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Colour variation between different lineages of a colour polymorphic lizard

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Abstract

Colour polymorphic animals offer useful models to study the evolution of polymorphisms and studies with colour polymorphic lizards have contributed many advances in this field. Unfortunately, few studies address basic questions such as how observers (e.g. conspecifics) perceive the polymorphism or whether there is chromatic variability among evolutionary lineages or distant geographic areas within a species' range. The common wall lizard (*Podarcis muralis*) shows a striking colour polymorphism in its ventral surface, presenting up to five alternative colour morphs, that is white, yellow and orange/red (depending on the lineage), and two intermediate mosaic morphs: white-orange and yellow-orange. Here we compare this polymorphism in two geographically distant areas, the Po valley (Northern Italy) and the Eastern Pyrenees (Iberian Peninsula), corresponding to separate phylogeographic lineages. Using objective techniques of colour measurement and lizard vision models, we examine the chromatic differences between these two polymorphic lineages. We also search for chromatic differences in other colour traits present in *P. muralis*: the cryptic dorsal coloration and the ultraviolet-blue spots of the outer ventral scales (UV-blue OVS) used for intraspecific communication. Although we detected significant differences among lineages in colour variables, the main variation was found between the alternative ventral colour morphs. The most striking inter-lineage divergence was between the orange Pyrenean morph and the red Italian morph, mainly caused by achromatic (but not chromatic) differences. In addition, although the UV-blue OVS show strong chromatic and achromatic variation between lineages, the dorsal coloration shows the smallest degree of variation, and mainly between localities rather than lineages. Overall, the ventral colour pattern of *P. muralis* is shared by at least two geographically and phylogenetically distant lineages. Nevertheless, body coloration also shows signs of historical divergence (Pyrenean orange vs. Italian red) and local adaptation (mainly in the dorsal pattern).

Introduction

The extraordinary diversity of animal colours is caused by the interaction of many selective forces. A particularly interesting case is that in which some colour variants coexist in the same population (colour polymorphisms; White & Kemp, 2016). These polymorphisms afford unique opportunities to explore how evolution promotes and maintains the coexistence of different phenotypes (Gray & McKinnon, 2006; Oliveira, Taborsky & Brockmann, 2008; McKinnon & Pierotti, 2010). Well-documented cases of colour polymorphism exist in insects, fish or birds (Roulin, 2004; Takahashi *et al.*, 2010; Maan & Sefc, 2013). Lizards show an exuberant diversity in coloration, from dull concolor (i.e. a single colour pattern) to striking and contrasting complex patterns, often involving conspicuous colour polymorphisms. Thus, lizards represent a useful model to study patterns of colour variation (Stuart-Fox & Ord, 2004; Chen *et al.*, 2012) and particularly to identify the evolutionary mechanisms underlying stable colour polymorphisms (Sinervo & Lively, 1996; Lattanzio & Miles, 2014; McLean, Stuart-Fox & Moussalli, 2015).

Lacertid lizards (Lacertidae) have highly variable coloration (Pérez i de Lanuza, Font & Monterde, 2013a; Pérez i de Lanuza & Font, 2016) and a complex colour vision system involving four types of single cones, as well as double cones, which allows colour vision from 320 to 700 nm (Pérez i de Lanuza & Font, 2014; Martin *et al.*, 2015). Lacertids often show striking ventral and ventrolateral colour patterns involving several contrasting colour patches that most likely act as chromatic signals (Pérez i de Lanuza & Font, 2015, 2016).

During close-range social interactions with conspecifics, including male–male agonistic interactions and interactions between males and females, lizards often compress their body in the sagittal plane and depress the gular area making their ventral and ventrolateral colour patches visible to observers located on the same plane (Kitzler, 1941; Verbeek, 1972; for *Podarcis muralis* references see Pérez i de Lanuza & Font, 2015; Ábalos *et al.*, 2016; MacGregor *et al.*, 2017).

Colour polymorphism is common among lacertids, some species being currently under intense scrutiny with the aim to test hypotheses for the evolution of polymorphisms (e.g. Carretero *et al.*, 2006; Huyghe *et al.*, 2007, 2009; Galeotti *et al.*, 2013; Pérez i de Lanuza, Font & Carazo, 2013b; San-José *et al.*, 2014; Pérez i de Lanuza, Font & Carretero, 2016; Pérez i de Lanuza, Carretero & Font, 2017; Pérez i de Lanuza, Sillero & Carretero, 2018b). A crucial question to properly address the study of colour polymorphisms is whether relevant observers of the polymorphism (i.e. conspecifics) actually discriminate alternative morphs. Although this necessary requirement for considering a species as chromatically polymorphic is generally assumed, very little empirical evidence is available to support this assumption (e.g. Teasdale, Stevens & Stuart-Fox, 2013; Merkling *et al.*, 2016) and explicit behavioural demonstrations are needed. In fact, in the absence of this kind of confirmation, the identification and description of morphs may be controversial, obscuring the interpretation of the results (e.g. Cote *et al.*, 2008; Vercken, Sinervo & Clobert, 2008).

A recent paper studying colour discrimination in the common wall lizard, *P. muralis* (Lacertidae), provided the first demonstration of discrimination of different colour morphs based on chromatic cues in lizards (Pérez i de Lanuza *et al.*, 2018a). Colour polymorphism in this species has recently received much attention. Efforts have mainly focused on testing the assumption that ventral colour morphs may be linked to some sort of alternative reproductive strategies, but results are far from conclusive (Sacchi *et al.*, 2007; Calsbeek, Hasselquist & Clobert, 2010; Galeotti *et al.*, 2013; Scali *et al.*, 2013; Pérez i de Lanuza & Font, 2015; Ábalos *et al.*, 2016). The available evidence suggests that several selective forces may interact in the maintenance of this polymorphism, probably in a complex balancing selection scenario (Pérez i de Lanuza *et al.*, 2017, 2018b). Most available results agree with the hypothesis that sexual selection is important for the maintenance of this polymorphism (Galeotti *et al.*, 2013; Pérez i de Lanuza *et al.*, 2013b, 2016, 2017; Ábalos *et al.*, 2016). However, evidence from geographic variation of local morph composition and habitat use by morphs in sympatry suggests that this polymorphism is also environmentally constrained (Pérez i de Lanuza & Carretero, 2018; Pérez i de Lanuza *et al.*, 2018a,b).

