ORIGINAL ARTICLE

Information content of ultraviolet-reflecting colour patches and visual perception of body coloration in the Tyrrhenian wall lizard *Podarcis tiliguerta*

Arnaud Badiane[1] · Enrique Font[2]

Abstract

Colour signals are ubiquitous in nature but only recently have researchers recognised the potential of ultraviolet (UV)-reflecting colour patches to function as signals of quality. Lacertid lizards often display UV-blue patches on their flanks and black spots over their entire body, both of which are under sexual selection. They also have a cryptic dorsum and some species have a conspicuous, polymorphic ventral coloration. In this study, we use the Tyrrhenian wall lizard *Podarcis tiliguerta* to investigate the information content of the lateral UV-blue patches and black melanin spots of males by assessing the relationship between colour features and individual quality traits. In addition, we use a visual modelling procedure to examine whether the coloration of the different body parts and different colour morphs can be distinguished by a wall lizard visual system. We found that larger males had more numerous and larger UV-blue patches, with a higher UV chroma, UV-shifted hue, but a lower spectral intensity than smaller males. The extent of black on the throat, dorsum, and flanks also correlated with male body size and size-corrected head length but not with colour features of the UV-blue patches. These results suggest that the UV-blue and melanic colour patches may provide different, non-redundant information about male resource holding potential, and thus act as condition-dependent indicators of male quality. Finally, we found that the different body parts can be chromatically distinguished from each other, and that the UV-blue patches are the most conspicuous while the dorsum is the least conspicuous.

Significance statement

Many animals use their coloration to convey information about their quality as rivals or mates. Yet, until recently researchers have not recognised the potential of ultraviolet colour patches to function as signals of quality. In this study, we first show that male Tyrrhenian wall lizards display ultraviolet-blue and black colour patches that correlate positively with some aspect of their quality such as body or head size. Furthermore, our visual modelling procedure suggests that these lizards are able to distinguish the colours of their body parts from each other, with dorsal colours being the least conspicuous and ultraviolet-blue coloration being the most conspicuous.

Keywords Colour signals · Visual modelling · Colour morph · Colour discrimination · Lacertidae

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✉ Arnaud Badiane
  arnaud.badiane@gmail.com

1   IMBE, Aix-Marseille Université, Avignon Université, CNRS, IRD, 13013 Marseille, France

2   Ethology Lab, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, APDO 22085, 46071 Valencia, Spain

Introduction

The display of conspicuous colour patches constitutes a ubiquitous and diverse class of signals that play a pivotal role in sexual selection (Hamilton and Zuk 1982; Endler 1983; Andersson 1994; Hill and McGraw 2006). In this context, colour signals typically convey information about the signaller's quality as a mate (e.g. direct and/or indirect benefits) or as a rival (e.g. fighting ability, social dominance; Hill and McGraw 2006; Morehouse and Rutowski 2010; Bradbury and Vehrencamp 2011). Colour production in animals results from the interaction of light with pigments (e.g. carotenoids,

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melanin), nanostructures, or a combination of both in the integument (Shawkey and D'Alba 2017). Our understanding of the signalling role and evolution of pigment-based colours has much improved over the past decades (Olson and Owens 1998; Svensson and Wong 2011; Roulin 2016). For example, carotenoid-based colour signals can in some cases function as honest signals of quality due to the trade-off involved in allocating carotenoids to signalling or to other important physiological functions (Svensson and Wong 2011; Weaver et al. 2017). In contrast, structurally produced colours, such as blue, violet, and ultraviolet (UV), have been tradition- ally considered cheap to produce and lacking in any obvious trade-offs, and therefore unlikely to accurately reflect inter- individual variations in quality (Kemp et al. 2012; Kemp and Grether 2015). However, mounting evidence reveals that many animals are equipped with UV-sensitive vision (Kelber et al. 2003; Cronin and Bok 2016), thus leading to an increasing appreciation of the potential of structural col- oration as honest signals of individual quality (White 2020). UV signalling has now been shown to occur in many taxa, including birds (e.g. Keyser and Hill 1999), lizards (e.g. Whiting et al. 2006), amphibians (e.g. Secondi et al. 2012), fish (e.g. Siebeck 2004; Rick et al. 2006), insects (e.g. Papke et al. 2007), and arachnids (e.g. Painting et al. 2016). Despite this evidence, we are still far from a complete understanding of the selective forces at play in the evolution of UV signals, and more generally of structural colour signals.

Many lizards possess conspicuous colour patches that reflect in the UV range (e.g. Macedonia 2001; Stoehr and Mcgraw 2001; Martin et al. 2013; Badiane et al. 2018b) and are displayed during social interactions (Whiting et al. 2006), suggesting a potential role as ornaments. In lacertid lizards, UV coloration is particularly widespread and often appears on the lizard's flanks, head, throat, or belly (Molina- Borja et al. 2006; Pérez i de Lanuza and Font 2007; Font et al. 2009; Badiane et al. 2018a). The signalling role of UV colour patches has been well established in several lacertid species, both via field studies showing correlations between the design of the UV patches and male fitness-related phe- notypic traits (Font and Molina-Borja 2004; Huyghe et al. 2005; Font et al. 2009; Molnár et al. 2012; Pérez i de Lanuza et al. 2014), and through experimental manipulations of the reflectance of the UV patches during intra-sexual and inter- sexual interactions (Bajer et al. 2010, 2011; Martin et al. 2015a, 2016; Names et al. 2019). While current evidence seems to indicate that, in lacertids, UV signals primarily evolved to resolve male-male conflicts and avoid contest escalation (Bajer et al. 2011; Pérez i de Lanuza et al. 2014; Martin et al. 2015a, 2016), UV coloration may also play a role in female mate choice in some species (Bajer et al. 2010; Badiane et al. 2020).

