

UV coloration influences spatial dominance but not agonistic behaviors in male wall lizards

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Abstract A bright ultraviolet (UV) component in the coloration of males may signal individual quality and thus determine the outcome of male-male contests. Yet, the role of the UV component of coloration in resolving conflicts is still controversial relative to factors such as residency status and seasonality. Here, we investigated whether a reduction of UV reflectance of lateral blue spots in male wall lizards (*Podarcis muralis*) interacts with residency status (resident vs. intruder) to influence agonistic behaviors, the outcome of contests, and basking time (a measure of spatial dominance). We performed this experiment during one breeding and one non-breeding season. The UV manipulation did not predict the outcome of contests. During the breeding season, the agonistic behaviors and basking time depended on the residency status of males but not on their UV treatment. During the non-breeding season, experimental factors affected basking time only. For a given male, the time spent basking depended in a complex manner on its residency status, its UV treatment, and those of its rival. UV reflectance of blue spots thus influences the processes of mutual assessment and spatial dominance, but is

not a critical determinant of fighting success. Altogether, these results evidence context-dependent effects of the UV reflectance of blue spots on territorial behaviors according to residency status and, potentially, season. They also suggest that UV signaling may be more important than expected for male-male interactions during the non-breeding season.

Keywords Intrasexual selection · *Podarcis muralis* · Seasonality · Structural coloration · Territorial conflict

Introduction

Many bird, reptile, amphibian, and fish species display color patches with a striking ultraviolet (UV) structural component, and most of these animals possess a visual system sensitive to UV light allowing them to perceive the UV component of coloration (Bowmaker 2008; Rick and Bakker 2008; Rémy et al. 2010; Bajer et al. 2011; Secondi et al. 2012). Evolutionary theory predicts that size and/or spectral characteristics of color patches may mediate the outcome of contests by playing the role of a badge of status. A badge of status can be an assessment signal conveying information about the fighting ability of the bearer (i.e., resource-holding potential) or a conventional signal revealing aggressiveness (i.e., willingness to escalate) and dominance status, thus allowing individuals to assess the potential fighting success of a rival (Rohwer 1975; Maynard Smith and Harper 2003; Searcy and Nowicki 2005). Under the badge of status hypothesis, individuals will fight with opponents with a similar badge, avoid conflict with opponents with a greater badge, but signal and then attack opponents with a smaller badge (Johnstone and Norris 1993; Hurd 1997).

There is growing evidence that the UV component of coloration can signal fighting ability or aggressiveness during

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male-male competition in some birds (Keyser and Hill 2000; Pryke and Griffith 2006, and references thereafter), lizards (Stapley and Whiting 2006; Whiting et al. 2006; Bajer et al. 2011), and fishes (Siebeck 2004; Rick and Bakker 2008). For example, a reduction of UV coloration in males decreased their reproductive success in wild sand lizards *Lacerta agilis* (Olsson et al. 2011). Yet, in blue tits *Cyanistes caeruleus*, the UV crown coloration influences contest outcomes and aggressive responses differently depending on the familiarity and degree of asymmetry between opponents (Alonso-Alvarez et al. 2004; Rémy et al. 2010; Vedder et al. 2010). Furthermore, in this species, UV coloration determines contest outcomes during the breeding season when competition for mates is maximal (Alonso-Alvarez et al. 2004) but is also important during the non-breeding season (Rémy et al. 2010; Vedder et al. 2010). In other species, it is still unclear whether UV coloration plays a different role during male-male interactions associated with competition for mates than during competition for food and space. We therefore need more studies that test the role of the UV component of coloration in different social contexts in the same species.

In territorial species, prior residency (automatic owner status of individuals who arrived first in an area) is a major determinant of the outcome of aggressive interactions during territorial intrusions (reviewed in Kokko et al. 2006). Prior residency implies a difference in initial motivation to fight and may be used as an arbitrary rule during territorial contests (the prior-resident effect or “bourgeois strategy”, see Maynard Smith and Parker 1976). Alternatively, territory ownership may confer a larger fighting ability (Hardy 1998). For example, resident speckled wood butterflies (*Pararge aegeria*) that defend sun spot territories can reach higher body temperatures than intruders and win contests due to increased fighting ability (Stutt and Willmer 1998). However, none of the previous studies that examined the role of UV coloration in animal contests have tested for the effects of resident-intruder status.

