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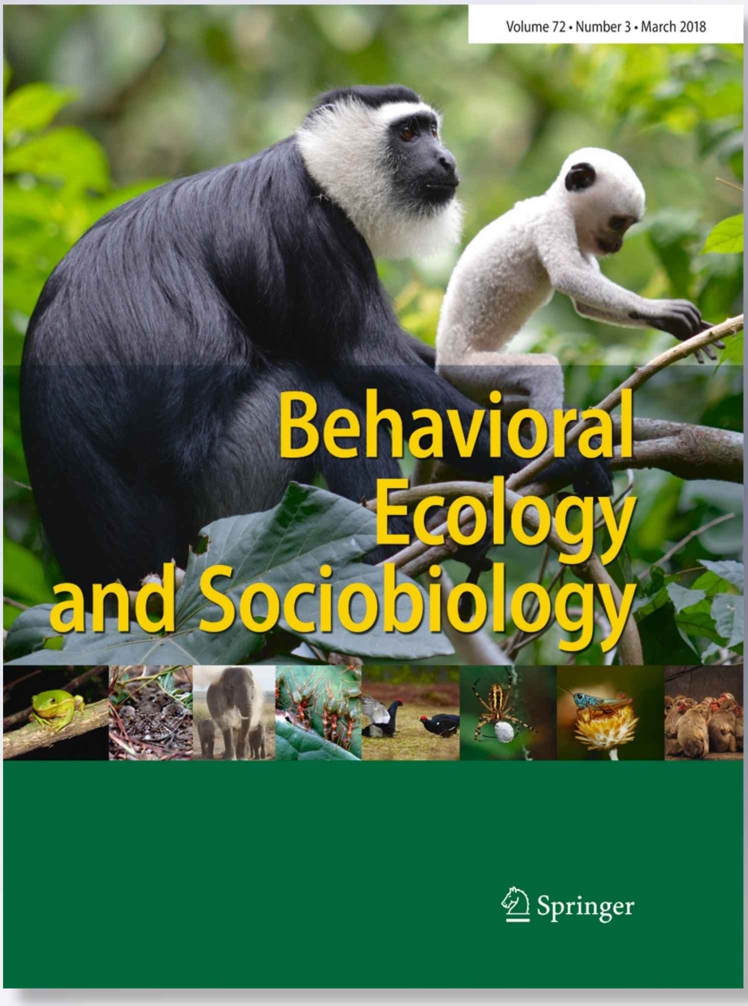

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ORIGINAL ARTICLE

Predictors of contest outcome in males of two subspecies of *Gallotia galloti* (Squamata: Lacertidae)

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Abstract

In many species, male coloration signals aggressiveness and/or fighting ability. Males of the Tenerife lizard (*Gallotia galloti*) have conspicuous ultraviolet (UV)-blue cheek and lateral color patches that are brighter in the breeding season and larger than those of females. We analyzed experimentally the effect of morphological and behavioral traits, including spectral variables from UV-reflecting color patches, on the outcome of staged dyadic contests between males of two subspecies of *G. galloti*. We performed two experiments: (1) using pairs of unmanipulated males and (2) reducing the UV reflectance of the UV-blue patches of one of the contestants with sunscreen lotion. Results from experiment 1 showed no significant difference between subspecies in the effect of any variable on contest outcome. Overall, winners had larger body mass, head width, and fore-limb length and showed a higher rate of aggressive behavior patterns than losers, whereas losers showed a higher rate of "tail shake," which is considered a submissive behavior. Winners also had lateral UV-blue patches with higher (more blue-biased) hue than losers, but no other spectral trait had a significant effect on contest outcome. Results from experiment 2 showed that reducing patch reflectance in the UV range had no effect in one subspecies but significantly increased fighting success in the other. The probability of winning was positively associated with the frequency of bites (irrespective of whether individuals had manipulated patches or not). Results from both experiments suggest that while multiple traits (morphometric, coloration, and behavioral) may influence the outcome of male contests in *G. galloti*, behavioral traits take prevalence over morphological, including coloration, traits.

Significance statement

The effect of several traits on the outcome of contests has been previously analyzed in males of several lizard species. These analyses have commonly considered the effect of a single trait on contest outcome. However, as even males of the same age and experience often vary across multiple morphological (including coloration), performance, and behavioral traits, it has been suggested that contest outcome could be influenced by several interacting traits. We tested this hypothesis by staging dyadic contests between males of two subspecies of the Tenerife lizard. Results from a first experiment showed that larger body mass, head width, fore-limb lengths, higher frequency of bites, throat extension, and higher peak reflectance (hue) of UV-blue patches significantly affected the probability of winning, while a large frequency of tail shakes was associated with losing. Results from a second experiment, in which we experimentally manipulated patch UV reflectance in one of the contestant lizards, showed that bite frequency and reduction of UV reflectance affected the probability of winning; we discuss the complex effect of this latter trait on contest outcome.

Keywords Lizard contests · Patch coloration · Ultraviolet reflectance · Behavioral traits · *Gallotia*

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Introduction

Conspicuously colored body parts function as social signals in many animal taxa such as fish, lizards, and birds (Cooper Jr and Vitt 1989; Cooper Jr and Greenberg 1992; Alatalo et al. 1994; García and Perera 2002). For example, conspicuous color patches have been shown to be involved in signaling sex (Cooper Jr and Greenberg 1992; Delhey and Peters 2008; Balogová and Uhrin 2015), status/fighting ability (lizards, Olsson 1994; Carpenter 1995), and individual quality in the context of female choice of male mates (birds, Sheldon et al. 1999; Siitari and Huhta 2002).

