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

3

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13

14 *Abstract*

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

33

34 *Significance Statement*

35 Many animals use their coloration to convey information about their quality as rivals or  
36 mates. Yet, until recently researchers have not recognized the potential of ultraviolet colour  
37 patches to function as signals of quality. In this study, we first show that male Tyrrhenian  
38 wall lizards display ultraviolet-blue and black colour patches that correlate positively with

39 some aspect of their quality such as body or head size. Furthermore, our visual modelling  
40 procedure suggests that these lizards are able to distinguish the colours of their body parts  
41 from each other, with dorsal colours being the least conspicuous and ultraviolet-blue  
42 coloration being the most conspicuous.

43

44

45 *Key words:* colour signals; visual modelling; colour morph; colour discrimination; Lacertidae

46

47 *Introduction*

48 The display of conspicuous colour patches constitutes a ubiquitous and diverse class of  
49 signals that play a pivotal role in sexual selection (Hamilton and Zuk 1982; Endler 1983;  
50 Andersson 1994; Hill and McGraw 2006). In this context, colour signals typically convey  
51 information about the signaller's quality as a mate (e.g. direct and/or indirect benefits) or as a  
52 rival (e.g. fighting ability, social dominance; Hill and McGraw 2006; Morehouse and  
53 Rutowski 2010; Bradbury and Vehrencamp 2011). Colour production in animals results from  
54 the interaction of light with pigments (e.g. carotenoids, melanin), nanostructures, or a  
55 combination of both in the integument (Shawkey and D'Alba 2017). Our understanding of the  
56 signalling role and evolution of pigment-based colours has much improved over the past  
57 decades (Olson and Owens 1998; Svensson and Wong 2011; Roulin 2016). For example,  
58 carotenoid-based colour signals can in some cases function as honest signals of quality due to  
59 the trade-off involved in allocating carotenoids to signalling or to other important  
60 physiological functions (Svensson and Wong 2011; Weaver et al. 2017). In contrast,  
61 structurally produced colours, such as blue, violet, and ultraviolet (UV), have been  
62 traditionally considered cheap to produce and lacking in any obvious trade-offs, and therefore  
63 unlikely to accurately reflect inter-individual variations in quality (Kemp et al. 2012; Kemp  
64 and Grether 2015). However, mounting evidence reveals that many animals are equipped with  
65 UV-sensitive vision (Kelber et al. 2003; Cronin and Bok 2016), thus leading to an increasing  
66 appreciation of the potential of structural coloration as honest signals of individual quality  
67 (White 2020). UV signalling has now been shown to occur in many taxa, including birds (e.g.  
68 Keyser and Hill 1999), lizards (e.g. Whiting et al. 2006), amphibians (e.g. Secondi et al.  
69 2012), fish (e.g. Siebeck 2004; Rick et al. 2006), insects (e.g. Papke et al. 2007), and  
70 arachnids (e.g. Painting et al. 2016). Despite this evidence, we are still far from a complete

71 understanding of the selective forces at play in the evolution of UV signals, and more  
72 generally of structural colour signals.

73 Many lizards possess conspicuous colour patches that reflect in the UV range (e.g.  
74 Macedonia 2001; Stoehr and McGraw 2001; Martin et al. 2013; Badiane et al. 2018a) and are  
75 displayed during social interactions (Whiting et al. 2006), suggesting a potential role as  
76 ornaments. In lacertid lizards, UV coloration is particularly widespread and often appears on  
77 the lizard's flanks, head, throat, or belly (Molina-Borja et al. 2006; Pérez i de Lanuza and  
78 Font 2007; Font et al. 2009; Badiane et al. 2018a). The signalling role of UV colour patches  
79 has been well established in several lacertid species, both via field studies showing  
80 correlations between the design of the UV patches and male fitness-related phenotypic traits  
81 (Font and Molina-Borja 2004; Huyghe et al. 2005; Font et al. 2009; Molnár et al. 2012; Pérez  
82 i de Lanuza et al. 2014), and through experimental manipulations of the reflectance of the UV  
83 patches during intra- and inter-sexual interactions (Bajer et al. 2010, 2011; Martin et al.  
84 2015a, 2016; Names et al. 2019). While current evidence seems to indicate that, in lacertids,  
85 UV signals primarily evolved to resolve male-male conflicts and avoid contest escalation  
86 (Bajer et al. 2011; Pérez i de Lanuza et al. 2014; Martin et al. 2015a, 2016), UV coloration  
87 may also play a role in female mate choice in some species (Bajer et al. 2010; Badiane et al.  
88 2020).

89 Wall lizards from the genus *Podarcis* comprise 24 species and the males of most of  
90 these species have conspicuous colour patches on some of their outer-ventral scales (OVS).  
91 These colour patches appear blue to the human eye but are in fact UV-reflecting and therefore  
92 best described as UV-blue. In the common wall lizard (*Podarcis muralis*), Pérez i de Lanuza  
93 et al. (2014) showed that the hue and UV chroma of the UV-blue patches are related to size-  
94 independent bite force (a proxy of male fighting ability in lizards, Huyghe et al. 2009) and  
95 body condition, respectively, suggesting condition-dependence and a role in male-male

96 interactions and contest behaviour. MacGregor et al. (2017) also found a relationship between  
97 the hue and UV chroma of the UV-blue patches and male reproductive success in two *P.*  
98 *muralis* lineages. Martin et al. (2015a) and Names et al. (2019) found that manipulating the  
99 reflectance and size of UV-blue patches affected male agonistic interactions. Finally, Abalos  
100 et al. (2016) reported that natural variation in the size and reflectance of the UV-blue patches  
101 does not predict the outcome of laboratory-staged contests between size-matched males, and  
102 proposed that the UV-blue patches may be important during the early stages of contests  
103 during which rival assessment takes place. Taken together, these results suggest that the UV-  
104 blue patches may play a role in male-male signalling, but the evidence for their role as signals  
105 of fighting ability remains equivocal.

