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# Behavioral Ecology and Sociobiology

## The relative importance of body size and UV coloration in influencing male-male competition in a Lacertid lizard

--Manuscript Draft--

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| <b>Abstract:</b>                                     | <p>Communication via color signals is common in natural systems. Ultraviolet (UV)-blue patches located on the outer-ventral scales of some Lacertid lizards are thought to be involved in male-male competition. However, the mechanisms that maintain their honesty remain unknown. Here, we use the common wall lizard <i>Podarcis muralis</i> to test whether the lateral UV-blue spots are conventional signals, the honesty of which is guaranteed by receiver-dependent costs, and discuss their potential role as an amplifier of body size. We first described the morphology and reflectance properties of lateral UV-blue spots in common wall lizards and investigated how they influence male-male competition. Spot size and number, UV chroma, and conspicuousness (calculated using vision models) were significantly greater in adult males relative to adult females and adult males relative to juveniles. Total spot area (and not spot number) of adult males was positively correlated with body size. We conducted staged competition encounters between focal males and smaller or larger rivals with control or manipulated spots. Spots were enlarged in small rivals and reduced in large rivals to disrupt the phenotypic correlation between spot area and body size. Aggressiveness and dominance were positively influenced by body size in control encounters. Spot manipulations resulted in greater submission and less aggressiveness in focal males. These results contradict the predictions associated with conventional signals and amplifiers, but suggest that spots contributed to opponent evaluation during short-distance encounters between competing males.</p> |                |
| <b>Response to Reviewers:</b>                        | <p>Response to Editor-in-Chief's Comments</p> <p>COMMENTS FOR THE AUTHOR:<br/>Associate Editors comments:<br/>This paper has undergone several rounds of reviews. It has been reviewed by one expert over these successive versions who agrees that it has improved considerably.</p>   |                |

The authors have also adequately addressed that reviewers minor comments from the most recent round of reviews. I am satisfied that the MS is now suitable for publication in BES.

My comments:

see Word file corrected with track change. Please check the corrections, and if agree, accept them and resubmit a clean version.

Our response: We thank the Editor-in-Chief for their corrections. All changes were made and a clean version of the manuscript has been submitted.

line 192 AND 850 AND 854: Indicate the meaning of "SVL"

Our response: We thank the Editor-in-Chief for catching this. SVL has been specified at all of the above locations.

line 368 AND 825: Indicate the meaning of "jnds"

Our response: We thank the Editor-in-Chief for this correction. Jnds has been specified at all of the above locations.

- Acknowledgments: you may wish to thank the reviewers

Our response: We thank the Editor-in-Chief for their suggestion. We have now thanked the reviewers in our acknowledgements.

- Methods: It is required that authors state in the Methods section whether blinded methods were used in papers submitted for publication in Behavioral Ecology and Sociobiology, for example by stating "To minimize observer bias, blinded methods were use when all behavioral data were recorded and/or analyzed." or "It was not possible to record data blind because our study involved focal animals in the field."  
Our response: We thank the Editor-in-Chief for catching this and have now added that methods and analyses were conducted blind (lines 331-332).

- Ethical Approval: ethical approval from ethics committee for this study is not clearly mentioned in the manuscript. Please add here or state that this was not required  
Our response: We thank the Editor-in-Chief for this information and have now added that ethical approval from an ethics committee was not necessary for this study (line 643).

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*and*

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MA, 02215 USA

Dear Prs. Bakker and Traniello,

Thank you for allowing us to submit a new version of our manuscript entitled "The relative importance of body size and UV coloration in influencing male-male competition in a Lacertid lizard" for publication in *Behavioral Ecology and Sociobiology*. We have made all minor corrections provided by Editor-in-Chief Bakker. We would like to thank the Editor-in-Chief for their corrections, and we hope that they will be satisfied by this new revision. As requested, we have uploaded a clean version of the manuscript and the ESM, as well as a document detailing the changes made in this round of revisions.

Our work has not been presented to any scientific meeting and is not under consideration by any other journal. All authors agreed to the submission of this original work and they declare that there are no conflicts of interest.

We look forward to your response.

In the name of all authors,  
Best regards,

Gabrielle Names

## Response to Editor-in-Chief's Comments

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1 **The relative importance of body size and UV coloration in influencing male-male**  
2 **competition in a Lacertid lizard**

3

4 Gabrielle Names<sup>a,b\*</sup>, Mélissa Martin<sup>a</sup>, Arnaud Badiane<sup>a</sup> and Jean-François Le Galliard<sup>a,b</sup>

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16 quality of the manuscript.

17

18 **ABSTRACT**

19 Communication via color signals is common in natural systems. Ultraviolet (UV)-blue patches  
20 located on the outer-ventral scales of some Lacertid lizards are thought to be involved in male-  
21 male competition. However, the mechanisms that maintain their honesty remain unknown. Here,  
22 we use the common wall lizard *Podarcis muralis* to test whether the lateral UV-blue spots are  
23 conventional signals, the honesty of which is guaranteed by receiver-dependent costs, and  
24 discuss their potential role as an amplifier of body size. We first described the morphology and  
25 reflectance properties of lateral UV-blue spots in common wall lizards and investigated how they  
26 influence male-male competition. Spot size and number, UV chroma, and conspicuousness  
27 (calculated using vision models) were significantly greater in adult males relative to adult  
28 females and adult males relative to juveniles. Total spot area (and not spot number) of adult  
29 males was positively correlated with body size. We conducted staged competition encounters  
30 between focal males and smaller or larger rivals with control or manipulated spots. Spots were  
31 enlarged in small rivals and reduced in large rivals to disrupt the phenotypic correlation between  
32 spot area and body size. Aggressiveness and dominance were positively influenced by body size  
33 in control encounters. Spot manipulations resulted in greater submission and less aggressiveness  
34 in focal males. These results contradict the predictions associated with conventional signals and  
35 amplifiers, but suggest that spots contributed to opponent evaluation during short-distance  
36 encounters between competing males.

37

38 **KEYWORDS:** Intrasexual competition, *Podarcis muralis*, UV coloration, Territorial conflict

39

40 **SIGNIFICANCE STATEMENT**

41 Many animals use color to communicate. During intraspecific resource competition, some  
42 species use color signals as an assessment tool to determine if they should engage in or avoid  
43 conflicts. Studies have found that in non-mammalian vertebrates, UV coloration can be a good  
44 indicator of fighting ability or aggressiveness. We tested whether and how the UV-blue spots of  
45 common wall lizards play a role in male-male competition by studying the properties of their  
46 spots, and then used that information to design and conduct competition experiments between  
47 males involving spot manipulation. Both body size and spot manipulation influenced aggression  
48 and submission during encounters. In particular, results suggest that spot manipulation disrupted  
49 mutual assessment and thus that spots play a role in competition signaling in male common wall  
50 lizards.

51

## 52 **INTRODUCTION**

53 Animals use conspicuous color patterns as signals in a variety of social interactions ranging from  
54 mate choice to competition, and these signals often convey information about individual quality  
55 (Bennett et al. 1994; Etman et al. 2001; Candolin 2003; Doucet and Montgomerie 2003;  
56 Seehausen and Schluter 2004; Searcy and Nowicki 2005; Pryke and Griffith 2007). Resource  
57 competition often involves signals that are honest indicators of the signaler's tendency or ability  
58 to fight (Rohwer 1975; Maynard Smith and Harper 2003). Several mechanisms have been  
59 proposed that guarantee signal honesty when interests of signalers and receivers oppose (e.g.,  
60 resource competition). Signal honesty can be maintained by an incorruptible, inherent  
61 relationship between signal and quality (i.e. low-cost indices) or by differential costs (or  
62 benefits) associated with signal expression that are conditional on the signaler's quality (i.e.  
63 strategic costs, Zahavi 1975; Dawkins and Guilford 1991; Searcy and Nowicki 2005; Bradbury



64 and Vehrencamp 2011). These costs may be directly related to the production and maintenance  
65 of signals (i.e. handicap signals, Searcy and Nowicki 2005) or behaviorally imposed by  
66 conspecifics based on an arbitrary convention (i.e. conventional signals, Guilford and Dawkins  
67 1995; Johnstone 1998; Candolin 2000; Vehrencamp 2000). Conventional signals, such as  
68 “badges of status” in birds, are cheap to produce but their honesty is maintained by social costs  
69 imposed by receivers that penalize signalers displaying a signaling level that does not match their  
70 fighting capacity or individual quality (Senar 1999; Searcy and Nowicki 2005; Ligon and  
71 McGraw 2016). In addition to indices and costly signals, Hasson suggests the evolution of  
72 amplifiers as yet another route to signal honesty (Hasson 1989, 1990, 1991). Amplifiers are low-  
73 cost signals that do not directly inform on the signaler’s quality, but act as a “standard” against  
74 which other signals or cues are evaluated (Castellano and Cermelli 2010). By improving the  
75 detection of signals or cues by intended receivers, amplifiers impose differential efficacy-related  
76 benefits on signalers rather than differential strategic costs (Hasson 1997; Heberts 2004; Harper  
77 2006).

