ORIGINAL ARTICLE

The relative importance of body size and UV coloration in influencing male-male competition in a lacertid lizard

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Abstract

Communication via color signals is common in natural systems. Ultraviolet (UV)-blue patches located on the outer-ventral scales of some lacertid lizards are thought to be involved in male-male competition. However, the mechanisms that maintain their honesty remain unknown. Here, we use the common wall lizard *Podarcis muralis* to test whether the lateral UV-blue spots are conventional signals, the honesty of which is guaranteed by receiver-dependent costs, and discuss their potential role as an amplifier of body size. We first described the morphology and reflectance properties of lateral UV-blue spots in common wall lizards and investigated how they influence male-male competition. Spot size and number, UV chroma, and conspicuousness (calculated using vision models) were significantly greater in adult males relative to adult females and adult males relative to juveniles. Total spot area (and not spot number) of adult males was positively correlated with body size. We conducted staged competition encounters between focal males and smaller or larger rivals with control or manipulated spots. Spots were enlarged in small rivals and reduced in large rivals to disrupt the phenotypic correlation between spot area and body size. Aggressiveness and dominance were positively influenced by body size in control encounters. Spot manipulations resulted in greater submission and less aggressiveness in focal males. These results contradict the predictions associated with conventional signals and amplifiers, but suggest that spots contributed to opponent evaluation during short-distance encounters between competing males.

Significance statement

Many animals use color to communicate. During intraspecific resource competition, some species use color signals as an assessment tool to determine if they should engage in or avoid conflicts. Studies have found that in non-mammalian vertebrates, UV coloration can be a good indicator of fighting ability or aggressiveness. We tested whether and how the UV-blue spots of common wall lizards play a role in male-male competition by studying the properties of their spots, and then used that information to design and conduct competition experiments between males involving spot manipulation. Both body size and spot manipulation influenced aggression and submission during encounters. In particular, results suggest that spot manipulation disrupted mutual assessment and thus that spots play a role in competition signaling in male common wall lizards.

Communicated by S. J. Downes

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Introduction

Animals use conspicuous color patterns as signals in a variety of social interactions ranging from mate choice to competition, and these signals often convey information about individual quality (Bennett et al. 1994; Etman et al. 2001; Candolin 2003; Doucet and Montgomerie 2003; Seehausen and Schluter 2004; Searcy and Nowicki 2005; Pryke and Griffith 2007). Resource competition often involves signals that are honest indicators of the signaler's tendency or ability to fight (Rohwer 1975; Maynard Smith and Harper 2003). Several mechanisms have been proposed that guarantee signal honesty when interests of signalers and receivers oppose (e.g.,

resource competition). Signal honesty can be maintained by an incorruptible, inherent relationship between signal and quality (i.e., low-cost indices) or by differential costs (or benefits) associated with signal expression that are conditional on the signaler's quality (i.e., strategic costs, Zahavi 1975; Dawkins and Guilford 1991; Searcy and Nowicki 2005; Bradbury and Vehrencamp 2011). These costs may be directly related to the production and maintenance of signals (i.e., handicap signals, Searcy and Nowicki 2005) or behaviorally imposed by conspecifics based on an arbitrary convention (i.e., conventional signals, Guilford and Dawkins 1995; Johnstone 1998; Candolin 2000; Vehrencamp 2000). Conventional signals, such as "badges of status" in birds, are cheap to produce, but their honesty is maintained by social costs imposed by receivers that penalize signalers displaying a signaling level that does not match their fighting capacity or individual quality (Senar 1999; Searcy and Nowicki 2005; Ligon and McGraw 2016). In addition to indices and costly signals, Hasson suggests the evolution of amplifiers as yet another route to signal honesty (Hasson 1989, 1990, 1991). Amplifiers are low-cost signals that do not directly inform on the signaler's quality, but act as a "standard" against which other signals or cues are evaluated (Castellano and Cermelli 2010). By improving the detection of signals or cues by intended receivers, amplifiers impose differential efficacy-related benefits on signalers rather than differential strategic costs (Hasson 1997; Hebets 2004; Harper 2006).

In recent years, studies have shown that ultraviolet (UV) coloration in non-mammalian vertebrates is widespread (Whiting et al. 2006; Roberts et al. 2009; Siebeck et al. 2010) and that many of these species have UV-sensitive vision systems (Bennett et al. 1994; Carleton et al. 2000; Smith et al. 2002; Pérez i de Lanuza and Font 2014). Mounting evidence suggests that UV coloration can act as an honest signal of male aggressiveness or fighting ability in birds, fishes, and reptiles (Keyser and Hill 2000; Siebeck 2004; Siefferman and Hill 2005; Pryke and Griffith 2006; Stapley and Whiting 2006; Whiting et al. 2006; Rick and Bakker 2008; Rémy et al. 2010; Bajer et al. 2011; Martin et al. 2015b; Martin et al. 2016). For example, in the Augrabies flat lizard *Platysaurus broadleyi*, UV throat color is an honest predictor of fighting ability (Whiting et al. 2006), and in the European green lizard *Lacerta viridis*, UV-blue nuptial coloration in males signals dominance (Bajer et al. 2011). UV signals have also been shown to co-vary with male phenotypic quality (e.g., Doucet and Montgomerie 2003), and their expression can be constrained in stressful environments (e.g., McGraw et al. 2002; Bajer et al. 2012). Although debated, it has also been suggested that UV signal expression may be subject to developmental costs due to the structural coloration production mechanisms (Keyser and Hill 2000; Siitari et al. 2007; Vedder et al. 2010). Other types of costs, such as receiver-dependent costs (e.g., social costs) associated with

conventional signals, could also maintain the honesty of UV signals (Searcy and Nowicki 2005), but empirical evidence is lacking.

Alternatively, a growing body of literature suggests that color signals could convey information as part of a multicomponent signaling mechanism (Grether et al. 2004). During male-male competition, signaling displays often involve multiple sensory modalities and convey pieces of information from various parts of the body (Rowe 1999; Hebets and Papaj 2005). For example, the dewlap extension signal in male anole lizards (used to signal bite force, Vanhooydonck et al. 2005) is enhanced by the dewlap's coloration (Fleishman et al. 1993; Fleishman 2000), and Ord et al. (2015) suggested that the dewlap's morphology and coloration evolved to amplify the detection of head bobbing behavior. In this context, UV patches could function as amplifiers (Bogaardt and Johnstone 2016; Hasson 1989) by facilitating the detection or discrimination of other signals or cues, such as body size, behavioral displays, or other attributes from the same or adjacent color patches (Fitzpatrick 1998; Taylor et al. 2000; Grether et al. 2004). UV color patches, in particular, are often located along body parts such as necks, mouth corners, and flanks, which makes them good candidates as amplifiers of other quality signals or cues (e.g., Lappin et al. 2006). For example, the male collared lizard *Crotaphytus collaris* has white and UV reflective mouth corners that function as amplifiers during gaping displays by drawing attention to the jaw muscles, which inform on physical strength (Lappin et al. 2006). However, to our knowledge, the amplifier hypothesis has not been experimentally tested on UV coloration displays.