To date, the great majority of studies on polymorphic *P. muralis* have been conducted in two geographically distant areas (the Po valley in Northern Italy and the Eastern Pyrenees), which are inhabited by two different lineages that originated, with many others within this species, during the Pleistocene (Salvi *et al.*, 2013). Although colour polymorphism has been reported in both regions, chromatic similarity between the two is assumed rather than tested and there is no consensus among researchers in the number and typology of morphs. For example, studies from the Pyrenees describe up to five ventral colour morphs in both adult males and females: white, yellow and orange pure morphs, and white-orange and yellow-orange intermediate morphs (Pérez i de Lanuza *et al.*, 2013b; but see the proposal for a sixth white-yellow morph in Calsbeek *et al.*, 2010; Zajitschek *et al.*, 2012). In contrast, studies from Northern Italy describe from four to six morphs and, remarkably, have reported the existence of a red (rather than orange) morph in this area (Sacchi *et al.*, 2007, 2009, 2013; Galeotti *et al.*, 2013; Scali *et al.*, 2013, 2016; Pellitteri-Rosa *et al.*, 2014, 2017). The discrepancy between the orange and the red morphs might indicate some underlying biological meaningful difference (e.g. differences in pigment composition; McGraw, 2006), but it may also be caused by the subjective perception of human observers. For these reasons, and with the aim to reach a consensus among researchers regarding the variability of colour morphs in *P. muralis*, the adoption of objective techniques for colour measurement (reflectance spectrophotometry) and analyses (visual modelling) is highly desirable.

Here we extend previous work to explore the chromatic differences between the Italian and Pyrenean polymorphic lineages, which are not geographically in contact and have undergone thousands of years of independent evolution (Salvi *et al.*, 2013). Our aim is to explore if the different morphs are chromatically equivalent across the two lineages taking into account the visual perception of conspecifics. Additionally, we also study colour variation in two other colour traits: the dorsal coloration and the ultraviolet (UV)-blue patches shown mainly by males in some of their outer ventral scales (OVS). Although the UV-blue OVS probably act as social signals (Pérez i de Lanuza, Carazo & Font, 2014; MacGregor *et al.*, 2017) and are extremely conspicuous when viewed in combination with ventral colours (Pérez i de Lanuza *et al.*, 2013b), the brown dorsal coloration seems mainly the result of selection for crypsis (Pérez i de Lanuza *et al.*, 2013b; Pérez i de Lanuza & Font, 2015).

In this context, our main questions are: (1) are ventral colours from both lineages chromatically different? and (2) are colour differences between the orange Pyrenean morph and the red Italian morph caused by achromatic and/or chromatic differences? Additionally, we also predict that the dorsal coloration (mainly related to crypsis; Pérez i de Lanuza & Font, 2015) will be more variable between localities than between lineages due to a potential local adaptation. Contrarily, as different Italian lineages of *P. muralis* differ in the chromatic properties of the UV-blue OVS (MacGregor *et al.*, 2017), we expect that those colour patches most likely used as social signals (i.e. UV-blue OVS, but also the ventral colour) will be more variable between lineages than between localities.

So far, no study has compared lizards from the Eastern Pyrenees and Northern Italy, which are now used for multiple studies of colour polymorphism in this species. The adoption of a general framework encompassing the two (and maybe other) lineages of *P. muralis* will allow us to determine if this polymorphism is similar across lineages, and if it is ancestral or, alternatively, is lineage-characteristic suggesting an independent origin. This study represents a first step in this direction.

Materials and methods

Sampling areas

We captured lizards in both Eastern Pyrenees and Northern Italy. In order to disentangle local from regional (i.e. lineage) variation, we sampled two different localities in each study area. In the Eastern Pyrenees, we sampled the villages of Angostrina (42°29′N, 1°57′E) and La Tor de Querol (42°27′N, 1°53′E). In Northern Italy, our samples come from the countryside of San Genesio ed Uniti (Pavia; 45°13′N, 9°11′E) and Bareggio (Milan; 45°27′N, 8°58′E). The distance between the Pyrenean localities is 7 km, and the distance between the Italian localities is 30 km. The distance between both areas is 660 km. Because data on population genetics are not available for the studied areas, here we use the term locality instead of population. The habitat of the Pyrenean localities consists of abandoned fields with dispersed granite rocks and dry-stone walls surrounded by shrubbery (*Crataegus monogyna* and *Rosa* sp.) and some trees (*Fraxinus excelsior*, *Corylus avellana*) (Pérez i de Lanuza & Carretero, 2018). The two Italian sampling sites are located in the typical man-made landscape of the Po plain. The habitat where the lizards were caught is composed by agricultural farms made of bricks and concrete, mainly surrounded by fields of rice (*Oryza sativa*) and corn (*Zea mays*). Trees (mainly *Robinia pseudoacacia* and *Populus* sp.) are sometimes present.

Lizards were captured by noose and transported to the laboratory in individual cloth bags. We only captured adult lizards (with adult SVL, body proportions and coloration; for a detailed description see Pérez i de Lanuza *et al.*, 2013b). After measurements, all lizards were released to their exact site of capture. As captures were not biased by morph, the sample size for each morph is roughly proportional to their availability in the field. Sample sizes for different colour patches differ because lizards showing intermediate morphs were discarded, some UV-blue OVS were too small to obtain appropriate spectrophotometric measurements (Badiane *et al.*, 2017) and dorsal spectra were only available from a subset of lizards (see detailed sample sizes in Table 1).

Table 1 Sample sizes for each colour patch classified by locality and sex

	Eastern Pyrenees		Northern Italy	
	Angostrina	Tor Querol	Bareggio	San Genesio
Overall per locality				
Males	287	69	33	39
Females	78	40	6	37
Samples per patch				
Dorsum				
Males	108	69	33	21
Females	58	40	6	37
OVS				
Males	287	47	31	39
Throat				
White				
Males	91	20	10	7
Females	38	12	3	12
Yellow				
Males	73	17	7	10
Females	23	8	2	17
Orange/red				
Males	58	10	5	2
Females	17	2	1	3

Only pure morph lizards were included in the sample (i.e. excluding intermediate colour morphs).

Reflectance spectrophotometry and colour variables

In order to obtain reflectance spectra of the relevant colour patches of *P. muralis*, we used a USB-2000 portable spectrometer and a PX-2 xenon strobe light source (Ocean Optics Inc.; Dunedin, FL, USA), calibrated with a Spectralon white diffuse reflectance standard (Labsphere) (see Badiane *et al.*, 2017 for technical specifications). As in some populations, the ventral colour polymorphism is only present in the throat of females (Pérez i de Lanuza *et al.*, 2013b; Sacchi *et al.*, 2013), and the coloration of male throats and bellies does not differ (Pérez i de Lanuza & Font, 2015), for ventral morphs we obtained reflectance spectra from the throat instead of the bellies (Fig. 1). We also measured the brown background dorsal colour from a central point of the dorsum avoiding black or grey small spots, and the second rostral-most UV-blue OVS on the right side of males (Pérez i de Lanuza & Font, 2015; Fig. 1). Spectra were collected placing the reading-illumination probe approximately perpendicular to the skin surface, that is illumination and recording angles of 90° (coincident normal measuring geometry; Pérez i de Lanuza *et al.*, 2013b, 2014; Pérez i de Lanuza & Font, 2015; Badiane *et al.*, 2017). For each measurement, the spectrophotometer averaged 20 consecutive spectra from the same patch (Pérez i de Lanuza & Font, 2015).

