



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

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

Received: 16 July 2021 / Revised: 23 December 2021 / Accepted: 6 January 2022
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

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 have considered the visible and the ultraviolet components of this ability. Thus, whether changes in ultraviolet play a role in settling 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 chameleon species, 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.

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, and possible

injury, and may increase predation risk (Glass and Huntingford 1988; Kelly and Godin 2001; Briffa and Elwood 2004). To avoid energy expenditure and potentially 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 consequently assess 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

Communicated by: Oliver Hawlitschek

✉ Alexis Y. Dollion
dollion.alexis.14340@gmail.com

- 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

2006). For example, *Anolis* lizards have been suggested 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 a signal expression that relies 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 producing and maintaining signals (i.e., handicap signals, Searcy and Nowicki 2005). Producing color signals is costly as it involves pigments like carotenoids or melanin, which are also involved in the immune response (Griffith et al. 2006) and 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 to 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 of 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 by punishing 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 appears to convey information on RHP (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 mainly through a social cost (Martin et al. 2016).

Interestingly, some animals can 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 change is found in a wide range of taxa: for example, cephalopods (Adamo et al. 2000), lizards (Korzán et al. 2006; Batabyal and Thaker 2017), and insects (Umbers et al. 2013). Nevertheless, most 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). Interestingly, the dynamics of color change likely offer as many 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). However, the UV component of color change has been neglected even though 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 show color changes in the visible spectrum and the UV range. This realization 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 ranges. Selection for conspicuous signals is likely to have driven the evolution of this group's color displays (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). Furthermore, some species exhibit complex color changes (Nečas 1999; Tolley and Herrel 2013; Teyssier et al. 2015) including in hue, brightness, and saturation, offering a large color-change repertoire. Finally, chameleons are tetrachromatic lizards with UV-sensitive photoreceptors ($\lambda_{\max} = 375\text{--}385\text{ nm}$; 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 light in the UV range. Finally, we 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 6 months old) captive-bred males *Furcifer pardalis* of the “Ambilobe” morph were used.

Animals were kept individually and were visually isolated from one another in mesh terraria (46 × 46 × 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 40 W heating bulb (Repti Basking Spot, ZooMed) were suspended above each cage. The photoperiod was set at 12/12 h. 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 × 50 × 80 cm) with opaque Plexiglas sides and a front made of transparent Plexiglas of 50 cm high to allow for 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 as described previously (Dollion et al. 2020). Combining the different light sources enabled us to cover most of the solar spectrum, including infrared with the halogen bulbs, UVs with the fluorescent tubes, and visible light with the other sources (Fig. S1). Hence, this combination provided a light environment in accordance with the chameleon visual system, which includes UVs in the UVA range (Bowmaker et al. 2005). In the middle

of the arena, a thin (~0.7 mm) transparent PVC plate (50 cm × 100 cm), hereafter called barrier, was placed to prevent direct attacks and injuries while allowing the animals to see one another (Fig. 1).

From April 2018 to May 2018, round-robin tournaments were performed to assess the dominance status between our 19 male panther chameleons. Males were split into four groups of four to five different males balanced in size and color pattern, meaning that individuals with similar color patterns (i.e., blue bar and red bar) or size were dispatched in different groups. The round-robin was performed within groups, resulting in three to four encounters per male, totaling 42 agonistic interactions. The encounters occurred at room temperature (26 °C) from 10 am to 6 pm, corresponding to their daily activity. The arena was sprayed and cleaned with clear water before each trial to prevent potential effects of odors remaining from a previous trial. Animals were able to interact for 30 min unless one of the animals crossed the barrier upon which the trial was halted to avoid physical injury to the animals. The behavior was recorded with an HD camera, HDCR-CX740VE (SONY, Minato-ku, Tokyo, Japan). It was impossible to record data blindly because our study involved focal animals, yet we randomized the order and time of the encounters. Agonistic interaction outcomes were assessed through behavioral observations (Table 1). Animals were considered as “winners” if they succeeded or tried to cross the barrier, if they chased (followed) their opponent from their side, or if they spent most of the interaction trying to climb the barrier (Table 1). Animals were considered as “losers” if they fled from their opponent while trying to maintain a considerable distance between them. In some cases, individuals exhibited “winner”-like behavior at the beginning of the interaction, but then the direction (winner/loser) of the interaction changed. In this case, we only considered the final behavior. We also observed some “ties” where both animals appeared to ignore each other or were facing and trying to fight each other (hitting the barrier violently in turn) until the end of the interaction (Table 1). We chose not to consider these “tie” situations for our statistical analysis, as, in nature, one of the individuals would likely have prevailed.

Color calibration and measurements

During the disputes, pictures of both protagonists were taken twice every 2 min with a full spectrum converted camera, Samsung NX-1000. One picture was taken in the visible range (VIS) and a second in the ultraviolet range (UV) immediately after the first. For pictures in the visible range, 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-s exposure. Immediately after the picture was taken, the filter