Due to their distinctive lateral UV-blue patches (hereafter referred to as "UV-blue spots," Pérez i de Lanuza et al. 2014), some lacertid lizards are good model systems to investigate alternative mechanisms of honest signaling, such as conventional signals or amplifiers. In several species, the UV-blue spots (located on the outer-ventral scales of the flanks) are highly sexually dimorphic and dichromatic. Although females of some species display faint spots, which appear blue to the human eye, males alone display UV-blue spots with a marked reflectance peak in the UV range, which is highly conspicuous (Pérez i de Lanuza and Font 2014, 2015; Martin et al. 2015a). Several lines of evidence suggest that UV-blue spots may serve in male-male resource competition, but the information content of these traits and the mechanisms responsible for their evolution are contested. First, although the strategic costs associated with these spots remain unknown, their presence both during and outside the breeding season suggests they respond to both natural and sexual selection (Martin et al. 2015b). Second, studies of spot condition dependence and status signaling have produced contradictory results regarding inter-individual variation in spot number, size, and UV reflectance. López et al. (2004) and Cabido et al. (2009) found that spot number correlated with body size and condition in

the Iberian rock lizard *Iberolacerta monticola*. Pérez i de Lanuza et al. (2014), however, demonstrated that the UV chroma of the second rostral-most spot correlated with body condition in the common wall lizard *Podarcis muralis*. In addition, while López et al. (2004) found a relationship between spot presence (vs. absence) and aggressiveness in *I. monticola*, Pérez i de Lanuza et al. (2014) emphasized the importance of UV hue in signaling combat ability in *P. muralis*. Then, Martin et al. (2015b) found that *P. muralis* spots play a role in opponents' mutual assessment of fighting ability. Also along these lines, some studies have found a relationship between spot number and body size (López et al. 2004; Martin et al. 2015b), thus raising the possibility that spot number may be an amplifier of body size, found to correlate with male fighting ability in *I. monticola* (López et al. 2002) and *P. muralis* (Edsman 1990; Sacchi et al. 2009). However, a manipulative study of the blue (but not UV) coloration of *I. monticola*, in which some spots were masked, failed to validate this hypothesis (López et al. 2004).

The above results suggest that UV-blue spots are involved in *P. muralis* signaling but that their effects may be subtle and/or depend on multiple features of the spots themselves or other qualities of the signaler (i.e., body size). *P. muralis* males display UV-blue spots, which run along a large portion of the flanks, and body size is a predictor of *P. muralis* aggressiveness and fighting ability (Edsman 1990; Sacchi et al. 2009). However, the relative roles of body size and UV reflectance in male-male competition are unknown. The aims of our study were to (1) investigate multiple color and morphological properties of the UV-blue spots, (2) experimentally examine whether the honesty of these UV-blue spots is maintained by social costs characteristic of conventional signals, and (3) explore their potential role as amplifiers of body size. We designed behavioral assays consisting of dyadic encounters between non-manipulated focal males and differently sized opponents (2–4 mm larger or smaller than the focal) with UV-blue spots that were or were not UV-enhanced/reduced (hereafter "manipulated" or "control" opponents, respectively). We manipulated the UV-blue spots to create an asymmetry between UV-blue spot area and body size, so as to obtain bluffers (small males with enlarged spots) and Trojans (large males with reduced spots). If spot area functions as a conventional signal, we would predict that deceptive males would pay a cost for being dishonest in the form of increased aggression from focal males (Ligon and McGraw 2016). Therefore, we expected deceptive males to produce fewer displays of aggression and greater displays of submission compared to their respective controls. If, however, spot area acts as an amplifier of body size, we predicted that conflicting body size and spot area traits would cause rival assessment to take longer or not be possible by visual assessment alone, thus resulting in an increase in physical assessment via aggression and fighting by both focals and opponents.

Materials and methods

Study species

The common wall lizard *P. muralis* is a small (snout-vent length, SVL, 48–67 mm), oviparous, polyandrous lacertid lizard widely distributed in semi-open habitats in Europe (Speybroeck et al. 2016). Adult males are territorial during reproduction; large males are more aggressive and defend large territories, while smaller males are less aggressive and defend small territories (Edsman 1990). *P. muralis* is characterized by a conspicuous, discrete belly color polymorphism (Speybroeck et al. 2016; Andrade et al. 2019). In the study area, males have white, orange, or yellow bellies and females have white or yellow bellies (though yellow is rare in both sexes, J-F Le Galliard personal observation; Sacchi et al. 2009; Galeotti et al. 2010). In this study sample, we captured no individuals with yellow bellies. Lateral UV-blue spots, which appear blue to the human viewer and span a large portion of the flank (see Fig. S2), are displayed by a majority of individuals, although previous analyses showed that spots are sexually dimorphic (reduced or absent in females) and sexually dichromatic (UV-reduced in females, Vacher and Geniez 2010; Pérez i de Lanuza et al. 2014; Martin et al. 2015a).

Sampling and measurements

Our study was conducted on a wild population of *P. muralis* located in central France (CEREEP-Ecotron IleDeFrance, France, 60 m a.s.l., 48° 17′ N, 2° 41′ E). All procedures complied with laws on animal experimentation and animal care in France and Europe (permit Ce5/2011/044). Lizards were captured by noosing during the breeding season in the second week of March of 2014. In total, 15 juvenile (4 male, 4 female, 7 unidentified sex) and 60 adult (37 male, 23 female) lizards were captured. Age class was identified by size (adults > 55 mm), and sex by presence of femoral pores (visible to the naked eye) and the hemipene caudal bulges in the proximate tail. Immediately following capture, we used a spectrometer (Jaz Series, JAZ-ULM-200; Ocean Optics Inc., Dunedin, FL, USA) to obtain ambient irradiance profiles of light at the capture locations, for use in models of the lizard vision system. Individuals were taken to the lab to measure body size (snout-vent length [SVL] and total length, ± 1 mm) and body mass (± 1 mg). Spots were counted and their surface area measured (± 0.00001 cm^2) in ImageJ (Schneider et al. 2012) using digital scans of lizard flanks (3.8 megapixels, produced using CanoScan LiDE 700F). To produce scans, lizard flanks were pressed securely but gently against the scanner, situated just below a grid (1 × 1 mm) to scale. Then, two ventral scales of each individual were marked using a non-invasive heat-branding method to allow for individual identification during behavioral experiments (Vervust and Van Damme 2009).