The European wall lizard *Podarcis muralis*, a small diurnal species commonly found in central and southern Europe, is an ideal model system to address these issues. In this species, adults (>2 years) of both sexes exhibit three main ventral color morphs (white, yellow, and red), contrasting in their morphology, immune defenses, and chemical profiles (Sacchi et al. 2007; Calsbeek et al. 2010; Galeotti et al. 2010; Sacchi et al. 2013; Pellitteri-Rosa et al. 2014) but not for their aggressiveness or fighting success (Sacchi et al. 2009). Adults also exhibit color patches on the marginal ventral scales that appear blue to humans but display a reflectance peak in the near UV (300–400 nm, see Figs. 1 and 2). This UV reflectance can be perceived by wall lizards, which possess a UV-sensitive visual system (Martin et al. 2015; Pérez i de Lanuza and Font 2014). During male-male interactions, wall lizards perform push-ups and present one flank to the sight of their opponent, suggesting that the blue spots on their marginal ventral scales might

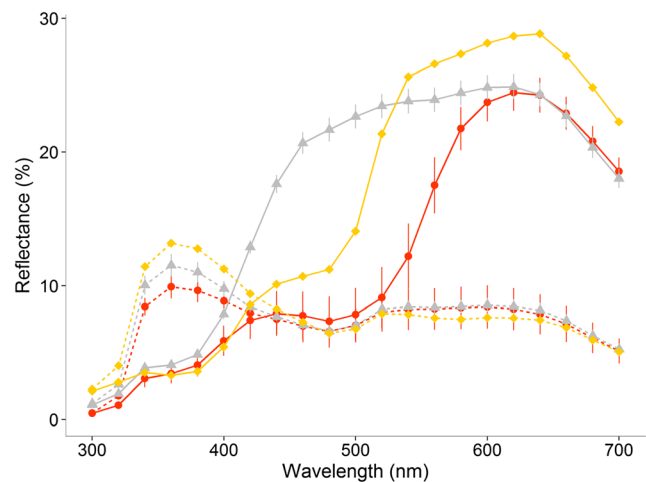


Fig. 1 Mean reflectance spectra during the breeding season of orange (orange circle, $N=8$), white (grey triangle, $N=33$), and yellow (yellow diamond, $N=1$) male wall lizards on the belly (solid line) and on blue spots (dashed line) located around the flanks. The standard error around the mean is indicated for orange and white males. Note that UV reflectance of males during the breeding season is smaller than after the breeding season (see Fig. 2)

be involved in intraspecific communication. In our study site, there are two or three peaks of breeding during a year between April and July (Mou 1987; Nembrini and Oppliger 2003; Barbault and Mou 1986). Large aggressive males defend territories that do not overlap, and small, subordinate males may also defend small territories unoccupied by large males (Edsman 1990). We observed pursuits among males until the middle of September (MM and JFLG, personal observation) suggesting that males maintain territories during the non-breeding season. It is thus likely that the quality of a territory is related to access to females but also to shelter and food.

At our study site, sampled male lizards had 3–15 blue spots on each flank. In closely related species, the total number of blue spots is positively correlated with body size and condition (López et al. 2004; Cabido et al. 2009) and the relative proportion of some chemical compounds of femoral secretion (López et al. 2006). In addition, López et al. (2004) found that the presence, but not the number, of blue spots may elicit aggressiveness in *Iberolacerta monticola*. Furthermore, the reflectance peak and UV chroma of blue spots are good predictors of fighting ability and body condition in wall lizards (Pérez i de Lanuza et al. 2014). Yet, it is not known if the UV component of blue spot color influences social interactions among males in these congeneric lizard species.