From reflectance spectra we extracted values of total reflectance (luminance), hue and chroma. Luminance was calculated as the sum of the reflectance over the 300–700 nm spectral range. Hue was calculated as the wavelength of maximum reflectance for the UV-blue OVS and the dorsum, and as the wavelength at which reflectance is halfway between its minimum and its maximum for ventral colours (Pryke, Lawes & Andersson, 2001; Smiseth *et al.*, 2001; Andersson *et al.*, 2002). Chroma was calculated as the sum of the relative reflectance between 450 and 700 nm divided by reflectance at 700 nm for dorsum and ventral morphs (Peters *et al.*, 2004), and as the sum of the relative reflectance between 300 and 400 nm divided by the sum of the relative reflectance over the entire spectral range for the UV-blue OVS.

Visual modelling

We used visual models to quantitatively determine the chromatic and achromatic distances between colour patches of lizards from each locality and lineage from the point of view of conspecifics. We performed these analyses using Vorobyev & Osorio's (1998) receptor noise model, with cone sensitivities of *P. muralis* (Martin *et al.*, 2015). As colour vision is largely

conserved among and within species of diurnal lizards (Fleishman *et al.*, 1997; Fleishman, Loew & Whiting, 2011), we assumed that the visual system of *P. muralis* is invariant across localities and lineages (Pérez i de Lanuza & Font, 2014; Martin *et al.*, 2015). To calculate chromatic distances, we assumed a cone abundance ratio of 1:1:1:4 (corresponding to the ultraviolet-, short-, middle- and long-wavelength-sensitive cones; Martin *et al.*, 2015), and a Weber fraction of 0.05 for the long-wavelength sensitive cone (Siddiqi *et al.*, 2004; previously used in lacertids: Marshall & Stevens, 2014; Martin *et al.*, 2015; Pérez i de Lanuza *et al.*, 2018a). To calculate achromatic distances, we assumed that lizards process the achromatic information using the long-wavelength sensitive cone as suggested in other lizards (Fleishman & Persons, 2001). Chromatic and achromatic distances are expressed as just noticeable differences (JND). It is traditionally assumed that pairs of colour patches generating chromatic distances above 3 JND are easily discriminable (Siddiqi *et al.*, 2004). We also calculated chromatic and achromatic distances between ventral colours and the UV-blue OVS as a measure of conspicuousness. Additionally, we used the relative stimulations of the four cone types to obtain a three-dimensional

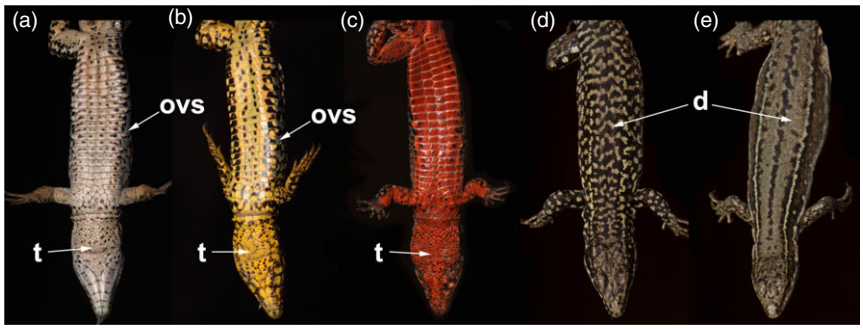

Figure 1 Body location of spectral measurements: t = throat (measured in a central position avoiding black spots), OVS = a UV-blue outer ventral scale (often the second rostral-most UV-blue OVS in the right flank), d = dorsum (the background brown coloration, avoiding black or grey small spots). (a, b and c) represent examples of pure white, yellow and orange males respectively. (d and e) represent examples of the dorsal coloration of an adult male (d) and an adult female (e).

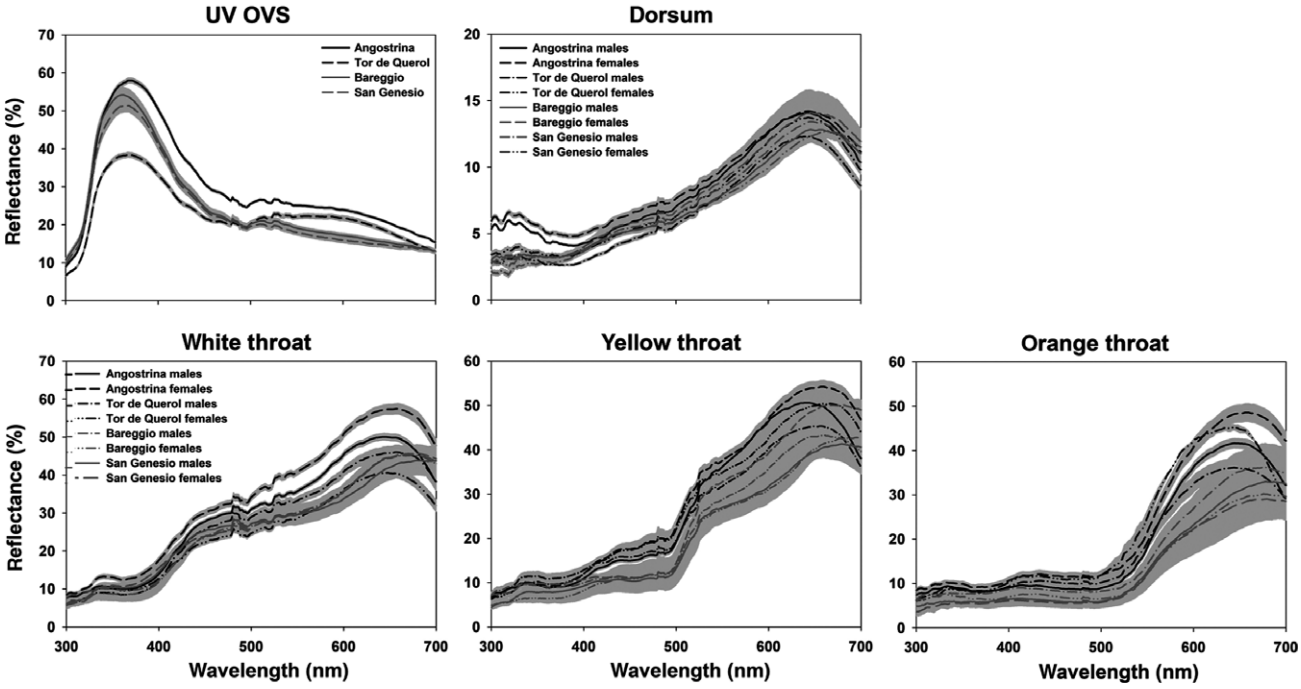

Figure 2 Reflectance spectra from the second rostral-most ultraviolet-blue outer ventral scales (UV-blue OVS) of males and the dorsal coloration of males and females (above), and from the throats of the three pure morphs (below). Lines represent means, grey areas represent ± 1 SEM. For sample sizes, see text.