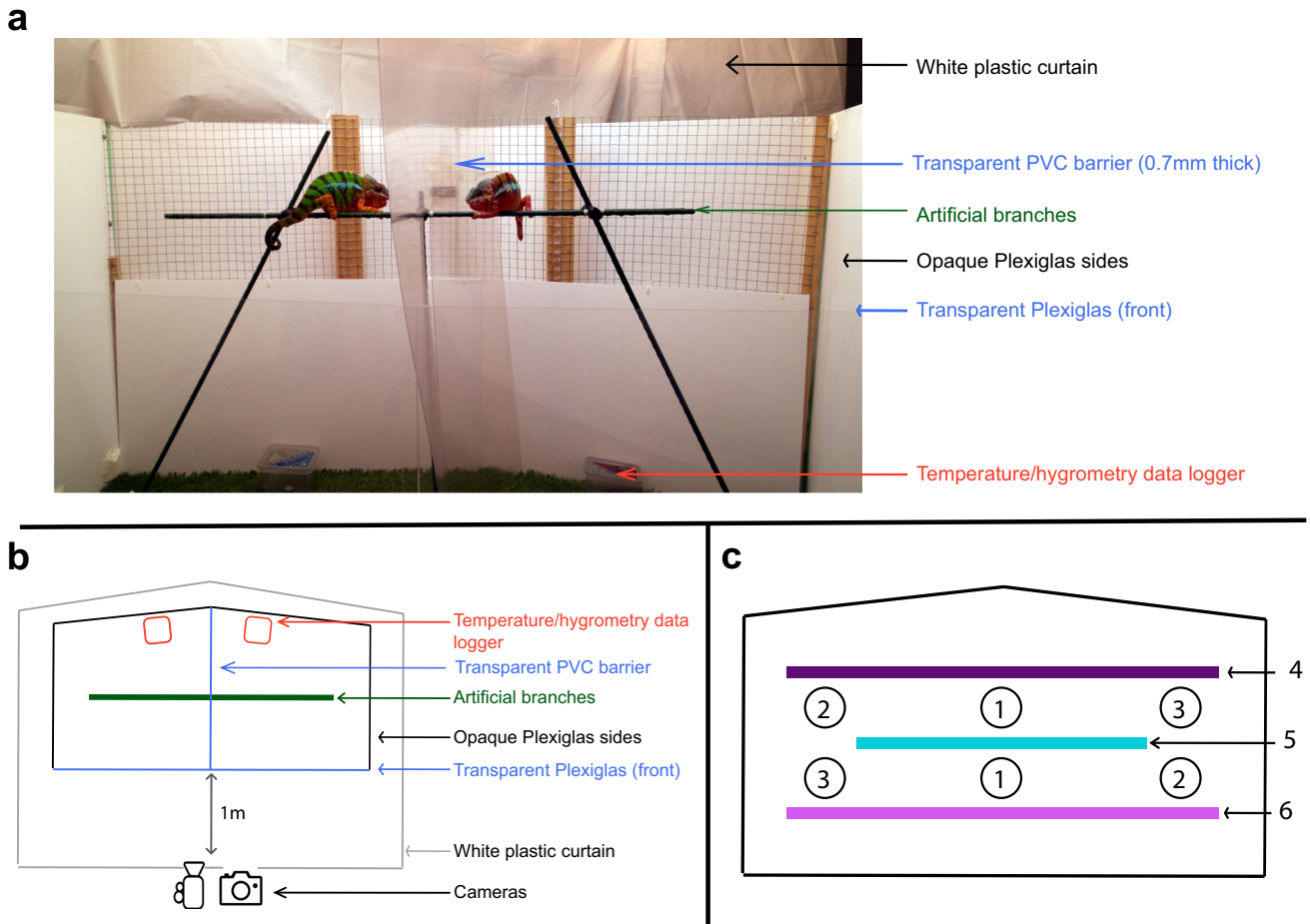


Fig. 1 Picture and schematic representation of the experimental setup. **a** Picture of the setup from one of our cameras. **b** Schematic drawing of the setup showing where the cameras were positioned. **c** Schematic drawing of the light source positions from the top: **1**= 100 Watt. 2800 Kelvin. 1320 lm halogen bulbs, **2**= 60 Watt. 2700

Kelvin incandescent bulbs, **3**=60 Watt. 4000 Kelvin. 806 lm 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 Dolliion et al. 2020)

Table 1 Ethogram used to determine the outcome of the agonistic interactions

Interaction outcomes	Number observed	Description
Win	24	<ul style="list-style-type: none"> - 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	<ul style="list-style-type: none"> -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	<ul style="list-style-type: none"> - 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

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-s 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. 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 it was either absorbing or reflecting UV according to the individual and time. 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 humans' color-making

attributes and color perception. As pictures were taken every 2 min, 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) (Eq. 1). The following 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 (Eq. 2), the overall absolute color change (Eq. 3), the maximum color variation (Eq. 4), and the overall color variation (Eq. 5). DEHSV values enable us to the changes occurring in the three dimensions of the HSV color space in one measurement. All variables (Fig. 3; Dollion et al.2020) were calculated independently for UV 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.

In our formulae, x represents a color value (H, S, V or DEHSV); t_{\min} represents the beginning of the interaction; t_{\max} represents the end of the interaction; $t_{x_{\max}}$ is the time at which x reaches its maximum value; $t_{x_{\min}}$ is the time at which x reaches its minimum value; $x_{t_{\max}}$ is the x value at the end of the interaction; and $x_{t_{\min}}$ is the x value at the beginning of the interaction. In Eq. 1, H is the hue value, S is the saturation value, and V is the brightness value.

$$DEHSV_{t_1 \rightarrow t_2} = \sqrt{(S_1 \cos H_1 - S_2 \cos H_2)^2 + (S_1 \sin H_1 - S_2 \sin H_2)^2 + (V_1 - V_2)^2} \quad (1)$$

Fig. 2 Color patterns sampled during male-male *F. pardalis* agonistic interactions. As inter-individual 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)

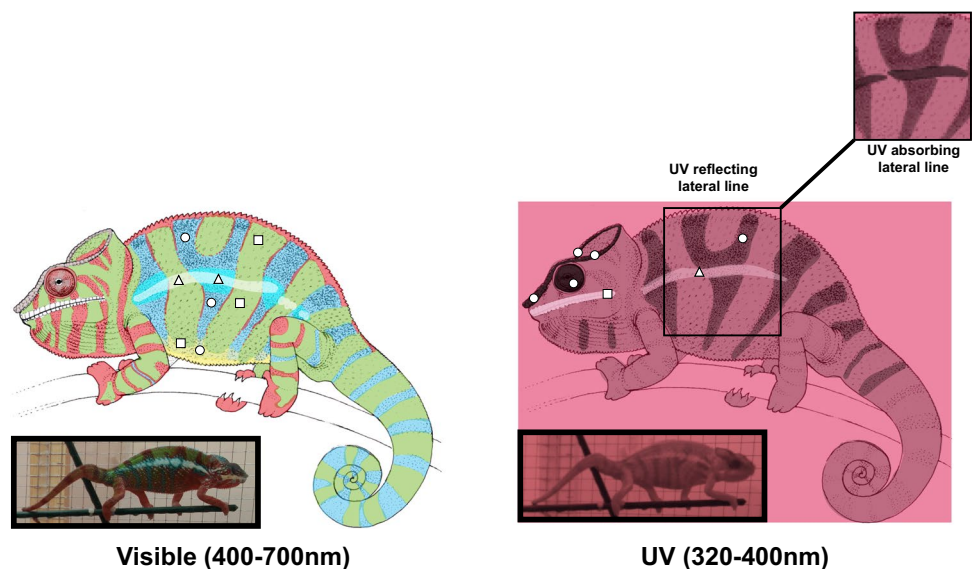
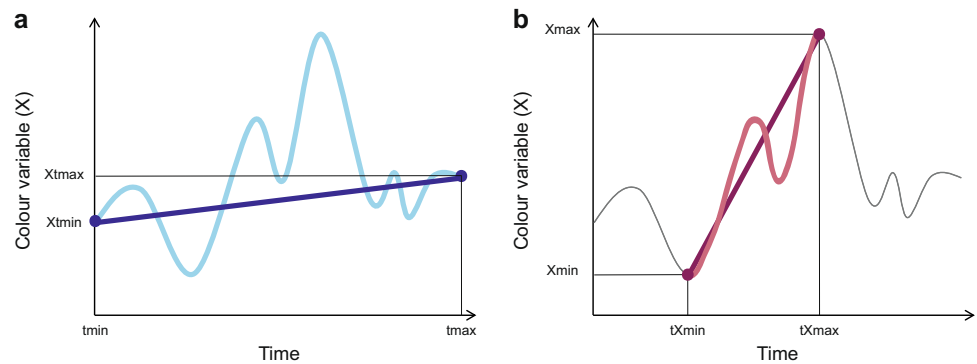


Fig. 3 Schematic representation of the different computed color change variables. Where X represents any color value (e.g., hue, saturation, brightness, or DEHSV). **a** Overall color variation in light blue and overall absolute color change in dark blue. **b** Maximum color variation in light red and maximum absolute color change dark red



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

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

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

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

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

Statistical analyses

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

We summarized color-change information using principal component analysis (PCA) on the centered and scaled individual values of each color change variable with the “ade4” package (Dray and Dufour 2007). For the visible range (VIS), all variables were incorporated in the PCA, while for the UV range (UV), only brightness and saturation were used, as the hue was constrained by the filter and nearly constant. The number of principal components (PCs) used for the subsequent analyses was chosen using the broken stick method (Legendre and Legendre 1998) while representing at least 70% of the variability and for which the contribution

of each variable to PCs provided a relevant interpretation of the color change.

