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The role of male coloration in the outcome of staged contests in the European common wall lizard (*Podarcis muralis*)

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Abstract

Colour signals play a key role in regulating the intensity and outcome of animal contests. Males of the common wall lizard (*Podarcis muralis*) show conspicuous ventrolateral ultraviolet (UV)-blue and black patches. In addition, some populations express a striking ventral colour polymorphism (i.e., discrete orange, white and yellow morphs). In this study, we set out to evaluate the potential signalling function of these colour patches by staging pairwise combats between 60 size-matched adult lizards (20 per morph). Combats were held in a neutral arena, with each lizard facing rivals from the three morphs in a tournament with a balanced design. We then calculated a fighting ability ranking using the Bradley–Terry model, and used it to explore whether ventral colour morph, the size of UV-blue and black patches or the spectral characteristics of UV-blue patches (i.e., brightness, hue, chroma) are good predictors of fighting ability. We did not find an effect of the UV-blue patches on contest outcome, but the size of black patches emerged as a good predictor of fighting ability. We also found that winners were more aggressive when facing rivals with black patches of similar size, suggesting that black patches play a role in rival assessment and fighting rules. Finally, we found that orange males lost fights against heteromorphic males more often than yellow or white males. In light of these results, we discuss the potential signalling function of ventrolateral and ventral colour patches in mediating agonistic encounters in this species.

Keywords

fighting ability, intrasexual competition, colour polymorphism, UV signals, melanin, *Podarcis muralis*.

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1. Introduction

In a world of limited resources, males of many vertebrate systems often engage in contests with members of their own species, either over access to females or resources that are necessary to attract potential mates. Chromatic signals mediate the intensity of these confrontations by allowing animals to assess rivals prior to physically interacting, thereby reducing the costs of aggressive conflicts (Briffa, 2014). For example, in male widow birds (*Euplectes ardens*) the size and spectral properties of the red collar predict territorial behaviour and the intensity of aggressive responses against simulated intruders (Pryke et al., 2001). Similar colour ornaments acting as agonistic signals (i.e., armaments) have been described in numerous vertebrates and invertebrates (e.g., Pryke & Griffith, 2006; Miyai et al., 2011; Todd et al., 2011). In lizards, several colour signals have been shown to convey information about dominance and male fighting ability in intrasexual confrontations (Stapley & Whiting, 2006; Baird, 2013; Olsson et al., 2013). For instance, in the Australian frillneck lizard (*Chlamydosaurus kingii*), the carotenoid-based colour of the frill acts as a reliable signal of fighting ability, and males exhibiting more colourful frills are dominant in size-matched dyadic contests (Hamilton et al., 2013). Similarly, research on *Anolis* has demonstrated that the display of brightly coloured dewlaps plays an important communicative role in several contexts, including male–male contests (Jenssen et al., 2000; Tokarz et al., 2003; Simon, 2011), its role in determining contest outcome being dependent on the degree of territoriality of the species (Lailvaux & Irschick, 2007).

Lacertid lizards comprise 42 different genera and more than 300 species inhabiting a wide variety of habitats across the Old World (Uetz & Hosek, 2015). Although their mating systems are insufficiently documented, they seem to be characterized by strong male–male competition over resources (e.g., territoriality in the genus *Podarcis*; Edsman, 1990; Font et al., 2012) or females (e.g., mate-guarding in *Lacerta agilis*; Olsson, 1994; and *Lacerta schreiberi*; Marco & Pérez-Mellado, 1999). The role of colour signals in this group has been relatively neglected, possibly because lacertids have been traditionally considered to be mainly chemosensory (Mason & Parker, 2010). Despite this historical bias, lacertids have a colour vision system as sophisticated as that of other lizards that rely heavily on vision for many aspects of their biology (Pérez i de Lanuza & Font, 2014; Martin et al., 2015a), and very often exhibit complex colour patterns that at least in some

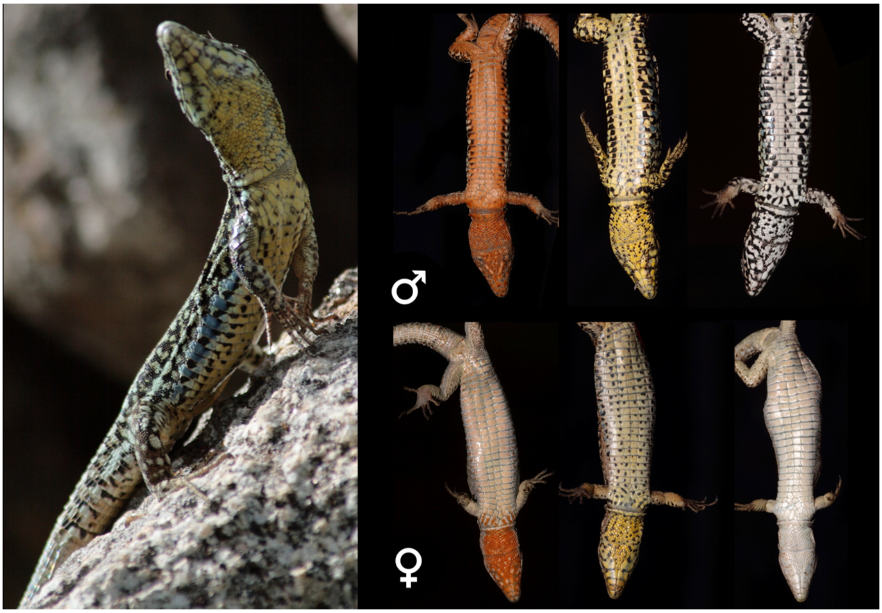

Figure 1. Left: male common wall lizard *Podarcis muralis*. This species has a relatively cryptic dorsum and conspicuous ventrolateral coloration. The ventrolateral area usually presents a complex pattern with black and UV-blue patches. Right: ventral view of both sexes to illustrate the colour polymorphism. Individuals from the three main morphs present orange, yellow or white ventral coloration. In our study population, the ventral colour is restricted to the throat in females, but extends to the belly in males. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

cases seem to have evolved under strong intrasexual competition in males (Bajer et al., 2011; Olsson et al., 2011; Pérez i de Lanuza et al., 2013a).