106         Previous studies of the communicative function of the UV-blue patches have focused  
107 on a single species of wall lizard, but other *Podarcis* species display colour ornaments similar  
108 to those of *P. muralis*. Here we consider the case of the Tyrrhenian wall lizard (*P. tiliguerta*),  
109 which is phylogenetically close to *P. muralis* and displays similar UV-blue patches that have  
110 not been empirically investigated so far. As in other lacertid lizards, body coloration in *P.*  
111 *tiliguerta* is a complex mosaic of colour patches that are likely subject to different selection  
112 pressures (Pérez i de Lanuza et al. 2013b). Dorsally, they show a dull brown-green coloration  
113 that probably evolved for antipredatory purposes (e.g. camouflage – Stuart-Fox et al. 2003;  
114 Marshall and Stevens 2014; Marshall et al. 2015a, b, 2016). Their ventral coloration, in  
115 contrast, is conspicuous and polymorphic, with three alternative ventral colours (i.e. orange,  
116 white, and yellow) that may be linked to different behavioural or life history strategies  
117 (Huyghe et al. 2010b; Pérez i de Lanuza et al. 2013a). Additionally, *P. tiliguerta* lizards have  
118 black melanin spots over their entire body surface which could also have a signalling role  
119 (e.g. Abalos et al. 2016). Our aim here is to characterize the coloration of the different body  
120 parts of *P. tiliguerta*, which has never been studied using objective methods of colour

121 assessment. To determine the potential information content of the UV-blue patches and the  
122 black melanic spots, we investigate whether black and UV-blue colour variables correlate  
123 with morphological or performance traits indicative of male quality. We also use visual  
124 modelling procedures to examine whether different body parts and different colour morphs  
125 can be distinguished from each other by a wall lizard visual system, and to explore which of  
126 these body colours are the most conspicuous when viewed against a natural background. This  
127 study should provide useful insights on the potential information content of UV-blue signals,  
128 thus improving our understanding of the role of structurally produced colours as  
129 communicative signals. In addition, our visual modelling approach will help us understand  
130 the roles of the multiple colours displayed by these lizards, and establish the foundations for  
131 future research involving this species.

132

### 133 *Materials and Methods*

#### 134 Study species

135 The Tyrrhenian wall lizard *Podarcis tiliguerta* is a small lacertid endemic to the  
136 Mediterranean islands of Corsica and Sardinia and their respective satellite islets, although  
137 recent evidence has shown marked phylogeographic patterns suggestive of a species complex  
138 (Capula 1996; Bruschi et al. 2006; Rodríguez et al. 2017; Salvi et al. 2017; Senczuk et al.  
139 2019). Several micro-insular subspecies have been described based on morphological  
140 variation, including body coloration (e.g. melanism, red ventral coloration – Brizzi and Lanza,  
141 1975). Tyrrhenian wall lizards inhabit semi-open rocky and shrubby areas as well as human  
142 constructions (e.g. stone walls) interspersed with vegetation (Vanhooydonck et al. 2000;  
143 Bombi et al. 2009). Like most *Podarcis* lizards, they have a cryptic dorsal coloration and a  
144 conspicuous polymorphic ventral coloration with three alternative colour morphs (i.e. orange,  
145 yellow, white). Laterally, males of this species display small UV-blue patches on some of



146 their OVS, often interspersed with black melanin-based spots (Fig. 1). In contrast to the  
147 ventral scales, which are white, yellow or orange, background colour of the outer-ventral  
148 scales is light blue-greenish to the human eye.

149

#### 150 Data collection

151 On 18-22 May 2016, we captured 50 male *P. tiliguerta* by noosing in central-western Corsica  
152 (lat: 42.059911; lon: 8.959600) alongside roads, human constructions, and water streams. On  
153 the day of capture, we measured body mass to the nearest 0.1 g using a light-line spring scale  
154 (Pesola), and snout-vent length (i.e. SVL) and head length to the nearest 0.1 mm using digital  
155 callipers (Mitutoyo). We also measured maximum bite force, which has been shown to be a  
156 good proxy for fighting ability and whole-organism performance in lizards (Huyghe et al.  
157 2005; Lappin and Husak 2005), using a purpose-built bite force meter. The bite force meter  
158 was constructed from a modified Sauter FK 25 N digital force meter with two metal plates on  
159 which each animal bites, one attached to the main body of the force meter, and the other  
160 attached to the fixed recording rod. We placed the lizards in a small plastic box with a heating  
161 mat underneath until the lizards reached a body temperature between 32°C and 37°C as  
162 measured with an infrared thermometer (preferred body temperature for this species is ca.  
163 35°C; Van Damme et al. 1989). We then retained the maximum score out of three bite force  
164 measurements. Unexpectedly, 21 lizards completely refused to bite the bite-force plate and  
165 the remaining 29 individuals showed an obvious lack of motivation resulting in very low bite  
166 force scores (i.e. typically below 0.3 N). This is unusual for *Podarcis* lizards, which are  
167 usually motivated to bite and bite harder than this  
168 (e.g. *P. muralis*, *P. melisellensis*, *P. filfolensis*, *P. liolepis*, *P. sicula*, *P. lilfordi* – AB and EF  
169 personal observations). Based on this evidence, we consider that our bite force scores are  
170 unreliable and do not reflect the maximum performance of the tested individuals (Lappin and

171 Jones 2014), and therefore we excluded them from further analyses. It was not possible to  
172 record data blind because our study involved focal animals in the field.