78         In recent years, studies have shown that ultraviolet (UV) coloration in non-mammalian  
79 vertebrates is widespread (Whiting et al. 2006; Roberts et al. 2009; Siebeck et al. 2010) and that  
80 many of these species have UV-sensitive vision systems (Bennett et al. 1994; Carleton et al.  
81 2000; Smith et al. 2002; Pérez i de Lanuza and Font 2014). Mounting evidence suggests that UV  
82 coloration can act as an honest signal of male aggressiveness or fighting ability in birds, fishes  
83 and reptiles (Keyser and Hill 2000; Siebeck 2004; Siefferman and Hill 2005; Pryke and Griffith  
84 2006; Stapley and Whiting 2006; Whiting et al. 2006; Rick and Bakker 2008; Rémy et al. 2010;  
85 Bajer et al. 2011; Martin et al. 2015b; Martin et al. 2016). For example, in the Augrabies flat  
86 lizard *Platysaurus broadleyi*, UV throat color is an honest predictor of fighting ability (Whiting

87 et al. 2006), and in the European green lizard *Lacerta viridis*, UV-blue nuptial coloration in  
88 males signals dominance (Bajer et al. 2011). UV signals have also been shown to co-vary with  
89 male phenotypic quality (e.g., Doucet and Montgomerie 2003) and their expression can be  
90 constrained in stressful environments (e.g., McGraw et al. 2002; Bajer et al. 2012). Although  
91 debated, it has also been suggested that UV signal expression may be subject to developmental  
92 costs due to the structural coloration production mechanisms (Keyser and Hill 2000; Siitari et al.  
93 2007; Vedder et al. 2010). Other types of costs, such as receiver-dependent costs (e.g., social  
94 costs) associated with conventional signals, could also maintain the honesty of UV signals  
95 (Searcy and Nowicki 2005), but empirical evidence is lacking.

96         Alternatively, a growing body of literature suggests that color signals could convey  
97 information as part of a multicomponent signaling mechanism (Grether et al. 2004). During  
98 male-male competition, signaling displays often involve multiple sensory modalities and convey  
99 pieces of information from various parts of the body (Rowe 1999; Hebets and Papaj 2005). For  
100 example, the dewlap extension signal in male anole lizards (used to signal bite force,  
101 Vanhooydonck et al. 2005) is enhanced by the dewlap's coloration (Fleishman et al. 1993;  
102 Fleishman 2000), and Ord et al. (2015) suggested that the dewlap's morphology and coloration  
103 evolved to amplify the detection of head bobbing behavior. In this context, UV patches could  
104 function as amplifiers (Bogaardt and Johnstone ; Hasson 1989) by facilitating the detection or  
105 discrimination of other signals or cues, such as body size, behavioral displays, or other attributes  
106 from the same or adjacent color patches (Fitzpatrick 1998; Taylor et al. 2000; Grether et al.  
107 2004). UV color patches, in particular, are often located along body parts such as necks, mouth  
108 corners, and flanks, which makes them good candidates as amplifiers of other quality signals or  
109 cues (e.g., Lappin et al. 2006). For example, the male collared lizard *Crotaphytus collaris* has

110 white and UV reflective mouth corners that function as amplifiers during gaping displays by  
111 drawing attention to the jaw muscles, which inform on physical strength (Lappin et al. 2006).  
112 However, to our knowledge, the amplifier hypothesis has not been experimentally tested on UV  
113 coloration displays.

114         Due to their distinctive lateral UV-blue patches (hereafter referred to as "UV-blue spots",  
115 Pérez i de Lanuza et al. 2014), some lacertid lizards are good model systems to investigate  
116 alternative mechanisms of honest signaling, such as conventional signals or amplifiers. In several  
117 species, the UV-blue spots (located on the outer-ventral scales of the flanks) are highly sexually  
118 dimorphic and dichromatic. Although females of some species display faint spots, which appear  
119 blue to the human eye, males alone display UV-blue spots with a marked reflectance peak in the  
120 UV range, which is highly conspicuous (Pérez i de Lanuza and Font 2014, 2015; Martin et al.  
121 2015a). Several lines of evidence suggest that UV-blue spots may serve in male-male resource  
122 competition, but the information content of these traits and the mechanisms responsible for their  
123 evolution are contested. First, although the strategic costs associated with these spots remain  
124 unknown, their presence both during and outside the breeding season suggests they respond to  
125 both natural and sexual selection (Martin et al. 2015b). Second, studies of spot condition-  
126 dependence and status signaling have produced contradictory results regarding inter-individual  
127 variation in spot number, size and UV reflectance. López et al. (2004) and Cabido et al. (2009)  
128 found that spot number correlated with body size and condition in the Iberian rock lizard  
129 *Iberolacerta monticola*. Pérez i de Lanuza et al. (2014), however, demonstrated that the UV  
130 chroma of the second rostral-most spot correlated with body condition in the common wall lizard  
131 *Podarcis muralis*. In addition, while López et al. (2004) found a relationship between spot  
132 presence (vs. absence) and aggressiveness in *I. monticola*, Pérez i de Lanuza et al. (2014)

133 emphasized the importance of UV hue in signaling combat ability in *P. muralis*. Then, Martin et  
134 al. (2015b) found that *P. muralis* spots play a role in opponents' mutual assessment of fighting  
135 ability. Also along these lines, some studies have found a relationship between spot number and  
136 body size (López et al. 2004; Martin et al. 2015b), thus raising the possibility that spot number  
137 may be an amplifier of body size, found to correlate with male fighting ability in *I. monticola*  
138 (López et al. 2002) and *P. muralis* (Edsman 1990; Sacchi et al. 2009). However, a manipulative  
139 study of the blue (but not UV) coloration of *I. monticola*, in which some spots were masked,  
140 failed to validate this hypothesis (López et al. 2004).

141         The above results suggest that UV-blue spots are involved in *P. muralis* signaling but that  
142 their effects may be subtle and/or depend on multiple features of the spots themselves or other  
143 qualities of the signaler (i.e. body size). *P. muralis* males display UV-blue spots, which run along  
144 a large portion of the flanks, and body size is a predictor of *P. muralis* aggressiveness and  
145 fighting ability (Edsman 1990; Sacchi et al. 2009). However, the relative roles of body size and  
146 UV reflectance in male-male competition are unknown. The aims of our study were to 1)  
147 investigate multiple color and morphological properties of the UV-blue spots, 2) experimentally  
148 examine whether the honesty of these UV-blue spots is maintained by social costs characteristic  
149 of conventional signals, and 3) explore their potential role as amplifiers of body size. We  
150 designed behavioral assays consisting of dyadic encounters between non-manipulated focal  
151 males and differently sized opponents (2-4 mm larger or smaller than the focal) with UV-blue  
152 spots that were or were not UV-enhanced/reduced (hereafter “manipulated” or “control”  
153 opponents, respectively). We manipulated the UV-blue spots to create an asymmetry between  
154 UV-blue spot area and body size, so as to obtain bluffers (small males with enlarged spots) and  
155 Trojans (large males with reduced spots). If spot area functions as a conventional signal, we

156 would predict that deceptive males would pay a cost for being dishonest in the form of increased  
157 aggression from focal males (Ligon and McGraw 2016). Therefore, we expected deceptive males  
158 to produce fewer displays of aggression and greater displays of submission compared to their  
159 respective controls. If, however, spot area acts as an amplifier of body size, we predicted that  
160 conflicting body size and spot area traits would cause rival assessment to take longer or not be  
161 possible by visual assessment alone, thus resulting in an increase in physical assessment via  
162 aggression and fighting by both focals and opponents.

## 163 **MATERIALS AND METHODS**

### 164 **Study species**

165 The common wall lizard *P. muralis* is a small (snout-vent length, SVL, 48-67 mm), oviparous,  
166 polyandrous lacertid lizard widely distributed in semi-open habitats in Europe (Speybroeck et al.  
167 2016). Adult males are territorial during reproduction; large males are more aggressive and  
168 defend large territories, while smaller males are less aggressive and defend small territories  
169 (Edsman 1990). *P. muralis* is characterized by a conspicuous, discrete belly color polymorphism  
170 (Speybroeck et al. 2016; Andrade et al. 2019). In the study area, males have white, orange, or  
171 yellow bellies and females have white or yellow bellies (though yellow is rare in both sexes, J-F  
172 Le Galliard personal observation; Sacchi et al. 2009; Galeotti et al. 2010). In this study sample,  
173 we captured no individuals with yellow bellies. Lateral UV-blue spots, which appear blue to the  
174 human viewer and span a large portion of the flank (see Fig. S2), are displayed by a majority of  
175 individuals, although previous analyses showed that spots are sexually dimorphic (reduced or  
176 absent in females) and sexually dichromatic (UV-reduced in females, Vacher and Geniez 2010;  
177 Pérez i de Lanuza et al. 2014; Martin et al. 2015a).