Conspicuous color patches are common in many lizard species and are usually located on the throat, belly, laterally on the head and/or body trunk, and in the tail of some iguanids, agamids, crotaphytids, varanids, and lacertids (Cooper Jr and Greenberg 1992; Olsson et al. 2013). The color patches are often sexually dimorphic, those of males being typically larger than those of females (Font et al. 2009). In some species color variation has been shown to provide information about the sex of the bearer (Bauwens et al. 1987; Cooper Jr and Vitt 1988), male fighting ability (Olsson 1994), or female reproductive condition (Cuadrado 2000). Moreover, the conspicuous, lateral coloration and the dorsal, generally cryptic coloration of some lizards have been shown to be tuned, respectively, to conspecific and predator vision (Marshall and Stevens 2014; Pérez i de Lanuza and Font 2015), suggesting that the lateral coloration has been selected for a social signaling function. It has also been found that coloration in several lizard species is related to morphological, behavioral, and performance traits that promote success in male-male contests (Quinn and Hews 2000; Stuart-Fox et al. 2006; Whiting et al. 2006; Hamilton et al. 2013; Yewers et al. 2016); a common result of these studies has been that larger or more colorful males have a higher probability of winning contests and/or obtaining access to a larger number or female partners (Baird 2014).

The reflectance of colored body parts in some vertebrates extends into wavelengths that are not visible to humans. Thus, for example, near ultraviolet (UV) reflectance (i.e., wavelengths between 300 and 400 nm) of color patches has been described in many vertebrates including birds, fish, and reptiles (Cuthill et al. 1999; García and Perera 2002; Font et al. 2009). For species capable of UV vision, UV reflectance potentially provides a “private” communication channel which has received much attention in recent decades. For example, feather reflectance in the UV range has been documented to play a role in signaling male status or condition in birds (Cuthill et al. 1999; Sheldon et al. 1999; Alonso-Alvarez et al. 2004).

Patches reflecting UV have been described in several lizard species (Blomberg et al. 2001; Pérez i de Lanuza and Font 2007; Font et al. 2009; Martin et al. 2013), but their functions have not yet been clearly established. The UV-reflecting throats of females of *Ctenophorus ornatus* have been shown to influence male mate choice (Lebas and Marshall 2000), while UV reflectance from males affects female mate choice in *Lacerta viridis* (Bajer et al. 2010). In other species, UV reflectance has been shown to be a good predictor of male fighting ability (Stapley and Whiting 2006; Whiting et al. 2006; Bajer et al. 2011; Olsson et al. 2011; Pérez i de Lanuza et al. 2014) or spatial dominance (Martin et al. 2015b). Perception of UV reflectance from these color patches is made possible by the complex color vision system of diurnal lizards (including lacertids), which has an all-cone retina with four types of cones, one of which is sensitive to near UV wavelengths (Fleishman et al. 2011; Pérez i de Lanuza and Font 2014).

Gallotia galloti is an endemic lizard species from Tenerife (Canary Islands), with two subspecies: *G.g. galloti* (from the center and south of the island, hereafter *Ggg*) and *G.g. eisentrauti* (hereafter *Gge*) from the northern coastal strip (Bischoff 1982). The two subspecies differ mainly in male coloration. Northern males have transverse yellow bars on the back and conspicuous UV-blue patches on the cheeks and lateral trunk. Southern males have larger UV-blue lateral patches and show much less developed UV-blue cheeks, which they may lack entirely (Molina-Borja et al. 1997). The two subspecies are relatively distant phylogenetically and are currently separated by a contact zone with restricted gene flow (Richard and Thorpe 2001; Thorpe and Richard 2001; Cox et al. 2010). Therefore, the question emerges about the possible role of morphological and behavioral traits, including aggressive patterns and contest strategies, in maintaining the genetic distance between the two subspecies. We therefore selected for our work individuals from spatially separated populations of each subspecies. Sexual dichromatism of the UV-blue patches has been described for both subspecies of *G. galloti*, the UV-blue lateral patches of males having lower hue and higher brightness (luminance) than those of females (Molina-Borja et al. 2006; Bohórquez-Alonso and Molina-Borja 2014). Though contests among southern males have been previously analyzed (Molina-Borja et al. 1998), information for the northern subspecies is more scant and the possible function of the UV-blue reflecting patches has not been experimentally assessed for either subspecies. Thus, in the present work, we conducted experiments to test if winning and losing probabilities are affected by several morphological and behavioral traits in males of the two subspecies of *G. galloti*.

Based on previous analyses in other lizard species, we hypothesized that winners of agonistic encounters would have larger UV-blue color patches (Huyghe et al. 2005), with more brightness (luminance), and/or different hue and chroma (*Platysaurus broadleyi*, Whiting et al. 2006; *Podarcis muralis*, Pérez i de Lanuza et al. 2014) than those of losers. However, as the probability of contest winning/losing in males from each population may be affected by multiple traits, we predicted that a combination of morphometric, coloration, and behavioral traits would influence winning/losing probability.

Materials and methods

Lizard sampling and maintenance

Lizards were collected in two localities in Tenerife: (1) El Pris (north of the island, *Gge*) with vegetation including *Rubus ulmifolius*, *Euphorbia regis-jubae*, *Artemisia* sp., and *Periploca laevigata* shrubs and (2) Malpaís de Güimar (henceforth Güimar, in the southeast, *Ggg*), a protected natural space with lava fields and dispersed xeric plants such as *E. canariensis*, *Plocama pendula*, *P. laevigata*, and *E. balsamifera*.

