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Original Article

UV color determines the issue of conflicts but does not covary with individual quality in a lizard

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Ultraviolet (UV) colors are visual signals potentially involved in territorial conflicts. However, the role of UV signals remains unclear relative to the prior resident effect and familiarity with the opponent, and the reliability of UV signals is still controversial. Male common lizards *Zootoca vivipara* exhibit substantial variation in the reflectance of their throat UV color patch. We tested whether UV reflectance was correlated with indicators of individual condition. We further manipulated throat UV reflectance of resident and intruder lizards and staged repeated encounters in the laboratory during the mating season. We found no evidence of condition dependence of the UV colors expression. During the first encounter among unfamiliar males, a reduction of UV reflectance of 1 of the 2 opponents influenced agonistic behaviors and the contest outcome, such that there was a significant advantage for residents over intruders. This advantage disappeared when both opponents were UV reduced. During the subsequent encounters among familiar males, fighting was more aggressive when opponents displayed similar UV signals, but UV signals did not influence the contest outcome. These results demonstrate that UV reflectance acted as a badge of status in male common lizards whose effects on the behavioral response were modulated, but not overridden, by the prior resident effect and by the familiarity effect. Male–male interactions are therefore mediated by UV signaling and competition for mates should play a major role in the evolutionary maintenance of this ornament. We discuss putative functions and reliability of UV signals.

Key words: **condition dependence, male–male competition, opponent familiarity, prior residency, structural coloration, *Zootoca vivipara*.**

INTRODUCTION

Color ornaments constitute some of the best-studied secondary sexual characters in vertebrates, and intensive work has been carried out on the ecology and evolution of sexually dichromatic coloration involving carotenoid and melanin pigments (reviewed in Ducrest et al. 2008; Svensson and Wong 2011). Yet, numerous nonmammalian taxa exhibit also structural colors, most notably in the ultraviolet (UV, 300–400 nm) range (e.g., birds, Andersson et al. 1998; fishes: Siebeck 2004; reptiles: Stapley and Whiting 2006; amphibians: Secondi et al. 2012), a spectral range to which the visual system of some vertebrate species is sensitive (reviewed by Bowmaker 2008). Despite a significant research effort during the last decade on this component of coloration, the proximate function and evolution of UV signals still remain poorly understood in vertebrates (Vedder et al. 2010 and references therein).

In several species, sexual dichromatism of UV coloration has been observed and males have usually brighter UV color patches than females (e.g., Andersson et al. 1998; Stuart-Fox and Ord 2004). This suggests a potential role of UV coloration in intrasexual communication and therefore sexual competition among males. During competition for resources, males assess the success of a potential rival through the use of phenotypic signals conveying information about the rival's fighting ability (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). Four decades ago, Rohwer (1975) proposed that size and/or spectral characteristics of color patches may influence competition among males by playing the role of a badge of status. Under this hypothesis, individuals should fight with opponents with a similar badge, avoid conflicts with opponents with a greater badge, but signal and attack opponents with a smaller badge (Johnstone and Norris 1993; Hurd 1997).

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Though the badge of status hypothesis offers a potential framework to understand how UV color patches mediate contests among males, it may not be sufficient when other factors such as familiarity and prior resident effects are taken into account (Alonso-Alvarez et al. 2004; Siebeck 2004; Stapley and Whiting 2006; Rémy et al. 2010; Vedder et al. 2010). Recognition of conspecifics based on UV signals might influence aggressiveness toward unfamiliar individuals but could have little effects when rivals are familiar (i.e., "dear enemy" phenomenon, Ydenberg et al. 1988; Rémy et al. 2010; Vedder et al. 2010). Furthermore, the outcome of aggressive interactions during territorial intrusions is strongly dependent on the prior residency status (reviewed in Kokko et al. 2006). Generally, territory owners are more likely to be winners than intruders because of a stronger motivation to fight or a larger fighting ability conferred by ownership of the resources (Maynard Smith and Parker 1976; Hardy 1998). Yet, the role of UV color patches in settling conflicts between residents and intruders still remains poorly understood.

Because UV colorations are produced by coherent light-reflecting and light-scattering microstructures of feathers or dermis (see Bradbury and Vehrencamp 2011), they were initially considered cheap to produce and ideal candidates for conventional signals (Gray 1996). If a UV color badge signals strong status, motivation, aggressiveness, or fighting ability, it should provoke attacks by strong individuals and dishonest signaling would be ruled out owing to costs of fights with stronger rivals (reviewed in Senar 1999). On the other hand, the honesty of color ornaments can be guaranteed by production and maintenance costs (Andersson 1994). Such costs have now been identified for UV color ornaments that can covary with indicators of male quality such as immune status, body condition, stamina, or fighting ability (e.g., McGraw et al. 2002; Griggio et al. 2010; Pérez i de Lanuza et al. 2014; and references therein). In male blue tits, the expression of UV color patches could reflect plasma levels of testosterone (Roberts et al. 2009), a hormone associated with a higher metabolism and aggressiveness and with a lower immunity (Folstad and Karter 1992). In lizards, the size and UV reflectance of UV-blue patches can act as quality index that informs rivals on bite force (Lappin et al. 2006; Pérez I de Lanuza et al. 2014). Therefore, what is the information content of UV colors and whether arbitrary conventions or production and maintenance costs explain best the evolution of these ornaments still remains unclear.

