1.55E-05	1.49E-05	78	0.89
Morph <sub>orange</sub> *OVS <sub>brightness</sub>	2.59E-05	1.67E-05	78	0.89
OVS <sub>brightness</sub>	3.44E-05	9.19E-05	80	0.91
Morph <sub>yellow</sub>	0.24	8.15E-01	81	0.92
Morph <sub>orange</sub>	-0.96	9.85E-01	81	0.92
OVS <sub>chroma</sub>	-12.37	1.95E+01	89	1

Colour variables: OVS<sub>chroma</sub>, OVS<sub>hue</sub>, OVS<sub>brightness</sub>, Throat<sub>chroma</sub> and Throat<sub>brightness</sub>. Covariables: colour morph. Importance rate > 0.8. Model averaging was calculated over the confidence set of candidate models (i.e.  $N = 89$ ).

limbs occurred as a result of manipulations, and all the lizards were released back at their capture location within 24 h of capture. Lizards in our sample were captured in an area in which we are conducting several longitudinal studies (Pérez i de Lanuza, Font, & Carazo, 2013). After measurements, lizards were marked with xylene-free pens (Pilot Corporation, Tokyo, Japan; Whiting et al., 2006) to prevent recapture within a season (markings last 2–3 weeks) and to avoid pseudoreplication. Painted numbers were inconspicuous at long distances (>5 m), but allowed lizard identification at close range (i.e. <3 m). In addition, 192 lizards (out of 372 lizards caught) were marked with a unique toe-clipping pattern prior to being released, ensuring that they could be individually identified across breeding seasons. Lizards that presented natural toe loss, scars or other unique characteristics allowing individual identification were not toe clipped. Toe clipping is less stressful than alternative marking methods and is considered the most adequate and ethically sound method for durable marking of small lizards (Perry, Wallace, Perry, Curzer, & Muhlberger, 2011). In agreement with the majority of studies that have addressed this issue (e.g. Borges-Landáez & Shine, 2003; Huey, Dunham, Overall, & Newman, 1990; Paulissen & Meyer, 2000), we did not observe any adverse effects of toe clipping. To minimize harm to the animals and comply with reptile care guidelines, we cut a maximum of two toes per lizard with a pair of sharp surgical scissors that were disinfected with ethanol before and after each lizard was toe clipped. We only clipped one toe per limb and selected small digits that did not usually draw blood. For toe clipping, lizards were restrained by hand. After clipping, injuries were cleaned with alcohol and treated with Terramycin ophthalmic ointment to prevent infection and to

provide analgesia; Terramycin contains hydrocortisone, which is an anti-inflammatory drug with well-known analgesic effects. Lizards were not anaesthetized for toe clipping to avoid potential adverse effects of anaesthetics. Also, anaesthesia increases the time the lizards must be held in captivity (to allow for complete recovery) and requires additional handling of the lizards which may itself cause more stress than toe clipping (Langkilde & Shine, 2006). Forty-four males were captured in more than one breeding season (43 toe-clipped and one with natural marks), in which cases we only consider the latest measurements in our analyses. Lizards were captured under research permit number 2013095-0001 from the Préfecture des Pyrénées-Orientales. This research complied with the ASAB/ABS Guidelines for the Use of Animals in Research.