Spectral reflectance of all UV-blue spots of all individuals was measured using a USB-2000 spectrophotometer, a HL 2000 (Halogen-Deuterium) light source, and a 400-μm R400-7-UV/VIS fiber-optic probe (all products of Ocean Optics Inc., Dunedin, FL, USA). Spots smaller than the size of the reflectance detector (< 2 mm) were not measured ($N = 519$ out of 1159) to avoid spectral contamination (Badiane et al. 2017). Reflectance spectra were analyzed using Avicol software version 6, which linearly interpolates spectra with one value per nanometer (Gomez 2006). For each spectrum, we quantified intensity ($R_{300-700}$), UV chroma ($R_{300-400}/R_{300-700}$), and UV hue (wavelength of the maximal reflectance in the UV range 300–400 nm). UV hue was not calculated when there was no UV reflectance peak, i.e., when the spectrum sloped up or down from 300 to 400 nm ($N = 93$ out of 640). We also calculated a mean spot reflectance spectrum for each individual. To determine extrinsic conspicuousness of spots, one to two flank scales dorsal to the UV-blue spots per lizard were measured to calculate a mean flank spectrum, which was used to simplify analyses. Then, to determine extrinsic conspicuousness, eight habitat background objects commonly found at capture sites (3 rocks, 2 bricks, 1 patch of grass, 1 tree branch, and 1 piece of plywood) were each measured (4–6 times) and the mean reflectance spectrum for each object was calculated.

Color vision model

P. muralis is a typical diurnal lizard species with tetrachromatic color vision based on a single-cone system that includes UV-, short wavelength-, medium wavelength-, and long wavelength-sensitive photoreceptors (Martin et al. 2015a). To model the ability of wall lizards to discriminate colors of conspecifics, we ran the Vorobyev and Osorio (1998) color opponent vision model in Avicol (Gomez 2006), parameterized with data on eye physiology and anatomy obtained from Martin et al. (2015a). This model assumes a receptor noise-limited color opponent discrimination mechanism and requires data on receptor spectral sensitivities, receptor abundance, and noise levels in the photoreceptors (e.g., see Vorobyev and Osorio 1998; Siddiqi et al. 2004 for applications). The model calculates relative quantum catch by each photoreceptor type given incident light entering the eye and the spectral sensitivity of the receptor (including lens, ocular media and oil droplet absorption, and visual pigment absorbance of single cones), which is then used to place color objects into a tetrahedral color space and to calculate a perceptual distance (ΔS) in the chromaticity diagram (Goldsmith 1990; Stoddard and Prum 2008). ΔS between two color objects was calculated following the Vorobyev and Osorio (1998) model and expressed in units of multiples of just noticeable differences (jnd). Values of ΔS below 1 indicate that colors are inconspicuous. Receptor spectral sensitivities and

receptor abundance were obtained from previous data on single cones (Martin et al. 2015a), and photoreceptor noise was assumed independent of light. Incident light was calculated by averaging ambient irradiance profiles taken during lizard captures (parameterization details in Appendix S1). We used the model to calculate ΔS of pairwise comparisons between spots vs. habitat objects, spots vs. the mean flank spectrum, and the mean flank spectra vs. habitat objects. This approach is similar to that used in Pérez i de Lanuza and Font (2015), but we found it important to conduct these analyses in our study population before proceeding to behavioral assays. Males had a greater number of UV-blue spots than adult females and juveniles, which accounts for the difference in UV-blue spot sample sizes of the groups.

Color manipulation and behavioral assays

Following measurements, 35 adult males were housed individually in opaque terraria ($25 \times 15.5 \times 15$ cm). Lizards were housed for a total of 15 days, which included a 4-day acclimation period and an 11-day experimental period. Animal care was performed by authorized personnel under permit DTTP-2008-449 issued to JFLG. Each terrarium contained a thick layer of soil bedding, a shelter, and a water dish. Heat and light were provided by a combination of halogen and UV lamps set to a 10:14-h light-dark regime, resulting in an ambient temperature ranging from 15 to 23 °C during the dark and light periods, respectively. Lizards were fed 300–400 mg of crickets every other day, and water was available ad libitum.

Behavioral assays were performed in a temperature-controlled room in neutral arenas, to eliminate the effect of residence advantage (López and Martín 2001; Kokko et al. 2006; Martin et al. 2016) and to focus on the effects of spots and body size on male-male competition. Arenas were composed of large opaque terraria ($45 \times 29 \times 22$ cm) containing a layer of white sand and divided by opaque plastic into two equally sized small compartments (17×14.5 cm) and one large compartment (28×29 cm). The small compartments served as solitary holding areas, which allowed lizards to acclimate to the new conditions. Two UVB neon tube lights (Reptisun 10.0) and one Exo Terra Solar-Glo lamp were suspended above the arena to provide UV-white light (producing an irradiance profile that included substantial UV irradiance and resembled natural lighting) and heat. The latter was positioned 20 cm directly over a 4×9-cm black PVC basking plate, placed on the sand in the large compartment, to which lizards competed for access.

Dyadic encounters occurred between a non-manipulated focal male and an opponent male 2 to 4 mm larger or smaller than the focal (opponent lizard size range = 59–71 mm, mean size difference with focal = 3.20 mm ± 0.89 SD). Opponents either were a control or had manipulated spots. For the latter,

spots were enlarged in smaller opponents (i.e., bluffers) or reduced in larger opponents (i.e., Trojans) based on a regression of spot area against SVL regression (0.8 mm^2/mm SVL; see below). The modified spot area was calculated by multiplying 0.8 mm^2 by twice the difference in size of the focal and opponent in order to exaggerate the spot area-SVL mismatch. Half of the total modified area was applied to each flank. Spot size of opponents was altered by applying a UV-reducing cream (UV−) or UV-enhancing marker (UV+) to add or subtract area from opponent spots. The UV− cream consisted of two inorganic agents (zinc oxide and titan dioxide) mixed with two fats (petroleum jelly and liquid paraffin) at a ratio of 6:4:50:40 per 100 g, a combination that successfully masked UV reflectance in Martin et al. (2015b). The UV+ marker was a light blue Edding 4500 T-shirt marker pen (color code 0.10), previously used to enhance UV coloration in blue tits (Johnsen et al. 2005; Kurvers et al. 2010; Rémy et al. 2010) and shown here to likely enhance UV coloration in *P. muralis* (see Fig. S3). When placed firmly on a surface at a perpendicular angle, the marker tip produced a circle of approximately 0.5 mm diameter (area 0.8 mm^2). As area to be added was in multiples of 0.8 mm^2 (see above), we calculated the number of spots necessary for the area manipulation and added that number of spots using firm application of the marker tip. Spots were added posterior to the lizard's middle spot (uneven number of spots) or to the anterior of the middle spots (even number of spots). Following marker application, we added a fat layer of petroleum jelly and liquid paraffin (55.6:44.4 per 100 g), with no effect on UV reflectance (see Fig. 2a of Martin et al. 2015b), to prevent marker rub off. Control individuals were given a fat layer treatment only. The UV cream and fat layer were applied with the thin end of a forceps. At the end of each trial, UV-reducing cream, fat, and marker treatments were removed through the gentle application of diluted ethanol.