Male common lizards *Zootoca vivipara* compete actively within their home range for access to foraging and basking sites as well as for females (Lecomte et al. 1994; Fitze et al. 2008). During behavioral displays, males signal themselves by exposing their UV-reflecting throat to the sight of rivals. Because common lizards vary importantly in throat UV reflectance and possess an effective UV-sensitive visual system for detecting small variations in throat coloration (Fitze et al. 2009; Martin et al. 2013, 2015a), we hypothesized that UV signaling plays an important role in conflict resolution in this species. We thus tested whether throat UV patch acts as a badge of status in males during the mating season. Given home ranges of male common lizards overlap in nature, we further asked whether effects of throat UV reflectance interact with residency and familiarity with rivals, 2 factors potentially critical in this species to settle behavioral conflicts. To investigate these issues, we staged repeated encounters between resident and intruder unfamiliar males in which UV reflectance was alternatively reduced or not in a full factorial design. We quantified behavioral strategies and contest outcomes to gain insights into fighting abilities and motivation to fight. If UV coloration signals fighting ability, the experimental reduction of UV reflectance should influence aggressive behaviors as well as the outcome of contests. If UV signaling is strongly modulated by familiarity, we expect stronger effects during the first encounters. Alternatively, if conflict resolution is solely mediated by an ownership effect, the residency status of individuals should override the effects of other factors. To investigate the information conveyed by UV reflectance, we also examined whether UV throat reflectance correlates with body condition, body size, head width (a correlate of bite force), immune status through inflammatory response, and blood parasite load as well as with aggressiveness via testosterone level.

MATERIALS AND METHODS

Study species

The common lizard, *Zootoca (Lacerta) vivipara*, is a small lacertid (45–70 mm) distributed across Eurasia. This species is characterized by a strong sexual dimorphism and dichromatism: males are smaller, with a larger head, and brighter than females. Head size strongly varies among males and, because it determines bite force, may be decisive to win a fight and to grasp females during mating (Lappin et al. 2006; Gvozdík and Van Damme 2003). Males bear a permanent, yellow-red coloration on the belly and a whitish coloration on the throat with yellow-red areas extending from the belly (Bauwens 1987). The yellow-red coloration is based on carotenoids and is partly influenced by environmental factors (Cote et al. 2008; Fitze et al. 2009). It is also a sexually selected trait (Vercken et al. 2007; Fitze et al. 2009) that plays a role in mate recognition (Bauwens 1987), intrasexual competition among females (Vercken and Clobert 2008), and female mate choice (Fitze PS, personal communication). In addition, the throat of males reflects importantly in the UV range, as evidenced by the whole-body pictures in the UV range (Martin et al. 2013). The sexual dichromatism of the throat in the UV range is only apparent in adults, and throat UV reflectance strongly varies among adult males (Fitze et al. 2009; Martin et al. 2013; and see below). Males also strongly differ in the expression of melanin-based ventral punctuation that can correlate with phytohemagglutinin (PHA)-induced inflammatory response and thus may signal immune status of males (Vervust et al. 2013).

When 2 male common lizards interact, they observe each other and lick the substrate to collect chemical cues. In lacertid lizards, chemoreception is thought to be critical in male–male competition and chemical cues are involved in territory advertisement, sex recognition, individual recognition, and competitor assessment (reviewed in López and Martín 2004). Then, 1 male generally takes the initiative of approaching its rival, which may end up in "gentle" contacts (probably to collect direct chemical information) or aggressive attacks, sometimes associated with a bite. In return, the other individual may display an apparent absence of response, produce tail undulations or vibrations, and/or flee the conflict or, more rarely, counterattack. In addition, common lizards signal themselves by extending their front legs and exposing their throat (Martin M, personal observation) such that conspecifics can cue on the coloration of the throat and, at a lesser extent of the belly, to take behavioral decisions. Behavioral repertoire of males also includes a twisting movement of the body resulting in an S-shaped posture (Martin M, personal observation) that could be interpreted as a demonstration behavior allowing to expose ventral and lateral colorations to conspecifics.

Sampling and measurements

All procedures complied with laws on animal experimentation in France and Europe (permit Ce5/2011/024). Hand captures took place in outdoor enclosures at the Centre de Recherche en Ecologie Expérimentale et Prédictive (48°17′N, 2°41′E) during the mating season in March 2011. Adult males ($N = 110$) raised in enclosures without females were brought to the laboratory where we recorded their body size (snout-vent length, SVL; ±1 mm) and body mass (±1 mg). In this study, males measured 57.97 ± 2.39 mm (mean ± standard deviation [SD], range = 55–64 mm) and were all sexually mature. For each male, we calculated body condition as the residual of the linear regression of body mass over SVL (log-transformed variables). In addition, based on digital pictures of each male, we measured head width at the maximum lateral extent of the temporal jaw-adductor musculature (HW-am) and at the articular jaw joints (HW-t). These 2 metrics are strongly correlated with bite force in lizards (for method details, see Lappin et al. 2006).

For each individual, we also scored the expression of melanin-based coloration (3 levels: 0–2%, 2–10%, and >10% of coverage of the ventral surface) and quantified the reflectance on the throat and belly (3 measures per location) using a spectrophotometer (see Martin et al. 2013 for material details). Each spectrum was imported into Avicol software v5 (Gomez 2006), where we extracted brightness, yellow-red hue, and saturation as well as UV hue (wavelength of maximal reflectance in the UV) and UV chroma (proportion of the UV reflectance relative to the total reflectance). More details on the calculation and interpretation of these spectral parameters are provided elsewhere (Martin et al. 2013). Throat UV chroma varied importantly among sampled individuals (mean ± SD = 0.16 ± 0.02; coefficient of variation [CV] = 0.15; Figure 1), whereas throat UV hue did not (mean ± SD = 355.1 ± 6.8; CV = 0.02). Consequently, this paper focuses on variation in throat UV chroma only.