173 We also took four pictures of each individual (i.e. dorsal, ventral, and both lateral  
174 profiles) using a Nikon D5300 DSLR camera with a Sigma 70-300 mm macro lens and the  
175 flash turned on. To maximize consistency, we held each lizard gently pressed against a glass  
176 plate at a fixed distance from the camera (Badiane et al. 2018a). Using lateral photographs  
177 and the colour threshold tool implemented in ImageJ (Schneider et al. 2012), we calculated  
178 the percentage of surface area covered by black coloration on the left and right rows of OVS  
179 of each lizard, on the dorsum (between the parietal-occipital scales and the insertion of the  
180 posterior limbs), and on the throat (between the infra-labial scales and the collar scale row).  
181 We did not measure the belly as it has no or very few black spots. Similarly, we counted the  
182 number of UV-blue patches and calculated the total surface covered by blue coloration  
183 present on the lizards' OVS (and occasionally on some of the adjoining dorsolateral granular  
184 scales). It should be noted that we used the percentage of black area (i.e. a relative  
185 measurement), but the total area of UV-blue patches (i.e. an absolute measurement) because  
186 measuring the total black area would include a non-negligible measurement error due to slight  
187 inconsistencies in the delimitation of the relevant body part (e.g. dorsum, throat). We kept the  
188 absolute UV-blue area because this coloration sometimes spreads over the granular scales  
189 above the OVS, which would lead to inconsistencies if we used a relative value. These  
190 variables have previously been measured similarly in other lizard species (Abalos et al. 2016).

191

## 192 Reflectance spectra and visual modelling

193 We obtained reflectance spectra of the belly (a single reading in the middle of the belly), and  
194 of the second and third UV-blue patches on both flanks using a JAZ portable diode-array  
195 spectrometer with a R200-7-VIS-NIR reading-illumination probe (Ocean Optics Inc.) and a

196 notebook computer running Ocean Optics Spectra Suite software. We took reflectance  
197 readings in a darkened room using a PX-2 xenon strobe light source (Ocean Optics Inc.) for  
198 full spectrum illumination. We recorded spectra in 0.37 steps and used a  
199 certified Spectralon 99% white diffuse reflectance standard (Labsphere) as a white reference.  
200 We took a dark reading and subtracted it from the signal just prior to gathering the spectral  
201 data. We averaged reflectance readings over 5 nm using a kernel smoothing function, and set  
202 integration time to 30 ms, scans to average to 10, and boxcar width to 10. For data  
203 acquisition, we hand-held the probe over the centre of the colour patch, and perpendicular to  
204 the patch surface (i.e. illumination and recording angles were both 90°; coincident normal  
205 measuring geometry, Anderson and Prager 2006). An entomological pin attached to the side  
206 of the probe allowed us to maintain a constant distance of 5 mm between the tip of the probe  
207 and the measured surface. We did not consider colour spots smaller than 2 mm in diameter  
208 because they cannot be measured using our spectrophotometer set-up (Badiane et al. 2017).

209 We processed spectral data in R v.3.6.2 (R Development Core Team 2017) using the  
210 software package *pavo* v.2.0 (Maia et al. 2019). We considered spectra from the throat, belly,  
211 dorsum, and the second UV-blue patch on the right side of each individual because the first  
212 one is often too small to measure reliably. For two individuals, we used the third UV-blue  
213 patch of the right side because the second one was too small to be measured (Badiane et al.  
214 2017). First, we cropped each spectrum between 300-700 nm and smoothed it using an  
215 interval of 0.2. Then, we extracted colorimetric variables from the spectra of the lateral UV-  
216 blue patches, namely spectral intensity (i.e.  $R_{300-700}$ ), UV chroma (i.e.  $R_{300-400}/R_{300-700}$ ), and hue  
217 (i.e. wavelength at the maximum reflectance peak).

218 Visual modelling was done using the Vorobyev and Osorio model (Vorobyev and  
219 Osorio 1998) implemented in the package *pavo* v.2.0 to score colour discrimination and  
220 conspicuousness in terms of chromatic and achromatic contrasts of each individual's body

221 parts (i.e. throat, belly, dorsum, and UV-blue patches) against different natural backgrounds.  
222 We obtained reflectance spectra of different natural backgrounds present in the lizards'  
223 habitat, namely a grass spectrum (i.e. average of three spectra), three types of rock (i.e. schist,  
224 slate, and limestone - average of five spectra for each rock type), a mean rock background  
225 (i.e. average of the spectra from the three rock types), and a black spectrum obtained from a  
226 black patch adjacent to the UV-blue patches on the lizards' OVS. We used the cone  
227 sensitivities (UVS:SWS:MSW:LSW, 367:456:497:562 nm; LSW-562 was used for the  
228 achromatic component) and relative cone densities (1:1:1:4) of *P. muralis* (Martin et al.  
229 2015b), which is the closest relative of *P. tiliguerta* for which these data are available. We  
230 used a standard daylight "D65" irradiance spectrum, as implemented in *pavo*. We set the  
231 Weber fraction to 0.1. Chromatic ( $\Delta S$ ) and achromatic ( $\Delta L$ ) contrasts were calculated in units  
232 of *just noticeable differences* (JND). A JND value greater than one indicates that two colours  
233 can be discriminated, whereas colours are indistinguishable if they have a contrast value  
234 inferior to one JND. The Euclidian distance between pairs of points in a chromaticity diagram  
235 and the receptor noise model yield similar results in terms of perceptual distance among  
236 colours (Fleishman et al. 2016), and colour distances provide accurate estimates of  
237 conspicuousness up to 10 JNDs (Santiago et al. 2020).