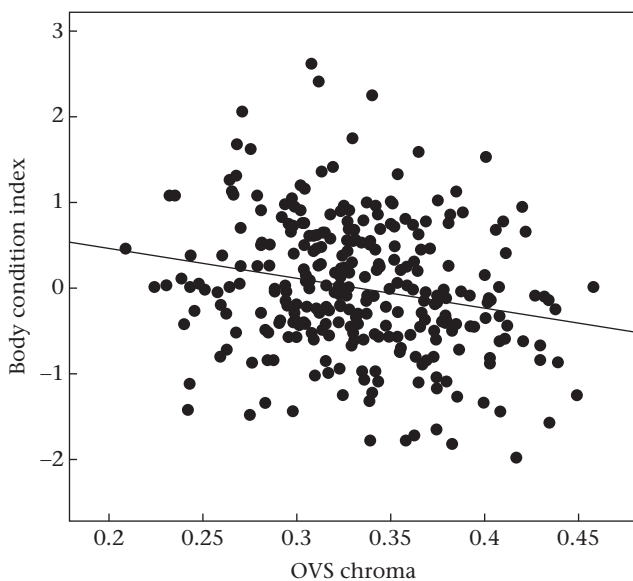
## RESULTS

### Morphological Relationships

Spectrophotometric data are shown in Table 1 and Appendix Fig. A2. Figure 2 shows morphometric, body condition and bite force data. Body condition and bite force were not significantly related ( $BF \sim BCI + Year$ ; whole model:  $r^2 = -0.005$ ,  $F_{2,190} = 0.496$ ,  $P = 0.610$ ;  $BF$ :  $t = 0.159$ ,  $P = 0.874$ ). As expected, we detected a highly significant effect of size (SVL) on bite force ( $F_{2,191} = 115.303$ ,  $P < 0.001$ ). We also found significant differences in BF between years ( $F_{2,191} = 61.300$ ,  $P < 0.001$ ), but not between different colour morphs ( $F_{2,191} = 0.736$ ,  $P = 0.480$ ). In contrast, we did not detect significant differences in BCI between years ( $F_{4,325} = 1.499$ ,  $P = 0.202$ ), but we did detect marginally significant differences between morphs ( $F_{2,325} = 3.255$ ,  $P = 0.040$ ). A post hoc Tukey HSD test suggests that this is due to white lizards exhibiting higher BCI than orange lizards, but differences were marginally nonsignificant (white versus orange: difference =  $0.223 \pm 0.239$ ,  $P = 0.072$ ; white versus yellow: difference =  $0.207 \pm 0.240$ ,  $P = 0.106$ ; yellow versus orange: difference =  $0.015 \pm 0.266$ ,  $P = 0.990$ ).

### Predictors of Body Condition

Our model selection procedure produced a 95% confidence set of 89 models (best model:  $BCI \sim 1 + Morph + Throat_{chroma} + OVS_{brightness} + OVS_{chroma} + Morph * OVS_{brightness}$ ,  $AICc = 506.05$ ,  $w_i = 0.060$ ).  $OVS_{chroma}$  was found to be negatively related to BCI, and appears as the variable with both the highest importance weight and the highest average coefficient estimate, and therefore as the main predictor of BCI, although morph also appears as an important predictor in the model (Table 2). An LM with all the variables that appeared as important in the exhaustive screening (Table 2) shows a highly significant effect of  $OVS_{chroma}$  ( $F_{1,283} = 12.668$ ,  $P < 0.001$ ; Fig. 3) and a marginally significant effect of morph ( $F_{2,283} = 3.099$ ,  $P = 0.047$ ), but no effect of  $OVS_{brightness}$  ( $F_{2,283} = 0.287$ ,  $P = 0.593$ ), or of the interaction between morph and  $OVS_{brightness}$  ( $F_{2,283} = 2.020$ ,  $P = 0.135$ ).



**Figure 3.** Scatterplot showing the relation between body condition index and the UV-blue OVS ( $OVS_{chroma}$ ).

**Table 3**  
Average coefficient estimates and relative importance for colour variables and covariables (year and SVL) identified as important predictors of bite force in *Podarcis muralis* male lizards

Term	Coefficient	SE	Models	Importance
Year <sub>2010</sub>	-315.10	157.80	91	1
Year <sub>2012</sub>	-37.10	136.79	91	1
OVS <sub>hue</sub>	49.36	16.30	91	1
SVL	294.22	87.85	91	1
OVS <sub>hue</sub> *SVL	-0.75	0.24	91	1

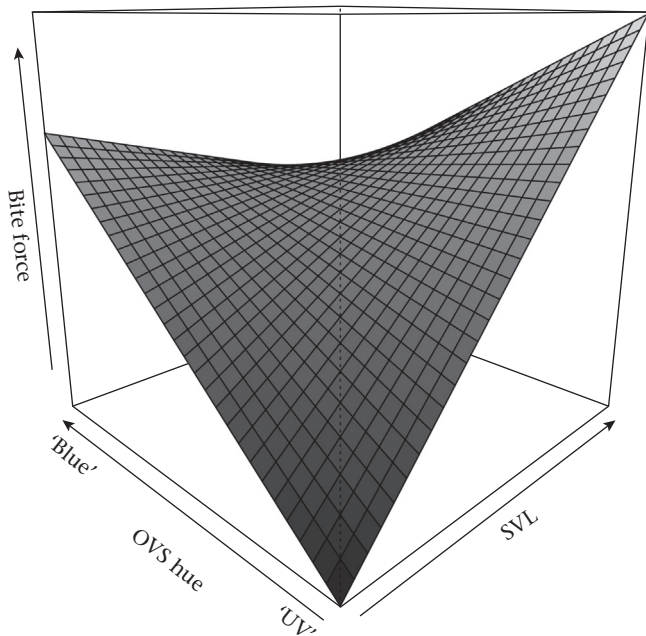
Colour variables: OVS<sub>chroma</sub>, OVS<sub>hue</sub>, OVS<sub>brightness</sub>, Throat<sub>chroma</sub> and Throat<sub>brightness</sub>. Covariables: year and SVL. Importance rate > 0.8. Model averaging was calculated over the confidence set of candidate models (i.e.  $N = 91$ ).

