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RESEARCH

Dual function of blue belly patches in the mesquite lizard

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Abstract

The armament–ornament model suggests that females may benefit from exploiting signals that indicate status or are used in male-male aggressive interactions as such traits may impose costs. Here, we investigated whether the blue belly patches displayed by mesquite male lizards, *Sceloporus grammicus*, are used during male-male and female-male interactions. In the first experiment, males interacted with another male of similar size whose blue belly patches were manipulated to appear dull or bright, or remained unmanipulated. In the second experiment, females observed two males paired by size featuring either unmanipulated, dull, or bright blue belly patches. We found that males were less aggressive toward males with brighter and bluer patches, and females displayed more behaviors toward brighter males than toward males with unmanipulated blue patches, although it remains unclear whether females courted or rejected these males. Our results suggest that the ventral blue belly patches have a dual function in mesquite lizards, influencing antagonistic interactions among males and interactions between females and males.

Significance statement

The armament–ornament model suggests that females may benefit from exploiting signals that indicate male status or are used in male-male aggressive interactions, because such traits may impose costs if faked. Accordingly, we show that brighter males in mesquite lizards, *Sceloporus grammicus*, are less likely to be attacked by opponents and are the target of more display behaviors from females. In mesquite lizards, the brightness of males' ventral blue belly patches has a dual function, influencing antagonistic interactions among males and between males and females.

Keywords Visual signals · Sexual selection · Armament–ornament model · Sceloporus grammicus · Male-male competition

Introduction

Intrasexual competition and intersexual choice are the primary mechanisms of sexual selection driving the evolution of sexual traits, which ultimately influence male and female fitness (Darwin 1871; Andersson 1994). Intrasexual competition, typically male-male competition, favors the evolution of sexual traits that function as armaments, or status badges used directly when competing for access to mates (Rico-Guevara and Hurme 2019). Intersexual choice, typically female mate choice, favors the evolution of sexual traits or ornaments that are usually honest indicators of the quality of the bearer (Zahavi 1975; Hamilton and Zuk 1982; but see Prum 2012). Hence, females who prefer more ornamented mates may gain direct or indirect benefits when these sexual traits are indicators of good genes or material benefits (Cuervo et al. 1996; Mays and Hill 2004; Griggio

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et al. 2005; Kemp 2007; Wells et al. 2016). Coloration traits as a visual signal in sexual contexts have been investigated in invertebrates (Mazel et al. 2004; Franklin et al. 2019) and vertebrates (White 2020; Emberts and Wiens 2022). In some species, the same sexual trait may function in both inter and intra-sexual interactions (reviewed in Berglund et al. 1996; Wong and Candolin 2005). For example, sexual traits such as the length of the black beard in the bearded tit, *Panurus biamircus* (Hoi and Griggio 2008), the male's sword in the swordfish *Xiphophorus helleri* (Basolo 1990; Benson and Basolo 2006), or the color of the spiny-footed lizard, *Acanthodactylus erythrurus*, where males prefer females with red tails over females with white tails (Belliure et al. 2018), play a role in male-male competition, female mate choice, and even in male mate choice. The dual utility hypothesis or armament–ornament model suggests that females may benefit from exploiting signals that indicate status or that are used in male-male aggressive interactions, as such traits are hard to be faked without incurring high costs (Berglund et al. 1996; Wong and Candolin 2005), or because male-male competition influences female mate choice by affecting the detectability, evaluation or choice of mates (Wong and Candolin 2005).

Lizards are ideal systems to test the dual utility hypothesis because some species display colorful signals in multiple settings. Signals can be used to deter predators (Pérez i de Lanuza et al. 2013; Perez-Martinez et al. 2020), to recognize sympatric individuals (Bastiaans et al. 2014), in female mate choice (Kwiatkowski and Sullivan 2002; Hamilton and Sullivan 2005; Healey et al. 2008; Chen et al. 2012; Martin et al. 2016; Lisboa et al. 2017; Pérez i de Lanuza et al. 2017; York and Baird 2017; Kawamoto et al. 2021), and in male-male agonistic encounters (Olsson 1994; Whiting et al. 2006; Martin et al. 2016; Perez i de Lanuza et al. 2017; Names et al. 2019; Kawamoto et al. 2021). The same signal can have a dual function, like in *Lacerta viridis*, where females prefer males with a throat patch with high UV chroma (Bajer et al. 2010), which also determines a male's fighting success (Bajer et al. 2011), and negatively correlates with the male's parasite load (Molnár et al. 2013). Although lizard species display a wide range of colorful traits, few studies have assessed whether the same colorful signal serves a dual purpose during both intra and inter-sexual interactions (Smith and John-Alder 1999; Sheldahl and Martins 2000; Martín and López 2009; Bajer et al. 2010, 2011; García-Rosales et al. 2021).

Here, we evaluated in the mesquite lizard *Sceloporus grammicus*, the prediction from the armament-ornament model (Berglund et al. 1996) that the male's blue belly patches have a dual utility by playing a role in male-male and female-male interactions. Most lizards of the genus *Sceloporus* are sexually dimorphic. Males from most *Sceloporus* species have blue patches in the ventral and gular region, a color patch partly regulated by testosterone (Cox and John-Alder 2005; Cox et al. 2005, 2008), while females have light orange ventral patches (Weiss 2006; Ossip-Drahos et al. 2016). In the mesquite lizard, males have two blue patches bordered internally by two black stripes (Sites 1982; Fig. 1), and females have two slight orange patches on the belly. The size and brightness of the blue patches are positively correlated with male size and body condition, and the mite loadings in males are negatively correlated with how bright the males' patches are, suggesting that blue patches indicate physical condition and competitive abilities (Zúñiga-Vega et al. 2021). Males exhibit blue belly patches through behaviors such as "push-ups" (raising and lowering their bodies) and more conspicuously, "full-shows" in which they flatten their body, and display the throat, curve the back, and move laterally, showing the ventral blue patches (Cooper and Burns 1987; Martins 1993). The male's blue belly patches are displayed in social interactions in different contexts, but for the mesquite lizard, there is no experimental evidence on their function.