Physiological characteristics

Immunocompetence was estimated by local inflammation assessed through the skin-swelling response to the primary injection of a mitogen (PHA). Primary PHA injection triggers a local hemagglutination and leukocyte infiltration and involves innate (mediated by granulocytes and macrophages) components of the immune system (Vinkler et al. 2010). One day after the end of all behavioral trials of an individual (see below), we injected subcutaneously in the right posterior leg 0.04 mL of a solution of phosphate-buffered saline (Sigma-Aldrich, St Louis, MO; reference D5773) containing 2.5 mg/mL of PHA (Sigma-Aldrich; reference L8754). Before and 12 h after the injection, we measured thickness of the leg to the nearest 0.01 mm with a spessimeter (ID-C Absolute Digimatic, Mitutoyo). PHA swelling response was calculated as the change in thickness of the leg between the 2 measurements (Meylan et al. 2010; Mugabo et al. 2015).

In addition, we collected blood samples (ca. 40–60 μL per individual) from the postorbital sinus and isolated plasmas by centrifugation for subsequent storage at −30 °C. We later determined circulating testosterone (T) plasma levels using colorimetric competitive enzyme immunoassays (Cayman Chemical, Cat. No. 582701). T levels averaged 32.72 ± 4.84 pg/mL (mean ± standard error), ranged from 1.57 to 217.98 pg/mL, and was not correlated with the PHA swelling response ($r = -0.08$, $P = 0.50$). When collecting blood, we also smeared a blood droplet on a microscope slide, which was later fixed in methanol and stained in Giemsa. We then counted haemogregarinid intraerythrocytic parasites (mean ± SD load = 26.13 ± 5.06 infected cells/10 000 erythrocytes; range = 0–247). Blood parasite load was not correlated with PHA swelling response ($r = -0.14$, $P = 0.25$) or T level ($r = 0.05$, $P = 0.65$).

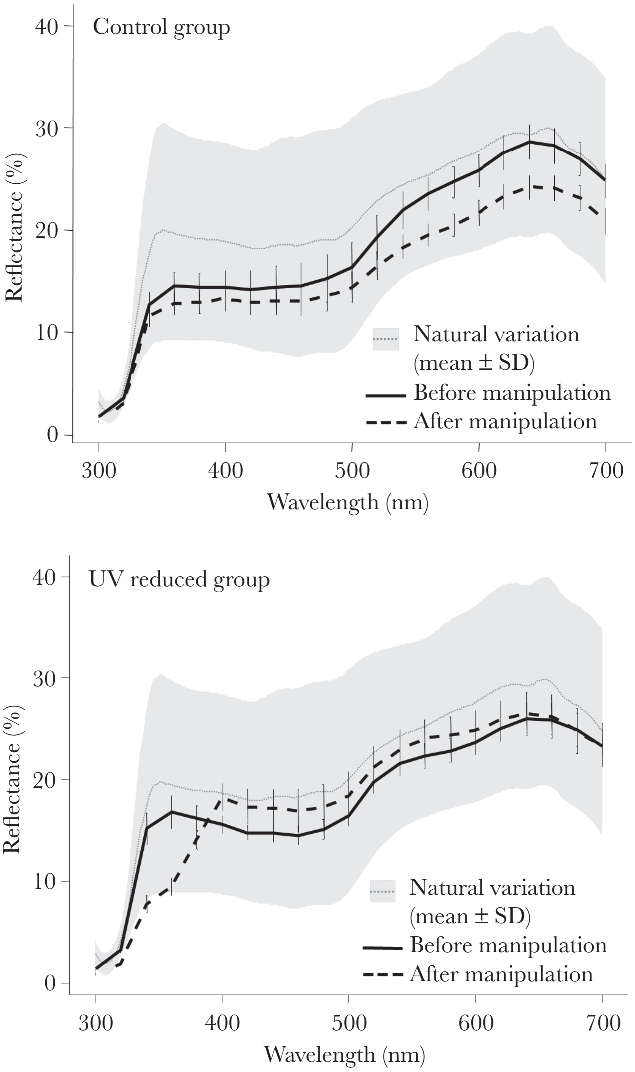


Figure 1
Natural range and experimental manipulation of throat coloration of male common lizards. Mean spectra (±SD) of individuals of the total sample ($N = 110$, gray line); and mean reflectance (±SE) of individuals from the control group (top panel) and the UV-reduced group (bottom panel), before and 30 min after treatment application ($N = 7$ per group, black lines).

UV manipulation

To reduce temporarily the UV skin reflectance, we used UV blocking (290–400 nm) inorganic agents (zinc oxide and titan dioxide) mixed with a fat combination of petroleum jelly and liquid paraffin (respectively, 6:4:50:40 g for 100 g, Martin et al. 2015b). The product was applied on the throat with a soft paintbrush from the tip of the nose. To validate our protocol, we measured skin reflectance on the throat of randomly selected males ($N = 7$ per group) before and after application of fat (control group) or of the UV-reducing treatment (UV-reduced group). After 30 min, control treatment did not change significantly spectral parameters (Wilcoxon paired test between measurements performed before and 30 min after application, $P > 0.16$), except for a marginal decrease in total brightness ($P = 0.078$, Figure 1). The UV-reducing treatment significantly increased the wavelength of maximal reflectance in the UV by 4.35 ± 2.86 nm ($P = 0.036$), reduced UV chroma by 4.54 ± 1.69% ($P = 0.016$), and did not change the other spectral parameters (all $P > 0.30$, Figure 1). Reduction of UV reflectance sat at the lower end of the natural range of variation (Figure 1) and was efficient for less than 6 h (Wilcoxon test for UV chroma, 2 h 30 min after treatment: $P = 0.017$; 6 h after treatment: $P = 0.21$; see also Martin et al. 2015b).