### Predictors of Bite Force

Our model selection procedure produced a 95% confidence set of 91 models (best model:  $BF \sim 1 + \text{Year} + \text{Throat}_{\text{chroma}} + \text{OVS}_{\text{hue}} + \text{SVL} + \text{SVL} * \text{OVS}_{\text{hue}} + \text{Year} * \text{Throat}_{\text{chroma}}$ ,  $AICc = 1962.43$ ,  $w_i = 0.034$ ). Year, SVL, OVS<sub>hue</sub> and the interaction between OVS<sub>hue</sub> and SVL all appear as highly important variables (Table 3). Again, an LM with all the variables that appeared as important in the exhaustive screening (Table 3) agrees with this finding, showing a highly significant effect of year ( $F_{2,158} = 75.550$ ,  $P < 0.001$ ), SVL ( $F_{1,158} = 87.190$ ,  $P < 0.001$ ), and the interaction between OVS<sub>hue</sub> and SVL ( $F_{1,158} = 10.567$ ,  $P = 0.001$ ). We explored this effect with a 3D plot, which suggest that this interaction is due to the existence of a positive relationship between BF and OVS<sub>hue</sub> in small males, where males with high BF exhibit OVS shifted towards the blue end of the spectrum, but a negative relationship between BF and OVS<sub>hue</sub> in large males, where males with high BF exhibit OVS shifted towards the UV end of the spectrum (Fig. 4).

### DISCUSSION

We report here that the UV-blue OVS located on the flanks of male *P. muralis* are a potential source of socially important information, with different colour variables of these patches relating to individual body condition and bite force. The ‘multiple messages’ hypothesis (Hebets & Papaj, 2005) states that different signals or



**Figure 4.** 3D plot exploring the relationship between bite force, reflectance peak location of UV-blue OVS (OVS<sub>hue</sub>) and body size (SVL) in male *P. muralis* lizards in our study. Dark–clear shading reflects the low–high bite force axis.

signal components produced simultaneously (or perceived simultaneously by receivers) convey information about different aspects of signaller quality. In accordance with this hypothesis, our results suggest that UV-blue OVS may play an important role as complex, multicomponent signals (see Grether, Kolluru, & Nersissian, 2004) conveying information about different, nonredundant male quality attributes. In contrast, the ventral pigment-based coloration of *P. muralis* was not found to be a good predictor of any of these quality indicators. Our findings agree with a recent comparative study of lacertid colour patterns, which suggests that the UV-blue patches (but not the ventral or dorsal coloration) play an important role in male intrasexual competition in this lizard clade (Pérez i de Lanuza, Font, & Monterde, 2013). Although carotenoid coloration represents the paradigm of chromatic honest signalling (Svensson & Wong, 2011), the results reported here highlight the relevance of structural condition-dependent colour patches for individual quality signalling in lizards.

### Short-wavelength Structural Coloration as Quality Signal

Previous studies have shown that UV-reflective patches may act as quality signals in fish (e.g. Siebeck, 2004), amphibians (e.g. Secondi, Lepetz, & Théry, 2012), birds (e.g. Siefferman & Hill, 2005) and lizards (e.g. Lappin et al., 2006; Stapley & Whiting, 2006; Whiting et al., 2006), including lacertids. For instance, the size of the UV-blue lateral badges of *Gallotia galloti* seems to convey information about male dominance (Huyghe et al., 2005; Molina-Borja, Font, & Mesa Ávila, 2006). More recent work on *Lacerta viridis* has shown that dominant males have throats with higher UV chroma than subordinates (Bajer, Molnár, Török, & Herczeg, 2011), and that females prefer such males over males with lower UV chroma (Bajer, Molnár, Török, & Herczeg, 2010). Moreover, several colour variables of the male throat have been shown to correlate with directional asymmetry, body size, relative head size and ectoparasite load in this species (Molnár, Bajer, Török, & Herczeg, 2012).

The honesty of structural colour signals, such as the UV-based coloration of *P. muralis*, could be guaranteed by the various costs associated with their production and maintenance (Kemp et al., 2012). Available evidence suggests that short-wavelength reflectance, and particularly UV chroma and hue, are costly features of structural coloration. At least in birds, the development and arrangement of the nanostructures responsible for UV coloration appear to be costly and condition dependent owing to a trade-off between investment in growth/body condition and investment in these chromatic signals (e.g. Keyser & Hill, 1999). Structural coloration in lizards results from a combination of iridophores that reflect short wavelengths and an underlying layer of melanophores that absorb the wavelengths that are not reflected by the iridophores (Bagnara et al., 2007; Grether et al., 2004). Short-wavelength reflectance (i.e. blue and UV) is produced by thin-layer interference of reflecting guanine platelets located inside the dermal iridophores (Kuriyama, Miyaji, Sugimoto, & Hasegawa,

2006; Morrison, Rand, & Frost-Mason, 1995). As the spectral properties of structural colours depend on the thickness, refractive index and distribution of guanine platelets (Morrison et al., 1995), we suggest the hue and chroma of UV signals in *P. muralis* may reflect a trade-off between these colour traits and investment in growth or body condition.

