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Abstract

The interplay between morphological (structures) and behavioral (acts) signals in contest assessment is still poorly understood. During contests, males of the common wall lizard (*Podarcis muralis*) display both morphological (i.e. static color patches) and behavioral (i.e. raised-body display, foot shakes) traits. We set out to evaluate the role of these putative signals in determining the outcome and intensity of contests by recording agonistic behavior in ten mesocosm enclosures. We find that contests are typically won by males with relatively more black coloration, which are also more aggressive. However, black coloration does not seem to play a role in rival assessment, and behavioral traits are stronger predictors of contest outcome and winner aggression than prior experience, morphology, and coloration. Contest intensity is mainly driven by resource- and self-assessment, with males probably using behavioral threat (raised-body displays) and de-escalation signals (foot shakes) to communicate their willingness to engage/persist in a fight. Our results agree with the view that agonistic signals used during contests are not associated with mutual evaluation of developmentally-fixed attributes, and instead animals monitor each other to ensure that their motivation is matched by their rival. We emphasize the importance of testing the effect of signals on receiver behavior and discuss that social recognition in territorial species may select receivers to neglect potential morphological signals conveying static information on sex, age, or intrinsic quality.

Introduction

Animal contests are frequently settled via ritualized agonistic displays without overt physical aggression (Lorenz 1963; Maynard-Smith and Price 1973; Kokko et al. 2014), yet the interplay between morphological (structures) and behavioral (acts) signals in contest assessment remains elusive (Fernández et al. 2018; Ligon and McGraw 2018; Bruinjé et al. 2019; Naretto and Chiaraviglio 2023; see Table S1 for a list of key conceptual definitions). Agonistic interactions are inherently characterized by a conflict of interest between opponents, and therefore agonistic signals require mechanisms ensuring they make reliable functional information available to receivers (Carazo and Font 2010; Font and Carazo 2010; Hardy and Briffa 2013). The outcome of contests is usually determined by asymmetries between opponents in resource-holding potential (RHP), which depends on the interplay between intrinsic quality (i.e. developmentally-fixed factors such as body size, weaponry, and baseline aggressiveness), performance (i.e. condition-dependent factors such as stamina and fighting ability), motivation (i.e. the individual's willingness to engage/persist in a contest, a function of subjective resource value), and experience (i.e. acquired status, individual recognition, and feedback effects from previous interactions) (Bradbury and Vehrencamp 2011; Hardy and Briffa 2013). Given the importance of these factors in contest resolution, selection has favored the evolution of signals allowing opponents to assess their mismatch for each of them (Setchell et al. 2008; Briffa 2015; Briffa and Lane 2017; Ligon and McGraw 2018).

Different agonistic signals may be better suited to convey different types of information depending on their honesty-ensuring mechanisms and design. An important aspect of signal design is whether the signal is morphological (a structure) or behavioral (an act) (Bradbury and Vehrencamp 2011). Morphological signals (e.g. weapon size, static color patches) become relatively fixed during early development, either because of physical or physiological constraints (Andersson 1994; Taylor et al. 2014; Lindsay et al. 2019). Morphological signals showing unimodal inter-individual variation are well suited to convey information about relatively static (developmentally-fixed) aspects of RHP, such as intrinsic quality (Senar et al. 2006; Stapley and Whiting 2006; Mercadante and Hill 2014; Tibbetts et al. 2017). Many of the agonistic signals described so far are color patches (either structural or pigmentary-based) that remain essentially unchanged (static) after sexual maturity and correlate with aspects of intrinsic quality such as body size, age, weaponry, and hormone levels (Hill and McGraw 2006; Ducrest et al. 2008; Svensson and Wong 2011; Johnson and Fuller 2014; Roulin 2016; Beltrão et al. 2021). In contrast, the expression and intensity of behavioral signals (e.g. weapon-flaring, raised postures, physiological colour changes) may vary in adults over short periods of time (Waas 1991; Hofmann and Schildberger 2001; Waas 2006; Font and Carazo 2010; Heathcote et al. 2018; Ligon and McGraw 2018; Naretto and Chiaraviglio 2023). Behavioral displays that may be produced once, repeatedly, or not at all during interactions are better suited to convey information about more dynamic aspects such as motivation, performance, and experience, which may vary according to context and current condition (Searcy and Nowicki 2005; Briffa 2015; Irschick et al. 2015). An important difference between morphological and behavioral signals is that honesty is enforced during development in the former and within the timeframe of interactions (or immediately after) for the latter (Briffa 2015). It is often the case that agonistic displays have both morphological and behavioral components (i.e. multicomponent signals; Hebets and Papaj 2005). For instance, during contests many crustaceans present their chelipeds to rivals through stationary postures and waving displays, and use them as weapons if contests escalate (Briffa 2013). Chelar size, the morphological signal component, determines pinch strength and other developmentally-fixed aspects of RHP (Sneddon et al. 2000; Bywater et al. 2008). Stationary postures facilitate the assessment of chelar size (and thus, intrinsic quality), but are also energetically costly, targeted towards a rival, and correlate with motivation (Smith and Taylor 1993; Rovero et al. 2000; Elwood et al. 2006). Waving displays are even more exhausting than postural displays, and may add a third layer of informational content on stamina (Briffa and Elwood 2000; Matsumasa and Murai 2005). It is thus pertinent to differentiate between morphological and behavioral (postural or dynamic) components of displays, as they may convey partially non-redundant information (i.e. multiple messages hypothesis; Hebets and Papaj 2005).

The agonistic behavioral repertoire of many species includes two different types of motivation signals: offensive threat signals, and de-escalation or appeasement signals. Offensive threat signals are intention-to-attack postures or movements (i.e. dynamic displays) designed to deter rivals from fighting by conveying the sender's willingness to escalate (Bradbury and Vehrencamp 2011). They often take the form of pre-attack postures performed at close distance of a well-defined target opponent (Számadó 2003). To qualify as a credible signal, threats need to be associated to an increased probability of attack/escalation and demand a response in the form of a retreat or counterattack on the part of the receiver (nonresponses should be answered with escalation; Számadó 2008; van Staaden et al. 2011). Much less attention has been devoted to de-escalation signals, which are submission signals aimed at conveying the sender's low valuation of the contested resource and/or unwillingness to fight. De-escalation signals often take a form that is antithetical to the threat signal of the species and, in opposition to threats, should be accompanied by an increased probability of rapid retreat (Bradbury and Vehrencamp 2011). Why opponents should signal motivation is not straightforward (Briffa 2015). Nonetheless, researchers have begun to characterize motivation signals and to investigate the conditions favoring their evolution, often finding that they form an important yet understudied aspect of animal contest behavior (Számadó 2000; Számadó 2003; Matsumura and Hayden 2006; Számadó 2008; Reddon et al. 2021).