Lizards were captured between April and June (2005 and 2006) using tomato-baited pitfall traps and were transported to the laboratory at the Universidad de La Laguna. We released immediately all captured juveniles and females and kept only adult males (larger than 85-mm SVL, Molina-Borja and Rodríguez-Domínguez 2004). In the laboratory, each lizard was housed singly in a terrarium (50 × 40 × 40-cm height) placed inside a temperature-controlled room. Light was provided by fluorescent tubes with daylight spectrum (UV-enriched light: Reptistar, F18W 6500 K, Sylvania) with a cycle of 13-h light and 11-h dark. We supplied food (pieces of tomato and banana, and *Tenebrio* larvae) two to three times weekly. Water was continuously available in water dishes. The temperature inside the rooms was 28 ± 0.5 °C. Lizards were held in captivity a maximum of 12 days and were released at their capture points once the experiments were completed.

Experimental procedures

Area of color patches

On the day they were captured (or at most the following day), we took a digital picture of each lizard's left and right flanks by gently pressing it against a transparent plastic sheet with an attached millimeter scale. Pictures were transferred to computer files and analyzed with UTHSCSA Image Tool v 2.0 software. We measured the total area (in mm^2) of all cheek and lateral UV-blue color patches from both body sides (TPA).

Lizard contests, behavioral patterns, and spectral measurements

We performed two experiments. In the first experiment (Exp. 1), after 7–10 days in their terraria, pairs of males from each population ($n = 24$ and 29 pairs from the northern and southern populations, respectively) were selected at random and introduced in a cage (40 × 50 × 40-cm height) located in a different room having the same temperature and light-dark cycle as described above (including UV-enriched illumination). The maximum body size difference between contestants was 2 cm. When at least one of the lizards resumed spontaneous activity, the behaviors of both contestants were continuously filmed with a video camera (mini DV Panasonic NV-DS15). Contests lasted a maximum of 30 min and were terminated as soon as a winner could unambiguously be determined (i.e., the other lizard fled if approached by its opponent or tried to escape the fighting arena). Each lizard was only used in a single contest. We measured ambient and lizard body temperatures both at the beginning and at the end of each contest; cloacal temperature was taken by means of a quick reading thermometer (Web and Miller, 0.1-°C precision). In addition, for each individual, we took the following morphometric measurements: snout-to-vent length (SVL, 0.5-mm precision), body mass (BM, 0.1-g precision), head width (HW), fore-limb, and hind-limb lengths (FLL, HLL, 0.01-mm precision), as defined elsewhere (Molina-Borja et al. 1997).

From every recorded video, we noted in check-sheets and separately for each lizard, the frequency of behavior patterns shown in each trial. The behaviors shown by *G. galloti* lizards in agonistic encounters have been previously described (Molina-Borja et al. 1998), and in the current study, we considered only the most frequent behaviors observed in male-male contests: "tongue-flicking" (TF), "throat extension" (TE), "bite" (B), and "tail shake" (TS) (see descriptions in Table 1). Throat extension is always accompanied by lateral body compression and both are commonly exhibited at the beginning of a contest, followed by bites (both individuals), and finally tail shakes by the loser as the contest escalates (Molina-Borja et al. 1998). To minimize observer bias, scoring of behavior data was done blind by a single observer.

As *G. galloti* do not undergo short-term physiological color changes (MMB unpublished observations), we waited until the end of the contests to measure the reflectance of the first lateral right patch (for both subspecies) and that of the cheek mark (only for *Gge*) by means of an Ocean Optics USB2000 portable diode-array spectrophotometer. UV-blue patches on both sides of the body had similar spectral shapes, and considering conspicuousness and likely communicative importance, we concentrated our analyses on the first rostral most right lateral patch and the right

Table 1 Short descriptions of the behavioral patterns analyzed in male contests of both subspecies of *Gallotia galloti*

Behavioral pattern	Description
Tongue-flicking	Extrusion of the tongue that is moved in the sagittal plane once outside the mouth.
Throat extension	The lizard extends its gular skin downwards and holds it in that position during several seconds.
Bite	A male opens its mouth and bites or tries to bite the opponent. The head is more frequently bitten but also the trunk or other body parts.
Tail shake	The whole tail is undulated sideways while being parallel and in contact with the substrate.

male cheek patch. A few specimens had large patches (7–8 mm in diameter) and as the optic probe reading spot was 2.5 mm in diameter (Badiane et al. 2017), we only took one measurement from the center of these patches.

Spectra were recorded in 0.37-nm steps from 300 to 700 nm and expressed as percent light reflected relative to a Spectralon white diffuse reflectance standard. For each color patch, the spectrometer averaged 20 spectra that were graphed using OOIBase32 software from Ocean Optics. Integration time was set at 55 ms using data-smoothing level 10. Brightness (luminance or total intensity of the light spectrum) was calculated for the entire spectrum (300–700 nm) and separately for the UV-blue and for the rest of the visible range by summing the percent reflectance across the 300–495-nm range of wavelengths (R300–495) and the 495–700-nm range (R495–700), respectively. These two wavelength segments were analyzed separately because winner-loser differences could be reflected in just one of them and not in the other. Hue (peak wavelength) was estimated as the wavelength of maximal reflectance (Rmax). Relative UV-blue reflectance or UV-blue chroma (the spectral purity or saturation of UV-blue colors) was calculated using the formula R300–495/R300–700, where R300–700 is the cumulative percent reflectance in the 300–700-nm spectral range.

