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1 **The colour of success: does female mate choice rely on male colour change in the**
2 **chameleon *Furcifer pardalis*?**

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20 **Abstract**

21 Colour change is involved in various functions ranging from thermo- and hydroregulation to
22 camouflage and communication. The role of colour change in communication has received
23 increased attention over the past few decades, yet has been studied predominantly in the
24 context of intrasexual competition. Here, we investigate the role of colour change in mate
25 choice in an animal that can change its colour, the panther chameleon (*Furcifer pardalis*). We
26 conducted behavioural experiments and colour analysis to investigate whether colour changes,
27 including in the UV range, are involved in mate choice. This study presents evidence of
28 female preference for specific aspects of colour change in courting males, both in the visible
29 and the UV range. Females chose males exhibiting more saturation changes regardless of the
30 body region and spectral range. In addition, females chose males showing fewer brightness
31 changes at the level of the lateral line and males showing lower hue changes at the level of the
32 bands and the interbands, in the visible range. In the UV, selected males showed more
33 brightness changes and higher maximum brightness. These results suggest that male colour
34 change is important in female mate choice in the panther chameleon.

35 **Keywords:** Chameleon, Intersexual selection, Colour signal, Animal communication

36 INTRODUCTION

37 Animal colouration is not as fixed as is often assumed. Indeed, many animals change colour
38 during their development (Booth, 1990) and/or in response to environmental variation
39 including season (Küderling *et al.*, 1984), food availability (Hill *et al.*, 2002), circadian
40 rhythms, breeding season (Keren-Rotem *et al.*, 2016b; McGraw and Hill, 2004), or predation
41 pressure (Hemmi *et al.*, 2006). This type of colour change, termed morphological colour
42 change (Leclercq *et al.*, 2009; Umbers *et al.*, 2014), can be achieved through pigments, the
43 anabolism or catabolism of photonic structures, changes in the number of chromatophores in
44 tissues, or the renewal of dead tissue (e.g. hairs, feathers, scales, or cuticula) containing
45 pigments or photonic structures through moulting (Detto *et al.*, 2008). These morphological
46 colour changes are typically achieved over time spans ranging from months to days.

47 However, some organisms can change colour in hours or even less than a second. This is
48 referred to as rapid colour change or physiological colour change (Ligon and McCartney,
49 2016). Physiological colour changes can be achieved by the contraction/expansion of
50 chromatophores (Cloney and Florey, 1968) or by the mobilisation of pigments or photonic
51 nanostructures within chromatophores. These types of colour changes are typically mediated
52 by hormones and/or neurotransmitters (Ligon and McCartney, 2016; Umbers *et al.*, 2014), or
53 through hydraulic infiltration into photonic nanostructures (Liu *et al.*, 2009). This ability has
54 been documented in cephalopods (Hanlon and Messenger, 2018), insects (Hinton and Jarman,
55 1973; Key and Day, 1954), arachnids (Wunderlin and Kropf, 2013), crustaceans (Brown and
56 Sandeen, 1948; Stevens *et al.*, 2014), fish (Iga and Matsuno, 1986; Nilsson Sköld *et al.*, 2013)
57 amphibians (Kindermann and Hero, 2016; Nilsson Sköld *et al.*, 2013), reptiles (Batabyal and
58 Thaker, 2017; Taylor and Hadley, 1970), and even some birds (Curio, 2004). The functions of
59 physiological colour change may differ in different taxa and include thermoregulation (Smith
60 *et al.*, 2016), hydroregulation (Whiters, 1995), camouflage (Allen *et al.*, 2010; Stuart-Fox *et*
61 *al.*, 2008; Zylinski and Johnsen, 2011), and intraspecific communication (Hutton *et al.*, 2015).

62 In the context of animal communication, colour change has mostly been studied during
63 intrasexual interactions suggesting intraspecific communication to be a prominent driver of
64 the evolution of physiological colour change. Surprisingly, few studies have investigated the
65 role of physiological colour change during intersexual interactions (Adamo *et al.*, 2000;
66 Batabyal and Thaker, 2017; Boal, 1997; Kelso and Verrell, 2002; Keren-Rotem *et al.*, 2016a).
67 Moreover, most of these studies focused on differences in colour change between intra- and

68 intersexual interactions, or which colours correspond to courtship, rather than evaluating the
69 variations in colour during the interaction itself. To date, no study has explored the role of
70 physiological colour change in mate choice, raising questions on the role of female mate
71 choice based on male colour change.

72 In some animals, like chameleons, sexual selection upon the ability to change colour is likely
73 to occur as a strong sexual dimorphism both in terms of colour and the ability to change
74 colour exists (Kelso and Verrell, 2002; Keren-Rotem *et al.*, 2016a; Tolley and Herrel, 2013).
75 Moreover, comparative studies have demonstrated that selection for conspicuous social
76 signals has likely driven the evolution of colour change in a clade of dwarf chameleons
77 (Stuart-Fox and Moussalli, 2008). Chameleons are thus an excellent model to study whether
78 females chose mates based on male physiological colour change. Chamaeleonid lizards are
79 famous for exhibiting striking and complex colour changes (Nečas, 1999; Teyssier *et al.*,
80 2015; Tolley and Herrel, 2013) with a large repertoire (Kelso and Verrell, 2002; Ligon and
81 McGraw, 2018). Despite previous studies describing the specific courtship colour patterns and
82 female receptive colours (Karsten *et al.*, 2009a; Kelso and Verrell, 2002; Keren-Rotem *et al.*,
83 2016a), the involvement of colour change in intersexual selection in chameleons has been
84 neglected.