In this study we found a negative relationship between UV chroma (i.e. the amount of reflected UV relative to the entire spectrum) and body condition that is in accordance with that reported by Molnár et al. (2012) for *L. viridis*, and by Whiting et al. (2006) for the cordylid *P. broadleyi*. In the latter species, this relationship seems to be mediated by territorial behaviour, that is, territorial lizards exhibit both higher UV chroma and relatively lower body condition than floater males. Whiting et al. (2006) argued that this result may be explained by the physiological costs associated with the defence of good territories. According to this hypothesis, the UV chroma of UV-reflecting colour patches would act as a general indicator of territorial status or social dominance in male lizards, and the observed relationship between UV chroma and body condition would be an indirect by-product. This would explain why, in our sample, males with high UV chroma were in poor body condition compared to males with low UV chroma.

Our results also indicate that the hue of UV-blue OVS of male *P. muralis* may function as a signal of male fighting ability. Chromatic ornaments have been shown to mediate the assessment of an opponent's fighting ability, and contribute to determining the intensity of aggressive behaviours in lizards (Lappin et al., 2006; Stapley & Whiting, 2006; Stuart-Fox et al., 2009). Our results agree with these findings, strongly suggesting that male *P. muralis* may use the hue of UV-blue OVS to assess the competitive ability of rivals without having to resort to physical contact, as occurs in other lizards (Whiting et al., 2006). However, our analyses detected an interaction between hue and body size (SVL). Given that lizards have indeterminate growth, this finding suggests that the relationship between OVS hue and bite force changes during development in adult lizards. Among small to medium-sized adult males (SVL between 56 and 65 mm), those with stronger bite force show long wavelength-biased UV-blue OVS (i.e. shifted towards the blue portion of the spectrum). In contrast, among large adult males (SVL > 67–70 mm, lizards more than 2 years old, E. Font, G. Pérez i de Lanuza, & P. Carazo, unpublished data), those with stronger bite force show short wavelength-biased UV-blue OVS (i.e. shifted towards 360 nm). Interpreting the intriguing interaction between body size and hue of UV-blue OVS in the absence of specific knowledge about individual ontogenetic changes in bite force and UV-blue OVS coloration is necessarily speculative.

If UV-shifted OVS function as a quality signal mediating male intrasexual competition, we suggest that selection will favour young males that exhibit more bluish, female-like OVS (female OVS peak reflectance is relatively displaced towards the blue end of the spectrum, mean  $\pm$  SEM: 378.61  $\pm$  2.23 nm,  $N = 27$ ; Pérez i de Lanuza, 2012) as a strategy to avoid social costs. There is widespread evidence that small and/or subadult males of many species mimic females and/or delay the adoption of male coloration to avoid associated social costs (e.g. Whiting, Webb, & Keogh, 2009), and what little evidence we have in this respect seems to indicate that the hue of OVS does indeed drop gradually during development in *P. muralis* (see Appendix Fig. A3). The fact that the bite force/OVS hue relationship is inverted through ontogeny could then be explained by the existence of a positive correlation between individual quality (i.e. fighting ability) and intragenerational individual phenotypic plasticity in OVS colour. Because phenotypic plasticity is inherently costly (e.g. Snell-Rood, Van Dyken, Cruickshank, Wade, & Moczek, 2010), it is likely that not

all individuals will be able to afford the same degree of ontogenetic change in the hue of their OVS. Under this scenario, evolution would favour high-quality males that are better able to shift from blue OVS to UV OVS during development, which means they would pay less signal maintenance costs when small and gain more benefits from signalling high fighting ability when large. While this is a speculative hypothesis at this stage, we suggest it is a plausible and exciting hypothesis worth addressing by future studies.

#### *Polymorphic Ventral Coloration and Male Quality*

Conspicuous long wavelength-reflective colours are used for honestly signalling status and fighting ability in many vertebrates. In lizards, long wavelength-reflective patches of some species may be condition dependent (Olsson et al., 2013), and may act as male quality signals that play a key role in the resolution of male–male contests (e.g. Hamilton, Whiting, & Pryke, 2013). However, and despite the large spectral variability found between and within ventral morphs of *P. muralis* (see Table 1, Appendix Fig. A1 and Pérez i de Lanuza, Font, & Carazo, 2013), our results argue against the possibility that ventral coloration conveys information about either male dominance or fighting ability. This conclusion agrees with a recent study that suggested that ventral coloration does not affect the outcome of male–male contests in Italian polychromatic populations of *P. muralis* with white, yellow and orange colour phenotypes (Sacchi et al., 2009). In short, the available evidence suggests that the ventral coloration of *P. muralis* may mediate mate assessment (i.e. positive assortative mating; Pérez i de Lanuza, Font, & Carazo, 2013), and may also reflect different female reproductive strategies (i.e. clutch size and egg size; Galeotti et al., 2013), but does not seem to convey information about individual male quality.

We have shown that different chromatic characteristics of structural OVS are good predictors of fighting ability and body condition, respectively, which suggests OVS may act as complex, multicomponent condition-dependent signals in this species. In contrast, pigment-based ventral coloration apparently does not indicate male quality in this species, which challenges the traditional idea of costly pigment-based indicators versus cheap structural-based coloration. Instead, we suggest that the different conspicuous ventral and ventrolateral colours may signal different information content, possibly aimed at different receivers. Finally, we identified an intriguing ontogenetic shift in the direction of the relationship between OVS structure and individual quality, which suggests a potential link between intragenerational phenotypic plasticity in OVS and individual quality that deserves further attention in future studies.