We further modeled color signals' perception by male common lizards. For each male of the validation protocol ($N = 14$), we calculated color distance (i.e., color contrast) between throat coloration before and after manipulation using the color discrimination model described in Martin et al. 2015a. Only colors with a distance above 1.0 just-noticeable-distance (jnd) can be visually discriminated, and the higher the color distance, the easier the discrimination of the 2 colors for a given visual system in a given environment (Vorobyev and Osorio 1998). We found that color distances between throat coloration before and after manipulation were not different from 1 jnd in the control group (mean ± SD = 1.95 ± 1.24 jnd, 2-tailed Wilcoxon test, $V = 24$, $P = 0.11$) but were significantly higher than 1 jnd in the UV-reduced group (mean ± SD = 4.39 ± 1.55 jnd, 1-tailed Wilcoxon test, $V = 28$, $P < 0.01$). Altogether, these results indicate that the control treatment was not or poorly distinguishable, whereas UV reduction was clearly discriminable but remained in the natural range of variation.

Behavioral trials

Lizards from different enclosures were matched pairwise by SVL (±2 mm), body mass (±600 mg) as well as by throat and belly coloration to ensure that individuals of a same pair were unfamiliar and as similar as possible ($N = 36$ pairs). For each pair, one lizard was attributed to the resident group and the other to the intruder group. Residents and intruders did not differ for SVL, mass, head width (HW-am and HW-jj), score of melanin-based coloration, and coloration features (brightness, yellow-red hue and chroma, UV hue and chroma) of the throat and belly (Student's or Wilcoxon paired tests depending on data normality, all $P > 0.05$). The "resident" lizard was housed in a terrarium (45 × 29 × 22 cm) for more than 5 days prior to the start of behavioral observations to ensure acclimation (Martin et al. 2015b). The "intruder" lizard was housed in another similar terrarium and transferred to the resident terrarium prior to each behavioral test. This design generated an asymmetry in prior residency, but also in stress and risk-taking levels (observation of differences in monopolization of the heat source and in scratching the wall), between residents and intruders (López and Martín 2001; Martin et al. 2015b). Terraria were layered with sand, equipped with a small water dish, 2 hides and a black plastic plate for basking. Heat was provided by an incandescent bulb (25 W) and white light was provided by UV-B neon light (Reptisun 10.0 UVB, Zoomed) during 8 h/day. Food (*Acheta domesticus*) and water were provided ad libitum.

Each pair was tested 4 times according to 4 resident–intruder treatments: "Control–Control," "Control–UV reduced," "UV reduced–Control," and "UV reduced–UV reduced." The sequence of treatments was random, and the 4 trials of a pair were spaced by 2 days and occurred at the same daytime. This full factorial, repeated measure design allowed testing for effects of UV coloration while controlling for variation among pairs and among individuals within pairs. Immediately before each trial, internal equipment was removed from the resident's terrarium, which was separated into 2 compartments by a removable opaque wall. Light was provided by 2 UV-B neon light located 70 cm above the ground and heat was provided by 2 incandescent bulbs located above each compartment. The room temperature was maintained at 20–21 °C. After the treatment application, the resident was left in one of the compartments, and the intruder was introduced in the other one. After 20 min of acclimation, heat was turned off, an incandescent bulb of 40 W was turned on above the resident's compartment only, the opaque wall was removed gently, and observations begun. This procedure encouraged the intruder to move toward the resident's compartment to bask. All trials of a pair were observed by the same experimenter placed behind a blind. Half of the pairs were observed by one person and the other half by another person. For each trial, behavior of residents and intruders was recorded during 20 min using Jwatcher V 1.0 (Blumstein et al. 2006). We recorded the number of agonistic behaviors including aggressions (attack toward the opponent or touch the opponent without bite), approaches, bites, demonstrative behaviors (S-shaped or throat displays toward the opponent), escapes, surveillance, and tail movements. We then used objective methods (dominance score and principal component analyses [PCAs]) to score each behavioral trial and the behavior of each lizard (see below) instead of a standard classification of lizards into winners and losers.

Data analyses

We used R 2.13.1 software (R Development Core Team 2011) to conduct all statistical analyses. To investigate the function and costs of UV reflectance, we analyzed the effects of SVL, body condition, head width, and physiological characteristics (PHA swelling response, T level, blood parasite load) on UV reflectance of the throat on capture (prior to manipulation) with a linear model ($N = 72$ individuals). Then, we run 2 sets of behavioral analyses. First, to evaluate the outcome of contests, we computed a contest score for each trial of each pair by measuring the difference between the aggression scores of the resident and of the intruder. Aggression score was calculated by subtracting the number of submissive behaviors (escapes and tail movements) from the number of aggressive behaviors (aggressions, approaches, and bites). Contest scores ($N = 136$) were then ranked relative to 0 such that positive values would denote the dominance of the resident over the intruder (see the method in Sacchi et al. 2009; Martin et al. 2015b). In average, contest scores were significantly positive (1-sample Student's *t*-test, $t_{135} = 4.80$, $P < 0.001$) indicating that residents invested more in aggressive than in submissive behaviors relative to intruders, like in other species of lizards investigated so far (e.g., Kokko et al. 2006; Sacchi et al. 2009; Martin et al. 2015b). Second, to gain insights into behavioral strategies, we examined the agonistic behaviors of each male in each contest ($N = 272$). Because correlations existed among agonistic behaviors, individual values of bite, aggression, approach, escape, tail movement, and surveillance behaviors were included into a PCA in order to summarize behavioral variation into a few, relevant principal component (PC) scores. Because the interpretation of S-shaped displays is not straightforward, demonstration behaviors were excluded from the analysis. Variables were root square transformed, centered, and scaled prior to PCA. We used the broken-stick method (Jackson 1993) to determine how many PCs represented significant variation with respect to the original data. We then extracted the absolute contributions of the decomposition of inertia for each selected PC with *ade4* package and interpreted only behaviors whose contribution exceeded the average. The selected PC scores fulfilled assumptions of normality and variance homogeneity.