In the second experiment (Exp. 2), we used a different set of lizards (29 pairs of *Ggg* and 25 pairs of *Gge*) to assess the effect of manipulating the UV reflectance of lateral patches on the outcome of aggressive contests. For this, we applied a commercial UV-absorbing sunscreen lotion (Anthélios XL, 60+, La Roche Posay) to all lateral patches from both body sides (and cheeks in *Gge*) of one of the contestant lizards (hereafter referred to as UV−). To confirm that this treatment effectively contributed to reducing UV reflectance, we obtained spectra from a small sample of lizards with sunscreen on their UV-blue patches (see Fig. 4c of "Results"). The animal receiving the UV treatment was selected by a coin flip. The other contestant (control UV+) received sunscreen over a similar total surface area but on body parts different from the lateral color patches (on areas of skin showing the dark brown background coloration and not immediately surrounding the UV-blue patches). For this second experiment, we took the same morphometric and behavioral measurements of all individuals; spectral measurements were not taken in this case because a lizard from each pair lacked reflectance in the UV range due to sunscreen application. All experimental trials of the two experiments were conducted between 10:00 and 13:00 h by the same researcher (MLBA).

Visual modeling

We used Vorobyev and Osorio's (1998) receptor noise limited model to quantify the discriminability between the unmanipulated and the UV-reduced color patches and between both types of UV-blue color patches and the background body coloration. Lacertids and other diurnal lizards have a phylogenetically conserved color vision system with four different types of single cone photoreceptors covering the visual spectrum from 320 to 700 nm (Fleishman et al. 1997; Loew et al. 2002; Pérez i de Lanuza and Font 2014; Martin et al. 2015a). As cone sensitivities of *Gallotia* are currently unavailable, we used cone absorbance spectra from another lacertid, *P. muralis* (Martin et al. 2015a). We selected visual parameters previously used in the literature. Thus, cone abundance ratio was fixed as 1:1:1:4 (corresponding to the UV-, short-, middle-, and long-wavelength-sensitive cones; based on results from Martin et al. 2015a), and the Weber fraction was 0.05 for the long-wavelength sensitive cone (Siddiqi et al. 2004; Marshall and Stevens 2014; Martin et al. 2015a). Calculations were performed in R 3.3.2 (R Core Team 2016) using the package PAVO (Maia et al. 2013). The discriminability (i.e., chromatic distance) between color patches was expressed as just noticeable differences (JND). It is traditionally assumed that chromatic distances below 1 JND are not discriminable, distances between 1 and 3 JND represent colors that are discriminable under good illumination conditions, and distances above 3 JND represent easily discriminable colors (Siddiqi et al. 2004; Marshall and Stevens 2014).

Data and statistics

As contest duration was 30 min or less, for each lizard, we calculated the relative frequency of each behavior pattern dividing its total frequency by the exact contest duration. Morphometric, behavioral, and patch hue data were standardized by $\log_{10}$ and brightness by arcsin square root.

In Exp. 1, as we did not obtain spectra from animals with nonshed skins or small lateral patches, the final sample sizes for spectral data analyses were 27 (*Ggg*) and 15 (*Gge*) male pairs. In the case of comparison of cheeks of *Gge*, the final sample size was 9 because at least one of the two individuals participating in the remaining contests did not have a cheek patch.

Data from Exp. 1 were analyzed with a generalized linear model (GLM) using the overall sample of lizards with winner/loser as the dependent variable (with a binomial distribution), population (i.e., subspecies) as a fixed factor, and morphometric, behavioral, and spectral traits as covariates. Given emphasis on biological and statistical significance, we generated a set of competing models and applied an information theoretic (IT) model selection procedure using Akaike's information criterion (AIC). The advantages of using an IT-AIC approach are likely to be slight, especially given recent emphasis on biological rather than statistical significance (Richards et al. 2011). AIC has a second order derivative (AICc) which contains a bias correction term for small sample sizes that should be used when the number of free parameters, p, exceeds $n/40$ (where n is sample size) (Burnham and Anderson 2002). We present AIC_c differences ($\Delta AIC_c = AIC_c - AIC_{min}$) for interpreting results of multiple models and we used a cutoff of $\Delta \leq 2$ to include only those models with substantial support from the data (Burnham and Anderson 2002).

In Exp. 2, to determine if there was a relationship between the UV treatment and contest outcome (i.e., winner/loser), we used a G-test of independence (Sokal and Rohlf 1995: alpha = 0.05) separately for *Ggg* and *Gge*. We also ran a GLM taking winner/loser as dependent variable, morphometric and behavioral data as independent variables, and population and treatment (UV+/UV−) as factors. As in Exp. 1, we included only those models with substantial support from the data (Burnham and Anderson 2002). Additionally, SVL and BM of males winning and losing contests and with and without sunscreen on their UV-blue patches were compared separately for *Gge* (multivariate ANOVA, factor: presence/absence of sunscreen) and for *Ggg* (Mann-Whitney *U* test, given that data did not fulfill the requirements of normality and homoscedasticity).

Finally, to establish if the absence of reflectance from lateral patches of one of the lizards affected the level of aggressiveness of the contest as a whole, we compared the relative frequency of all agonistic patterns (all the behaviors included in Table 1, except "tongue-flicking," which is not an aggressive behavior) performed in this type of contest with that of trials without manipulation of UV-blue patches (two-tailed Mann Whiney *U* test).

Data availability All data generated during the current work are included in the manuscript or are available from the authors on request.

Results

Exp. 1: morphometric, behavioral, and spectral traits of winners and losers

Basic statistics for all morphometric and behavioral variables of winning and losing lizards from both populations are presented in Supplementary Table S1. Total UV-blue patch area (TPA) increased with SVL but the relationship only reached statistical significance for losers of *Ggg*: Spearman rho (r) = 0.193, $p = 0.32$, and $r = 0.47$, $p = 0.01$, respectively, for winners and losers of *Ggg*, and $r = 0.15$, $p = 0.54$, $r = 0.32$, $p = 0.17$, respectively, for winners and losers of *Gge*.