To determine whether the color change exhibited by an individual could explain the outcome of an intrasexual agonistic interaction, generalized linear mixed-effects models (GLMM) (“glmer”) using “lme4” package (Bates et al. 2015) were performed. We tested for the effect of color change (i.e., PCs and maximum brightness and saturation for the UV range) either in the visible range or in the UV range, on the agonistic interaction outcome, considering the male identity and the test order as random factors. These were tested for each body region separately because we found a significant effect of the body region on most of the color change variables ($P < 0.01$) in both VIS and UV (see Table S1). Male size (i.e., snout-vent-length) was not incorporated in any model as there was no significant effect on the agonistic interaction outcome (GLMM: $X^2 = 3.77$; $P = 0.052$).

We evaluated the relative importance (RI) of each predictor variable using model-averaging approaches (Burnham et al. 2011) within model sets for each body region from each spectral range to build one model per region. From the model averaging results for each region, we kept the variables with an RI value exceeding 50%.

All statistical analyses were conducted in R version 3.6.1 (R Core Team 2019); model selection and model-averaging were also undertaken using the R package MuMIn (Barton 2019).

Results

PCA results and interpretation

The first three principal components accounted for 70.47% of the total variance in the visible spectrum. The first principal component (PC1) of our PCA describes hue and saturation changes, and the second principal component (PC2) depicts brightness and DEHSV changes (Table 2). The third principal component (PC3) describes brightness

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 ultra-violet 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 *Furci-fer pardalis*. In each image, the color was measured from the band, interband, and lateral lines in the range of 400–700 nm and from UV-absorbing region, UV-reflecting region, and lateral line in the UV range (320–400 nm)

Spectral range	VIS _(400–700 nm)			UV _(320–400 nm)	
	PC1	PC2	PC3	PC1	PC2
Principal component (% of the variability explained)					
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		

Are in bold the loadings values of the variables that significantly participate to the according PC

changes (Table 2). In the UV, the first two principal components accounted for 73.93% of the total variability. The first principal component (PC1) represents UV color changes, whereas the second principal (PC2) describes UV brightness changes (Table 2).

Male color change and agonistic interaction outcome

In the visual range, multi-model averaging uncovered PC2 (i.e., brightness and DEHSV changes) as being the best predictor for the band models (RI PC2 = 95%) and lateral line models (RI PC2 = 99%; Fig. 4D). Similarly, multi-model averaging on the interbands models uncovered PC1 (i.e., hue and saturation changes) (RI = 65%) and PC2 (RI = 99%; Fig. 3D) as important predictors. GLMM on those selected models show that males displaying more brightness and DESHV changes (PC2) at the bands (Fig. 4a; Fig. 5a) and

the interbands (Fig. 4b; Fig. 5b) are significantly more likely to win. Although a tendency could also be observed for the lateral line, GLMM results are not significant for this body region (Fig. 4c). For the interbands, GLMM results did not show a significant effect of the hue and saturation changes (PC1) on the probability of winning (Fig. 4b). In the UV range, multi-model averaging did not uncover any of our UV variables to be good predictors of the winning probability (i.e., $RI < 50%$; Fig. 4d; Fig. 6).

Discussion

This study highlighted that color change in the visible range plays a key role in agonistic interaction outcomes in male *F. pardalis*. We showed that animals that exhibited more brightness and DEHSV changes (PC2) were more likely to win a contest. These results suggest that