Preliminary tests revealed that the contest outcome and agonistic behaviors changed significantly between the first encounter and each of the subsequent trials (Tukey post hoc tests between trial 1 and trials 2, 3, or 4 on contest scores: all $P < 0.001$, and on PC scores: all $P < 0.02$), which may suggest an important effect of familiarity. Consequently, contest scores and PC scores for data from the first trial and for data from subsequent trials were calculated and analyzed separately (Table 1). For contest scores, we tested the effects of the UV treatment of the resident, the UV treatment of the intruder, and their interaction on contests scores with a linear model (analysis of trial 1) or a linear mixed-effect model (trials 2–4) with pair identity as a random factor. The linear mixed-effect model was implemented with the *lme* procedure from the nlme package (Pinheiro and Bates 2000). For PC scores, we tested the effects of the residency status of the male (resident or intruder), the UV treatment of the male (thereafter called T_{male}), and the UV treatment of the rival (thereafter called T_{rival}), and their 2-way and 3-way interactions on PC scores. We used a linear mixed-effect model in the *lme* procedure with pair identity (all trials) and individual identity (trials 2–4) as random factors. All analyses started with a full model including all covariates listed above as fixed effects. Because the scoring of behaviors can differ substantially between observers, we treated observer name as a blocking factor and introduced it as the first covariate in all the models. Knowing that variance analysis is sequential in R (sum squares depend on the introduction order of variables), the effect of experimental factors were therefore tested after having took into account the observer effect. The best model was then chosen by backward elimination of nonsignificant terms.

RESULTS

UV chroma in relation to individual traits

Neither physiological variables (PHA swelling response, T level, and blood parasite load) nor morphological variables (SVL, body condition, HW-am, HW-t) were significantly correlated with UV chroma on the throat prior to the experimentation (all $P > 0.14$).

Effect of UV reduction on interactions between unfamiliar rivals

During the first trial, the contest score was influenced by an interaction between the UV treatment of the resident and of the intruder ($F_{1,29} = 8.27$, $P = 0.008$). Contest scores were higher in pairs where residents and intruders had different UV treatments than in pairs where residents and intruders displayed the same UV treatment (Figure 2a). Other factors did not influence contest scores (all $P > 0.44$). The PCA summarized 65.19% of variation of behavioral data from the first trial into 2 major axes (Table 1). The first principal component (PC1) was positively associated with aggression, approach, bite, and surveillance behaviors and contrasted individuals with low versus high levels of aggression and investigation. The second principal component (PC2) was positively correlated with escapes and tail movements and thus could indicate more submissive behaviors.

Table 1

Contribution (loading scores) of agonistic behaviors to each of the significant PC obtained from a PCA applied to data of the first trial and data of the subsequent trials of each male pair

	Trial 1		Trials 2-3-4	
Loadings	PC1	PC2	PC1	PC2
Aggression	**0.86**	0.09	**0.79**	−0.37
Approach	**0.79**	0.19	**0.79**	−0.23
Bite	**0.67**	0.01	0.43	−0.17
Escape	−0.54	**0.57**	0.16	**0.77**
Tail	−0.19	**0.88**	0.35	**0.72**
Surveillance	**0.71**	0.35	**0.68**	0.25
Eigenvalue	2.65	1.27	2.07	1.39
Variance (%)	44.09	21.10	34.46	23.13

Bold values are behaviors with a significant contribution to a PC.

Interestingly, the residency status interacted with the UV treatment of the male and the UV treatment of the rival to affect both PC1 and PC2 (Table 2). Residents and intruders had similar scores of PC1 and PC2 in “Control–Control” trials (Figure 2b,c). By contrast, in the “Control–UV reduced” and “UV reduced–Control” trials, residents had higher PC1 and lower PC2 scores than intruders (Figure 2b,c). During “UV reduced–UV reduced” trials, residents and intruders did not differ in PC1 and PC2 scores (Figure 2b,c), but both of them invested then less in submissive behaviors than during “Control–Control” trials (1-tailed Mann–Whitney tests on PC2 scores of individuals from the control group vs. the UV-reduced group, for residents and intruders: $P < 0.05$).