Spectra of the first UV-blue lateral patch show a characteristic shape in all males from both populations, with reflectance concentrated in the UV-blue range and with a peak around 380 nm (Fig. 1a, b; see also Molina-Borja et al. 2006).

GLM showed that, taking into account all covariates, there was no significant difference between populations (i.e., subspecies) (Table 3). In both subspecies, larger BM, HW, FLL, a higher frequency of the behaviors "tongue-flicking" and "bite,"

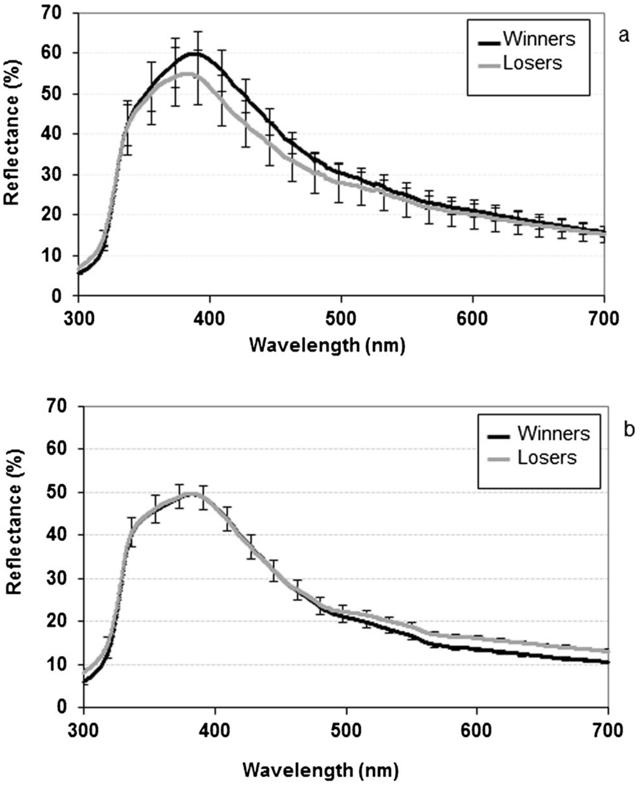

Fig. 1 Reflectance spectra (mean ± 1 SE) of the first lateral UV-blue patch of winner (dark line) and loser (gray line) lizards participating in male-male contests of *Ggg* (**a**) and *Gge* (**b**)

Table 2 Results of the generalized linear model analysis applied to all morphological, behavioral, and spectral traits of lizards from experiment 1. Bold variables significantly contributed to differentiate between winner and loser lizards

	Wald's chi-square	df	*p*
Intersect	3.653	1	0.056
Population	0.680	1	0.410
SVL	1.630	1	0.202
BM	**7.426**	**1**	**0.006**
HW	**5.263**	**1**	**0.022**
FLL	**7.137**	**1**	**0.008**
HLL	0.005	1	0.943
TPA	0.075	1	0.784
TE	3.587	1	0.058
TF	**6.376**	**1**	**0.012**
Bites	**8.271**	**1**	**0.004**
TS	**9.471**	**1**	**0.002**
R300_495	0.016	1	0.898
R495_700	0.762	1	0.383
R300_700	0.007	1	0.935
UVB_chroma	0.553	1	0.457
Peak	**6.697**	**1**	**0.010**

Table 3 Summary of AIC$_c$ candidate models. $\Delta AICc = AIC_c - AIC_{min}$

Model	AIC$_c$	$(\Delta AIC_C)_i$
Null[a]	105.693	33.079
Full[b]	72.614	17.951
Significant variables[c]	55.059	0.000
Biological meaningful[d]	96.866	39.702
Morph[e]	133.917	77.088
Behav[f]	90.422	35.234
Spectral[g]	113.329	56.273

[a] Null model (only intercept is included in the model)

[b] All covariates and the factor

[c] The significant variables in the GLM

[d] Biological meaningful variables: SVL, BM, HW, bites, R300–495, peak

[e] Morphometric variables

[f] Behavioral variables

[g] Spectral variables

and more blue-biased hue of the lateral UV-blue patches were significantly associated to winners, whereas losers showed a higher frequency of TS (Table S1, Fig. 2, Table 2). In Table 3, we present AIC values for different models including all or different subsets of variables; considering a cutoff of $\Delta \leq 2$, the most informative model is model c in Table 3.

In the case of the cheek patches of *Gge*, winners had larger mean brightness in the 300–700-nm range than losers (Fig. 3), but the difference was not statistically significant and no spectral trait of cheek patches was significantly associated with fighting success ($p > 0.05$ in all cases).

Exp. 2: effect of UV treatment

In Table S2, we present morphometric and behavioral data for lizards participating in Exp. 2. Sunscreen application reduced the UV-reflectance of the UV-blue patches almost completely while leaving the reflectance in the human-visible range largely unaffected (Fig. 4c).