Wall lizards from the genus *Podarcis* comprise 24 species and the males of most of these species have conspicuous colour patches on some of their outer-ventral scales (OVS). These colour patches appear blue to the human eye but are in fact UV-reflecting and therefore best described as UV- blue. In the common wall lizard (*Podarcis muralis*), Pérez i de Lanuza et al. (2014) showed that the hue and UV chroma of the UV-blue patches are related to size-independent bite force (a proxy of male fighting ability in lizards, Huyghe et al. 2009) and body condition, respectively, suggesting condition dependence and a role in male-male interactions and contest behaviour. MacGregor et al. (2017) also found a relationship between the hue and UV chroma of the UV- blue patches and male reproductive success in two *P. mura- lis* lineages. Martin et al. (2015a) and Names et al. (2019) found that manipulating the reflectance and size of UV-blue patches affected male agonistic interactions. Finally, Abalos et al. (2016) reported that natural variation in the size and reflectance of the UV-blue patches does not predict the out- come of laboratory-staged contests between size-matched males, and proposed that the UV-blue patches may be impor- tant during the early stages of contests during which rival assessment takes place. Taken together, these results suggest that the UV-blue patches may play a role in male-male sig- nalling, but the evidence for their role as signals of fighting ability remains equivocal.

Previous studies of the communicative function of the UV-blue patches have focused on a single species of wall lizard, but other *Podarcis* species display colour ornaments similar to those of *P. muralis*. Here we consider the case of the Tyrrhenian wall lizard (*P. tiliguerta*), which is phyloge- netically close to *P. muralis* and displays similar UV-blue patches that have not been empirically investigated so far. As in other lacertid lizards, body coloration in *P. tiliguerta* is a complex mosaic of colour patches that are likely subject to different selection pressures (Pérez i de Lanuza et al. 2013b). Dorsally, they show a dull brown-green coloration that prob- ably evolved for antipredatory purposes (e.g. camouflage— Stuart-Fox et al. 2003; Marshall and Stevens 2014; Marshall et al. 2015a, b, 2016). Their ventral coloration, in contrast, is conspicuous and polymorphic, with three alternative ventral colours (i.e. orange, white, and yellow) that may be linked to different behavioural or life history strategies (Huyghe et al. 2010b; Pérez i de Lanuza et al. 2013a). Additionally, *P. tiliguerta* lizards have black melanin spots over their entire body surface which could also have a signalling role (e.g. Abalos et al. 2016). Our aim here is to characterise the col- oration of the different body parts of *P. tiliguerta*, which has never been studied using objective methods of colour assess- ment. To determine the potential information content of the UV-blue patches and the black melanic spots, we investigate whether black and UV-blue colour variables correlate with morphological or performance traits indicative of male qual- ity. We also use visual modelling procedures to examine whether different body parts and different colour morphs can

be distinguished from each other by a wall lizard visual system, and to explore which of these body colours are the most conspicuous when viewed against a natural background. This study should provide useful insights on the potential information content of UV-blue signals, thus improving our understanding of the role of structurally produced colours as communicative signals. In addition, our visual modelling approach will help us understand the roles of the multiple colours displayed by these lizards, and establish the foundations for future research involving this species.

Materials and methods

Study species

The Tyrrhenian wall lizard *Podarcis tiliguerta* is a small lacertid endemic to the Mediterranean islands of Corsica and Sardinia and their respective satellite islets, although recent evidence has shown marked phylogeographic patterns suggestive of a species complex (Capula 1996; Bruschi et al. 2006; Rodríguez et al. 2017; Salvi et al. 2017; Senczuk et al. 2019). Several micro-insular subspecies have been described based on morphological variation, including body coloration (e.g. melanism, red ventral coloration—Brizzi and Lanza 1975). Tyrrhenian wall lizards inhabit semi-open rocky and shrubby areas as well as human constructions (e.g. stone walls) interspersed with vegetation (Vanhooydonck et al. 2000; Bombi et al. 2009). Like most *Podarcis* lizards, they have a cryptic dorsal coloration and a conspicuous polymorphic ventral coloration with three alternative colour morphs (i.e. orange, yellow, white). Laterally, males of this species display small UV-blue patches on some of their OVS, often interspersed with black melanin-based spots (Fig. 1). In contrast to the ventral scales, which are white, yellow, or orange, background colour of the outer-ventral scales is light blue-greenish to the human eye.

Data collection

On 18–22 May 2016, we captured 50 male *P. tiliguerta* by noosing in central-western Corsica (lat: 42.059911; lon: 8.959600) alongside roads, human constructions, and water streams. On the day of capture, we measured body mass to the nearest 0.1 g using a light-line spring scale (Pesola), and snout-vent length (i.e. SVL) and head length to the nearest 0.1 mm using digital callipers (Mitutoyo). We also measured maximum bite force, which has been shown to be a good proxy for fighting ability and whole-organism performance in lizards (Huyghe et al. 2005; Lappin and Husak 2005), using a purpose-built bite force meter. The bite force meter was constructed from a modified Sauter FK 25 N digital force meter with two metal plates on which each animal

Fig. 1 Photograph of a male Tyrrhenian wall lizard *P. tiliguerta* (above) on which the UV-blue patches on some of the outer-ventral scales are visible. Below, a close-up view of the UV-blue patches (another individual) on the outer-ventral scales. The lizard's orange belly is visible in the lower part of the picture

bites, one attached to the main body of the force meter, and the other attached to the fixed recording rod. We placed the lizards in a small plastic box with a heating mat underneath until the lizards reached a body temperature between 32 and 37 °C as measured with an infrared thermometer (preferred body temperature for this species is ca. 35 °C; Van Damme et al. 1989). We then retained the maximum score out of three bite force measurements. Unexpectedly, 21 lizards completely refused to bite the bite force plate and the remaining 29 individuals showed an obvious lack of motivation resulting in very low bite force scores (i.e. typically below 0.3 N). This is unusual for *Podarcis* lizards, which are usually motivated to bite and bite harder than this (e.g. *P. muralis*, *Podarcis melisellensis*, *Podarcis filfolensis*, *Podarcis liolepis*, *Podarcis sicula*, *Podarcis lilfordi*—AB and EF personal observations). Based on this evidence, we consider that our bite force scores are unreliable and do not reflect the maximum performance of the tested individuals (Lappin and Jones 2014), and therefore we excluded them from further analyses. It was not possible to record data blind because our study involved focal animals in the field.