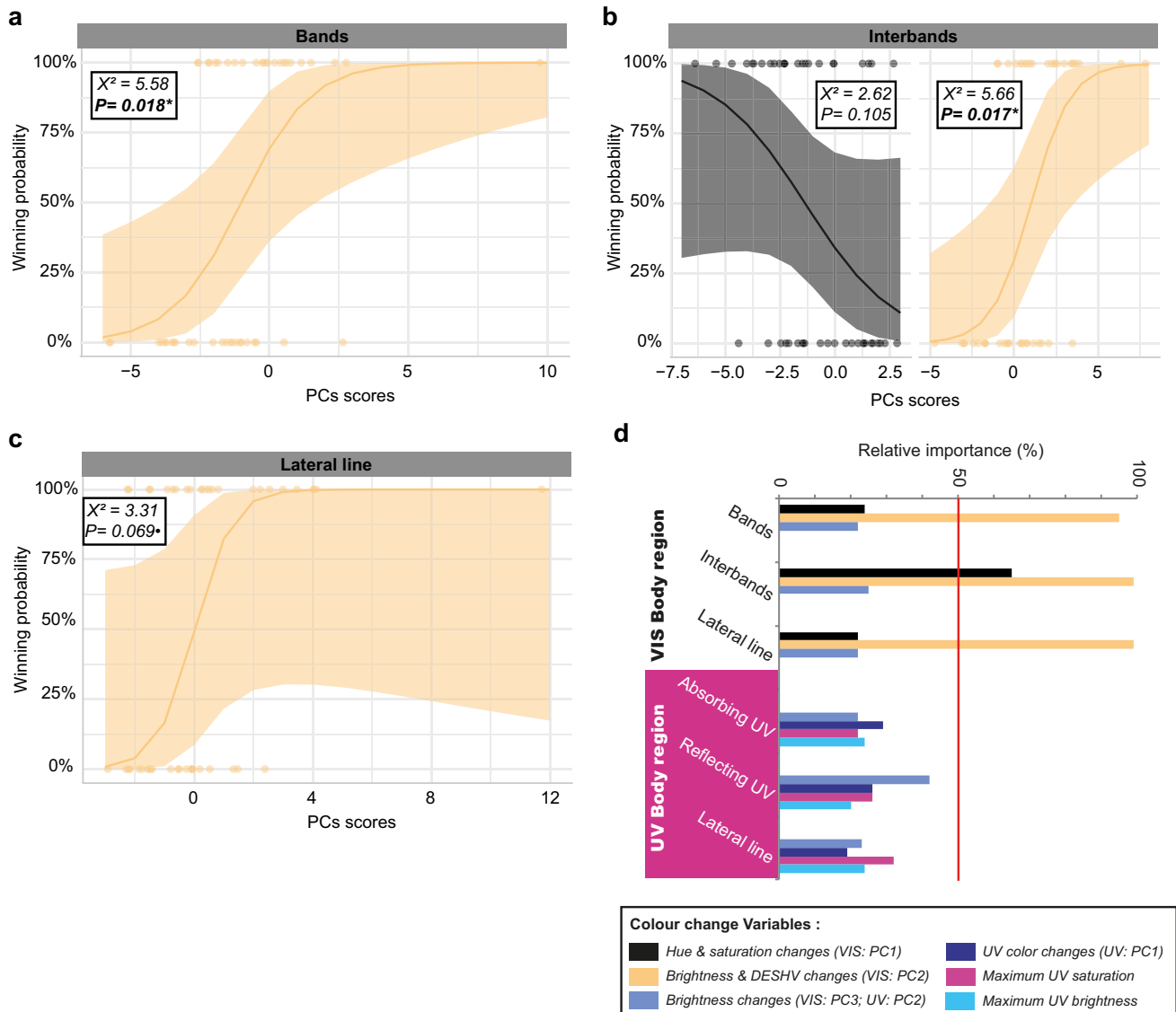


Fig. 4 Relationships between winning probability and color change variables in the visible range (VIS) selected by the model selection by AICc and the relative importance of color variables to models, based on multi-model averaging, in both visible and UV range. Ribbons illustrate the 95% confidence interval. A winning probability of 100% corresponds to “winner,” while zero corresponds to “loser”. **a** Rela-

tionship 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 **d** *RI* values of color change variables (PCs) in the visible range predicting intrasexual agonistic interaction outcome

brightness changes play a prominent role in agonistic interactions in *F. pardalis*. This is likely the case for chameleons in general as our results align with previously published data for the veiled chameleon (*Chamaeleo calypttratus*, Duméril and Duméril 1851) (Ligon and McGraw 2013). Similar to our results, the dynamics of the brightness changes matter in *C. calypttratus* (Ligon and McGraw 2013). In this species, males that brighten faster were more likely to win a fight. Furthermore, brightness changes affected the likelihood of winning, but only at specific body regions, namely the bands and interbands.

Hence, those two regions seem to have significant involvement in communication during agonistic interactions. Contrary to bands and interbands, the lateral line color change did not significantly explain the agonistic interaction outcome in male *F. pardalis*. Therefore, the lateral line appears not to be involved in intraspecific communication. However, it likely plays a role in antipredator defense as a disruptive coloration pattern (Stevens and Merilaita 2009). To better understand the importance of patterns in communication in chameleons, further studies would benefit from quantifying those patterns using quantitative color pattern

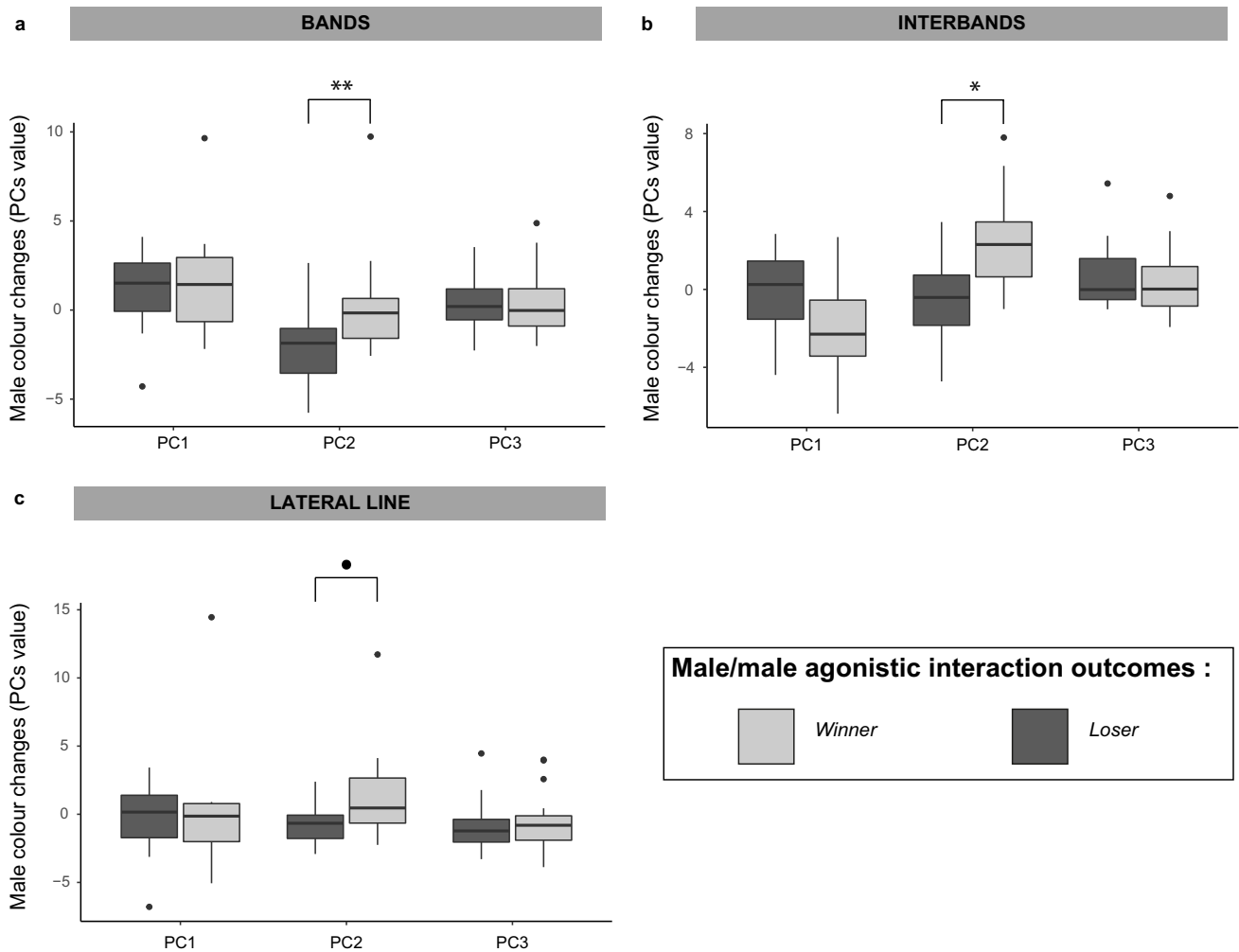


Fig. 5 Effect of the color change in the visible range in adult males *F. pardalis* on the outcomes of intrasexual agonistic interaction. Box-plots showing respectively: **a** Color changes occurring at the bands. **b**

Color changes occurring at the interbands. **c** Color changes occurring at the lateral line. PC1 = hue and saturation changes, PC2 = brightness and DEHSV changes, PC3 = brightness changes

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

Our results highlight the dynamic properties of color change and pinpoint the importance of the frequency of color change (i.e., maximum color variations and overall color variations; see Fig. 3). In other words, the number of times an individual changes color is a, important factor. Consequently, what we might observe here is that winners exhibit several brightness changes while losers exhibit a few or only one, namely darkening. During our experiments, we noticed that losers were generally darker than the winners at the end of the interaction. As in *C. calypttratus* (Ligon 2014), we can hypothesize that male *F. pardalis* darken to communicate submission. Submissive behaviors are quite common (Lorenz 1966) and should be favored by natural selection because they would avoid unnecessary expenditure of time and energy on both sides (Matsumura and Hayden 2006). Brightness changes in

chameleons are also involved in the context of camouflage in some species of *Bradypodion*, which decrease their brightness when exposed to highly visual predators (Stuart-Fox et al. 2008). Consequently, we might predict chameleons to increase their brightness to increase conspicuousness to communicate or to decrease it to prevent injuries from conspecifics and from being spotted by predators.