Contests end when one of the opponents decides to withdraw, which it does based on information on themselves, its opponent, and the contested resource. Game theoretic models on contest assessment have largely focused on distinguishing between self-assessment (SA) and mutual assessment (MA) (Hardy and Briffa 2013; Chapin et al. 2019). Theoretical models of rival assessment make testable predictions regarding the relationship between the opponents' RHP (often equated with intrinsic quality) and contest intensity (Taylor and Elwood 2003; Elwood and Arnott 2013). Under pure SA (e.g. energetic war-of-attrition), fights will continue until the weaker individual reaches its threshold and therefore contest intensity should show a strong and positive relationship with loser RHP (and a weaker positive relationship with winner RHP) (Mesterton-Gibbons et al. 1996; Payne and Pagel 1996; Payne and Pagel 1997). The cumulative assessment model (CAM) is also a SA model, but it assumes that animals inflict costs upon each other (i.e. injuries). Under CAM, contest intensity is expected to show a positive relationship with loser RHP and a negative relationship with winner RHP (Payne 1998). This same pattern is expected under the sequential assessment model (SAM), a MA model in which contest intensity depends on the relative RHP of both opponents (Enquist and Leimar 1983; Enquist et al. 1990; Arnott and Elwood 2008). To draw the distinction between CAM and MA, Pinto et al. (2019) suggested taking a closer look at 1) the relationship between contest duration and RHP-linked traits for rivals showing a high degree of similarity in these traits (RHP-matched rivals), as well as at 2) the relationship between contest escalation and RHP difference for randomly-paired rivals. Relative RHP remains the same across the range of RHP variation in RHP-matched contests, and therefore contest duration and the mean RHP of the pair should be unrelated under MA (and positively related under CAM) (Arnott and Elwood 2009). Under MA, contests should be less likely to escalate with increasing difference between rivals in RHP-linked traits (Enquist and Leimar 1983). No relationship between contest escalation and RHP difference is expected under CAM (Payne 1998). Due to its lower cognitive demands, SA is thought to be the default strategy in animals (Elwood and Arnott 2012; Fawcett and Mowles 2013), and was found to be the most common assessment rule in a recent metanalysis of empirical contest studies (Pinto et al. 2019). Despite significant progress in our understanding of contest assessment, the role of communication during contests remains elusive. While signaling is essential for MA, the use of agonistic signals in species that rely on SA may seem paradoxical (Briffa 2015; Chapin et al. 2019). Empirical studies testing the predictions of the main assessment models in species showing a rich repertoire of multicomponent agonistic signals are especially valuable to clarify how signaling may be integrated into contest assessment theory.

Male aggression often plays a central role in structuring lizard social systems, especially in territorial species where males compete to secure resources attractive to females within a patch of suitable habitat, and female mate choice seems largely absent (Baird 2013). Lizard agonistic behavior ranges from overt physical attacks (which entail a risk of injury) to more or less costly signals, often in the form of stereotyped motor patterns, conspicuous coloration, and chemical signals (i.e. scent marks) (Whiting and Miles 2019). Although traditionally considered mainly chemosensory (Mason and Parker 2010), lacertid lizards have a visual system as sophisticated as that of many diurnal animals that rely heavily on vision, including four types of cones in their retina extending their sensitivity to the ultraviolet (UV) waveband (Pérez i de Lanuza and Font 2014a; Martin, Le Galliard, et al. 2015; Fleishman and Font 2019). Among lacertid lizards, the genus *Podarcis* is recently attracting attention in studies of the impact of visual signals on contest behavior (López et al. 2004; Sacchi et al. 2009; Martin, Meylan, Perret, et al. 2015; Martin, Meylan, Haussy, et al. 2015; Abalos et al. 2016; Names et al. 2019). Like other wall lizards, the common wall lizard (*P. muralis*) shows a resource-defense promiscuous mating system where males try to secure fertilizations by investing significant time and energy in the defense of territories offering resources valuable to females (e.g. shelters, basking spots, egg-lying sites) against other males (Edsman 1990; Font, Barbosa, et al. 2012). Females seem to be attracted to high-quality territories rather than to males with certain phenotypic traits and hence patterns of shared paternity often reflect spatial and social dominance among males (Edsman 2001; Heathcote et al. 2016). During social interactions (including contests between males), *P. muralis* show a suite of agonistic visual signals, comprising exposure of normally hidden static color patches and behavioral displays (Fig. 1). Males (and also some females) of many *Podarcis* species — including *P. muralis*— present a complex ventrolateral color pattern in their outer ventral scales (OVS), with conspicuous ultraviolet (UV)-blue reflecting patches that are often surrounded by more or less extensive black melanin-based blotches (Pérez i de Lanuza and Font 2010; Pérez i de Lanuza et al. 2014; Abalos et al. 2016; Badiane and Font 2021). These color patches are absent in newborn lizards and believed to remain largely static after their development (Pérez i de Lanuza et al. 2014; Martin, Meylan, Perret, et al. 2015; Names et al. 2019). Although previous studies suggest positive associations between these color patches and RHP, their role as agonistic signals remains unclear (While et al. 2015; Abalos et al. 2016; Names et al. 2019). Importantly, the interplay between the morphological and behavioral components of *P. muralis* agonistic signals has been largely overlooked. Males approaching conspecifics typically adopt a raised-body posture extending the throat, arching the back with the head pointing downwards, and laterally flattening the body (Kitzler 1941; Weber 1957; Verbeek 1972). This raised-body display is thought to intimidate rivals by projecting a larger image onto their retina while rendering the OVS color patches visible (López and Martín 2001; Font and Carazo 2010; Pérez i de Lanuza and Font 2010). Much less attention have received the foot shake displays that are also produced by both males and females during social interactions. Foot shakes consist of one or more up and down, roughly circular movements of the hand or the entire forelimb that may engage one or both forelegs, either sequentially or simultaneously. In common with other lacertid species, *P. muralis* show at least three types of foot shake displays (named I, II, and III; Font et al. 2012b; de la Cruz et al. 2023) that differ in the structure and overall body posture of the displaying lizard, as well as in the context in which they are performed. Type I foot shakes are broadcast (non-directed, spontaneous) displays similar to the assertion/advertisement displays of iguanid lizards (e.g. Jenssen 1977; Martins and Lacy 2004), and Type III foot shakes function as pursuit-deterrent signals directed at potential predators (Font et al., 2012). Type II foot shakes, on the other hand, are social signals used in interactions with conspecifics of either sex (Steward 1965; Verbeek 1972; Gomez et al. 1993; Font and Desfilis 2002; Pérez i de Lanuza et al. 2016a; Abalos et al. 2020). Despite the appeal of a potential dynamic signal with a social function, controlled observations and experiments to establish the communicative role of Type II foot shakes are lacking.

Here we set out to shed light on the uncertainties surrounding the role of communication in contest assessment by investigating the role of *P. muralis* morphology, coloration, and behavior (i.e. postures and dynamic displays) on male-male competition. To do so, we recorded agonistic confrontations in ten mesocosm enclosures designed to encourage resource-defense competition. Specifically, the aims of this study are: i) to explore the relative importance of morphological and behavioral traits on determining contest outcome and escalation, ii) to assess the informative content of these putative signals by examining their effects on receiver behavior, and iii) to identify the assessment strategy used by males during contests by testing predictions of theoretical models.

Materials and methods

Lizard capture

We captured 190 lizards (100 females and 90 males) from 12 localities across the Cerdanya plateau (Eastern Pyrenees). In each of these localities, we captured 2-8 adult lizards of each sex (snout-to-vent-length; SVL ≥ 56 mm; see Fig. S2 in Abalos et al. 2020). We spotted lizards by slowly walking across suitable patches of habitat (e.g. paths lined with stone-walls in rural areas) and captured them by noosing. Lizards were placed in moistened individual cloth bags (which minimizes stress and ensures ventilation), and then transferred to the Station d'Ecologie Théorique et Expérimentale (SETE, Moulis, France). To facilitate paternity estimates (published elsewhere; Abalos et al. 2020), we captured females at the end of the previous breeding season (September 2017) and males at the start of the following breeding season, in May 2018 (see Appendix S1).