We carried out two experiments to evaluate if the male's ventral blue patches have a dual utility playing a role in two social contexts: male-male interactions and female-male interactions. In the first experiment, we evaluated whether brighter males, and/or males with higher blue chroma are attacked less frequently than duller males, as expected if brighter or bluer males (bluer chroma) are of better physiological condition and more competitive. In the second experiment, we evaluated if females display more behaviors towards brighter males and/or towards bluer males, as expected if male blue belly coloration is an honest indicator of male quality.

Methods

General methods

Lizard collection

We captured sexually mature males and females (snout-vent length [SVL] > 44 mm; (Jiménez-Cruz et al. 2005), between March and April 2009 (for male – male interactions), and between March and April 2011 (for female – male interactions), in the surroundings of "Pedregal de San Ángel" in southern Mexico City (19.31826 N, 99.19431 W), and the experiments were carried out in each year between May and June, a period of intensive mating activity for *S. grammicus*. Populations of *S. grammicus* from the Mexican Central

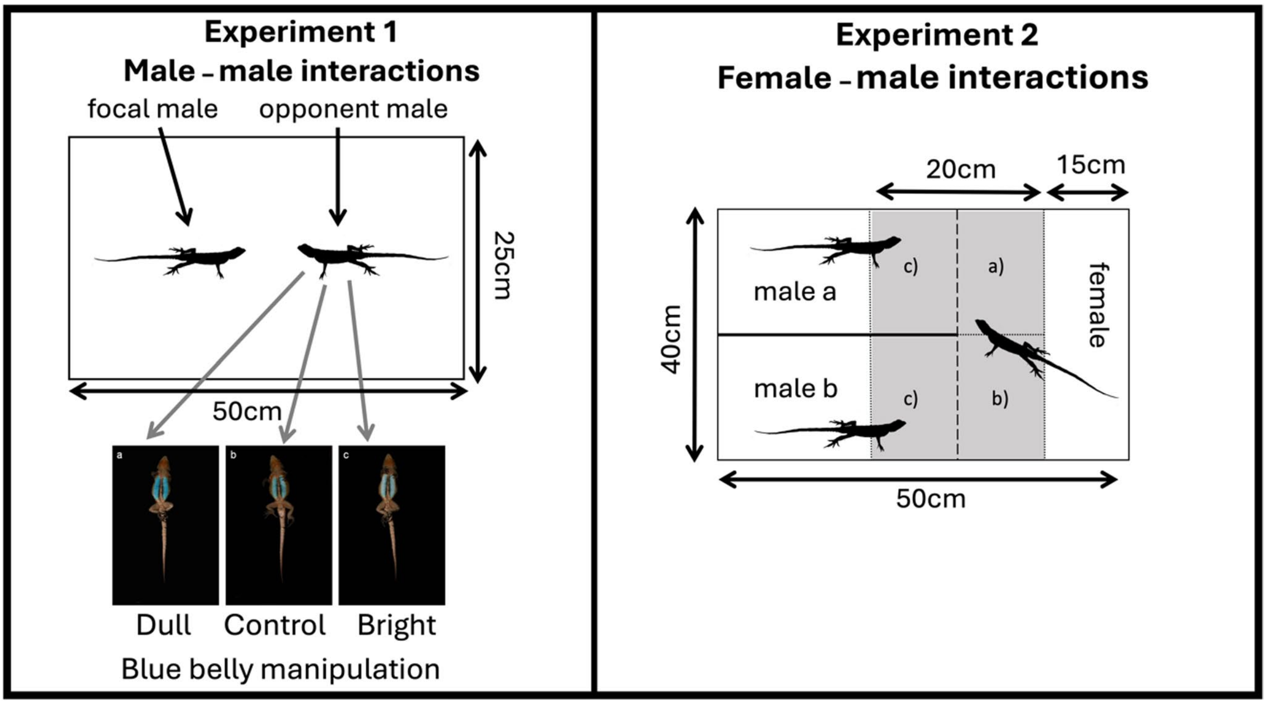

Fig. 1 Experimental designs. Experiment 1 (left): Male-male interactions. The same focal male encountered three different opponent males matched by size. One of his opponents had dull blue belly patches, one bright belly patches, and one unmanipulated (control) belly patches. Experiment 2 (right): Female-male interactions. Females observed two males in each trial, matched by size. The bold line depicts the opaque wall that separates the two males. The dotted line shows the transparent division between the males and the female. The shaded areas indicate the female's preference zone for male (**a**) or (**b**), and the shaded areas **c**) indicate the areas where male behavior towards the female was recorded

Plateau exhibit male and female synchronous breeding and reproductive activity all year (Ramírez-Bautista et al. 2012; Lozano et al. 2015). Males' testicular recrudescence begins in October, and maximum testis size is maintained from December to July, while females with vitellogenic follicles are observed from October to July. Neonates and juveniles are observed all year (Ramírez-Bautista et al. 2012). Similarly, in our study site, mating activity and neonates are observed all year (Argaez 2015). All lizards were sampled from the same population, and to minimize recognition effects between lizards, individuals were collected at intervals greater than 100 m. We measured each lizard's SVL, tail length (±0.01 mm), and mass (±0.01 g), as well as the brightness (reflectance) of the blue belly patches (see below). We kept each lizard in individual terraria (50 × 25 × 30 cm; width × length × height). Terraria were set with UV lamps and had controlled temperature (27–29 °C, following the temperature of Mexico City during the months when the experiment was carried out, according to CONAGUA 2011), and a 12 h. light/dark photoperiod. Lizards were fed three mealworms (*Tenebrio molitor*) daily and provided with water *ad libitum*.

Blue belly brightness, chroma manipulation, and spectrophotometry

In both experiments, we manipulated the brightness and blue chroma of the blue belly patches with non-toxic, wax-based makeup (Laukrom brand), following (López et al. 2003; Healey et al. 2008). We applied white makeup to increase the brightness, and decrease blue chroma (bright males), and blue makeup to decrease the brightness and increase blue chroma (dull males). Our experimental manipulation generated a negative correlation between the brightness and the chroma of the blue belly patches (Fig. 2; Fig. S1). To simulate the manipulation, control males received a belly massage that mimicked the treatment given to the experimental males, but without any color modification. Additionally, a wax application was placed below their tail to homogenize smells.