85 Here, we explore whether mate choice outcome relies on specific aspect of male colour
86 change in the panther chameleon (*Furcifer pardalis* Cuvier 1829). The panther chameleon (*F.*
87 *pardalis*) is an ideal study species as it possesses a strong dichromatism with males being
88 brightly coloured and females being dull. Female colouration remains constant between
89 populations while a strong variability is observed in males depending on the population
90 (Ferguson, 2004). We conducted sequential mate choice experiments and investigated
91 whether female preference and mate choice relies on male colour change. We predict mate
92 choice outcome should be related to brightness changes as these changes have been shown to
93 be involved in intrasexual interactions in chameleons (Ligon, 2014; Ligon *et al.*, 2016; Ligon
94 and McGraw, 2013, 2018).

95 **METHODS**

96 *Animals and husbandry*

97 *Furcifer pardalis* is endemic to Madagascar and found in a wide range of habitats along the
98 northern and eastern coasts. They are diurnal tree-dwelling lizards living in relatively intact
99 forests and forest edges, gardens, plantations, and degraded habitats. This species exhibits a
100 strong sexual dimorphism and exceptionally large intraspecific variation in male colouration:
101 females and juveniles are tan to brown with hints of pink or orange, while adult males are
102 much larger and have various combinations of bright red, green, blue, and yellow. This
103 polychromatism among males, also referred to as morphs or localities, depends on the region
104 of origin. Local variation also appears to exist within morphs (Ferguson, 2004). It has even
105 been suggested that most of the colour morphs in *F. pardalis* could be considered as separated
106 subspecies (Grbic *et al.*, 2015). For the present study, 28 adult (over six months old) captive-
107 bred *F. pardalis* ‘Ambilobe’ morphs were used ($N_{\text{male}} = 19$; $N_{\text{female}} = 9$).

108 Animals were kept in a dedicated room in the Parc Zoologique de Paris in mesh terraria (46 x
109 46 x 91 cm, ReptiBreeze, ZooMed) outfitted with branches and plastic plants to provide
110 hiding spots. The room temperature was maintained at 26°C and fluorescent tubes, providing
111 12% UVB (Reptile Lamp 12% T8, Arcadia) and a 40W heating bulb (Repti Basking Spot,
112 ZooMed) were suspended above each cage. The photoperiod was set at 12/12h. Animals were
113 fed thrice weekly and crickets were calcium-dusted once a week. Water was provided to the
114 animals during three daily misting periods (9 am, 12 pm, and 4 pm) using an automated
115 misting system (Vivaria project) and 20 cL drippers. Males were individually housed, while
116 females were kept in groups of 2-3 individuals, but all terraria were visually isolated from one
117 another.

118 *Experimental design*

119 We used a large arena (144 x 50 x 80 cm) with opaque Plexiglas sides and a front made of
120 transparent Plexiglas of 50 cm high to allow behavioural observations and photo/video
121 recordings (Fig. 1). As chameleons are arboreal, we provided artificial branches to mimic an
122 arboreal environment. As chameleons have a spectral sensitivity that includes the UV
123 (Bowmaker *et al.* 2005), we used a combination of different light sources, allowing to cover a
124 spectrum close to the solar spectrum, including the UV. The overall set up was illuminated
125 with a combination of nine light sources placed 56 cm above the set-up: two 60 Watt, 4000
126 Kelvin, 806 lumen LED bulbs (Lexman ®), two 60 Watt, 2700 Kelvin incandescent bulbs
127 (OSRAM ®, Munich, Germany), two 100 Watt, 2800 Kelvin, 1320 lumen halogen bulbs
128 (OSRAM ®, Munich, Germany), one UVB fluorescent tube ReptiSun® 10.0 High Output

129 UVB Bulb (ZooMed Laboratoires inc., San Luis Obispo, California, United-States), one
130 Arcadia T5 D3+ Desert 12% Reptile Fluorescent Lamp (Arcadia, Croydon, United-
131 Kingdom), and one Reptile systems New Dawn T5 LED (Aquariums systems ®, Sarrebourg,
132 France).