The common wall lizard (*Podarcis muralis*) is a suitable lacertid model in which to test ideas about the role of colour signals in animal contests. Males of *P. muralis* exhibit a complex ventrolateral pattern on their outer ventral scales (OVS) combining black melanin-based patches (Bowker et al., 1987) and conspicuous ultraviolet (UV)-blue structurally based patches (Figures 1, 2b; Pérez i de Lanuza & Font, 2015). Chromatic variables of male UV-blue patches have been found to correlate with bite force and body condition (Pérez i de Lanuza et al., 2014a), while a recent study showed that the overall area covered by black patches correlates positively with male dominance status (While et al., 2015). In addition to ventrolateral colour patches, some populations of *P. muralis* express a pigment-based ventral colour polymor-

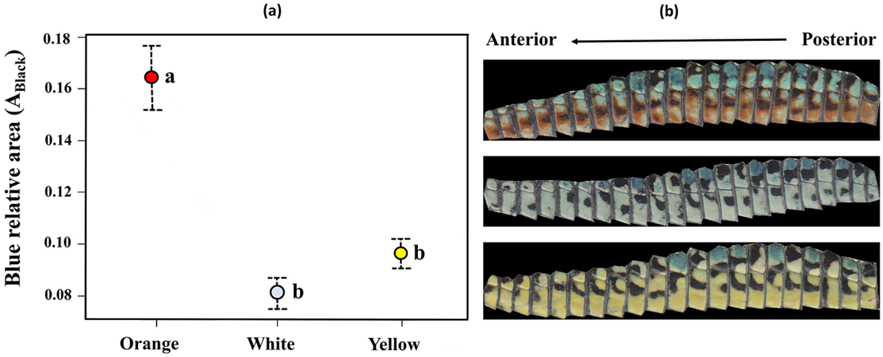

Figure 2. (a) Means of the relative blue area (A_{Blue}) in the ventrolateral patches, for each morph. Error bars represent the standard error of the mean. (b) Representative pictures of the ventrolateral pattern in males of the three pure morphs. Blue coloration sometimes extends to the second row of ventral scales in orange males, while this is rare in white or yellow morph males. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

phism with discrete white (w), orange (o) or yellow (y) pure morphs, as well as intermediate orange-yellow and white-orange morphs (Figure 1; Pérez i de Lanuza et al., 2013b). Although recent studies suggest that different phenotypic optima and breeding strategies may be favoured in each morph, the evolutionary origins and functional significance underlying colour polymorphism in *P. muralis* are still far from resolved (Calsbeek et al., 2010; Galeotti et al., 2013; Pérez i de Lanuza et al., 2013b; but see Sacchi et al., 2015). As in many *Podarcis* species, *P. muralis* shows a resource-based polygynous mating system in which males set out territories that overlap with the home ranges of several females, engaging in frequent contests with intruding males (Edsman, 1990). During these male–male interactions, lizards compress their body laterally (Kitzler, 1941; Olsson, 1992, 1994) in a way that exposes the ventrolateral colour patches, but also the ventral coloration, which could hence also be involved in signalling during agonistic encounters (see Huyghe et al., 2012). These territorial contests are pivotal for the reproductive success of males, since females seem to be attracted to good quality territories rather than to males of certain phenotypic characteristics (Font et al., 2012; Olsson et al., 2013), and frequently remain within the same territory even when the owner is removed and another male takes his place (Edsman, 2001).

In this study we explored the effect of ventral and ventrolateral colour patches during pairwise agonistic interactions between size-matched males with no previous experience that confronted each other in a neutral arena (i.e., no residency effect). We designed our dyadic encounters as a tournament in order to calculate an overall fighting ability for each individual that we could relate to chromatic variables of ventral and ventrolateral colour patches and to levels of winner/loser aggression. We calculated individual fighting ability using a Bradley–Terry model (B-T; Bradley & Terry, 1952; Firth & Turner, 2012), which allows for simultaneous analysis of the relative influence of multiple individual traits on fighting ability, can accommodate an incomplete matrix of confrontations, and takes proper account of dependency among contests involving the same individual (Stuart-Fox et al., 2006).

2. Materials and methods

2.1. Study species

Animals participating in this study came from a colour polymorphic population of *P. muralis* from the Cerdanya valley in the eastern Pyrenees (France). To minimize potential previous fighting experience between opponents, lizards were captured in eight different areas at least 300 m apart, or separated by a geographic barrier (e.g., river). Between 17 and 19 May 2014, we captured 20 adult males of each pure morph (i.e., w, white; y, yellow; o, orange) by noosing, and transported them to the laboratory at the University of Valencia (Valencia, Spain). We only captured lizards with a snout-to-vent length (SVL) larger than 65 mm to restrict the sample to large adult males, ensuring that all individuals participating in the tournament had fully developed colour patches (Pérez i de Lanuza et al., 2013b, 2014a) and were large enough to exhibit full-blown agonistic behaviour (Edsman, 1990), while minimising the range of possible size differences between potential contestants (Sacchi et al., 2009). For each lizard, we used SVL (± 1 mm) and body mass (± 0.1 g) measures at the time of capture to calculate a body condition index (BCI) as the residual from a least-squares linear regression of log(body mass) against log(SVL) (Green, 2001).