After manipulation, we measured the average spectral brightness (reflectance) of the blue belly patches of each male at three nonoverlapping points of each patch using a portable spectrophotometer that determines reflectance from 360 to 740 nm at 10-nm intervals (Minolta CM-2600d;

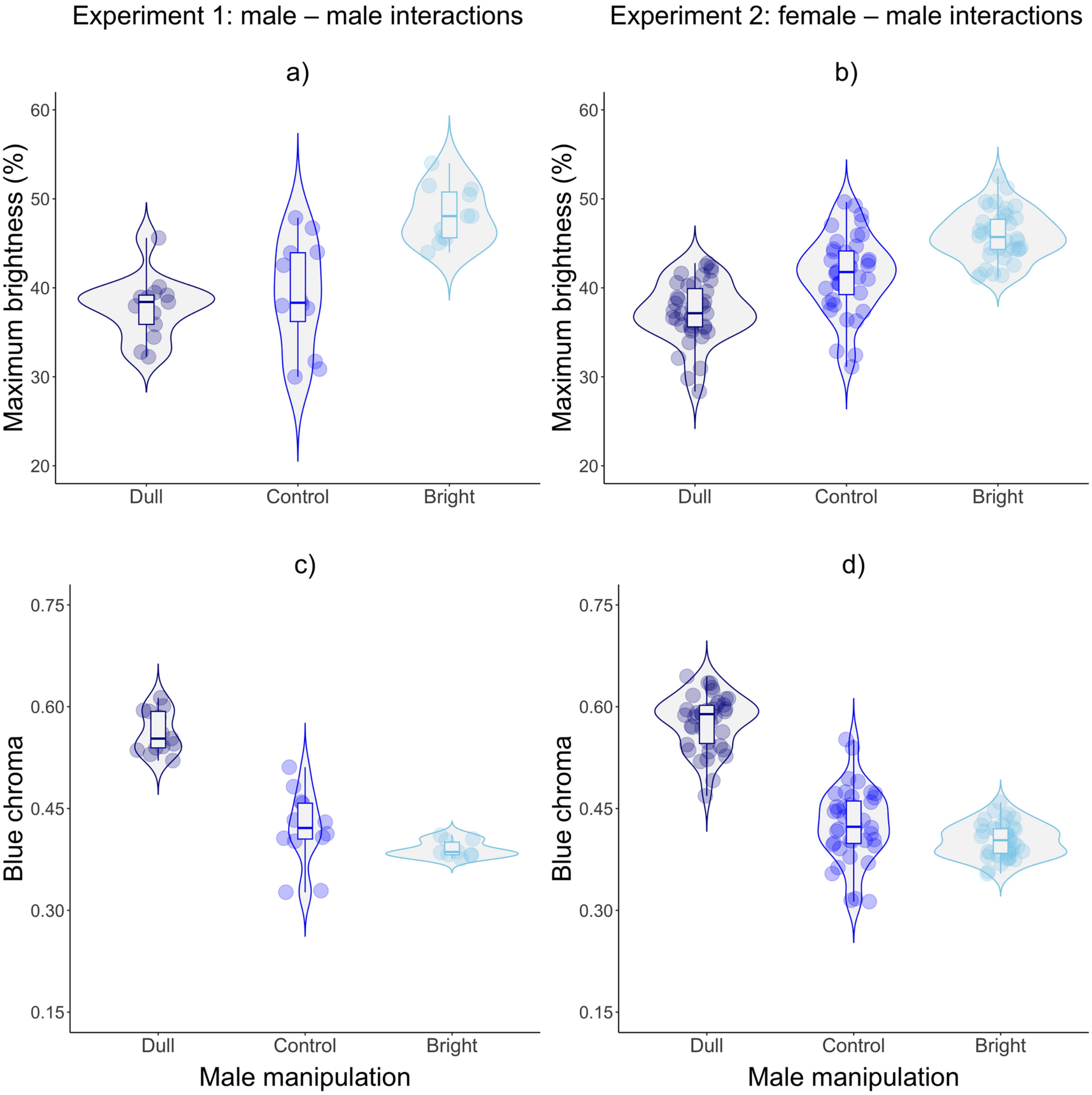

Fig. 2 Maximum brightness (**a** and **b**) and blue chroma (**c** and **d**) of the male blue belly patches according to the experimental manipulation. Experiment one (**a** and **c**): male – male interactions. Experiment two (**b** and **d**): female – male interactions. The horizontal line inside each box shows the median brightness percentage (**a** and **b**) or median blue chroma (**c** and **d**), the box shows where the middle of the data falls (interquartile range), and whiskers represent 1.5x the inter-quartile range

Minolta Co. Ltd, Osaka, Japan). The spectrophotometer was set with a target mask of 3 mm in diameter, and before every trial we calibrated it against a standard white calibration plate and a zero target. From the color curves, we calculated the maximum brightness within the blue reflectance range (the maximum percentage of brightness between wavelengths 400 and 520 nm, which corresponds to the only peak in the color curve) and the blue chroma as the sum of the brightness from 400 to 520 nm divided by the total sum of brightness (Montgomerie 2006). Color manipulation increased and decreased the maximum brightness within the range of natural variation in the blue spectrum (Fig. S2). Maximum brightness was highly correlated with the total brightness ($r = 0.92$, $P < 0.0001$; Fig. S1).

Experiment 1: male – male interactions

We used 17 sexually mature males in the experiment, 14 as focal males. All 17 males were used as non-focal males. Each trial consisted of two males, a focal (unmanipulated) male and an opponent, whose belly blue patches were manipulated just before the trial. Each focal male entered a trial with three different males on different days: a bright, dull or control male. In each trial, the focal male and the opponent were matched by size (comparison of body length of the two males in a trial: Wilcoxon rank sum test = 743.5, $P = 0.52$). We randomized the order of the trials for all focal males. All lizards (focal and manipulated) entered only one trial per day.