133 From April 2018 to September 2018, sequential mate choice experiments were performed to
134 assess mate choice outcomes. This experimental design mimicked the reproductive behaviour
135 of chameleons, as perch-dwelling lizards are likely to approach mates in a sequential manner
136 during the mating season. Males were split into four different pools of four to five individuals
137 and females in four pools of two to three individuals. To each pool of females, we assigned
138 one specific pool of males from a different breeder with which the sequential mate choice
139 experiment was run. Every female from each pool was exposed to all males of the paired pool
140 (*i.e.* four-five males). The sequential mate choice experiment was repeated four times per
141 female. Sequential mate choice was repeated because mate guarding has been observed in
142 chameleons (Cuadrado, 2006). Consequently, it is likely that females copulate several times
143 with the same chosen male. However, if a female engaged in copulation, meaning potentially
144 gravid, the experiment was not repeated more than twice to prevent potential stress-related
145 dystocia (DeNardo, 2005). Potential gravid females were isolated in specific terraria and
146 allowed to lay their eggs. The mate choice experiments were performed at room temperature
147 (26°C) from 10 am to 6 pm, corresponding to their daily active period. The arena was sprayed
148 with clear water and cleaned before each trial to prevent potential effects of odours remaining
149 from a previous trial. The animals were able to interact for one hour or less if the male
150 attempted to attack the female. Each female was exposed to three different males maximum
151 per day and individuals were allowed to rest at least 90 minutes between each trial. The mate
152 choice experiment was repeated if necessary, with at least a week interval. The behaviour of
153 the animals was recorded with an HD camera, HDCR-CX740VE (SONY, Minato-ku, Tokyo,
154 Japan) (Fig. 1).

155 *Colour calibration and measurements of male colouration*

156 During the interactions, pictures of the male were taken twice every two minutes with a full
157 spectrum converted camera (Samsung NX-1000), one picture in the visible spectrum (VIS)
158 and one in the ultraviolet spectrum (UV). For pictures in the visual spectrum, a filter blocking
159 ultraviolet and infrared was manually placed in front of the camera (UV/IR cut/L Filter,
160 Baader ©, Mammendorf, Germany) and pictures were taken with a 1/640-second exposure.

161 Immediately after the picture was taken, the filter was changed for a filter blocking all
162 wavelengths except those ranging from 320 to 400 nm (Venus-U Planetary Filter, Optolong
163 ©, Kunming City, China) and a picture was taken with a 1-second exposure.

164 For the colour calibration of pictures in the visual range, pictures of a colour checker
165 (SpyderCHECKR™) placed at 13 different regions of the arena were taken once empty.
166 Colour calibration was performed using Adobe Photoshop Lightroom 6, and the
167 SpyderCheckr software (version 1.2.2) provided with the SpyderCHECKR™ following the
168 instructions. As individuals might be in different regions of the arena, images were cropped to
169 isolate each individual and then according to the position of the individuals in the arena, the
170 corresponding colour calibration was applied. Calibrated images were then used for colour
171 measurements. As the UV filter imposes a narrow hue range resulting in a constant pink
172 colouration, colour calibration was not required.

173 Colour measurements were performed by retrieving RGB values, using the RGB measure
174 ImageJ plugin. Here, ten squares of sixteen pixels ($N_{VIS} = 5$; $N_{UV} = 5$; Fig. 2), describing the
175 specific colour patterns of male *F. pardalis* were quantified: the bands ($N = 2$), interbands (N
176 $= 2$) and lateral line ($N = 1$). In the UV, we considered the bands, eyelid, and the head bony
177 tubercles as colour patterns “absorbing” UV ($N=3$), the highly “reflecting” lips ($N=1$), and the
178 “lateral line” ($N=1$) which either absorbs or reflects UV. RGB values were then compiled in R
179 (R Core Team, 2019) and converted into HSV values (H: Hue, S: Saturation, V: Brightness)
180 using the Colourscience package (Gamma and Davis, 2018). HSV is an alternative
181 representation of the RGB colour model that aligns with colour-making attributes and colour
182 perception. As pictures were taken every two minutes, each picture corresponds to a time step
183 of two minutes with the first picture of each interaction corresponding to $t=0$ min.

184 From our measurements, Euclidian distances between colours over two time steps in the 3D
185 HSV colour space (DEHSV) (Eqn 1) and then six variables, which allows to describe the
186 colour changes occurring during social interactions were computed for each colour value (i.e.
187 hue, saturation, brightness, and DEHSV) at each of the ten squares: the variance, the
188 maximum speed of change between two-time steps, maximum absolute colour change (Eqn
189 2), overall absolute colour change (Eqn 3), maximum colour variations (Eqn 4) and overall
190 colour variations (Eqn 5). DEHSV value enables us to summarise in one measurement the
191 changes occurring in the three dimensions of the HSV colour space. All variables (Fig. 3)
192 were calculated independently for UV pictures and VIS pictures, and averaged by body region

193 (VIS: bands, interbands and lateral line; UV: absorbing, reflecting and lateral line). Maximum
 194 UV brightness and maximum UV saturation were also retrieved.

$$195 \quad DEHSV_{x_1-x_2} = \sqrt{(S_1 \cos H_1 - S_2 \cos H_2)^2 + (S_1 \sin H_1 - S_2 \sin H_2)^2 + (V_1 - V_2)^2} \quad (1)$$

196

$$197 \quad \frac{X_{max} - X_{min}}{|t_{Xmax} - t_{Xmin}|} \quad (2)$$

$$198 \quad \frac{|X_{tmax} - X_{tmin}|}{t_{max} - t_{min}} \quad (3)$$

$$199 \quad \frac{\sum_{t=t_{Xmin}}^{t_{Xmax}} (|X_{t+1} - X_t|)}{|t_{Xmax} - t_{Xmin}|} \quad (4)$$

$$200 \quad \frac{\sum_{t=t_{min}}^{t_{max}} (|X_{t+1} - X_t|)}{t_{max} - t_{min}} \quad (5)$$

201 For colour measurements, across all sequential mate choice experiments ran, we only
 202 included sequential mate choice experiments, during which the female exhibited receptive
 203 colouration in her resting state. Hence, out of the 169 interactions, we quantified pictures from
 204 56 interactions only.