2.2. Animal housing and maintenance

In the laboratory, we housed lizards individually in glass terraria (20 × 40 and 25 cm high) with an artificial grass substrate, a water dish, a shelter, and a small brick for basking over which we suspended a 40 W incandescent lamp. Shelters consisted of two tiles (one serving as base and one serving as a removable lid) separated with felt so as to leave a 90 × 90 × 12 mm cavity for the lizard to take refuge. We covered all but the front wall of every terrarium with brown cardboard paper to prevent visual contact between animals from adjoining terraria. We set the temperature and light cycle to mimic average field conditions during the reproductive season at the capture site (15°C at night, 26°C during the day; 12.5L:11.5D), and additionally provided all lizards with full spectrum light (Reptistar 5.0: Sylvania, Danvers, MA, USA) for 1 h three times weekly (12.00–13.00 h) to ensure an effective calcium metabolism, preventing avitaminosis and metabolic bone disease (Adkins et al., 2003). We fed lizards *Tenebrio molitor* larvae dusted with vitamins (Exo Terra, Montreal, QC, Canada) three times weekly and allowed lizards to acclimate to laboratory conditions for 14 days before the experiments. Overall, animals stayed in the laboratory less than two months (19 May–13 July) before being released back to their capture location in the field.

2.3. Experimental design

In order to examine the effect of colour patches on male–male contest outcome, we used a tournament design in which every male faced three different rivals (one of each morph) with a minimum of three days between consecutive contests. The order of contests was randomized for each morph combination to control for a potential order effect. At the conclusion of the 90 initially planned contests, we staged nine additional heteromorphic fights between the three more successful individuals of each morph in order to increase the nestedness of the final tournament network and give additional resolving power to the B-T model (Stuart-Fox et al., 2006); note these fights were pooled with the rest in our analyses. To reduce the potential noise introduced by size asymmetry and prior experience (Baird, 2013), we allowed a maximum size difference between contestants of 10% in SVL, and only confronted males from different capture areas (see above). Finally, to eliminate the effect of residency, we staged the encounters in a neutral experimental arena consisting of a glass terrarium (70 × 30 and 40 cm high) divided into two equal compartments by an opaque partition. Each compartment was illuminated by a 40 W lamp and a full spectrum lamp (Reptistar 5.0) equipped with a high frequency ballast (Quicktronic, Osram, Munich, Germany) (Evans et al., 2006). We performed five combats daily between

Table 1.
Behaviours used to calculate the individual Aggression Score (AS) of lizards participating in the tournament (see text for details).

Behaviour	Description	Score
No response		0
Stare	Looks toward rival	1
Approach	Reduces distance with rival	2
Chase	Quickly follows fleeing rival	3
Display	Throat extension, trunk compression and back arching	4
Mouth gaping	Opens mouth	5
Lunge	Hits rival with closed mouth	6
Bite	Holds rival for <2 s	7
Bite-hold	Holds rival for >2 s	8

4 June and 1 July 2014 at the natural peak activity hours for this population (10.00–13.30 and 16.00–19.00 local time). Immediately before each trial, we randomly determined the initial side of the arena for each opponent, chased the lizards into their shelter, and transferred them into the experimental arena along with their own basking stone. We then disassembled the shelter leaving the base tile in the arena and allowed a 30 min acclimation period before withdrawing the opaque partition and allowing the opponents to interact. All contests were filmed with a digital video camera (XM2, Canon®, Tokyo, Japan). The experimental arena was thoroughly cleaned with water, then alcohol, and again with water after every combat.

In each contest, we designated a winner only if one of the males ceased agonistic behaviours (Table 1) and repeatedly fled if approached by its opponent. In addition to this categorical measure, we also calculated a quantitative variable based on the level of aggression shown by each lizard in each staged contest. In order to do this, we played back filmed contests and recorded each time a lizard performed any of the behaviours described in Table 1. We assigned a score to each of these behaviours based on Carazo et al. (2008), which allowed us to calculate an individual aggression score as the sum of every agonistic behaviour performed by each lizard in each contest (i.e., one aggression score per lizard and contest). We also calculated a measure of aggression ratio for each contest as the quotient between the winner aggression score and the sum of both winner and loser aggression scores (i.e., one aggression ratio per contest). We interrupted combats if they escalated to the point of risking injuries (bite-holds in head or limbs lasting more than

1 min), which was only necessary in one combat. None of the contests resulted in observable injuries.

2.4. Colour measurements

We determined morph visually at the time of capture in the field (Pérez i de Lanuza et al., 2013b). We recorded spectrophotometric measurements in a single session at the conclusion of all contests to minimize the stress induced by manipulation prior to the experiments. We recorded reflectance spectra of the UV-blue patches with a portable USB-2000 spectrometer equipped with a PX-2 Xenon strobe light (Ocean Optics, Dunedin, FL, USA; for further details see Font et al., 2009). Measurements encompassed the 300–700 nm range to cover the entire visual spectrum of *P. muralis* (Pérez i de Lanuza & Font, 2014; Martin et al., 2015a). We recorded spectra from the second, third and fourth UV-blue patches in both sides and averaged them to provide an individual mean spectrum for each lizard. We then extracted data for the standard variables describing colour: brightness (spectral intensity), chroma, and hue (Endler, 1990; Bradbury & Vehremcamp, 2011). We calculated brightness of the UV-blue patches (OVS-Qt) as the total area under the 300–700 nm reflectance curve, hue (OVS-hue) as the wavelength where peak reflectance is located, and UV-chroma (OVS-C_{UV}) as the area under the 300–400 nm reflectance curve divided by the area under the entire spectral curve (i.e., 300–700 nm) (Endler, 1990; Molina-Borja et al., 2006; Pérez i de Lanuza et al., 2014a).