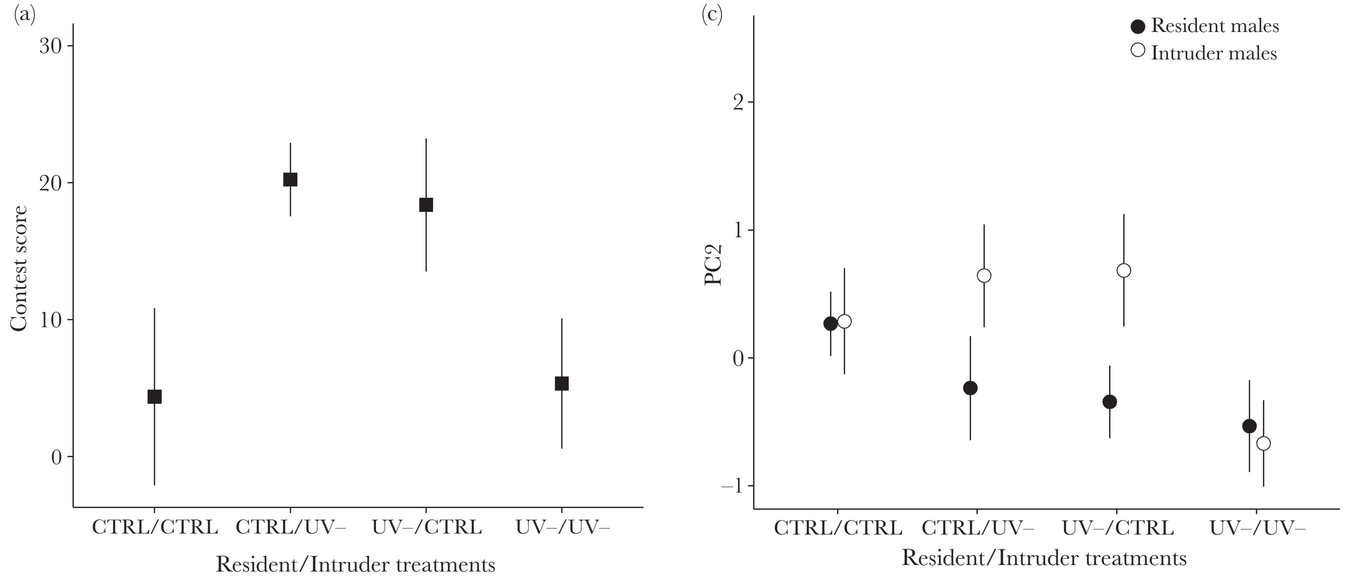
Effect of UV reduction on interactions between familiar rivals

For the subsequent trials, the contest score did not depend on the UV treatments of male pairs (all $P > 0.25$), but on sequence number ($F_{2,64} = 5.88$, $P = 0.005$) with lower contest scores during trial 4 compared with trials 2 and 3 (Tukey post hoc comparisons, trial 2 or 3 vs. 4: all $P > 0.01$, trial 2 vs. 3: $P = 0.95$). Two axes explained 57.59% of the behavioral variability (Table 1), with the same loading pattern than in the first encounter. PC1 score was significantly affected by the interaction between the UV treatment of the focal male and of the rival (Table 2). On average, the 2 males tended to have a higher PC1 score in “Control–Control” and “UV reduced–UV reduced” pairs (Figure 3). PC2 score was affected by the residency effect only (Table 2), with more submissive behaviors for intruders than for residents.

DISCUSSION

In line with previous experimental studies in birds, fishes, and 3 species of lizards (Alonso-Alvarez et al. 2004; Siebeck 2004; Stapley and Whiting 2006; Rick and Bakker 2008; Vedder et al. 2010; Bajer et al. 2011; Martin et al. 2015b), our behavioral study revealed that the UV color patch influences male–male competition. In male common lizards matched for other traits known to influence territorial contests, UV signals directly influenced the process of conflict resolution and effects of UV signals were not overridden by a prior resident effect nor by a familiarity effect.

During the first interaction, when animals were unfamiliar, contest scores (a measure of the degree of behavioral dominance of residents over intruders, Sacchi et al. 2009; Martin et al. 2015b), aggression–investigation behaviors (PC1 score) and submission behaviors (PC2 score) were both influenced by the UV manipulation. These treatment effects depended on the prior resident status. In situations of signal symmetry between males, contest scores were close to 0 because residents and intruders behaved quite similarly. The fact that UV-reduced male pairs displayed a behavioral pattern close



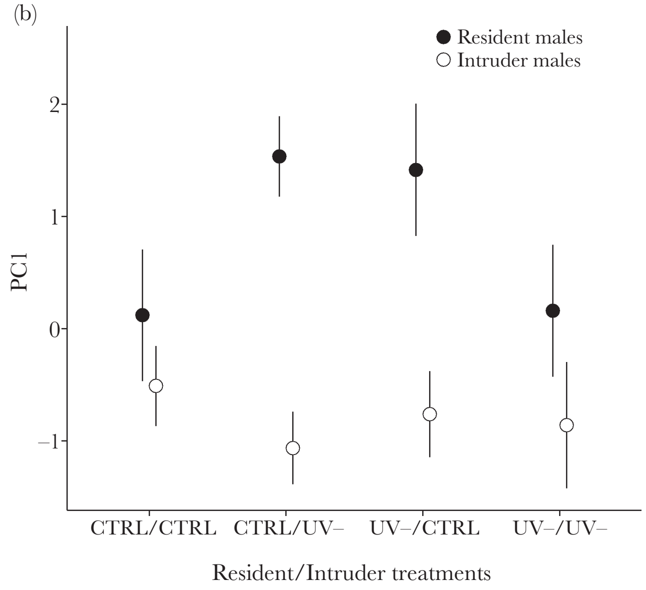


Figure 2

Effects of the UV manipulation on behavioral interactions during the first encounter. (a) Mean (±SE) contest score of male pairs for each resident–intruder treatment group, where CTRL indicates control treatment and UV− indicates UV-reduced treatment. Higher positive values indicate stronger dominance of the resident over the intruder. (b, c) Mean (±SE) PC1 and PC2 score, respectively, of residents and intruders for each treatment group. Higher PC1 values indicate more aggression and surveillance behaviors, whereas higher PC2 values indicate more submissive behaviors.

