



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

Alexis Dollion, Anthony Herrel, Olivier Marquis, Mathieu Leroux-Coyau,
Sandrine Meylan

► To cite this version:

Alexis Dollion, Anthony Herrel, Olivier Marquis, Mathieu Leroux-Coyau, Sandrine Meylan. The colour of success: does female mate choice rely on male colour change in the chameleon *Furcifer pardalis*?. *Journal of Experimental Biology*, 2020, 223 (20), 10.1242/jeb.224550 . hal-02990221

HAL Id: hal-02990221

<https://hal.science/hal-02990221>

Submitted on 7 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Alexis Y. Dollion^{1,2,3}, Anthony Herrel³, Olivier Marquis⁴, Mathieu Leroux-Coyau² and Sandrine Meylan²

¹ Université de Paris, 75006, Paris, France

² Sorbonne Université, CNRS, IRD, INRA, Institut d'Ecologie et des Sciences de l'Environnement-Paris, iEES-Paris, 75252, Paris, France

³ Département Adaptations du vivant, UMR 7179 C.N.R.S./M.N.H.N, 75005, Paris, France

⁴ Muséum national d'Histoire naturelle, Parc Zoologique de Paris, 75012 Paris, France

Funding information: Ecole Doctorale Frontières de l'Innovation en Recherche et Education - Programme Bettencourt"; Université de Paris.

#Pages: 21

#Tables: 2

#Figure: 4

Corresponding Address

Alexis Y. Dollion

e-mail: dollion.alexis.14340@gmail.com

phone: +33 (0)7 83 67 96 55

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

INTRODUCTION

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

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

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

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

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

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

METHODS

Animals and husbandry

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

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

Experimental design

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

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

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

Colour calibration and measurements of male colouration

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

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

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

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

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

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

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

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

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

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

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

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

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

Female mate choice assessment

For each of these 56 interactions, female mate choice was established based on a previous study on male-female interactions in other species of *Furcifer* (Karsten *et al.*, 2009) and personal observations (Table 1). Based on this, the mate choice observed during those 56 interaction was classified into one of two categories: the male is “selected” (n=27) (table 1: 2, 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 ($\Delta AICc$) 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

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

Male colour change and female mate choice in the UV range

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

Acknowledgements

We thank the two anonymous reviewers and Dr. Ylenia Chairi for helpful and constructive reviews of an earlier version of this manuscript. We thank Dr. Sylvie Laidebeur, Dr. Laetitia Redon, Dr. Alexis Lecu, Fabrice Bernard, Morgane Denis and Mickaël Leger for assistance with chameleon husbandry and care. We thank Cedric Bordes, Denis Lebon and Loïc Laumalle-Waddy from the “ferme tropicale” for their help in providing us with materials for husbandry. We thank Hugue Clamouze and Thierry Decamps for helping us with the experimental arena. Finally, we thank the “Ecole Doctorale FIRE - Programme Bettencourt” for funding.

References

- Adamo, S. A., Brown, W. M., King, A. J., Mather, D. L., Mather, J. A., Shoemaker, K. L. and Wood, J. B.** (2000). Agonistic and reproductive behaviours of the cuttlefish *Sepia officinalis* in a semi-natural environment. *Journal of Molluscan Studies* **66**, 417–418.
- Allen, J. J., Mäthger, L. M., Barbosa, A., Buresch, K. C., Sogin, E., Schwartz, J., Chubb, C. and Hanlon, R. T.** (2010). Cuttlefish dynamic camouflage: responses to substrate choice and integration of multiple visual cues. *Proc. R. Soc. B* **277**, 1031–1039.
- Asar, Ö., İlk, O. and Dag, O.** (2017). Estimating Box-Cox power transformation parameter via goodness-of-fit tests. *Communications in Statistics-Simulation and Computation* **46**, 91–105.
- Baeta, R., Faivre, B., Motreuil, S., Gaillard, M. and Moreau, J.** (2008). Carotenoid trade-off between parasitic resistance and sexual display: an experimental study in the blackbird (*Turdus merula*). *Proceedings of the Royal Society B: Biological Sciences* **275**, 427–434.