In addition, we measured the relative ventrolateral area covered by black and blue patches in each lizard. For this purpose, we obtained an image of both sides of every lizard using a portable digital scanner (Lide 700F, Canon®), and then calculated the proportion of black and blue coloured area out of the total ventrolateral surface (Figure 2b) using ImageTool Version 3.0 (Wilcox et al., 2002). We defined total ventrolateral surface as the area covered by the first two rows of OVS, between the insertions of the fore and hind limbs. We determined the proportion of coloured area by dividing the blue or black area by total ventrolateral surface; the same researcher (J.A.) measured all areas following a blind protocol. We confirmed the reliability of these measurements by calculating repeatability (r) as defined by Lessels & Boag (1987) in a subsample of lizards ($N = 15$; $r_{\mathrm{blue}} = 0.97$; $r_{\mathrm{black}} = 0.97$). Due to an endoparasitic infection unnoticed at the time of capture, one lizard died in the laboratory before its colour patches could be measured, reducing the final sample for colour variables to 59 individuals.

2.5. Statistical analyses

We used the Bradley–Terry model (B-T model) for planned comparisons to extract a global index of fighting ability for each contestant (Bradley & Terry, 1952). Staged contests can be considered as a subset of all the possible interactions between rivals from which relative fighting ability can be estimated. The B-T model is a type of generalized linear model that takes proper account of dependencies within and between contests while accommodating an incomplete matrix of all possible interactions (Firth, 2005). This model assumes every contestant has a positive value of fighting ability, such that the most likely contest outcome is given by the ratio of the abilities of both contestants (Whiting et al., 2006), and estimates a hierarchy based on transitivity (Stuart-Fox et al., 2006). Using the R package BradleyTerry2 (Firth & Turner, 2012) in R 2.1.5.1 (R Core Team, 2014) we fitted B-T models to 99 fights involving 60 lizards, obtaining a ranking based on individual fighting ability estimates. The model was calculated with 'bias reduction', as is recommended when players face each other only once, and coding ties as half a win for each rival (Firth & Turner, 2012).

We used a generalized linear model (GLM) to explore the relationship between ventral colour morph (considered as a fixed factor), the three spectral variables of the UV-blue patches (i.e., OVS-Qt, OVS-Hue, OVS-C_{UV}), the relative area of blue (A_{Blue}) and black (A_{Black}) colour patches, body size (SVL), and fighting ability estimates as the dependent variable. We checked that all variables conformed to heteroscedasticity and normality assumptions, and assumed a Gaussian distribution for fitting the GLM. We started with the following full model representing our main hypothesis: Fighting ability $\sim$ Morph $+$ SVL $+$ OVS-Qt $+$ OVS-C_{UV} $+$ OVS-Hue $+$ A_{Blue} $+$ A_{Black}. Model fitting was done manually in R 2.1.5.1 (R Core Team, 2014) and model selection was conducted using backward single term deletions ($p \leqslant 0.05$) of the saturated model followed by model comparisons via likelihood ratio tests.

We run linear mixed effects models to explore the relationship between individual aggression score and colour variables. We also explored potential receptor-dependent costs of coloration (i.e., variation in aggression score caused by rival coloration) by running linear mixed models with SVL, OVS-Hue, OVS-C_{UV}, OVS-Qt, Morph, A_{Blue}, A_{Black} and rival aggressive score as fixed factors, and intercepts for winner and loser identity as random effects. Finally, in order to assess the relationship between aggression ratio, body size, morph, and the size of black colour patches, we run the following post hoc linear mixed effects model: Aggression ratio $\sim$ Winner $A_{\text{Black}} \times$ Loser A_{Black} + Winner Morph × Loser Morph + Winner SVL × Loser SVL + (1|Winner) + (1|Loser). p-values were obtained via likelihood ratio tests of the full model after single-term deletions.

3. Results

We could identify a winner in 76 out of 99 contests (Figure A1 in the Appendix). Overall, the mean aggression score of each individual male across contests was significantly correlated with the estimate of fighting ability calculated with the B-T model from the global tournament network (Mean aggression score $\sim$ Fighting ability, $R = 0.59$, $t_{56} = 5.515$, $p < 0.0001$, Figure A2 in the Appendix).