We investigated whether the UV component of blue spot color acts as a badge of status and interacts with residency to influence conflict resolution in male-male pairs during one breeding season and one non-breeding season. To do so, we staged repeated encounters between resident and intruder males in each season. In order to test its effect on the behavior of resident males, we either reduced UV reflectance of the intruder or left it intact. We also manipulated UV reflectance

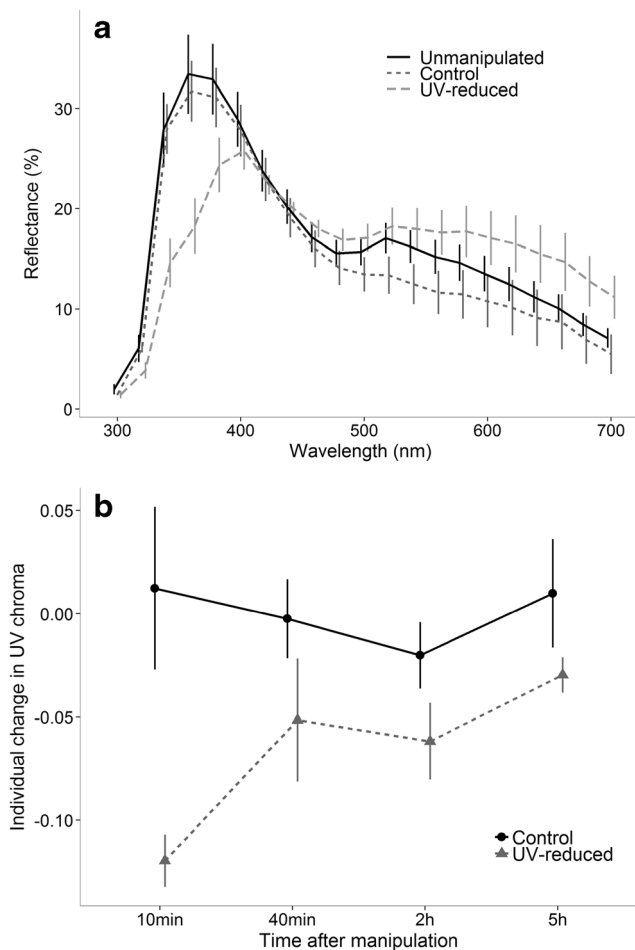


Fig. 2 **a** Experimental manipulation of UV reflectance during the non-breeding season. Mean reflectance (\pm SE) in the 300–700-nm range on blue spots of male wall lizards from a non-manipulated group, a control group treated with a fat cream, and a UV-reduced group treated with a UV-reducing cream. The data was obtained 10 min after application ($N=7$ per group). **b** Mean individual change of UV chroma (\pm SE) in the control and UV-reduced treatments ($N=7$ per group). Change was calculated as the difference between UV chroma after and before application for each individual. Individual change in UV chroma differed significantly between treatment groups 10 min after application

of residents in order to investigate its impact on the behavior of intruders and the potential for mutual assessment processes between males, where opponents assess each other's motivation and strength relative to their own (Arnott and Elwood 2009). We quantified contest outcomes and behavioral strategies to gain insights into fighting abilities and motivation to fight. If UV color signals fighting ability or aggressiveness, the experimental reduction of UV reflectance should influence mutual assessment and decision-making processes, including agonistic interactions, spatial dominance, and contest outcome. If UV signaling is in fact strongly involved in mate competition, we expect stronger effects of UV reflectance during the breeding season. Finally, if conflict resolution is mediated by a prior residency convention, the residency status of individuals should override the effects of UV coloration.