- 432 **Bagnara, J. T. and Hadley, M. E.** (1973). *Chromatophores and color change : the*
 433 *comparative physiology of animal pigmentation*. Englewood Cliffs, N.J. : Prentice-
 434 Hall.
- 435 **Bartoń, K.** (2019). *MuMIn: multi-model inference*.
- 436 **Batabyal, A. and Thaker, M.** (2017). Signalling with physiological colours: high contrast
 437 for courtship but speed for competition. *Animal Behaviour* **129**, 229–236.
- 438 **Bates, D., Mächler, M., Bolker, B. and Walker, S.** (2015). Fitting Linear Mixed-Effects
 439 Models Using lme4. *Journal of statistical software* **67**, 1–48.
- 440 **Belliure, J., Fresnillo, B. and Cuervo, J. J.** (2018). Male mate choice based on female
 441 coloration in a lizard: the role of a juvenile trait. *Behavioral Ecology* **29**, 543–552.
- 442 **Boal, J. G.** (1997). Female Choice of Males in Cuttlefish (Mollusca: Cephalopoda). *Behav*
 443 **134**, 975–988.
- 444 **Bowmaker, J. K., Loew, E. R. and Ott, M.** (2005). The cone photoreceptors and visual
 445 pigments of chameleons. *Journal of Comparative Physiology A* **191**, 925–932.
- 446 **Brown, F. A. and Sandeen, M. I.** (1948). Responses of the Chromatophores of the Fiddler
 447 Crab, *Uca*, to Light and Temperature. *Physiological Zoology* **21**, 361–371.
- 448 **Burnham, K. P., Anderson, D. R. and Huyvaert, K. P.** (2011). AIC model selection and
 449 multimodel inference in behavioral ecology: some background, observations, and
 450 comparisons. *Behav Ecol Sociobiol* **65**, 23–35.
- 451 **Butler, M. W., Toomey, M. B. and McGraw, K. J.** (2011). How many color metrics do we
 452 need? Evaluating how different color-scoring procedures explain carotenoid pigment
 453 content in avian bare-part and plumage ornaments. *Behav Ecol Sociobiol* **65**, 401–413.
- 454 **Cloney, R. A. and Florey, E.** (1968). Ultrastructure of cephalopod chromatophore organs.
 455 *Zeitschrift für Zellforschung* **89**, 250–280.
- 456 **Courtiol, A., Etienne, L., Feron, R., Godelle, B. and Rousset, F.** (2016). The Evolution of
 457 Mutual Mate Choice under Direct Benefits. *The American Naturalist* **188**, 521–538.
- 458 **Cuadrado, M.** (2006). Mate guarding and social mating system in male common chameleons
 459 (*Chamaeleo chamaeleon*): Mate guarding and spatial organization in male
 460 chameleons. *Journal of Zoology* **255**, 425–435.
- 461 **Cummings, M. E., Rosenthal, G. G. and Ryan, M. J.** (2003). A private ultraviolet channel
 462 in visual communication. *Proc. R. Soc. Lond. B* **270**, 897–904.
- 463 **Curio, E.** (2004). On ornamental maturation of two Philippine hornbill species with a note on
 464 physiological colour change. *J Ornithol* **145**,.
- 465 **Darwin, C.** (1874). *The descent of man: and selection in relation to sex*. Albemarle Street,
 466 London, UK: John Murray.

467 **DeNardo, D. F.** (2005). Dystocias. In *Reptile Medecine and Surgery*, pp. 787–792. St. Louis,
468 Missouri: Elviesier Health Sciences.

469 **Detto, T., Hemmi, J. M. and Backwell, P. R. Y.** (2008). Colouration and Colour Changes of
470 the Fiddler Crab, *Uca capricornis*: A Descriptive Study. *PLoS ONE* **3**, e1629.