Results of visual modeling show that the spectra of the manipulated and UV-reduced lateral UV-blue patches and the brown skin background color are clearly segregated in color space (Fig. 4a, b). The chromatic distances measured in JND between

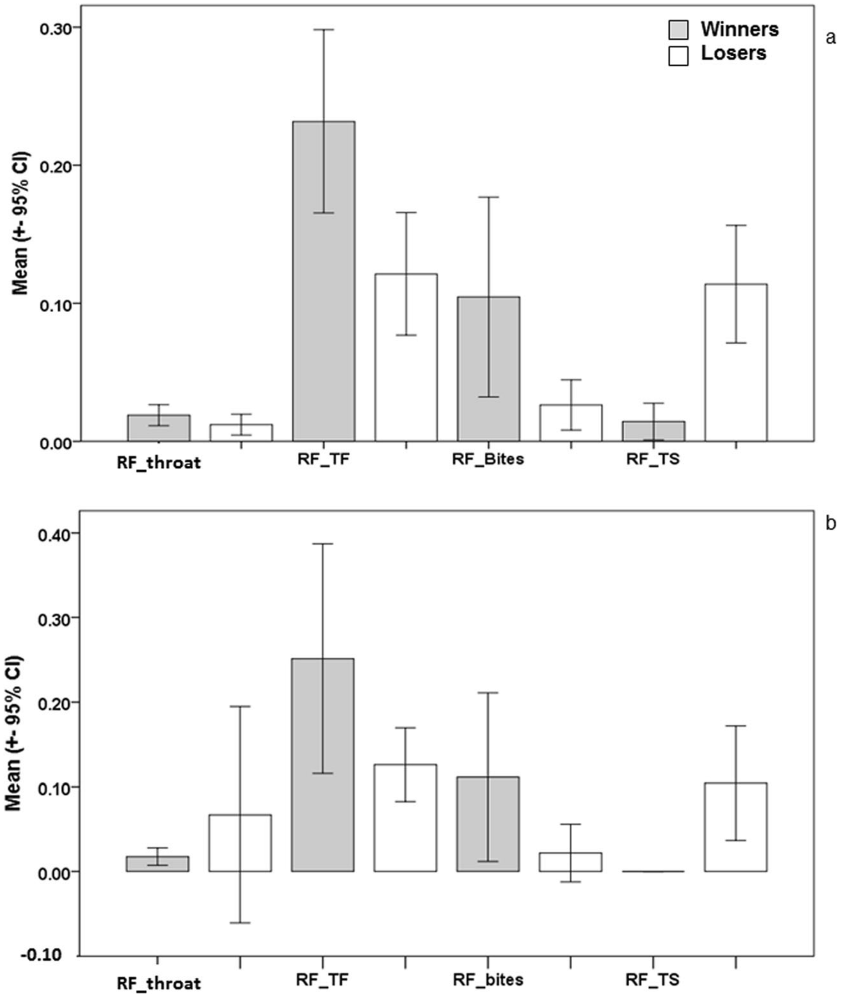

Fig. 2 Mean (± 95% CI) relative frequencies (RF) of "throat extension" (throat), "tongue-flicking" (TF), "bite" (bites), and "tail-shake" (TS) from winner (gray) and loser (white) lizards of *Ggg* (**a**) and *Gge* (**b**)

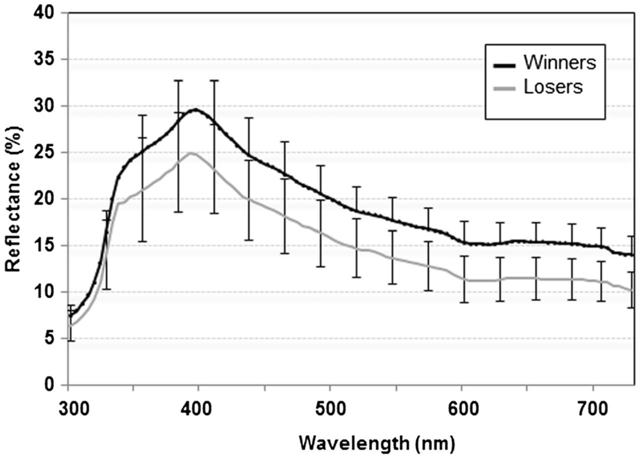

Fig. 3 Reflectance spectra (mean ± 1 SE) of the cheek patch of winner (dark line) and loser (gray line) lizards participating in male-male contests of *Gge*

them are (mean ± SEM): unmanipulated vs UV-reduced lateral UV-blue patches = 14.25 ± 0.44, UV-reduced patch vs background = 10.49, unmanipulated UV-blue patches vs background = 17.57 ± 0.50. Thus, assuming a conservative discrimination threshold of 3 JND, the three colors are chromatically discriminable to lizards considering all paired combinations.

In *Ggg*, there were significantly more UV− winners and more UV+ losers than expected by chance (Table 4). Thus, the UV treatment had an effect on contest outcome. The same trend was found for *Gge*, but in this case, the association did not reach statistical significance (Table 4). On the other hand, GLM showed that considering all morphological and behavioral traits, no variable contributed to differentiate winner and losers, except UV treatment (UV+ and UV−) (Table 5 and full model of Table 6). When morphological and behavioral traits were considered separately, the latter contributed the most to explaining contest outcome (Table 6). The second best model included behavioral traits and UV treatment (Table 6). UV− and UV+ males of *Gge* did not significantly differ in SVL ($F_{1,48} = 1.64$, $p = 0.205$) or BM ($F_{1,48} = 1.28$, $p = 0.263$) nor did they differ in *Ggg* ($F_{1,53} = 0.039$, $p = 0.843$ and $F_{1,53} = 0.042$, $p = 0.839$, respectively, for SVL and BM). Moreover, winners and losers from each subspecies did not significantly differ in these two variables (*Ggg*: $F_{1,53} = 1.543$, $p = 0.22$ and $F_{1,53} = 0.778$, $p = 0.382$, respectively, for SVL and BM; *Gge*: $F_{1,46} = 0.127$, $p = 0.723$ and $F_{1,46} = 0.067$, $p = 0.797$, respectively).