Materials and methods

Sampling and measurements

Capture sessions took place in August 2011 and March 2012, i.e., during one non-breeding and one breeding season, respectively. All captured individuals originated from a wild population (CEREAP-Ecotron Ile-De-France, France, 60 m a.s.l., 48° 17' N, 2° 41' E). Adult males were brought to the laboratory where we measured body size (snout-vent length SVL; ± 1 mm) and body mass (± 1 mg) and counted by eye the total number of blue spots on each flank. The number of blue spots was positively correlated with SVL ($N=43$, Pearson's correlation test, $r=0.35$, $t_{41}=2.37$, $p=0.023$). We quantified the reflectance on the first three blue spots of the right flank starting from the front legs using a spectrophotometer as described by Martin et al. (2013). Reflectance spectra were imported into Avicol software v5 (Gomez 2006), where we calculated brightness (total reflectance over the range 300–700 nm), chroma (difference between maximal and minimal reflectance divided by the average reflectance), UV hue (wavelength of the maximal reflectance in the UV range), and UV chroma (proportion of the UV reflectance relative to the total reflectance). We also performed spectral measurements on the animals' belly during the breeding season (Fig. 1). We extracted brightness and chroma from these spectra and found that the spectral variables of the UV coloration of blue spots were independent of spectral characteristics of ventral coloration ($N=38$, Pearson's correlation tests, for all the variables $p>0.18$). The number of blue spots corrected by SVL (residuals from regression between log-transformed variables) was different between color morphs (ANOVA: $F_{2,70}=3.63$; $p=0.032$): red morph had more blue spots than white morph (white vs. red: $p=0.022$; yellow vs. red or white, $p>0.78$). In addition, brightness, chroma, and UV chroma were significantly higher during the non-breeding season than during the breeding season (Welch's t test for brightness: $t_{52.5}=-17.77$, $p<0.001$; chroma: $t_{68.63}=-4.80$, $p<0.001$; UV chroma: $t_{62.9}=-5.72$, $p<0.001$; UV hue: $t_{69}=1.45$, $p=0.28$).

When choosing individuals to form a pair for the experiment ($N=34$ per season), we ensured that the two males were as similar as possible in their SVL (± 2 mm) and body mass (± 500 mg) as well as in their ventral color morph and total number of blue spots ($N=17$ pairs per season with a total of 22 white pairs, 7 red pairs, and 5 mixed pairs). For each pair, one male was given the residency status and the other was given the intruder status. No differences were detected between residents and intruders in SVL, body mass, and number of blue spots (Student's paired t tests, all $p>0.18$). Each resident male was housed in an individual terrarium (45 \times 29 \times 22 cm) where all behavioral tests took place after 5–6 days of acclimation. Intruders were transferred to the resident terrarium prior to each test. This

design generates an asymmetry in ownership, stress level, and risk-taking between residents and intruders during the behavioral tests (López and Martín 2001a). In the housing, all terraria were layered with sand, equipped with a small water dish, two hides, and a black PVC plate for basking (4×9 cm). Heat was provided by means of an incandescent bulb (25 W), and light was provided by a UVB neon light (Reptisun 10.0 UVB, Zoomed, see Fig. S1 for a spectrum of light environment) during 8 h per day. Lizards were fed with 200 mg of crickets (*Acheta domesticus*) per day, and water was provided *ad libitum*.

Color manipulation

To temporarily reduce the UV skin reflectance, we designed a cream based on two UV-blocking (290–400 nm) inorganic agents (zinc oxide and titan dioxide) that do not penetrate the epidermis (particles of 200–500 nm) mixed with a combination of petroleum jelly and liquid paraffin called fat thereafter (6:4:50:40 for 100 g). The cream was applied on all blue spots with a soft paintbrush. To validate our protocol, we measured the reflectance of blue spots from randomly selected males belonging to a non-manipulated group, a control group treated with fat only, or a treatment group ($N=7$ per group). After 10 min, the treatment shifted up the wavelength of maximal UV reflectance by 23.7 ± 8.7 (SD) nm ($t_{5,34}=-3.66$, $p=0.013$), and reduced UV chroma by 12 ± 2.5 (SD) % ($t_{3,61}=3.19$, $p=0.038$, Fig. 2a), but it did not change brightness ($t_{5,5}=-0.86$, $p=0.43$) and chroma ($t_{3,08}=1.26$, $p=0.29$) significantly. The treatment was efficient during at least 5 h and reduced UV reflectance within the natural range after less than half an hour (Fig. 2b).

