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Do male panther chameleons use different aspects of color change to settle disputes?

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Abstract

In many animals, males engage in agonistic interactions. Color signals are commonly used to mitigate these potentially harmful interactions. Both pigment-based color and structural color, notably ultraviolet coloration, are used in this context to convey information, including an animal's resource holding potential (RHP) or social status. Despite extensive previous work on this topic, the ability to change color in this context has received relatively little attention. Moreover, no studies to date have considered both the visible and the ultraviolet component of this ability. Thus, whether changes in ultraviolet play a role in the settling of intraspecific disputes remains unknown. Here, we investigate the role of color change during intrasexual agonistic interactions in male panther chameleons (*Furcifer pardalis*). To do so, we combined behavioral experiments and color analysis. Our results show that the outcome of male intrasexual agonistic interactions depends on particular aspects of color change in the visible spectrum. Dominant males exhibit more brightness changes and Euclidian distance changes within the HSV color space at the level of the bands and interbands, suggesting a prominent role of these patterns in panther chameleon communication. Our results also align with previous studies in another species of chameleon, thus supporting the key role of brightness changes in chameleon communication, at least in a competitive context. Interestingly, although our species did exhibit UV coloration neither this coloration nor its changes seem to be involved in intrasexual agonistic interactions among males, possibly because those signals may be used for other purposes like attracting mates, repelling predators, or deception.

Significance statement:

There is a growing body of evidence that animal color change is used for communication. The dynamics of color change have been suggested to play a prominent role in settling agonistic interactions. To date, the ultraviolet component (<400nm) of color change remains largely neglected despite the fact that many animals, including chameleons, can perceive colors in the UV range. Using image analysis techniques, we investigated male *F. pardalis* color change during agonistic interactions, in both the visible and UV range. We demonstrate that male *F. pardalis* settle agonistic interactions through specific aspects of color change. Interestingly, while our species did show UV coloration and UV color change, these appeared not to be involved in settling agonistic interactions.

Keywords: Chameleon, Intrasexual competition, Color signals, Animal communication

INTRODUCTION

In many animal species, males engage in agonistic interactions varying from threat displays to physical fighting. They do so to compete over sexual partners or over resources to attract potential mates. Physical fighting is costly, in terms of energy (Briffa and Sneddon 2007), time, possible injury, and may result in an increase in predation risk (Glass and Huntingford 1988; Kelly and Godin 2001; Briffa and Elwood 2004). To avoid energy expenditure and potential lethal injuries linked to fighting, many species rely on signals to assess the quality of the opponent and to mitigate the outcome of the agonistic interactions (Maynard-Smith and Harper 2003; Briffa 2014). These signals are thought to convey information on fighting ability or overall male strength or quality, often referred to as resource holding potential (RHP) (Parker 1974; Andersson 1994). Individuals may consequentlyassess asymmetries in RHP between themselves and opponents during intrasexual agonistic interactions using these signals (Taylor and Elwood 2003) and thus settle the interaction without escalation.

It has been suggested that intrasexual agonistic interactions may be mediated by color traits, sometimes referred to as badges of status (Rohrlich and Rubin 1975; Maynard-Smith and Harper 2003). These badges can be used to assess the RHP of the opponent if they reflect the social status or dominance of the individual (Whiting et al. 2003; Senar 2006). For example, *Anolis* lizards have been suggested to be able to assess an opponent's bite force by evaluating dewlap color, size, and display rate (Vanhooydonck et al. 2005; Steffen and Guyer 2014). Signal honesty can be maintained by an incorruptible, inherent relationship between signal and quality (*i.e.* relatively "cost-free") or costs associated with signal expression that rely on the quality of the signaller (Zahavi 1975; Searcy and Nowicki 2005; Bradbury and Vehrencamp 2011; Weaver et al. 2017). This cost could be associated with the production and maintenance of signals (i.e. , handicap signals, Searcy and Nowicki 2005). Producing color signals is indeed costly as it involves pigments like carotenoids or melanin which are also involved in the immune response (Griffith et al. 2006) and the oxidative barrier (Henschen et al. 2016). Moreover, the production of melanin-based color is linked to testosterone levels which have an immunodepressive effect (Buchanan et al. 2003; Foo et al. 2017). Therefore, there appears to be a potential trade-off in the pigment allocation into badges of status versus immunocompetence and/or oxidative barriers as predicted by the handicap theory (Zahavi 1975) and the immunocompetence handicap theory (Folstad and Karter 1992). Nevertheless, the cost ensuring signal honesty can also be from a social nature, which is mostly the case for badges of status. Here, the signal honesty is mainly guaranteed by conspecifics imposing a high cost on dishonest individuals through the punishment of those individuals (*i.e.* significantly more aggressive behavior toward cheaters) (Rohwer 1982; Tibbetts and Dale 2004; Tibbetts and Izzo 2010).

Although pigment-based colors have been extensively studied in this context, structural colors are clearly also important, notably ultraviolet (UV) coloration. Over the past decade a growing body of

evidence has been accumulated on the involvement of UV coloration in intrasexual competition and the role of these UV color traits as badges of status (Lim and Li 2013; Xu and Fincke 2015; Martin et al. 2016; Sabol et al. 2017). A higher UV reflectance eappears to convey information onRHP (Stapley and Whiting 2006; Whiting et al. 2006; Tringali and Bowman 2012; Lim and Li 2013), a better immune response (Doucet and Montgomerie 2003; Griggio et al. 2010; Megía-Palma et al. 2016), or a higher testosterone level (Roberts et al. 2009). The signal honesty of UV signals has been suggested to be ensured by the immunocompetence handicap mechanism (Folstad and Karter 1992; Roberts et al. 2009) but mostly through a social cost (Martin et al. 2016).

Interestingly, some animals are able to exhibit rapid color change (in a few minutes or even less than a second) which they may use in the course of intraspecific disputes to communicate (Hutton et al. 2015). This is found in a wide range of taxa: for example, cephalopods (Adamo et al. 2000), lizards (Korzan et al. 2006; Batabyal and Thaker 2017), and insects (Umbers et al. 2013). Nevertheless, most of the studies on the use of color change during social interactions have investigated this ability as a simple ON/OFF feature, without considering the dynamic aspect of color change (*i.e.* speed, temporal variation, direction). Yet, the dynamics of color change likely offer as much communication possibilities and complexity as vocalizations. For example, a previous study by Ligon and McGraw (2013) investigated the role of dynamic color change in intrasexual agonistic interactions in chameleons. They demonstrated not only that chameleons exhibit submissive behavior through the exhibition of darker colors (Ligon 2014) and that brighter colors act as badges of status (Ligon and McGraw 2016), but also that the speed by which the color change occurs matters (Ligon and McGraw 2013). They further suggested that the honesty of this signal is guaranteed by a social cost (Ligon and McGraw 2016). Yet, the UV component of color change has been neglected despite the fact that numerous color changing animals are sensitive to UV (Briscoe and Chittka 2001; Bowmaker 2008), including chameleons (Bowmaker et al. 2005). During intrasexual agonistic interactions, these animals likely do not only show color changes in the visible spectrum, but also in the UV range. This raises the question of whether they rely on color change in the visible range only or on both the visible and UV range to communicate and settle social interactions.

Chameleons (Squamata: *Chameleonidae*) are an excellent biological model to investigate the role of dynamic color change in intrasexual agonistic interactions in both the visible and UV range. Selection for conspicuous signals is likely to have driven the evolution of color displays in this group (Stuart-Fox and Moussalli 2008). Moreover, they are highly territorial animals that often engage in physical and sometimes even deadly fights (Tolley and Herrel 2013). Moreover, some species exhibit complex color changes (Nečas 1999; Tolley and Herrel 2013; Teyssier et al. 2015) that may include changes in hue, brightness and saturation, offering a large color change repertoire. Finally, chameleons are tetrachromatic lizards with UV sensitive photoreceptors ($\lambda_{max} = 375\text{-}385$ nm; Bowmaker *et al.*, 2005).