3.1. *Inter-morph differences*

Yellow males won 66% of heteromorphic combats ($N = 36$), while white males won 58% ($N = 39$) and orange males only 24% ($N = 37$). Yellow and white males defeated orange males in the majority of contests (W > O: 76%, $N = 17$; Y > O: 75%, $N = 20$), while results for contests between white and yellow males were more balanced (Y > W: 58%, $N = 19$). However, males with different ventral coloration did not differ in their mean aggression score across contests (Mean AS, $F_{2,58} = 1.73$, $p = 0.187$). We found no significant differences in body size (SVL, $F_{2,60} = 1.84$, $p = 0.168$) or body condition (BCI, $F_{2,60} = 2.858$, $p = 0.0658$) among morphs, despite a trend for yellow males in our sample to show lower BCI than males of the other two morphs (Figure A3 in the Appendix). UV-blue spectral variables did not differ between morphs (OVS-Qt, $F_{2,59} = 2.807$, $p = 0.0691$; OVS-Hue, $F_{2,59} = 0.088$, $p = 0.916$; OVS-C_{UV}, $F_{2,59} = 1.349$, $p = 0.268$). A_{Black} showed marginally non-significant differences between morphs (A_{Black}, $F_{2,58} = 3.038$, $p = 0.0561$), likely due to males of the white morph having slightly larger A_{Black} than males from the orange morph (Tukey's post hoc, W-O ± SEM = 0.058 ± 0.024, $t_{2,58} = 2.39$, $p = 0.052$; Y-O ± SEM = 0.042 ± 0.025, $T_{2,58} = 1.69$, $p = 0.218$; Y-W ± SEM = -0.016 ± 0.025, $t_{2,58} = -0.64$, $p = 0.801$). Orange morph males had higher A_{Blue} than white and yellow males (Figure 2; A_{Blue}, $F_{2,58} = 25.49$, $p < 0.0001$; Tukey's post hoc, W-O ± SEM = -0.083 ± 0.012, $t_{2,58} = -6.75$,

$p < 0.0001$; Y-O ± SEM $= -0.067 \pm 0.013$, $t_{2,58} = -5.33$, $p < 0.0001$), while the white and yellow morphs did not differ (Tukey's post hoc, Y-W ± SEM $= 0.016 \pm 0.013$, $t_{2,58} = 1.24$, $p = 0.434$).

3.2. *Predictors of fighting ability*

In accordance with the observed differences in contest outcome, we detected a marginally significant difference in the fighting ability of different morphs (one way-ANOVA: Fighting ability ∼ Morph, $T_{2,59} = 3.337$, $p = 0.043$; Figure 3). Orange males seem to have slightly lower fighting ability than yellow males (Tukey's post hoc, W-O ± SEM $= 0.007 \pm 0.003$, $t_{2,58} = 2.08$, $p = 0.104$; Y-O ± SEM $= 0.008 \pm 0.003$, $t_{2,58} = 2.37$, $p = 0.054$; Y-W ± SEM $= -0.001 \pm 0.003$, $t_{2,58} = 0.35$, $p = 0.93$).

However, after model selection, only A_{Black} (mean ± SEM $= 0.249 \pm 0.128$) remained as a significant predictor of individual fighting ability (Fighting ability $\sim A_{\mathrm{Black}}$, $t_{56} = 2.453$, Std. Coef. = 0.31, $p = 0.017$, Figure 4). A_{Black} was not related to mean aggression score (Spearman correlation: $S_{56} = 26808$, $\rho = 0.175$, $p = 0.188$), BCI ($T_{56} = 0.032$, $p = 0.974$) or A_{Blue} ($t_{56} = -1.23$, $p = 0.223$). We found no relationship between the spectral variables of UV-blue patches and fighting ability ($R < 0.1$, $p > 0.2$ in all cases).

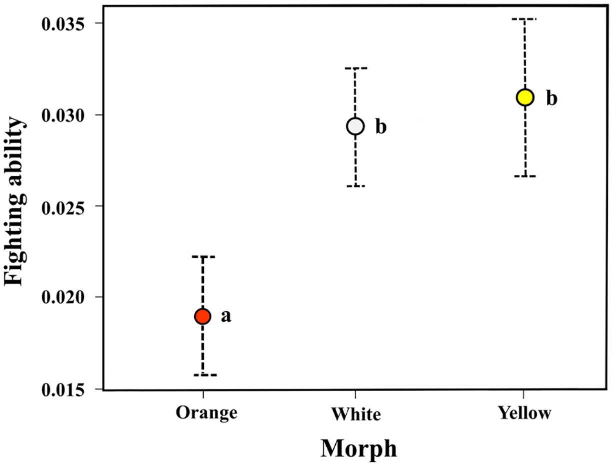

Figure 3. Within-morph means of fighting ability estimates obtained with the Bradley–Terry model. Error bars represent the standard error of the mean. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

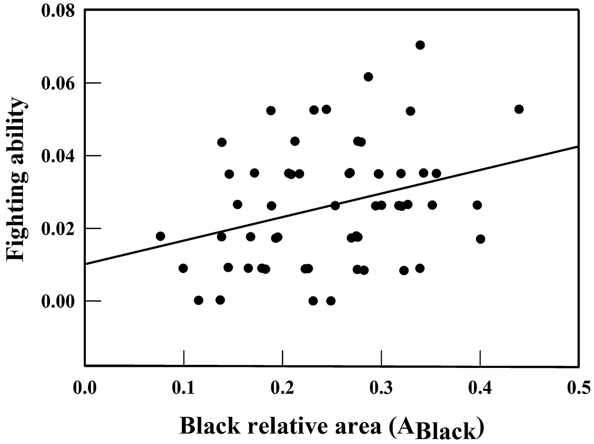

Figure 4. Scatterplot showing the relationship between fighting ability and black relative area in the ventrolateral scales (A_{Black}) for each individual participating in the tournament.