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 finding suggests that UV signals are likely not involved in chameleon communication during intrasexual competition, contrary to color changes in the visible range. This might be explained 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

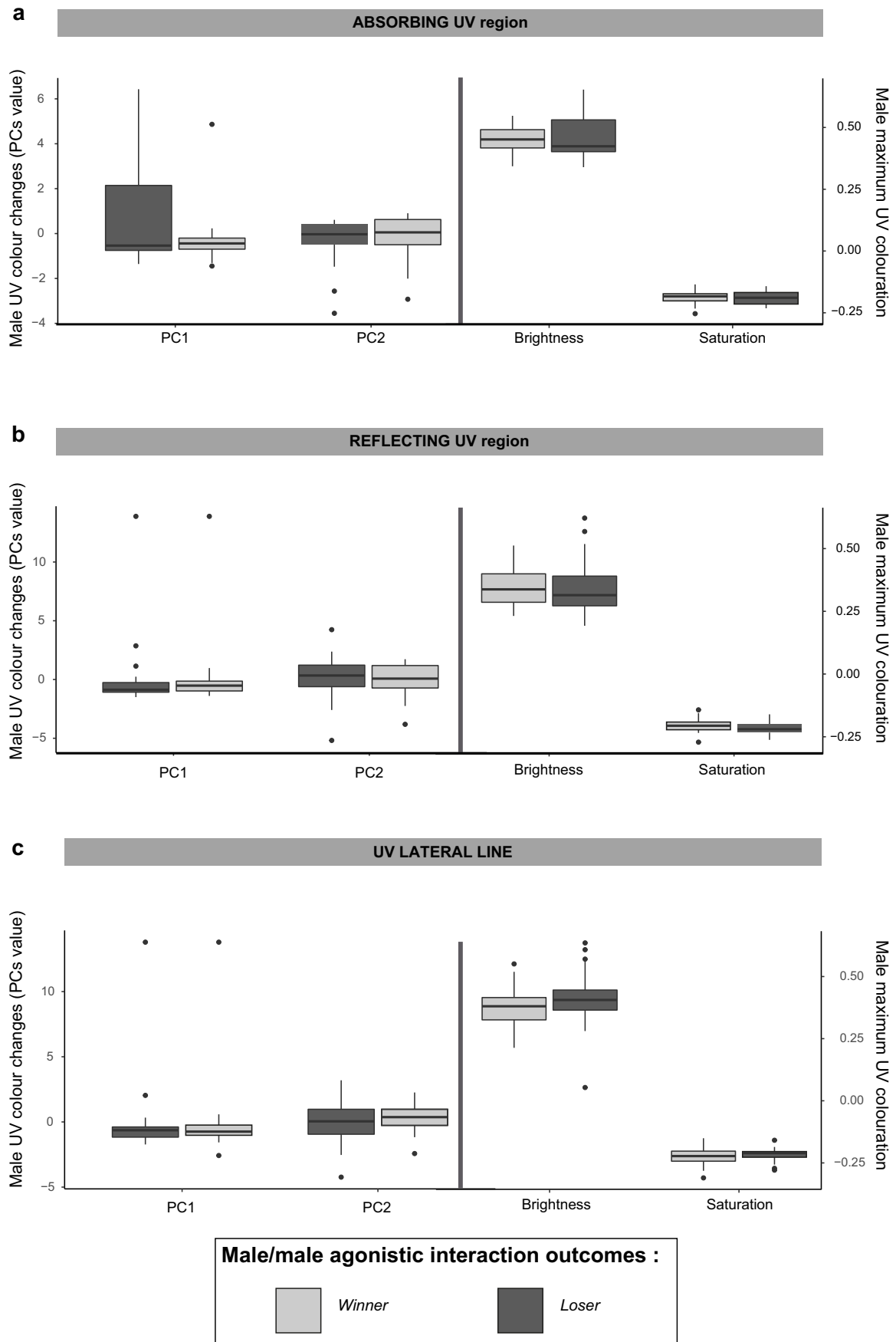


Fig. 6 Effect of the color change in the UV range in adult males *F. pardalis* on the outcomes of intrasexual agonistic interaction. Box-plots showing respectively: **a** Color changes occurring in regions that absorb UVs. **b** Color changes occurring in regions that reflect UVs. **c** Color changes occurring at the lateral line. PC1 = UV-color changes. PC2 = UV-brightness changes

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 our individuals to detect those. The use of UV within this specific range would be beneficial for this chameleon because the spectral range around 430 nm 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 this specific range as private signals, but we could not assess this with our experimental design. Even though UV color change might not be involved in agonistic interactions, 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 other 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 a 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 modeling (Vorobyev and Osorio 1998; Siddiqi 2004; Troscianko and Stevens 2015) as this would have provided an animal vision perspective of the observed color changes. 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 might vary greatly between genera. Future studies would benefit from measuring spectral sensitivity in *Furcifer pardalis*. These data could then be used to define color patterns based on the spectral sensitivity of *F. pardalis* using JND (just noticeable difference) approach (Pike 2012), similarly to Ligon and McGraw (2013) but here taking into account the 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.

The cost of different physiological pathways associated with different components of color change may be different. For example, changes in brightness are the result of the dispersion of melanosomes within dermal melanophores. The process of melanosome translocation is assumed to be achieved by the microtubules and actin filaments of the cytoskeleton and the associated motors, kinesin and dynein (Ligon and McCartney 2016). However, these motors consume energy (Hackney 1996), suggesting that brightness changes may be costly. Although the mechanisms through which melanophores and xantho-erythrophores allow color change are very similar, the function of iridophores is quite different. Iridophores enable color change thanks to the modification of the space between photonic nanostructures, here guanine platelets, within the iridophores (Teyssier et al. 2015; Ligon and McCartney 2016). Iridophores are thought to be the principal actors of color change in the panther chameleon, in which small changes in the space between guanine platelets lead to noticeable differences in color (i.e., hue) (Teyssier et al. 2015). Changing the arrangement of guanine platelets might thus be cheaper than manipulating brightness through melanosome translocation. If so, winners might invest more energy in changing brightness, yet the actual cost of color change remains unknown to date.