205 Here, we were unable to model the colour vision of the panther chameleon because the raw
 206 data required to calculate the cone-catch values for visual system modeling (Siddiqi, 2004;
 207 Troscianko and Stevens, 2015; Vorobyev and Osorio, 1998) are no longer available for
 208 *Furcifer pardalis* (Bowmaker, personal communication).

209 *Female mate choice assessment*

210 For each of these 56 interactions, female mate choice was established based on a previous
 211 study on male-female interactions in other species of *Furcifer* (Karsten *et al.*, 2009) and
 212 personal observations (Table 1). Based on this, the mate choice observed during those 56
 213 interaction was classified into one of two categories: the male is “selected” (n=27) (table 1: 2,
 214 3, 4; 5 & 6) or “non-selected” (n=29) (table 1: 0 & 1) by the female. In the case of “selected”,

215 only pictures prior copulation or copulation attempts were analysed as female mate choice
216 should be based on male colours seen before choosing to mate with a male.

217 *Statistical analysis*

218 Prior to analyses, the distribution of each colour change variable was transformed where
219 needed using a Box-Cox power function with “AID” package to meet the requirements of
220 normal distribution (Asar *et al.*, 2017).

221 We summarised colour change information using a principal components analysis (PCA) on
222 the centered and scaled individual values of each colour change variable with the “ade4”
223 package (Dray and Dufour, 2007). For the visible range (VIS), all variables were incorporated
224 in the PCA, while for the UV range (UV) only brightness and saturation were used as the
225 filter used for UV range captures imposed a constant hue. The number of principal
226 components (PCs) used for the subsequent analyses was identified using the broken stick
227 method (Legendre and Legendre, 1998) while accounting for at least 70% of the variability in
228 the data set and for which the contribution of each variable to PCs provided a relevant
229 interpretation of the colour change.

230 To determine whether the male colour change exhibited during an intersexual interaction
231 could explain female mate choice, a generalised linear mixed-effects model (GLMM) fit with
232 a binomial error (‘glmer’) using ‘lme4’ package (Bates *et al.*, 2015) was performed. We tested
233 for the effect of colour change (*i.e.* PCs and maximum brightness and saturation for the UV
234 range) either in the visible range or in the UV range, on female mate choice, considering the
235 female and the order of males as random factors. These were tested for each body region
236 separately because we found a significant effect of the body region on most of the colour
237 change variables ($P < 0.01$) in both visible and UV range (Table S1).

238 We performed model selection based on Akaike’s information criterion (AICc) with a
239 difference in AICc (Δ AICc) superior or equal to two, and evaluated the relative importance
240 (RI) of each predictor variable using model-averaging approaches (Burnham *et al.* 2011)
241 within model sets for each body region from each spectral range.

242 All statistical analyses were conducted in R version 3.6.1 (R Core Team, 2019). Additionally,
243 model selection and model-averaging were undertaken using the R package MuMIn (Bartoń,
244 2019).

245 *Ethical Note*

246 Experiments were carried out in compliance with French legislation and animals were given
247 regular health checks by Zoo veterinarians. Animals were alive and healthy after the
248 experiments and showed no weight loss. In accordance to the directive 2010/63/EU of the
249 European Parliament and French legislation, our study did not require specific authorisation
250 because our observations did not cause any pain, suffering, distress, or lasting harm.

251 **RESULTS**

252 *PCA results and interpretation*

253 In the visible spectrum, the first four principal components accounted for 75.72 % of the total
254 variability. The first principal component (PC1) of our PCA described hue changes and the
255 second principal component (PC2) depicted saturation changes (Table 2). The third principal
256 component (PC3) described brightness changes. The fourth principal component (PC4)
257 described the overall absolute colour change (Table 2). In the UV, the first three principal
258 components accounted for 73.68 % of the total variability. The first principal component
259 (PC1) represented UV brightness changes, whereas the second principal (PC2) described UV
260 saturation changes. The third principal component (PC3) depicted the overall absolute UV
261 colour change (Table 2).