Trials were carried out in neutral terraria (50 × 25 × 30 cm), to eliminate any effect of residence advantage (Martin et al. 2016; Names et al. 2019). Each terrarium had a clean plywood base, and an internal vertical wood division connected to a pulley which allowed us to remotely remove the division. We gently placed each male on one side (randomly chosen) of the terraria for 10 min of habituation. After this time, we gently lifted the division and allowed the males to interact for 20 min (Fig. 1). Each terrarium was set with a 100 W bulb at the top, and a UV lamp in the room, as lizards see in this wavelength (Adkins et al. 2003; Whiting et al. 2006). Trials were carried out between 10 am and 12 h. Males could not observe other trials.

We recorded all trials with a video-camera (Sony DCR SR 80; CANON Gl2). At the end of each trial, we cleaned makeup from the male lizards' belly patches using a paper moistened with water and neutral soap, then dried them with a cloth, and returned them to their individual housing. Three observers naive to the color manipulation recorded from the videos the number and duration of push-ups, full-shows, lateral compression, back arching, gular sac deployment, tail waving, and bites (description in Table S1, Electronic Supplementary Material). These behaviors have been considered as agonistic behaviors in the context of male-mele interactions (Bastiaans et al. 2013). We ran four intra and inter-observer reliability tests on different days using the concordance index and ensured consistency was above 95% (Martin et al. 1991).

Experiment 2: female – male interactions

We used 20 females and 30 males. Each trial consisted of one female with visual access to two males. All lizards (males and females) were matched by size. Glass partitions separated the three lizards to prevent olfactory contact. Additionally, black cardboard was placed between the compartments of the males to avoid visual contact among them. Each terrarium had black cardboard on the walls to avoid external disturbances, clean plywood sheets as substrate, and a UV lamp. In each trial the female observed one of the following combinations of males: bright-control, bright-dull, and control-dull. All 20 females entered three trials, one every two days. We randomly assigned the males to the color treatments, and the order in which the females were exposed to the different combinations of males. We made 'preference zones' by drawing 10 cm lines from the separation glass in the male and female compartments (Fig. 1), and only recorded and analyzed behaviors within that area, to ensure female behaviors were directed towards a specific male, and similarly considered male's behavior only in the area close to the female.

Once inside the terraria, the lizards were maintained without visual contact for 10 min for acclimatation before the trial. Behavioral recordings lasted 30 min and were recorded using video cameras. An observer naive to the male treatments recorded from the videos, all the behaviors exhibited by males and females. The behaviors recorded for males were the same behaviors recorded in Experiment 1. For females, we recorded push-ups, lateral compression, as well as horizontal and vertical tail waves. In *Sceloporus* genus, females' push-ups and lateral compression have been reported as agonistic or rejection behaviors, while tail waves and tail vibrations have been reported as mate acceptance behaviors (Electronic Supplementary Material, Table S1). However, these behaviors are used by males and females in different contexts (Greenberg 1977; Martins 1993; Kelso and Martins 2008; Swierk et al. 2012; Hardwick et al. 2013), and we have recorded females displaying these behaviors to males before copulation, in contexts when females are allowed to choose to mate or not (Electronic Supplementary Video). Hence, although the significance of *S. grammicus* female behavioral displays in the context of mate choice is not clear, for the analyses, we calculated the total frequency of female behaviors other than tail waves (hereafter, female behaviors), and the total frequency of female horizontal and vertical tail waves (hereafter, female tail waves). Four intra-observer reliability tests on different days were conducted using the concordance index, indicating 97% intra-observer reliability through time (Martin et al. 1991).

Statistical analyses

All analyses were conducted using R studio 4.1.1 (R Development Core Team 2014), with 'glmer', 'lmer', 'glm' and 'gls' functions (Bates et al. 2013). We evaluated the residuals in both analyses to ensure they followed a normal distribution, showed no patterns, and had similar variance between factors and across values of continuous covariates

(Zuur et al. 2009). We included the lizard's identities as random effects since we had multiple measurements for each lizard.

Experiment 1: male – male interactions

First, we compared the maximum brightness and blue chroma of the blue belly patches of the opponent lizards according to the manipulation (dull, control, bright) before entering the experiment, but after the color manipulation, using GLMMs with normal error distribution. The blue patches of all manipulated groups differed in maximum brightness and blue chroma ($\chi^2 = 37.7$, $P < 0.0001$ and $\chi^2 = 141.18$, $P < 0.0001$; respectively; Fig. 2a, c). However, the blue chroma only differed marginally between manipulated bright and control males (post-hoc comparison: $P = 0.066$). Furthermore, upon further exploration, we found that some focal males saw opponent males with very similar maximum brightness and/or with similar blue chroma (Fig. 2). Therefore, instead of comparing the focal male's behavior according to the treatment, we used a GLMM that included as response variable the total behaviors of the focal male, and as explanatory variable his maximum brightness, his opponent's maximum brightness, his blue chroma, and his opponent's blue chroma. None of these traits were strongly correlated with each other (all $r < 0.30$; Fig. S3). We included as random effects the identity of the focal male and of the opponent male since we had multiple measurements for each lizard. Because each of the focal male's specific aggressive behaviors were highly correlated to one another (e.g., most correlations were above $r > 0.50$; Fig. S4), we analyzed the total frequency of behaviors. As we found heteroscedasticity in the residuals, we used the 'gls' function to control for trends in the variance of the residuals using the *varFixed* variance structure, and we verified the normalized residuals (Zuur et al. 2009). To further explore whether the relative difference in maximum brightness and blue chroma between males within a trial influence the aggressive behavior of the focal male, using a GLMM, we analyzed the total behaviors of the focal male as the response variable, and as explanatory variable the difference between his maximum brightness and his opponent's maximum brightness, and the difference between his blue chroma and his opponent's blue chroma. We included as random effects the identity of the focal male and the identity of the opponent.

Experiment 2: female – male interactions

In this experiment, we faced some statistical limitations. The maximum brightness and the blue chroma of the male's belly patches differed between treatments after the manipulation ($\chi^2 = 551.63$, $P < 0.001$, all treatments comparisons: $P < 0.004$; $\chi^2 = 340.87$, $P < 0.001$, all treatments comparisons: $P < 0.001$; respectively; Fig. 2b). However, in many replicates, the brightness or chroma of the two males were very similar, meaning females observed very similar-sized and similar-bright or similar-blue males. Furthermore, the correlation between a male's brightness and his blue chroma was $r = -0.54$, meaning we could not include within the same model a male's brightness and his chroma as independent explanatory variables.