We also took four pictures of each individual (i.e. dorsal, ventral, and both lateral profiles) using a Nikon D5300 DSLR camera with a Sigma 70–300-mm macro lens and the flash turned on. To maximise consistency, we held each lizard gently pressed against a glass plate at a fixed distance from the camera (Badiane et al. 2018b). Using lateral photographs and the colour threshold tool implemented in ImageJ

(Schneider et al. 2012), we calculated the percentage of surface area covered by black coloration on the left and right rows of OVS of each lizard, on the dorsum (between the parietal-occipital scales and the insertion of the posterior limbs), and on the throat (between the infra-labial scales and the collar scale row). We did not measure the belly as it has no or very few black spots. Similarly, we counted the number of UV-blue patches and calculated the total surface covered by blue coloration present on the lizards' OVS (and occasionally on some of the adjoining dorsolateral granular scales). It should be noted that we used the percentage of black area (i.e. a relative measurement), but the total area of UV-blue patches (i.e. an absolute measurement) because measuring the total black area would include a non-negligible measurement error due to slight inconsistencies in the delimitation of the relevant body part (e.g. dorsum, throat). We kept the absolute UV-blue area because this coloration sometimes spreads over the granular scales above the OVS, which would lead to inconsistencies if we used a relative value. These variables have previously been measured similarly in other lizard species (Abalos et al. 2016).

Reflectance spectra and visual modelling

We obtained reflectance spectra of the belly (a single reading in the middle of the belly), and of the second and third UV-blue patches on both flanks using a JAZ portable diode-array spectrometer with an R200-7-VIS–NIR reading-illumination probe (Ocean Optics Inc.) and a notebook computer running the Ocean Optics Spectra Suite software. We took reflectance readings in a darkened room using a PX-2 xenon strobe light source (Ocean Optics Inc.) for full spectrum illumination. We recorded spectra in 0.37 steps and used a certified Spectralon 99% white diffuse reflectance standard (Labsphere) as a white reference. We took a dark reading and subtracted it from the signal just prior to gathering the spectral data. We averaged reflectance readings over 5 nm using a kernel smoothing function, and set integration time to 30 ms, scans to average to 10, and boxcar width to 10. For data acquisition, we hand-held the probe over the centre of the colour patch, and perpendicular to the patch surface (i.e. illumination and recording angles were both 90°; coincident normal measuring geometry, Anderson and Prager 2006). An entomological pin attached to the side of the probe allowed us to maintain a constant distance of 5 mm between the tip of the probe and the measured surface. We did not consider colour spots smaller than 2 mm in diameter because they cannot be measured using our spectrophotometer set-up (Badiane et al. 2017).

We processed spectral data in R v.3.6.2 (R Development Core Team 2017) using the software package *pavo* v.2.0 (Maia et al. 2019). We considered spectra from the throat, belly, dorsum, and the second UV-blue patch on the right

side of each individual because the first one is often too small to measure reliably. For two individuals, we used the third UV-blue patch of the right side because the second one was too small to be measured (Badiane et al. 2017). First, we cropped each spectrum between 300 and 700 nm and smoothed it using an interval of 0.2. Then, we extracted colorimetric variables from the spectra of the lateral UV-blue patches, namely spectral intensity (i.e. $R_{300-700}$), UV chroma (i.e. $R_{300-400}/R_{300-700}$), and hue (i.e. wavelength at the maximum reflectance peak).

Visual modelling was done using the Vorobyev and Osorio model (Vorobyev and Osorio 1998) implemented in the package *pavo* v.2.0 to score colour discrimination and conspicuousness in terms of chromatic and achromatic contrasts of each individual's body parts (i.e. throat, belly, dorsum, and UV-blue patches) against different natural backgrounds. We obtained reflectance spectra of different natural backgrounds present in the lizards' habitat, namely a grass spectrum (i.e. average of three spectra), three types of rock (i.e. schist, slate, and limestone—average of five spectra for each rock type), a mean rock background (i.e. average of the spectra from the three rock types), and a black spectrum obtained from a black patch adjacent to the UV-blue patches on the lizards' OVS. We used the cone sensitivities (UVS:SWS:MSW:LSW, 367:456:497:562 nm; LSW-562 was used for the achromatic component) and relative cone densities (1:1:1:4) of *P. muralis* (Martin et al. 2015b), which is the closest relative of *P. tiliguerta* for which these data are available. We used a standard daylight "D65" irradiance spectrum, as implemented in *pavo*. We set the Weber fraction to 0.1. Chromatic (ΔS) and achromatic (ΔL) contrasts were calculated in units of *just noticeable differences* (JND). A JND value greater than one indicates that two colours can be discriminated, whereas colours are indistinguishable if they have a contrast value inferior to one JND. The Euclidian distance between pairs of points in a chromaticity diagram and the receptor noise model yield similar results in terms of perceptual distance among colours (Fleishman et al. 2016), and colour distances provide accurate estimates of conspicuousness up to 10 JNDs (Santiago et al. 2020).

Statistical analyses

We conducted all statistical analyses in R v.3.6.2. (R development Core Team 2017). First, to investigate the relationship between the UV-blue patches and male quality, we ran linear models (LMs) using the *lm* R function with all the colour variables as response variables (see below) except for the number of UV-blue patches, for which we assumed a Poisson distribution and used generalised linear models (GLMs) using the *glm* R function. We included the following colour variables as response variables: spectral intensity, UV chroma, hue, number of UV-blue patches, and total area of

UV-blue patches. In each case, the full model included all the following independent variables as predictors: body size (SVL), size-corrected head length (HLres; i.e. residuals from a regression of head length against SVL), and body condition (i.e. residuals from a regression of body mass against SVL). We then proceeded with a stepwise backward model selection consisting of discarding the non-significant terms until obtaining the model with the lowest Akaike Information Criterion (AIC). Additionally, we performed the same models and the same model selection procedure as above to explore potential correlations between the relative amount of black coloration and male quality. We thus used LMs and a GLM to test the effect of body size, size-corrected head length, body condition, and throat colour (predictor variables) on the percentage of black coloration on the OVS, on the dorsum, and on the belly (response variables). Model residuals were checked for normality and homoscedasticity and, to comply with these assumptions, the variable hue was rank-transformed and chromatic contrasts of the dorsum were log-transformed. All Gaussian variables were previously centred and scaled (Schielzeth 2010).