262 *Male colour change and female mate choice in the visible spectrum*

263 In the visual spectrum, model selection by AICc retained the model which included PC1 (*i.e.*
264 hue changes), PC2 (*i.e.* saturation changes) and PC4 (*i.e.* overall absolute colour change) for
265 the bands (Table S2). Multimodel averaging on the band models did uncover PC1 (RI=94%),
266 PC2 (RI=95%), and PC4 (RI=97%) to be the best predictors of mate choice outcome (Fig.
267 4D). Specifically, males that exhibited fewer hue changes (PC1) but also more saturation
268 changes (PC2) and that showed a higher overall absolute colour change were significantly
269 more likely to be “selected” by females, thus having a higher mating probability (Fig. 4A;
270 Fig. 5A). For the lateral line, model selection by AICc selected the model with PC2 and PC3
271 (*i.e.* brightness change; Table S2). Multimodel averaging for the lateral line models did
272 uncover PC2 (RI=99%) and PC3 (RI=83%) to be the best predictors of female mate choice
273 (Fig. 4D). More specifically, we found that males exhibiting fewer brightness changes, but
274 more saturation changes were more likely to mate (Fig. 4C; Fig. 5C). However, for the

275 interband model selection by AICc did not allow us to discriminate between models (Table
276 S2). Consequently, we relied on the multimodel averaging to retrieve the best predictors for
277 the interband model. According to multimodel averaging, the best predictors were PC2
278 (RI=65%), PC3 (RI=67%), and PC4 (RI=74%) (Fig. 4D). This model showed that males with
279 a higher overall absolute colour change (PC4) are “selected” by females (Fig. 4B; Fig. 5B).
280 We also found that males exhibiting more brightness changes (PC3) tend to be less “selected”
281 by the females. At the level of the interbands, it there seems to be no link between female
282 mate choice and saturation changes (PC2).

283 *Male colour change and female mate choice in the UV range*

284 In the UV, at the level of the lateral line and UV absorbing regions, model selection by AICc
285 selected PC1 (*i.e.* UV brightness changes), PC2 (*i.e.* UV saturation changes), and UV
286 maximum brightness (maxV; Table S3). Multimodel averaging selected those variables as
287 best predictors of female mate choice (Fig. 6D) for the following regions: *UV absorbing*
288 *regions*: PC1 RI=95%, PC2= 100%, maxV RI=89%; *lateral line*: PC1 RI=85%, PC2= 92%,
289 maxV RI=79%. Our results show that “selected” males are those which exhibited more UV
290 brightness (PC1) and UV saturation changes (PC2), yet lower UV brightness (Fig. 6A,C; Fig.
291 7A, C). At the level of the UV reflecting regions, model selection by AICc failed to
292 discriminate among models. Hence, we used the best predictors uncovered by model
293 averaging, PC1 and PC2. At the level of the reflecting UV region, as in the UV absorbing
294 region and the lateral line, males were more likely to be “selected” by the females, when they
295 exhibited more brightness (PC1) and saturation (PC2) changes during the interaction (Fig. 6B;
296 Fig. 7B).

297 **DISCUSSION**

298 *Female mate choice relies on specific aspects of male colour change in the visible range*

299 This study presents evidence of female mate choice based on specific aspects of male colour
300 change during courtship. Males that exhibited lower lateral line and interband brightness
301 changes in the visible range (PC3) were more likely to be successful and engage in copulation
302 attempts or actual copulation. This result follows our prediction that, as in the context of other
303 social interactions (Ligon and McGraw, 2013), brightness changes should be involved in
304 intersexual interactions. Brightness changes in chameleons are also involved in the context of

305 camouflage in some species and are used to decrease their conspicuousness when exposed to
306 highly visual predators (Stuart-Fox *et al.*, 2008). Consequently, we might assume that
307 chameleons would increase their brightness to increase their conspicuousness to
308 communicate. This is strongly supported by our results and previous studies on chameleon
309 social interactions, suggesting a keystone role of brightness changes in chameleon agonistic
310 interactions (Ligon, 2014; Ligon and McGraw, 2013). However, we showed that “non-
311 selected” males exhibited more brightness changes than “selected” males, possibly because
312 “non-selected” males darken, similar to the submissive behaviour described for the veiled
313 chameleon (*Chamaeleo calyptratus* Duméril 1851) (Ligon *et al.*, 2014). In both cases, males
314 may increase crypsis or signal submission through an active darkening. This may prevent
315 injuries by conspecifics and may prevent chameleons from being spotted by predators.

316 In addition, we found that “selected” males were those exhibiting greater overall absolute
317 colour changes (PC4) at the bands and interbands. Hence, females chose males that exhibited
318 the greatest colour difference between their initial colour and final colour (prior to
319 copulation). Females seem to pay particular attention to the overall absolute colour change
320 from the bands compared to other areas (Fig. 4 and 5). Females also seem to choose males
321 showing fewer hue changes at the bands and interbands and more saturation changes at the
322 bands and the lateral line in the visible range. Even though guanine platelet translocation in
323 iridiphores is likely causing the hue changes in *F. pardalis* (Teyssier *et al.* 2015), it is thought
324 that xantho-erythrophores also play a role in colour change by varying the extent of light
325 filtration by this chromatophore layer (Satake 1980; Kotz 1994; Oshima *et al.* 2001; Sato *et*
326 *al.* 2004). Hence, both chromatophores act collectively to achieve hue changes. Xantho-
327 erythrophores achieve colour change through the translocation of pigment granules
328 containing carotenoids/pteridines pigments. However, the amount of those pigments may also
329 impact the filtering range capabilities, with greater amount leading to wider filtering
330 possibilities and thus wider colour change repertoires. In general, animals with a more
331 developed carotenoid-based colouration have a better immune system (McGraw and Ardia,
332 2003; Baeta *et al.*, 2008) and antioxidant function (Henschen *et al.*, 2016), because of
333 immunostimulant and antioxidant properties of carotenoids and pteridines (Svensson and
334 Wong 2011; Simons *et al.* 2012) (McGraw 2005). Saturation and hue metrics of carotenoid-
335 based colouration are good proxies of carotenoid concentration in some birds (Butler *et al.*,
336 2011; Inouye *et al.*, 2001). Consequently, it is expected that a female would preferentially opt
337 for males exhibiting a greater overall colour change as well as greater hue and saturation

338 changes, as it may reflect a better immune system and antioxidant function. In accordance, we
339 did find that chosen males exhibited greater saturation changes and greater overall colour
340 changes.