Because of this, we carried out the following analyses. We eliminated a priori replicates where the difference in maximum brightness (analysis 1: female's behaviors; analysis 2: female's tail waves; but note that there was a positive, significant correlation between the frequency of tail waves, and the frequency of all other behaviors; $r = 0.36$, $P = 0.005$) or in blue chroma (analyses 3 and 4; female's behaviors and tail waves, respectively) between males within a trial was close to zero (falling within -5 and 5 or within -0.06 and 0.06; for brightness and blue chroma, respectively). This left us with 12 replicates in the dull-control, 14 in the bright-dull, and 11 in the bright-control for the analysis of maximum brightness (analyses 1 and 2), and 18 replicates in the dull-control and 19 in the bright-dull (only four replicates in the bright-control treatment had different blue chroma and were thus eliminated) for the analysis of blue chroma (analyses 3 and 4).

We carried out analyses with these reduced datasets, in which females observed similar sized males but that differed in maximum brightness (analyses 1 and 2) or in blue chroma (analyses 3 and 4). For both set of analyses we carried out GLMMs with normal error distribution and included as response variable the difference in the frequency of behaviors displayed by the female to the two males (frequency of behaviors towards one male – frequency of behaviors towards the other male, including all behaviors for analyses 1 and 3, and just tail waves for analyses 2 and 4), within the choice area. In all analyses, we included as an explanatory variable the combination of males she saw (treatment with three levels), and as random effects the identity of the female, and the identity of each of the two males. We included as covariable the difference in the frequency of behaviors of both males within a replicate (following the same order as the difference of behaviors displayed by the female, i.e., bright male minus control male). We kept full models. After finding differences according to the treatment for the maximum brightness analyses, we carried out a GLM per treatment and included the intercept (if it was significantly different from zero it means the female displayed more behaviors to one male than to the other) and included as covariable the difference in the frequency of behaviors of both males within a replicate. We also replicated this analysis using total brightness and not just maximum brightness, and found qualitatively similar results (see ESM).

Results

Experiment 1: male – male interactions

Males displayed fewer aggressive behaviors towards brighter males than towards duller males (value = −1.42, SE = 0.58, $t = -2.42$, $P = 0.02$). Neither the focal's maximum brightness (value = 0.67, SE = 0.61, $t = 1.10$, $P = 0.27$) nor his blue chroma (value = 172.05, SE = 110.64, $t = 1.55$, $P = 0.13$) predicted the behavior of the focal male. After removing one outlier, a male that performed over 90 behaviors, our results were quantitatively similar regarding the opponent's brightness (value = −1.41, SE = 0.47, $t = -3.01$, $P = 0.005$). Males also displayed fewer aggressive behaviors towards opponents with higher blue chroma (value = −87.22, SE = 39.40, $t = -2.21$, $P = 0.03$; Fig. 3). Similarly, with the alternative analysis, we found that focal males showed more aggressive behaviors when his opponent was less bright than himself (estimate = 0.99, SE = 0.46, $t = 2.14$, $P = 0.039$; Fig. 4). However, we did not detect the same effect with blue chroma (estimate = 42.65, SE = 46.72, $t = 0.91$, $P = 0.37$).

Experiment 2: female – male interactions

In the first analysis we found that the female's behavior depended on the combination of males to choose from (analysis 1, effect of the treatment: $\chi^2 = 7.24$, $P = 0.02$; Fig. 5), and that she also displayed more behaviors towards the male that displayed more behaviors to her (estimate = 0.14, SE = 0.05, $t = 2.75$, $P = 0.01$). Females displayed more behaviors towards a bright than a control male (the intercept was significantly different from zero and positive; intercept = 6.64, SE = 2.12, $t = 3.12$, $P = 0.01$). However, the intercept was not significantly different from zero in the model including only bright-dull males ($P = 0.76$). In the bright-dull treatment, females displayed more behaviors towards the male that displayed more behaviors to her (estimate = 0.30, SE = 0.10, $t = 2.81$, $P = 0.01$). Female's tail waves did not depend on the combination of males she saw (analysis 2, effect of treatment: $\chi^2 = 2.62$, $P = 0.27$). Furthermore, in trials where males differed in blue chroma, females did not discriminate between males as no differences between treatments in the frequency of either female's overall behaviors