### 178 **Sampling and measurements**

179 Our study was conducted on a wild population of *P. muralis* located in central France (CEREEP-  
180 Ecotron IleDeFrance, France, 60 m a.s.l., 48°17'N, 2°41'E). All procedures complied with laws  
181 on animal experimentation and animal care in France and Europe (permit Ce5/2011/044).  
182 Lizards were captured by noosing during the breeding season in the second week of March of  
183 2014. In total, 15 juvenile (4 male, 4 female, 7 unidentified sex) and 60 adult (37 male, 23  
184 female) lizards were captured. Age class was identified by size (adults > 55mm), and sex by  
185 presence of femoral pores (visible to the naked eye) and the hemipene caudal bulges in the  
186 proximate tail. Immediately following capture, we used a spectrometer (Jaz Series, JAZ-ULM-  
187 200; Ocean Optics Inc., Dunedin, FL, USA) to obtain ambient irradiance profiles of light at the  
188 capture locations, for use in models of the lizard vision system. Individuals were taken to the lab  
189 to measure body size (snout-vent length [SVL] and total length,  $\pm 1$  mm) and body mass ( $\pm 1$  mg).  
190 Spots were counted and their surface area measured ( $\pm 0.001$  mm<sup>2</sup>) in ImageJ (Schneider et al.  
191 2012) using digital scans of lizard flanks (3.8 megapixels, produced using CanoScan LiDE  
192 700F). To produce scans, lizard flanks were pressed securely but gently against the scanner,  
193 situated just below a grid (1x1 mm) to scale. Then, two ventral scales of each individual were  
194 marked using a non-invasive heat-branding method to allow for individual identification during  
195 behavioral experiments (Vervust and Van Damme 2009).

196 Spectral reflectance of all UV-blue spots of all individuals was measured using a USB-  
197 2000 spectrophotometer, a HL 2000 (Halogen-Deuterium) light source, and a 400- $\mu$ m R400-7-  
198 UV/VIS fiber optic probe (all products of Ocean Optics Inc., Dunedin, FL, USA). Spots smaller  
199 than the size of the reflectance detector (< 2 mm) were not measured (N = 519 out of 1159) to  
200 avoid spectral contamination (Badiane et al. 2017). Reflectance spectra were analyzed using  
201 Avicol software version 6, which linearly interpolates spectra with one value per nm (Gomez

202 2006). For each spectrum, we quantified intensity ( $R_{300-700}$ ), UV chroma ( $R_{300-400}/R_{300-700}$ ), and  
203 UV hue (wavelength of the maximal reflectance in the UV range 300-400 nm). UV hue was not  
204 calculated when there was no UV reflectance peak, i.e. when the spectrum sloped up or down  
205 from 300 to 400 nm ( $N = 93$  out of 640). We also calculated a mean spot reflectance spectrum  
206 for each individual. To determine extrinsic conspicuousness of spots, one to two flank scales  
207 dorsal to the UV-blue spots per lizard were measured to calculate a mean flank spectrum, which  
208 was used to simplify analyses. Then, to determine extrinsic conspicuousness, eight habitat  
209 background objects commonly found at capture sites (3 rocks, 2 bricks, 1 patch of grass, 1 tree  
210 branch and 1 piece of plywood) were each measured (4-6 times) and the mean reflectance  
211 spectrum for each object was calculated.

## 212 **Color vision model**

213 *P. muralis* is a typical diurnal lizard species with tetrachromatic color vision based on a single-  
214 cone system that includes UV, short wavelength, medium wavelength, and long wavelength  
215 sensitive photoreceptors (Martin et al. 2015a). To model the ability of wall lizards to  
216 discriminate colors of conspecifics, we ran the Vorobyev and Osorio (1998) color opponent  
217 vision model in Avicol (Gomez 2006), parameterized with data on eye physiology and anatomy  
218 obtained from Martin et al. (2015a). This model assumes a receptor noise-limited color opponent  
219 discrimination mechanism and requires data on receptor spectral sensitivities, receptor  
220 abundance, and noise levels in the photoreceptors (e.g., see Vorobyev and Osorio 1998; Siddiqi  
221 et al. 2004 for applications). The model calculates relative quantum catch by each photoreceptor  
222 type given incident light entering the eye and the spectral sensitivity of the receptor (including  
223 lens, ocular media and oil droplet absorption, and visual pigment absorbance of single cones),  
224 which is then used to place color objects into a tetrahedral color space and to calculate a

225 perceptual distance ( $\Delta S$ ) in the chromaticity diagram (Goldsmith 1990; Stoddard and Prum  
226 2008).  $\Delta S$  between two color objects was calculated following the Vorobyev and Osorio (1998)  
227 model and expressed in units of multiples of just noticeable differences (jnd). Values of  $\Delta S$   
228 below 1 indicate that colors are inconspicuous. Receptor spectral sensitivities and receptor  
229 abundance were obtained from previous data on single cones (Martin et al. 2015a), and  
230 photoreceptor noise was assumed independent of light. Incident light was calculated by  
231 averaging ambient irradiance profiles taken during lizard captures (parameterization details in  
232 Appendix S1). We used the model to calculate  $\Delta S$  of pairwise comparisons between spots vs.  
233 habitat objects, spots vs. the mean flank spectrum, and the mean flank spectra vs. habitat objects.  
234 This approach is similar to that used in Pérez i de Lanuza and Font (2015), but we found it  
235 important to conduct these analyses in our study population before proceeding to behavioral  
236 assays. Males had a greater number of UV-blue spots than adult females and juveniles, which  
237 accounts for the difference in UV-blue spot sample sizes of the groups.

### 238 **Color manipulation and behavioral assays**

239 Following measurements, 35 adult males were housed individually in opaque terraria  
240 (25x15.5x15 cm). Lizards were housed for a total of 15 days, which included a 4-day acclimation  
241 period and an 11-day experimental period. Animal care was performed by authorized personnel  
242 under permit DTTP-2008-449 issued to JFLG. Each terrarium contained a thick layer of soil  
243 bedding, a shelter, and a water dish. Heat and light were provided by a combination of halogen  
244 and UV lamps set to a 10:14-h light-dark regime, resulting in an ambient temperature ranging  
245 from 15 to 23°C during the dark and light periods, respectively. Lizards were fed 300-400 mg of  
246 crickets every other day and water was available *ad libitum*.



247 Behavioral assays were performed in a temperature-controlled room in neutral arenas, to  
248 eliminate the effect of residence advantage (López and Martín 2001; Kokko et al. 2006; Martin  
249 et al. 2016) and to focus on the effects of spots and body size on male-male competition. Arenas  
250 were composed of large opaque terraria (45×29×22 cm) containing a layer of white sand and  
251 divided by opaque plastic into two equally sized small compartments (17×14.5 cm) and one large  
252 compartment (28×29 cm). The small compartments served as solitary holding areas, which  
253 allowed lizards to acclimate to the new conditions. Two UVB neon tube lights (Reptisun 10.0)  
254 and one Exo Terra Solar-Glo lamp were suspended above the arena to provide UV-white light  
255 (producing an irradiance profile that included substantial UV irradiance and resembled natural  
256 lighting) and heat. The latter was positioned 20 cm directly over a 4×9 cm black PVC basking  
257 plate, placed on the sand in the large compartment, to which lizards competed for access.

258 Dyadic encounters occurred between a non-manipulated focal male and an opponent  
259 male 2 to 4 mm larger or smaller than the focal (opponent lizard size range = 59-71 mm, mean  
260 size difference with focal =  $3.20 \text{ mm} \pm 0.89 \text{ SD}$ ). Opponents were either a control or had  
261 manipulated spots. For the latter, spots were enlarged in smaller opponents (i.e. bluffers) or  
262 reduced in larger opponents (i.e. Trojans) based on a regression of spot area against SVL  
263 regression ( $0.8 \text{ mm}^2/\text{mm SVL}$ , see below). The modified spot area was calculated by multiplying  
264  $0.8 \text{ mm}^2$  by twice the difference in size of the focal and opponent in order to exaggerate the spot  
265 area-SVL mismatch. Half of the total modified area was applied to each flank. Spot size of  
266 opponents was altered by applying a UV-reducing cream (UV-) or UV-enhancing marker (UV+)  
267 to add or subtract area from opponent spots. The UV- cream consisted of two inorganic agents  
268 (zinc oxide and titan dioxide) mixed with two fats (petroleum jelly and liquid paraffin) at a ratio  
269 of 6:4:50:40 per 100 g, a combination that successfully masked UV reflectance in Martin et al.