Morphometry and color measurements

Two days before the onset of the experiment, we measured SVL (± 0.1 mm) and mass (± 0.01 g) of each lizard with a ruler and a spring balance (Pesola balance light line 10 g), and we quantified head length in males (HL) using a digital caliper (± 0.01 mm; Mitutoyo, Telford, UK) (Olsson et al. 2002). We estimated an index of body condition (BCI) for each sex as the residual from a least-squares linear regression of log(body mass) against log(SVL) (Green, 2001; Peig and Green, 2010).

We conducted color measurements in a single session at the end of the experiment to minimize the stress induced by manipulation prior to the introduction of the lizards into the experimental enclosures. To quantify color patch size we obtained an image of both sides for every lizard using a portable digital scanner (Lide 700F, Canon®, Tokyo, Japan), and then calculated the proportion of blue and black-colored area out of the total left or right ventrolateral surface using ImageJ 1.53e (Schneider et al. 2012). We defined left and right ventrolateral surfaces as the area covered by the OVS and the adjacent row of ventral scales, between the insertions of the left/right fore and hind limbs (Fig. 1). To obtain the OVS absolute area covered in black we adjusted the color threshold tool implemented in ImageJ to the following values: hue = 0-255, saturation= 0-255, brightness= 1-75. Blue absolute area was calculated by setting these parameters to: hue = 100-190, saturation= 0-255, brightness= 90-255. We determined the proportion of colored area by dividing the blue or black area by total ventrolateral surface; the same researcher (JA) measured all areas following a blind protocol.

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; Pérez i de Lanuza et al. 2014; Badiane et al. 2017). Measurements encompassed the 300–700 nm range to cover the entire visual spectrum of *P. muralis* (Pérez i de Lanuza and Font 2014a; Martin, Le Galliard, et al. 2015). In a single session, GPL recorded spectra from the second anteroposterior UV-blue patch on both sides and averaged them to provide an individual mean spectrum for each lizard. Spectral data were analysed in R v.4.0.3 (R Development Core Team, 2017) using the package *pavo 2* (Maia et al. 2013). Spectra were smoothed (span = 0.2) and normalized by making the reflectance at all wavelengths proportional to the minimum reflectance. We then extracted three standard variables describing color: luminance (spectral intensity), chroma, and hue (Endler 1990; Maia et al. 2013; Renoult et al. 2017). We calculated luminance as the sum of reflectance across a range including the spectrum perceived by wall lizards (i.e., $R_{300\text{-}700}$) and hue as the wavelength of peak reflectance (λ_{max}). To study saturation of UV coloration we calculated UV chroma (CUV) as the area under the reflectance curve in the UV range divided by the area under the entire spectral curve (i.e., $R_{300\text{-}400}/R_{300\text{-}700}$)) (Endler 1990; Molina-Borja et al. 2006; Pérez i de Lanuza et al. 2014; Badiane and Font 2021).

Mesocosm design

To study social behavior in *P. muralis,* we released a total of 180 lizards into ten experimental enclosures (47 m^2 each) in at the Metatron research facility (Caumont, France; Legrand et al., 2012). Within each of these enclosures, we created two types of sites that varied in structural complexity (HQ = high quality, LQ = low quality). Each site consisted of a wooden pallet (~1.2 m^2) with differing number of bricks, cinderblocks, rocks, and logs piled above, which acted both as shelter and perching/basking sites (Fig. S1).

On May 23 2018, we released nine males within each of the enclosures. We monitored male behavior (see below) for seven days before releasing nine females within each enclosure. Prior to release, we marked each lizard permanently on the ventral scales using a disposable medical cautery unit (Ekner et al. 2011) and drew a dorsal number with a toluene xylene-free permanent marker to facilitate individual recognition during behavioral observations (Ferner and Plummer, 2016; see video V1 in Abalos *et al.*, 2020). To minimize the noise introduced by size asymmetries and prior social interactions, we allowed a maximum SVL difference of 2 mm (within sexes) and only put lizards together in the same experimental enclosure if they had been captured at least 300 m apart. On June 22, we removed the males from the enclosures and released them at their capture location (previously determined using a GPS device), while we housed females individually in the laboratory until oviposition (Abalos *et al.*, 2020).

Behavioral observations

From May 23 to June 22, we conducted observations of spatial and social behavior within the experimental enclosures during the natural activity hours for the lizards (9.00 –19.30; Fig. S2), spacing consecutive visits to the same enclosure at least 1 h. To ensure that observations were evenly distributed across different enclosures and time periods, we numbered the enclosures and systematically varied the visiting sequence (Table S2). Each day, the starting enclosure for observation by each observer was rotated, and the sequence of visits was alternated between ascending and descending order. One observer (OL) performed sequential rounds visiting all the enclosures every 2.5 h to collect data on the lizards' spatial behavior (i.e. positional data). Using scan sampling, we determined the identity and location of every lizard in sight on a scale map of the enclosure that included the six wooden pallets. To balance sampling effort across enclosures, scanning of a single enclosure was restricted to a maximum period of 15 min after the first lizard was spotted. Meanwhile, two researchers (JA, AB) recorded the identity, position and behaviors of the lizards participating in social interactions using a behavior sampling rule in recording sessions lasting 40 min. A social interaction was considered to occur whenever a marked lizard in our visual range directed any of the behaviors listed in Table 1 towards a conspecific. Consecutive interactions involving the same lizards were recorded as different events whenever the participants remained further than 30 cm apart for longer than 2 min.. For further details, see Abalos et al. (2020).

Behavior analyses

Behavioral observations were used to study male aggressive behaviour and socio-spatial dominance. To account for habitat use within the enclosures, we estimated range areas by adjusting the smoothing factor in a fixed-kernel contour analysis on each male positional data until it matched the area of the 95% MCP (smoothing multiplier = 0.75, matrix cell number = 40; (Row and Blouin-Demers 2006; Kie 2013; MacGregor et al. 2017; Abalos et al. 2020). Lizards with fewer than nine sightings (*N* = 3) were excluded from the analysis (see Appendix S1). Each lizard was assigned to a specific site (i.e. residency) based on the position where the 50% kernel estimate indicated peak density. For each male, we calculated range size and overlap with females at the 95% (home-range; k95) and 50% (core-range; k50) isopleth levels. When calculating home-range estimates, we excluded the positional data collected during the first six days of the experiment to allow for an acclimation period. All spatial analyses were conducted in Ranges 9 (Anatrack Ltd., UK; Kenward *et al.*, 2014).