Table 2 Results from generalized linear models testing differences in luminance, chroma and hue in the UV-blue OVS, dorsum and throat

	Luminance	Chroma	Hue
UV-blue OVS			
Lineage	**0.32 ± 0.05**	**0.17 ± 0.03**	−0.01 ± 0.01
	(6.3; <0.00001)	**(6.3; <0.00001)**	(−0.1; 0.923)
Lineage:locality	−0.06 ± 0.01	−0.02 ± 0.01	−0.01 ± 0.01
	(−7.9; <0.00001)	(−4.4; <0.00001)	(−1.1; 0.262)
Dorsum			
Sex	0.05 ± 0.04	0.04 ± 0.05	−0.01 ± 0.01
	(1.2; 0.29)	(0.9; 0.37)	−0.8 (0.41)
Lineage	0.04 ± 0.04	−0.02 ± 0.05	0.01 ± 0.01
	(0.9; 0.36)	(−0.5; 0.64)	1.2 (0.22)
Sex * lineage	−0.01 ± 0.03	−0.03 ± 0.04	0.01 ± 0.01
	(−0.3; 0.77)	(−0.8; 0.44)	1.7 (0.09)
Lineage:locality	−0.04 ± 0.01	−0.02 ± 0.01	−0.01 ± 0.01
	(−3.6; 0.0003)	(−1.3; 0.20)	−0.8 (0.42)
Throat			
Sex	0.06 ± 0.03	−0.05 ± 0.04	−0.01 ± 0.01
	(2.3; 0.02)	(−1.2; 0.24)	(−0.3; 0.74)
Morph	−0.06 ± 0.02	**−0.26 ± 0.03**	0.04 ± 0.01
	(−3.7; 0.0003)	**(−9.4; < 0.00001)**	(10.7; < 0.00001)
Lineage	**0.12 ± 0.05**	−0.17 ± 0.09	0.04 ± 0.01
	(2.2; 0.03)	(−1.8; 0.07)	(2.7; 0.008)
Sex * lineage	0.01 ± 0.02	−0.01 ± 0.03	−0.01 ± 0.01
	(0.4; 0.72)	(−0.1; 0.97)	(0.8; 0.42)
Morph * lineage	−0.03 ± 0.01	−0.01 ± 0.02	−0.01 ± 0.01
	(−1.8; 0.07)	(−0.1; 0.96)	(−1.0; 0.31)
Lineage:locality	−0.02 ± 0.01	−0.01 ± 0.01	−0.01 ± 0.01
	(−3.3; 0.001)	(−0.1; 0.90)	(−2.3; 0.02)
White			
Sex	0.07 ± 0.04	**−0.15 ± 0.07**	0.01 ± 0.01
	(2.0; 0.047)	**(−2.2; 0.03)**	(0.3; 0.80)
Lineage	**0.22 ± 0.07**	**−0.27 ± 0.12**	0.05 ± 0.03
	(3.4; 0.0009)	**(−2.2; 0.03)**	(1.9; 0.06)
Sex * lineage	−0.02 ± 0.03	0.06 ± 0.05	0.01 ± 0.01
	(−0.5; 0.59)	(1.1; 0.25)	(0.3; 0.78)
Lineage:locality	−0.04 ± 0.01	0.01 ± 0.02	−0.01 ± 0.01
	(−4.4; < 0.00001)	(0.2; 0.83)	(−1.7; 0.08)
Yellow			
Sex	0.01 ± 0.04	−0.01 ± 0.06	−0.01 ± 0.01
	(0.0; 1.0)	(−0.0; 0.99)	(−3.0; 0.003)
Lineage	−0.08 ± 0.07	−0.18 ± 0.12	0.01 ± 0.01
	(−1.1; 0.27)	(−1.6; 0.12)	(1.9; 0.06)
Sex * lineage	0.03 ± 0.03	−0.03 ± 0.05	0.01 ± 0.00
	(1.2; 0.21)	(−0.7; 0.49)	(2.9; 0.004)
Lineage:locality	−0.01 ± 0.01	0.01 ± 0.02	−0.01 ± 0.01
	(−0.9; 0.35)	(0.3; 0.77)	(−2.5; 0.01)
Orange/red			
Sex	**0.20 ± 0.08**	0.04 ± 0.09	−0.01 ± 0.01
	(2.7; 0.008)	(0.4; 0.68)	(−0.3; 0.75)
Lineage	0.18 ± 0.12	−0.29 ± 0.15	0.03 ± 0.01
	(1.5; 0.14)	(−1.9; 0.06)	(3.1; 0.003)
Sex * lineage	**−0.12 ± 0.06**	−0.04 ± 0.07	0.01 ± 0.01
	(−2.0; 0.049)	(−0.6; 0.55)	(0.0; 0.97)
Lineage:locality	−0.03 ± 0.02	0.04 ± 0.02	−0.01 ± 0.01
	(−1.3; 0.20)	(1.7; 0.09)	(−2.5; 0.02)

Each cell indicates the coefficient ± SE, and the *t* and *P* values in parenthesis. Significant results with high coefficients (>0.10) are highlighted in bold.