270 (2015b). The UV+ marker was a light blue Edding 4500 T-shirt marker pen (color code 0.10),  
271 previously used to enhance UV coloration in blue tits (Johnsen et al. 2005; Kurvers et al. 2010;  
272 Rémy et al. 2010) and shown here to likely enhance UV coloration in *P. muralis* (see Fig. S3).  
273 When placed firmly on a surface at a perpendicular angle, the marker tip produced a circle of  
274 approximately 0.5 mm diameter (area 0.8 mm<sup>2</sup>). As area to be added was in multiples of 0.8 mm<sup>2</sup>  
275 (see above), we calculated the number of spots necessary for the area manipulation and added  
276 that number of spots using firm application of the marker tip. Spots were added posterior to the  
277 lizard's middle spot (uneven number of spots) or to the anterior of the middle spots (even  
278 number of spots). Following marker application, we added a fat layer of petroleum jelly and  
279 liquid paraffin (55.6:44.4 per 100g), with no effect on UV reflectance (see Fig. 2a of Martin et al.  
280 2015b), to prevent marker rub off. Control individuals were given a fat layer treatment only. The  
281 UV- cream and fat layer were applied with the thin end of a forceps. At the end of each trial, UV  
282 reducing cream, fat, and marker treatments were removed through the gentle application of  
283 diluted ethanol.

284 Out of the 35 males, 22 focal males and 13 opponent males were chosen based on size to  
285 ensure the 2 to 4 mm difference in size between focal and opponent males. Each focal male  
286 participated in a total of 4 encounters, each involving a different, randomly chosen opponent of  
287 the following types: (1) control and SVL 2-4 mm longer than focal; (2) control and SVL 2-4 mm  
288 shorter than focal; (3) manipulated (UV- spot area) and SVL 2-4 mm longer than focal; (4)  
289 manipulated (UV+ spot area) and SVL 2-4 mm shorter than focal. Each opponent male  
290 participated in no more than 8 encounters. We chose novel opponents for each test to avoid  
291 familiarity among males, which has been found to significantly influence male aggressiveness in

292 *P. muralis* (Martin et al. 2016). Encounters were spaced out by at least 1.5 days to avoid fatigue,  
293 and the order of the encounters (1-4 above) was randomized.

294 Before each experiment, individuals were removed from their home terraria, spot  
295 treatments were applied, and each male was placed in one of the two holding compartments.  
296 After a 10-min acclimation period, the experiment began with the removal of the opaque walls.  
297 One of two observers was randomly chosen to observe encounters from behind a one-way mirror  
298 for a period of 10 min. Using Jwatcher (Blumstein and Daniel 2007), we recorded the number of  
299 agonistic behaviors in real-time and the number and total time of non-agonistic behaviors and  
300 total time wall scratching using played-back video recordings. Video was recorded in black and  
301 white using a Nikon D70 digital camera positioned 30 cm directly above the arena. Behaviors are  
302 summarized in Table 1 below (modified from Martin et al. 2016). Observers were trained to  
303 interrupt experiments if fighting escalated to the point that it could compromise the welfare of  
304 the individuals but we observed no repeated biting or other tactile aggression events, or other  
305 serious distress signs, during the 88 trials. At the end of experimentation, lizards were  
306 individually released to their respective capture sites. To minimize observer bias, all behavioral  
307 data were recorded and analyzed blind.

### 308 **Statistical analyses**

309 We used R version 3.1.2 (R Core Team 2014) for all statistical analyses and Figs. To determine  
310 differences in spot and flank conspicuousness and spot coloration (intensity, hue, and UV  
311 chroma) of adult males, adult females, and juveniles, we used linear mixed-effects models  
312 (LMEs) with a “group” variable (three levels: adult males, adult females, and juveniles) as the  
313 fixed effect and individual identity as a random effect (multiple spots or flank scales measured  
314 per lizard). To account for heteroscedasticity in our “group” variable, we used the weights

315 argument in our models to allow variance of the residuals to differ among group levels.  
316 Residuals were tested for normality and intensity was log-transformed, hue and UV chroma were  
317 rank-transformed, and chromatic contrast of flank and habitat objects was square root-  
318 transformed. We performed *post hoc* Tukey's test to conduct pairwise comparisons of groups.  
319 We also calculated variance components for spot intensity, hue (for males only), and UV chroma  
320 to determine intra- and inter-individual variation for males and females.

321 We investigated the effect of sex and age on spot morphology, including total spot area,  
322 total spot number, area of largest left flank spot, and area of largest right flank spot, using linear  
323 models (LMs). Prior evidence suggests that these spot features may be indicators of male  
324 behavior and/or dominance (López et al. 2004; Cabido et al. 2009; Pérez i de Lanuza et al. 2014;  
325 Martin et al. 2015b). Using adult male data only, we then tested for an effect of belly color  
326 morph and SVL on total spot area, total number of spots, largest left flank spot area, largest right  
327 flank spot area, and mean spot UV chroma to identify spot properties that could be good  
328 conventional signals or amplifiers of body size. We applied the Benjamini-Hochberg correction  
329 to account for the testing of multiple spot characteristics (see Table S2). Residuals were tested  
330 for normality and total spot number was log-transformed while largest left and right spots were  
331 transformed using the square root function.

332 Analysis of behavioral experiment data began by summing total counts and total time data  
333 for each male in each experiment. This information was used to calculate aggression score,  
334 submission score, and dominance score for each male in each experiment (see Table 1), as in  
335 Martin et al. (2016). We began with an analysis of control social interactions to validate previous  
336 findings regarding the effect of body size and color (belly morph and spots) on male competitive  
337 behavior (López and Martín 2001; Martin et al. 2015b). Using LMEs, we tested the additive

338 effect of SVL, belly color morph, opponent size difference, and total spot area (the most likely  
339 amplifier of SVL based on spot and morphology analyses) on time basking, time wall scratching,  
340 aggression score, submission score, and dominance score. Random effects included lizard  
341 identity and assay pair number. To determine the effect of body size and spots on behavior, we  
342 conducted a second set of analyses using only data from focal males, since manipulated  
343 opponents were not aware of manipulations to their spots and could therefore not respond to  
344 those manipulations. We tested the effect of SVL, opponent size difference (smaller or larger  
345 SVL) and color manipulation (control or manipulated) as well as the two-way interaction of the  
346 latter on focal male time basking, time wall scratching, aggression score, submission score, and  
347 dominance score. The Benjamini-Hochberg correction was used to account for the testing of  
348 multiple behaviors and scores (see Table S3). All behavioral data were analyzed with LMEs, and  
349 Satterhwaite approximations of degrees of freedom were used for control analyses. In addition to  
350 the fixed effects listed above, all models included experiment observer (2 persons), lizard  
351 sequence number (lizards were used 4 to 8 times, categorical factor), and experiment time of day  
352 (morning or afternoon) in order to control for variables related to experimental logistics. To  
353 control for the specific experimental trial, analyses of control interactions data also included  
354 experimental trial number. Prior to behavioral analyses, residuals were tested for normality, and  
355 dominance score was rank transformed. For all analyses, we began with the full model including  
356 all effects and chose the best model using stepwise model selection by AIC. Results are reported  
357 as mean  $\pm$  SE unless otherwise stated.

### 358 **Data availability**

359 The datasets generated and analyzed during the current study are available from the  
360 corresponding author on reasonable request.

## 361 **RESULTS**

### 362 **Color conspicuousness**

363 Perceptual distances between flank and habitat object colors had a mean of  $6.67 \pm 0.15$  jnds (just  
364 noticeable differences) with 2.5% of distances inferior to 1 jnd. There was no significant  
365 difference in the chromatic contrast of habitat objects against flanks of adult males and adult  
366 females ( $p = 0.92$ ,  $\beta_{\text{adult male vs. adult female}} = 0.040 \pm 0.10$ ), adult males and juveniles ( $p = 0.16$ ,  $\beta_{\text{adult$   
367  $\text{male vs. juvenile}} = -0.23 \pm 0.13$ ), or juveniles and adult females ( $p = 0.12$ ,  $\beta_{\text{juvenile vs. adult female}} = 0.27 \pm$   
368  $0.14$ ; Table 2). Then, chromatic contrast of UV-blue spots against habitat objects had a mean of  
369  $22.79 \pm 0.14$  jnds with 0.23% of distances inferior to 1 jnd, and chromatic contrast of UV-blue  
370 spots against the mean flank had a mean of  $22.18 \pm 0.36$  jnds with 0.15% of distances inferior to  
371 1 jnd. In both cases, the chromatic contrast of adult male spots was significantly greater than that  
372 of adult female spots (spot and habitat:  $p < 0.001$ ,  $\beta_{\text{adult male vs. adult female}} = 14.62 \pm 1.43$ ; spot and  
373 flank:  $p < 0.001$ ,  $\beta_{\text{adult male vs. adult female}} = 15.00 \pm 1.49$ ) and juvenile spots (spot and habitat:  $p <$   
374  $0.001$ ,  $\beta_{\text{adult male vs. juvenile}} = 7.08 \pm 1.89$ ; spot and flank:  $p < 0.001$ ,  $\beta_{\text{adult male vs. juvenile}} = 7.15 \pm 1.96$ ),  
375 and the chromatic contrast of juvenile spots was significantly greater than that of adult female  
376 spots (spot and habitat:  $p < 0.001$ ,  $\beta_{\text{juvenile vs. adult female}} = 7.55 \pm 2.02$ ; spot and flank:  $p < 0.001$ ,  
377  $\beta_{\text{juvenile vs. adult female}} = 7.85 \pm 2.11$ ; Table 2). Histograms of perceptual distances can be found in  
378 Fig. S1.

