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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*

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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 (ΔS) and achromatic (ΔL) 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 ΔS_{bkg} and ΔL_{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 ΔS_{bkg} and ΔL_{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 ± 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 β 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 ± 0.13 , $p = 0.074$; HLres: 0.33
325 ± 0.13 , $p = 0.017$), on the OVS (SVL: 0.29 ± 0.13 , $p = 0.038$; HLres: 0.28 ± 0.13 , $p = 0.038$),
326 and on the dorsum (SVL: 0.49 ± 0.12 , $p = 0.0001$; HLres: 0.27 ± 0.12 , $p = 0.031$). All error
327 terms associated with β 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 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 – 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 (ΔS_{bkg}) and achromatic (ΔL_{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 (β),
819 standard errors (SE), and adjusted p-values (Bonferroni corrections) are reported. Statistical
820 significance is also indicated (*)
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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 – 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

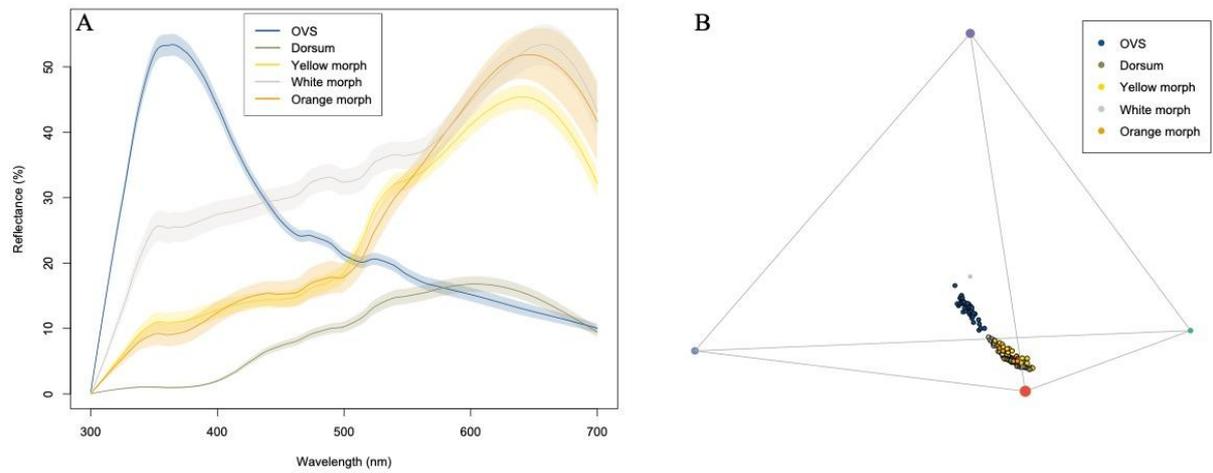
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826 Fig. 1

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.



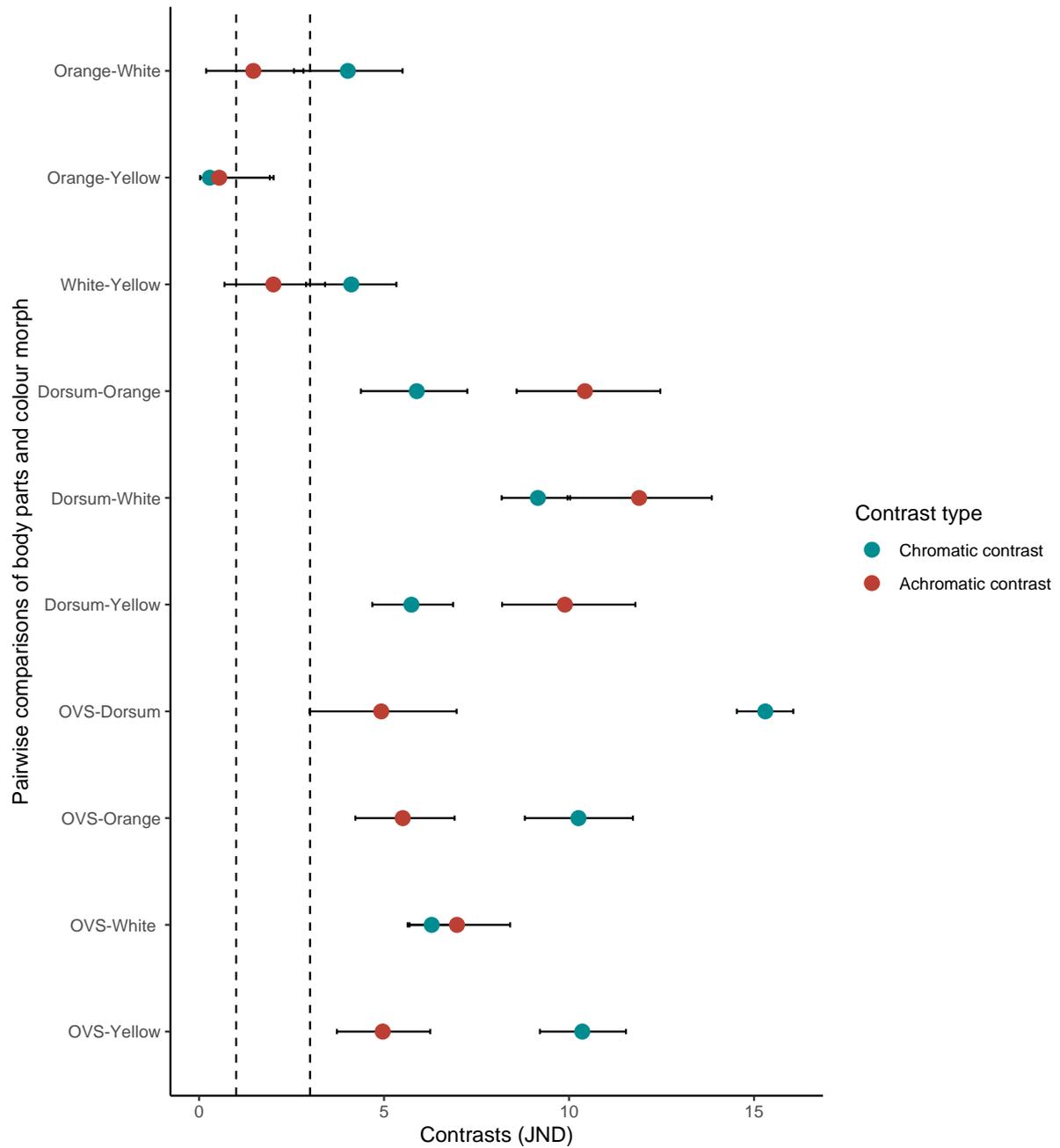
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832 Fig. 2