Finally, the level of aggressiveness did not differ significantly between contests without manipulation of patch reflectance (Exp. 1) and those in which one of the lizards had reduced UV reflectance of its lateral patches (Exp. 2): Mann-Whitney *U* test, $Z = -0.17$, $n = 27$ and 29, $p = 0.87$ (for *Ggg*), and $Z = -0.147$, $n = 15$ and 25, $p = 0.88$ (for *Gge*).

Discussion

Our results show that individuals from both subspecies of *G. galloti* do not differ in the type of behavior patterns expressed during agonistic encounters (see also Molina-Borja 2002) or in the effect of morphometric, behavioral, or spectral traits on fighting success. Therefore, despite their phylogenetic distance, no divergence in male aggressive behavior seems to have taken place between the two subspecies; however, future experiments conducting inter-subspecific

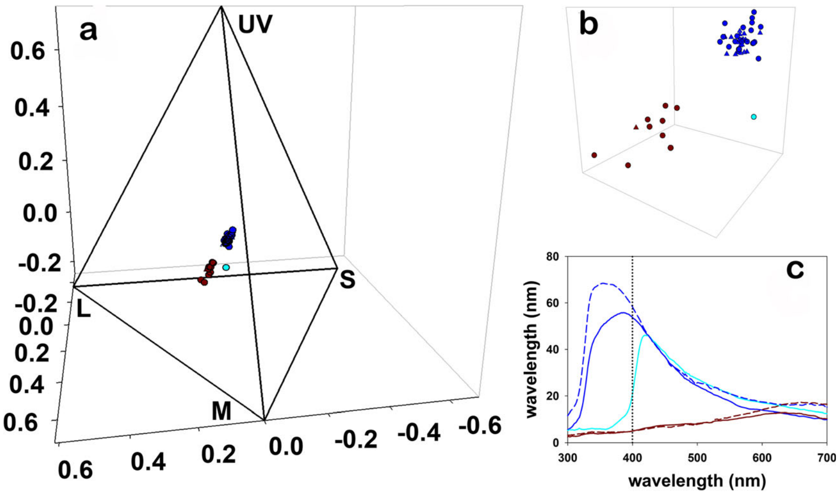

Fig. 4 Chromatic points of UV-blue lateral patches and background dorsal coloration of *G. galloti* modeled with *P. muralis* cone sensitivities in TetraColorSpace (for details see text). **a** Chromatic points are shown in the overall tetrahedron. UV, S, M, and L correspond to the chromatic points in which only the UV, short, medium, and long wavelengths are stimulated. **b** Detail of the volume occupied by the chromatic points. Chromatic points of the background coloration are shown in brown and those of UV-blue patches in dark blue. The light blue circle is a single UV-blue patch of *Gge* painted with sunscreen lotion. **c** Representative reflectance spectra from unmanipulated first lateral patches (dark blue lines), from a patch painted with sunscreen (light blue line), and from background color (brown lines). Circles and continuous lines correspond to *Gge*; triangles and dashed lines to *Ggg*

Table 4 Test of independence of UV treatment (UV+, UV−) and contest outcome for both subspecies. G: *G* statistic, *p*: significance level

	Winners	Losers	*G*	*p*
Güimar (*Ggg*)				
UV+	9	22	12.15	0.0005
UV−	20	7		
Pris (*Gge*)				
UV+	10	15	2.014	0.156
UV−	15	10		

contests with both males and females may reveal currently undetected differences between the two subspecies.

Results of Exp. 1 show that three morphometric, three behavioral, and one spectral trait are good predictors of the outcome of male contests in *G. galloti*. The main result from the second experiment, where we eliminated UV reflectance from the UV-blue lateral patches of one of the contestants, is that individuals having their patches painted with sunscreen won contests more often than control UV+ lizards (at least in *Ggg*). Moreover, as in Exp. 1, winners performed the behavior "bite" with a significantly higher frequency than losers.

Morphological and behavioral traits (Exp. 1)

Our results show that a combination of body mass, fore-limb length, head width, and the relative frequency of the behaviors "throat extension" and "bite" contribute to contest outcome, winners having significantly larger values for all those variables than losers. These results confirm previous findings obtained by our group in the southern subspecies (Molina-Borja et al. 1998; Huyghe et al. 2005) and agree with results from studies on other species showing that large body size is one of the main determinants of fighting success in lizards (Hews 1990; Carpenter 1995; Umbers et al. 2012; reviewed in Baird 2014). However, in contrast with previous experiments in *G. galloti* (Huyghe et al. 2005), our results did not reveal winner/loser differences in the surface area covered by the UV-blue patches. A higher relative frequency of aggressive behavior patterns ("bite," "throat extension") in winners than in losers during contests is also a common finding in other species (Simon 2011; Steffen and Guyer 2014) and confirms our own previous results with *Ggg* (Molina-Borja et al. 1998). On the other hand, we found that the behavior "tail shake" was performed at the end of contests and with significantly higher frequency in losers than in winners; this suggests that this behavior pattern is a submissive display given in an appeasement context (Martins and Lacy 2004).