To test these ideas, future work should focus on the physiological cost associated with each component of color change. This work would provide insight into the information content of this dynamic signal which remains poorly investigated. Along the same vein, color change involves several types of pigments, including carotenoids in xantho-erythrophores and melanins in melanophores, pigments known to play key roles in immunoregulation, immunostimulation, lymphocyte proliferation, and free radical scavenging (Moller et al. 2000; Galván and Solano 2009). Thus, the differences in color-change ability observed in this study may be related to high quantities of circulating pigments in dominant individuals. These individuals would then also be able to allocate these pigments to both immune system functioning and antioxidant protection in addition to their use in color signals. It would also be interesting to explore this for UVs as UV coloration can also reflect individual quality, including immunocompetence (Martín and López 2009; Griggio et al. 2010) and testosterone levels (Roberts et al. 2009).

To conclude, this study underlines the importance of brightness changes in the visual spectrum to settle agonistic interactions in male *F. pardalis*. Unexpectedly, UV seems not to be involved in male intrasexual interactions in this species.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00114-022-01784-y>.

Acknowledgements We would like to thank Marc Thery for letting us use his spectrophotometer to measure the irradiance spectrum of the experimental arena. We acknowledge 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 Karim Daoues, Cédric Bordes, and Denis Lebonand LoïcLaumalle-Waddy from the “fermetropicale” for their help in providing us with materials for husbandry. We thank Hugues Clamouze and Thierry Decamps for helping us with the experimental arena. Finally, we thank the “Ecole Doctorale Frontières de l’Innovation en Recherche et Education—Programme Bettencourt” for financial support. And, we would like to acknowledge all the reviewers that have reviewed our work and led us to this actual manuscript.

Author contribution Study conception: A. Y. Dollion, S. Meylan and A. Herrel.

Experimental design: A. Y. Dollion, S. Meylan, O. Marquis, and A. Herrel.

Acquisition of data: A. Y. Dollion and M. Leroux-coyau.

Analysis and interpretation of data: A. Y. Dollion, S. Meylan, and A. Herrel.

Drafting of the manuscript: A. Y. Dollion, S. Meylan, and A. Herrel.

Critical revision: A. Y. Dollion, S. Meylan, O. Marquis, and A. Herrel.

Funding This study is financially supported by the “Ecole Doctorale Frontières de l’Innovation en Recherche et Education—Programme Bettencourt,” Université de Paris.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Ethics approval Experiments were carried out in compliance with French legislation, and animals were given regular health checks by zoo veterinarians. Animals were alive and healthy after the experiments and showed no weight loss. Following the directive 2010/63/EU of the European Parliament and French legislation, our study did not require specific authorization because our observations did not cause any pain, suffering, distress, or lasting harm.

Consent to participate Not applicable.

Consent for publication Dr. Alexis Y. Dollion, Pr. Sandrine Meylan, Dr. Olivier Marquis, Mr. Mathieu Leroux-Coyau, and Dr. Anthony Herrel, authors of the following article entitled “Do male panther chameleons (*Furcifer pardalis*) use different aspects of color change in the visible and the ultraviolet range to settle intrasexual agonistic interactions?”, acknowledge and consent to the submission of the article to *The Science of Nature* journal and its later potential publication in *The Science of Nature*.

Conflict of interest The authors declare no competing interests.

References

- Adamo SA, Brown WM, King AJ et al (2000) Agonistic and reproductive behaviours of the cuttlefish *Sepia officinalis* in a semi-natural environment. *J Molluscan Stud* 66:417–418
- Andersson M (1994) Coloration and other visual signals. In: *Sexual Selection*. Princeton University Press, Princeton, New-Jersey
- Asar Ö, İlk O, Dag O (2017) Estimating Box-Cox power transformation parameter via goodness-of-fit tests. *Commun Stat Simul Comput* 46:91–105. <https://doi.org/10.1080/03610918.2014.957839>
- Barton K (2019) MuMIn: multi-model inference. Version 1. 43. 6URL <https://CRAN.R-project.org/package=MuMIn>
- Batabyal A, Thaker M (2017) Signalling with physiological colours: high contrast for courtship but speed for competition. *Anim Behav* 129:229–236. <https://doi.org/10.1016/j.anbehav.2017.05.018>
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. arXiv preprint arXiv: 1406.5823
- Bowmaker JK (2008) Evolution of vertebrate visual pigments. *Vision Res* 48:2022–2041. <https://doi.org/10.1016/j.visres.2008.03025>
- Bowmaker JK, Loew ER, Ott M (2005) The cone photoreceptors and visual pigments of chameleons. *J Comp Physiol A* 191:925–932. <https://doi.org/10.1007/s00359-005-0014-4>
- Bradbury JW, Vehrencamp SL (2011) *Principles of animal communication*, 2nd edn. Sinauer Associates, Sunderland, Massachusetts
- Briffa M, Elwood RW (2004) Use of energy reserves in fighting hermit crabs. *Proc R Soc Lond B* 271:373–379. <https://doi.org/10.1098/rspb.2003.2633>
- Briffa M, Sneddon LU (2007) Physiological constraints on contest behaviour. *Funct Ecol* 21:627–637. <https://doi.org/10.1111/j.1365-2435.2006.01188.x>
- Briffa M (2014) Agonistic signals: integrating analysis of functions and mechanisms. In: J. Irschick D, Briffa M, Podos J (eds) *Animal Signaling and Function*. John Wiley & Sons, Inc., Hoboken, pp 141–173
- Briscoe AD, Chittka L (2001) The evolution of color vision in insects. *Ann Rev Entomol* 46:471–510
- Buchanan KL, Evans MR, Goldsmith AR (2003) Testosterone, dominance signalling and immunosuppression in the house sparrow, *Passer domesticus*. *Behav Ecol Sociobiol* 55:50–59. <https://doi.org/10.1007/s00265-003-0682-4>
- Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav Ecol Sociobiol* 65:23–35. <https://doi.org/10.1007/s00265-010-1029-6>
- Dollion AY, Herrel A, Marquis O et al (2020) The colour of success: does female mate choice rely on male colour change in the chameleon *Furcifer pardalis*? *J Exp Biol* 223:jeb224550. <https://doi.org/10.1242/jeb.224550>
- Doucet SM, Montgomerie R (2003) Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. *Behav Ecol* 14:503–509. <https://doi.org/10.1093/beheco/arg035>
- Dray S, Dufour A-B (2007) The ade4 package: implementing the duality diagram for ecologists. *J Stat Softw* 22:1–20
- Duméril C, Duméril AHA (1851) *Catalogue méthodique de la collection des reptiles* (Vol. 2). Gide et Baudry
- Ferguson G (2004) *The Panther chameleon: color variation, natural history, conservation, and captive management*. Krieger Pub. Co., Malabar
- Folstad I, Karter AJ (1992) Parasites, bright males, and the immunocompetence handicap. *Am Nat* 139:603–622
- Foo YZ, Nakagawa S, Rhodes G, Simmons LW (2017) The effects of sex hormones on immune function: a meta-analysis. *Biol Rev* 92:551–571. <https://doi.org/10.1111/brv.12243>