238

### 239 Statistical analyses

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

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

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

266         Following Maia and White (2018), we tested whether or not different body parts and  
267 throat colour morphs can be discriminated from each other by a wall lizard visual system. To  
268 do so, we used a distance-based PERMANOVA (Anderson 2001) on the chromatic and  
269 achromatic contrasts using the *pairwise.adonis* function from the *pairwiseAdonis* R package  
270 (Arbizu 2019), a modified version of the *adonis* function from the *vegan* R package (Oksanen

271 et al. 2017) allowing for multilevel pairwise comparisons. We created a group variable  
272 including the following levels for pairwise comparison: OVS, dorsum, white throat, orange  
273 throat, and yellow throat. We tested the assumption of multivariate homogeneity of group  
274 dispersions (variances) and found that our group levels have unequal variances for both the  
275 chromatic and achromatic contrasts, but not in a way that would substantially affect our  
276 distance-based PERMANOVA procedure since the largest group had the highest variance  
277 (Anderson and Walsh 2013). For each pairwise comparison, we recorded statistical  
278 significance ( $\alpha = 0.05$ ) using 999 permutations, a pseudo F-statistic, and  $R^2$  as an effect size  
279 estimate. Adjusted p-values for multiple comparisons were obtained using a Bonferroni  
280 procedure. As significance thresholds do not necessarily match the theoretical perceptual  
281 threshold of one JND above which colours can be said to be distinguishable, we used a  
282 bootstrap procedure to generate confidence intervals for the mean colour distance between the  
283 different colours. We used the *bootcoldist* function from the *pavo* R package on the visual  
284 model described above with 1000 replicates and a 0.95 level for confidence intervals. This  
285 procedure was repeated six times, once for each visual model with a different natural  
286 background (i.e. grass, schist, slate, limestone, mean rock, and black patch).

287       Next, to explore which body part and colour morph are the most conspicuous when  
288 viewed by a wall lizard against a natural background (i.e. grass, rocks, black patch), we built  
289 the same visual model as above, except that now we included an ideal black as visual  
290 background in the model instead of the natural background spectra. This time, we included  
291 the natural background spectra as if it were another body part to be compared but could not  
292 use the same PERMANOVA procedure as before because we had only one spectrum per  
293 natural background. Instead, we created  $\Delta S_{\text{bkg}}$  and  $\Delta L_{\text{bkg}}$  variables such that only the  
294 chromatic and achromatic contrasts (respectively) between each individual spectrum of each  
295 body part and colour morph and the natural background spectrum were included. Next, we

296 fitted linear models using the generalised least squares method using the *gls* function from the  
297 *nlme* R package (Pinheiro et al. 2019) with  $\Delta S_{\text{bkg}}$  and  $\Delta L_{\text{bkg}}$  as response, and body parts (i.e.  
298 five levels: OVS, dorsum, and the three throat colour morphs) as explanatory variable. To  
299 account for heteroscedasticity in our “body parts” variable, we used the weights argument in  
300 our models to allow variance of the residuals to differ among group levels. To explore  
301 differences among different body parts and throat colour morph, we performed *post hoc*  
302 Tukey tests on these two factors using the *multcomp* R package (Hothorn et al. 2008),  
303 adjusting p-values for multiple comparison with a Bonferroni method. Model residuals were  
304 checked for normality and homoscedasticity. Finally, we used the same bootstrap procedure  
305 as above to generate confidence intervals for the mean colour distance between the different  
306 body parts and background colour.

307

### 308 *Results*

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

314         Regarding the relationship between the UV-blue patches and male traits, we found that  
315 larger males in terms of SVL had higher UV chroma ( $F_{1-43} = 4.85$ ,  $R^2 = 0.08$ ,  $\beta = 0.34 \pm 0.16$ ,  
316  $p = 0.033$ ), a larger area of UV-blue ( $F_{1-47} = 1.47$ ,  $R^2 = 0.33$ ,  $\beta = 0.59 \pm 0.12$ ,  $p < 0.001$ ), more  
317 UV-blue patches ( $\beta = 0.14 \pm 0.03$ ,  $p < 0.001$ ), but a lower spectral intensity ( $F_{3-42} = 3.25$ ,  $R^2 =$   
318  $0.13$ ,  $\beta = -0.36 \pm 0.15$ ,  $p = 0.021$ ), and a lower (i.e. more UV-biased) hue ( $F_{1-48} = 6.73$ ,  $R^2 =$   
319  $0.10$ ,  $\beta = -0.35 \pm 0.14$ ,  $p = 0.013$ ) than smaller males. We also found that spectral intensity  
320 correlated negatively with male relative head size ( $F_{3-42} = 3.25$ ,  $R^2 = 0.13$ ,  $\beta = -0.31 \pm 0.15$ ,  $p$

321 = 0.047) but not with body condition ( $F_{3,42} = 3.25$ ,  $R^2 = 0.13$ ,  $\beta = 0.21 \pm 0.15$ ,  $p = 0.152$ ). All  
322 the error terms associated with  $\beta$  coefficients correspond to standard errors

323 In addition, we found that body size and relative head size both correlated positively  
324 with the percentage of black on the throat (trend for SVL:  $0.24 \pm 0.13$ ,  $p = 0.074$ ; HLres:  $0.33$   
325  $\pm 0.13$ ,  $p = 0.017$ ), on the OVS (SVL:  $0.29 \pm 0.13$ ,  $p = 0.038$ ; HLres:  $0.28 \pm 0.13$ ,  $p = 0.038$ ),  
326 and on the dorsum (SVL:  $0.49 \pm 0.12$ ,  $p = 0.0001$ ; HLres:  $0.27 \pm 0.12$ ,  $p = 0.031$ ). All error  
327 terms associated with  $\beta$  coefficient correspond to standard errors.