### 379 **Age and sex differences in spot coloration**

380 First, we found that blue spots of adult males had significantly higher UV chroma compared to  
381 those of adult females ( $p < 0.001$ ,  $\beta_{\text{adult male vs. adult female}} = 268.22 \pm 29.87$ , see Fig. 1) and juveniles  
382 ( $p < 0.001$ ,  $\beta_{\text{adult male vs. juvenile}} = 153.61 \pm 38.34$ ), and the UV chroma of juvenile spots was  
383 significantly higher than that of adult female spots ( $p = 0.015$ ,  $\beta_{\text{juvenile vs. adult female}} = 114.61 \pm$

384 41.35). Then, we found that adult female spots had significantly higher hue compared to those of  
385 adult males ( $p < 0.0001$ ,  $\beta_{\text{adult female vs. adult male}} = 278.79 \pm 31.43$ ) and juveniles ( $p = 0.0001$ ,  $\beta_{\text{adult$   
386  $\text{female vs. juvenile}} = 206.06 \pm 45.64$ ), but adult male and juvenile spots did not differ in hue ( $p = 0.20$ ,  
387  $\beta_{\text{adult male vs. juvenile}} = -72.73 \pm 42.74$ ). We also found no significant differences in spot intensity for  
388 adult males and adult females ( $p = 0.98$ ,  $\beta_{\text{adult male vs. adult female}} = -0.010 \pm 0.051$ ), adult males and  
389 juveniles ( $p = 0.073$ ,  $\beta_{\text{adult male vs. juvenile}} = 0.14 \pm 0.063$ ), or juveniles and adult females ( $p = 0.091$ ,  
390  $\beta_{\text{juvenile vs. adult female}} = -0.15 \pm 0.070$ ). Finally, males showed greater inter-individual variation in  
391 terms of spot intensity and UV chroma compared to females (Table S1).

### 392 **Size scaling of spot characteristics**

393 Our results revealed that total spot area, total number of spots, largest left flank spot area, and  
394 largest right flank spot area were all significantly greater in males compared to females as well as  
395 in adults compared to juveniles with the exception of total number of spots (see Table 3). The  
396 difference in mean total spot area was especially striking, with mean spot area more than twice  
397 as large in males compared to females (males:  $2.0 \text{ mm}^2 \pm 0.15$ , females:  $0.73 \text{ mm}^2 \pm 0.097$ ,  $\beta_{\text{males$   
398  $\text{vs. females}} = 0.18 \pm 0.026$ ), and more than twice as large in adults as compared to juveniles (adults:  
399  $1.5 \text{ mm}^2 \pm 0.13$ , juveniles:  $0.66 \text{ mm}^2 \pm 0.14$ ,  $\beta_{\text{adults vs. juveniles}} = 0.14 \pm 0.040$ ). In addition, male  
400 total spot area, largest right spot area, and largest left spot area were positively correlated with  
401 SVL (Table 4), but not total number of spots ( $t_{1, 33} = 0.48$ ,  $p = 0.63$ ,  $\beta = 0.0079 \pm 0.017$ , Table 4,  
402 Fig. 2a). The relationship between total spot area and SVL was not significant for juveniles ( $t_{1, 12}$   
403  $= 0.89$ ,  $p = 0.39$ ,  $\beta = 0.0024 \pm 0.0027$ ) or females ( $t_{1, 25} = 0.25$ ,  $p = 0.80$ ,  $\beta = 0.00057 \pm 0.0022$ ,  
404 Fig. 2b). Mean UV chroma of male spots was higher in orange-bellied as compared to white-  
405 bellied individuals, but was not related to SVL (Table 4).

### 406 **Behavior experiments**

407 Regarding control experiment analyses, individual SVL, but not size difference from the rival  
408 nor total spot area, was negatively correlated with indicators of submission (wall scratching time,  
409  $F_{1, 40.19} = 8.48, p = 0.006, \beta = -9.30 \text{ sec/mm} \pm 3.20$ ) and positively correlated with aggression  
410 (higher dominance score,  $F_{1, 39.23} = 5.66, p = 0.023, \beta = 2.69 \text{ mm}^{-1} \pm 1.13$ , see Fig. 3). Analyses  
411 of focal male data indicated that spot manipulation (area added or removed) and opponent size  
412 (larger or smaller than the focal) did not significantly affect wall scratching time or aggression  
413 score. However, focal males facing manipulated individuals had significantly higher submission  
414 scores than focal males facing control individuals ( $F_{1, 57} = 6.57, p = 0.013, \beta_{\text{manipulated vs. control}} =$   
415  $5.46 \pm 2.13$ ) and also tended to have lower dominance scores (marginally significant,  $F_{1, 57} =$   
416  $3.86, p = 0.054, \beta_{\text{manipulated vs. control}} = -8.43 \pm 4.29$ ).

## 417 **DISCUSSION**

418 According to our vision model, the *P. muralis* visual system can distinguish the majority of UV-  
419 blue spots when viewed against a mean *P. muralis* flank spectrum and objects commonly found  
420 in their natural environments, thus corroborating previous findings involving the same species  
421 (Pérez i de Lanuza and Font 2015). UV-blue spots also had a higher extrinsic compared to  
422 intrinsic conspicuousness, which seems to reinforce the idea that visual systems are more  
423 sensible to extrinsic than intrinsic conspicuousness (Aronsson and Gamberale-Stille 2009). In  
424 addition, the relative inconspicuousness of the lizards' flanks (in this study) and dorsal surfaces  
425 (in Pérez i de Lanuza and Font 2015) seems to indicate strong selection for background matching  
426 to avoid predation, as observed in other lizard species (LeBas and Marshall 2000; Marshall and  
427 Stevens 2014).

428         Based on the hypothesis that male-male competition shapes the evolution of UV-blue  
429 spots, sexual selection theory predicts that adult males should evolve exaggerated UV-blue spots,



430 while this trait should be minimized or absent in females, as it may be detrimental and reduce  
431 their fitness via associated costs (Promislow et al. 1992; Andersson 1994; López et al. 2004;  
432 Pérez i de Lanuza et al. 2013). Additionally, juveniles should also have reduced UV-blue spots,  
433 since young, subdominant lizards should avoid competition with adults (e.g., Mugabo et al.  
434 2013). Previous studies have revealed strong sexual dimorphism for several UV-blue spot  
435 characteristics in adult *P. muralis* but have found no clear correlation between UV coloration and  
436 adult body size. In males, a slight negative correlation between UV chroma and body condition,  
437 as well as a correlation between UV chroma and bite force (dependent on male body size), have  
438 been reported (Pérez i de Lanuza et al. 2014; Martin et al. 2015b). The number of spots also  
439 correlates positively with body size in male Iberian rock lizards *I. monticola*, a sister species of  
440 *P. muralis* (López et al. 2004). Together, these results, along with those showing an influence  
441 (albeit weak) of spots on behavior during competitive encounters (López et al. 2004; Pérez i de  
442 Lanuza et al. 2014; Martin et al. 2015b, 2016), suggest that UV-blue spots function as potential  
443 signals of individual quality, age and/or sex (Candolin 2003).

444 Our study revealed age differences and a strong sexual dimorphism in the expression of  
445 UV-blue spots. Adult males had exaggerated number, area, and UV chroma of UV-blue spots  
446 while adult females and juveniles had only a few faint blue spots (see also López et al. 2004;  
447 Pérez i de Lanuza et al. 2014), indicating very limited trait expression in these groups. In adult  
448 males, we found a significant correlation between body size and both total spot area and largest  
449 left/right spot area, but considered that total spot area is likely to be more biologically relevant  
450 because it spans a large part of the length of the lizard, while largest spots do not. Our results  
451 therefore indicate that longer, possibly older, adult males have larger and more interspaced UV-  
452 blue spots, possibly making them more conspicuous against their natural visual background. This

453 result is noteworthy, as previous studies have not measured the coloration and morphological  
454 properties of all spots of a single lizard (Pérez i de Lanuza et al. 2013; Martin et al. 2015b).  
455 Different interpretations can be drawn to explain this relationship. First, UV-blue spot area may  
456 be an honest signal of male quality and correlate with quality indicators not measured in this  
457 study such as bite force, which has been shown to be related to male quality in lizards, especially  
458 lacertids (Huyghe et al. 2005; Salvador et al. 2007; Henningsen and Irschick 2012; Pérez i de  
459 Lanuza et al. 2014). Second, UV-blue spot area may be directly related to body size either  
460 through an inherent relationship, in which case they would act as indices, or as amplifiers of  
461 body size, to facilitate receivers' assessment of body size. Baeckens et al. (2018), for example,  
462 argue that displaying sexual signals that are redundant with body size may be useful in the first  
463 stages of a confrontation, when cryptic lizards must assess one another's quality at a certain  
464 distance. Third, ontogenetic processes could also explain this relationship, which could be tested  
465 in longitudinal studies following the same males as they age. For example, Bonnaffé et al. (2018)  
466 showed that, in male common lizards *Zootoca vivipara*, UV chroma increased with age, likely  
467 due to ontogenetic processes.