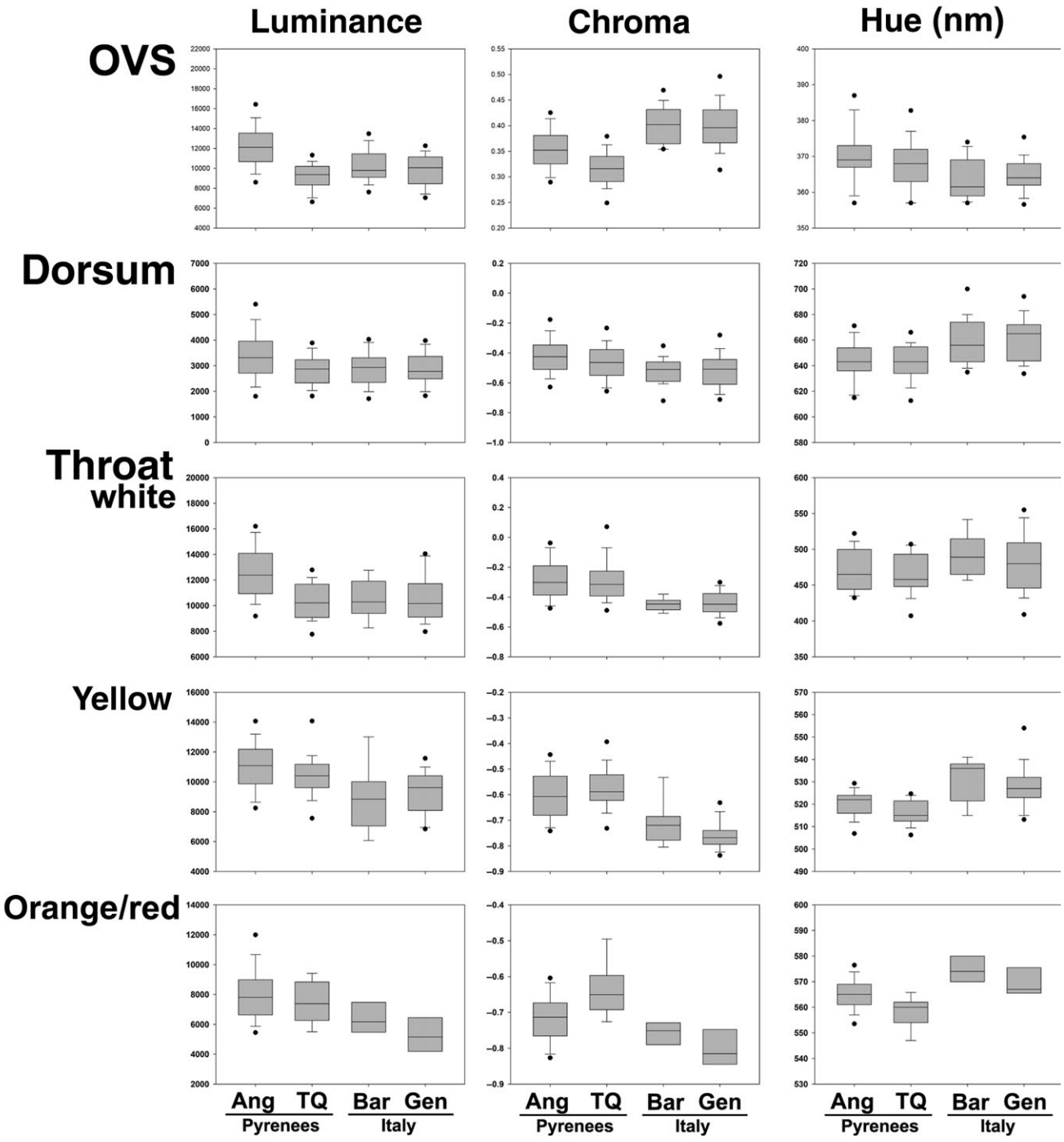

Figure 3 Colour variables of the UV-blue outer ventral scales (OVS), dorsum and the throat of the three pure morphs of *Podarcis muralis* (see details of each variable in the Material and methods section). Males and females are pooled for clarity. Ang = Angostrina, TQ = Tor de Querol, Bar = Bareggio and Gen = San Genesio. Horizontal lines, boxes, error bars and points indicate the median, the 25–75% range, the 10th and 90th percentiles, and the 5th and 95th percentiles, respectively.

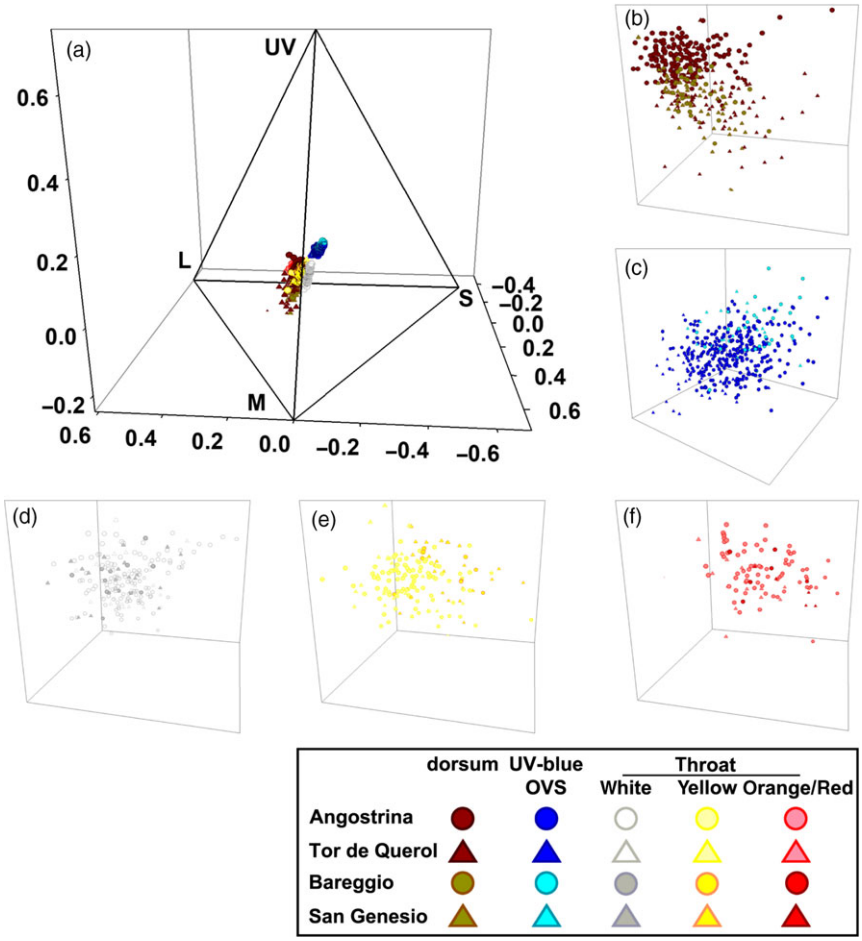

Figure 4 Chromaticity diagram showing the location of chromatic points obtained from the different colour patches of *Podarcis muralis*. (a) The entire colour space showing all the chromatic points; UV, S, M and L represent the ultraviolet-, short-, medium- and long-wavelength vertices. (b) Dorsal coloration. (c) Ultraviolet-blue outer ventral scales (UV-blue OVS). (d–f) White, yellow and orange throats respectively.

chromaticity diagram to graphically explore the chromatic diversity of the different colour patches. Visual models were performed in R 3.3.2 (R Core Team 2016) using the package PAVO (Maia *et al.*, 2013).