In the present study, we investigate the role of color change, in the visible and the ultraviolet range, during intrasexual agonistic interactions in panther chameleons (*Furcifer pardalis,* Cuvier 1829*)*. To do so, we staged dyadic agonistic encounters among male *F. pardalis* under appropriate light conditions (*i.e.* including UV) and examined the dynamic color change, during those interactions. We predict that, as in *C. calyptratus* (Ligon and McGraw 2013; Ligon 2014)*,* male *F. pardalis* will rely on brightness changes, to settle agonistic interactions. Moreover, we predict that ultraviolet signals may also be used, as chameleons perceive UV. Finally, we also tested whether saturation and hue changes are involved in settling agonistic interactions among males.

Material and methods

Animals and husbandry

Furcifer pardalis is a diurnal and arboreal lizard, endemic to Madagascar and found in a wide range of habitats along the northern and eastern coasts of Madagascar. This species exhibits a strong sexual dimorphism and considerable intraspecific variation in male coloration: 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 depends on the region of origin and is either termed a "morph" or "locality". Local variation also appears to exist within morphs (Ferguson 2004). For this study, nineteen adult (over six months old) captive-bred male *Furcifer pardalis* of the 'Ambilobe' morph were used.

Animals were kept individually and were visually isolated from one another in mesh terraria (46 x 46 x 91 cm, ReptiBreeze, ZooMed) outfitted with branches and plastic plants to provide hiding spots. Animals were kept in a dedicated room at the Paris Zoo (Parc Zoologique de Paris). The room temperature was maintained at 26°C during the day and the temperature dropped to 22°C at night. 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. The 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) with an automated misting system (Vivaria project) and 20cL drippers.

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 behavioral observations and photo/video recordings. As chameleons are perch-dwelling lizards, we provided artificial branches to simulate an arboreal environment. The overall setup was illuminated with a combination of nine light sources placed 56 cm above the setup

185 as described previously (Dollion et al. 2020). The combination of those different light sources enabled

186 us to cover most of the solar spectrum, including infrared with the halogen bulbs, UVs with the

187 fluorescent tubes, and visible light with the other sources (Fig. S1). Hence, this combination provided

188 a light environment in accordance with the chameleon visual system which includes UVs in the UVA

189 range (Bowmaker et al. 2005). In the middle of the arena, a thin (~0. 7mm) transparent PVC plate (50

190 cm x 100 cm), hereafter called barrier, was placed to prevent direct attacks and injuries while allowing

191 the animals to see one another (Fig. 1).

192 From April 2018 to May 2018 round-robin tournaments were performed to assess the dominance

193 status between our 19 male panther chameleons. Males were split into four groups of four to five

194 different males balanced in size and color pattern, meaning that individuals with similar color patterns

195 (*i.e.* blue bar and red bar) or size were dispatched in different groups. The round-robin was performed

196 within groups, resulting in three to four encounters per male, totalling 42 agonistic interactions. The

197 encounters occurred at room temperature (26°C) from 10 am to 6 pm, corresponding to their daily

198 activity period. The arena was sprayed and cleaned with clear water before each trial to prevent

199 potential effects of odors remaining from a previous trial. Animals were able to interact for 30 minutes

200 unless one of the animals crossed the barrier upon which the trial was halted to avoid physical injury

201 to the animals. The behavior was recorded with an HD camera, HDCR-CX740VE (SONY, Minato-ku,

202 Tokyo, Japan). It was not possible to record data blindly because our study involved focal animals, yet

203 we randomized the order and time of the encounters. Agonistic interaction outcomes were assessed

204 through behavioral observations (Table 1). Animals were considered as "winners" if they succeeded or

205 tried to cross the barrier, if they chased (followed) their opponent from their side, or if they spent most

206 of the interaction trying to climb the barrier (Table 1). Animals were considered as "losers" if they fled

207 from their opponent while trying to maintain a large distance between them. In some cases, individuals

208 exhibited "winner"-like behavior at the beginning of the interaction but then the direction

209 (winner/loser) of the interaction changed. In this case, we only considered the final behavior. We also

210 observed some "ties" where both animals appeared to ignore each other or were facing and trying to

211 fight each other (hitting the barrier violently in turn) until the end of the interaction (Table 1). We

212 chose not to consider these "tie" situations for our statistical analysis as in nature one of the

213 individuals would likely have prevailed.

214 *Color calibration and measurements*

215 During the disputes, pictures of both protagonists were taken twice every two minutes with a full

216 spectrum converted camera, Samsung NX-1000. One picture was taken in the visible range (VIS) and

217 a second in the ultraviolet range (UV) immediately after the first. For pictures in the visible range, a

218 filter blocking ultraviolet and infrared was manually placed in front of the camera (UV/IR cut/L Filter,

219 Baader ©, Mammendorf, Germany) and pictures were taken with a 1/640-second exposure.

7

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 one-second exposure.

For the color calibration in the visual range, a color checker (SpyderCHECKR ™) was photographed while placed at thirteen different regions of the arena, once empty. Color calibration was performed using Adobe Photoshop Lightroom 6, and the SpyderCheckr software (version 1. 2. 2) provided with the SpyderCHECKR ™, following the instructions. As each of the two opponents might be in different regions of the arena, images were cropped to isolate each opponent and then according to the position of the individuals in the arena the corresponding color calibration was applied. Calibrated images were then used for color measurements. As the UV filter imposes a narrow hue range resulting in a constant pink coloration, color calibration was not required for the UV pictures.

Color measurements were performed by retrieving RGB values using the RGB measure tool in ImageJ. We measured fifteen squares of sixteen pixels (NVIS = 8; NUV = 7; Fig. 2), describing the specific color patterns of male *F. pardalis*. In the visual spectrum, we quantified color at the bands (N=3), interbands (N=3) and the lateral line (N=2); in the UV, areas were defined as absorbing UV (N=5) (*i.e.* bands, eyelid and head bony tubercles), or reflecting UV (N=1) (*i.e.* lips) and the lateral line (N=1) (Fig. 2). The lateral line was considered independently because according to the individual and time, it was either absorbing or reflecting 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 Colorscience package (Gamma and Davis 2018). HSV is an alternative representation of the RGB color model that aligns with color-making attributes and color perception, in humans. 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 colors over two time steps (1 and 2) in the 3D HSV color space were calculated (DEHSV) (Eqn 1). The next six derived variables which allow us to describe the color changes occurring during social interactions were computed for each color value (i.e. hue, saturation, brightness, and DEHSV) at each of the fifteen squares selected on the body of the chameleon: the variance, the maximum speed of change between two time steps, the maximum absolute color change (Eqn 2), the overall absolute color change (Eqn 3), the maximum color variation (Eqn 4), and the overall color variation (Eqn 5). DEHSV values enable us to summarise in one measurement the changes occurring in the three dimensions of the HSV color space. All variables (Fig. 3; Dollion et al. 2020) 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.

254 In our formulae x represents a color value (H, S, V or DEHSV); t_{min} represents the beginning of the

255 interaction; t_{max} represents the end of the interaction, t_{xmax} is the time at which x reaches its maximum

256 value; t_{xmin} is the time at which x reaches its minimum value; x_{tmax} is the x value at the end of the

257 interaction; and x_{tmin} is the x valueat the beginning of the interaction. In Eqn 1, H is the hue value, S

258 isthe saturation value and V is the brightness value.

259 $$DEHSV_{x1-x2} = \sqrt{(S_1 \cos H_1 - S_2 \cos H_2)^2 + (S_1 \sin H_1 - S_2 \sin H_2)^2 + (V_1 - V_2)^2} \quad (1)$$

260 $$\frac{X_{max} - X_{min}}{|t_{Xmax} - t_{Xmin}|} \quad (2)$$

261 $$\frac{|X_{tmax} - X_{tmin}|}{t_{max} - t_{min}} \quad (3)$$

262 $$\frac{\sum_{t=t_{Xmin}}^{t_{Xmax}} (|X_{t+1} - X_t|)}{|t_{Xmax} - t_{Xmin}|} \quad (4)$$

263 $$\frac{\sum_{t=t_{min}}^{t_{max}} (|X_{t+1} - X_t|)}{t_{max} - t_{min}} \quad (5)$$

264 We were unable to model the color vision of the panther chameleon because the raw data required to

265 calculate the cone-catch values for visual system modeling (Vorobyev and Osorio 1998; Siddiqi 2004;

266 Troscianko and Stevens 2015) are no longer available for *Furcifer pardalis* (Bowmaker, personal

267 communication).