Out of the 35 males, 22 focal males and 31 opponent males were chosen based on size to ensure the 2- to 4-mm difference in size between focal and opponent males. Each focal male participated in a total of 4 encounters, each involving a different, randomly chosen opponent of the following types: (1) control and SVL 2–4 mm longer than focal; (2) control and SVL 2–4 mm shorter than focal; (3) manipulated (UV− spot area) and SVL 2–4 mm longer than focal; (4) manipulated (UV+ spot area) and SVL 2–4 mm shorter than focal. Each opponent male participated in no more than 8 encounters. We chose novel opponents for each test to avoid familiarity among males, which has been found to significantly influence male aggressiveness in *P. muralis* (Martin et al. 2016). Encounters were spaced out by at least 1.5 days to avoid fatigue, and the order of the encounters (1–4 above) was randomized.

Before each experiment, individuals were removed from their home terraria, spot treatments were applied, and each male was placed in one of the two holding compartments. After a 10-min acclimation period, the experiment began with the removal of the opaque walls. One of two observers was randomly chosen to observe encounters from behind a one-way mirror for a period of 10 min. Using Jwatcher (Blumstein and Daniel 2007), we recorded the number of agonistic behaviors in real time and the number and total time of non-agonistic behaviors and total time wall scratching using played-back video recordings. Video was recorded in black and white using a Nikon D70 digital camera positioned 30 cm directly above the arena. Behaviors are summarized in Table 1 (modified from Martin et al. 2016). Observers were trained to interrupt experiments if fighting escalated to the point that it could compromise the welfare of the individuals, but we observed no repeated biting or other tactile aggression events, or other serious distress signs, during the 88 trials. At the end of experimentation, the lizards were individually released to their respective capture sites. To minimize observer bias, all behavioral data were recorded and analyzed blind.

Statistical analyses

We used R version 3.1.2 (R Core Team 2014) for all statistical analyses and figures. To determine differences in spot and flank conspicuousness and spot coloration (intensity, hue, and UV chroma) of adult males, adult females, and juveniles, we used linear mixed-effects models (LMEs) with a "group" variable (three levels: adult males, adult females, and juveniles) as the fixed effect and individual identity as a random effect (multiple spots or flank scales measured per lizard). To account for heteroscedasticity in our "group" variable, we used the weights argument in our models to allow variance of the residuals to differ among group levels. Residuals were tested for normality and intensity was log-transformed, hue and UV chroma were rank-transformed, and chromatic contrast of flank and habitat objects was square root-transformed. We performed post hoc Tukey's test to conduct pairwise comparisons of groups. We also calculated variance components for spot intensity, hue (for males only), and UV chroma to determine intra- and inter-individual variation for males and females.

We investigated the effect of sex and age on spot morphology, including total spot area, total spot number, area of largest left flank spot, and area of largest right flank spot, using linear models (LMs). Prior evidence suggests that these spot features may be indicators of male behavior and/or dominance (López et al. 2004; Cabido et al. 2009; Pérez i de Lanuza et al. 2014; Martin et al. 2015b). Using adult male data only, we then tested for an effect of belly color morph and SVL on total spot area, total number of spots, largest left flank spot area, largest right flank spot area, and mean spot UV chroma to identify spot properties that could be good conventional signals or amplifiers of body size. We applied the Benjamini-Hochberg

Table 1   List and description of (1) behaviors displayed by *P. muralis* during male encounters and (2) scores used in analyses of behavior data

Behaviors/scores		Description
Agonistic	Aggression	Rapid approach towards the opponent OR touch the opponent without bite
	Approach	Slow cautious approach to the opponent
	Bite	Prehension of a body part of the opponent with teeth
	Demonstration	Stationary position with alternately, jerked up and down movements of the hind legs OR wide sustained opening of jaws OR exhibiting one flank by postural adjustment towards the opponent
	Escape	Bypass OR rapid movement away from the opponent
	Wall scratching	Scratching the wall of the terrarium, a sign of moderate stress or avoidance behavior
Non-agonistic	Basking	The body is flattened onto the substrate and oriented at right angles to a heat source
	Movement	Movement from one place to another
	Immobility	No movement while on feet
Scores	"Aggression"	Aggressions + approaches + demonstrations
	"Submission"	Escapes + tail wag events + wall scratching events
	"Dominance"	Aggression score − submission score

correction to account for the testing of multiple spot characteristics (see Table S2). Residuals were tested for normality and total spot number was log-transformed while the largest left and right spots were transformed using the square root function.

Analysis of behavioral experiment data began by summing total counts and total time data for each male in each experiment. This information was used to calculate aggression score, submission score, and dominance score for each male in each experiment (see Table 1), as in Martin et al. (2016). We began with an analysis of control social interactions to validate previous findings regarding the effect of body size and color (belly morph and spots) on male competitive behavior (López and Martín 2001; Martin et al. 2015b). Using LMEs, we tested the additive effect of SVL, belly color morph, opponent size difference, and total spot area (the most likely amplifier of SVL based on spot and morphology analyses) on time basking, time wall scratching, aggression score, submission score, and dominance score. Random effects included lizard identity and assay pair number. To determine the effect of body size and spots on behavior, we conducted a second set of analyses using only data from focal males, since manipulated opponents were not aware of manipulations to their spots and could therefore not respond to those manipulations. We tested the effect of SVL, opponent size difference (smaller or larger SVL), and color manipulation (control or manipulated) as well as the two-way interaction of the latter on focal male time basking, time wall scratching, aggression score, submission score, and dominance score. The Benjamini-Hochberg correction was used to account for the testing of multiple behaviors and scores (see Table S3). All behavioral data were analyzed with LMEs, and Satterhwaite

approximations of degrees of freedom were used for control analyses. In addition to the fixed effects listed above, all models included experiment observer (2 persons), lizard sequence number (lizards were used 4 to 8 times, categorical factor), and experiment time of day (morning or afternoon) in order to control for variables related to experimental logistics. To control for the specific experimental trial, analyses of control interactions data also included experimental trial number. Prior to behavioral analyses, residuals were tested for normality, and dominance score was rank transformed. For all analyses, we began with the full model including all effects and chose the best model using stepwise model selection by AIC. Results are reported as mean ± SE unless otherwise stated.

Data availability

The datasets generated and analyzed during the current study are available in the Zenodo repository, https://zenodo.org/record/3246981.