471 **Dray, S. and Dufour, A.-B.** (2007). The ade4 package: implementing the duality diagram for
472 ecologists. *Journal of statistical software* **22**, 1–20.

473 **Drickamer, L. C., Gowaty, P. A. and Wagner, D. M.** (2003). Free mutual mate preferences
474 in house mice affect reproductive success and offspring performance. *Animal*
475 *Behaviour* **65**, 105–114.

476 **Edward, D. A. and Chapman, T.** (2011). The evolution and significance of male mate
477 choice. *Trends in Ecology & Evolution* **26**, 647–654.

478 **Ferguson, G.** (2004). *The Panther chameleon: color variation, natural history, conservation,*
479 *and captive management*. Malabar, Fla.: Krieger Pub. Co.

480 **Gamma, J. and Davis, G.** (2018). *Colorscience : Color Science Methods and Data*.

481 **Grbic, D., Saenko, S. V., Randriamoria, T. M., Debry, A., Raselimanana, A. P. and**
482 **Milinkovitch, M. C.** (2015). Phylogeography and support vector machine
483 classification of colour variation in panther chameleons. *Molecular Ecology* **24**, 3455–
484 3466.

485 **Griggio, M., Zanollo, V. and Hoi, H.** (2010). UV plumage color is an honest signal of
486 quality in male budgerigars. *Ecol Res* **25**, 77–82.

487 **Hanlon, R. T. and Messenger, J. B.** (2018). Body Patterning and Colour Change. In
488 *Cephalopod Behaviour*, pp. 45–73. Cambridge University Press.

489 **Hart, N. S. and Hunt, D. M.** (2007). Avian Visual Pigments: Characteristics, Spectral
490 Tuning, and Evolution. *The American Naturalist* **169**, S7–S26.

491 **Hart, N. S. and Vorobyev, M.** (2005). Modelling oil droplet absorption spectra and spectral
492 sensitivities of bird cone photoreceptors. *J Comp Physiol A* **191**, 381–392.

493 **Hemmi, J. M., Marshall, J., Pix, W., Vorobyev, M. and Zeil, J.** (2006). The variable
494 colours of the fiddler crab *Uca vomeris* and their relation to background and predation.
495 *Journal of Experimental Biology* **209**, 4140–4153.

496 **Henschen, A. E., Whittingham, L. A. and Dunn, P. O.** (2016). Oxidative stress is related to
497 both melanin- and carotenoid-based ornaments in the common yellowthroat. *Funct*
498 *Ecol* **30**, 749–758.

499 **Hill, G. E., Inouye, C. Y. and Montgomerie, R.** (2002). Dietary carotenoids predict plumage
500 coloration in wild house finches. *Proc. R. Soc. Lond. B* **269**, 1119–1124.

501 **Hinton, H. E. and Jarman, G. M.** (1973). Physiological colour change in the elytra of the
502 hercules beetle, *Dynastes hercules*. *Journal of Insect Physiology* **19**, 533–549.