Experiment

Each pair was tested four times with different combinations of UV treatments for the resident and the intruder male in a full factorial design (i.e., for resident-intruder pair: “Control – Control,” “Control – UV reduced,” “UV reduced – Control,” and “UV reduced – UV reduced”). The sequence of treatments was random, and trials of a pair occurred at the same hour every other day. This design allowed testing for effects of UV coloration while controlling for variation between pairs and among individuals within pairs. Immediately, prior to each trial, internal equipments were removed from the resident’s terrarium, which was separated into two compartments by a removable opaque wall. Light was provided by two UVB neon lights located 70 cm above the ground, and heat was provided by two incandescent bulbs of 20 W located above each compartment. Room temperature was maintained at 20–21 °C. After the application of the cream on all blue spots, the resident was introduced by hand in one compartment and the intruder 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, and observations begun. This protocol ensured that the intruder was encouraged to move towards the resident to bask.

Trials were observed independently by two experimenters placed behind a blind. For each trial, behaviors of both males were recorded during 20 min using Jwatcher (Blumstein and Daniel 2007). As previously observed in wall lizards, pairwise interactions rarely escalated into physical fights (López and Martín 2001b; Sacchi et al. 2009), and aggressive displays were not ritualized. Thus, we used dominance score and principal component analysis to analyze agonistic behaviors (see below). For each trial of a pair, we recorded the number of agonistic behaviors including aggression (rapid approach towards the opponent or touch the opponent without bite), approach, bite, demonstration (push-up, wide sustained opening of jaws, or display of one flank towards the opponent), escape, surveillance, and tail movement (see details in Table S1 provided as supplementary data). In addition, to evaluate spatial dominance, we quantified the total time spent basking (flattened body onto the substrate oriented at right angle to a heat source), which can be interpreted as a monopolization of the heat resource (de Fraipont et al. 2000; Le Galliard and Ferrière 2008).

To assess the outcome of each trial, we computed a contest score by measuring the difference between the dominance score of the resident and of the intruder. The dominance score of each individual was calculated by subtracting the number of its submissive behaviors (escapes and tail movements) from the number of its aggressive behaviors (aggressions, approaches, and bites). The contest score provides a quantitative measure of the contest outcome, where positive values of contest score denote the “superiority” of the resident over the intruder, and negative values denote the “superiority” of the intruder (López and Martín 2001b; Sacchi et al. 2009).

Statistical analyses

We used the R 2.13.1 software (R Development Core Team 2011) to separately analyze variation in agonistic behaviors and basking time during and after the breeding season. Agonistic behaviors were studied through two complementary methods—contest score and principal component analysis (PCA)—allowing to describe behavioral variation at the pair level on the one hand and at the individual level on the other hand. We first analyzed the effects of the UV treatment on the resident, of the UV treatment on the intruder, and of their interaction (fixed effects) on contest scores. Contest scores ($N=68$ observations per season) were rank-transformed in order to fulfill assumptions of normality and variance homogeneity.

Second, we investigated the influence of UV manipulation on the behavior of each male within a pair depending on its residency status and on the treatments they were submitted to. For each individual, we scored residency status (resident or intruder), UV treatment (thereafter called focal treatment or Tfocal), and UV treatment of its opponent (thereafter called rival treatment or Trival). We tested for the effects of these factors and their two-way and three-way interactions on basking time and agonistic behaviors. Given that significant correlations existed among descriptors of agonistic behaviors, individual values of aggression, approach, escape, tail movement, demonstration, and surveillance behaviors were square root-transformed, centered, and scaled. A PCA was then used to calculate individual principal component (PC) scores. The data for the number of bites was excluded from the PCA because only two pairs displayed this behavior during the breeding season. We determined how many axes represented a significant variation with the broken-stick model (Jackson 1993). We then extracted the absolute contributions of the decomposition of inertia for each axis with the *inertia.pca* procedure implemented in the *ade4* package and interpreted only behavioral parameters whose contribution exceeded the average contribution. PC scores fulfilled assumptions of normality and variance homogeneity.