328 Results and test statistics of our PERMANOVA procedure are summarised in Table 2.  
329 We found that the UV-blue patches and dorsum colours were statistically different from all  
330 the other body parts in terms of chromatic and achromatic contrasts. In addition, the white  
331 throat was chromatically different from both the yellow and orange throat; however, yellow  
332 and orange throats were not statistically different. Also, the three throat colours were not  
333 statistically different from each other in terms of achromatic contrast.

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



345 The results and test statistics of our generalised least squares models using a grass  
346 background are summarised in Table 3, and results using the five other background types are  
347 shown in Supplementary Information S2. We found that the UV-blue patches are  
348 chromatically more conspicuous against all types of background than all other body part  
349 colours, except against a black background, for which dorsum colour was the most  
350 conspicuous.

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

356

### 357 *Discussion*

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

371           In lizards, body size is the primary factor that determines male contest outcome, larger  
372 males winning more fights than smaller ones (Carpenter 1995; Karsten et al. 2009; Baird  
373 2013; Names et al. 2019). The relationship between some features of the UV-blue patches and  
374 male body size in *P. tiliguerta* suggests that the UV-blue patches may function as signals that  
375 convey information on male resource holding potential (RHP) or fighting ability during  
376 aggressive contests. In *P. muralis*, a sister species, previous studies identified hue and UV  
377 chroma of the UV-blue patches as predictors of fighting ability, male condition, and  
378 reproductive success (Pérez i de Lanuza et al. 2014; MacGregor et al. 2017). Also, in *P.*  
379 *muralis*, Names et al. (2019) reported a correlation between the number and size of the UV-  
380 blue patches and male – but not female - body size. The positive relationship between body  
381 size and the number and size of the UV-blue patches in males of these two *Podarcis* species  
382 could arise simply as a consequence of ontogenetic processes: as individuals grow larger, so  
383 do their colour patches. Hue and UV chroma, on the other hand, more likely act as signals  
384 since they seem to convey information about size-independent fighting ability (bite force) and  
385 body condition, at least in *P. muralis* (Pérez i de Lanuza et al. 2014). A role for the UV-blue  
386 patches as signals of body size is unlikely considering that aggressive interactions between  
387 males typically take place at very close range. This makes signalling of body size  
388 unnecessary, i.e. a receiver capable of perceiving the UV-blue patches of its rival should also  
389 be capable of ascertaining its body size through direct assessment. Instead, it seems likely that  
390 the UV-blue patches provide information about phenotypic traits related to RHP that are not  
391 directly observable, such as bite force, fighting ability, or experience.

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

396 of black coloration as a signal of male quality and/or condition. Previous studies have also  
397 identified black melanic coloration to signal male quality and/or condition in other vertebrate  
398 species (see San-Jose and Roulin 2018 for a review), including lacertid lizards such as *P.*  
399 *muralis* (Abalos et al. 2016) and *Zootoca vivipara* (San-Jose et al. 2017). Males of *Podarcis*  
400 may thus be using multiple signals – UV-blue and melanic coloration -- to advertise their  
401 quality. UV-blue and melanic coloration could convey information about different aspects of  
402 the individual quality of the signaller (multiple message hypothesis; Johnstone 1996). For  
403 example, in males of Dickerson’s collared lizard (*Crotaphytus dickersonae*) the blue body  
404 colour conveys information about RHP, whereas the black collar is related to immune  
405 condition (Plasman et al. 2015). Alternatively, multiple signals could convey and reinforce  
406 information about the same component of the signaller’s individual quality (redundant or  
407 back-up signal hypothesis; Johnstone 1996). For example, in the South Indian rock agama  
408 (*Psammophilus dorsalis*) display behaviour and the colour of the red dorsal strip convey  
409 redundant information about male quality which affects female mate choice (Deodhar and  
410 Isvaran 2018). Unfortunately, the available information does not allow us to discriminate  
411 conclusively between these alternative explanations for the maintenance of multiple  
412 chromatic signals of quality in *Podarcis*. However, a strong co-variation between the different  
413 signals involved is expected in the case of redundant signals. In *P. tiliguerta*, however the  
414 variables derived from the UV-blue patches and the black coloration do not correlate strongly  
415 (Supplementary Information S3), thus supporting a multiple message hypothesis.