Statistical analyses

We used generalized linear models (GLM) to assess the differences between colour variables, chromatic and achromatic distances of each colour patch (i.e. UV-blue OVS, dorsum) and morph (i.e. white, yellow, orange/red throats) between localities, and chromatic and achromatic distances (i.e. conspicuousness) between each throat colour and the UV-blue OVS, which represents the most conspicuous chromatic combination in this species (Pérez i de Lanuza & Font, 2015). When colour variables were compared, sex (except for the UV-blue OVS), morph (if applicable) and lineage were considered as independent factors, locality being nested within lineage, and considering the interactions between both sex and lineage and morph and lineage. When chromatic and achromatic distances between lineages and between colour patches (i.e. conspicuousness) were compared, sex (except for the UV-blue OVS), morph (if applicable) and if the pair of localities belonged to the same lineage or not were considered as independent factors, the pair of localities being nested into the latter factor. Before analyses, luminance and hue variables, as well as chromatic and achromatic distances, were log-transformed, and chroma variables were arcsin-transformed to ensure normality and homoscedasticity.

Results

Colour variables and spectral shape

We did not find striking differences between lineages and localities in the spectral shape of ventral colours, UV-blue OVS and dorsum (Fig. 2). However, we found small (but statistically significant) differences in some colour variables (Table 2; Fig. 3). The UV-blue OVS differ in luminance and chroma between lineages. Both variables also vary between

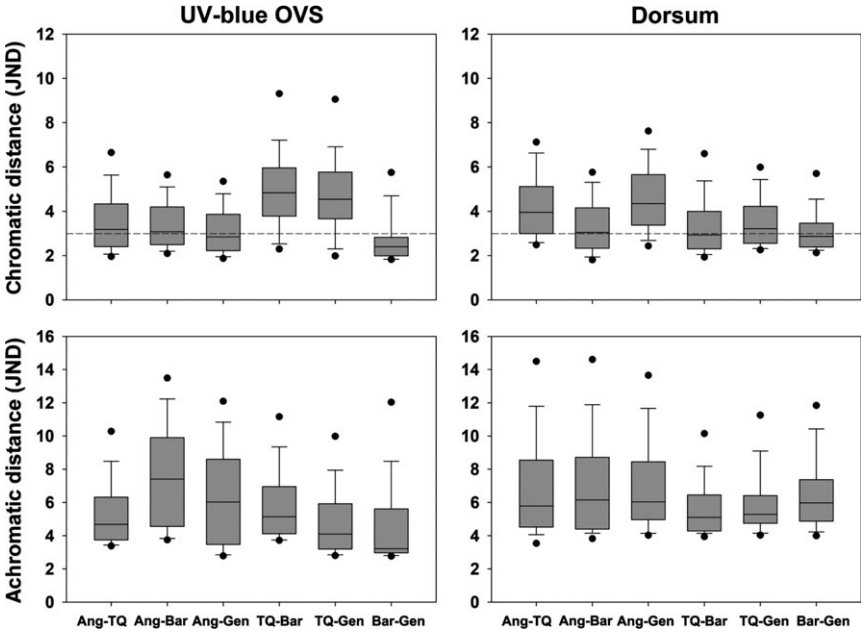

Figure 5 Chromatic (above) and achromatic (below) distances between pairs of localities for the second rostral-most ultraviolet-blue outer ventral scales (left) and the dorsal coloration (right). Ang = Angostrina, TQ = Tor de Querol, Bar = Bareggio and Gen = San Genesio. Horizontal lines, boxes, error bars and points indicate the median, the 25–75% range, the 10th and 90th percentiles, and the 5th and 95th percentiles respectively. Horizontal dashed lines in the chromatic panels indicate 3 JND, the threshold traditionally assumed for chromatic discrimination.

localities, but the magnitude of the variation is much smaller than that obtained comparing lineages (Table 2). The dorsal coloration only differs in luminance between localities. As expected, the ventral coloration differs in chroma among morphs (and to a lesser extent in luminance and hue), but also among lineages, especially in luminance and chroma. Within morphs, white males and females differ in chroma, and lineages strongly differ in luminance and chroma of the white morph. The yellow morph differs in hue between sexes when considering the interaction between sex and lineage. The orange/red morph differs in luminance between the sexes, with a significant interaction between sex and lineage. Differences between lineages especially affect chroma. Although we find significant within-morph differences between localities in some variables, they are rather small. The chromaticity diagram (Fig. 4) shows the spatial segregation between the UV-blue OVS chromatic points and the chromatic points of the other patches. There exists a relative segregation between morphs, but also some intra-morph variation between lineages.

Chromatic and achromatic distances

The chromatic and achromatic distances for the UV-blue OVS and dorsum are shown in Fig. 5, and the corresponding statistics in Table 3. Regarding the UV-blue OVS, the largest difference corresponds to the achromatic distances between pairs of localities belonging to the same lineage. Both chromatic and achromatic distances of the dorsum do not differ either by sex or depending on whether pairs of localities belong the same lineage, but vary between pairs of localities, though the magnitude of the difference is small.

The chromatic and, especially, the achromatic distances of ventral colours (Fig. 6, Table 3) differ depending on the morph and lineage. The achromatic, but not the chromatic, distance varies depending on pairs of localities, and there are no differences between sexes. Among morphs, the differences are significant between the white and the orange/red morphs (chromatic distance: $Z = -5.97$, $P < 0.0001$; achromatic distance: $Z = 9.95$, $P < 0.0001$), and between the yellow and the orange/red morphs (chromatic distance: $Z = -7.17$, $P < 0.0001$; achromatic distance: $Z = 8.62$, $P < 0.0001$), but not between the white and the yellow morphs (chromatic distance: $Z = 1.72$, $P = 0.20$; achromatic distance: $Z = 0.19$, $P = 0.54$).

Conspicuousness

The chromatic distances between the UV-blue OVS and each throat colour (Fig. 7, Table 3) mainly differ by lineage and only secondarily depending on the locality within each lineage. The difference between morphs is non-significant. The achromatic distances differ between morphs and depending on whether pairs of localities are from the same lineage or not, but not between pairs of localities, differing the white and the yellow morphs ($Z = -2.97$, $P = 0.009$), the white and the orange/red morphs ($Z = -16.98$, $P < 0.0001$), and the yellow and the orange/red morphs ($Z = -14.01$, $P < 0.0001$).