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#### **References**

- Andersson, S., Pryke, S. R., Lawes, M. J., & Andersson, M. (2002). Multiple receivers, multiple ornaments and a trade-off between agonistic and epigamic signaling in a widowbird. *American Naturalist*, 160, 683–691. <http://dx.doi.org/10.1086/342817>.

- Bagnara, J. T., Fernández, P. J., & Fujii, R. (2007). On the blue coloration of vertebrates. *Pigment Cell Research*, 20, 14–26. <http://dx.doi.org/10.1111/j.1600-0749.2006.00360.x>.
- Bajer, K., Molnár, 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. <http://dx.doi.org/10.1007/s00265-010-1012-2>.
- Bajer, K., Molnár, O., Török, J., & Herczeg, G. (2011). Ultraviolet nuptial colour determines fight success in male European green lizards (*Lacerta viridis*). *Biology Letters*, 7, 866–868. <http://dx.doi.org/10.1098/rsbl.2011.0520>.
- Blount, J. D., & McGraw, K. J. (2008). *Signal functions of carotenoid colouration*. In G. Britton, S. Llaaen-Jensen, & H. Pfander (Eds.), *Carotenoids, natural functions* (Vol. 4); (pp. 213–236). Basel, Switzerland: Birkhauser Verlag.
- Borges-Landáez, P. A., & Shine, R. (2003). Influence of toe-clipping on running speed in *Eulamprus quoyii*, an Australian scincid lizard. *Journal of Herpetology*, 37, 592–595. <http://dx.doi.org/10.1670/26-02N>.
- Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York: Springer.
- Calcagno, V., & de Mazancourt, C. (2010). glmulti: an R package for automated model selection with (generalized) linear models. *Journal of Statistical Software*, 34, 1–29.
- 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. <http://dx.doi.org/10.1111/j.1420-9101.2010.01978.x>.
- Endler, J. A. (1990). On the measurement and classification of color in studies of animal colour patterns. *Biological Journal of the Linnean Society*, 41, 315–352. <http://dx.doi.org/10.1111/j.1095-8312.1990.tb00839.x>.
- Fitze, P. S., Cote, J., San-Jose, L. M., Meylan, S., Isaksson, C., Andersson, S., et al. (2009). Carotenoid-based colours reflect the stress response in the common lizard. *PLoS One*, 4, e5111. <http://dx.doi.org/10.1371/journal.pone.0005111>.
- Fleishman, L. J., Loew, E. R., & Whiting, M. J. (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 B: Biological Sciences*, 278, 2891–2899. <http://dx.doi.org/10.1098/rspb.2011.0118>.
- Font, E., & Carazo, P. (2010). Animals in translation: why there is meaning (but probably no message) in animal communication. *Animal Behaviour*, 80, e1–e6. <http://dx.doi.org/10.1016/j.anbehav.2010.05.015>.
- 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. <http://dx.doi.org/10.1111/j.1095-8312.2009.01251.x>.
- Freeman, P. W., & Lemen, C. A. (2008). Measuring bite force in small mammals with a piezo-resistive sensor. *Journal of Mammalogy*, 89, 513–517. <http://dx.doi.org/10.1644/07-MAMM-A-101R.1>.
- Galeotti, P., Sacchi, R., Pellitteri-Rosa, D., Bellati, A., Cocca, W., Gentilli, A., et al. (2013). Colour polymorphism and alternative breeding strategies: effects of parent's colour morph on fitness traits in the common wall lizard. *Evolutionary Biology*, 40, 385–394. <http://dx.doi.org/10.1007/s11692-012-9222-3>.
- Green, A. J. (2001). Mass/length residuals: measures of body condition or generators of spurious results? *Ecology*, 82, 1473–1483. [http://dx.doi.org/10.1890/0012-9658\(2001\)082\[1473:MLRMOB\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2001)082[1473:MLRMOB]2.0.CO;2).
- Grether, G. F., Kolluru, G. R., & Nersissian, K. (2004). Individual colour patches as multicomponent signals. *Biological Reviews of the Cambridge Philosophical Society*, 79, 583–610. <http://dx.doi.org/10.1017/S1464793103006390>.
- Hamilton, D. G., Whiting, M. J., & Pryke, S. R. (2013). Fiery frills: carotenoid-based coloration predicts contest success in frillneck lizards. *Behavioral Ecology*, 24, 1138–1149. <http://dx.doi.org/10.1093/beheco/art041>.
- Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, 57, 197–214. <http://dx.doi.org/10.1007/s00265-004-0865-7>.
- Henningsen, J. P., & Irschick, D. J. (2011). An experimental test of the effect of signal size and performance capacity on dominance in the green anole lizard. *Functional Ecology*, 26, 3–10. <http://dx.doi.org/10.1111/j.1365-2435.2011.01893.x>.
- Huey, R., Dunham, A., Overall, K., & Newman, R. (1990). Variation in locomotor performance in demographically known populations of *Sceloporus merriami*. *Physiological Zoology*, 63, 845–872.
- Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-Borja, M., & Van Damme, R. (2005). Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology*, 19, 800–807. <http://dx.doi.org/10.1111/j.1365-2435.2005.01038.x>.
- Kemp, D. J., Herberstein, M. E., & Grether, G. F. (2012). Unraveling the true complexity of costly color signaling. *Behavioral Ecology*, 23, 233–236. <http://dx.doi.org/10.1093/beheco/arr153>.
- Keyser, A. J., & Hill, G. E. (1999). Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proceedings of the Royal Society B: Biological Sciences*, 266, 771–777. <http://dx.doi.org/10.1098/rspb.1999.0704>.
- Kuriyama, T., Miyajiri, K., Sugimoto, M., & Hasegawa, M. (2006). Ultrastructure of the dermal chromatophores in a lizard (Scincidae: *Plestiodon laticaudatus*) with conspicuous body and tail coloration. *Zoological Science*, 23, 793–799. <http://dx.doi.org/10.2108/zsj.23.793>.
- Langkilde, T., & Shine, R. (2006). How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. *Journal of Experimental Biology*, 209, 1035–1043. <http://dx.doi.org/10.1242/jeb.02112>.