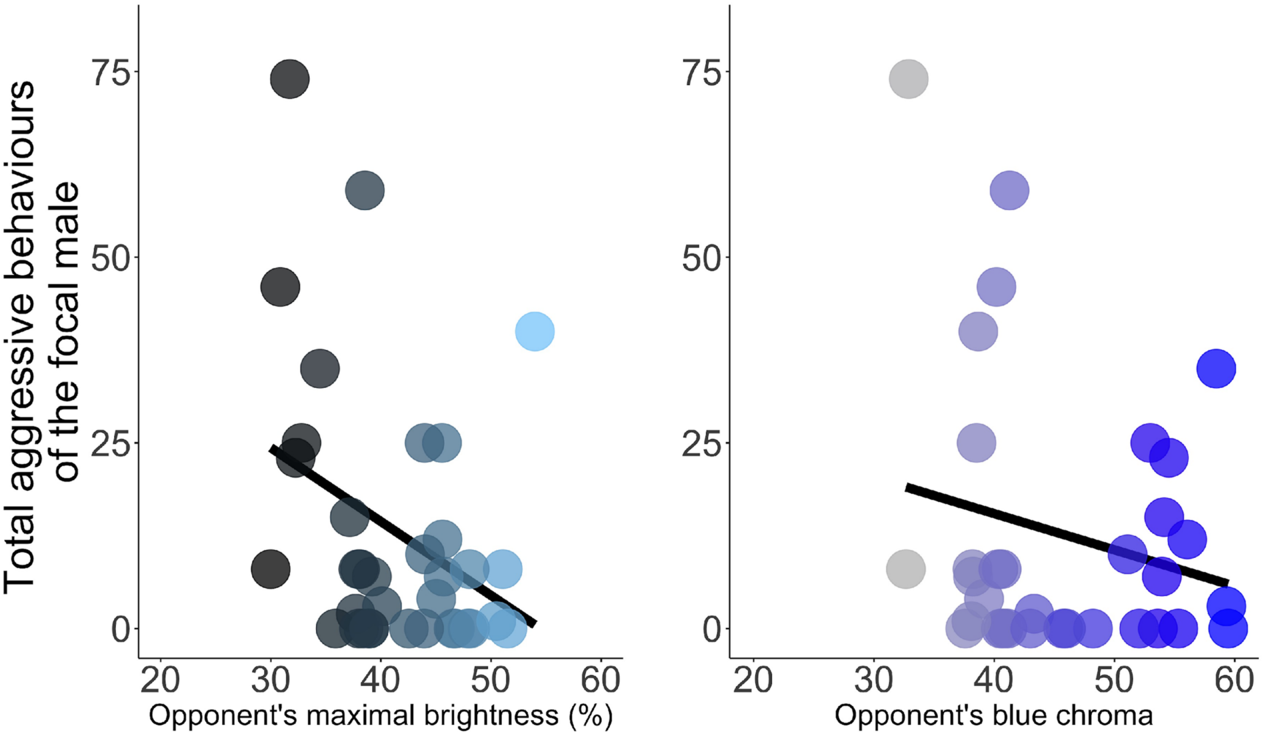

Fig. 3 Focal males were less aggressive towards males with brighter and bluer belly patches. The left panel shows a linear relationship between the total aggressive behaviors displayed by the focal male (y axis), and the maximum brightness of the opponent (x axis). The colors reflect the brightness of the opponent male. The right panel shows a linear relationship between the total aggressive behaviors displayed by the focal male, and the opponent male's blue chroma

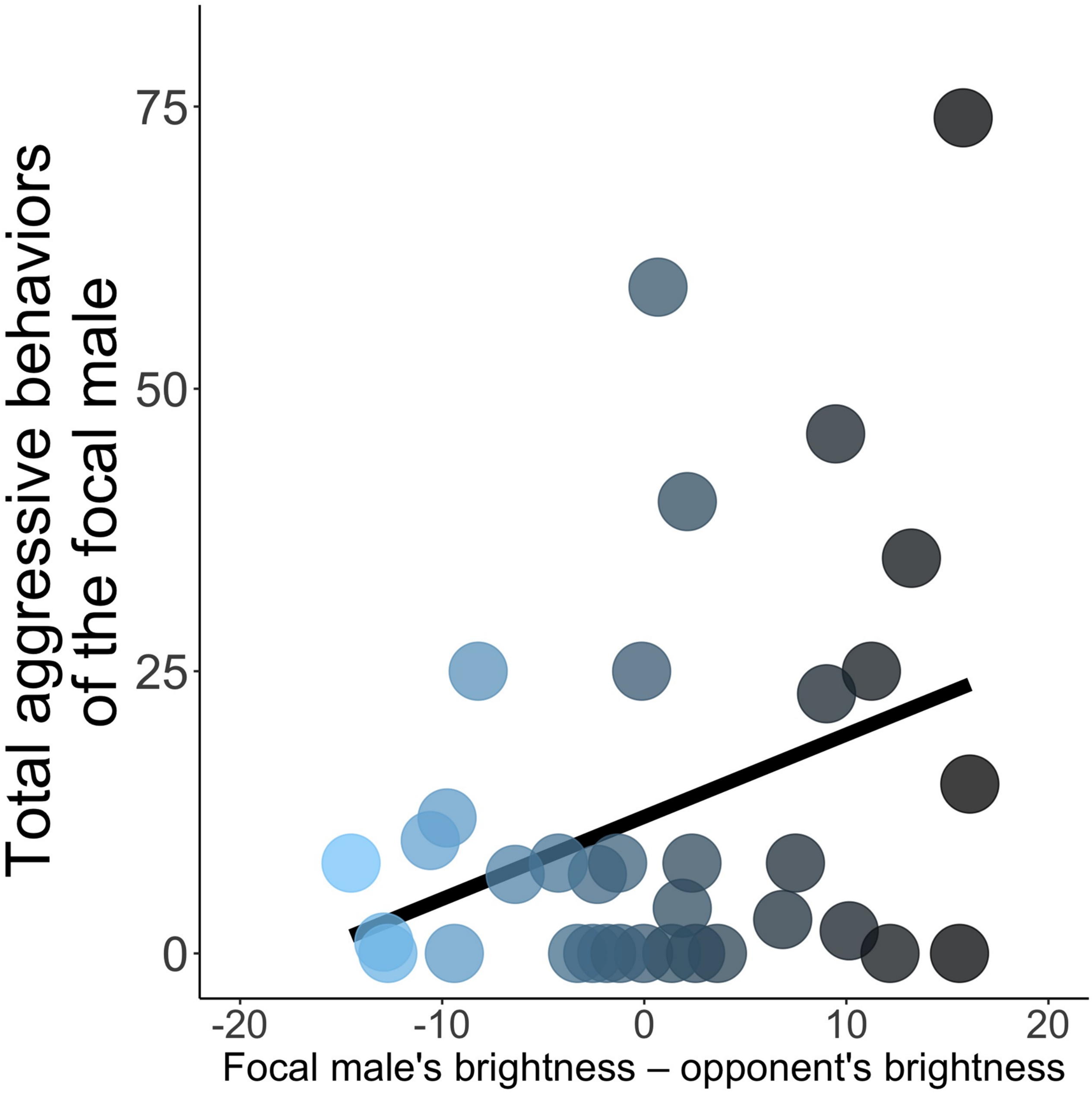

Fig. 4 Focal males were less aggressive towards males that were brighter than themselves. The graph shows a linear relationship between the total aggressive behaviors displayed by the focal male (y axis), and the difference in brightness among the males (x axis). Negative values reflect a brighter opponent than a focal male within a replicate, positive values reflect brighter focal than opponent male within a replicate. The light blue color reflects brighter opponents than focal males

(analysis 3, effect of treatment: $\chi^2 = 0.02$, $P = 0.87$), nor tail waves (analysis 4, effect of treatment: $\chi^2 = 0.39$, $P = 0.53$) were detected. In these last two analyses, females displayed more tail waves towards the male that displayed more overall behaviors to her (both $P < 0.008$).