We analyzed all data with linear mixed-effect models in the *lme* procedure, with pair identity as random factor when studying contest score, and with pair and individual identities when studying basking time and PC scores. In addition, observer name (two persons per season) and sequence number (trial 1 to 4, categorical factor) were included in the models. This latter factor allowed controlling for behavioral variation related to the effect of familiarity between opponents (unfamiliar vs. familiar rivals) and/or any form of habituation to the experimental environment. There was no relationship between the color morphs and the behavior (influence of color morphs on PC scores and basking time: all $p > 0.12$). Analyses started with a full model including all effects, and the best model was chosen by backward elimination of non-significant terms starting with interaction terms.

Results

Breeding season

Contest scores of male pairs were not influenced by UV treatments (all $p > 0.11$; effects of observer identity and sequence number: all $p > 0.09$). The PCA summarized behavioral variation into two major axes (Table 1). The first principal component (PC1) was positively associated with aggression and approach behaviors, while the second principal component (PC2) was positively correlated with escape and tail movements. We found that residency status influenced the time

Table 1 Scores and contribution of agonistic behaviors for the two first PCs from a PCA of behavioral data during and after the breeding season

	Breeding season		Non-breeding season	
	PC1	PC2	PC1	PC2
Eigen value	1.78	1.47	2.02	1.24
Variance (%)	29.72	24.49	33.61	20.73
Loadings				
Aggression	0.67	-0.25	0.47	0.76
Approach	0.69	-0.29	0.68	0.50
Demonstration	0.55	-0.09	0.62	-0.47
Escape	0.52	0.72	0.60	-0.12
Tail movement	0.13	0.88	0.44	-0.28
Surveillance	0.53	-0.14	0.63	-0.34

Bold values are behaviors with a “significant” contribution in the associated principal component (PC)

spent basking as well as scores for PC1 and PC2 (Table 2). On average, residents spent more time basking, aggressed and approached more (higher scores for PC1), and displayed less escape and tail movement behaviors (lower scores for PC2) than intruders. Results also indicated that PC1 scores changed significantly during a sequence because of a difference between trial 1 and the next trials (Tukey’s post-hoc tests; trials 2, 3, and 4 vs. 1: all $p < 0.03$, other comparisons: $p > 0.29$, Table 2). None of the individual variables was influenced by UV treatments (Table 2).

Non-breeding season

Contest scores were not influenced by UV treatments or other factors (all $p > 0.09$). The PCA summarized agonistic behavioral data into two major axes (Table 1). PC1 was positively associated with approach, demonstration, escape, and surveillance behaviors while PC2 was positively correlated with aggression behaviors. We observed a sequence effect on PC1 scores, with differences between the first and the other trials (Tukey’s post-hoc tests; trial 2, 3, and 4 vs. 1 and trials 4 vs. 2: $p < 0.005$, trial 3 vs. 2 and 4: $p > 0.082$, Table 2). Neither the residency status nor the UV treatments significantly influenced PC1 and PC2 scores (Table 2). However, the basking time was significantly affected by a three-way interaction between residency status, the UV treatment of the focal male, and that of the rival (Table 2 and Fig. 3). When both residents and intruders had the control treatment, they had similar basking times. By contrast, when the two contestants displayed a different UV treatment, residents seemed to spend more time basking than intruders; intruders seemed to spend more time basking than residents when both residents, and intruders had the UV reducing treatment.

Table 2 Results of backward elimination on non-significant terms from the full model (12 parameters, 136 observations) describing variation among males in PC scores (PCA applied to agonistic behaviors, see Table 1) and basking time during and after the breeding season

Fixed effects	Breeding season			Non-breeding season		
	PC1	PC2	Bask.	PC1	PC2	Bask.
Observer	5.04*	5.16*	1.13	9.11**	0.07	<0.01
Sequence	7.01***	0.55	0.49	39.61***	0.62	0.30
Status	6.18*	4.77*	5.48*	0.63	0.13	<0.01
Tfocal	0.08	1.39	1.91	0.27	1.27	0.51
Trival	0.01	0.78	0.16	0.80	0.01	1.50
Status×Tfocal	0.18	0.01	0.02	0.22	0.85	0.59
Status×Trival	0.08	0.55	0.29	0.55	0.40	1.19
Tfocal×Trival	3.26	3.08	0.69	1.47	2.00	0.47
Status×Tfocal×Trival	0.06	0.08	0.32	0.06	0.78	4.91*
Random effects						
Pairs	37.99	<0.01	9.85	25.65	13.67	<0.01
Individuals nested in pairs	10.23	48.83	53.53	17.64	35.21	73.21
Residuals	51.78	51.17	36.62	56.71	51.12	26.79