Results

Color conspicuousness

Perceptual distances between flank and habitat object colors had a mean of 6.67 ± 0.15 just noticeable differences (jnds) with 2.5% of distances inferior to 1 jnd. There was no significant difference in the chromatic contrast of habitat objects against flanks of adult males and adult females ($p = 0.92$, $\beta_{\text{adult male vs. adult female}} = 0.040 \pm 0.10$), adult males and juveniles ($p = 0.16$, $\beta_{\text{adult male vs. juvenile}} = -0.23 \pm 0.13$), or juveniles and adult females ($p = 0.12$, $\beta_{\text{juvenile vs. adult female}} = 0.27$

± 0.14; Table 2). Then, chromatic contrast of UV-blue spots against habitat objects had a mean of 22.79 ± 0.14 jnds with 0.23% of distances inferior to 1 jnd, and chromatic contrast of UV-blue spots against the mean flank had a mean of 22.18 ± 0.36 jnds with 0.15% of distances inferior to 1 jnd. In both cases, the chromatic contrast of adult male spots was significantly greater than that of adult female spots (spot and habitat: $p < 0.001$, $\beta_{\text{adult male vs. adult female}} = 14.62 \pm 1.43$; spot and flank: $p < 0.001$, $\beta_{\text{adult male vs. adult female}} = 15.00 \pm 1.49$) and juvenile spots (spot and habitat: $p < 0.001$, $\beta_{\text{adult male vs. juvenile}} = 7.08 \pm 1.89$; spot and flank: $p < 0.001$, $\beta_{\text{adult male vs. juvenile}} = 7.15 \pm 1.96$), and the chromatic contrast of juvenile spots was significantly greater than that of adult female spots (spot and habitat: $p < 0.001$, $\beta_{\text{juvenile vs. adult female}} = 7.55 \pm 2.02$; spot and flank: $p < 0.001$, $\beta_{\text{juvenile vs. adult female}} = 7.85 \pm 2.11$; Table 2). Histograms of perceptual distances can be found in Fig. S1.

Age and sex differences in spot coloration

First, we found that blue spots of adult males had significantly higher UV chroma compared to those of adult females ($p < 0.001$, $\beta_{\text{adult male vs. adult female}} = 268.22 \pm 29.87$, see Fig. 1) and juveniles ($p < 0.001$, $\beta_{\text{adult male vs. juvenile}} = 153.61 \pm 38.34$), and the UV chroma of juvenile spots was significantly higher than that of adult female spots ($p = 0.015$, $\beta_{\text{juvenile vs. adult female}} = 114.61 \pm 41.35$). Then, we found that adult female spots had significantly higher hue compared to those of adult males ($p < 0.0001$, $\beta_{\text{adult female vs. adult male}} = 278.79 \pm 31.43$) and juveniles ($p = 0.0001$, $\beta_{\text{adult female vs. juvenile}} = 206.06 \pm 45.64$), but adult male and juvenile spots did not differ in hue ($p = 0.20$, $\beta_{\text{adult male vs. juvenile}} = -72.73 \pm 42.74$). We also found no significant differences in spot intensity for adult males and adult females ($p = 0.98$, $\beta_{\text{adult male vs. adult female}} = -0.010 \pm 0.051$), adult males and juveniles ($p = 0.073$, $\beta_{\text{adult male vs. juvenile}} = 0.14 \pm 0.063$), or juveniles and adult females ($p = 0.091$, $\beta_{\text{juvenile vs. adult female}} = -0.15 \pm 0.070$). Finally, males showed greater inter-individual variation in terms of spot intensity and UV chroma compared to females (Table S1).

Size scaling of spot characteristics

Our results revealed that total spot area, total number of spots, largest left flank spot area, and largest right flank spot area were all significantly greater in males compared to females as well as in adults compared to juveniles with the exception of total number of spots (see Table 3). The difference in mean total spot area was especially striking, with mean spot area more than twice as large in males compared to females (males, 0.20 cm^2 ± 0.015; females, 0.073 cm^2 ± 0.0097; $\beta_{\text{males vs. females}} = 0.18 \pm 0.026$), and more than twice as large in adults as compared to juveniles (adults, 0.15 cm^2 ± 0.013; juveniles, 0.066 cm^2 ± 0.014; $\beta_{\text{adults vs. juveniles}} = 0.14 \pm 0.040$). In addition, male total spot area, largest right spot area, and largest left spot area were positively correlated with SVL (Table 4), but not total number of spots ($t_{1, 33} = 0.48$, $p = 0.63$, $\beta = 0.0079 \pm 0.017$, Table 4, Fig. 2a). The relationship between total spot area and SVL was not significant for juveniles ($t_{1, 12} = 0.89$, $p = 0.39$, $\beta = 0.0024 \pm 0.0027$) or females ($t_{1, 25} = 0.25$, $p = 0.80$, $\beta = 0.00057 \pm 0.0022$, Fig. 2b). Mean UV chroma of male spots was higher in orange-bellied as compared to white-bellied individuals, but was not related to SVL (Table 4).

Behavior experiments

Regarding control experiment analyses, individual SVL, but not size difference from the rival nor total spot area, was negatively correlated with indicators of submission (wall scratching time, $F_{1, 40.19} = 8.48$, $p = 0.006$, $\beta = -9.30$ s/mm ± 3.20) and positively correlated with aggression (higher dominance score, $F_{1, 39.23} = 5.66$, $p = 0.023$, $\beta = 2.69$ mm^{-1} ± 1.13, see Fig. 3). Analyses of focal male data indicated that spot manipulation (area added or removed) and opponent size (larger or smaller than the focal) did not significantly affect wall scratching time or aggression score. However, focal males facing manipulated individuals had significantly higher submission scores than focal males facing control individuals ($F_{1, 57} = 6.57$, $p = 0.013$, $\beta_{\text{manipulated vs. control}} = 5.46 \pm 2.13$) and also tended to have lower dominance scores (marginally significant, $F_{1, 57} = 3.86$, $p = 0.054$, $\beta_{\text{manipulated vs. control}} = -8.43 \pm 4.29$).

Table 2 Mean $\pm$ SE chromatic contrast of flank and spot spectra in just noticeable differences (jnds). Flank vs. habitat and spot vs. habitat analyses compared individual flank and spot spectra, respectively, to each of 8 habitat object spectra. Spot vs. flank analyses compared individual spot spectra to a mean flank spectrum. N_1 and N_2 represent the number of spectra of the 1st and 2nd comparison elements, respectively