416 Our results also show that large and presumably high-quality males of *P. tiliguerta* have  
417 darker UV-blue patches than smaller males. This finding may seem contrary to the  
418 expectation, based on studies of chromatic signals of quality in other taxa, that high-quality  
419 males should be more brightly coloured than low-quality males (e.g. Molnár et al. 2012).  
420 However, the relationship between spectral intensity and several indices of the signaller’s

421 quality is not always positive (Whiting et al. 2006; Merklings et al. 2018). In the Brazilian  
422 lizard *Tropidurus semitaeniatus* males with darker yellow chests are more dominant and have  
423 a greater probability of winning aggressive encounters, suggesting a negative relationship  
424 between spectral intensity and RHP (Bruinjé et al. 2019). Aggressiveness, RHP and head and  
425 body size are directly influenced by testosterone levels in lizards (Cooper et al. 1987; Rhen  
426 and Crews 2000; Husak et al. 2007; Cox et al. 2009; Huyghe et al. 2010a; Wade 2011), which  
427 in turn have a pronounced effect on body coloration, especially melanic coloration (Quinn and  
428 Hews 2003). High testosterone levels are associated with increased deposition of dermal  
429 melanin, which in *Podarcis* could be responsible both for the larger relative amount of black  
430 coloration and the darker, more saturated UV-blue patches of large, high-quality males. In  
431 support of this hypothesis, castrated males of Yarrow's spiny lizard (*Sceloporus jarrovi*),  
432 have brighter, less saturated abdominal blue patches than intact males, while testosterone  
433 replacement therapy restores coloration to levels similar to those of intact males, turning the  
434 blue patches of castrated males darker and more saturated (Cox et al. 2008).

435         Bite force is a widely used proxy of male dominance and fighting ability, and more  
436 generally of whole-organism performance in lizards (Lailvaux et al. 2004; Huyghe et al.  
437 2005). However, in our study, male *P. tiliguerta* refused to, or clearly lacked the motivation  
438 to bite the bite force device, thus leading to unusually low bite force scores. As pointed out by  
439 Losos et al. (2002), performance measurements are only meaningful if the data reflect the  
440 maximum voluntary performance of each individual. Maximum bite force scores may actually  
441 capture a significant amount of variation in motivation in addition to variation in maximum  
442 bite force performance. We thus advocate for a cautious use of bite force as a proxy of whole-  
443 organism performance, especially in a comparative framework, as the contribution of  
444 differences in motivation to variation in bite force scores is generally unknown, and may be  
445 high.

446           Showing that lizards perceive as different the colours of different body parts is the first  
447 step to be able to determine their functional role. Results of our visual modelling procedure  
448 show that the dull brown-green dorsum, the UV-blue patches, and the polychromatic throat,  
449 can be visually distinguished from each other by a wall lizard. The sole exception is the  
450 orange and yellow throats, which cannot be reliably distinguished from each other. This could  
451 be due to the low sample size for the orange morph ( $n = 8$ ); more orange spectra would have  
452 led to more points in the tetrahedral colour space (Fig. 1B) therefore increasing the  
453 probability of distinguishing between these two colours. It would indeed be surprising if *P.*  
454 *tiliguerta* was not able to distinguish between two of its three colour morphs, especially given  
455 that this ability has been demonstrated in the closely related *P. muralis* (Pérez i de Lanuza  
456 and Font 2015; Pérez i de Lanuza et al. 2018). That the yellow and orange morphs are two  
457 extremes of continuous colour variation seems unlikely because in *P. muralis*, the yellow and  
458 orange ventral coloration are regulated by two different genes (carotenoid- and pterin-related  
459 gene, respectively). In addition, we found that the dorsal coloration was the least conspicuous  
460 of all body parts against a natural background, thus reinforcing the idea that the dorsal  
461 coloration plays a role as camouflage. The lateral UV-blue patches are the most conspicuous  
462 colour patches. This is because the habitat of *P. tiliguerta* generally lacks UV reflective  
463 objects, thus increasing the contrasts between UV-blue patches and the natural background  
464 colours. Furthermore, these UV-blue patches are surrounded by patches of the same colour as  
465 the belly and the dorsum, against which they are highly conspicuous (Fig. 3). These results  
466 add to previous evidence showing that UV-blue patches function as communicative signals.  
467 Ventral coloration was highly conspicuous in *P. tiliguerta*, suggesting that it must also play a  
468 role in the visual socio-ecology of this species, although the selective processes responsible  
469 for the origin and maintenance of ventral colour polymorphism in wall lizards remain  
470 unresolved (Abalos et al. 2020). In summary, male *P. tiliguerta* show a body partitioning of

471 their coloration with the ventral and lateral body parts likely responding to selective pressures  
472 related to signalling and dorsal coloration being shaped by camouflage-related selective  
473 pressures.

474

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478

#### 479 *Declarations*

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##### 483 Ethics approval

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

##### 489 Data availability

490 The data used in this study are available <https://doi.org/10.5281/zenodo.4423275>

##### 491 Authors' contributions

492 AB and EF designed the study, conducted fieldwork and collected the data. AB performed the  
493 statistical analyses and wrote the manuscript. EF revised the manuscript. Both authors consent  
494 to publish this manuscript.