Data reported are F-ratios calculated during backward elimination in the case of non-significant variables and type III F-ratios for fixed effects and percentage of variability explained by inter-individual and inter-pair random effects. Bold values correspond to final models

Tfocal UV treatment of the male, *Trival* UV treatment of the rival, *Bask.* basking time

Stars are significant values with * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$

Inter-individual variation

In both seasons, the estimation of random effects (see Table 2) revealed consistent inter-individual differences especially for PC2 scores and basking time (percentage of variation higher than 35 %). Conversely, PC1 scores varied much more or similarly between pairs than between individuals during the breeding season or the non-breeding season, respectively. Thus, behavioral traits connected to basking, submission during the breeding season, and aggressiveness during

the non-breeding season were related to personality when we controlled for experimental factors (see Dingemanse et al. 2010 for a discussion of personality traits).

Discussion

Blue spots of male wall lizards displayed an important variation in the UV chroma (range=10–40 %, CV=0.24), and UV chroma was higher during one non-breeding season than during one breeding season. UV reflectance of blue spots in another lizard, *Gallotia galloti*, also shows striking inter-individual differences and progressively increases during the breeding season and then decreases to a value higher than the basal level, which may reflect changes in the hormonal state of animals (Bohórquez-Alonso & Molina-Borja 2014). Our staged encounter experiments showed that UV manipulation affected spatial dominance but not aggressive interactions differently according to male residency status, only during the non-breeding season. These complex results suggest context-dependent effects of the UV component of blue spot coloration on territorial behaviors.

UV visual signals in aggressive interactions

In line with predictions of the badge of status hypothesis (Rohwer 1975; Maynard Smith and Harper 2003), UV reflectance influences either aggressive behaviors of male rivals or the outcome of contest in blue tits, sticklebacks, damselfishes,

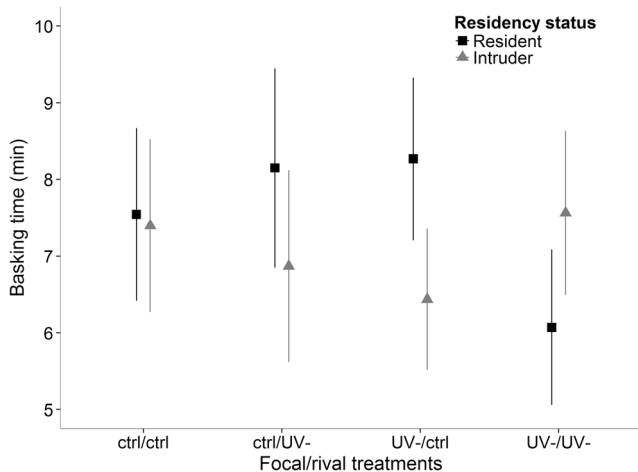


Fig. 3 Basking time of residents (*black squares*) and intruders (*grey triangle*) during the non-breeding season depending on their UV treatment and the UV treatment of their rival. Basking time data are mean duration (\pm SE)

and several species of lizards (Alonso-Alvarez et al. 2004; Siebeck 2004; Stapley and Whiting 2006; Whiting et al. 2006; Rick and Bakker 2008; Rémy et al. 2010; Vedder et al. 2010; Bajer et al. 2011; and see a review by Olsson et al. 2013). Yet, in wall lizards, we found no difference in contest scores and agonistic behaviors between male rivals in relation to UV treatments. In addition, we observed a significant resident effect on agonistic behaviors during the breeding season; resident males were on average more aggressive, approached the intruder more often, and were less submissive than intruders, in agreement with the results of several other studies (e.g., Olsson 1992; López and Martín 2001a). Thus, the prior-resident effect seems to override potential responses to differences in the UV component of coloration, and UV coloration is likely to be of limited importance during aggressive interactions when an asymmetry in residency status was present.