We classified interactions according to their sociosexual context into four types: intrasexual competitive and non-competitive, and male–female reproductive and nonreproductive (examined elsewhere; Abalos et al. 2020). Intrasexual interactions were deemed competitive whenever one lizard (i.e., the loser) used fast-paced locomotion to flee from another lizard (i.e., the winner) showing display behavior and/or physical aggression (i.e., display, bite, or chase). In males, where competitive interactions where numerous, we used the

R package BradleyTerry2 to investigate the relative importance of color patches, behavioral displays, and other contest-specific traits in predicting the probability of winning a contest (Bradley and Terry 1952; Firth and Turner 2012a). Contest-specific traits are variables that, unlike individual-specific traits (i.e. morphology, coloration), vary between contests (i.e. behavior, residency, etc) and can interact with the two players' probability of winning a contest. Bradley-Terry models are a type of logistic models for paired comparisons, and their standard equation can be expressed in a logit-linear form:

$$\text{logit}\ [pr(i \text{ beats } j)] = \lambda_i - \lambda_j$$

where i and j are the lizards in a contest and the probability of lizard i beating lizard j is a function of their difference in "fighting ability" (λ). Bradley-Terry models are especially suitable to study animal contests because they can accommodate an incomplete matrix of encounters, estimate a coefficient β for each of the predictors of contest outcome introduced, and calculate an individual index of fighting ability for every male (further details in Stuart-Fox et al. 2006; Firth and Turner 2012b; McLean and Stuart-Fox 2015; Abalos et al. 2016; Kar et al. 2016). Model coefficients and predicted fighting abilities are expressed in the logit scale (i.e. as the logarithm of odd ratios), so that probabilities can be calculated using the formula:

$$\text{Probability of winning} = (\exp(k^*\beta))/(1+(\exp(k^*\ \beta))$$

Where k is the z-score for a given predictor variable in the focal lizard and β is the coefficient for that same predictor according to the Bradley-Terry model. We examined the intercorrelation between the individual-level predictors of fighting ability (i.e. morphometric and color traits) using a Pearson correlation matrix provided by the "*PerformanceAnalytics*" package (Fig. S2) (Peterson et al. 2018). To account for false discovery rate in multiple correlation tests we estimated q-values using the *p.adjust* function of the *stats* package in R (Benjamini and Yekutieli 2001), and included only SVL and the residuals of head length on SVL (HL res) as morphometric predictors to avoid model over-parameterization. Hence, we assessed the following male-specific traits on the probability of winning: SVL, HL res, proportion of UV-blue coloration, UV-blue luminance, UV-blue hue, UV-blue chroma (CUV), and proportion of black coloration. As contest-specific traits we included 1) whether the male performed a raised-body display, Type II foot shake or bite (Table 1) during the interaction (binary 1/0), 2) prior contest history (i.e. 1 if the male won the most recent contest, 0 if it lost), and 3) residency (i.e. 1 if the fight took place in the pallet where the male was attributed residency, 0 if the fight took place elsewhere; see below). The first fight of every male was given a score of 0 for prior contest history, as contestants did not have any prior wins yet (Stuart-Fox et al. 2006; Kar et al. 2016).

We examined the association among the binary behavioral variables Raised-body display, Bite, Foot shake, Chase, and Flight across all contests using two Pearson correlation matrices (equivalent to phi coefficients): one at the within-individual level and another one confronting loser and winner behavior. To examine predictors of winner aggression, we fitted two logistic mixed models on the full dataset of contests observed: one on the probability of the winner biting the loser, and another on the probability that the winner chased the fleeing rival. To avoid model over-parameterization, predictors were selected among the factors found to be determinant for contest outcome in the BT models. Therefore, in these two models we included the binary variables describing the occurrence of raised-body displays and foot shakes by each rival as well as residency and the interaction between winner and loser black area as fixed factors. In the model on chases, we also included bites from both opponents among the predictors. To control for pseudo-replication in our dataset, in both models we included the identity of each rival and the enclosure as random factors.

Models of rival assessment

As intra-sexual confrontations rarely lasted longer than 1s, we operationally defined the number of interactions observed between any two pair of potential rivals (i.e. males released within the same enclosure) as a proxy for contest duration. We then estimated escalation for each resolved contest by summing up the binary occurrence of displays, bites and chases performed by both opponents. To obtain an individual score of RHP exclusively based on contest outcomes, we fitted a Bradley–Terry model without specifying any explanatory variables to the observed matrix of contest outcomes within each enclosure. We then used the function "*BTabilities*" to calculate the "direct estimates of ability" (hereafter, RHP) provided by the standard Bradley-Terry model (Firth and Turner 2012b).

Following the Taylor-Elwood method (Taylor and Elwood 2003), we first tested for contrasting predictions of contest assessment models by fitting separate mixed models of contest duration and escalation against RHP and individual-specific morphological traits (i.e. SVL, HL res, Blue area, UV-blue luminance, UV-blue hue, UV-blue CUV, and Black area). For each predictor we fitted two negative binomial models. In models on contest duration, we corrected for zero-inflation and used either the data corresponding to the male showing a higher value for said predictor in each pair of possible rivals (i.e. high-value male), or the data corresponding to the males showing a lower value (e.g. low-value male). For contest escalation we fitted one model on the winner's data and another on the loser's data.

We then followed Pinto et al. (2019) to discern between self- (CAM) and mutual assessment models in order to evaluate the possible signaling role of morphological traits during contest assessment. For each predictor included in the previous models, we obtained a different subset of our dataset on contests duration excluding contests between rivals showing a difference in the focal trait larger than 1 SD. We then examined the relationship between contest duration and mean predictor value in this subset of matched contests by fitting separate GLMMs with a negative binomial distribution for each predictor. In addition, we examined patterns of contest escalation by fitting a separate GLMM with a negative binomial distribution for each predictor variable, including the difference between winner and loser values as the only fixed factor.

Lastly, we examined the importance of resource value in contest assessment by recording site combination (i.e. LQ-LQ, HQ-LQ, HQ-HQ, according to the quality of the site assigned to each opponent) both in the dataset with all possible pair combinations and in the dataset of resolved contests. We then fitted one GLMM on contest duration and another on contest escalation, both with a negative binomial distribution and including site combination as a fixed factor. The identity of both opponents and enclosure were included as random factors in all models. Fitting separate models including a single predictor instead of using composite measures is recommended to independently evaluate the potential effect of the individual traits of each opponent (Taylor and Elwood 2003; Arnott and Elwood 2009; Elwood and Arnott 2012)

Statistical analyses

To explore phenotypic correlates of male space use and social behavior we ran generalized linear mixed models (GLMMs) using the *lme4* and the *glmTMB* packages (Bates et al. 2014; Brooks et al. 2017) in R (R Core Team 2023). For non-binary response variables, we chose model distribution (i.e. among Gaussian, Poisson, negative binomial and Gamma) based on AIC reduction and by comparing the homoscedasticity and normality of the residuals (simulated using the package *DHARMa*; Hartig 2017). All numerical variables were centered and scaled before running the models (Schielzeth, 2010). Model selection was conducted using backwards single term deletions ($P < 0.05$) of the saturated model followed by model comparisons via likelihood ratio tests (at $\alpha = 0.05$). We then calculated marginal *pseudo*-r^2 on the final model (following (Nakagawa et al. 2017), checked the absence of multicollinearity among predictors, influential data points, and graphically explored that residuals conformed to homoscedasticity and normality assumptions (when pertinent) using the *performance* package in R (Lüdecke et al. 2020). For logistic models, we checked that there was a linear relationship between the logit of the outcome and each of the predictor variables. We also checked for overdispersion using the *PsychHelperFunctions* package (Huff 2020). For further details on the statistical analyses see Appendix S1.