After the above analyses were done and the results were obtained, we performed linear models to test whether the area of the UV-blue patches (absolute value—predictor variable) correlated positively with the relative amount of black on the dorsum, on the OVS, and on the throat (absolute values—response variables). This correlation provides insight into the role of these two chromatic traits in the context of the multiple message and redundant signal hypotheses (see discussion; Johnstone 1996).

Following Maia and White (2018), we tested whether or not different body parts and throat colour morphs can be discriminated from each other by a wall lizard visual system. To do so, we used a distance-based PERMANOVA (Anderson 2001) on the chromatic and achromatic contrasts using the *pairwise.adonis* function from the *pairwiseAdonis* R package (Arbizu 2019), a modified version of the *adonis* function from the *vegan* R package (Oksanen et al. 2017) allowing for multilevel pairwise comparisons. We created a group variable including the following levels for pairwise comparison: OVS, dorsum, white throat, orange throat, and yellow throat. We tested the assumption of multivariate homogeneity of group dispersions (variances) and found that our group levels have unequal variances for both the chromatic and achromatic contrasts, but not in a way that would substantially affect our distance-based PERMANOVA procedure since the largest group had the highest variance (Anderson and Walsh 2013). For each pairwise comparison, we recorded statistical significance ($\alpha = 0.05$) using 999 permutations, a pseudo F-statistic, and R^2 as an effect size estimate. Adjusted p-values for multiple comparisons were obtained using a Bonferroni procedure. As significance thresholds do not necessarily match the theoretical perceptual threshold of

one JND above which colours can be said to be distinguishable, we used a bootstrap procedure to generate confidence intervals for the mean colour distance between the different colours. We used the *bootcoldist* function from the *pavo* R package on the visual model described above with 1000 replicates and a 0.95 level for confidence intervals. This procedure was repeated six times, once for each visual model with a different natural background (i.e. grass, schist, slate, limestone, mean rock, and black patch).

Next, to explore which body part and colour morph are the most conspicuous when viewed by a wall lizard against a natural background (i.e. grass, rocks, black patch), we built the same visual model as above, except that now we included an ideal black as visual background in the model instead of the natural background spectra. This time, we included the natural background spectra as if it were another body part to be compared but could not use the same PERMANOVA procedure as before because we had only one spectrum per natural background. Instead, we created ΔS_{bkg} and ΔL_{bkg} variables such that only the chromatic and achromatic contrasts (respectively) between each individual spectrum of each body part and colour morph and the natural background spectrum were included. Next, we fitted linear models using the generalised least squares method using the *gls* function from the *nlme* R package (Pinheiro et al. 2019) with ΔS_{bkg} and ΔL_{bkg} as response, and body parts (i.e. five levels: OVS, dorsum, and the three throat colour morphs) as explanatory variable. To account for heteroscedasticity in our "body parts" variable, we used the weights argument in our models to allow variance of the residuals to differ among group levels. To explore differences among different body parts and throat colour morph, we performed post hoc Tukey tests on these two factors using the *multcomp* R package (Hothorn et al. 2008), adjusting p-values for multiple comparison with a Bonferroni method. Model residuals were checked for normality and homoscedasticity. Finally, we used the same bootstrap procedure as above to generate confidence intervals for the mean colour distance between the different body parts and background colour.

Results

Some of the males captured in this study had different throat and ventral colours, which has rarely been described in other *Podarcis* species. For example, some males had a white belly and a yellow or orange throat, while others had a yellow belly and an orange throat. The UV-blue patches have a reflectance peak in the near UV range, at 364 ± 2 nm (mean ± standard error; Fig. 2a) and the colour characteristics of each body part are reported in Table 1.

Regarding the relationship between the UV-blue patches and male traits, we found that larger males in terms of
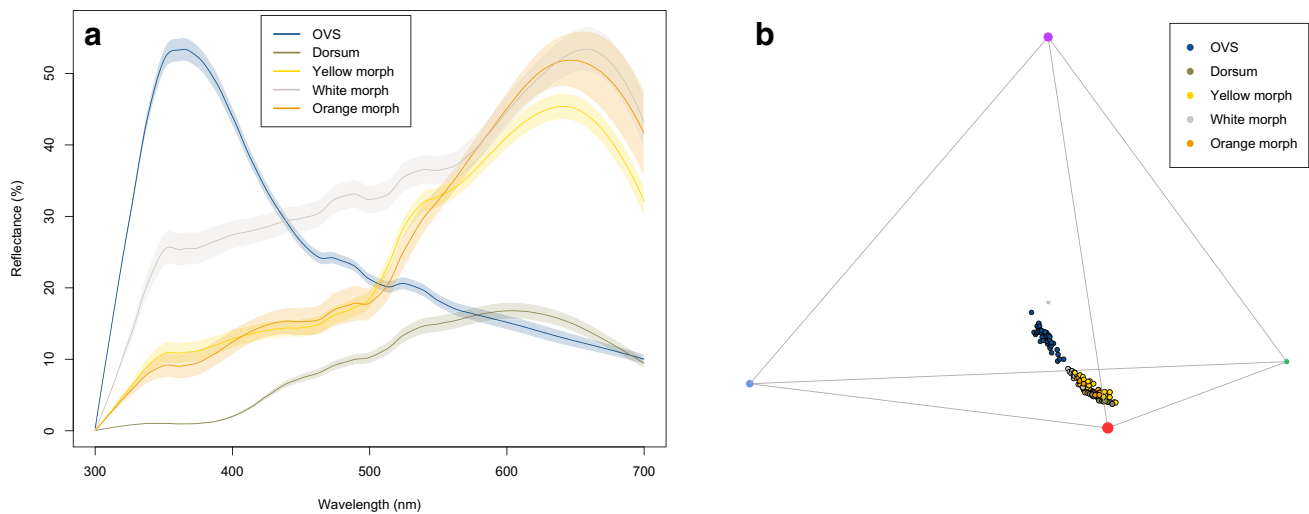
Fig. 2 **a** Mean spectra (plain curve) and their standard errors (shaded curve) of the UV-blue patches on the outer-ventral scales (OVS; $n=48$), the dorsal coloration (dorsum; $n=50$), and the three throat colours: white ($n=12$), yellow ($n=30$), orange ($n=8$). **b** Representa-tion of each individual spectrum from the different body parts of liz-ards (dorsum, outer-ventral scales (OVS), and throat (white, yellow, orange)) in a tetrahedral colour space built from a wall lizard visual system