- Lappin, A. K., Brandt, Y., Husak, J. F., Macedonia, J. M., & Kemp, D. J. (2006). Gaping displays reveal and amplify a mechanically based index of weapon performance. *American Naturalist*, 168, 100–113. <http://dx.doi.org/10.1086/505161>.
- Lim, M. L. M., & Li, D. (2013). UV-green iridescence predicts male quality during jumping spider contests. *PLoS One*, 8, e59774. <http://dx.doi.org/10.1371/journal.pone.0059774>.
- Losos, J. B., Creer, D. A., & Schulte, J. A. (2002). Cautionary comments on the measurement of maximum locomotor capabilities. *Journal of Zoology*, 258, 57–61. <http://dx.doi.org/10.1017/S0952836902001206>.
- Luna, S., Pérez i de Lanuza, G., & Font, E. (2013). Use of an infrared thermographic camera to measure field body temperatures of small lacertid lizards. *Herpetological Review*, 44, 59–62.
- Macedonia, J. M., Lappin, A. K., Loew, E. R., McGuire, J. A., Hamilton, P. S., Plasman, M., et al. (2009). Conspicuousness of Dickerson's collared lizard (*Crotaphytus dickersonae*) through the eyes of conspecifics and predators. *Biological Journal of the Linnean Society*, 97, 749–765. <http://dx.doi.org/10.1111/j.1095-8312.2009.01217.x>.
- Mason, R. T., & Parker, M. R. (2010). Social behavior and pheromonal communication in reptiles. *Journal of Comparative Physiology A*, 196, 729–749. <http://dx.doi.org/10.1007/s00359-010-0551-3>.
- Molina-Borja, M., Font, E., & Mesa Ávila, G. (2006). Sex and population variation in ultraviolet reflectance of colour patches in *Gallotia galloti* (Fam. Lacertidae) from Tenerife (Canary Islands). *Journal of Zoology*, 268, 193–206. <http://dx.doi.org/10.1111/j.1469-7998.2005.00008.x>.
- Møller, A. P., Biard, C., Blount, J. D., Houston, D. C., Ninni, P., Saino, N., et al. (2000). Carotenoid-dependent signals: indicators of foraging efficiency, immunocompetence or detoxification ability? *Avian and Poultry Biology Reviews*, 11, 137–159.
- Molnár, 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. <http://dx.doi.org/10.1111/j.1469-7998.2012.00916.x>.
- Morrison, R. L., Rand, M. S., & Frost-Mason, S. K. (1995). Cellular basis of color differences in three morphs of the lizard *Sceloporus undulatus erythrocheilus*. *Copeia*, 1995, 397–408.
- Olsson, M., Stuart-Fox, D., & Ballena, C. (2013). Genetics and evolution of colour patterns in reptiles. *Seminars in Cell & Developmental Biology*, 24, 529–541. <http://dx.doi.org/10.1016/j.semcdb.2013.04.001>.
- Olsson, M., Wapstra, E., & Uller, T. (2005). Differential sex allocation in sand lizards: bright males induce daughter production in a species with heteromorphic sex chromosomes. *Biology Letters*, 1, 378–380. <http://dx.doi.org/10.1098/rsbl.2005.0327>.
- Paulissen, M. A., & Meyer, H. A. (2000). The effect of toe-clipping on the gecko *Hemidactylus turcicus*. *Journal of Herpetology*, 34, 282–285.
- Peig, J., & Green, A. J. (2010). The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology*, 24, 1323–1332. <http://dx.doi.org/10.1111/j.1365-2435.2010.01751.x>.
- Pérez i de Lanuza, G. (2012). *Visió en color i coloracions dels lacèrtids* (doctoral dissertation). València: University of València. Retrieved from: <http://roderic.uv.es/handle/10550/23877>.
- Pérez i de Lanuza, G., & Font, E. (2011). Lizard blues: blue body colouration and ultraviolet polychromatism in lacertids. *Revista Española de Herpetología*, 24, 67–84.
- Pérez i de Lanuza, G., Font, E., & Carazo, P. (2012). Colour assortative mating in a colour polymorphic lacertid lizard. *Behavioral Ecology*, 24, 273–279. <http://dx.doi.org/10.1093/beheco/ars164>.
- Pérez i de Lanuza, G., Font, E., & Monterde, J. L. (2013). Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids. *Journal of Evolutionary Biology*, 26, 1826–1835. <http://dx.doi.org/10.1111/jeb.12185>.
- Pérez i de Lanuza, G., Luna, S., González, L., & Font, E. (2012, October). *Carotenoid content of conspicuous ventral colorations in a polychromatic lizard* (*Podarcis muralis*). Paper presented at the XII Congreso Luso-Español de Herpetología–XVI Congreso Español de Herpetología, Murcia, Spain. Abstract retrieved from: [https://dl.dropboxusercontent.com/u/87463444/0libro\\_resumenes.pdf](https://dl.dropboxusercontent.com/u/87463444/0libro_resumenes.pdf).
- Perry, G., Wallace, M. C., Perry, D., Curzer, H., & Muhlberger, P. (2011). Toe clipping of amphibians and reptiles: science, ethics, and the law. *Journal of Herpetology*, 45, 547–555. <http://dx.doi.org/10.1670/97-04n>.
- Sacchi, R., Pupin, F., Gentilli, A., Rubolini, D., Scali, S., Fasola, M., et al. (2009). Male-male combats in a polymorphic lizard: residency and size, but not color, affect fighting rules and contest outcome. *Aggressive Behavior*, 35, 274–283. <http://dx.doi.org/10.1002/ab.20305>.
- Saks, L., McGraw, K., & Horak, P. (2003). How feather colour reflects its carotenoid content. *Functional Ecology*, 17, 555–561. <http://dx.doi.org/10.1046/j.1365-2435.2003.00765.x>.
- Salvador, A., Díaz, J. A., Veiga, J. P., Bloor, P., & Brown, R. P. (2008). Correlates of reproductive success in male lizards of the alpine species *Iberolacerta cyreni*. *Behavioral Ecology*, 19, 169–176. <http://dx.doi.org/10.1093/beheco/arm118>.
- Searcy, W. A., & Nowicki, S. (2005). *The evolution of animal communication: Reliability and deception in signaling systems*. Princeton, NJ: Princeton University Press.
- 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. <http://dx.doi.org/10.1371/journal.pone.0030391>.