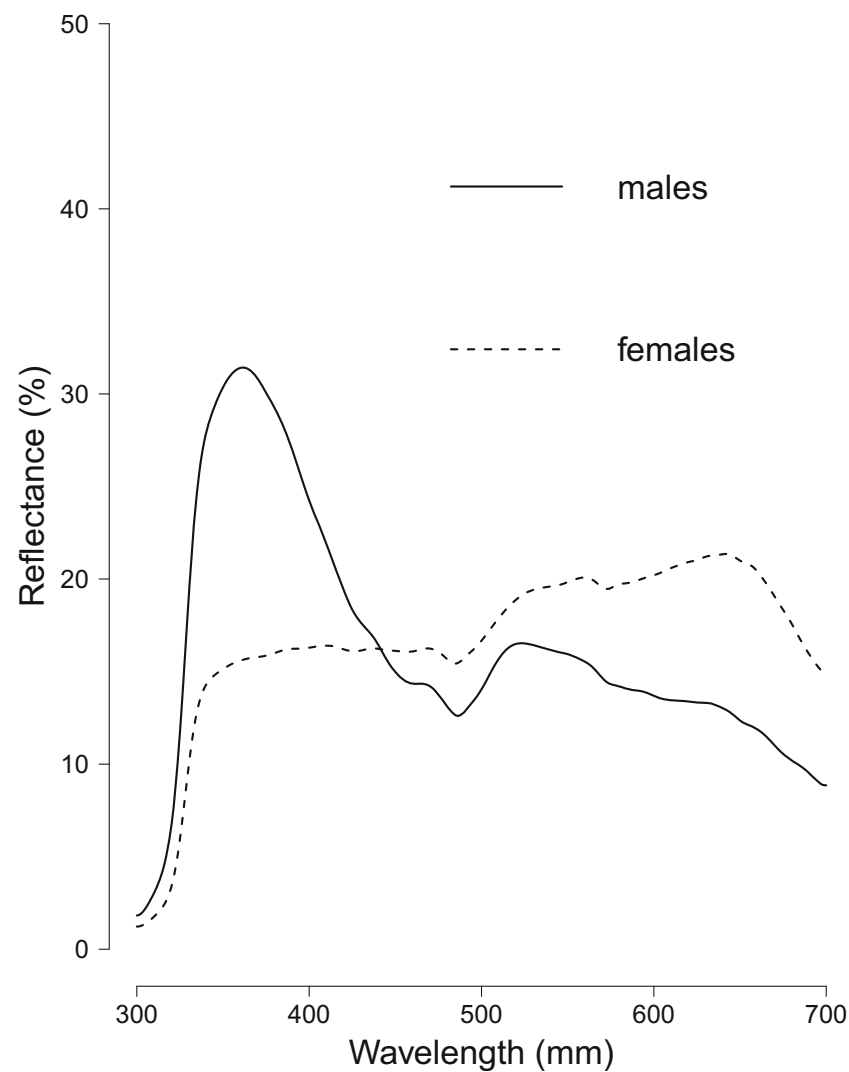|	Flank vs. habitat			Spots vs. habitat			Spots vs. mean flank		
	N_1	N_2	Mean $\pm$ SE	N_1	N_2	Mean $\pm$ SE	N_1	N_2	Mean $\pm$ SE
Adult males	67	8	6.50 ± 0.18	454	8	26.25 ± 0.14	454	1	25.72 ± 0.32
Adult females	25	8	6.45 ± 0.30	125	8	11.97 ± 0.27	125	1	11.02 ± 0.68
Juveniles	13	8	7.97 ± 0.52	72	8	19.78 ± 0.36	72	1	19.14 ± 0.90

Fig. 1 Mean reflectance spectra and 95% confidence interval curves of UV-blue spots for males and females. The male mean spectrum distinctly peaks in reflectance in the UV region (λmax = 360–365 nm) while the female mean spectrum has a weak UV reflectance and a flat reflectance curve in the visible range. Curves were calculated from raw data without smoothing, and confidence intervals assume a normal distribution

Discussion

According to our vision model, the *P. muralis* visual system can distinguish the majority of UV-blue spots when viewed against a mean *P. muralis* flank spectrum and objects commonly found in their natural environments, thus corroborating previous findings involving the same species (Pérez i de Lanuza and Font 2015). UV-blue spots also had a higher extrinsic compared to intrinsic conspicuousness, which seems to reinforce the idea that visual systems are more sensible to

Table 3 Age (A = adults, J = juveniles) and sex (M = males, F = females) differences in spot morphology qualities. Except total number of spots, all factors are in square centimeters. β were calculated on the transformed scale

Spot properties	Sex (df = 1,65)			Age (df = 1,72)		
	F	p	β (M vs. F)	F	p	β (A vs. J)
Total spot area	46.46	< 0.0001	0.18 ± 0.026	12.49	0.00072	0.14 ± 0.040
Total number of spots	5.28	0.025	3.40 ± 1.48	3.75	0.057	3.72 ± 1.92
Largest left flank spot area	47.39	< 0.0001	0.0083 ± 0.0012	14.42	0.00030	0.0068 ± 0.0018
Largest right flank spot area	49.34	< 0.0001	0.047 ± 0.0066	14.12	0.00035	0.040 ± 0.011

Table 4   Effects of belly color morph (O = orange, W = white) and SVL on spot characteristics in adult males. Except total number of spots and mean spot chroma, all factors are in square centimeters. β were calculated on the transformed scale

| Spot properties	Color (df = 1,33)			SVL (df = 1,33)		
	F	p	β (O vs. W)	t	p	β
Total spot area	2.08	0.16	0.27 ± 0.18	2.27	0.030	0.057 ± 0.025
Total number of spots	3.81	0.059	0.24 ± 0.12	0.48	0.63	0.0079 ± 0.017
Largest left flank spot area	0.33	0.57	-0.0011 ± 0.0019	2.61	0.014	0.0006 ± 0.0002
Largest right flank spot area	0.063	0.80	$6.50 \times 10^{-4} \pm 2.59 \times 10^{-4}$	2.67	0.012	0.0009 ± 0.0003
Mean spot UV chroma	7.49	0.010	0.062 ± 0.023	1.09	0.28	0.0034 ± 0.0031