Table 2

Results from the full model describing variation among males in PC scores (PCA applied to agonistic behaviors, see Table 1) for data of the first trial and data of the subsequent trials of each male pair

	Trial 1		Trials 2-3-4	
Effects	PC1	PC2	PC1	PC2
Fixed effects				
Observer	**4.19***	**6.60***	**20.82*****	1.41
Sequence	—	—	**3.43***	3.06
Status	**23.28***	4.027	0.61	**4.85***
T_{focal}	0.23	1.75	0.18	0.6
T_{rival}	0.08	2.12	0.20	0.02
Status × T_{male}	0.06	0.02	0.02	0.21
Status × T_{rival}	0.04	0.16	0.75	<0.01
T_{male} × T_{rival}	1.74	0.73	**7.77****	0.91
Status × T_{male} × T_{rival}	**5.41***	**5.22***	0.07	0.03
Random effects				
Pair	<0.01	35.44	33.95	<0.01
Individual in pair	—	—	25.29	57.91
Residuals	100.00	64.56	40.76	42.08

T_{male}, UV treatment of the focal male; T_{rival}, UV treatment of the rival. Bold values correspond to final models and asterisks are significant values with *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Data reported are type III *F*-ratios calculated during backward elimination in the case of nonsignificant variables for fixed effects and percentage of variability explained by interindividual and inter-pair random effects.

to the one of control pairs points to a mutual assessment process where lizards adjusted their behavior according to the behavior and color signal of their rival (Arnott and Elwood 2009). Control and UV-reduced male pairs invested moderately in aggression–investigation behaviors as expected due to the high costs of a fight with an opponent of similar strength. Given that we controlled pairwise assignments for visual signals but not for chemical cues, these results also confirm that males of a same pair were highly similar and that UV reduction did not result in odd-looking animals. Nevertheless, the 2 types of male pairs differed in their submission behaviors. Interestingly, when the 2 rivals were UV reduced, males of the same pair displayed less submission behaviors and thus avoided each other less strongly than males of control pairs did. This result suggests that UV-reduced individuals could signal a lower "strength" and thus be assessed as a lower threat by their opponent resulting in a decrease of the level of distrust in these latter ones.

In sharp contrast, in situations of signal asymmetry when only one opponent was UV reduced, a strong prior resident advantage existed. Residents performed more aggression–investigation behaviors and intruders invested more in submission behavior. For pairs with a control resident and a UV-reduced intruder, these findings support the badge of status hypothesis (Hurd 1997; Pryke et al. 2002; Stapley and Whiting 2006; Rémy et al. 2010), which predicts

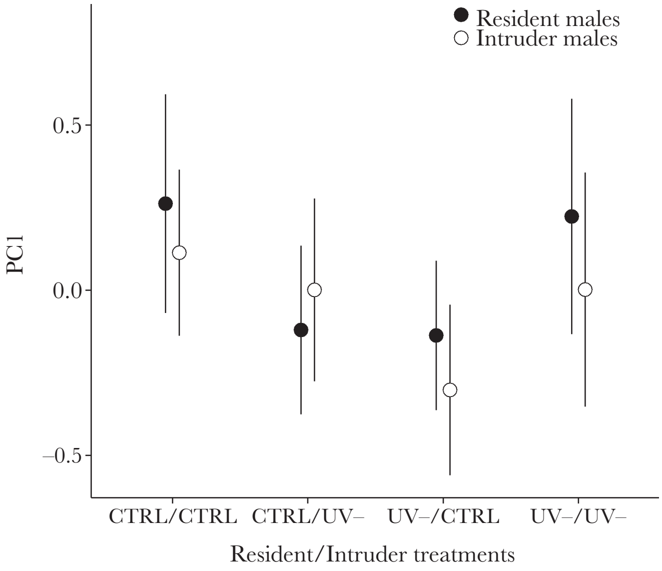


Figure 3
Effects of the UV manipulation on behavioral interactions between familiar rivals (trials 2-3-4). Data are mean (±SE) PC1 score for residents and intruders for each resident–intruder treatment group, where CTRL indicates control treatment and UV− indicates UV-reduced treatment. A higher PC1 score indicates more aggression, approach, and surveillance behaviors during the interaction.

that individuals with duller UV colors on the throat would be more often challenged if they represent a lower potential threat. Surprisingly, we found exactly the same behavioral pattern in pairs with a UV-reduced resident and a control intruder. One possible explanation is that UV-reduced residents that were not conscious of their signaling status assessed the intruder as a rival of similar "strength," whereas the intruder behaved as a dominant in response to the message of "low strength" conveyed by UV-reduced color of the resident. Under this scenario, UV-reduced residents could then perceive a mismatch between the public information conveyed by the behavior of intruders and their UV coloration and might evaluate the intruders as cheaters and punish them in consequence (Rohwer 1977; Maynard Smith and Harper 2003). A rigorous test of this hypothesis is still needed in common lizards, but these results are consistent with findings of experiments in wasps where a mismatch between the behavior and signal of a rival was sufficient to induce punishment by congeners (Tibbetts and Izzo 2010).