Setchell, J. M., & Wickings, E. J. (2005). Dominance, status signals and coloration in mandrills (*Mandrillus sphinx*). *Ethology*, 111, 25–50. <http://dx.doi.org/10.1111/j.1439-0310.2004.01054.x>.

Siebeck, U. E. (2004). Communication in coral reef fish: the role of ultraviolet colour patterns in damselfish territorial behaviour. *Animal Behaviour*, 68, 273–282. <http://dx.doi.org/10.1016/j.anbehav.2003.11.010>.

Siefferman, L., & Hill, G. E. (2005). UV-blue structural coloration and competition for nestboxes in male eastern bluebirds. *Animal Behaviour*, 69, 67–72. <http://dx.doi.org/10.1016/j.anbehav.2003.12.026>.

Snell-Rood, E. C., Van Dyken, J. D., Cruickshank, T., Wade, M. J., & Moczek, A. P. (2010). Toward a population genetic framework of developmental evolution: the costs, limits, and consequences of phenotypic plasticity. *Bioessays*, 32, 71–81. <http://dx.doi.org/10.1002/bies.200900132>.

Stapley, J., & Whiting, M. J. (2006). Ultraviolet signals fighting ability in a lizard. *Biology Letters*, 2, 169–172. <http://dx.doi.org/10.1098/rsbl.2005.0419>.

Stuart-Fox, D. M., Godinho, R., Goüy de Bellocq, J., Irwin, N. R., Brito, J. C., Moussalli, A., et al. (2009). Variation in phenotype, parasite load and male competitive ability across a cryptic hybrid zone. *PLoS One*, 4, e5677. <http://dx.doi.org/10.1371/journal.pone.0005677>.

Stuart-Fox, D. M., & Ord, T. J. (2004). Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society B: Biological Sciences*, 271, 2249–2255. <http://dx.doi.org/10.1098/rspb.2004.2802>.

Svensson, P. A., & Wong, B. B. M. (2011). Carotenoid-based signals in behavioural ecology: a review. *Behaviour*, 148, 131–189. <http://dx.doi.org/10.1163/000579510X548673>.