468         As argued above, recent evidence suggests that UV-blue spots are a signal of male  
469 quality. The eventual strategic costs associated with these signals remain unknown. Thus, we  
470 subsequently tested the prediction that total spot area may act as a conventional signal of male  
471 quality (the honesty of which would be maintained by social costs) by conducting behavioral  
472 assays between unfamiliar males of varying body size and manipulated spot area. During control  
473 encounters, we found a positive relationship between body size and dominance score, and a  
474 negative relationship between body size and wall scratching time. These results corroborated  
475 previous findings showing that body size influences aggressive and submissive behaviors in male

476 lizards (e.g., López and Martín 2001; Martin et al. 2015b). When we artificially created a  
477 mismatch between body size and UV-blue spot area, we found that UV-blue spot area was not a  
478 significant explanatory factor of dominance. If, as we aimed to test here, the UV-blue spots  
479 functioned as conventional signals, the honesty of which is guaranteed by receiver-dependent  
480 costs, we expected deceptive males to pay a socially induced cost for being dishonest (Maynard  
481 Smith and Harper 2003; Ligon and McGraw 2016). Focal males were thus expected to invest  
482 more in combat behaviors and escalation (both aggression and submission) when faced with a  
483 deceptive male rather than a control male, with larger males eventually dominating smaller ones.  
484 We, however, found that when facing deceptive opponents, the submission score of focal males  
485 significantly increased while their dominance score tended to decrease. These results do not  
486 support the prediction of a “conventional signal” hypothesis, in which deceptive males (i.e.  
487 bluffers and Trojans) pay a social cost for being dishonest (Maynard Smith and Harper 2003;  
488 Ligon and McGraw 2016), and suggest that other types of strategic costs must maintain signal  
489 honesty (e.g., handicaps).

490         In addition, if the UV-blue spots act as an amplifier of body size, we would have  
491 expected mismatching body size and spot area combinations to lead to combat escalation,  
492 because visual assessment of opponents would fail to clearly establish dominance (Hasson 1989;  
493 Maynard Smith and Harper 2003; Martin et al. 2015b). Unfortunately, in our behavioral assays,  
494 it was generally not possible to establish a clear “winner” or “loser” over the course of the  
495 competitive encounter, and thus we were not able to quantify combat escalation time. Yet, our  
496 results showed that the artificial mismatch between UV-blue spot area and body size did  
497 influence the competitive behavior of focal males. On one hand, focal males were more  
498 submissive against bluffers than against controls, which could be expected if spot area serves as

499 an amplifier of body size. On the other hand, focal males were also more submissive when faced  
500 with Trojans, which contradicts the predictions of the amplifier hypothesis.

501         One explanation for the weak effect of the combination of body size and spot  
502 manipulation treatments on encounters, apart from the submissive behavior of focal males, is that  
503 body size contrasts between males were small relative to the wall lizard body size range and,  
504 thus, that absolute body size was a better predictor of male behavior than size contrasts. In  
505 addition, the correlation between total spot area and body size was not strong (albeit significant,  
506 see Fig. 2), possibly suggesting that manipulation of total spot area might not have been  
507 perceived as a change in apparent body size. Experiments with a stronger size contrast and  
508 modifying the information content of the UV-blue spots in multiple ways (e.g., masking the first  
509 and last spots to reduce total length of the lateral rows) could shed light on this possibility.

510 Another explanation is that color traits, such as UV-blue spots, may be more relevant to mutual  
511 assessment in outdoor conditions when direct assessment of body size is more difficult, such as  
512 signaling over long distances or in the presence of vision-impairing factors (e.g., poor lighting,  
513 presence of objects or other organisms, Henningsen and Irschick 2012). Wall lizards typically  
514 defend territories using behavioral displays performed at maximal distances of several meters in  
515 outdoor conditions (Edsman 1990), and physical pairwise interactions are often aggressive at our  
516 study site (J-FLG personal observation). Thus, in the future, the effects of spot manipulation on  
517 territory defense and male-male interactions should be tested outdoors. Then, although we did  
518 account for and found no relationship between belly morph and behavior in this study, Abalos et  
519 al. (2016) found consistent physiological and morphological differences in morph types that  
520 could, in turn, be related to morph-specific behavioral syndromes. It would be worth  
521 investigating whether morphs are associated with certain personality types that could influence

522 competitive encounters. Finally, as was the case in studies involving blue tits (Johnsen et al.  
523 2005; Rémy et al. 2010), the UV enhancing marker increased reflectance in the UV as well as  
524 the 450-700 wavelength range (although the increase was less in the latter, see Fig. S3). The  
525 increase in reflectance outside the UV could have affected opponent response to the manipulated  
526 males and it would be ideal to find a UV enhancing product that increased reflectance only in the  
527 UV-blue range of the spectrum.

528         Despite the lack of a strong effect, we did find that spot manipulation of the rival resulted  
529 in increased submission and slightly decreased dominance in focal males irrespective of  
530 opponent size. We suggest that this result could be explained if rivals enter into aggressive  
531 encounters only if they believe they have a chance of winning based on a comparison of their  
532 own and their opponents' color signals (Rohwer 1975; Rémy et al. 2010; Vedder et al. 2010). If  
533 we assume that body size is a physical trait easily detected at short distances, large and small  
534 focal males initially evaluating a manipulated opponent would likely behave as they normally  
535 would against a small or big opponent. In manipulated individuals, focal males facing large  
536 opponents would likely back down immediately and no change in their behavior would result  
537 due to the manipulation. In focal males facing small opponents, the focal male may initially have  
538 been aggressive. Upon approaching their opponent and detecting their enlarged spot area,  
539 however, the focal male may back down or exhibit greater submission behaviors due to the  
540 mismatch between body size and the signal, resulting in a decrease in overall dominance and  
541 increase in overall submission. Another factor that could have reduced aggression is inadvertent  
542 modification of black spots next to UV-blue spots. Black spots, sometimes adjacent to UV-blue  
543 spots (see Fig. S2), have not been extensively investigated but have been found in one study  
544 (Abalos et al. 2016) to be a predictor of fighting ability, with winners showing greater aggression

545 in encounters with opponents of similar black spot area. It is possible that UV-blue spot  
546 manipulations reduced black spot area, resulting in encounters between lizards with more  
547 dissimilar black spot area and thus lower aggression. Altogether, however, these results suggest  
548 that the relationship between UV-blue spots and male dominance is ambiguous in *P. muralis*,  
549 similar to findings of Martin et al. (2015b) about spot UV reflectance. Spot properties are  
550 involved in mutual assessment during male-male competition but do not influence behavioral  
551 dominance as we would expect from a conventional signal or an amplifier of body size.

## 552 **COMPLIANCE WITH ETHICAL STANDARDS**

### 553 **Funding**

554 This research was supported by the Centre National de la Recherche Scientifique (CNRS).

### 555 **Conflicts of Interest**

556 We, the authors, declare no conflicts of interest.

### 557 **Ethical Approval**

558 Authorization No. Ce5/2011/044 allowed us to capture and manipulate wild animals for this  
559 study. Ethical approval from an ethics committee was not necessary. All applicable international,  
560 national, and/or institutional guidelines for the care and use of animals were followed. All  
561 procedures performed in studies involving animals were in accordance with the ethical standards  
562 of the institution at which the studies were conducted.

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749

## 750 **FIGURE AND TABLE CAPTIONS**

751 **Table 1** List and description of 1) behaviors displayed by *P. muralis* during male encounters, 2)  
752 scores used in analyses of behavior data

753 **Table 2** Mean  $\pm$  SE chromatic contrast of flank and spot spectra in jnds (just noticeable  
754 differences). Flank vs. habitat and spot vs. habitat analyses compared individual flank and spot  
755 spectra, respectively, to each of 8 habitat object spectra. Spot vs. flank analyses compared  
756 individual spot spectra to a mean flank spectrum.  $N_1$  and  $N_2$  represent the number of spectra of  
757 the 1<sup>st</sup> and 2<sup>nd</sup> comparison elements, respectively

758 **Table 3** Age (A = adults, J = juveniles) and sex (M = males, F = females) differences in spot  
759 morphology qualities. Except total number of spots, all factors are in  $\text{cm}^2$ .  $\beta$  were calculated on  
760 the transformed scale

761 **Table 4** Effects of belly color morph (O = orange, W = white) and SVL on spot characteristics in  
762 adult males. Except total number of spots and mean spot chroma, all factors are in  $\text{cm}^2$ .  $\beta$  were  
763 calculated on the transformed scale

764 **Fig. 1** Mean reflectance spectra and 95 % confidence interval curves of UV-blue spots for males  
765 and females. The male mean spectrum distinctly peaks in reflectance in the UV region ( $\lambda_{\text{max}} =$   
766 360-365 nm) while the female mean spectrum has a weak UV reflectance and a flat reflectance