- Galván I, Solano F (2009) The evolution of eu- and pheomelanin traits may respond to an economy of pigments related to environmental oxidative stress. *Pigment Cell Melanoma Res* 22:339–342. <https://doi.org/10.1111/j.1755-148X.2009.00559.x>
- Gamma J, Davis G (2018) *Colorscience : color science methods and data*. Version v1. 0. <https://CRAN.R-project.org/package=colourscience>
- Glass CW, Huntingford FA (1988) Initiation and resolution of fights between swimming crabs (*Liocarcinus depurator*). *Ethology* 77:237–249. <https://doi.org/10.1111/j.1439-0310.1988.tb00207.x>
- Griffith SC, Parker TH, Olson VA (2006) Melanin- versus carotenoid-based sexual signals: is the difference really so black and red? *Anim Behav* 71:749–763. <https://doi.org/10.1016/j.anbehav.2005.07.016>
- Griggio M, Zanollo V, Hoi H (2010) UV plumage color is an honest signal of quality in male budgerigars. *Ecol Res* 25:77–82. <https://doi.org/10.1007/s11284-009-0632-3>
- Hackney DD (1996) The kinetic cycles of myosin, kinesin, and dynein. *Annu Rev Physiol* 53:731–750
- Henschen AE, Whittingham LA, Dunn PO (2016) Oxidative stress is related to both melanin- and carotenoid-based ornaments in the common yellowthroat. *Funct Ecol* 30:749–758. <https://doi.org/10.1111/1365-2435.12549>
- Hutton P, Seymoure BM, McGraw KJ et al (2015) Dynamic color communication. *Curr Opin Behav Sci* 6:41–49. <https://doi.org/10.1016/j.cobeha.2015.08.007>
- Kelly CD, Godin J-GJ (2001) Predation risk reduces male-male sexual competition in the Trinidadian guppy (*Poecilia reticulata*). *Behav Ecol Sociobiol* 51:95–100. <https://doi.org/10.1007/s002650100410>
- Korzan WJ, Øverli Ø, Summers CH (2006) Future social rank: forecasting status in the green anole (*Anolis carolinensis*). *Acta Ethol* 9:48–57. <https://doi.org/10.1007/s10211-006-0015-5>
- Legendre P, Legendre L (1998) *Numerical ecology*, 2nd english edn. Elsevier, Amsterdam
- Ligon RA (2014) Defeated chameleons darken dynamically during dyadic disputes to decrease danger from dominants. *Behav Ecol Sociobiol* 68:1007–1017. <https://doi.org/10.1007/s00265-014-1713-z>
- Ligon RA, McCartney KL (2016) Biochemical regulation of pigment motility in vertebrate chromatophores: a review of physiological color change mechanisms. *Curr Zool* 62:237–252. <https://doi.org/10.1093/cz/zow051>
- Ligon RA, McGraw KJ (2013) Chameleons communicate with complex colour changes during contests: different body regions convey different information. *Biol Lett* 9:20130892–20130892. <https://doi.org/10.1098/rsbl.2013.0892>
- Ligon RA, McGraw KJ (2016) Social costs enforce honesty of a dynamic signal of motivation. *Proc R Soc B* 283:20161873. <https://doi.org/10.1098/rspb.2016.1873>
- Lim MLM, Li D (2013) UV-green iridescence predicts male quality during jumping spider contests. *PLoS ONE* 8:e59774. <https://doi.org/10.1371/journal.pone.0059774>
- Lorenz K (1966) *On aggression*, 1st edn. Methuen & Co., London
- Martin M, Meylan S, Haussy C et al (2016) UV color determines the issue of conflicts but does not covary with individual quality in a lizard. *BEHECO* 27:262–270. <https://doi.org/10.1093/beheco/arv149>
- Martín J, López P (2009) Multiple color signals may reveal multiple messages in male Schreiber's green lizards, *Lacerta schreiberi*. *Behav Ecol Sociobiol* 63:1743–1755. <https://doi.org/10.1007/s00265-009-0794-6>
- Matsumura S, Hayden TJ (2006) When should signals of submission be given?—A game theory model. *J Theor Biol* 240:425–433. <https://doi.org/10.1016/j.jtbi.2005.10.002>
- Maynard-Smith J, Harper D (2003) *Animal signals*. Oxford University Press, Oxford
- Megía-Palma R, Martínez J, Merino S (2016) A structural colour ornament correlates positively with parasite load and body condition in an insular lizard species. *Sci Nat* 103:52. <https://doi.org/10.1007/s00114-016-1378-8>
- Moller AP, Biard C, Blount JD et al (2000) Carotenoid-dependent signals: indicators of foraging efficiency, immunocompetence or detoxification ability? *Avian Poult Biol Rev* 11:137–160
- Nečas P (1999) Chameleons: nature's hidden jewels. Krieger Pub Co
- Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. *J Theor Biol* 47:223–243. [https://doi.org/10.1016/0022-5193\(74\)90111-8](https://doi.org/10.1016/0022-5193(74)90111-8)
- Pike TW (2012) Preserving perceptual distances in chromaticity diagrams. *Behav Ecol* 23:723–728. <https://doi.org/10.1093/beheco/ars018>
- R Core Team (2019) *R: A language and environment for statistical computing*. Version 3.6.1. The R Foundation for Statistical Computing
- Roberts ML, Ras E, Peters A (2009) Testosterone increases UV reflectance of sexually selected crown plumage in male blue tits. *Behav Ecol* 20:535–541. <https://doi.org/10.1093/beheco/arp028>
- Rohrlich ST, Rubin RW (1975) Biochemical characterization of crystals from the dermal iridophores of a chameleon *Anolis carolinensis*. *J Cell Biol* 66:635–645. <https://doi.org/10.1083/jcb.66.3.635>
- Rohrer S (1982) The evolution of reliable and unreliable badges of fighting ability. *Am Zool* 22:531–546. <https://doi.org/10.1093/icb/22.3.531>
- Sabol AC, Hellmann JK, Gray SM, Hamilton IM (2017) The role of ultraviolet coloration in intrasexual interactions in a colonial fish. *Anim Behav* 131:99–106. <https://doi.org/10.1016/j.anbehav.2017.06.027>
- Searcy WA, Nowicki S (2005) *The evolution of animal communication : reliability and deception in signaling systems*. Princeton University Press, Princeton, Oxford
- Senar JC (2006) Color displays as intrasexual signals of aggression and dominance. In: *Bird Coloration: Function and evolution*. Harvard University Press, pp 87–136
- Siddiqi A (2004) Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J Exp Biol* 207:2471–2485. <https://doi.org/10.1242/jeb.01047>
- Stapley J, Whiting MJ (2006) Ultraviolet signals fighting ability in a lizard. *Biol Lett* 2:169–172. <https://doi.org/10.1098/rsbl.2005.0419>
- Steffen JE, Guyer CC (2014) Display behaviour and dewlap colour as predictors of contest success in brown anoles. *Biol J Linn Soc* 111:646–655. <https://doi.org/10.1111/bij.12229>
- Stevens M, Merilaita S (2009) Defining disruptive coloration and distinguishing its functions. *Philo Trans R Soc B* 364:481–488. <https://doi.org/10.1098/rstb.2008.0216>
- Stuart-Fox D, Moussalli A (2008) Selection for social signalling drives the evolution of chameleon colour change. *Plos Biol* 6:e25. <https://doi.org/10.1371/journal.pbio.0060025>
- Stuart-Fox D, Moussalli A, Whiting MJ (2008) Predator-specific camouflage in chameleons. *Biol Lett* 4:326–329. <https://doi.org/10.1098/rsbl.2008.0173>
- Taylor PW, Elwood RW (2003) The mismeasure of animal contests. *Anim Behav* 65:1195–1202. <https://doi.org/10.1006/anbe.2003.2169>
- Teysier J, Saenko SV, van der Marel D, Milinkovitch MC (2015) Photonic crystals cause active colour change in chameleons. *Nat Commun* 6:6368. <https://doi.org/10.1038/ncomms7368>
- Tibbetts EA, Dale J (2004) A socially enforced signal of quality in a paper wasp. *Nature* 432:218–222. <https://doi.org/10.1038/nature02949>