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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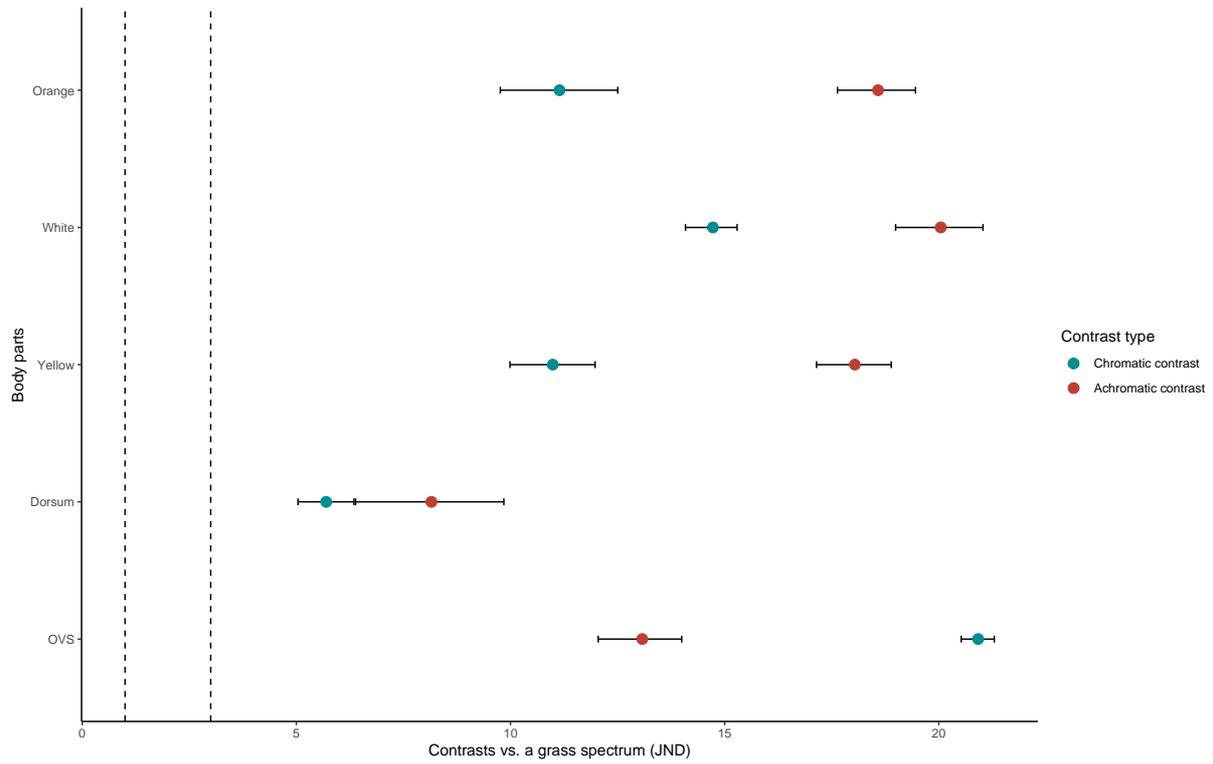


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841 Fig. 3

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.