268 *Statistical analyses*

269 Before analyses, the distribution of each color change variable was transformed where needed using a

270 Box-Cox power function with "AID" package to meet the requirements of a normal distribution (Asar

271 et al. 2017) .

272 We summarized color change information using principal component analysis (PCA) on the centred

273 and scaled individual values of each color change variable with the "ade4" package (Dray and Dufour

274 2007). For the visible range (VIS) all variables were incorporated in the PCA, while for the UV range

275 (UV) only brightness and saturation were used, as hue was constrained by the filter and nearly

276 constant. The number of principal components (PCs) used for the subsequent analyses was chosen

277 using the broken stick method (Legendre and Legendre 1998), while representing at least 70% of the

278 variability and for which the contribution of each variable to PCs provided a relevant interpretation of

279 the color change.

9

280 To determine whether the color change exhibited by an individual could explain the outcome of an

281 intrasexual agonistic interaction, generalized linear mixed-effects models (GLMM) ('glmer') using

282 'lme4' package (Bates et al. 2015) were performed. We tested for the effect of color change (*i.e.* PCs

283 and also maximum brightness and saturation for the UV range) either in the visible range or in the UV

284 range, on the agonistic interaction outcome, considering the male identity and the test order as random

285 factors. These were tested for each body region separately because we found a significant effect of the

286 body region on most of the color change variables ($P <0.01$) in both VIS and UV (See Table S1).

287 Male size (*i.e.* snout-vent-length) was not incorporated in any model as there was no significant effect

288 of male size on the agonistic interaction outcome (GLMM: $X^2=3.77$; *P=0.052*).

289 We evaluated the relative importance (RI) of each predictor variables using model-averaging

290 approaches (Burnham et al. 2011) within model sets for each body region from each spectral range, to

291 build one model per region. From the model averaging results for each region we kept the variables

292 with an RI value exceeding 50%.

293 All statistical analyses were conducted in R version 3.6.1 (R Core Team 2019). Additionally, model

294 selection and model-averaging were undertaken using the R package MuMIn (Barton 2019).

295 **RESULTS**

296 *PCA results and interpretation*

297 In the visible spectrum, the first three principal components accounted for 70.47 % of the total

298 variance. The first principal component (PC1) of our PCA describes hue and saturation changes and

299 the second principal component (PC2) depicted brightness and DEHSV changes (Table 2). The third

300 principal component (PC3) describes brightness changes (Table 2). In the UV, the first two principal

301 components accounted for 73.93 % of the total variability. The first principal component (PC1)

302 represents UV color changes, whereas the second principal (PC2) describes UV brightness changes

303 (Table 2).

304 *Male color change and agonistic interaction outcome*

305 In the visual range, multimodel averaging uncovered PC2 (i.e. brightness & DEHSV changes) as

306 being the best predictor for the band models (RI PC2=95%) and lateral line models (RI PC2=99%;

307 Fig. 4D). Similarly, multimodel averaging on the interbands models uncovered PC1 (i.e. hue and

308 saturation 310 changes) (RI=65%) and PC2 (RI=99%; Fig. 3D) as important predictors. GLMM on

309 those selected 311 models show that males displaying more brightness and DESHV changes (PC2) at

310 the bands (Fig. 4a; Fig. 5a) and the interbands (Fig. 4b; Fig. 5b) are significantly more likely to win.

311 Although a tendency could also be observed for the lateral line, GLMM results are not significant for

312 this body region (Fig. 4c). For the interbands, GLMM results did not show a significant effect of the

313 hue and saturation changes (PC1) on the probability of winning (Fig. 4b). In the UV range,

314 multimodel averaging did not uncover any of our UV variables to be good predictors of the winning

315 probability (i.e. RI< 50%; Fig. 4d; Fig. 6).

DISCUSSION

317 This study highlighted that color change in the visible range plays a key role in agonistic interaction

318 outcomes in male *F. pardalis*. We showed that animals that exhibited more brightness and DEHSV

319 changes (PC2) were more likely to win a contest. These results suggest that brightness changes play a

320 prominent role in agonistic interactions in *F. pardalis*. This is likely the case for chameleons in general

321 as our results align with previously published data for the veiled chameleon (*Chamaeleo calyptratus,*

322 Duméril 1851) (Ligon and McGraw 2013). Similar to our results, the dynamics of the brightness

323 changes matter in *C. calyptratus* (Ligon and McGraw 2013). In this species males that brighten faster

324 were more likely to win a fight. Furthermore, brightness changes affected the likelihood of winning,

325 but only at specific body regions, namely the bands and interbands. Hence, those two regions seem to

326 have significant involvement in communication during agonistic interactions. Contrary to bands and

327 interbands, the lateral line color change did not significantly explain the agonistic interaction outcome

328 in male *F. pardalis*. Therefore, the lateral line appears not be involved in intraspecific communication.

329 Yet, it likely plays a role in antipredator defence as a disruptive coloration pattern (Stevens and

330 Merilaita 2009). To better understand the importance of patterns in communication in chameleons,

331 further studies would benefit from quantifying those patterns using Quantitative Color Pattern

332 Analysis (QPCA) (van den Berg et al. 2020) and doing so across time to investigate pattern changes as

333 well.

334 Our results highlight the dynamic properties of color change, but also pinpoint the importance of the

335 frequency of color change (*i.e.* maximum color variations and overall color variations; *see* Fig. 3). In

336 other words, the number of times an individual changed color. Consequently, what we might observe

337 here is that winners exhibit several brightness changes while losers exhibit a few or only one, namely

338 darkening. During our experiments, we noticed that losers were generally darker than the winners at

339 the end of the interaction. We can hypothesize that, as in *C. calyptratus* (Ligon 2014), male *F.*

340 *pardalis* darken to communicate submission. Submissive behaviors are quite common (Lorenz 1966)

341 and should be favored by natural selection because they would avoid unnecessary expenditure of time

342 and energy on both sides (Matsumura and Hayden 2006). Brightness changes in chameleons are also

343 involved in the context of camouflage in some species of *Bradypodion,* which decrease their

344 brightness when exposed to highly visual predators (Stuart-Fox et al. 2008). Consequently, we might

345 predict chameleons to increase brightness to increase conspicuousness to communicate, or

346 alternatively to decrease it to prevent injuries from conspecifics and from being spotted by predators.

11

Unexpectedly, we found no relationship between UV coloration nor its dynamics and the outcome of intrasexual agonistic interactions, despite its presence in male *F. pardalis* (Fig. 1). This suggests that UV signals are likely not involved in chameleon communication during intrasexual competition, contrary to color changes in visible range. This might be explaining by the fact that our illumination spectrum (Fig. S1) presents a gap (low number of photons) between 360 and 420 nm which corresponds to the peak sensitivity for the chameleon photoreceptors (375-385 nm; Bowmaker et al. 2005). Hence, our individuals may use UV signals, yet our illumination spectrum may not be bright enough for them to detect those. The use of UV within this specific range would be beneficial for this chameleon because 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 UV signals within specific range as private signals, but we were not able to assess this with our experimental design. Even though UV color change might not be involved in agonistic integrations, UV coloration and UV color change may still be involved in chameleon communication in other kinds of social interactions than agonistic. Investigating agonistic intrasexual interactions among males to study the function of rapid color change is of interest and has been studied in detail (Adamo and Hanlon 1996; O'Connor et al. 1999; Korzan et al. 2006; Umbers et al. 2013; Ligon and McGraw 2013; Batabyal and Thaker 2017). However, the role of color change in others contexts like mate choice remains poorly investigated. Yet, a recent study (Dollion et al. 2020) showed that color change is involved in chameleon mate choice and that females seem to rely on color change in both the visible and UV range. Consequently, our understanding of chameleon communication, and more broadly the communication function of rapid color change, will benefit from future studies investigating this phenomenon across diverse social contexts.