- 503 **Hutton, P., Seymoure, B. M., McGraw, K. J., Ligon, R. A. and Simpson, R. K.** (2015).
504 Dynamic color communication. *Current Opinion in Behavioral Sciences* **6**, 41–49.
- 505 **Iga, T. and Matsuno, A.** (1986). Motile iridophores of a freshwater goby, *Odontobutis*
506 *obscura*. *Cell Tissue Res.* **244**,.
- 507 **Inouye, C. Y., Hill, G. E., Stradi, R. D., Montgomerie, R. and Bosque, C.** (2001).
508 Carotenoid pigments in male house finch plumage in relation to age, subspecies, and
509 ornamental coloration. *The Auk* **118**, 900–915.
- 510 **Karsten, K. B., Andriamandimbiarisoa, L. N., Fox, S. F. and Raxworthy, C. J.** (2009).
511 Social behavior of two species of chameleons in Madagascar: insights into sexual
512 selection. *Herpetologica* **65**, 54–69.
- 513 **Kelso, E. C. and Verrell, P. A.** (2002). Do male veiled chameleons, *Chamaeleo calyptratus*,
514 adjust their courtship displays in response to female reproductive status? *Ethology*
515 **108**, 495–512.
- 516 **Keren-Rotem, T., Levy, N., Wolf, L., Bouskila, A. and Geffen, E.** (2016a). Male
517 preference for sexual signalling over crypsis is associated with alternative mating
518 tactics. *Animal Behaviour* **117**, 43–49.
- 519 **Keren-Rotem, T., Levy, N., Wolf, L., Bouskila, A. and Geffen, E.** (2016b). Alternative
520 Mating Tactics in Male Chameleons (*Chamaeleo chamaeleon*) Are Evident in Both
521 Long-Term Body Color and Short-Term Courtship Pattern. *PLOS ONE* **11**, e0159032.
- 522 **Key, K. and Day, M.** (1954). The physiological mechanism of colour change in the
523 grasshopper *Kosciuscola Tristis* Sjöst. (Orthoptera:Acrididae). *Aust. J. Zool.* **2**, 340.
- 524 **Kindermann, C. and Hero, J.-M.** (2016). Rapid dynamic colour change is an intrasexual
525 signal in a lek breeding frog (*Litoria wilcoxii*). *Behavioral Ecology and Sociobiology*
526 **70**, 1995–2003.
- 527 **Kokko, H., Brooks, R., Jennions, M. D. and Morley, J.** (2003). The evolution of mate
528 choice and mating biases. *Proc. R. Soc. Lond. B* **270**, 653–664.
- 529 **Kotz, K. J.** (1994). Intracellular calcium and cAMP regulate directional pigment movements
530 in teleost erythrophores. *The Journal of Cell Biology* **124**, 463–474.
- 531 **Krinsky, N. I. and Johnson, E. J.** (2005). Carotenoid actions and their relation to health and
532 disease. *Molecular Aspects of Medicine* **26**, 459–516.
- 533 **Küderling, I., Cedrini, M. C., Fraschini, F. and Spagnesi, M.** (1984). Season-dependent
534 effects of melatonin on testes and fur color in mountain hares (*Lepus timidus* L.).
535 *Experientia* **40**, 501–502.
- 536 **Leclercq, E., Taylor, J. F. and Migaud, H.** (2009). Morphological skin colour changes in
537 teleosts: Morphological skin colour changes in fish. *Fish and Fisheries* **11**, 159–193.
- 538 **Legendre, P. and Legendre, L.** (1998). *Numerical ecology*. 2nd english edn. Amsterdam,
539 Netherlands: Elviesier.