Fig. 2 Size scaling of the number and area of UV-blue spots. **a** Total number of spots as a function of snout-vent length (SVL) for adult male and adult female data with their respective best-fit linear trend lines. The relationship between SVL and number of spots was not significant for male or female data. **b** Total spot area as a function of SVL. The relationship between SVL and total spot area is significant for males and not for females (see text)
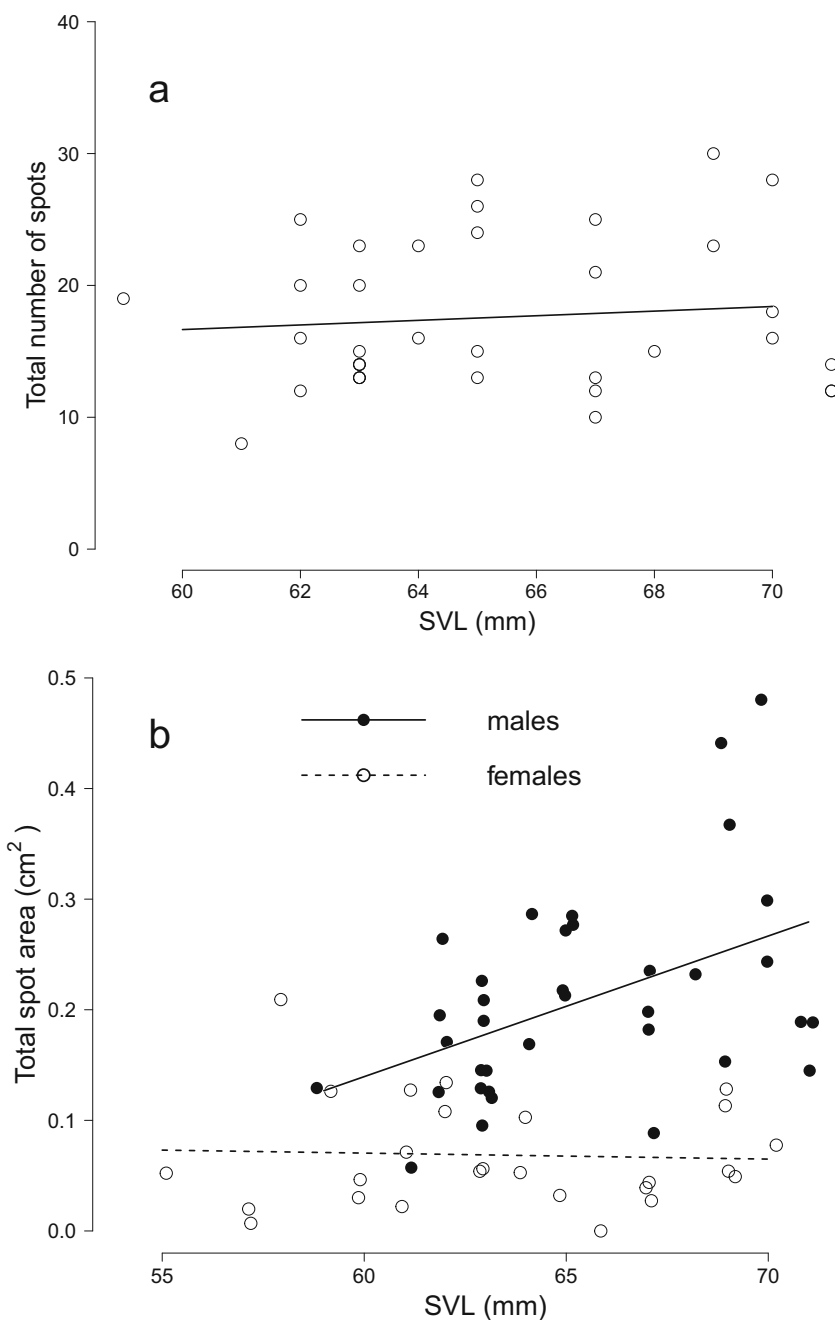
Fig. 3 Dominance score in the control experiments as a function of snout-vent length (SVL) with the corresponding best-fit linear trend line. The relationship between SVL and dominance score is significant (see text). The zero line represents situations in which males performed equal numbers of aggressive and submissive behaviors
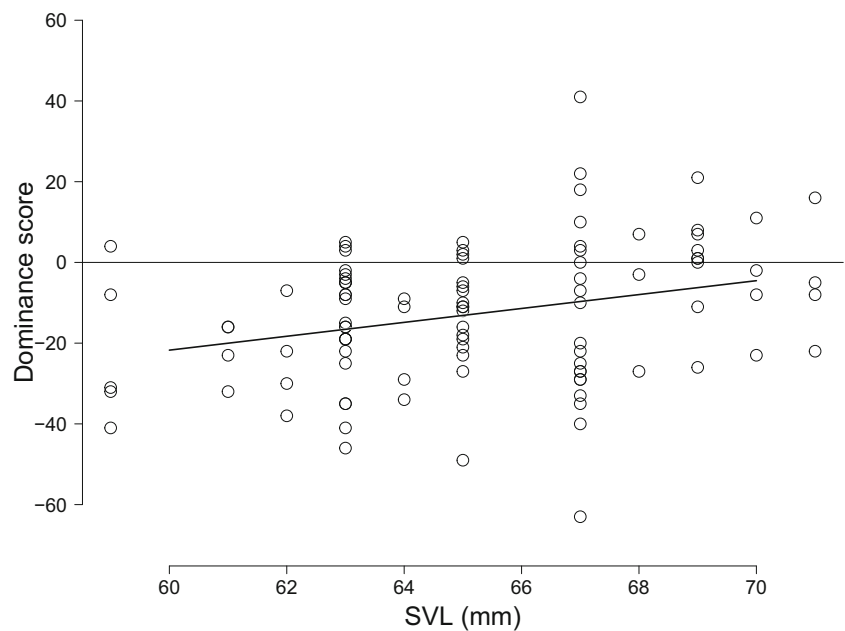
extrinsic than intrinsic conspicuousness (Aronsson and Gamberale-Stille 2009). In addition, the relative inconspicuousness of the lizards' flanks (in this study) and dorsal surfaces (in Pérez i de Lanuza and Font 2015) seems to indicate strong selection for background matching to avoid predation, as observed in other lizard species (LeBas and Marshall 2000; Marshall and Stevens 2014).

Based on the hypothesis that male-male competition shapes the evolution of UV-blue spots, sexual selection theory predicts that adult males should evolve exaggerated UV-blue spots, while this trait should be minimized or absent in females, as it may be detrimental and reduce their fitness via associated costs (Promislow et al. 1992; Andersson 1994; López et al. 2004; Pérez i de Lanuza et al. 2013). Additionally, juveniles should also have reduced UV-blue spots, since young, subdominant lizards should avoid competition with adults (e.g., Mugabo et al. 2013). Previous studies have revealed strong sexual dimorphism for several UV-blue spot characteristics in adult *P. muralis* but have found no clear correlation between UV coloration and adult body size. In males, a slight negative correlation between UV chroma and body condition, as well as a correlation between UV chroma and bite force (dependent on male body size), have been reported (Pérez i de Lanuza et al. 2014; Martin et al. 2015b). The number of spots also correlates positively with body size in male Iberian rock lizards *I. monticola*, a sister species of *P. muralis* (López et al. 2004). Together, these results, along with those showing an influence (albeit weak) of spots on behavior during competitive encounters (López et al. 2004; Pérez i de Lanuza et al. 2014; Martin et al. 2015b, 2016), suggest that UV-blue spots function as potential signals of individual quality, age, and/or sex (Candolin 2003).

Our study revealed age differences and a strong sexual dimorphism in the expression of UV-blue spots. Adult males had exaggerated number, area, and UV chroma of UV-blue spots while adult females and juveniles had only a few faint blue spots (see also López et al. 2004; Pérez i de Lanuza et al. 2014), indicating very limited trait expression in these groups. In adult males, we found a significant correlation between body size and both total spot area and largest left/right spot area, but considered that total spot area is likely to be more biologically relevant because it spans a large part of the length of the lizard, while the largest spots do not. Our results therefore indicate that longer, possibly older, adult males have larger and more interspaced UV-blue spots, possibly making them more conspicuous against their natural visual background. This result is noteworthy, as previous studies have not measured the coloration and morphological properties of all spots of a single lizard (Pérez i de Lanuza et al. 2013; Martin et al. 2015b). Different interpretations can be drawn to explain this relationship. First, the UV-blue spot area may be an honest signal of male quality and correlate with quality indicators not measured in this study such as bite force, which has been shown to be related to male quality in lizards, especially lacertids (Huyghe et al. 2005; Salvador et al. 2007; Henningsen and Irschick 2012; Pérez i de Lanuza et al. 2014). Second, the UV-blue spot area may be directly related to body size either through an inherent relationship, in which case they would act as indices, or as amplifiers of body size, to facilitate receivers' assessment of body size. Baeckens et al. (2018), for example, argue that displaying sexual signals that are redundant with body size may be useful in the first stages of a confrontation, when cryptic lizards must assess one another's quality at a certain distance. Third, ontogenetic

processes could also explain this relationship, which could be tested in longitudinal studies following the same males as they age. For example, Bonnaffé et al. (2018) showed that, in male common lizards *Zootoca vivipara*, UV chroma increased with age, likely due to ontogenetic processes.