Results

Correlations among morphological and color variables in males

We detected several significant correlations among pairs of morphological and color variables in males (Fig. S3). Variation in relative black area was independent from variation in relative blue area, but the latter was positively related with CUV (Pearson $R = 0.36$, *q-value* = 0.004). Luminance was found to correlate positively with Hue (Pearson $R = 0.57$, *q-value* < 0.001) and negatively with CUV (Pearson $R = -0.28$, *q-value* < 0.01), while CUV showed a negative correlation with hue (Pearson $R = -0.44$, *q-value* < 0.001). Weight showed a weak negative correlation with CUV (Pearson $R = -0.25$, *q-value* < 0.092). SVL and HLres showed the weakest correlation among morphometric variables (Pearson $R < 0.001$).

Predictors of contest outcome and winner aggression

We recorded 927 intrasexual interactions (614 in males and 384 in females) in 156 observation sessions. Competitive interactions were more common among males ($N = 544$; 89% of total male–male interactions) than among females ($N = 25$; 7%), which were often observed co-perching in groups ($N = 338$. 88%). In males, raised-body displays and/or Type II foot shakes (Tables 1 and S3) were observed in 60% of these competitive encounters, a third of them (36%) ended with a rapid chase/flight, and 16% involved physical aggression (i.e., bites). At the individual level, Raised-body display was positively correlated with Bite and Chase and negatively correlated with Foot shake and Flight (Fig. 2a). Bite correlated positively with Chase and negatively with Foot shake, while Foot shake correlated negatively with Chase. Correlations between winner and loser behavior show that loser Raised-body display correlated positively with winner Raised-body display, Bite, and Foot shake (Fig. 2b). Loser Bite correlated positively with winner Bite and Chase, while Loser Foot shake correlated positively with winner Raised-body display and negatively with winner Chase. Over half of the confrontations (62%) took place in a location were neither of the rivals was considered resident. Winner lizards were residents in 22% of the contests and loser lizards in 11%. Lastly, 5% of the contests took place in locations were both rivals were residents. When only one of the males was resident at the contest location, the resident lizard won in 66% of the occasions (N = 183 fights).

Using a B-T model on the full dataset of fights (M1, 544 fights) we found that black coloration and the occurrence of raised-body displays (scored as 1/0) during the fight were positively related with winning confrontations, while foot shaking lizards tended to lose. Significant predictors in first fights (in which no lizard had previous contest history, M3, 66 fights) included HLres, black coloration, and raised-body displays (Table 2). When these first fights were excluded from the B-T model (M2, 478 encounters), we found evidence of an effect for the same predictors as when running the full dataset plus a positive effect of prior contest history (Fig. 3a). This B-T model successfully predicted the outcome in 85.7% of the contests when considering predicted probabilities greater or equal to 0.75 as sufficient to assign the winner of a contest. Males multiply their odds of winning contests by a factor of 2.32 for each 1 SD advantage in black area over their rival (Fig. 3b). This effect is similar in magnitude to the positive effect we found for prior contest history (2.69 more likely to win after a victory), but smaller than the effect of behavioral displays. Males that performed raised-body displays had 7.32 higher odds of winning contests (probability of 0.88) and males that performed Type II foot shakes had 16.67 higher odds of losing contests (probability of 0.94). We also found weak evidence for a positive effect of residency (Table 2; Fig. 3b). The strongest predictor of RHP (i.e. BT estimates of ability exclusively based on contest outcome) was black coloration (Table S4; Fig. 3c).

A similar prevalence of behavioral displays over morphological traits was found when examining the factors influencing winner aggression. The occurrence of raised-body displays by the winner and foot shakes by the loser were found to be significant predictors of winner aggression ($P < 0.01$, overdispersion test: P = 0.86, Nakagawa's *pseudo*-r^2 = 0.09; Table S5). Winners were 3.39 times more likely to bite the loser when the former performed raised-body displays, but 3.33 times less likely if the loser performed foot shakes (Fig. 2c). Visual signals were also found to play a role regulating whether the contest ended up in a chase ($P < 0.01$, overdispersion test: P = 0.128, Nakagawa's *pseudo*-r^2 = 0.20; Table S6). Winners were 7.26 times more likely to chase the fleeing rival after biting it or if showing a higher proportion of black coloration (odds multiplied by 1.87 with each 1 SD increase), while loser foot shakes decreased the probability of a chase taking place by a factor of 3.23 (Fig. 2d).

Predictors of contest intensity

We recorded contests between 60% of all potential rivals. The number of interactions between pairs of potential rivals (i.e. contest duration; range = 0-15) was positively related with the RHP and black area of both opponents (although the effect was not significant for the low-value male's black area; Fig. 4a). Contest duration was also weakly related with the blue area of both opponents (positive for high-value males, negative for low-value males; Table S7; Fig. 4a). Mean RHP and mean black area showed a positive relationship with contest duration in the models fitted on matched pair combinations, although the relationship was only significant for RHP (Table S8, Fig. 4b).

Contest escalation (range = 0-5) showed a positive and significant relationship with the RHP and black area of both opponents. The relationship was positive for the loser and negative for the winner in models fitted on HL res (loser: $P < 0.05$), SVL, CUV, and blue area (Table S7; Fig. 4d). Contest escalation showed a negative relationship with the asymmetry between contestants in HL res ($P < 0.05$), SVL, CUV, and blue area (Table S9, Fig. 4e).

Site combination was strongly related with contest intensity. Contest duration between males settled in LQ sites was 3.1 times shorter than between males settled in HQ sites, and 2.1 times shorter than between males settled in sites of different quality. Contest escalation was 1.3 times higher in HQ-LQ pairs with respect to LQ-LQ pairs (Table S7, Figs. 4c and 4f). More than half of the observed fights corresponded to HQ-LQ pairs, and 75% of the fights that took place in HQ sites confronted males settled in sites of different quality (Table S10).

Socio-spatial behavior

Overall, we accumulated 7,190 re-sightings of the marked lizards in 614 scan samplings. We found a strong sex bias in the tendency to occupy high- or low-quality sites (Table S11). In fact, even though lizards were evenly distributed among sites (HQ: $N = 91$, LQ: $N = 89$), females had 3.5 times higher odds of settling in HQ sites. Lizards settled in HQ sites were resighted more often than lizards in LQ sites, and males were resighted more often than females (Table S11). As expected, males had larger home- and core ranges than females, and lizards settling in HQ sites occupied smaller areas than lizards in LQ sites (Table S11).

In males, only a subset of highly dominant individual managed to settle in HQ sites (HQ: $N = 21$, LQ: $N = 69$), with each 1 SD increase in RHP increasing the odds of occupying a HQ pallet by a factor of 4.5

(Table S12; see Fig. 3d for effect on probability). Males settled in HQ sites did not differ in body size, weight, or head length from males settled in LQ sites (LMM: $\chi 2 < 1$, $P > .2$). Males in HQ sites were sighted significantly more often than males in LQ pallets (Table S12). Variation in home- and core-range size was explained by RHP, with more socially dominant males (i.e. more RHP) presenting significantly smaller ranges (Table S12). Spatial overlap with females was significantly predicted by site quality and core-range size (i.e. males in HQ pallets overlapped with 2.2 ± 0.3 more females; Table S12). For further details on the positive correlation between access to HQ sites and male fitness in this experiment see Abalos et al. (2020).