495

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796 **Table 1** Mean and standard errors of the spectral intensity, hue, and UV chroma (only for the  
797 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	13707 ± 787	10415 ± 689
Hue	364 ± 2	614 ± 6	646 ± 3	663 ± 5	654 ± 8
UV chroma	0.410 ± 0.010	-	-	-	-

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

810

Pairwise comparisons	Chromatic contrast $\Delta S$				Achromatic contrast $\Delta L$			
	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 – White throat	268.52	0.81	0.001	0.01 *	42.45	0.40	0.001	0.01 *
OVS – Orange throat	248.16	0.82	0.001	0.01 *	16.28	0.23	0.001	0.01 *
OVS – Dorsum	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

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814 **Table 3** Pairwise comparisons among the different body parts and throat colour morphs  
815 resulting from the *post hoc* Tukey tests related to the generalized least square models  
816 performed on chromatic ( $\Delta S_{\text{bkg}}$ ) and achromatic ( $\Delta L_{\text{bkg}}$ ) contrasts between different body parts  
817 and a grass background colour. In other words, these results allow us to determine which  
818 body colour are more conspicuous than other against a grass background. Estimates ( $\beta$ ),  
819 standard errors (SE), and adjusted p-values (Bonferroni corrections) are reported. Statistical  
820 significance is also indicated (\*)  
821

Pairwise comparisons	Chromatic contrast $\Delta S_{\text{grass}}$			Achromatic contrast $\Delta L_{\text{grass}}$		
	$\beta$	SE	p	$\beta$	SE	p
OVS – Yellow throat	9.979	0.564	< 0.001 *	-1.157	0.640	0.367
OVS – White throat	6.324	0.404	< 0.001 *	-2.688	0.688	< 0.001 *
OVS – Orange throat	9.931	0.961	< 0.001 *	-1.220	0.638	0.307
OVS – Dorsum	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

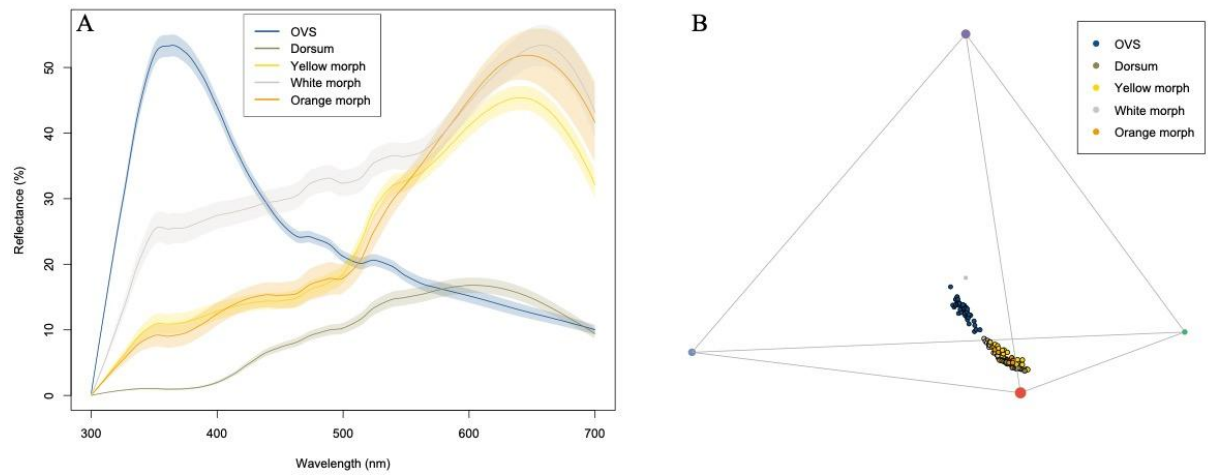
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826 Fig. 1

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



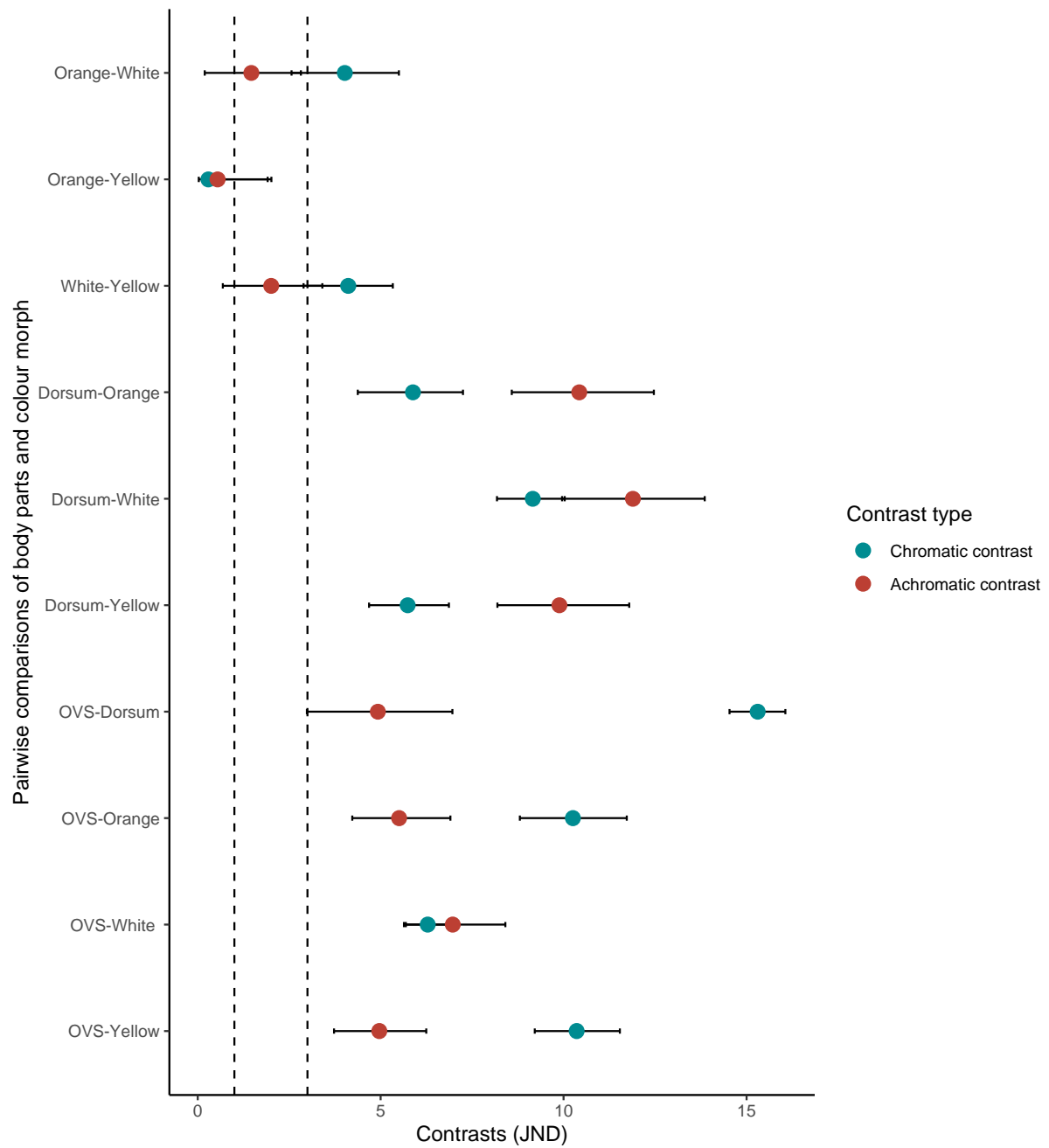
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832 Fig. 2