3.3. Predictors of aggression score and aggression ratio

Winner or loser aggression scores were unrelated to colour variables from any of the contestants. In every mixed model, the aggression score of one rival was best predicted only by the aggression score of its opponent (Winner aggression score $\sim$ Loser aggression score, $t_{5,76} = 5.6$, $p < 0.0001$). In contrast, aggression ratio showed a significant relationship with the A_{Black} of both contestants. Specifically, combats between males with similar A_{Black} resulted in higher aggression ratios. After model selection, aggression ratio was found to be significantly related to the interaction between the A_{Black} of each contestant (Winner A_{Black} × Loser A_{Black}; $\chi^2 = 4.74$, df $= 1$, $p = 0.029$) (Table 2), but not with their morph (Winner Morph × Loser Morph; $\chi^2 = 6.63$, df $= 1$, $p = 0.16$), nor their SVL (Winner SVL × Loser SVL; $\chi^2 = 0.0003$, df $= 1$, $p = 0.99$). To examine the significance of this interaction, we used a 3D plot, which suggests that aggression ratio increases as the asymmetry between winner and loser A_{Black} decreases (Figure 5).

4. Discussion

In this study, we set out to assess the potential role of *P. muralis* ventral (i.e., morph; orange, yellow or white) and ventrolateral (i.e., UV-blue and black) colour patches in determining contest outcome in male–male conflicts. Neither the size nor the spectral variables of UV-blue patches affected contest

Table 2.
Mixed effects linear model used to explore the relationship between body size, morph, black coloration and aggression ratio in staged contests between *Podarcis muralis* male lizards.

Term	Coefficient	SE	Variance	SD	χ^2	df	p
Fixed factors							
Winner A_{Black} × Loser A_{Black}	0.19	0.09			4.74	1	0.029
Winner A_{Black}	−0.09	0.12			0.53	1	0.47
Loser A_{Black}	−0.02	0.13			0.03	1	0.87
Random factors							
Loser identity			0.41	0.64			
Winner identity			0.33	0.57			

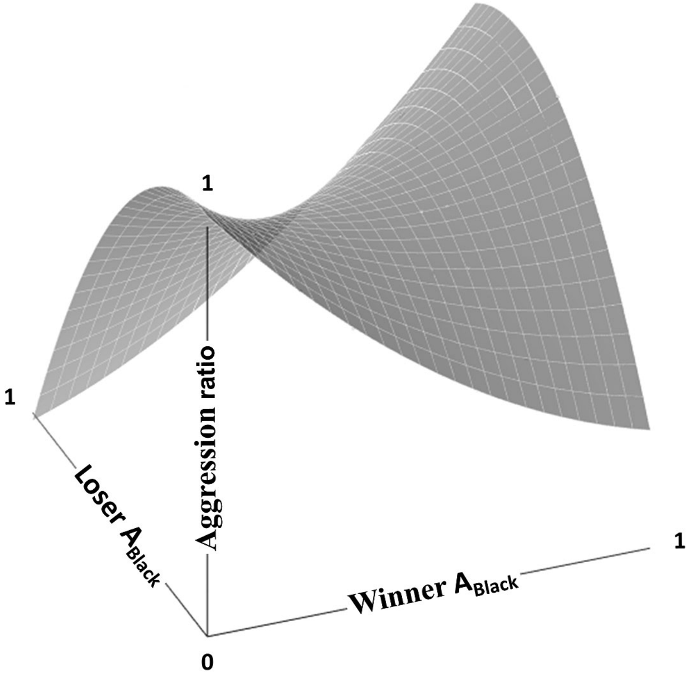

Figure 5. 3D plot exploring the relationship between aggression ratio and the interaction between the black relative area (A_{Black}) of both opponents.

outcome, but both A_{Black} and ventral colour morph did. A_{Black} was a particularly good predictor of fighting ability that also affected the difference in aggression score between winners and losers, in a way that suggests it may be functional as an agonistic signal (see below).

4.1. Black ventrolateral patches as chromatic signals of fighting ability

As stated, A_{Black} was the best predictor of fighting ability in our models, and we also found that the interaction between winner and loser A_{Black} was a significant predictor of the aggression ratio of a contest. Namely, winners behaved relatively more aggressively towards losers as the difference in winner-loser A_{Black} decreased, and less so as it increased. This effect was strong and persisted despite controlling for the interaction between both rivals' SVL in our post hoc model. Hence black coloration does not appear to act as a simple surrogate of size (Gosá, 1987) but rather as an agonistic signal used by males to assess their rivals' fighting ability, and adjust their investment in the fight accordingly. This is in agreement with a recent study reporting that the amount of ventral black coloration strongly correlates with dominance status in two different lineages of *P. muralis* (i.e., Tuscany and Western Europe lineages; While et al., 2015). Furthermore, results from this study strongly suggest that the introgression of the Italian lineage (with exaggerated black coloration) onto Western France is likely driven by male–male competition favouring this character (While et al., 2015).

Several studies across different taxa have also documented the influence of black (melanin-based) coloration in the formation of hierarchies, dominance status, and in the resolution of contests (insects: Tibbetts et al., 2010; fish: Horth, 2003; Johnson & Fuller, 2014; birds: González et al., 2002; Chaine et al., 2011; reptiles: Lebas & Marshall, 2001; Osborne, 2005; Mafli et al., 2011; Qi et al., 2011). Interestingly, and in agreement with predictions from the sequential assessment game model (Enquist & Leimar, 1983), we found that the most aggressive contests were those involving opponents with similarly-sized melanin patches, which has also been reported in organisms as phylogenetically distant as the paper wasp (*Polistes dominulus*; Tibbetts et al., 2010; Tibbets & Sheehan, 2011), or the bluefin killifish (*Lucania goodie*; Johnson & Fuller, 2014). Thus, melanin-based signals seem to convey valuable information about opponents' fighting abilities in a broad diversity of taxa.