Discussion

What limits aggression in animal contests remains a key question in ethology. Here we investigate the role of *P. muralis* morphological and behavioral traits on male-male competition. Our results suggest that visual displays play a more important role than morphology (including coloration) in male-male competition by influencing contest outcome and overall aggression.

Predictors of contest outcome and informational content of agonistic visual signals

Among the morphological traits examined, only melanin-based black coloration was found to correlate with contest outcome. The effect of black coloration was similar in magnitude to the positive effect we found for prior contest history (a proxy for experience), but smaller than the effect of behavioral displays (Fig. 3). A similar prevalence of behavior over color patches was found when examining the factors influencing winner aggression (Fig. 2).

Black coloration has been found to correlate with RHP in a previous study on *P. muralis* from Eastern Pyrenees (Abalos et al. 2016), and in studies of two different *P. muralis* lineages from the Italian peninsula (While et al. 2015; MacGregor et al. 2017). However, covariation between melanin-based coloration and RHP is not restricted to wall lizards. Many studies in vertebrates and invertebrates show a positive association between melanin-based coloration and baseline aggressiveness or other behaviors that provide a high RHP and social dominance (Ducrest et al. 2008; Roulin 2016; Carranza et al. 2020). Shared genetic architecture and developmental pathways may explain why covariations between darker coloration and RHP-related traits have evolved so often, especially in vertebrates (Morgan et al. 2004; Ducrest et al. 2008; San-Jose and Roulin 2018; de la Peña et al. 2020a; 2020b; San-Jose and Roulin 2020). Some melanin-based patches have been hypothesized to function as conventional quality signals subject to socially-enforced costs (i.e. badges of status), or unfakeable indices of quality (Rohwer 1975; Tibbetts and Dale 2004; Chaine et al. 2011; de la Peña et al. 2021). However, the signaling role of melanin-based coloration is debated and empirical evidence is inconclusive (Nakagawa et al. 2007; Roulin 2016; Sánchez-Tójar et al. 2018). Despite their frequent association with RHP, black melanin-based patches may not be assessed during fights, in which case they should be best regarded as by-products or pleiotropic consequences of selection on other traits rather than agonistic signals (Kemp and Grether 2015; San-Jose and Roulin 2018).

In contrast to black, we did not find evidence for an effect of UV-blue patches on contest outcome, and several empirical studies aimed at examining the signaling role of UV-blue patches during contests have likewise produced inconclusive results (Martin, Meylan, Perret, et al. 2015; Abalos et al. 2016; Names et al. 2019). Bohórquez-Alonso et al. (2018) failed to replicate earlier findings by Huyghe et al. (2005) in the Tenerife lizard (*Gallotia galloti*) suggesting that winner males tended to show larger UV-blue lateral patches, and instead found that reducing patch reflectance in the UV range significantly increased fighting success. In *P. muralis,* reducing UV reflectance was apparently irrelevant to fighting success, and Martin et al. (2015c) concluded that the function of UV-blue patches may be related to spatial dominance. These negative results may seem surprising, since there are compelling reasons to believe that lacertid UV-blue patches play a role in male-male competition. First, UV-blue patches are often sexually-dimorphic, being larger, more numerous, and conspicuous in males than females (Pérez i de Lanuza and Font 2015; de la Cruz et al. 2023). Second, unlike melanin-based coloration (which occurs all over the body) UV-blue patches are restricted to the OVS and some of the surrounding scales, allowing males to control their visibility through postural changes (Pérez i de Lanuza et al. 2016b). In fact, any potential impact of UV-blue patches on contest outcome may be nested within the effect of raised-body displays, as they may only be visible to conspecifics during such displays. Third, their spectral properties are tuned to the visual system of conspecifics (Marshall and Stevens 2014; Pérez i de Lanuza and Font 2014b). Fourth, lower UV chroma and UV-biased hues have been found to correlate with better body condition and stronger bite force, respectively (Pérez i de Lanuza et al. 2014; Badiane and Font 2021). Encounters within our enclosures occurred in a much more natural context that in previous studies, allowing us to refute the often-raised concern that negative results could be due to the artificiality of the short-range encounters enforced in the lab. However, there are several potential explanations for why the UV-blue patches emerge as poor predictors of contest outcome in our analyses. First, the UV-blue patches could convey categorical information on the bearer’s sexual maturity and play a role on sexual maturity and play a role influencing the receiver decision to confront a potential competitor, but fail to predict outcome if a contest takes place (Arnott and Elwood 2008; Elwood and Arnott 2012; Abalos et al. 2016; Pinto et al. 2019). Another possibility is that our analysis of the OVS pattern as separate blue and black color patches neglects important aspects of the integration between these adjoining color patches. For instance, brokenness and light-and-dark spacing have sometimes been found to be aspects of color signals relevant to receivers (Bulatov et al. 1997; Tibbetts and Sheehan 2011; Feng et al. 2017). Finally, an important shortcoming of this and other recent studies is that quantification of the UV-blue color surface is based on the analysis of images tuned to human color vision. Applying recently developed methods based on UV photography to study *P. muralis* color patches according to lacertid acuity and color vision will improve our understanding on their function and design (Stevens et al. 2007; Font et al. 2009; Troscianko and Stevens 2015).

Behavioral displays were found to influence contest outcome and intensity in a way that suggests their role as motivation signals. Raised-body displays increased the odds of prevailing in male-male encounters and were also associated with biting and chasing the opponent. Stationary postural displays such as the cheliped presentation in crustaceans or the broadside displays observed in many taxa have generally been interpreted as index signals revealing the sender's morphological correlates of intrinsic quality (weaponry/body size), with their potential additional role as motivation signals having been often overlooked (Elwood et al. 2006; Font and Carazo 2010; Briffa 2015). Lacertid raised-body displays are similar to these stationary postural displays in that they reveal the sender's body size while rendering the OVS pattern visible. In addition, lateral compression of the thorax may interfere with respiration and thus convey condition-dependent information on stamina (Brandt 2003; Bradbury and Vehrencamp 2011). However, raised-body displays include a pointing component (males look straight to their opponent while approaching using a characteristic lateral walk) and are associated to increased odds of physical attack (Noble and Bradley 1933; Kitzler 1941; Molina-Borja et al. 1998). Thus, we deem reasonable to suggest their dual role as offensive threat and intrinsic quality signals (Andersson 1980; Adams and Mesterton-Gibbons 1995; Hurd and Enquist 2001; Számadó 2003; Számadó 2008; Bradbury and Vehrencamp 2011; van Staaden et al. 2011). While the costs of producing the OVS color pattern (i.e. the morphological signal component) are paid during development, honesty for the behavioral signal component is enforced during interactions. Animal communication theory is abandoning the idea that only costly signals can be honest (i.e. handicaps; Zahavi and Zahavi 1999), for a framework in which honesty is enforced by signaling trade-offs (Számadó 2011; Penn and Számadó 2020; Számadó et al. 2022). In agreement with Számadó (2003), lacertid raised-body displays are not handicaps making the sender especially vulnerable to attack, but pre-attack postures by which males often point their gaped mouth towards the opponent. However, winners tended to bite more often opponents that performed a raised-body display (Fig. 3), suggesting that the honesty of lacertid raised-body displays may result from a signaling trade-off between the benefits gained from adopting a pre-attack posture, the inherent proximity risks of being close to the rival (which are a necessity for credible threat signals), and the socially-enforced costs of bluffing (Számadó 2008; van Staaden et al. 2011).