Symonds, M. R. E., & Moussalli, M. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65, 13–21. <http://dx.doi.org/10.1007/s00265-010-1037-6>.

Umbers, K. D. L. (2013). On the perception, production and function of blue colouration in animals. *Journal of Zoology*, 289, 229–242. <http://dx.doi.org/10.1111/jzo.12001>.

Vroonen, J., Vervust, B., & Van Damme, R. (2013). Melanin-based colouration as a potential indicator of male quality in the lizard *Zootoca vivipara* (Squamata: Lacertidae). *Amphibia-Reptilia*, 34, 539–549.

Whiting, M. J., Stuart-Fox, D. M., O'Connor, D., Firth, D., Bennett, N. C., & Blomberg, S. P. (2006). Ultraviolet signals ultra-aggression in a lizard. *Animal Behaviour*, 72, 353–363. <http://dx.doi.org/10.1016/j.anbehav.2005.10.018>.

Whiting, M. J., Webb, J. K., & Keogh, J. S. (2009). Flat lizard female mimics use sexual deception in visual but not chemical signals. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1585–1591. <http://dx.doi.org/10.1098/rspb.2008.1822>.

Appendix

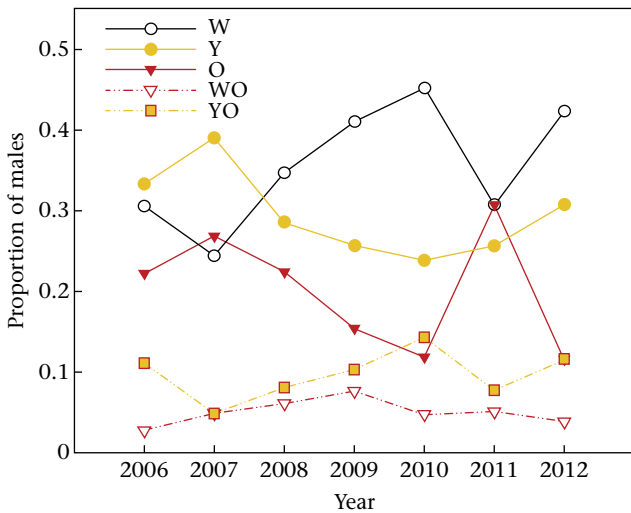


Figure A1. Population variation in colour morph frequencies of male *Podarcis muralis* during a 7-year period.

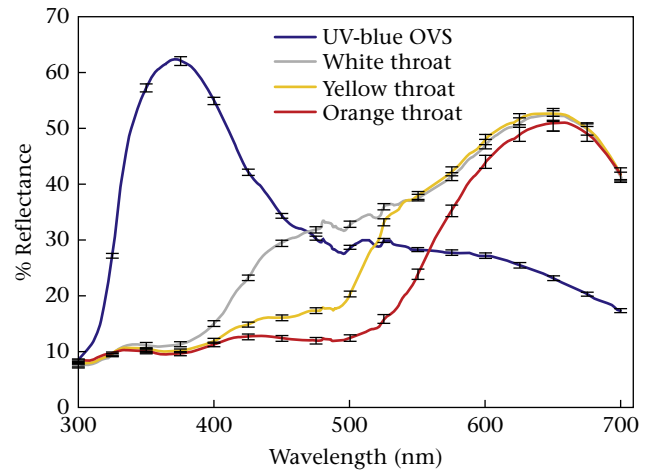


Figure A2. Reflectance spectra from UV-blue OVS and white, yellow and orange throats of male *Podarcis muralis*. Vertical lines: error bars ( $\pm 1$  SEM). See sample sizes in Table 1.

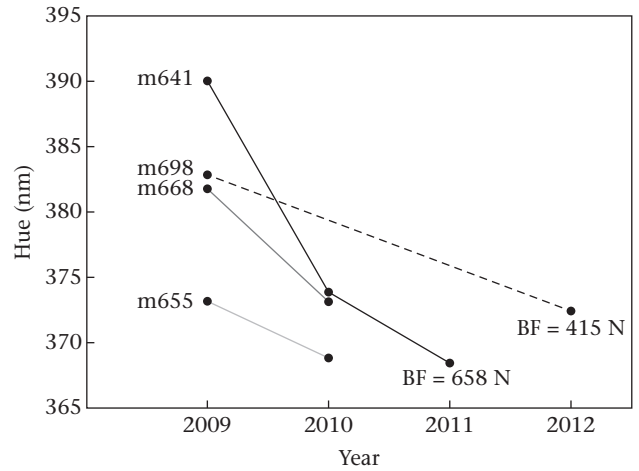


Figure A3. Ontogenetic changes in the hue of UV-blue OVS of four *Podarcis muralis* males. All males were captured as subadults (i.e. SVL < 56 mm) in 2009, and were recaptured (and their UV-blue OVS remeasured) occasionally during the ensuing years.