Discussion

Despite lizards displaying a wide variety of colorful traits, until recently, few studies evaluated whether the same signals displayed by males functioned in male-male and

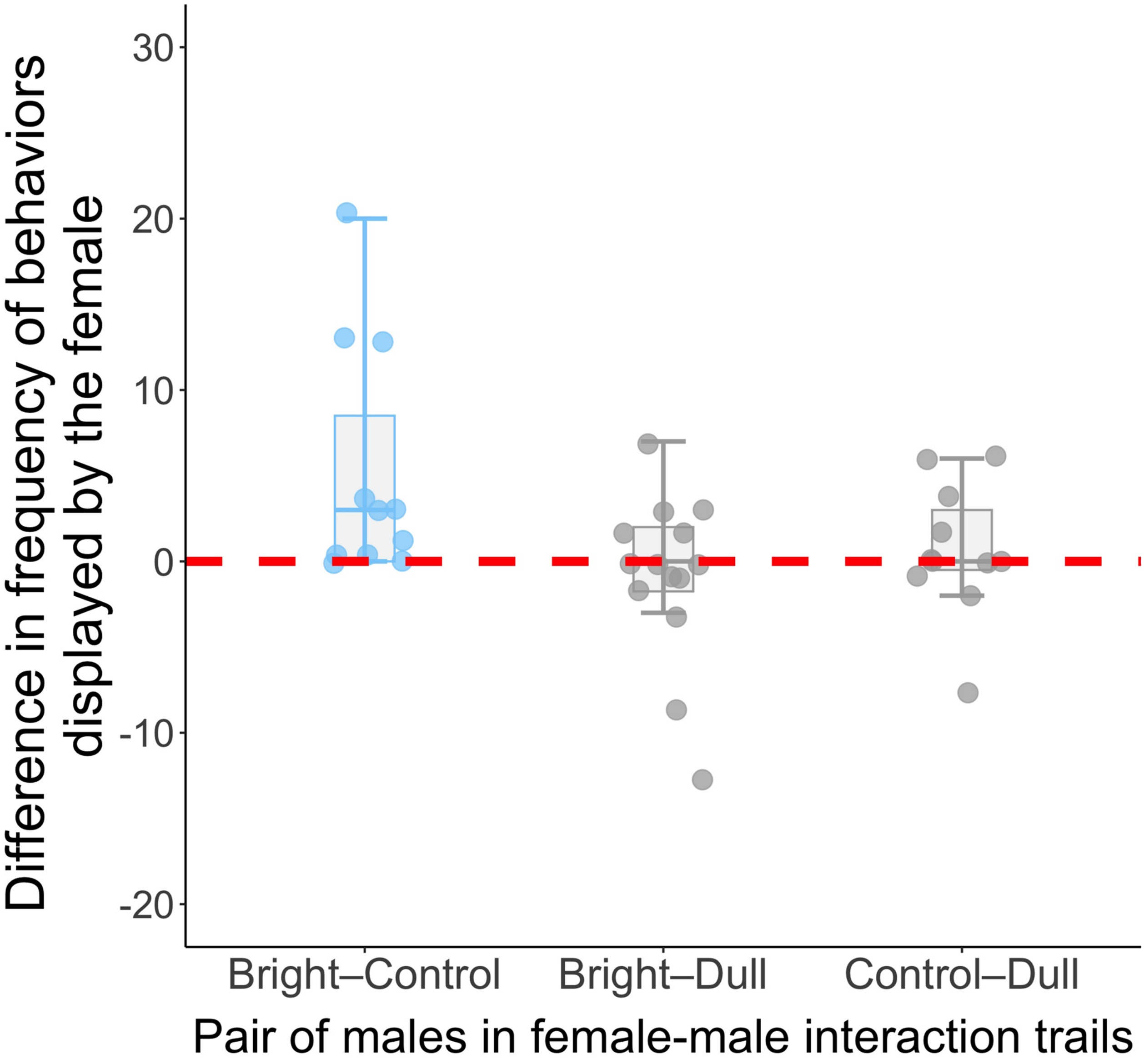

Fig. 5 Females displayed more behaviors to bright than to control males (difference in behavior of the female towards the males she saw). Each point represents a female. The horizontal line inside each box shows the median value per pair of males that the female saw, the data inside the boxes includes the middle 50% of the data (interquartile range), and whiskers represent 1.5x the inter-quartile range. The dashed red line shows zero differences in the behavior of the female towards the two males. Significantly different intercept from 0 is marked in light blue

female-male interactions. Here, we provide evidence that in *S. grammicus*, the brightness of the ventral blue belly patches of the males is used in two different contexts: in male-male and in female-male interactions. In the male-male experiment, males with brighter and higher blue chroma in their belly patches received fewer aggressive behaviors from focal males. In the female-male experiment, females displayed more behaviors towards brighter males, only when compared to control males. We did not detect females changing their behavior according to the males' blue chroma. Our experiments suggest that blue belly patches of *S. grammicus* function as a status badge in male-male competition and as a trait used by females in inter-sexual interactions, but it remains unclear whether females courted or rejected these males.