- 540 **Ligon, R. A.** (2014). Defeated chameleons darken dynamically during dyadic disputes to
541 decrease danger from dominants. *Behavioral Ecology and Sociobiology* **68**, 1007–
542 1017.
- 543 **Ligon, R. A. and McCartney, K. L.** (2016). Biochemical regulation of pigment motility in
544 vertebrate chromatophores: a review of physiological color change mechanisms.
545 *Current Zoology* **62**, 237–252.
- 546 **Ligon, R. A. and McGraw, K. J.** (2013). Chameleons communicate with complex colour
547 changes during contests: different body regions convey different information. *Biology*
548 *Letters* **9**, 20130892–20130892.
- 549 **Ligon, R. A. and McGraw, K. J.** (2016). Social costs enforce honesty of a dynamic signal of
550 motivation. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20161873.
- 551 **Ligon, R. A. and McGraw, K. J.** (2018). A chorus of color: hierarchical and graded
552 information content of rapid color change signals in chameleons. *Behavioral Ecology*
553 **29**, 1075–1087.
- 554 **Lim, M. L. M., Li, J. and Li, D.** (2007). Effect of UV-reflecting markings on female mate-
555 choice decisions in *Cosmophasis umbratica*, a jumping spider from Singapore.
556 *Behavioral Ecology* **19**, 61–66.
- 557 **Liu, F., Dong, B. Q., Liu, X. H., Zheng, Y. M. and Zi, J.** (2009). Structural color change in
558 longhorn beetles *Tmesisternus isabellae*. *Opt. Express* **17**, 16183.
- 559 **Martin, M., Meylan, S., Haussy, C., Decenci re, B., Perret, S. and Le Galliard, J.-F.**
560 (2016). UV color determines the issue of conflicts but does not covary with individual
561 quality in a lizard. *BEHECO* **27**, 262–270.
- 562 **McGraw, K. J.** (2005). The antioxidant function of many animal pigments: are there
563 consistent health benefits of sexually selected colourants? *Animal Behaviour* **69**, 757–
564 764.
- 565 **McGraw, K. J. and Ardia, D. R.** (2003). Carotenoids, Immunocompetence, and the
566 Information Content of Sexual Colors: An Experimental Test. *The American*
567 *Naturalist* **162**, 704–712.
- 568 **McGraw, K. J. and Hill, G. E.** (2004). Plumage color as a dynamic trait: carotenoid
569 pigmentation of male house finches (*Carpodacus mexicanus*) fades during the
570 breeding season. *Can. J. Zool.* **82**, 734–738.
- 571 **Myhre, L. C., de Jong, K., Forsgren, E. and Amundsen, T.** (2012). Sex Roles and Mutual
572 Mate Choice Matter during Mate Sampling. *The American Naturalist* **179**, 741–
573 755
- Ne as, P.** (1999). *Chameleons: Nature’s Hidden Jewels*. Krieger Pub Co.
- 574 **Nilsson Sk ld, H., Asp ngren, S. and Wallin, M.** (2013). Rapid color change in fish and
575 amphibians - function, regulation, and emerging applications. *Pigment Cell &*
576 *Melanoma Research* **26**, 29–38.
- 577 **Oshima, N., Nakamaru, N., Araki, S. and Sugimoto, M.** (2001). Comparative analyses of
578 the pigment-aggregating and -dispersing actions of MCH on fish chromatophores.

579 *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology* **129**,
580 75–84.

581 **Prötzel, D., Heß, M., Scherz, M. D., Schwager, M., Padje, A. van't and Glaw, F.** (2018).
582 Widespread bone-based fluorescence in chameleons. *Scientific Reports* **8**.

583 **R Core Team** (2019). *R: A Language and Environment for Statistical Computing*. Vienna,
584 Austria: R Foundation for Statistical Computing.

585 **Rick, I. P. and Bakker, T. C. M.** (2008). UV wavelengths make female three-spined
586 sticklebacks (*Gasterosteus aculeatus*) more attractive for males. *Behav Ecol Sociobiol*
587 **62**, 439–445.

588 **Satake, N.** (1980). Effect of methionine-enkephalin on xanthophore aggregation. *Peptides* **1**,
589 73–75.

590 **Sato, M., Ishikura, R. and Oshima, N.** (2004). Direct Effects of Visible and UVA Light on
591 Pigment Migration in Erythrophores of Nile Tilapia. *Pigment Cell Res* **17**, 519–524.

592 **Schantz, T. von, Bensch, S., Grahn, M., Hasselquist, D. and Wittzell, H.** (1999). Good
593 genes, oxidative stress and condition-dependent sexual signals. *Proc. R. Soc. Lond. B*
594 **266**, 1–12.

595 **Siddiqi, A.** (2004). Interspecific and intraspecific views of color signals in the strawberry
596 poison frog *Dendrobates pumilio*. *Journal of Experimental Biology* **207**, 2471–2485.

597 **Simons, M. J. P., Cohen, A. A. and Verhulst, S.** (2012). What Does Carotenoid-Dependent
598 Coloration Tell? Plasma Carotenoid Level Signals Immunocompetence and Oxidative
599 Stress State in Birds—A Meta-Analysis. *PLoS ONE* **7**, e43088.