Foot shakes were strongly associated with losing contests and had a tempering effect on winner aggression, which confirms their role as appeasement displays. Notably, foot shakes have also been found to act as de-escalation signals in other lizards (Carpenter et al. 1970; Martins and Lacy 2004; Van Dyk and Evans 2008; Woo and Rieucau 2012). De-escalation signals are expected to take a form that is antithetical to the threat signal of the species (e.g. defeated chameleons darken their body, in contrast with the bright colors exhibited by winners; Ligon and McGraw 2013, 2016; Ligon 2014). In *P. muralis*, Type II foot shakes are often produced while pressing the belly against the substrate (thus making the adoption of the raised-body display posture impossible), however this is not always the case (Fig. 1) and other components of display behavior can be simultaneously produced (e.g. gular extension). Limited gestures of submission may not satisfy an aggressor, so de-escalation signals are generally not graded (Reddon et al. 2021). Here we recorded Type II foot shakes as a binary variable per individual and contest, though the number, duration, and amplitude of Type II foot shakes may vary among bouts, suggesting they could function as graded signals. Future research on lacertid de-escalation should detail how signal forms vary with context and evaluate whether differences among foot-shake bouts ensure signal perception amidst environmental noise and/or reflect varying levels of submission (Stevens 2013; Fleishman and Font 2019).

Prior contest history (a proxy for experience) was also found to affect contest outcome, with lizards that won their last fight being more likely to come out as winners in subsequent confrontations. Winner-loser effects, by which individuals gather information on their relative RHP through the experience of fighting, are a cognitively undemanding rule-of-thumb that many animals use to adjust their effort in costly contests (Chase 1986; Chase et al. 1994; Hsu and Wolf 1999; Dugatkin and Earley 2004; Reichert and Quinn 2017). The experience effect detected may be also due to social recognition and the establishment of dominance relationships. Many territorial lizards show a “dear enemy” effect by which competing neighbors (after some initial confrontations to establish territories) direct low-intensity aggressive behavior toward familiar males, but fiercely attack unfamiliar males (Qualls and Jaeger 1991; Olsson 1994; Whiting 1999; López and Martín 2002; Husak and Fox 2003). Moreover, research on wall lizards has shown that males are able to discriminate even between familiar individuals based solely on their scent marks, remembering the spatial location of scent marks and behaving more aggressively toward males that consistently marked in the middle, rather than along the periphery, of their experimental terrarium (Carazo et al. 2008; Font, Barbosa, et al. 2012). Disentangling these different processes falls beyond the scope of this study and should be tackled in future experiments altering rival distinctiveness and threat level.

Predictors of contest intensity and models of assessment

Contest intensity increased with both opponents' RHP and in contests involving lizards from HQ sites, while morphology was a weaker predictor of the number of interactions and aggression levels (Fig. 4). Black coloration stands out as the only morphological trait showing a strong and nearly significant relationship with contest duration in both randomly-paired and matched contests. However, no significant relationship exists between contest escalation and rival asymmetry in black coloration. These results follow the pattern expected for non-signaling traits under SA, suggesting that —despite their association with RHP— black patches do not play a communicative role in rival assessment. In contrast, model coefficients for SVL, HL res, and blue area (though generally non-significant) follow the pattern expected for intrinsic quality signals involved in MA: positive for low-value and loser males, negative for high-value and winner males, no relationship with contest duration in matched pairs, and a negative relationship between winner-loser asymmetry and contest escalation (Taylor and Elwood 2003; Elwood and Arnott 2012; Pinto et al. 2019). Overall, these results are compatible with the existence of a plastic strategy in *P. muralis* by which males rely mainly on resource value and SA to decide when to withdraw from a fight, but occasionally incorporate information about the opponent's intrinsic quality (through MA of HL res, SVL, or blue area) (Arnott and Elwood 2009; Elwood and Arnott 2012; Chapin et al. 2019). This is in agreement with growing theoretical and empirical evidence suggesting that assessment mode is not fixed at the species or individual level (Mesterton-Gibbons and Heap 2014; Reichert 2019). For instance, opponents are expected to shift from MA strategies to SA with increasing costs of escalation (Hsu et al. 2008), resource value (Chapin and Hill-Lindsay 2016), and decreasing cost-effectiveness of mutual assessment (Prenter et al. 2006; Mesterton-Gibbons and Heap 2014). Our finding of a higher prevalence of physical fights in HQ-LQ pairs shows that *P. muralis* males can escalate conflicts in response to changes in subjective resource value, which is in agreement with previous lab-staged studies (Sacchi et al. 2009; Sacchi et al. 2021). Elsewhere we showed that the outcome of confrontations over access to HQ sites was the main factor driving male fitness in our experiment (Abalos et al. 2020). Evidence from field studies also attests to the high resource value of territories in lacertid lizards, where the outcome of agonistic confrontations often tracks patterns of shared paternity (Edsman 1990; Uller and Olsson 2008; Font, Barbosa, et al. 2012; Olsson et al. 2019). A heavier reliance of *P. muralis* on self and contested-resource information is thus consistent with theoretical predictions.

Empirical support for SA in species showing a broad repertoire of agonistic signals may seem paradoxical. However, signaling can coexist with SA (despite the nomenclature suggesting otherwise) if agonistic signals involve mutual evaluations of RHP components other than intrinsic quality (Pinto et al. 2019). Intrinsic quality signals may be assessed mainly prior to interacting (Morrell et al. 2005), with contests then proceeding based on SA (Mesterton-Gibbons and Heap 2014) where individuals use other agonistic signals in their repertoire to assess each other and ensure their energetic investments matches their rival's (Briffa 2015). Our analyses considering all pairs of potential rivals suggest no effect of morphological traits on pre-contest MA, likely because of the obscuring effect of other contingent factors (e.g. motivation, experience, social recognition). However, we found evidence that visual displays (likely conveying information on motivation) are better predictors of contest outcome and overall aggression levels than morphological traits, including color patches putatively related with developmentally-fixed aspects of RHP. This lends support to the ideas put forward by Pinto et al. (2019) and is in agreement with previous findings in the lacertid lizard *Gallotia galloti* (Bohórquez-Alonso et al. 2018), where behavioral traits also outperformed morphological traits in predicting contest outcome. To further establish the association of behavioral displays with motivation, future studies should measure the correlation between signaling intensity and latency to resume contest behavior after an experimentally-induced startle (Elwood et al. 2006; Briffa 2013).