- Tibbetts EA, Izzo A (2010) Social punishment of dishonest signalers caused by mismatch between signal and behavior. *Curr Biol* 20:1637–1640. <https://doi.org/10.1016/j.cub.2010.07.042>
- Tolley KA, Herrel A (2013) The biology of chameleons. Univ of California Press
- Tringali A, Bowman R (2012) Plumage reflectance signals dominance in Florida scrub-jay, *Aphelocoma coerulescens*, juveniles. *Anim Behav* 84:1517–1522. <https://doi.org/10.1016/j.anbehav.2012.09.025>
- Troscianko J, Stevens M (2015) Image calibration and analysis toolbox – a free software suite for objectively measuring reflectance, colour and pattern. *Methods Ecol Evol* 6:1320–1331. <https://doi.org/10.1111/2041-210X.12439>
- Umbers KDL, Tatarnic NJ, Holwell GI, Herberstein ME (2013) Bright turquoise as an intraspecific signal in the chameleon grasshopper (*Kosciuscola tristis*). *Behav Ecol Sociobiol* 67:439–447. <https://doi.org/10.1007/s00265-012-1464-7>
- van den Berg CP, Troscianko J, Endler JA et al (2020) Quantitative colour pattern analysis (QCPA): a comprehensive framework for the analysis of colour patterns in nature. *Methods Ecol Evol* 11:316–332. <https://doi.org/10.1111/2041-210X.13328>
- Vanhooydonck B, Herrel AY, Van Damme R, Irschick DJ (2005) Does dewlap size predict male bite performance in Jamaican Anolis lizards? *Funct Ecology* 19:38–42. <https://doi.org/10.1111/j.0269-8463.2005.00940.x>
- Vorobyev M, Osorio D (1998) Receptor noise as a determinant of colour thresholds. *Proc R Soc Lond B* 265:351–358. <https://doi.org/10.1098/rspb.1998.0302>
- Weaver RJ, Koch RE, Hill GE (2017) What maintains signal honesty in animal colour displays used in mate choice? *Phil Trans R Soc B* 372:20160343. <https://doi.org/10.1098/rstb.2016.0343>
- Whiting MJ, Stuart-Fox DM, O'Connor D et al (2006) Ultraviolet signals ultra-aggression in a lizard. *Anim Behav* 72:353–363. <https://doi.org/10.1016/j.anbehav.2005.10.018>
- Whiting MJ, Nagy KA, Bateman PW (2003) Evolution and maintenance of social status-signaling badges: experimental manipulations in lizards. In: *Lizard Social Behavior*. JHU Press, pp 47–82
- Xu M, Fincke OM (2015) Ultraviolet wing signal affects territorial contest outcome in a sexually dimorphic damselfly. *Anim Behav* 101:67–74. <https://doi.org/10.1016/j.anbehav.2014.12.018>
- Zahavi A (1975) Mate selection—a selection for a handicap. *J Theor Biol* 53:205–214. [https://doi.org/10.1016/0022-5193\(75\)90111-3](https://doi.org/10.1016/0022-5193(75)90111-3)

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Terms and Conditions

Springer Nature journal content, brought to you courtesy of Springer Nature Customer Service Center GmbH (“Springer Nature”).

Springer Nature supports a reasonable amount of sharing of research papers by authors, subscribers and authorised users (“Users”), for small-scale personal, non-commercial use provided that all copyright, trade and service marks and other proprietary notices are maintained. By accessing, sharing, receiving or otherwise using the Springer Nature journal content you agree to these terms of use (“Terms”). For these purposes, Springer Nature considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the relevant terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). For Creative Commons-licensed articles, the terms of the Creative Commons license used will apply.

We collect and use personal data to provide access to the Springer Nature journal content. We may also use these personal data internally within ResearchGate and Springer Nature and as agreed share it, in an anonymised way, for purposes of tracking, analysis and reporting. We will not otherwise disclose your personal data outside the ResearchGate or the Springer Nature group of companies unless we have your permission as detailed in the Privacy Policy.

While Users may use the Springer Nature journal content for small scale, personal non-commercial use, it is important to note that Users may not:

1. use such content for the purpose of providing other users with access on a regular or large scale basis or as a means to circumvent access control;
2. use such content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval, sponsorship, or association unless explicitly agreed to by Springer Nature in writing;
4. use bots or other automated methods to access the content or redirect messages
5. override any security feature or exclusionary protocol; or
6. share the content in order to create substitute for Springer Nature products or services or a systematic database of Springer Nature journal content.

In line with the restriction against commercial use, Springer Nature does not permit the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Springer Nature journal content cannot be used for inter-library loans and librarians may not upload Springer Nature journal content on a large scale into their, or any other, institutional repository.

These terms of use are reviewed regularly and may be amended at any time. Springer Nature is not obligated to publish any information or content on this website and may remove it or features or functionality at our sole discretion, at any time with or without notice. Springer Nature may revoke this licence to you at any time and remove access to any copies of the Springer Nature journal content which have been saved.

To the fullest extent permitted by law, Springer Nature makes no warranties, representations or guarantees to Users, either express or implied with respect to the Springer nature journal content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Springer Nature that may be licensed from third parties.

If you would like to use or distribute our Springer Nature journal content to a wider audience or on a regular basis or in any other manner not expressly permitted by these Terms, please contact Springer Nature at

onlineservice@springernature.com