341 However, females also preferentially chose males showing lower hue changes. This could be
342 possibly be explained by the fact that animals rely on numerous other compounds for
343 antioxidant function including vitamin A, vitamin E, vitamin C, polyphenols, polyunsaturated
344 fatty acids (i.e. omega 3 and 6), L-arginine, transferrin and ubiquinol (reviewed in Vertuani *et al.*
345 *al.* 2004). Therefore, carotenoid-based colouration does not always reflect oxidative stress or
346 immune system quality as other compounds may take over. (Schantz *et al.*, 1999; Krinsky and
347 Johnson, 2005; Svensson and Wong, 2011). Understanding the information conveyed by the
348 colour change is a core question that would need further investigation. To do so, the links
349 between fitness-related traits and different aspects of colour change need to be explored.

350 Another hypothesis that may explain why males selected by females exhibited lower hue
351 changes might be linked to the energetic cost of colour change or more precisely the cost to
352 maintain a specific colour. However, the cost of colour change remains unknown to date.
353 Consequently, it would be beneficial for future studies to quantify the energetic requirements
354 of each component of colour change (*i.e.* melanosome translocation within melanophores,
355 pigment granule translocation within xantho-erythrophores, and guanine platelet translocation
356 within iridophores). Even though general sexual selection hypotheses (Darwin, 1874) involve
357 female mate choice over courting males, there is a growing body of evidence for male mate
358 choice (Belliere *et al.*, 2018; Edward and Chapman, 2011; Kokko *et al.*, 2003) and even
359 mutual mate choice (Courtiol *et al.*, 2016; Drickamer *et al.*, 2003; Myhre *et al.*, 2012). Our
360 data may reflect male mate choice where male *F. pardalis* may express rejection with more
361 hue changes. During our mate choice experiments, we did observe cases where a female
362 exhibited active receptive behaviour, yet males did not respond to those signals (See Table 1)
363 (N=16). In some cases, the male even fiercely rejected the female (*i.e.* biting or lunging at the
364 female). Although this is suggestive of male mate choice, the female traits upon which male
365 preference might be based remain to be investigated.

366 *Female mate choice relying on specific aspect of male UV colouration and UV colour change*

367 Chameleons, including *F. pardalis*, have a spectral sensitivity that includes the UV range
368 (Bowmaker *et al.*, 2005) and there is evidence that chameleons have UV patterns and UV

369 absorbing fluorescent patterns (Prötzel *et al.*, 2018). However, previous studies investigating
370 dynamic colour changes in intrasexual interactions in chameleons (Ligon, 2014; Ligon *et al.*,
371 2016; Ligon and McGraw, 2013, 2018) did not investigate the role of UV and the associated
372 changes thereof. Literature data, in contrast, suggests a role of UV colouration in either
373 intrasexual (Martin *et al.*, 2016; Whiting *et al.*, 2006) or intersexual (Griggio *et al.*, 2010; Lim
374 *et al.*, 2007; Rick and Bakker, 2008) interactions in a diversity of taxa. In the present study,
375 we did find a relation between UV colouration and female mate choice. Selected males
376 showed lower UV brightness along with more brightness changes and more saturation
377 changes. It appears thus that females choose males with higher UV absorbance and males that
378 change more in UV colouration. Interestingly, some of the UV absorbing colour patterns we
379 sampled are head bony tubercles, which are known to be fluorescent under UV light (Prötzel
380 *et al.*, 2018). Consequently, higher absorbing UV properties might lead to higher
381 fluorescence. Thus, females may prefer higher fluorescence rather than higher UV absorbing
382 properties *per se*. This fluorescence emits around 430 nm, which is close to the mean
383 maximum absorbance of short wave sensitive photoreceptors (*i.e.* 440 nm with a maximum at
384 430 nm) in *F. pardalis* (Bowmaker *et al.*, 2005). Interestingly, the spectral range around
385 430nm also seems to correspond to a spectral sensitivity gap in avian vision (Hart and Hunt,
386 2007; Hart and Vorobyev, 2005). Therefore chameleons might use fluorescence as a private
387 communication channel (Cummings *et al.*, 2003) to avoid predation risk from avian predators
388 during mate choice interactions.