As argued above, recent evidence suggests that UV-blue spots are a signal of male quality. The eventual strategic costs associated with these signals remain unknown. Thus, we subsequently tested the prediction that total spot area may act as a conventional signal of male quality (the honesty of which would be maintained by social costs) by conducting behavioral assays between unfamiliar males of varying body size and manipulated spot area. During control encounters, we found a positive relationship between body size and dominance score, and a negative relationship between body size and wall scratching time. These results corroborated previous findings showing that body size influences aggressive and submissive behaviors in male lizards (e.g., López and Martín 2001; Martin et al. 2015b). When we artificially created a mismatch between body size and UV-blue spot area, we found that UV-blue spot area was not a significant explanatory factor of dominance. If, as we aimed to test here, the UV-blue spots functioned as conventional signals, the honesty of which is guaranteed by receiver-dependent costs, we expected deceptive males to pay a socially induced cost for being dishonest (Maynard Smith and Harper 2003; Ligon and McGraw 2016). Focal males were thus expected to invest more in combat behaviors and escalation (both aggression and submission) when faced with a deceptive male rather than a control male, with larger males eventually dominating smaller ones. We, however, found that when facing deceptive opponents, the submission score of focal males significantly increased while their dominance score tended to decrease. These results do not support the prediction of a "conventional signal" hypothesis, in which deceptive males (i.e., bluffers and Trojans) pay a social cost for being dishonest (Maynard Smith and Harper 2003; Ligon and McGraw 2016), and suggest that other types of strategic costs must maintain signal honesty (e.g., handicaps).

In addition, if the UV-blue spots act as an amplifier of body size, we would have expected mismatching body size and spot area combinations to lead to combat escalation, because visual assessment of opponents would fail to clearly establish dominance (Hasson 1989; Maynard Smith and Harper 2003; Martin et al. 2015b). Unfortunately, in our behavioral assays, it was generally not possible to establish a clear "winner" or "loser" over the course of the competitive encounter, and thus, we were not able to quantify combat escalation time. Yet, our results showed that the artificial mismatch between UV-blue spot area and body size did influence the competitive behavior of focal males. On one hand, focal males were more submissive against bluffers than against controls, which could be expected if spot area serves as an amplifier of body size. On the other hand, focal males were also more submissive when faced with Trojans, which contradicts the predictions of the amplifier hypothesis.

One explanation for the weak effect of the combination of body size and spot manipulation treatments on encounters, apart from the submissive behavior of focal males, is that body size contrasts between males were small relative to the wall lizard body size range and, thus, that absolute body size was a better predictor of male behavior than size contrasts. In addition, the correlation between total spot area and body size was not strong (albeit significant, see Fig. 2), possibly suggesting that manipulation of total spot area might not have been perceived as a change in apparent body size. Experiments with a stronger size contrast and modifying the information content of the UV-blue spots in multiple ways (e.g., masking the first and last spots to reduce total length of the lateral rows) could shed light on this possibility. Another explanation is that color traits, such as UV-blue spots, may be more relevant to mutual assessment in outdoor conditions when direct assessment of body size is more difficult, such as signaling over long distances or in the presence of vision-impairing factors (e.g., poor lighting, presence of objects or other organisms, Henningsen and Irschick 2012). Wall lizards typically defend territories using behavioral displays performed at maximal distances of several meters in outdoor conditions (Edsman 1990), and physical pairwise interactions are often aggressive at our study site (J-FLG, personal observation). Thus, in the future, the effects of spot manipulation on territory defense and male-male interactions should be tested outdoors. Then, although we did account for and found no relationship between belly morph and behavior in this study, Abalos et al. (2016) found consistent physiological and morphological differences in morph types that could, in turn, be related to morph-specific behavioral syndromes. It would be worth investigating whether morphs are associated with certain personality types that could influence competitive encounters. Finally, as was the case in studies involving blue tits (Johnsen et al. 2005; Rémy et al. 2010), the UV enhancing marker increased reflectance in the UV as well as the 450–700 wavelength range (although the increase was less in the latter; see Fig. S3). The increase in reflectance outside the UV could have affected opponent response to the manipulated males and it would be ideal to find a UV enhancing product that increased reflectance only in the UV-blue range of the spectrum.

Despite the lack of a strong effect, we did find that spot manipulation of the rival resulted in increased submission and slightly decreased dominance in focal males

irrespective of opponent size. We suggest that this result could be explained if rivals enter into aggressive encounters only if they believe they have a chance of winning based on a comparison of their own and their opponents' color signals (Rohwer 1975; Rémy et al. 2010; Vedder et al. 2010). If we assume that body size is a physical trait easily detected at short distances, large and small focal males initially evaluating a manipulated opponent would likely behave as they normally would against a small or big opponent. In manipulated individuals, focal males facing large opponents would likely back down immediately and no change in their behavior would result due to the manipulation. In focal males facing small opponents, the focal male may initially have been aggressive. Upon approaching their opponent and detecting their enlarged spot area, however, the focal male may back down or exhibit greater submission behaviors due to the mismatch between body size and the signal, resulting in a decrease in overall dominance and increase in overall submission. Another factor that could have reduced aggression is inadvertent modification of black spots next to UV-blue spots. Black spots, sometimes adjacent to UV-blue spots (see Fig. S2), have not been extensively investigated but have been found in one study (Abalos et al. 2016) to be a predictor of fighting ability, with winners showing greater aggression in encounters with opponents of similar black spot area. It is possible that UV-blue spot manipulations reduced black spot area, resulting in encounters between lizards with more dissimilar black spot area and thus lower aggression. Altogether, however, these results suggest that the relationship between UV-blue spots and male dominance is ambiguous in *P. muralis*, similar to findings of Martin et al. (2015b) about spot UV reflectance. Spot properties are involved in mutual assessment during male-male competition but do not influence behavioral dominance as we would expect from a conventional signal or an amplifier of body size.

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflicts of interest.

Ethical approval   Authorization No. Ce5/2011/044 allowed us to capture and manipulate wild animals for this study. Ethical approval from an ethics committee was not necessary. 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 at which the studies were conducted.

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