Under the badge of status hypothesis, the effects of color signals are expected to disappear once individuals gain experience about their opponents (Searcy and Nowicki 2005; but see Pryke et al. 2002; Pryke and Andersson 2003), an assumption supported for UV signals in blue tits (Rémy et al. 2010; Vedder et al. 2010). In the present study, aggression–investigation behaviors (PC1 score), but not contest scores, were influenced by an interaction between the UV treatment of the male and of the rival once rivals were familiar. As a general rule, males performed more aggression and investigation behaviors in situation of signal symmetry than in situation of signal asymmetry. Thus, effects of UV throat coloration were not anymore in accordance with the badge of status hypothesis because (1) the outcome of contest was not affected by the UV manipulation and (2) signal asymmetry did not increase aggression and dominance hierarchy. Instead, behavioral data were more consistent with the predictions of a sequential assessment model according to which contests would escalate more often when the 2 opponents signal equal strength (Enquist and Leimar 1983; Maynard Smith and Harper 2003). To our knowledge, this is the first demonstration that a UV color patch influences behavioral interactions during a conflict between familiar individuals.

Given the behavioral effects of UV manipulation in male common lizards, it is important to understand the function and information content of UV signals for male conspecifics as well as the basis of signal honesty. Previous studies suggested that UV colors can reflect testosterone levels and inform on aggressiveness in males (Whiting et al. 2006; Roberts et al. 2009; Rémy et al. 2010) but neither our behavioral data nor physiological data support this hypothesis in the common lizard. In the last decade, evidence of UV colors as signals of fighting ability has been growing in birds and lizards (i.e., Stapley and Whiting 2006; Rémy et al. 2010; Vedder et al. 2010; Bajer et al. 2011) and it was therefore proposed that honesty of these signals could be explained by production and maintenance costs (i.e., condition-dependent signals, Zahavi 1975; Morrison et al. 1995). Indeed, UV chroma of feathers is correlated with indicators of individual quality in several bird species (e.g., Roberts et al. 2009; Griggio et al. 2010; McGraw et al. 2002). In lizards, UV reflectance of nuptial UV-blue color patches can covary with predictors of fighting ability such as body size and condition, bite force, and access to good basking sites (Lappin et al. 2006; Bajer et al. 2012; Pérez I de Lanuza et al. 2014). Yet, we found no relationship between UV chroma and body size, body condition, bite force proxies (head width indices), and immune status proxies (PHA skin-swelling response and blood parasite infection) in male common lizards (see also Martin et al. 2013). A recent experiment also demonstrated that manipulation of plasma corticosterone levels and carotenoid supplementation does not affect UV reflectance of the skin (San-Jose et al. 2013).

The fact that UV manipulation affects the contest outcome strongly supports the hypothesis of UV colors as fighting ability signals, yet the absence of correlations with predictor traits does not allow us to draw conclusions about their condition dependence. One possible explanation for this nonsignificant condition dependence has been proposed by Bradbury and Vehrencamp (2011): UV signals might belong to a multimodal fighting ability signal where reliability of UV signals might be guaranteed because there are index signals subjected to physic or physiological constraints, whereas another component of the signal might be kept honest because of its condition dependence. According to this scenario of multimodal signaling, our experimental UV reduction would generate inconsistency between the information conveyed by the UV signal and the information conveyed by the other components of the fighting ability signal. Given that this inconsistency should make harder the assessment of the fighting ability of UV-reduced animals, we would expect conspecifics to be more distrustful toward these individuals and thus display more aggressiveness and/or avoidance behaviors. However, the fact that males of "UV reduced–UV reduced" pairs did not differ in aggression–investigation behaviors and avoided less each other than males of "Control–Control" pairs contradicts this expectation.

Alternatively, the absence of correlation with male quality predictors might reflect an absence of physiological costs related to the production and maintenance of a high UV reflectance of the skin. Indeed, the honesty of fighting ability signals can be distinctly guaranteed by socially imposed costs (i.e., conventional signals, see Bradbury and Vehrencamp 2011). At least 1 study in birds provides clear evidence of UV colors as conventional signals, where cheating is socially controlled by aggression from dominant individuals toward individuals with exaggerated UV colors (Pryke and Andersson 2003). Even though we did not increase UV reflectance and measure costs of aggression to test this hypothesis, the fact that intruders with UV-reduced coloration were more often challenged by control residents suggests that this explanation is implausible. Finally, another alternative possibility is that UV signals have no information content but act as amplifier signals enabling an easier evaluation of head size, as previously suggested for UV-blue mouth-corner patches of the collared lizards (Lappin et al. 2006). Yet again, our behavioral data do not support this hypothesis. If UV reduction made more difficult the assessment of rival head size, we should observed more aggression–investigation behaviors in "UV reduced–UV reduced" male pairs than in "Control–Control"' male pairs, but we did not. All these putative explanations point out the need of new studies to disentangle the function and reliability of UV colors in common lizards, and more generally in lizards and birds.

Altogether, our results suggest that a reduction of the UV reflectance during the mating season changed behavioral interactions differently depending on the prior residency and degree of familiarity between opponents in male common lizards. Thus, social selection and notably sexual selection should play a major role in the evolutionary maintenance of this ornament. During the first encounter, the UV throat color patch acts like a badge of status but not when males were familiar. In general, the behavioral response of an individual depended on its residency status and on a nonadditive effect of the UV reflectance of the 2 opponents. These findings reinforce conclusions from previous studies in blue tits (Vedder et al. 2010) and wall lizards (Martin et al. 2015b) that effects of UV signaling are context dependent. This emphasizes that the understanding of the behavioral mechanisms involved in the sexual selection on cryptic color polymorphism requires a careful investigation of the social context.

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