Males in our experiment were less aggressive towards male opponents that displayed brighter and bluer belly patches. Our results support previous findings that colorful patches modulate antagonistic interactions among male lizards (Stuart-Fox and Johnston 2005; Olsson et al. 2013; Martin et al. 2016; Names et al. 2019; Megía-Palma et al. 2024). In lizards, blue patches may include reflectance in UV, which in some species is used as a signal that advertises the competitive ability of the bearer (Stapley and Whiting 2006; Whiting et al. 2006; Bajer et al. 2010, 2011; Bohórquez-Alonso et al. 2018). In *S. grammicus*, color curves of ventral patches exhibit a single peak (on average 40%) in the range of blue reflectance and a low UV reflectance (on average 5%; Fig. S2), suggesting that UV may not be crucial for communication. Besides color traits, the intensity and frequency of specific behaviors can influence male-male interactions and the battles outcome (Bohórquez-Alonso et al. 2018), as well as previous experience (Stuart-Fox and Johnston 2005), and individual differences in reproductive tactics (e.g. territorial versus floater) (Thompson and Moore 1991; Sinervo and Lively 1996; Whiting et al. 2006). Future analyses in *S. grammicus* could evaluate how colorful signals, behavior, and differences in other life history traits interact to determine the outcomes of antagonistic interactions. In *S. jarrovii* and *S. undulatus*, testosterone levels are positively correlated with the area and saturation of blue patches (Cox et al. 2005, 2008), while in *S. grammicus* they are associated with the brightness of ventral coloration (Argaez et al. 2021). Additionally, the area and brightness of a male's blue patches are positively correlated with his size (Zúñiga-Vega et al. 2021). Collectively, these findings suggest that the color and size of blue ventral patches could be honest signals of male competitive ability, influencing the outcomes of male-male antagonistic interactions.

Our second experiment revealed that females behave differently towards males, generally showing more displays to brighter males, but it remains unclear whether these displays indicate mate preference or rejection. Unlike males, whose visual displays such as push-ups, lateral compression, back arching, and gular sac displays, are linked to intraspecific competition and head-bobbing to courtship, there is uncertainty regarding the significance of these behaviors for *Sceloporus* females. Females display the same behaviors in mate selection and rejection contexts (Kelso and Martins 2008; Martins et al. 2005). Indeed, some behaviors traditionally considered aggressive have been recorded in females across different social contexts, suggesting they may have a dual role in communication. For example, females of different *Sceloporus* species perform push-ups during territorial interactions (Carpenter and Ferguson 1977). However, in *S. grammicus*, push-ups and lateral compression are negatively associated with the likelihood of copulation (Bastiaans et al. 2014), but females of several *Sceloporus* species perform push-ups, lateral compression, and tail waves when being courted by males (Kelso and Martins 2008; Swierk et al. 2012; Hardwick et al. 2013; Bastiaans et al. 2014). In our study, the frequency of push-ups and lateral compression by females were correlated with the frequency of tail waves, a behavior recorded in contexts where females freely approach a male and copulates (Bastiaans et al. 2014), and we have observed and recorded females displaying these behaviors before mating, both in the field and in laboratory settings (Electronic Supplementary video), suggesting that push-ups and lateral compression are not limited solely to aggressive interactions, and could be tentatively associated with mating behavior. Therefore, the higher frequency of behaviors towards brighter males may reflect courtship and mate preference or rejection, as these behaviors are used in both contexts, but our experimental design does not allow us to disentangle preference from rejection. Future studies are needed to clarify when do females' displays indicate mate choice, and when mate rejection. Independently of whether choosing or rejecting a male, our results suggest that females use the brightness of the belly blue patches of males to adjust their behavior.

We do not have a clear explanation as to why, when faced with the combination of males' bright versus dull, females displayed equally to both males. The fact that females discriminate among some males based on the male's color suggests that female lizards may use colorful patches during mate evaluation, as has been found in other species (Bajer et al. 2010; Carreira Bruinjé et al. 2022). Females could prefer brighter males if brighter males have access to better territories and more food resources (Sinervo and Lively 1996; Sinervo et al. 2000), or if brighter males have lower parasite load (Molnár et al. 2013).

Females only performed more behaviors when faced with a brighter than a control male. Contrary to our expectations, females did not perform more behaviors when faced with a brighter and dull male or with a dull and control male. Our experimental design had some limitations, as our manipulation simultaneously influenced two attributes, the brightness and the blue chroma of the ventral color patches of males. Particularly in the dull treatment, blue chroma increased, and maximum brightness decreased. If brightness plays a more important role than blue chroma, or their relative combination modulates female behavioral responses, it is possible that changes in different directions in two color attributes may have influenced the lack of discrimination by females in trials with dull males. Additionally, these results suggest that female behavior may be dynamic and context dependent. Females of some species have been shown to display negative frequency-dependent preference for the rare-male types in swordfish (Royle et al. 2008), and previous mating experience influences female mate choice in *Zootoca vivipara* (Fitze et al. 2010; Badiane et al. 2020). A possible explanation for the pattern found in *S. grammicus* could be related to potential costs associated with reproduction, as forced copulations can occur (Chan et al. 2009). In lizards, mating can lead to injuries for females when males bite the female's neck, and in some species, females avoid mating with the more colorful, ultra-dominant and territorial males and choose to mate with non-territorial males (Lattanzio et al. 2014), or with males defending small territories instead of males defending large territories (Carazo et al. 2011). Perhaps *S. grammicus* females, when choosing between males that largely differ in both brightness and blue chroma does not discriminate between them, if these traits reflect different aspects of male quality. The context-dependent female mate choice, the specific information that each color attribute may convey to females and whether previous mating experience influences female mate choice, are promising lines of research to be carried out by future work.

In conclusion, our results partially support the armament-ornament model as the brightness of ventral blue belly patches have a dual function in *S. grammicus*, influencing antagonistic interactions among males and female-male interactions, possibly linked to mate preferences. This study suggests that female choice in lizards may rely on the same colorful signals used in male-male interactions. However, the significance of female behavior in the context of mate preference, as well as the female's rules of choice, still need to be investigated in greater detail, particularly in viviparous species where reproduction is costly, and females are expected to be choosier. Our study highlights the idea that the evolution and maintenance of sexual traits may result from the combined effect of male-male competition and of female-male interactions (Berglund et al. 1996; Wong and Candolin 2005).

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Data availability All data and scripts are available at Figshare [https://figshare.com/s/47024bf3b37f44fb973d](https:/figshare.com/s/47024bf3b37f44fb973d).

Declarations

Ethics approval No ethical approval from the Ethics Committee was required. All animal procedures adhered to UNAM's ethical guidelines. This research complies with current Mexican laws and the Animal Behavior Guidelines for the use of animals for research.

Competing interests The authors declare no competing interests.

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