Our study would have benefited from using visual modelling (Vorobyev and Osorio 1998; Siddiqi 2004; Troscianko and Stevens 2015) as this would have provided an animal vision perspective of the observed changes in colour. Unfortunately, the raw data required for such analyses were not available at the time of our study (Bowmaker, personal communication). Although the spectral sensitivities of other chameleons, like *Chameleo dilepis*, could have been used, the study of Bowmaker and colleagues (2005) showed that the spectral sensitivity of chameleons may vary greatly between genera. Future studies would obviously benefit from measuring spectral sensitivity in *Fucifer pardalis*. These data could be then use to define color pattern based on the spectral sensitivity of *F. pardalis* using JNDs (Just Noticeable difference) approach (Pike 2012)similarly to Ligon and McGraw (2013), but here taking into account UV range as well. Moreover, given the subspecies diversity and strong dichromatism in *Furcifer pardalis*, it would be of interest to investigate whether the spectral sensitivity differs between subspecies and/or between males and females.

12

381   The cost of different physiological pathways associated with different components of color change

382   may be different. For example, changes in brightness are the result of the dispersion of melanosomes

383   within dermal melanophores. The process of melanosome translocation is assumed to be achieved by

384   the microtubules and actin filaments of the cytoskeleton and the associated motors, kinesin and dynein

385   (Ligon and McCartney 2016). However, these motors consume energy (Hackney 1996), suggesting

386   that brightness changes may be costly. Although the mechanisms through which melanophores and

387   xantho-erythrophores allow color change are very similar, the function of iridiphores is quite different.

388   Iridophores enable color change thanks to the modification of the space between photonic

389   nanostructures, here guanine platelets, within the iridophores (Teyssier et al. 2015; Ligon and

390   McCartney 2016). Iridiphores are thought to be the major actors of color change in the panther

391   chameleon, in which small changes in the space between guanine platelets lead to noticeable

392   differences in color (*i.e.* hue) (Teyssier *et al.* , 2015). Changing the arrangement of guanine platelets

393   might thus be cheaper than manipulating brightness through melanosome translocation. If so, winners

394   might invest more energy in changing brightness, yet the real cost of color change remains unknown

395   to date.

396   To test these ideas, future work should focus on the physiological cost associated with each

397   component of color change. This would provide insight into the information content of this dynamic

398   signal which remains poorly investigated. Along the same vein, color change involves several types of

399   pigments including carotenoids in xantho-erythrophores, and melanins in melanophores; pigments

400   known to play key roles in immunoregulation and immunostimulation, lymphocyte proliferation, and

401   free radical scavenging (Moller et al. 2000; Galván and Solano 2009). Thus, the differences in color

402   change ability observed in this study may be related to high quantities of circulating pigments in

403   dominant individuals. These individuals would then also be able to allocate these pigments to both

404   immune system functioning and antioxidant protection in addition to their use in color signals. It

405   would be interesting to explore this for UVs as well since UV coloration can also reflect individual

406   quality, including immunocompetence (Martín and López 2009; Griggio et al. 2010)and testosterone

407   levels (Roberts et al. 2009).

408   To conclude, this study underlines the importance of brightness changes in the visual spectrum to

409   settle agonistic interactions in male *F. pardalis*. Unexpectedly, UV seems not to be involved in male

410   intrasexual interactions in this species.

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594

595 **Table 1: Ethogram used to determine the outcome of the agonistic interactions.**

Interaction outcomes	Number observed	Description
Win	24	- The individual goes to the barrier, tries to get as close as possible to its opponent by any means (*i.e.* tries to climb the barrier). The opponent exhibits one of the losing behaviors. - The individual spends most of the interaction close to the barrier. The opponent exhibits one of the losing behaviors. - The individual tries to attack its opponent by hitting the barrier. The opponent exhibits one of the losing behaviors. - The individual succeeds in crossing the barrier by pushing it fiercely at the bottom of the arena. The opponent exhibits one of the losing behaviors.
Tie	18	-Both individuals face each other and both hit the barrier fiercely trying to attack the opponent. - Both individuals seem to act indifferently towards the opponent's behaviors.
Lose	24	- The individual stays far from the barrier for most of the interaction. The opponent exhibits one of the winning behaviors. - The individual turns back from its opponent and maintains a large distance from it. The opponent exhibits one of the winning behaviors.

596

Table 2: Contributions of original variables to principal components (PC) retained for further analysis. Components accounted for at least 70% of the total variability. In the visible range (VIS) 3 PCs were kept and accounted for 70.46 % of the total variability. In the ultraviolet range (UV) 2 PCs were kept and accounted for 73.94% of the total variability. Bold values represent high loadings. Variables were computed from the images of the 42 interactions among male *Furcifer pardalis*. In each image, the color was measured from the band, interband, and lateral lines in the range of 400-700nm and from UV absorbing region, UV reflecting region and lateral line in the UV range (320-400nm).

Spectral range	VIS (400-700 nm)			UV (320-400 nm)	
Principal component (% of the variability explained)	PC1	PC2	PC3	PC1	PC2
Variables	**(29.77%)**	**(27.73 %)**	**(12.97 %)**	**(57.96 %)**	**(15.97 %)**
Brightness variance	0.47	**6.06**	**10.36**	4.95	**27.99**
Saturation variance	**9.17**	0.36	0.02	**13.08**	0.87
Hue variance	**7.97**	3.49	0.00		
DEHSV variance	0.09	**8.68**	**6.39**		
Maximum speed of brightness change between two time steps	0.91	**5.68**	**15.21**	**9.27**	**8.83**
Maximum speed of saturation change between two time steps	**8.28**	0.02	2.30	**8.74**	5.15
Maximum speed of hue change between two time steps	**6.97**	4.05	0.55		
Maximum speed of DEHSV change between two time steps	0.35	4.08	0.03		
Maximum Brightness variation	0.69	**7.21**	**8.38**	**9.64**	**9.00**
Maximum Saturation variation	**8.48**	0.05	0.30	**12.59**	0.11
Maximum Hue variation	**8.07**	3.01	0.01		
Maximum DEHSV variation	0.06	**8.79**	1.28		
Maximum absolute Brightness change	0.56	**8.10**	**4.27**	**9.16**	7.45
Maximum absolute Saturation change	**8.36**	0.15	0.32	**9.64**	0.01

Maximum absolute Hue change	**8.11**	2.30	0.53		
Maximum absolute DESHV change	0.25	3.72	**13.66**		
Overall Brightness variation	1.54	**8.46**	**5.28**	5.39	**26.17**
Overall Saturation variation	**10.18**	1.14	0.12	**9.94**	2.67
Overall Hue variations	**9.24**	1.95	0.39		
Overall DESHV variation	0.06	**8.79**	1.28		
Overall absolute Brightness change	0.76	**6.22**	1.97	7.59	0.62
Overall absolute Saturation change	4.11	2.79	**6.42**	0.01	**11.15**
Overall absolute Hue change	**5.11**	0.12	**5.58**		
Overall absolute DEHSV change	0.21	**4.79**	**15.38**		

606

607

Figures captions:

Figure 1: Picture and schematic representation of the experimental setup. a:. Picture of the setup from one of our cameras. **b**: Schematic drawing of the setup showing where the cameras where 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 and **6** = Arcadia T5 D3+ Desert 12% Reptile Fluorescent Lamp (Figure adapted from Dollion *et al.* 2020).