833 A- Mean spectra (plain curve) and their standard errors (shaded curve) of the UV-blue patches  
 834 on the outer-ventral scales (OVS; n = 48), the dorsal coloration (dorsum; n = 50), and the  
 835 three throat colours: white (n = 12), yellow (n = 30), orange (n = 8).

836 B- Representation of each individual spectrum from the different body parts of lizards  
 837 (dorsum, outer-ventral scales [OVS], and throat [white, yellow, orange]) in a tetrahedral  
 838 colour space built from a wall lizard visual system.

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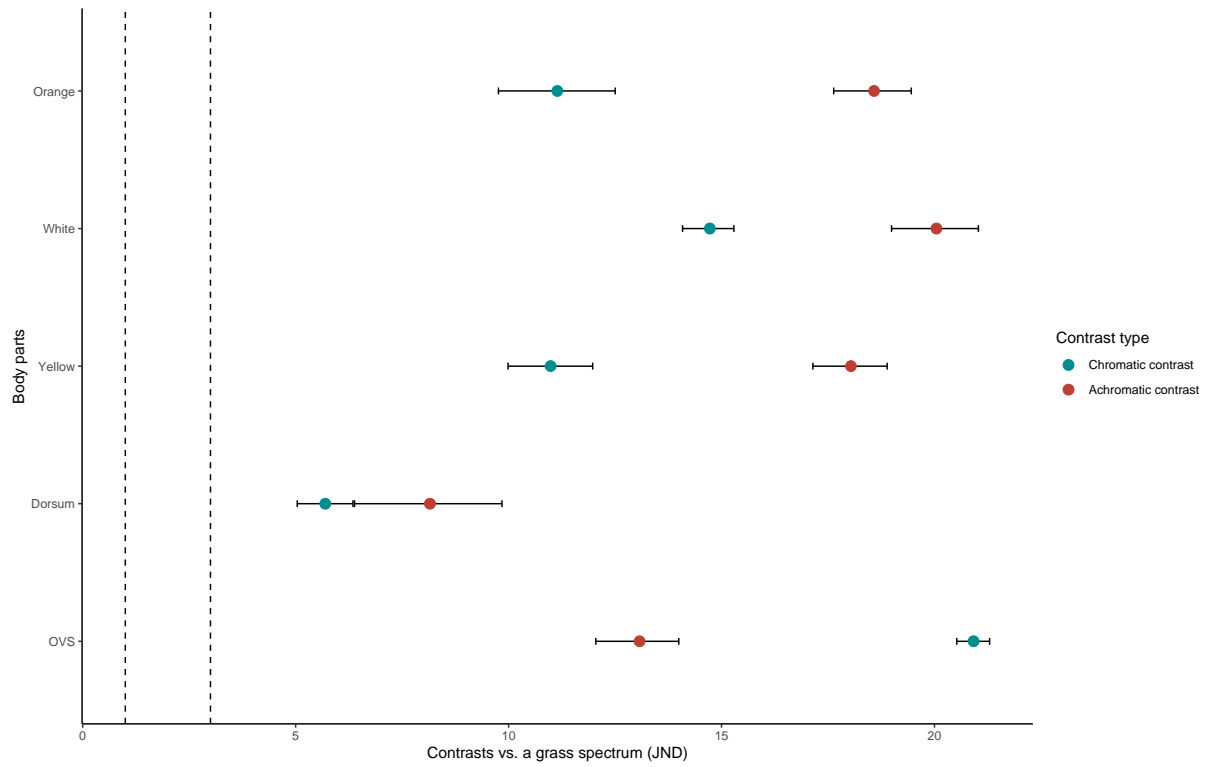


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841 Fig. 3

842 Mean and 95% confidence intervals of the chromatic and achromatic contrasts between the  
 843 coloration of each body part (dorsum, outer-ventral scales [OVS], and throat [white, yellow,  
 844 orange]) when viewed against a grass background. Two dashed lines at 1 and 3 JNDs  
 845 represent two discriminability thresholds. When the confidence intervals of a point include a  
 846 discriminability threshold, it means that the two colours are not distinguishable according to  
 847 this threshold.

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850 Fig. 4

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