Table 3 Results from generalized linear models testing differences in chromatic and achromatic within-patch distances (i.e. intra-patch distances), and chromatic and achromatic distances generated by the UV-blue OVS and ventral colours (i.e. conspicuousness)

	Chromatic distance	Achromatic distance
Intra-patch distances		
UV-blue OVS		
Lineage combination	−0.04 ± 0.02	**0.21 ± 0.02**
	(−2.6; 0.009)	**11.1 (<0.00001)**
Lineage combination: localities	0.01 ± 0.01	−0.03 ± 0.01
	(−4.8; <0.00001)	(−8.6; <0.00001)
Dorsum		
Sex	−0.01 ± 0.01	−0.01 ± 0.01
	(−0.9; 0.38)	(−0.6; 0.53)
Lineage combination	0.01 ± 0.02	0.03 ± 0.02
	(0.7; 0.52)	(1.7; 0.10)
Lineage combination: localities	−0.01 ± 0.01	−0.01 ± 0.01
	(−3.4; 0.0008)	(−3.4; 0.0007)
Throat		
Sex	0.01 ± 0.01	0.02 ± 0.01
	(0.1; 0.92)	(1.6; 0.12)
Morph	−0.04 ± 0.01	**0.13 ± 0.02**
	(−6.7; <0.00001)	**(6.8; <0.00001)**
Lineage combination	−0.05 ± 0.02	**0.13 ± 0.02**
	(−2.9; 0.004)	**(6.5; <0.00001)**
Lineage combination: localities	−0.01 ± 0.01	−0.01 ± 0.01
	(−0.1; 0.90)	(−3.0; 0.002)
UV-blue OVS vs morph distances (conspicuousness)		
Morph	0.01 ± 0.01	**−0.12 ± 0.01**
	(1.6; 0.12)	**(−17.1; <0.00001)**
Lineage combination	**0.33 ± 0.02**	**0.16 ± 0.07**
	(16.3; <0.00001)	**(2.4; 0.02)**
Lineage combination: localities	−0.05 ± 0.01	−0.02 ± 0.01
	(−15.2; <0.00001)	(−1.8; 0.08)

Each cell indicates the coefficient ± SE, and the *t* and *P* values in parenthesis. Significant results with high coefficients (>0.10) are highlighted in bold.

Discussion

Ventral polymorphic coloration

The results presented here confirm that the alternative colours involved in the ventral polymorphism shown by *P. muralis* are shared by two different polymorphic lineages of the species despite their independent Pleistocene origins and the wide geographic separation. Although clear differences exist in colour variables between lineages, hue differences are very small, most variation being due to luminance or purity (chroma). Moreover, according to the results of visual modelling, these differences seem subtle in comparison to inter-morph differences. In fact, chromatic distances between localities and lineages are around the 3 JND threshold (Fig. 6), suggesting that ventral morphs of the different localities are chromatically discriminable by lizards, but the magnitude of these differences is small (see, for example, the chromatic distances between morphs from Angostrina in Pérez i de Lanuza *et al.*, 2018a). The overlap between the clouds of chromatic points corresponding to the different lineages (Fig. 4) also argues in favour of this conclusion.

The main inter-lineage difference is between the orange Pyrenean morph and the red Italian morph. Interestingly, this apparent disparity seems caused by differences in luminance. Thus, the achromatic distances between localities from different lineages are higher than those generated when comparing localities within the same lineage. In general, there exists a consistent pattern within and between ventral colours, suggesting that most morph variation is mainly dependent on the lineage, but not on locality. Moreover, we found little sexual dichromatism within morphs in colour variables, only involving luminance and chroma in the white and orange/red morphs, suggesting that the chromatic properties of ventral colours are shared by both sexes.

Overall, these results suggest that colour morphs are largely shared by lineages, and probably ancestral in *P. muralis* (and maybe in other lacertids; Huyghe *et al.*, 2007, 2009; Runemark *et al.*, 2010), although we cannot discard an alternative explanation based on convergent evolution. However, there exists some historical divergence between lineages in colour properties, and local adaptation (e.g. background coloration, natural illumination, the type and/or density of predators) probably plays a small (or null) role in the design of ventral colours. The relative constancy of ventral colours despite variation in background coloration reinforces the hypothesis of colour partitioning in *P. muralis* (Pérez i de Lanuza & Font, 2015) and other lizards (Marshall & Stevens, 2014).

UV-blue OVS

The UV-blue OVS show a strong geographic variation in luminance and chroma, the Italian lizards having higher UV chroma than the Pyrenean ones. This result is confirmed by the relative bias of chromatic points in the chromaticity diagram, in which Italian chromatic points are biased toward the UV vertex (see Fig. 4). Previous results suggested that the UV-blue patches of *P. muralis* may act as social signals informing about male quality. In particular, chromatic variables (especially UV chroma) seem good predictors of fighting ability and body condition (Pérez i de Lanuza *et al.*, 2014), and are related to male mating success (MacGregor *et al.*, 2017). This suggests that inter-lineage differences in this character may be driven by different competitive scenarios, probably associated to present or past differences in the intensity or direction of sexual selection pressures.

Dorsal coloration

The dorsal coloration shows the smallest degree of variation compared to other colour patches. In fact, the dorsal brown coloration only differs between localities in luminance, and in the chromatic and achromatic distances, showing a bias in the chromaticity diagram. These results suggest local adaptation of the dorsal design, presumably caused by differences in visual ecology mainly related to crypsis and predator avoidance (Marshall & Stevens, 2014; Pérez i de Lanuza & Font, 2015). As the