Fig. 2:Color patterns sampled during male-male *F. pardalis* agonistic interactions. As interindividual variation exists. we focused on common patterns. Body regions were characterized 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 characterized 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**)** (Figure adapted from Dollion *et al.* 2020).
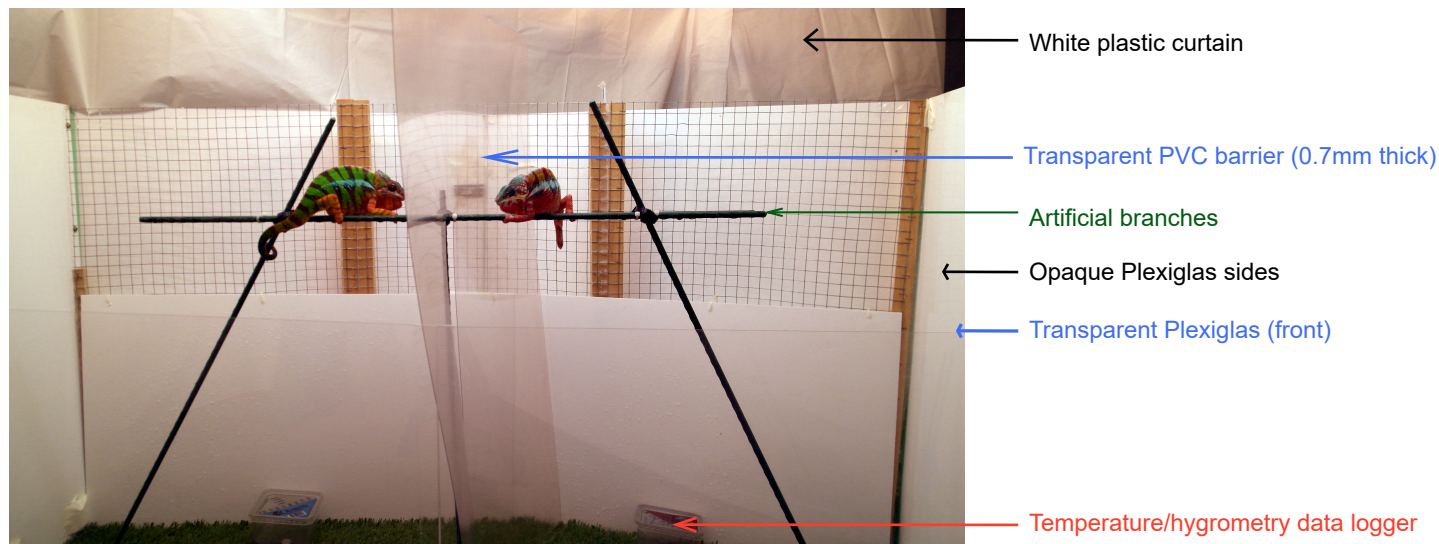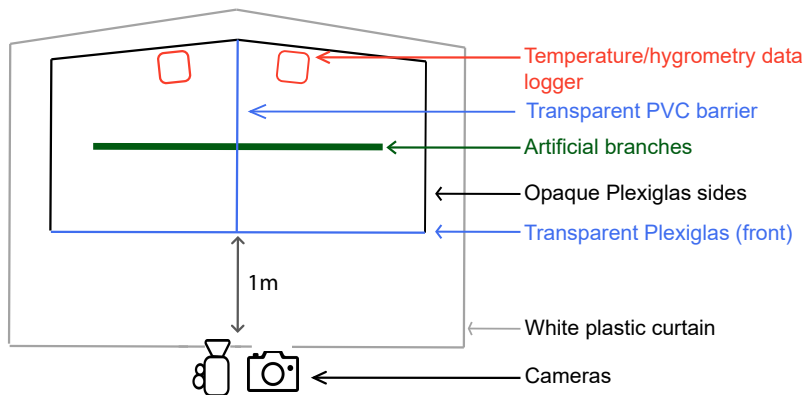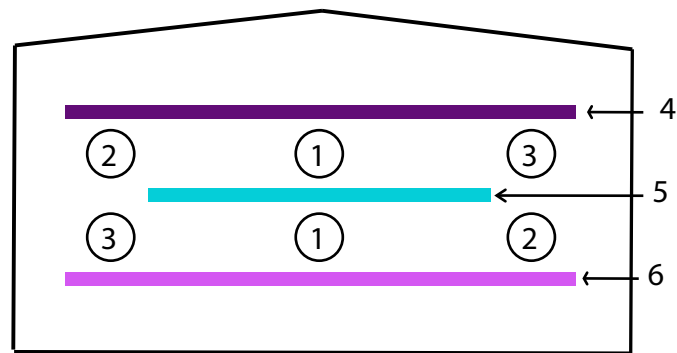
Fig. 3:Schematic representation of the different computed color change variables. Where X represents any color value (*e. g.* hue. saturation. brightness or DEHSV). **a**: Overall color variation in light blue and overall absolute color change in dark blue; **b**: Maximum color variation in light red and maximum absolute color change dark red.

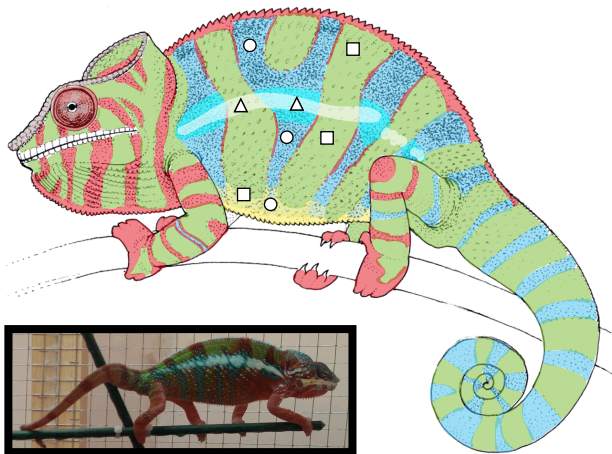**Fig. 4:Relationships between winning probability and color change variables in the visible range (VIS) selected by the model selection by AICc; and the relative importance of color variables to models. based on multimodel averaging. in both visible and UV range.** Ribbons illustrate the 95% confidence interval. A winning probability of 100 % corresponds to "winner", while zero corresponds to "loser". **a**: Relationship between winning probability and color change at the bands. **b**: Relationship between winning probability and color change at the interbands. **c**: Relationship between winning probability and color change at the lateral line and **b**: RI values of color change variables (PCs) in the visible range predicting intrasexual agonistic interaction outcome.

Figure 5: Effect of the color change in the visible range in adult males *F. pardalis* on the outcomes of intrasexual agonistic interaction. Boxplots showing respectively: **a**: Color changes occurring at the bands, **b**: Color changes occurring at the interbands and **c**: Color changes occurring at the lateral line. PC1 = hue and saturation changes, PC2 = brightness and DEHSV changes, PC3 = brightness changes.
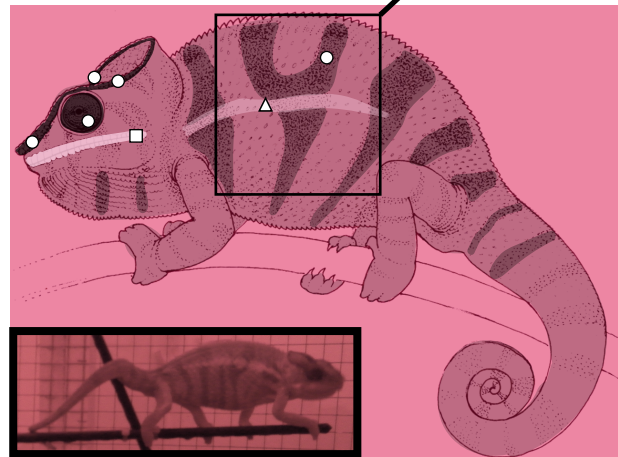
Fig. 6: Effect of the color change in the UV range in adult males *F. pardalis* on the outcomes of intrasexual agonistic interaction. Boxplots showing respectively: **a**: Color changes occurring in regions that absorb UVs, **b**: Color changes occurring in regions that reflect UVs and **c**: Color changes occurring at the lateral line. PC1 = UV color changes. PC2 = UV brightness changes.
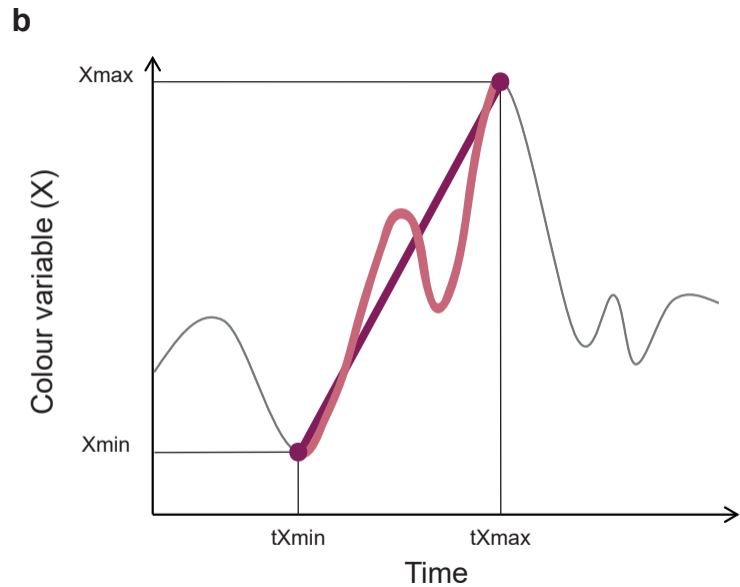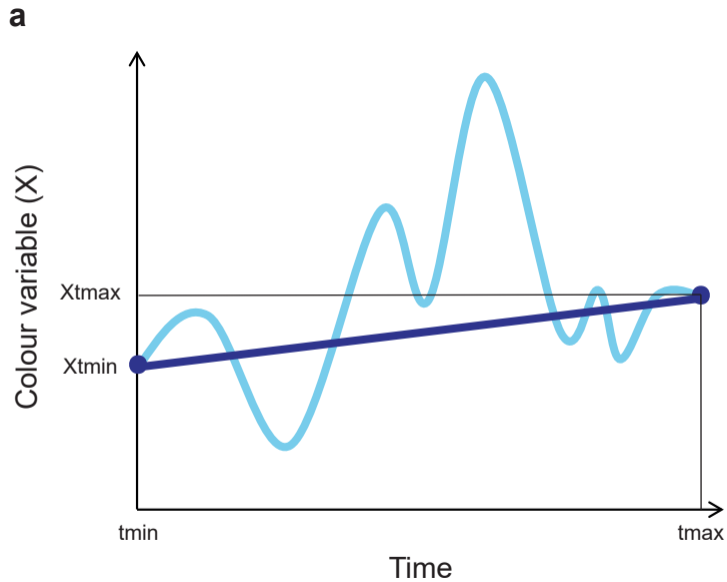
a