389 Females rejected the males with the lowest UV brightness and saturation changes. Non-
390 selected males may possibly favour crypsis to avoid predation or injuries from conspecific by
391 maintaining a constant UV colouration. In contrast, selected males should actively change UV
392 colouration to communicate their motivation to mate. We expected UV changes at the lateral
393 line to be more important than other UV colour patterns. UV colours at the lateral line are due
394 to the photonic crystals, within iridophores, which chameleons can manipulate to change
395 colour (Teyssier *et al.*, 2015). In contrast, the UV absorption from bony tubercles is due to
396 specific structures within the bone itself rather than the skin (Prötzel *et al.*, 2018).
397 Nevertheless, our results suggest that panther chameleons may be able to tune UV colouration
398 even at the level of the bony tubercles. How this is possible remains to be investigated, but a
399 possible role for melanosomes present in the skin overlying the tubercles can be envisaged.

400 To conclude, we here provide evidence of female mate choice for specific aspects of dynamic
401 colour change in male chameleons, including UV colouration and colour change in the visible
402 range. We showed that females rely on different aspects of colour change according to the
403 body region to assess mates. Female mate choice consistently appears to be for colour
404 changes between body regions. This poses the question of whether different aspects of colour
405 change from different body regions convey different information. Moreover, whether some
406 aspects of colour change participate more in signal design rather than to information content
407 remains to be elucidated.

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641 **Table 1: Mate choice outcome assessment.** Table based on the definitions of social
 642 behaviour used during male-male and male-female interactions from Karsten *et al.* (2009) and
 643 our behavioural observations.

| Mate choice outcome | Preference index | Behaviour | Description |
|----------------------------|-------------------------|----------------------------------|---|
| Non-selected | 0 | Rejection | Perpendicular exposure of a laterally flattened body; tail curled; expansion of lungs to as large a size as possible; Dark/Black colouration |
| | 1 | Non-receptivity | Dark/Black colouration; Slight perpendicular exposure of the body; tail curled; female is not initiating any actions toward the male |
| | 2 | Passive receptivity | Female elevates tail from normal and tilts the pelvis up, exposing cloaca when not moving |
| | 3 | Active receptivity | Female exhibits 'passive receptivity' behaviour and initiates actions toward the male (<i>i.e.</i> female going towards the male), but the male does not try to copulate with the female |
| Selected | 4 | Male biased copulation attempt | Female exhibits 'passive receptivity' behaviour; the male take actions (<i>i.e.</i> male going toward the female); male tries to ride the female |
| | 5 | Female biased copulation attempt | Female exhibits 'active receptivity' behaviour; and male tries to copulate with the female |
| | 6 | Copulation | Female exhibits 'receptive' behaviour, active or passive and the male successfully engages in |

644 **Table 2: contributions of original variables to principal components (PC) retained for**
645 **further analysis. Components accounted for at least 70% of the total variability.** In the
646 visible range (VIS) 4 PCs were kept and accounted for 75.7 % of the total variability. In the
647 ultraviolet range (UV) 3 PCs were kept and accounted for 73.7% of the total variability. Bold
648 values represent high loadings.

| Spectral range | VIS (400-700 nm) | | | | UV (320-400 nm) | | |
|---|-------------------------|---------------|---------------|--------------|------------------------|---------------|---------------|
| Principal component (% of the variability explained) | PC1 | PC2 | PC3 | PC4 | PC1 | PC2 | PC3 |
| Variables | (25.6) | (21.1) | (19.5) | (9.5) | (37.4) | (21.7) | (14.6) |
| Brightness variance | 0.09 | 1.04 | 15.82 | 1.92 | 7.87 | 12.55 | 0.57 |
| Saturation variance | 2.99 | 9.85 | <0.01 | 0.87 | 12.27 | 3.879 | 4.18 |
| Hue variance | 13.27 | 0.05 | 0.26 | 1.15 | | | |
| DEHSV variance | 5.42 | 7.51 | 0.02 | 2.03 | | | |
| Maximum speed of brightness change between two time step | 0.09 | 0.79 | 12.86 | 9.20 | 5.68 | 21.83 | 3.46 |
| Maximum speed of saturation change between two time step | 3.25 | 7.35 | 0.42 | 10.77 | 12.94 | 0.80 | 15.25 |
| Maximum speed of hue change between two time step | 13.61 | 0.08 | 0.01 | 0.04 | | | |
| Maximum speed of DEHSV change between two time step | 2.75 | 8.21 | 0.97 | 2.91 | | | |
| Maximum Brightness variations | 0.26 | 0.08 | 16.27 | 2.90 | 7.02 | 10.38 | 9.99 |
| Maximum Saturation variations | 1.63 | 9.63 | 0.18 | 6.10 | 13.04 | 6.78 | 1.07 |
| Maximum Hue variation | 12.4 | 0.21 | 0.31 | 0.62 | | | |
| Maximum DEHSV variations | 3.86 | 8.79 | <0.01 | <0.01 | | | |
| Maximum absolute Brightness change | 0.66 | <0.01 | 15.4 | 0.01 | 5.50 | 1.21 | 27.83 |