767 curve in the visible range. Curves were calculated from raw data without smoothing and  
768 confidence intervals assume a normal distribution

769 **Fig. 2** Size scaling of the number and area of UV-blue spots. a) Total number of spots as a  
770 function of SVL (snout-vent length) for adult male and adult female data with their respective  
771 best-fit linear trend lines. The relationship between SVL and number of spots was not significant  
772 for male or female data. b) Total spot area as a function of SVL. The relationship between SVL  
773 and total spot area is significant for males and not for females (see text)

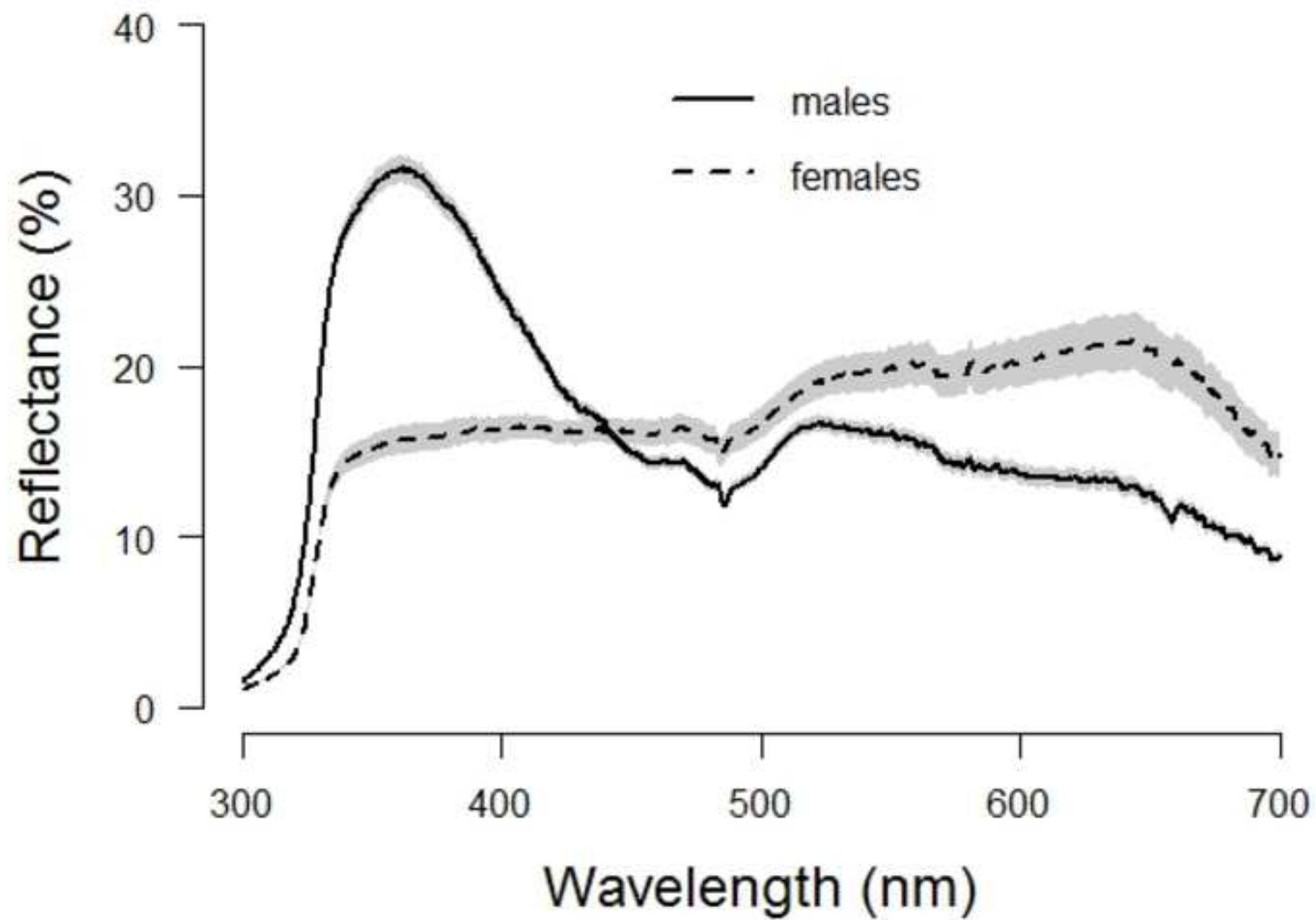
774 **Fig. 3** Dominance score in the control experiments as a function of SVL (snout-vent length) with  
775 the corresponding best-fit linear trend line. The relationship between SVL and dominance score  
776 is significant (see text). The zero line represents situations in which males performed equal  
777 numbers of aggressive and submissive behaviors