Melanin-based signals are usually considered to have low production costs in vertebrates (Hill & Brawner, 1998; Badyaev & Young, 2004; Stoehr, 2006; but see Roulin, 2016), but there is evidence in different species suggesting they frequently act as badges of status with socially-enforced costs (e.g., Møller, 1987; Senar & Camerino, 1998; Tibbets & Dale, 2004; Diep & Westneat, 2013; Roulin, 2016). In addition, activity in the melanocortin system — which is responsible for the production of melanin-based coloration — co-varies with several behavioural and physiological traits in vertebrates, such that darker individuals are often more aggressive, sexually more active and more resistant to various sources of stress than lighter animals (Ducrest et al., 2008). We suggest future studies should examine the mechanisms underlying honest signalling by means of melanin-based colour patches in *P. muralis*.

4.2. *Size and reflectance of UV-blue patches are not related to contest outcome*

We did not find a relationship between fighting ability or aggression score and the size or any of the spectral characteristics of UV-blue patches. Taken at face value, these results seem to argue against the possibility that conspicuous UV-blue patches convey information about male competitive skills. However, there is now compelling evidence suggesting that UV-blue patches may play an important role in intra-sexual competition in several *Podarcis* species (Marshall & Stevens, 2014; Pérez i de Lanuza et al., 2014a; Martin et al., 2015b), including *Podarcis muralis* (McGregor et al., 2016, unpublished data). It is possible that UV-blue patches play a significant role in more natural contexts than the short-range encounters artificially enforced by our experimental design (see also Martin et al., 2015b). It is also possible that, due to potential within-season changes in coloration, our spectrophotometric measurements, taken after the experiment was completed and towards the end of the reproductive season in this population, failed to reflect the true characteristics of UV-blue patches during combats (Martin et al., 2015b). Finally, our negative results may be due to UV-blue patches playing an important role only in the early stages of contests (when assessment takes place), but failing to predict contest outcome if the conflict escalates into physical aggression (Baird et al., 2013). We suggest future studies should aim to experimentally manipulate the area and spectral variables of the UV-blue patches, and set up contests in larger enclosures.

4.3. Morph-specific bias in fighting ability

Our finding that orange males have a propensity to lose heteromorphic confrontations seems to contradict a previous study that did not report any inter-morph differences in fighting ability in Italian polychromatic populations of *P. muralis* (Sacchi et al., 2009).

Although this discrepancy might arise from geographical/phylogenetic differences between the Italian and French lineages, it could also have originated from crucial differences in the experimental design and data analysis. Sacchi et al. (2009) found no differences among morphs in the aggression exhibited during contests, and no effect of ventral coloration over contest score (calculated as the difference in aggression score between contestants). In agreement with these results, in the present study we found no differences in levels of mean aggression score among morphs, nor of an effect of the opponents' ventral coloration on aggression ratio. However, the analysis of fighting ability estimates revealed significant inter-morph differences in the ability to win intrasexual confrontations. Estimating fighting ability directly from contest outcome in a nested tournament experimental design (rather than extrapolating it from aggressive scores obtained from independent subsets of contests; Sacchi et al., 2009), may have allowed for a more powerful analysis of the role played by ventral coloration in the agonistic context. Additionally, as Sacchi et al. (2009) performed combats in a resident-intruder scenario, residency — a strong determinant of contest outcome in lizard encounters (Whiting, 1999; Olsson & Shine, 2000) — may have easily masked the relatively weaker effect of ventral coloration (Stuart-Fox & Johnston, 2005). In *Lacerta agilis*, for example, resident males defeated intruder males in all staged combats regardless of their coloration (Olsson, 1993), while males with larger colour patches were more likely to win fights when confrontations took place in a neutral arena (Olsson, 1994). Other previous studies with lizards have also linked colour polymorphisms to differences in fighting ability using experimental designs that control for a residency effect. For example, in the agamid *Ctenophorus decresii* orange males consistently showed the highest levels of aggression when confronted to the other morphs (Yewers et al., 2016), while in *Ctenophorus pictus* red-headed males outcompeted yellow-headed males in dyadic contests (Healey et al., 2007). In the phrynosomatid *Urosaurus ornatus* blue–green throated males were more likely to defeat orange throated males (Carpenter, 1995). In contrast to our results, in populations of *Podarcis melisellensis* with the same type of orange–yellow–white ventral polymorphism as *P. muralis*, orange males show greater fighting ability than yellow or white males (Huyghe et al., 2012).

Sexual selection often plays a role in the origin and maintenance of population polymorphisms as strong intra-sexual competition might promote the evolution and maintenance of alternative mating strategies (Taborsky, 2008), which frequently correlate with discrete phenotypic traits (e.g., colour morphs; Wellenreuther et al., 2014). For example, in *Uta stansburiana* periodic oscillations in the relative frequencies of three discrete morphs reflect a cyclical 'rock–paper–scissors' game that is driven by frequency-dependent selection on three alternative reproductive strategies (Sinervo & Lively, 1996). Following these results, much attention has been paid to the possibility that other lizard colour polymorphisms might similarly reflect the existence of alternative reproductive tactics maintained by 'rock–paper–scissors' dynamics of selection. For instance, San-José et al. (2014) found that the lacertid *Zootoca vivipara* experiences similar fluctuations in the relative frequencies of morphs that appear to be consistent with frequency-dependent cycles of cumulative selection. However, the reason why alternative mating strategies should be associated with different colorations remains an intriguing question far from being resolved (Pérez i de Lanuza et al., 2013b; but see Sinervo et al., 2006), and future experimental studies in polymorphic systems should test the presumed signalling role of the alternative ventral colours.