White plastic curtain
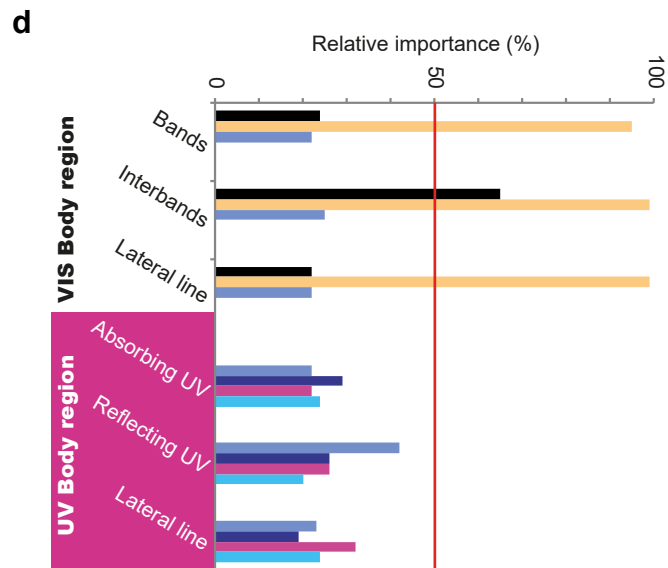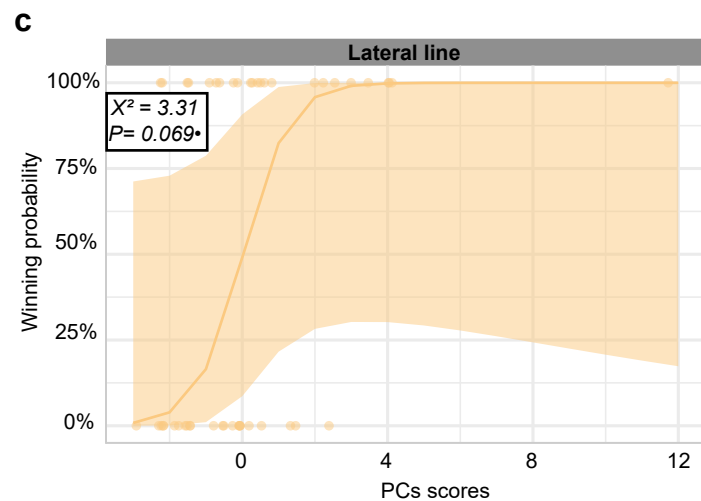
Transparent PVC barrier (0.7mm thick)

Artificial branches

Opaque Plexiglas sides

Transparent Plexiglas (front)

Temperature/hygrometry data logger

b

Temperature/hygrometry data logger

Transparent PVC barrier

Artificial branches

Opaque Plexiglas sides

Transparent Plexiglas (front)

White plastic curtain

Cameras

1m

c

4

② ① ③

5

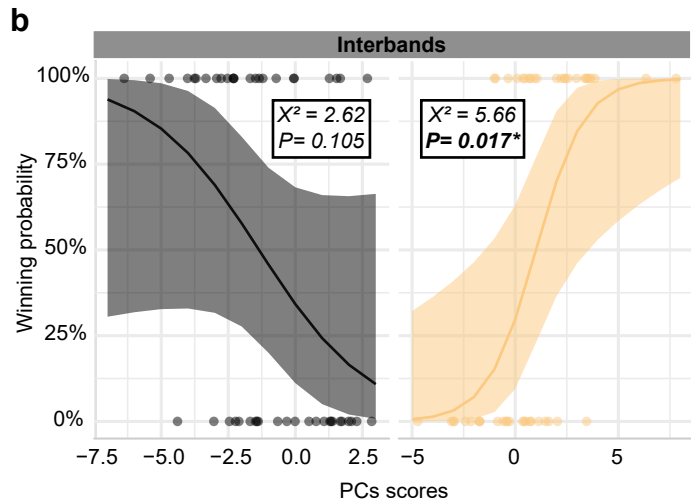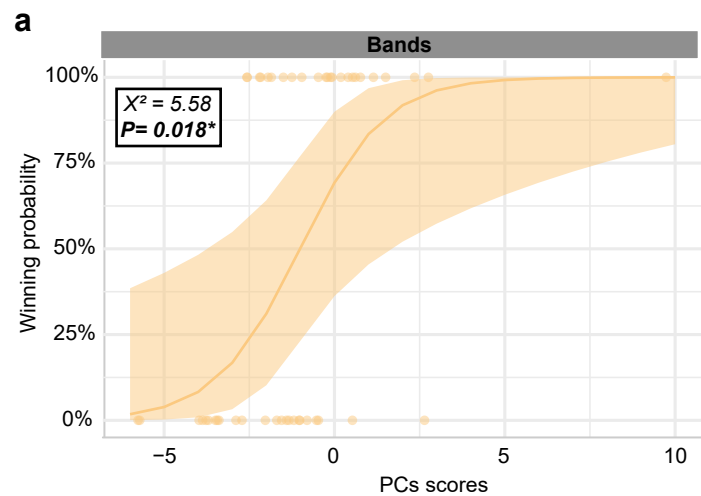③ ① ②

6

UV reflecting lateral line
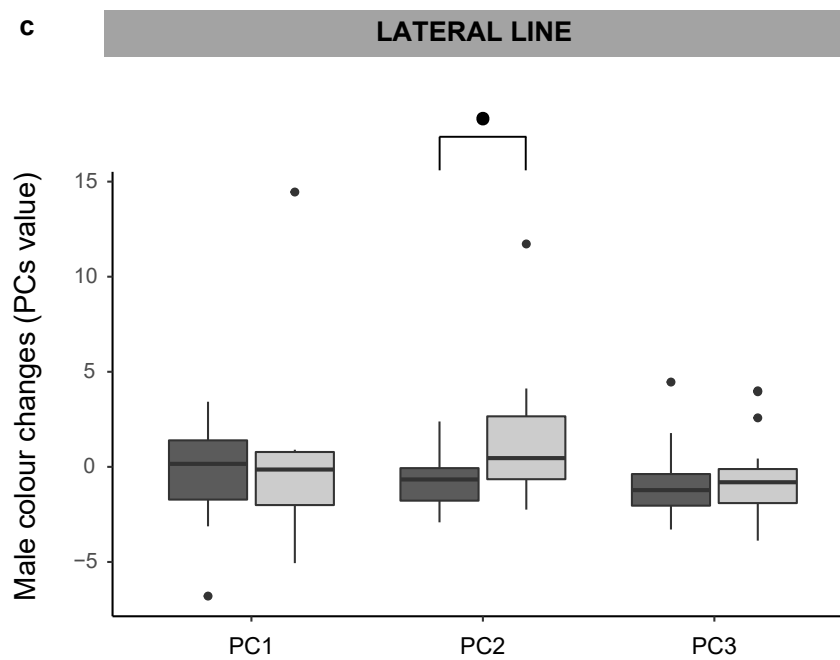
UV absorbing lateral line