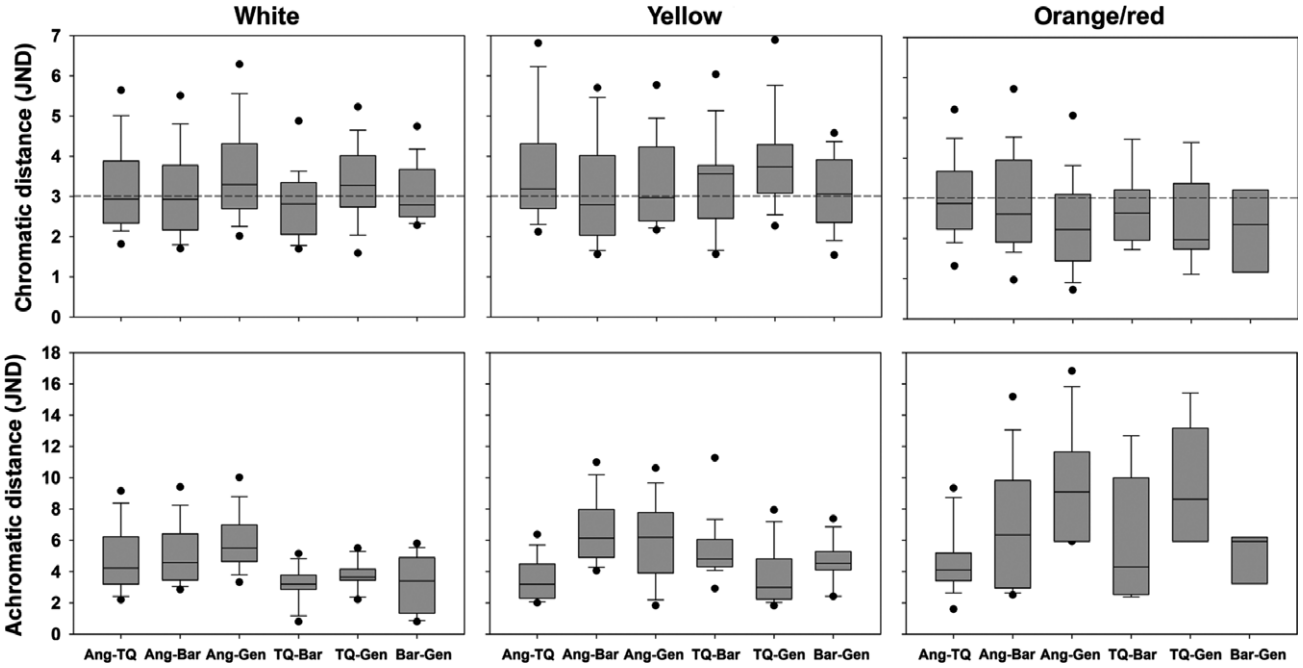

Figure 6 Chromatic (above) and achromatic (below) distances from the three pure morphs, measured from throats. Ang = Angostrina, TQ = Tor de Querol, Bar = Bareggio and Gen = San Genesio. Horizontal lines, boxes, error bars and points indicate the median, the 25–75% range, the 10th and 90th percentiles, and the 5th and 95th percentiles respectively. Horizontal dashed lines in the chromatic panels indicate 3 JND, the threshold traditionally assumed for chromatic discrimination.

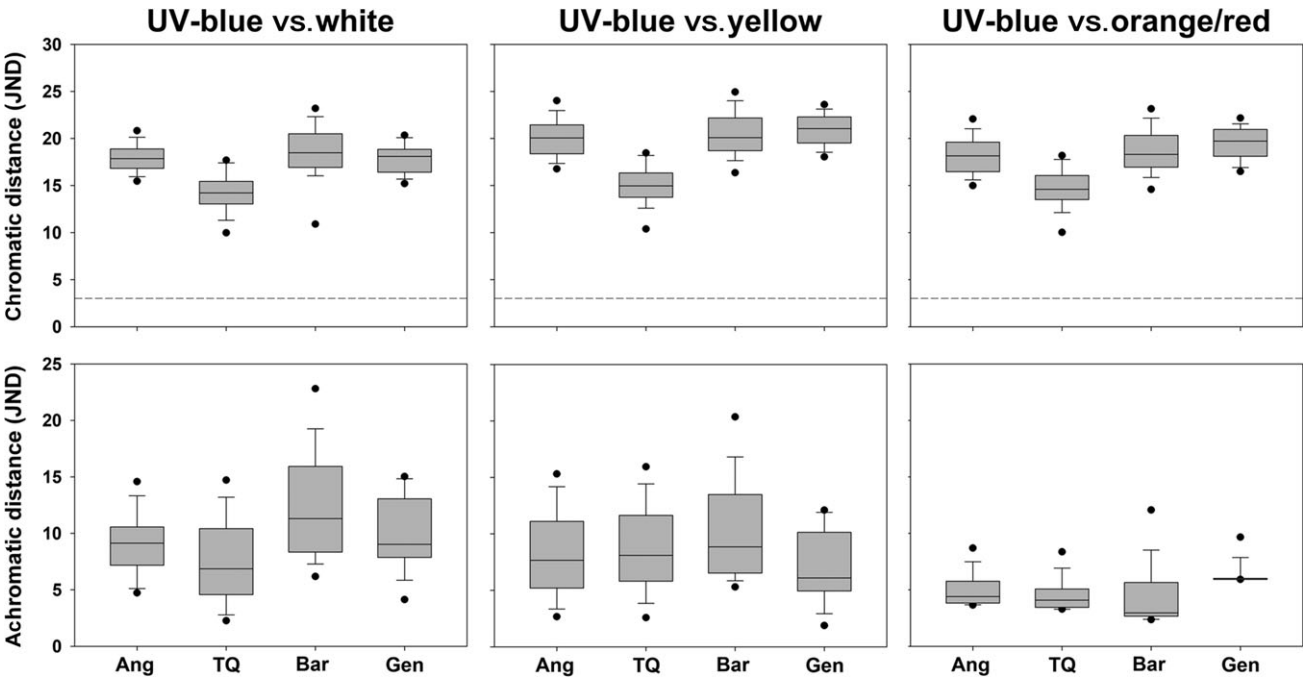

Figure 7 Chromatic (above) and achromatic (below) distances (i.e. conspicuousness) generated by the combination of the UV-blue OVS and the ventral colour morphs in each locality (Ang = Angostrina, TQ = Tor de Querol, Bar = Bareggio, Gen = San Genesio). Horizontal lines, boxes, error bars and points indicate the median, the 25–75% range, the 10th and 90th percentiles, and the 5th and 95th percentiles, respectively. Horizontal dashed lines in the achromatic panels indicate 3 JND, the threshold traditionally assumed for chromatic discrimination.

magnitude of these differences is smaller than that found in ventral colour and in the UV-blue OVS, the dorsal coloration is probably more conserved and/or constrained. This result also suggests that selection acting on conspicuous colour patches (i.e. ventral colour and UV-blue OVS) produces more variable colorations than that driving the design of dorsal coloration.

Conclusion

Taking these results together, we conclude that the general chromatic pattern of *P. muralis* is conserved and shared by at least two geographically and genetically distant polymorphic lineages of the species (Salvi *et al.*, 2013). The orange Pyrenean and the red Italian morphs should be considered analogous but not identical (i.e. whether or not they correspond to the same morph is a moot point considering how little we know about the mechanisms of colour production). Finally, although not surprisingly, our results confirm that the colour partitioning described for the different colour patches of Pyrenean *P. muralis* (Pérez i de Lanuza & Font, 2015) is found in other populations as well, and possibly in the whole species.

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