Until now, research on colour polymorphism in *P. muralis* has revealed several between-morph differences in morphological and physiological traits (Sacchi et al., 2007a, b; Calsbeek et al., 2010; Galeotti et al., 2010, 2013) that might suggest that different phenotypic optima are being favoured in each morph (i.e., increased body size and susceptibility to infection in the orange morph; Calsbeek et al., 2010), but it is still unclear whether these differences correlate with morph-specific behavioural syndromes and/or mating strategies (but see Sacchi et al., 2009; Pérez i de Lanuza et al., 2013b; Sacchi et al., 2015). The lower fighting ability of orange males in our experiments could be explained by a number of causes, such as by inter-morph behavioural differences in territory acquisition and defence or in inherent fighting ability. The relative impact of colour signals on contest outcome has been found to vary in species of *Anolis* with different levels of territoriality (Lailvaux

& Irschick, 2007). It would be interesting to investigate whether the differences we observed in the fighting ability and black coloration of orange males might be explained by differences in territorial behaviour, and hence in the relative importance of black coloration, across morphs. We suggest future studies should take a closer look at inter-morph differences in fighting ability and other behavioural and physiological aspects relevant to male–male competition (e.g., territoriality and sperm competition).

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Appendix

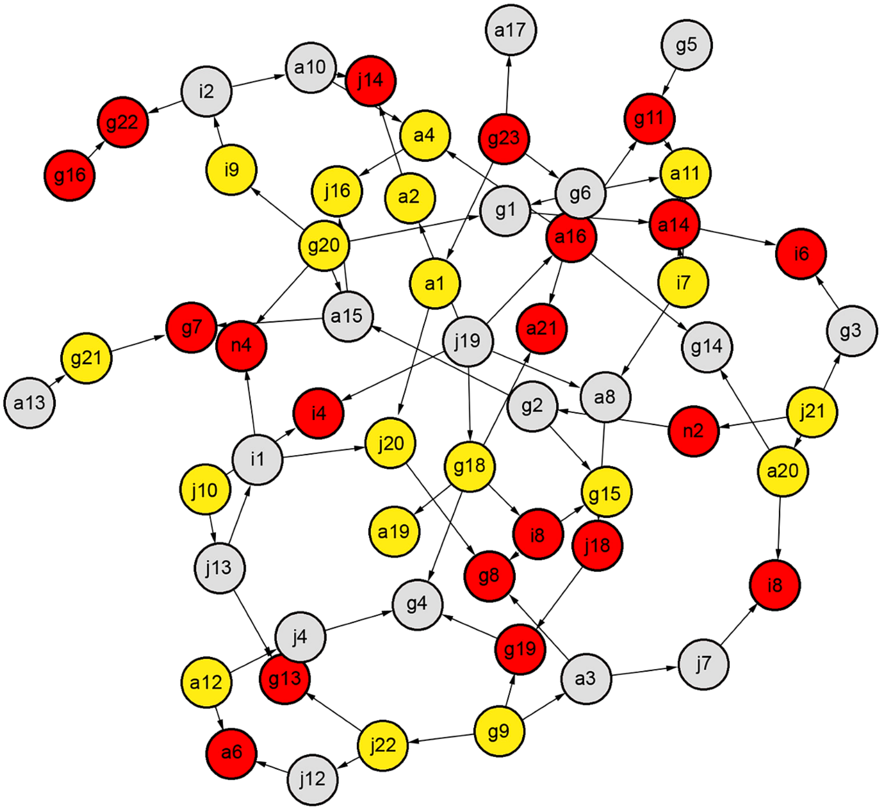

Figure A.1. Tournament network including all the 76 contests (out of 99 staged) in which a winner could be determined. Numbers inside circles denote individuals and the colour represents their morph (o, red; w, grey; y, yellow). Arrows connect opponents that were confronted, pointing toward the loser. The Bradley–Terry model calculates individual fighting ability estimates from nested tournament networks such as this one. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

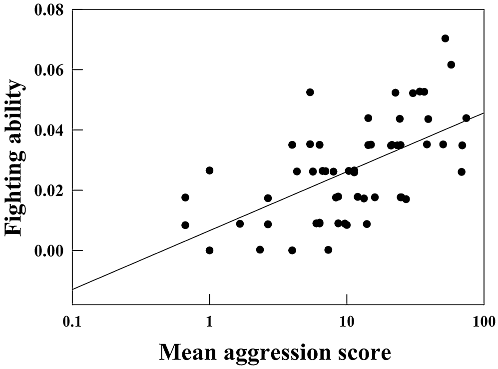

Figure A.2. Scatterplot showing the relationship between mean aggression score (AS) and fighting ability for each individual participating in the tournament.

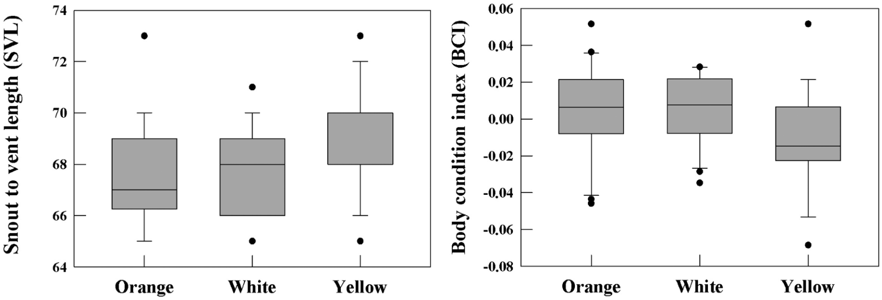

Figure A.3. Box plots showing the values of BCI and SVL separated by colour morph.