Visible (400-700nm)

UV (320-400nm)

a

Colour variable (X)

Xtmax

Xtmin

tmin   tmax

Time

b

Colour variable (X)

Xmax

Xmin

tXmin   tXmax

Time

a Bands

$X^2 = 5.58$
$P = 0.018*$

b Interbands

$X^2 = 2.62$
$P = 0.105$

$X^2 = 5.66$
$P = 0.017*$

c Lateral line

$X^2 = 3.31$
$P = 0.069•$

d Relative importance (%)

VIS Body region
- Bands
- Interbands
- Lateral line

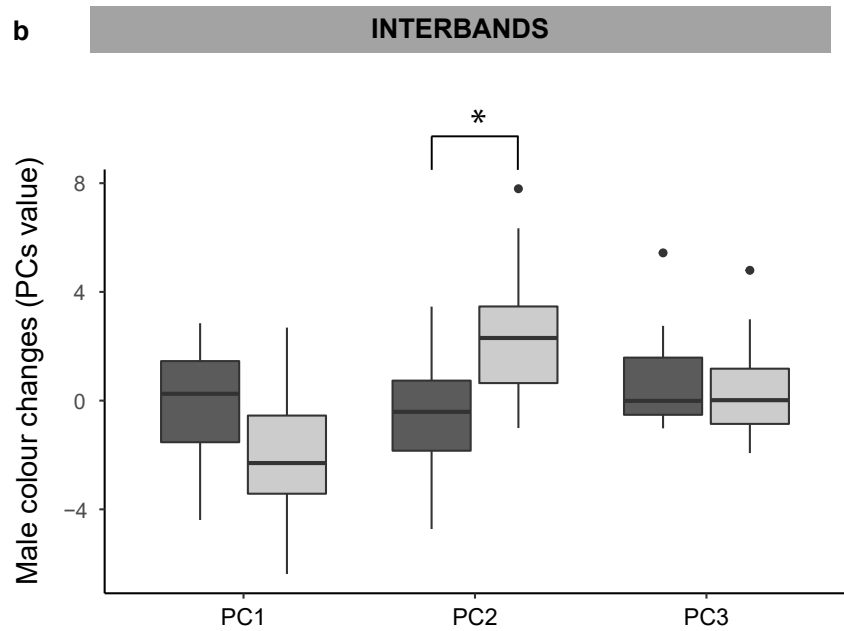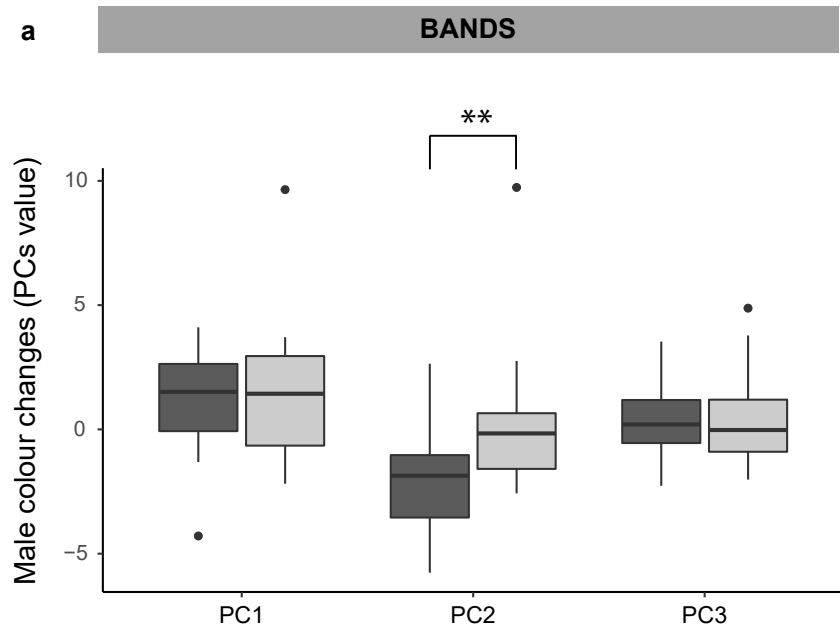UV Body region
- Absorbing UV
- Reflecting UV
- Lateral line

Colour change Variables :