SVL had higher UV chroma ($F_{1-43}=4.85$, $R^2=0.08$, $\beta=0.34\pm0.16$, $p=0.033$), a larger area of UV-blue ($F_{1-47}=1.47$, $R^2=0.33$, $\beta=0.59\pm0.12$, $p<0.001$), more UV-blue patches ($\beta=0.14\pm0.03$, $p<0.001$), but a lower spectral intensity ($F_{3-42}=3.25$, $R^2=0.13$, $\beta=-0.36\pm0.15$, $p=0.021$), and a lower (i.e. more UV-biased) hue ($F_{1-48}=6.73$, $R^2=0.10$, $\beta=-0.35\pm0.14$, $p=0.013$) than smaller males. We also found that spectral intensity corre-lated negatively with male relative head size ($F_{3-42}=3.25$, $R^2=0.13$, $\beta=-0.31\pm0.15$, $p=0.047$) but not with body condition ($F_{3-42}=3.25$, $R^2=0.13$, $\beta=0.21\pm0.15$, $p=0.152$). All the error terms associated with β coefficients correspond to standard errors.

In addition, we found that body size and relative head size both correlated positively with the percentage of black on the throat (trend for SVL: 0.24 ± 0.13, $p=0.074$; HLres: 0.33 ± 0.13, $p=0.017$), on the OVS (SVL: 0.29 ± 0.13, $p=0.038$; HLres: 0.28 ± 0.13, $p=0.038$), and on the dor-sum (SVL: 0.49 ± 0.12, $p=0.0001$: HLres: 0.27 ± 0.12, $p=0.031$). All error terms associated with β coefficient cor-respond to standard errors.

Results and test statistics of our PERMANOVA proce-dure are summarised in Table 2. We found that the UV-blue patches and dorsum colours were statistically different from

all the other body parts in terms of chromatic and achromatic contrasts. In addition, the white throat was chromatically different from both the yellow and orange throat; however, yellow and orange throats were not statistically different. Also, the three throat colours were not statistically different from each other in terms of achromatic contrast.

Moreover, our theoretical perceptual threshold analyses based on the bootstrap procedure revealed that, with a per-ceptual threshold of 1 JND, the colour of all body parts and throat morphs can be distinguished from each other by a wall lizard in terms of chromatic contrasts, except for the orange and yellow throats. This was also the case in terms of achromatic contrasts, except that none of the three throat col-ours could be distinguished from each other by a wall lizard visual system. Using a more conservative perceptual thresh-old of 3 JNDs (Siddiqi et al. 2004), the three throat colours become chromatically and achromatically indistinguishable, and the UV-blue patches become almost achromatically indistinguishable from the dorsum colour (Fig. 3). Results were almost identical irrespective of the natural background that was included (i.e. grass, schist, slate, limestone, mean rock, black—Supplementary Information S1).

The results and test statistics of our generalised least squares models using a grass background are summarised

Table 1 Mean and standard errors of the spectral intensity, hue, and UV chroma (only for the UV-blue patches) for each body part and throat colour. Sample size (n) is indicated

	UV-blue patches	Dorsum	Yellow throat	White throat	Orange throat
n	48	50	30	12	8
Intensity	9976 ± 341	3658 ± 260	9773 ± 489	$13,707\pm787$	$10,415\pm689$
Hue	364 ± 2	614 ± 6	646 ± 3	663 ± 5	654 ± 8
UV chroma	0.410 ± 0.010	-	-	-	-

Table 2 Pairwise comparison among the different body parts and throat colour morph as part of a distance-based PERMANOVA performed on the chromatic and achromatic contrasts. In other words, these results allow us to determine whether wall lizards can distinguish between the different colour patches on their body. Pseudo F-statistics, R^2 as an effect size estimate, p-values, and adjusted p-values (Bonferroni corrections) are reported. Statistical significance is also indicated (*)

Pairwise comparisons	Chromatic contrast ΔS				Achromatic contrast ΔL			
	F	R^2	p	Adj. p	F	R^2	p	Adj. p
OVS – Yellow throat	345.82	0.90	0.001	0.01 *	36.03	0.32	0.001	0.01 *
OVS – Yellow throat	268.52	0.81	0.001	0.01 *	42.45	0.40	0.001	0.01 *
OVS – Yellow throat	248.16	0.82	0. 001	0.01 *	16.28	0.23	0.001	0.01 *
OVS – Yellow throat	869.90	0.90	0.001	0.01 *	17.48	0.15	0.001	0.01 *
Dorsum – Yellow throat	60.49	0.42	0.001	0.01 *	34.42	0.29	0.001	0.01*
Dorsum – White throat	149.94	0.68	0. 001	0.01 *	23.54	0.25	0.001	0.01 *
Dorsum – Orange throat	24.81	0.29	0. 001	0.01 *	10.92	0.15	0.004	0.04 *
Yellow throat – White throat	23.54	0.34	0. 001	0.01 *	6.19	0.12	0.009	0.09
Yellow throat – Orange throat	0.07	0.001	0.949	1.00	0.50	0.01	0.564	1.00
White throat – Orange throat	26.05	0.53	0. 001	0.01 *	2.78	0.11	0.091	0.91

in Table 3, and results using the five other background types are shown in Supplementary Information S2. We found that the UV-blue patches are chromatically more conspicuous against all types of background than all other body part colours, except against a black background, for which dorsum colour was the most conspicuous.

Finally, our bootstrap procedure showed that the colour of all body parts was distinguishable from the natural background coloration by a wall lizard visual system. Dorsal coloration was the least conspicuous of all body parts while the UV-blue patches were the most chromatically conspicuous. The white throat was the most achromatically conspicuous, followed by the yellow throat (Fig. 4).