Table 5 Results of GLM analysis investigating the effect of all morphological and behavioral variables of lizards from Exp. 2 on contest outcome, taking into account population and sunscreen treatment as factors (full model in Table 6)

Parameters	Wald's chi-square	Hypothesis contrast	
		df	*p*
Intersect	0.010	1	0.919
Population	0.014	1	0.905
Sunscreen factor	**7.692**	**1**	**0.006**
TE	0.853	1	0.356
TF	1.042	1	0.307
Bites	2.716	1	0.099
SVL	0.546	1	0.460
BM	0.000	1	0.988
HW	0.097	1	0.756
HD	0.062	1	0.803
FLL	1.022	1	0.312
HLL	0.019	1	0.890

Table 6 Summary of AIC$_c$ candidate models. ΔAICc = AIC$_c$ − AIC$_{min}$ for data of experiment 2

Model	AIC$_c$	Δ_i
Null[a]	148.948	110.115
Full[b]	142.563	103.73
Variables with *p* value < 0.5[c, j]	131.223	92.39
Morphological variables ISF[d]	148.953	110.12
Morphological variables (WSF)[e]	158.025	119.192
Only behavioral variables (ISF)[f]	112.991	74.158
Only behavioral variables (WSF)[g]	109.87	71.037
Bites (ISF)[h)] (variables with $p < 0.25$)	38.833	0
Morphological and behavioral variables (ISF)[i]	137.457	98.624
Morphological and behavioral variables (WSF)[i]	142.519	103.686

ISF: including sunscreen factor; WSF: without sunscreen factor

[a] Null model (only intercept is included in the model)

[b] All covariates and factors

[c] The significant variables in the GLM

[d, g] Morphological and behavioral variables, separately

[h, i] Morphological and behavioral variables together

[j] See Table 5

Comparison of spectral data

Color patches along the lateral body surfaces are more likely involved in lizard intraspecific communication than in antipredator defense (Stuart-Fox and Ord 2004) and have been interpreted as reflecting individual status in several lizard species (Thompson and Moore 1991; Zucker 1994; Stuart-Fox and Johnston 2005). There is already compelling evidence that UV-reflecting color patches are important during intrasexual competition in lacertids (Bajer et al. 2011; Olsson et al. 2011; Pérez i de Lanuza and Font 2014; Martin et al. 2015b; McGregor et al.

2017) and in other lizards (Whiting et al. 2006; Steffen and Guyer 2014). Our results suggest that spectral traits from UV-blue patches may likewise influence the outcome of male-male contests in *G. galloti*. In our experiments, winners had more blue-shifted UV-blue patches than losers. Also, in two out of three comparisons, winners had brighter UV-blue patches than losers (Figs. 1a and 3), although the difference did not reach statistical significance.

On the other hand, we found no significant difference for cheek spectral data between winners and losers of *Gge*. This result was contrary to expectations given that the cheek patches are much larger than the lateral patches in this subspecies, and they are very conspicuous during the breeding season (Molina-Borja et al. 1997). However, the reduced sample size for this trait could account for this negative result and further experiments are needed to settle the issue.

Effects of UV manipulation on fighting success

Results from Exp. 2 show that behavior is the best predictor of contest outcome in fights between control lizards and lizards with reduced UV reflectance. Results of this experiment further confirm a relationship between UV reflectance and contest outcome, although the results are not in the predicted direction. In fact, for *Ggg*, lizards with UV-reduced reflectance were more often winners than losers of contests. This is unexpected given the abundant literature that shows that UV reduction generally has the effect of reducing rather than increasing the probability of winning contests (e.g., Vedder et al. 2010; Xu and Fincke 2015). However, the results obtained in experiments with lizards are somewhat paradoxical. Bajer et al. (2011) showed that males of *L. viridis* to whom UV-absorbing sunscreen was applied lost in approximately 90% of staged contests with size-matched rivals. It is difficult to interpret this result because the lizards receiving the sunscreen should not be aware of the manipulation and therefore should not have changed their behavior to accommodate their artificially altered reflectance. More likely, the absence of UV-reflectance may have made the UV-reduced lizard appear as a competitively inferior individual to its rival thereby increasing the probability of an attack (see Olsson et al. 2011). If lizards assess the UV reflectance of rivals during contests, artificially reducing the reflectance of UV-blue patches may result in a signal that underestimates the manipulated lizard's fighting ability. This mismatch could in some cases lead to the UV-reduced lizard losing contests (through reduced deterrence of rivals), but in others, it could have the opposite effect if it increases the probability that UV-reduced lizards will return the challenge of their unmanipulated rivals. It has also been suggested that UV reflectance could play a role in opponent assessment during the initial stages of male-male contests and not determine completely contest outcome in escalated fights (Baird et al. 2013; Olsson et al. 2013; Abalos et al. 2016). Martin et al. (2015b), for example, found that reducing the UV reflectance of UV-blue color patches in *P. muralis* affects mutual assessment and spatial dominance but is not a primary determinant of fighting success.

Contest outcome can be affected by multiple male traits (e.g., Stuart-Fox et al. 2006) and this was also our prediction for contests between males of *G. galloti*. Our results confirm this prediction and further show that the behavior of the contestants is a key factor affecting the result of dyadic male-male contests. In particular, the frequency of bites had a significant positive effect on the probability of winning, which agrees with work showing that bite force is an important trait affecting contest outcome in several lizards (Huyghe et al. 2005; McLean and Stuart-Fox 2015). Taken together, our results suggest that in *G. galloti*, while some spectral characteristics of UV-blue color patches may be important for assessing rival fighting ability, behavioral traits seem to be better predictors of the outcome of dyadic aggressive contests.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

Ethical statement At the completion of the experiments, all the lizards were released unharmed at their original capture sites. During their stay in captivity, the animals were cared for in accordance with guidelines published by Animal Behaviour (ASAB/ABS 2012; Anim Behav 83:301–309); the research received official approval from the Ethics and Animal Welfare Committee of the University of La Laguna (reference CEIBA2011-0020).

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