However, the absence of significant effects of a reduced UV coloration on agonistic behaviors and contest outcomes is not entirely surprising because the badge of status hypothesis predicts that color patches are more influential during the first stages of conflict resolution, when individuals are not familiarized to each other. For example, Rémy et al. (2010) and Vedder et al. (2010) demonstrated effects of UV coloration on male-male interactions between unfamiliar individuals only. In our study, the behavioral profiles of males changed significantly after the first trial, suggesting that rivals quickly became familiar. A preliminary exploration of the behavioral data collected during the first trial only showed that UV manipulation exclusively affected submissive behaviors of unfamiliar males (results not shown). However, these analyses remain questionable because we were unable to rigorously investigate differences among treatment groups owing to a lack of statistical power. Whether UV coloration is used as a badge of status during agonistic behaviors among unfamiliar males in the wall lizard therefore remains uncertain. Hence, the question should be tested with a larger sample size in the future.

UV visual signals in spatial dominance

Although agonistic behaviors are the most frequent interaction traits used to study the role of color signals in male-male interaction, we also recorded basking time, which is associated with the monopolization of the heat resource and, presumably, with dominance in space use in heliothermic lizard species (de Fraipont et al. 2000; Le Galliard and Ferrière 2008). Basking time was only well predicted by the residency status during the breeding season while during the non-breeding season, and it varied differently among residents and intruders in response to different combinations of their UV treatments and that of their rivals. Thus, the effects of UV signal intensity on spatial dominance of male wall lizards were complex and

context-dependent. Residents from the control group confronted to UV-reduced intruders seemed to increase their basking time relative to control intruders, while intruders seemed to respond in the opposite way. This result is consistent with the badge of status hypothesis, which predicts that UV reflectance is used by resident males to evaluate the strength of intruders and that intruders generally avoid conflicts for space use when territory owners signal higher dominance (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). However, we found opposite patterns of variation when residents belonged to the UV-reduced group. UV-reduced residents confronted to UV-reduced intruders decreased their basking time relative to control intruders. Thus, in wall lizards, residents tended to monopolize the heat resource whenever their UV signals differed from those of their rival. A potential explanation is that, in such cases, resident detects a mismatch between the signal of the intruder and its behavior (mutual assessment process, Arnott and Elwood 2009). For example, a control resident assesses a UV-reduced intruder as a weaker rival, but the intruder behaves as a rival of similar strength since it relies on its own evaluation of the resident's strength. Such a situation might then incite residents to invest in dominance behaviors (Rohwer 1977; Maynard Smith and Harper 2003).

Social evolution of UV visual signals

In summary, our study suggests that UV signaling is not a major determinant of fighting success in wall lizard. Yet, UV signals were involved in the process of behavioral assessment among rivals and influenced spatial dominance behaviors of males in a complex manner that depended on residency status and, potentially, seasons. We found differences in UV-treatment effects between the two experiments, and an exciting possibility is that these differences may be related to conditions during and outside of the breeding season. During the breeding season, when territory ownership is presumably related to access to females and the value of a territory is high, a resident effect was observed with more aggression and dominance in space use in residents as predicted by evolutionary game theory (Kokko et al. 2006). There was no competitive advantage in males with control UV coloration, suggesting that intrasexual competition for mates is unlikely to be a strong selective factor for the maintenance of that trait in this population. At the same time, the influence of UV signals on spatial dominance during the non-breeding season as well as the higher mean value of UV chroma at that time of the year suggest that UV signaling may have a more important role than expected during competition for food and space. More studies should be performed to confirm that these seasonal shifts in behaviors are not confounded with year or other temporal effects, because we sampled one breeding and one non-breeding season in two separate years. Replicate studies of

animal behaviors across seasons are rare, and our findings highlight the need to study color signals both during and outside of the breeding season to deepen our understanding of their functions.

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Compliance with ethical standards Authorization No. 2007-189-005 allowed us to capture and manipulate wild animals for this study. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

Conflicts of interest The authors declare that they have no competing interests.

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