| | | | | | | | |
|---|--------------|-------------|--------------|------------------|-------------|--------------|--------------|
| Maximum absolute Saturation change | 0.56 | 8.24 | 1.24 | 0.65 | 8.90 | 10.96 | 0.43 |
| Maximum absolute Hue change | 10.56 | 0.11 | 1.17 | 2.72 | | | |
| Maximum absolute DESHV change | 1.96 | 7.27 | 0.91 | 3.67 | | | |
| Overall Brightness variations | 0.25 | 0.09 | 17.46 | 2.38 9 | 8.52 | 16.5 | 0.25 |
| Overall Saturation variations | 2.77 | 11.5 | 0.1 | 3.56 | 14.3 | 5.22 | 1.38 |
| Overall Hue variations | 13.2 | 0.09 | 0.40 | 0.61 | | | |
| Overall DESHV variations | 5.19 | 7.64 | 0.01 | 0.04 | | | |
| Overall absolute Brightness change | 0.82 | 0.05 | 10.09 | 6.76 | 1.85 | 2.09 | 20.44 |
| Overall absolute Saturation change | 0.11 | 6.48 | 1.41 | 11.2 5 | 2.10 | 7.80 | 15.12 |
| Overall absolute Hue change | 2.049 | 0.24 | 3.04 | 14.4 5 | | | |
| Overall absolute DEHSV change | 2.25 | 4.68 | 1.63 | 15.3 7 | | | |

650 **Figure legends**

651 **Figure 1: Picture and schematic representation of the experimental set up.** **A:** Picture of
652 the set-up from one of our cameras. **B:** schematic drawing of the set up showing where the
653 cameras were positioned, **C:** schematic drawing of the light source positions from the top: 1
654 = 100 Watt, 2800 Kelvin, 1320 lumen halogen bulbs, 2 = 60 Watt, 2700 Kelvin incandescent
655 bulbs, 3 = 60 Watt, 4000 Kelvin, 806 lumen LED bulbs, 4 = UVB fluorescent tube
656 ReptiSun® 10.0 High Output UVB Bulb, 5 = Reptile systems New Dawn T5 LED, 6 =
657 Arcadia T5 D3+ Desert 12% Reptile Fluorescent Lamp.

658 **Figure 2: Body regions sampled on males for colour analysis during *F. pardalis* mate**
659 **choice experiments.** As interindividual variation exists, we focused on common patterns.
660 Body regions were characterised as bands (○), interbands (□) and lateral line (Δ) in the
661 visible spectrum (VIS; 400 to 700 nm). However, for the UV range (UV: 320 to 400 nm),
662 body regions were different and characterised by their UV properties as Absorbing (○),
663 reflecting (□) and lateral line (Δ) which either absorb or reflect through time and according to
664 the individual. (Illustration by Julien Norwood and pictures by Alexis Y. Dollion)

665 **Figure 3: Schematic representation of the different colour change variables computed.** X
666 represents any colour value (*e.g.* hue, saturation, brightness or DEHSV). **A:** Overall colour
667 variation in light blue and overall absolute colour change in dark blue; **B:** Maximum colour
668 variation in light red and maximum absolute colour change dark red.

669 **Figure 4: Relationships between mating probability and colour change variables in the**
670 **visible range with the relative importance (RI) exceeding 50% based on multimodel**
671 **averaging. Ribbons illustrate the 95% confidence interval.** **A** mating probability of 100 %
672 corresponds to “selected” female mate choice (copulation or at least copulation attempt),
673 while zero corresponds to “non-selected” mate choice outcome. **A:** Relationship between
674 mating probability and colour change at the bands, **B:** Relationship between mating
675 probability and colour change at the interbands, **C:** Relationship between mating probability
676 and colour change at the lateral line and **D:** RI values of colour change variables (PCs) in the
677 visible range predicting mate choice outcome.

678 **Figure 5: Effect of the colour change in the visible range in adult males *F. pardalis* on**
679 **female mate choice.** Boxplots showing respectively: **A:** Colour changes occurring at the

680 bands, **B**: Colour changes occurring at the interbands and **C**: Colour changes occurring at the
681 lateral line. PC1 = Hue changes, PC2 = Saturation changes, PC3 = Brightness changes and
682 PC4 = Overall absolute colour change.

683 **Figure 6: Relationships between mating probability and colour change variables in the**
684 **UV range with the highest relative importance (RI) based on multimodel averaging.**
685 **Ribbons illustrate the 95% confidence interval.** A mating probability of 100 % corresponds
686 to a “selected” female mate choice (copulation or at least copulation attempt), while zero
687 corresponds to a “non-selected” mate choice outcome **A** : Relationship between mating
688 probability and colour change in UV absorbing regions, **B**: Relationship between mating
689 probability and colour change in UV reflecting regions, **C**: Relationship between mating
690 probability and colour change in lateral line, and **D**: RI values of colour change variables
691 (PCs and maximum UV colour values) in the UV range predicting mate choice outcome.

692 **Figure 7: Effect of the colour change in the UV range in adult males *F. pardalis* on**
693 **female mate choice.** Boxplots showing respectively: **A**: Colour changes occurring in regions
694 that absorb UVs, **B**: Colour changes occurring in regions that reflect UVs and **C**: Colour
695 changes occurring at the lateral line. PC1 = UV Brightness changes, PC2 = UV Saturation
696 changes and PC3 = Overall absolute UV colour change.