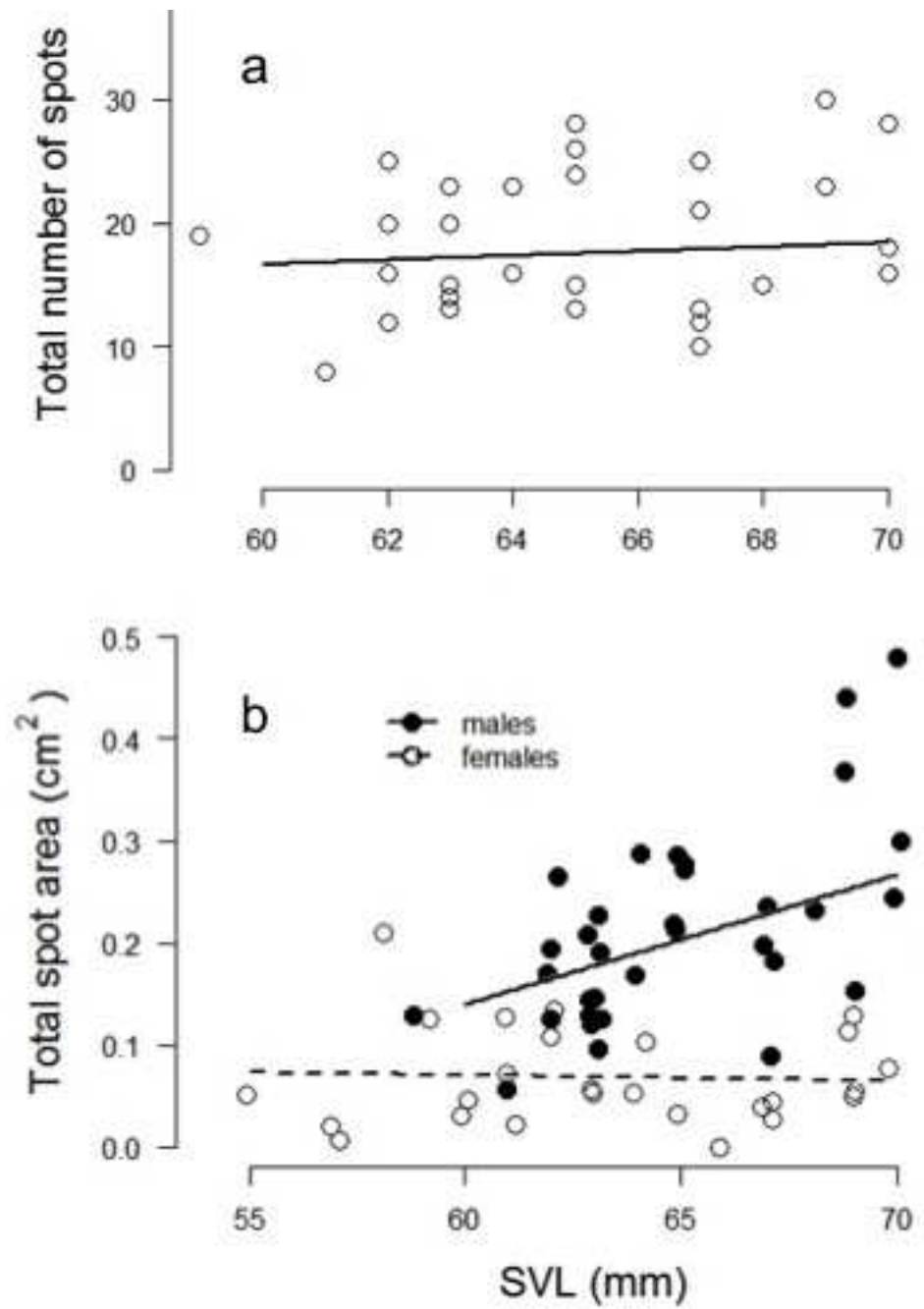


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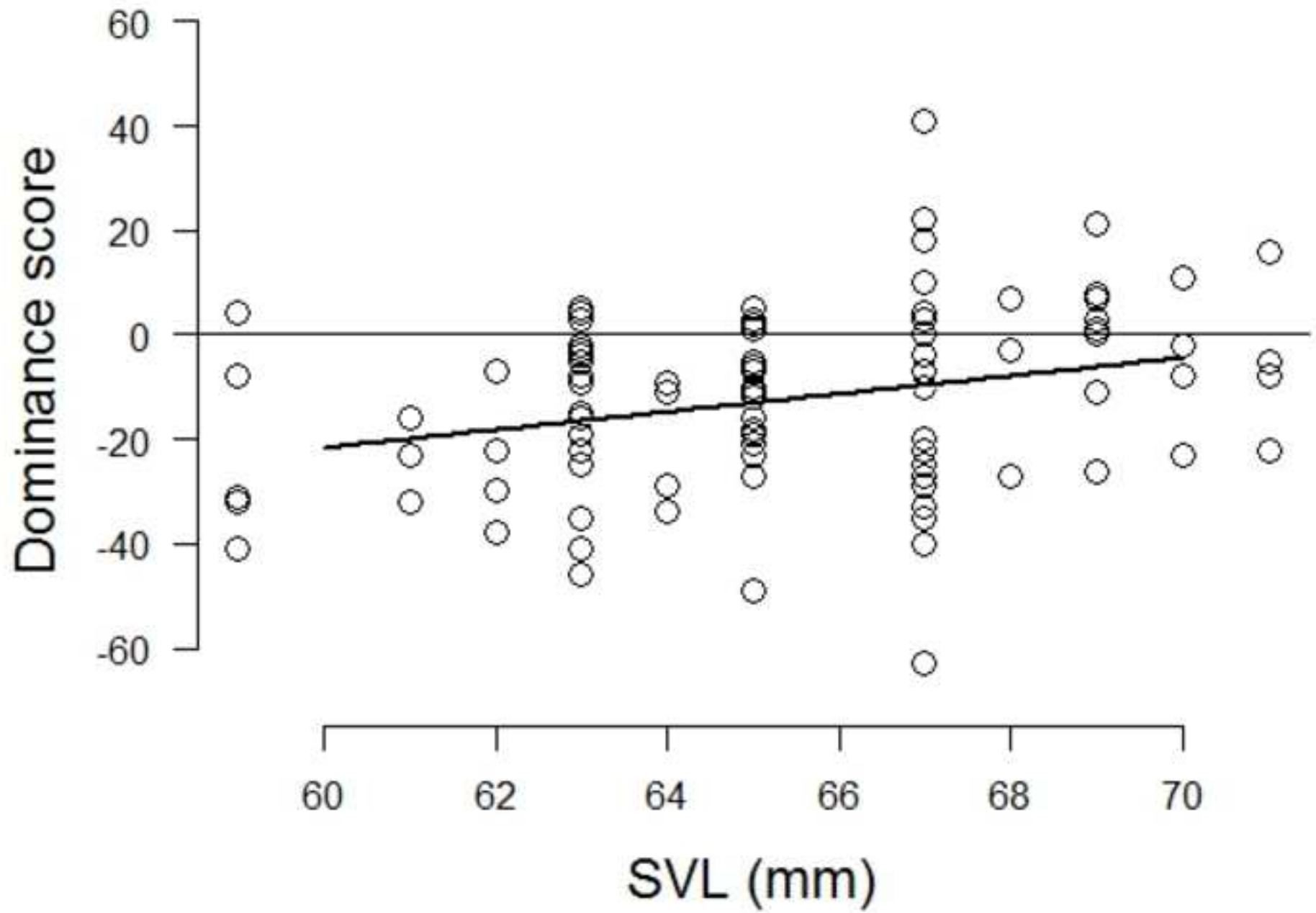


Table1

| <b>Behaviors/Scores</b> |                 | <b>Description</b>  |
|-------------------------|-----------------|---|
| <b>Agonistic</b>        | Aggression      | Rapid approach towards the opponent OR touch the opponent without bite  |
|                         | Approach        | Slow cautious approach to the opponent  |
|                         | Bite            | Prehension of a body part of the opponent with teeth  |
|                         | Demonstration   | Stationary position with alternately, jerked up and down movements of the hind legs OR wide sustained opening of jaws OR exhibiting one flank by postural adjustment towards the opponent |
|                         | Escape          | Bypass OR rapid movement away from the opponent   |
|                         | Wall scratching | Scratching the wall of the terrarium, a sign of moderate stress or avoidance behavior   |
| <b>Non-agonistic</b>    | Basking         | The body is flattened onto the substrate and oriented at right angles to a heat source  |
|                         | Movement        | Movement from one place to another  |
|                         | Immobility      | No movement while on feet.  |
| <b>Scores</b>           | "Aggression"    | Aggressions + approaches + demonstrations   |
|                         | "Submission"    | Escapes + tail wag events + wall scratching events  |
|                         | "Dominance"     | Aggression score – submission score   |

Table2

|                      | Flank vs. Habitat |                |             | Spots vs. Habitat |                |              | Spots vs. Mean flank |                |              |
|----------------------|-------------------|----------------|-------------|-------------------|----------------|--------------|----------------------|----------------|--------------|
|                      | N <sub>1</sub>    | N <sub>2</sub> | mean ± SE   | N <sub>1</sub>    | N <sub>2</sub> | mean ± SE    | N <sub>1</sub>       | N <sub>2</sub> | mean ± SE    |
| <b>Adult Males</b>   | 67                | 8              | 6.50 ± 0.18 | 454               | 8              | 26.25 ± 0.14 | 454                  | 1              | 25.72 ± 0.32 |
| <b>Adult Females</b> | 25                | 8              | 6.45 ± 0.30 | 125               | 8              | 11.97 ± 0.27 | 125                  | 1              | 11.02 ± 0.68 |
| <b>Juveniles</b>     | 13                | 8              | 7.97 ± 0.52 | 72                | 8              | 19.78 ± 0.36 | 72                   | 1              | 19.14 ± 0.90 |

Table3

| <b>Spot properties</b>               | <b>Sex (df = 1,65)</b> |          |                     | <b>Age (df = 1,72)</b> |          |                     |
|--------------------------------------|------------------------|----------|---------------------|------------------------|----------|---------------------|
|                                      | <i>F</i>               | <i>p</i> | $\beta$ (M vs. F)   | <i>F</i>               | <i>p</i> | $\beta$ (A vs. J)   |
| <b>Total spot area</b>               | 46.46                  | <0.0001  | $0.18 \pm 0.026$    | 12.49                  | 0.00072  | $0.14 \pm 0.040$    |
| <b>Total number of spots</b>         | 5.28                   | 0.025    | $3.40 \pm 1.48$     | 3.75                   | 0.057    | $3.72 \pm 1.92$     |
| <b>Largest left flank spot area</b>  | 47.39                  | <0.0001  | $0.0083 \pm 0.0012$ | 14.42                  | 0.00030  | $0.0068 \pm 0.0018$ |
| <b>Largest right flank spot area</b> | 49.34                  | <0.0001  | $0.047 \pm 0.0066$  | 14.12                  | 0.00035  | $0.040 \pm 0.011$   |

Table4

| Spot properties                      | Color (df = 1,33) |          |   | SVL (df = 1,33) |          |                     |
|--------------------------------------|-------------------|----------|---|-----------------|----------|---------------------|
|                                      | F                 | <i>p</i> | $\beta$ (O vs. W)                             | t               | <i>p</i> | $\beta$             |
| <b>Total spot area</b>               | 2.08              | 0.16     | $0.27 \pm 0.18$                               | 2.27            | 0.030    | $0.057 \pm 0.025$   |
| <b>Total number of spots</b>         | 3.81              | 0.059    | $0.24 \pm 0.12$                               | 0.48            | 0.63     | $0.0079 \pm 0.017$  |
| <b>Largest left flank spot area</b>  | 0.33              | 0.57     | $-0.0011 \pm 0.0019$                          | 2.61            | 0.014    | $0.0006 \pm 0.0002$ |
| <b>Largest right flank spot area</b> | 0.063             | 0.80     | $6.50 \times 10^{-4} \pm 2.59 \times 10^{-4}$ | 2.67            | 0.012    | $0.0009 \pm 0.0003$ |
| <b>Mean spot UV chroma</b>           | 7.49              | 0.010    | $0.062 \pm 0.023$                             | 1.09            | 0.28     | $0.0034 \pm 0.0031$ |



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We, the authors, declare no conflicts of interest.

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**New Author Contributions statement:**

**Dr. Badiane made a major contribution to the last substantial revision of the manuscript. Thanks to Dr. Badiane’s expertise in the signalling literature, we were able to substantially**

modify the introduction and discussion of the manuscript in order to focus more heavily on the conventional signal hypothesis and less on the amplifier hypothesis in response to the concerns of one of the reviewers. These changes would not have been possible without Dr. Badiane’s assistance.


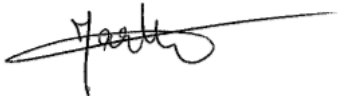

**New Acknowledgement Section:**

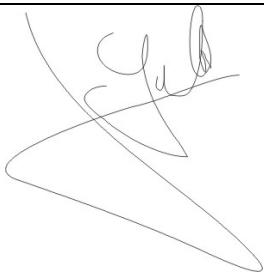
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