- *Hue & saturation changes (VIS: PC1)*
- *Brightness & DESHV changes (VIS: PC2)*
- *Brightness changes (VIS: PC3; UV: PC2)*
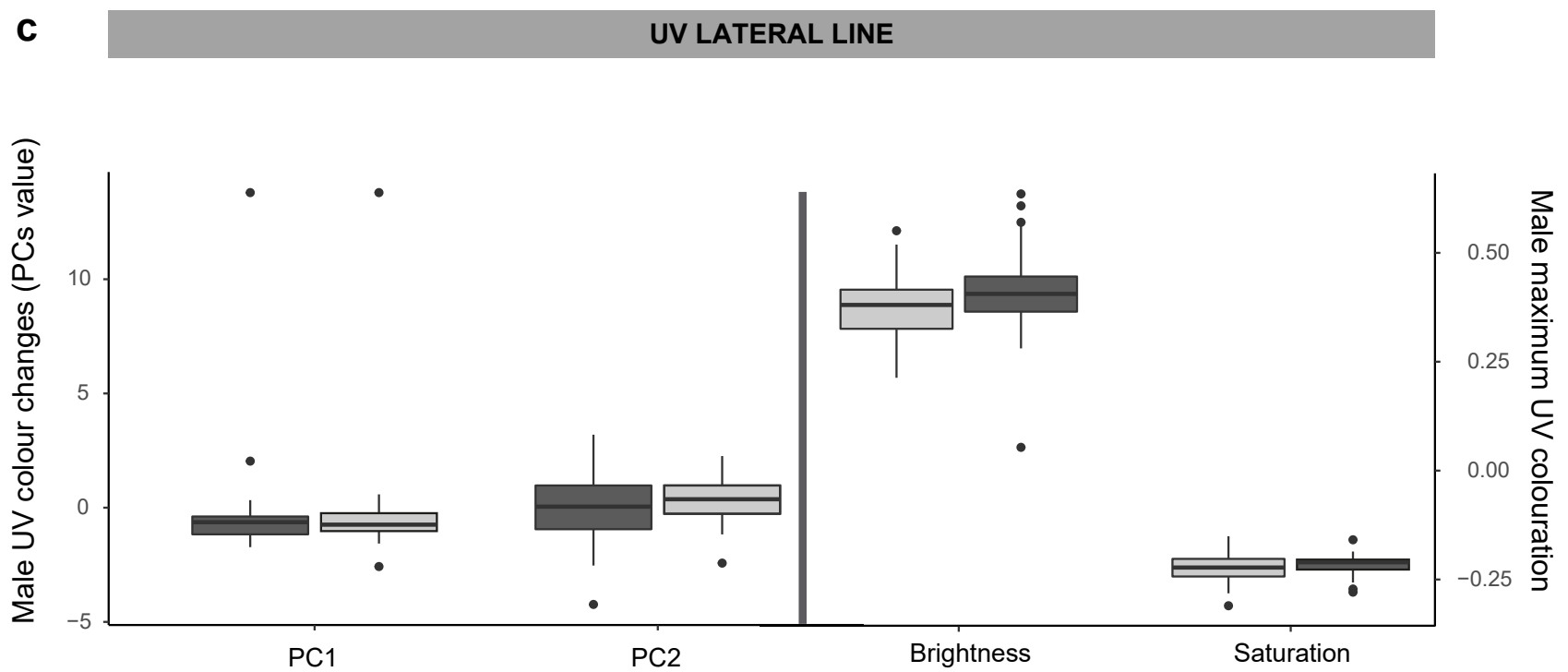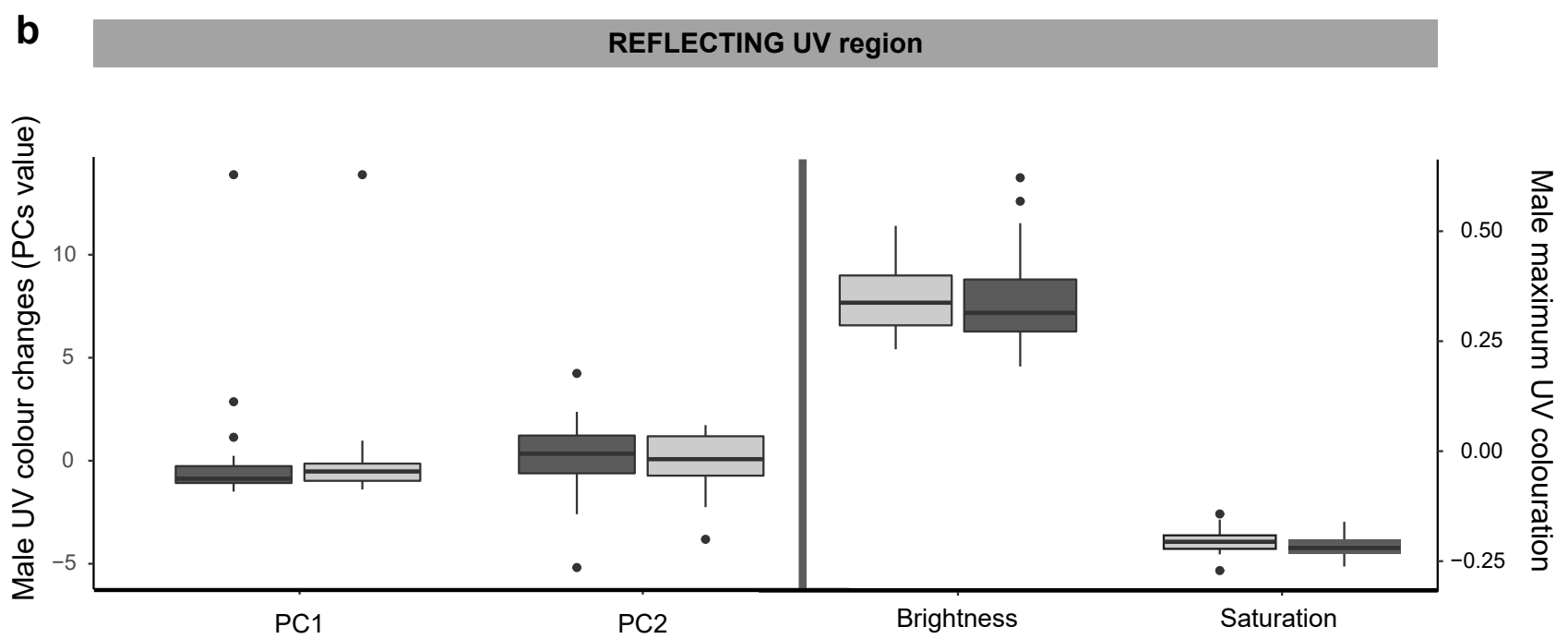- *UV color changes (UV: PC1)*
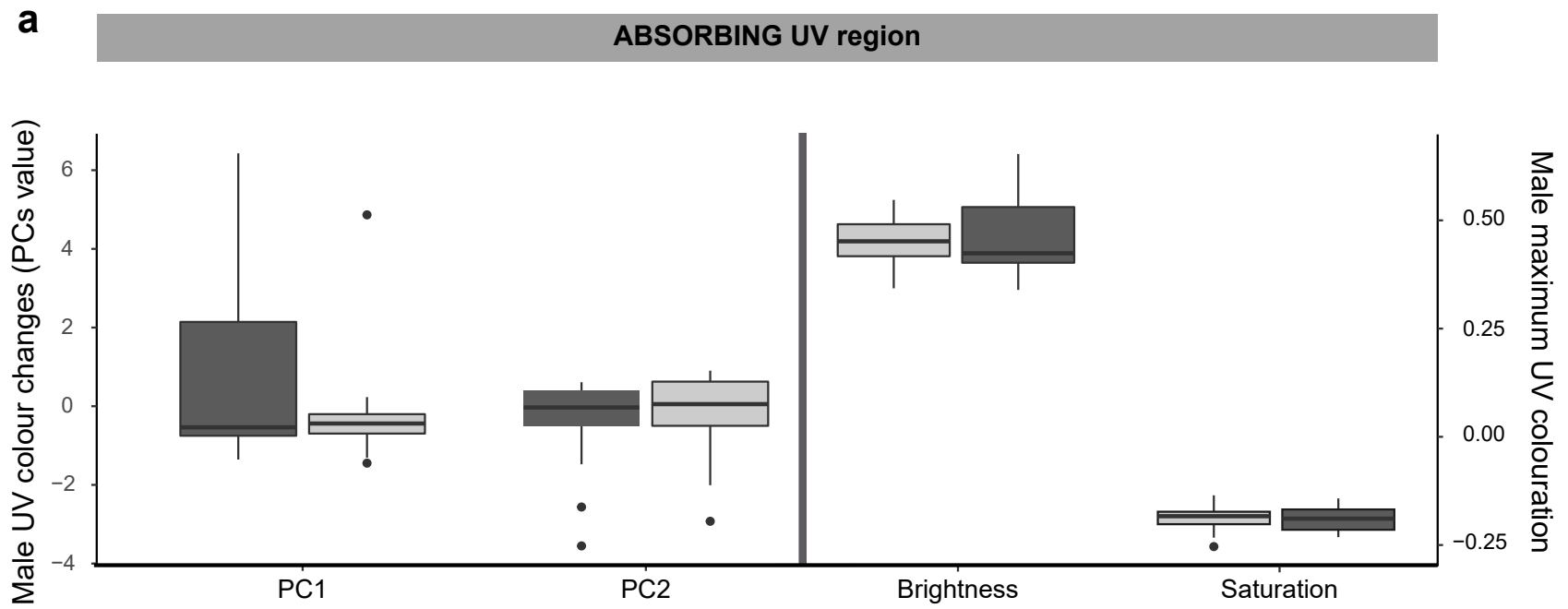- *Maximum UV saturation*
- *Maximum UV brightness*

a BANDS

b INTERBANDS

c LATERAL LINE

Male/male agonistic interaction outcomes :

Winner   Loser

a ABSORBING UV region

b REFLECTING UV region

c UV LATERAL LINE

Male/male agonistic interaction outcomes :

Winner   *Loser*

SUPPLEMENTARY MATERIAL

Do male panther chameleons (*Furcifer pardalis*) use different aspects of colour change in the visible and the ultraviolet range to settle intrasexual agonistic interactions?

running title: Male mate agonistic interaction and colour change

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Table S1. Results of linear mixed-effects models testing for the effect of mate Body region on the color changes variables in both visible and UV range

Spectral range	Color variable	Body region		UV body region	
		$F_{2.123}$	P	$F_{2.122}$	P
VISIBLE	PC1(Hue & Saturation changes)	10.90	**<0.001***		
	PC2(Brightness & DEHSV changes)	12.34	**<0.001***		
	PC3(Brightness changes)	14.04	**<0.001***		
UV	PC1(UV color change changes)			0.12	0.89
	PC2(UV brightness changes)			1.59	0.208
	Maximum UV saturation			23.80	**<0.001***
	Maximum UV brightness			45.29	**<0.001***

Figure S1: Irradiance spectra of the arena used for the behavioural experiments. For irradiance measurements, we used an AvaSpec-2048 spectrometer calibrated between 200 and 850 nm using an Ocean Optics cosine-corrected (CC3-UV) sensor and an optic fiber (FC-UV600-2-ME) calibrated in micromoles per square meter per second with an Avantes AvaLight-DHS deuterium-halogen light source and then converted into microwatt per square centimeter per nanometer. (D= distance from the light sources)