600 **Smith, K. R., Cadena, V., Endler, J. A., Porter, W. P., Kearney, M. R. and Stuart-Fox,**
601 **D.** (2016). Colour change on different body regions provides thermal and signalling
602 advantages in bearded dragon lizards. *Proceedings of the Royal Society B: Biological*
603 *Sciences* **283**, 20160626.

604 **Stevens, M., Lown, A. E. and Wood, L. E.** (2014). Color change and camouflage in juvenile
605 shore crabs *Carcinus maenas*. *Frontiers in Ecology and Evolution* **2**.

606 **Stuart-Fox, D. and Moussalli, A.** (2008). Selection for Social Signalling Drives the
607 Evolution of Chameleon Colour Change. *PLoS Biol* **6**, e25.

608 **Stuart-Fox, D., Moussalli, A. and Whiting, M. J.** (2008). Predator-specific camouflage in
609 chameleons. *Biology Letters* **4**, 326–329.

610 **Svensson and Wong** (2011). Carotenoid-based signals in behavioural ecology: a review.
611 *Behav* **148**, 131–189.

612 **Taylor, J. D. and Hadley, M. E.** (1970). Chromatophores and color change in the lizard,
613 *Anolis carolinensis*. *Z. Zellforsch.* **104**, 282–294.

614 **Teyssier, J., Saenko, S. V., van der Marel, D. and Milinkovitch, M. C.** (2015). Photonic
615 crystals cause active colour change in chameleons. *Nature Communications* **6**.

- 616 **Tolley, K. A. and Herrel, A.** (2013). *The Biology of Chameleons*. Univ of California Press.
- 617 **Troschianko, J. and Stevens, M.** (2015). Image calibration and analysis toolbox - a free
618 software suite for objectively measuring reflectance, colour and pattern. *Methods Ecol*
619 *Evol* **6**, 1320–1331.
- 620 **Umbers, K. D. L., Fabricant, S. A., Gawryszewski, F. M., Seago, A. E. and Herberstein,**
621 **M. E.** (2014). Reversible colour change in Arthropoda: Arthropod colour change.
622 *Biological Reviews* **89**, 820–848.
- 623 **Vertuani, S., Angusti, A. and Manfredini, S.** (2004). The Antioxidants and Pro-
624 Antioxidants Network: An Overview. *CPD* **10**, 1677–1694.
- 625 **Vorobyev, M. and Osorio, D.** (1998). Receptor noise as a determinant of colour thresholds.
626 *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265**, 351–
627 358.
- 628 **Whiters, P. C.** (1995). Evaporative water loss and colour change in the Australian desert tree
629 frog *Litoria rubella* (Amphibia: Hylidae). *Record of the Western Australian Museum*
630 **17**, 277–281.
- 631 **Whiting, M. J., Stuart-Fox, D. M., O'Connor, D., Firth, D., Bennett, N. C. and**
632 **Blomberg, S. P.** (2006). Ultraviolet signals ultra-aggression in a lizard. *Animal*
633 *Behaviour* **72**, 353–363.
- 634 **Wunderlin, J. and Kropf, C.** (2013). Rapid Colour Change in Spiders. In *Spider*
635 *Ecophysiology* (ed. Nentwig, W.), pp. 361–370. Berlin, Heidelberg: Springer Berlin
636 Heidelberg.
- 637 **Zylinski, S. and Johnsen, S.** (2011). Mesopelagic Cephalopods Switch between
638 Transparency and Pigmentation to Optimize Camouflage in the Deep. *Current Biology*
639 **21**, 1937–1941.
- 640

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

	copulation; hemipenis insertion
--	---------------------------------

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 (25.6)	PC2 (21.1)	PC3 (19.5)	PC4 (9.5)	PC1 (37.4)	PC2 (21.7)	PC3 (14.6)
Variables							
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	10.7 7	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	<0.0 1			
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			

Figure legends

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

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

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

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

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

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

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

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