Discussion

Our results identify some variables related to the UV-blue patches and the black melanic coloration in the Tyrrhenian wall lizard that correlate with male traits (i.e. head and body size) known to be important in male-male competition. We found that larger males have more numerous and larger UV-blue patches, with a higher UV chroma, and a UV-shifted hue. The relative extent of black coloration on the dorsum, throat, and outer-ventral scales also correlates positively with male body size and male relative head size. These correlations suggest that both UV-blue and black colour may act as honest signals of male quality. Furthermore, our analyses involving visual modelling revealed that the colours of most body parts can be distinguished from each other by a wall lizard visual system. Finally, we found that the UV-blue patches are the most chromatically conspicuous against a natural background while the dorsum coloration is the least conspicuous. These results

confirm that lizard body coloration is a mosaic of colour patches that play different roles and are shaped by different evolutionary forces.

In lizards, body size is the primary factor that determines male contest outcome, larger males winning more fights than smaller ones (Carpenter 1995; Karsten et al. 2009; Baird 2013; Names et al. 2019). The relationship between some features of the UV-blue patches and male body size in *P. tiliguerta* suggests that the UV-blue patches may function as signals that convey information on male resource holding potential (RHP) or fighting ability during aggressive contests. In *P. muralis*, a sister species, previous studies identified hue and UV chroma of the UV-blue patches as predictors of fighting ability, male condition, and reproductive success (Pérez i de Lanuza et al. 2014; MacGregor et al. 2017). Also, in *P. muralis*, Names et al. (2019) reported a correlation between the number and size of the UV-blue patches and male—but not female—body size. The positive relationship between body size and the number and size of the UV-blue patches in males of these two *Podarcis* species could arise simply as a consequence of ontogenetic processes: As individuals grow larger, so do their colour patches. Hue and UV chroma, on the other hand, more likely act as signals since they seem to convey information about size-independent fighting ability (bite force) and body condition, at least in *P. muralis* (Pérez i de Lanuza et al. 2014). A role for the UV-blue patches as signals of body size is unlikely considering that aggressive interactions between males typically take place at very close range. This makes signalling of body size unnecessary, i.e. a receiver capable of perceiving the UV-blue patches of its rival should also be capable of ascertaining its body size through direct assessment. Instead, it seems likely that the UV-blue patches provide information about phenotypic traits related to RHP
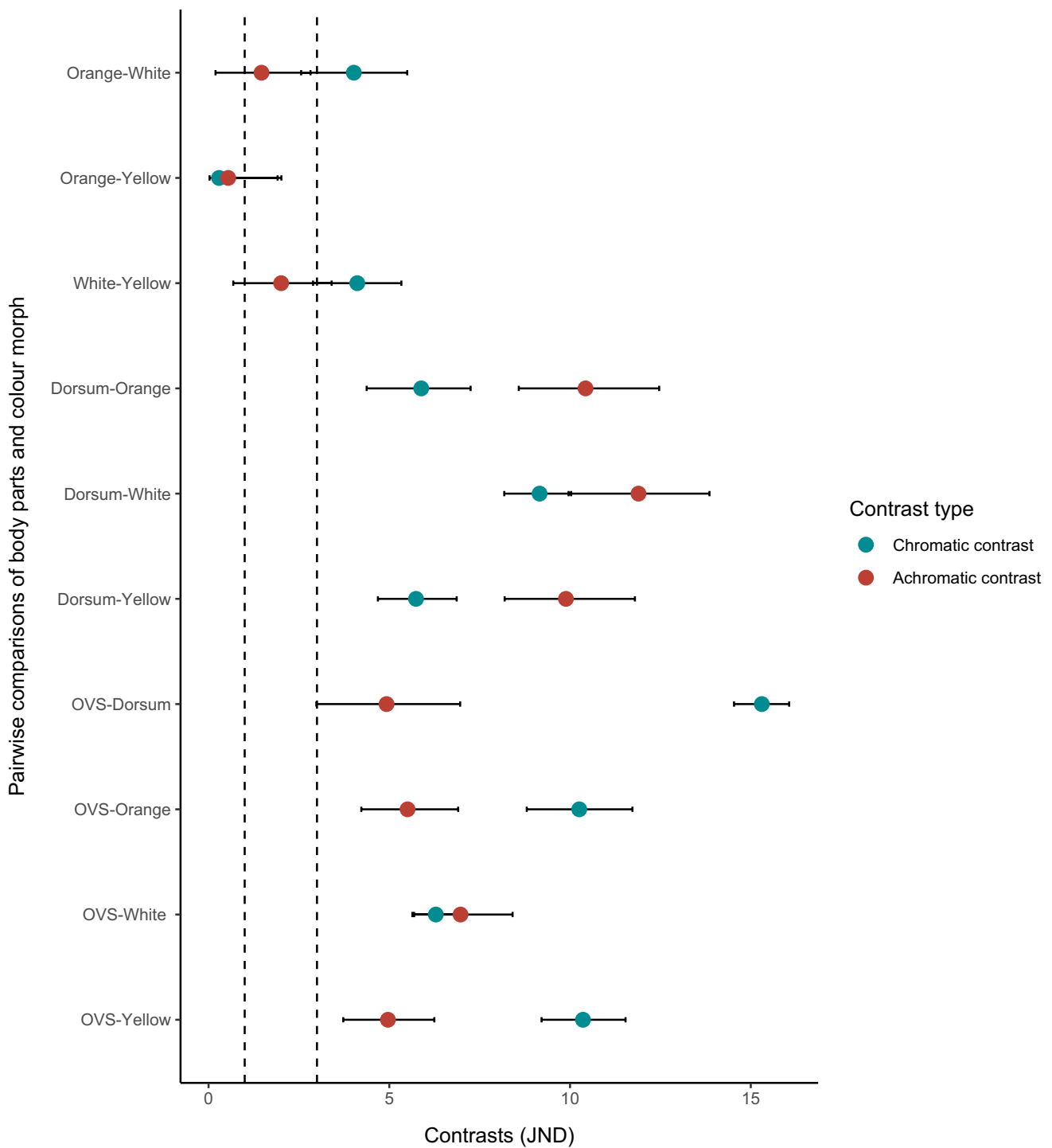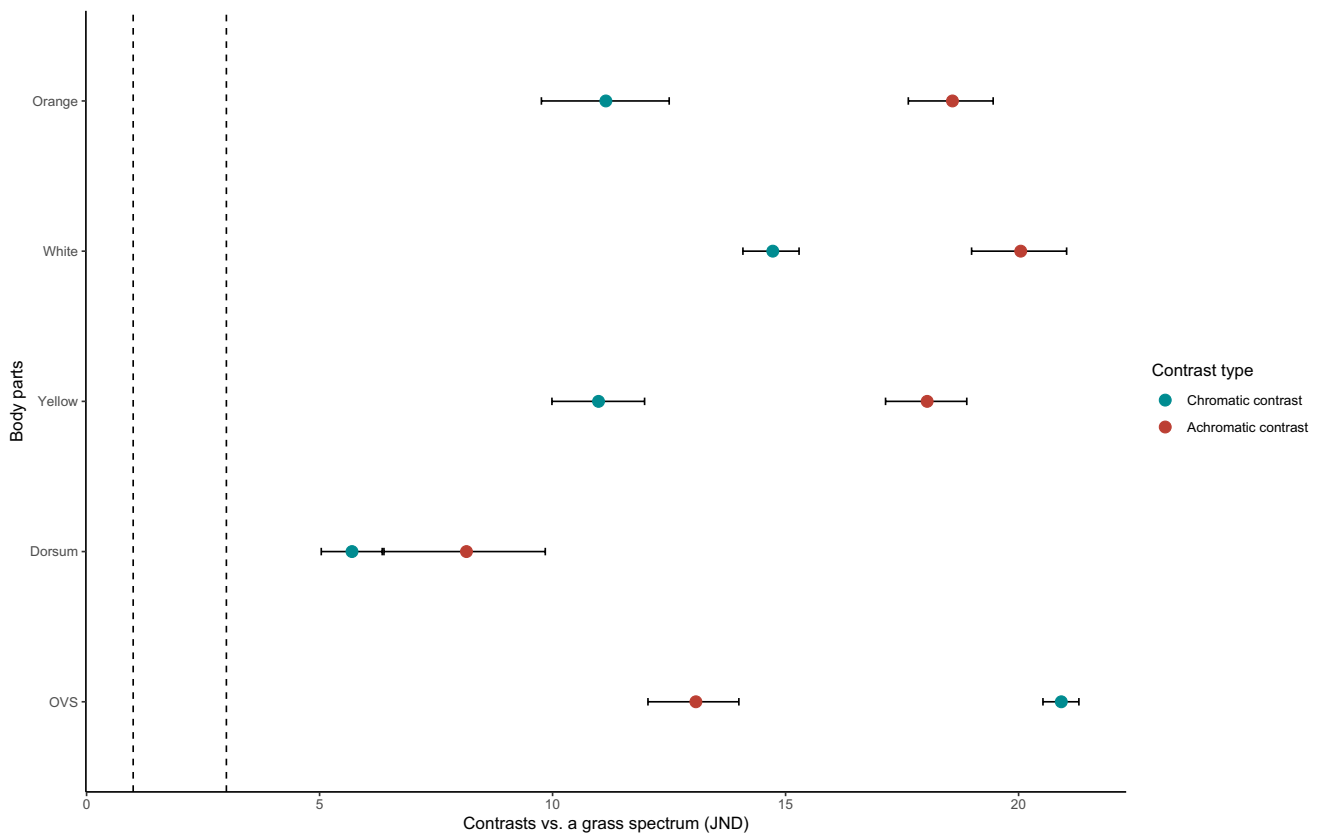
Fig. 3 Mean and 95% confidence intervals of the chromatic and achromatic contrasts between the coloration of each body part (dorsum, outer-ventral scales (OVS), and throat (white, yellow, orange)) when viewed against a grass background. Two dashed lines at 1 and 3 JNDs represent two discriminability thresholds. When the confidence intervals of a point include a discriminability threshold, it means that the two colours are not distinguishable according to this threshold

that are not directly observable, such as bite force, fighting ability, or experience.

In addition, we found that males with darker (i.e. less spectral intensity) UV-blue patches, and those with more numerous black spots on their body (throat, OVS, and dorsum), were larger and had a larger head relative to their body size. In other words, male black coloration also correlates with proxies of fighting ability and RHP, strongly suggesting

Table 3 Pairwise comparisons among the different body parts and throat colour morphs resulting from the post hoc Tukey tests related to the generalised least square models performed on chromatic (ΔS_{bkg}) and achromatic (ΔL_{bkg}) contrasts between different body parts and a grass background colour. In other words, these results allow us to determine which body colours are more conspicuous than other against a grass background. Estimates (β), standard errors (SE), and adjusted p-values (Bonferroni corrections) are reported. Statistical significance is also indicated (*)

Pairwise comparisons	Chromatic contrast ΔS_{grass}			Achromatic contrast ΔL_{grass}		
	β	SE	p	β	SE	p
OVS – Yellow throat	9.979	0.564	<0.001 *	−1.157	0.640	0.367
OVS – Yellow throat	6.324	0.404	<0.001 *	−2.688	0.688	<0.001 *
OVS – Yellow throat	9.931	0.961	<0.001 *	−1.220	0.638	0.307
OVS – Yellow throat	10.299	0.289	<0.001 *	3.374	0.764	<0.001 *
Dorsum – Yellow throat	−0.321	0.581	0.979	−4.532	0.760	<0.001 *
Dorsum – White throat	−3.976	0.429	<0.001 *	−6.063	0.801	<0.001 *
Dorsum – Orange throat	−0.368	0.971	0.995	−4.595	0.758	<0.001 *
Yellow throat – White throat	−3.655	0.647	<0.001 *	−1.531	0.684	0.164
Yellow throat – Orange throat	−0.047	1.085	1.00	−0.064	0.633	1.00
White throat – Orange throat	3.608	1.012	0.003 *	1.467	0.681	0.196

a role of black coloration as a signal of male quality and/ or condition. Previous studies have also identified black melanic coloration to signal male quality and/or condition in other vertebrate species (see San-Jose and Roulin 2018 for a review), including lacertid lizards such as *P. muralis* (Abalos et al. 2016) and *Zootoca vivipara* (San-Jose et al. 2017). Males of *Podarcis* may thus be using multiple signals— UV-blue and melanic coloration—to advertise their quality.

Fig. 4 Mean and 95% confidence intervals of the chromatic and achromatic contrasts between the coloration of each body part (dorsum, outer-ventral scales (OVS), and throat (white, yellow, orange)) and a natural grass spectrum. Two dashed lines at 1 and 3 JNDs represent two discriminability thresholds

UV-blue and melanic coloration could convey information about different aspects of the individual quality of the signaller (multiple message hypothesis; Johnstone 1996). For example, in males of Dickerson's collared lizard (*Crotaphytus dickersonae*), the blue body colour conveys information about RHP, whereas the black collar is related to immune condition (Plasman et al. 2015). Alternatively, multiple signals could convey and reinforce information about the same component of the signaller's individual quality (redundant or back-up signal hypothesis; Johnstone 1996). For example, in the South Indian rock agama (*Psammophilus dorsalis*), displayed behaviour and the colour of the red dorsal strip convey redundant information about male quality which affects female mate choice (Deodhar and Isvaran 2018). Unfortunately, the available information does not allow us to discriminate conclusively between these alternative explanations for the maintenance of multiple chromatic signals of quality in *Podarcis*. However, a strong co-variation between the different signals involved is expected in the case of redundant signals. In *P. tiliguerta*, however, the variables derived from the UV-blue patches and the black coloration do not correlate strongly (Supplementary Information S3), thus supporting a multiple message hypothesis.

Our results also show that large and presumably high-quality males of *P. tiliguerta* have darker UV-blue patches than smaller males. This finding may seem contrary to the expectation, based on studies of chromatic signals of quality in other taxa, that high-quality males should be more brightly coloured than low-quality males (e.g. Molnár et al. 2012). However, the relationship between spectral intensity and several indices of the signaller's quality is not always positive (Whiting et al. 2006; Merkling et al. 2018). In the Brazilian lizard *Tropidurus semitaeniatus*, males with darker yellow chests are more dominant and have a greater probability of winning aggressive encounters, suggesting a negative relationship between spectral intensity and RHP (Bruinjé et al. 2019). Aggressiveness, RHP, and head and body size are directly influenced by testosterone levels in lizards (Cooper et al. 1987; Rhen and Crews 2000; Husak et al. 2007; Cox et al. 2009; Huyghe et al. 2010a; Wade 2011), which in turn have a pronounced effect on body coloration, especially melanic coloration (Quinn and Hews 2003). High testosterone levels are associated with increased deposition of dermal melanin, which in *Podarcis* could be responsible both for the larger relative amount of black coloration and the darker, more saturated UV-blue patches of large, high-quality males. In support of this hypothesis, castrated males of Yarrow's spiny lizard (*Sceloporus jarrovi*) have brighter, less saturated abdominal blue patches than intact males, while testosterone replacement therapy restores coloration to levels similar to those of intact males, turning the blue patches of castrated males darker and more saturated (Cox et al. 2008).

Bite force is a widely used proxy of male dominance and fighting ability, and more generally of whole-organism performance in lizards (Lailvaux et al. 2004; Huyghe et al. 2005). However, in our study, male *P. tiliguerta* refused to, or clearly lacked the motivation to bite the bite force device, thus leading to unusually low bite force scores. As pointed out by Losos et al. (2002), performance measurements are only meaningful if the data reflect the maximum voluntary performance of each individual. Maximum bite force scores may actually capture a significant amount of variation in motivation in addition to variation in maximum bite force performance. We thus advocate for a cautious use of bite force as a proxy of whole-organism performance, especially in a comparative framework, as the contribution of differences in motivation to variation in bite force scores is generally unknown, and may be high.

Showing that lizards perceive as different the colours of different body parts is the first step to be able to determine their functional role. Results of our visual modelling procedure show that the dull brown-green dorsum, the UV-blue patches, and the polychromatic throat can be visually distinguished from each other by a wall lizard. The sole exception is the orange and yellow throats, which cannot be reliably distinguished from each other. This could be due to the low sample size for the orange morph ($n = 8$); more orange spectra would have led to more points in the tetrahedral colour space (Fig. 1b) therefore increasing the probability of distinguishing between these two colours. It would indeed be surprising if *P. tiliguerta* was not able to distinguish between two of its three colour morphs, especially given that this ability has been demonstrated in the closely related *P. muralis* (Pérez i de Lanuza and Font 2015; Pérez i de Lanuza et al. 2018). That the yellow and orange morphs are two extremes of continuous colour variation seems unlikely because in *P. muralis*, the yellow and orange ventral coloration are regulated by two different genes (carotenoid-related and pterin-related gene, respectively; Andrade et al. 2019). In addition, we found that the dorsal coloration was the least conspicuous of all body parts against a natural background, thus reinforcing the idea that the dorsal coloration plays a role as camouflage. The lateral UV-blue patches are the most conspicuous colour patches. This is because the habitat of *P. tiliguerta* generally lacks UV reflective objects, thus increasing the contrasts between UV-blue patches and the natural background colours. Furthermore, these UV-blue patches are surrounded by patches of the same colour as the belly and the dorsum, against which they are highly conspicuous (Fig. 3). These results add to previous evidence showing that UV-blue patches function as communicative signals. Ventral coloration was highly conspicuous in *P. tiliguerta*, suggesting that it must also play a role in the visual socio-ecology of this species, although the selective processes responsible for the origin and maintenance of ventral colour polymorphism

in wall lizards remain unresolved (Abalos et al. 2020). In summary, male *P. tiliguerta* show a body partitioning of their coloration with the ventral and lateral body parts likely responding to selective pressures related to signalling and dorsal coloration being shaped by camouflage-related selective pressures.

Declarations

Ethics approval This study was authorised by permit n°16–0660 issued on 12 April 2016 by DREAL Corse allowing the capture, transport, and detention of this protected species. The use of animals adheres to the guidelines set forth by the Animal Behaviour Society/Association for the Study of Animal Behaviour and was approved by the Macquarie University Animal Ethics Committee (reference 2015/044–2).

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