Interestingly, the conditions favoring the adoption of SA partly match those favoring the evolution of motivation signals (Adams and Mesterton-Gibbons 1995; Számadó 2003; Számadó 2008; Mesterton-Gibbons and Heap 2014; Reddon et al. 2021). Stable submission-signaling systems are expected to evolve i) when the value of the contested resource is not too high relative to the cost of injury, ii) when winners do not gain additional benefits from winning escalated conflicts instead of abbreviated, iii) when ecological or morphological constraints limit the loser's ability to safely retreat, and iv) when the ability of rivals to assess the opponent's intrinsic quality is accurate, but not perfect (Matsumura and Hayden 2006). These conditions apply to territorial species in which fights can get physical (i) and males meet regularly at territory boundaries (Temeles 1994; Tumulty 2018; Pinto et al. 2019). Males that are unable to usurp its neighbors' territory will not gain additional benefits from winning escalated conflicts (ii). Likewise, their ability to safely retreat is constrained by the costs of abandoning their own territory (iii) (Waltz 1982). Past experiences (e.g. winner effect) or social recognition may significantly affect an individual's performance in agonistic contests without being reflected in intrinsic quality signals, thus limiting the ability of rivals to accurately assess each other (iv) (Stuart-Fox and Johnston 2005; Stuart-Fox et al. 2006; Briffa 2015; Irschick et al. 2015; Kar et al. 2016). As territory-owners alternate between resident and intruder roles, motivational signals conveying contextual changes in subjective resource value become more informative to receivers than intrinsic quality signals. In turn, the existence of an evolutionary trade-off favoring SA and motivation signals over MA in territorial species may prevent the stabilization of candidate traits as intrinsic quality signals —or lead to a loss of function in established signals— (Sheehan and Bergman 2016), a possibility that could underlie our results on color patches. Altogether, these different lines of evidence suggest the positive payoff of limited war strategies such as dear enemy effects or individual recognition in territorial species, with de-escalation signals offering a mechanism to limit aggression compatible with SA (Pinto et al. 2019).

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Data Availability Statement

Analyses reported in this article can be reproduced using the data provided by Abalos (2024).

Conflicts of Interest

The authors declare no conflicts of interest.

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1065 Tables

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Table 1. Partial ethogram of *P. muralis* including social behaviors used to collect data on interactions during behavioral observations within the experimental enclosures.

Behavior	Description
Approach*	Movement toward a non-fleeing conspecific
Raised-body display	Gular extension, back-arching, shoulders raised, head down, sagittal compression (any combination)
Bite	One or more bites to another individual (excluding tail grab)
Retreat*	Movement away from a non-chasing conspecific
Chase	Rapidly following another FLEEING lizard
Flight	Fast-paced movement to withdraw from a CHASING lizard
Type II foot shakes	Rapid large amplitude vertical movements of forelimbs (belly down, head up posture), often accompanied by TAIL WAVE/SHAKE
Tail grab	A male bites the tail or inguinal region of a female. Often followed by copulation
Tail wave/shake	Vibrating entire tail (or its distal portion) swiftly from side to side
Mating	Two lizards engage in copulation
Co-perching	Two or more lizards lying together in close vicinity (<15 cm; >30 s)

* We classified the mode of locomotion used as either running (fast-paced) or any other mode of locomotion (slow-paced).

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Table 2. Results from Bradley–Terry (B-T) model examining the effects of morphometry, color patches, behavioral displays, prior contest history and residency on the log odds of winning a contest. M1 was fitted on the full dataset of contests (i.e. including all contestants' first fights). M2 excluded every contestant first contest so that every male had prior experience. M3 included only contests where both rivals had no prior experience. Significant predictors are highlighted in bold ($\alpha = 0.95$, $P < 0.05$). Statistics for non-significant factors are included at the point of their deletion from the model.

Model	Predicted	Variable	β	SEM	*df*	*Z*	*P*
M1 544 fights	77.6%	SVL	0.00	0.55	1	0.00	0.999
		HL res	-0.26	0.39	1	-0.67	0.504
		Blue area	0.38	0.38	1	0.99	0.324
		UV-blue Luminance	-0.42	0.37	1	-1.14	0.255
		UV-blue Hue	0.52	0.50	1	1.05	0.294
		UV-blue CUV	-0.04	0.44	1	-0.09	0.926
		Black area	0.94	0.35	1	2.69	0.007
		Raised-body display	1.75	0.30	1	5.77	<0.001
		Foot shake	-2.54	0.88	1	-2.87	0.004
		Bite	0.42	0.45	1	0.92	0.357
		Prior contest history	0.53	0.28	1	1.93	0.053
		Resident	0.45	0.34	1	1.35	0.179
		ID (Std. dev)	2.34	[0.61; 4.07]	66	7.54	<0.001
M2 478 fights	85.7%	SVL	0.20	0.57	1	0.35	0.727
		HL res	-0.53	0.35	1	-1.52	0.129
		Blue area	0.42	0.45	1	0.94	0.350
		UV-blue Luminance	-0.72	0.42	1	-1.73	0.083
		UV-blue Hue	-0.07	0.60	1	-0.12	0.908
		UV-blue CUV	-0.21	0.38	1	-0.60	0.552
		Black area	0.84	0.35	1	2.38	0.018
		Raised-body display	1.99	0.34	1	5.78	<0.001
		Foot shake	-2.83	1.07	1	-2.64	0.008
		Bite	0.58	0.56	1	1.04	0.297
		Prior contest history	1.00	0.32	1	3.13	0.002
		Resident	0.56	0.39	1	1.45	0.147
		ID (Std. dev)	2.11	[1.49; 2.73]	66	6.75	<0.001
M3 66 fights	65.2%	SVL	0.36	0.56	1	0.64	0.519
		HL res	0.81	0.34	1	2.39	0.017
		Blue area	-0.17	0.29	1	-0.61	0.545
		UV-blue Luminance	-0.05	0.35	1	-0.16	0.875
		UV-blue Hue	-0.51	0.32	1	-1.56	0.116
		UV-blue CUV	-0.35	0.33	1	-1.05	0.295
		Black area	0.89	0.36	1	2.44	0.015
		Raised-body display	3.48	0.89	1	3.88	<0.001
		Foot shake	0.49	1.29	1	0.38	0.707
		Bite	0.26	0.00	1	0.00	0.999
		Null deviance	91.49	-	66	-	-
		Residual deviance	49.15	-	63	-	-

Figure legends

Figure 1. Agonistic visual signals in *Podarcis muralis.* A & B) Representative frames of a social interactions involving a male approaching a co-perching pair, extracted from the video sequence V1 available in the Supporting information of Abalos et al. (2020). A) The approaching male (blue) performs a raised-body display and the female (orange) responds by performing Type II foot shakes and tail waves. B) After the female moves, the approaching male is faced with the resident male and performs Type II foot shakes before fleeing. Numbers shown in each frame are milliseconds from the beginning of the foot shake bout. C) Pair of photographs of the same male *P. muralis* individual showing both UV-blue and black patches in its outer ventral scales (OVS). Pictures were obtained with a full-spectrum camera and two filters, each transmitting either in the visible (400-700 nm) or the near-UV range (320-380 nm). Brighter areas in the UV image have higher UV reflectance (i.e. UV-blue patches). D) Photographs of two immobilized male *P. muralis* showing variation in the OVS coloration pattern.

Figure 2. Behavioral correlations and predictors of winner aggression A) Pearson correlation matrix among binary behavioral variables at the individual level across all contests (N = 1088). B) Pearson correlation matrix among winner and loser behavior across all contests. Color gradient reflects positive (green) or negative (orange) relationships. Significance level is indicated with asterisks (· <0.1; * < 0.05; ** < 0.01; *** < 0.001). C) Forest plot showing the estimated effect size and sign (odd ratios ± CI_{95}, obtained from the logit-scale coefficients) for the predictors of winner aggression included in the logistic model. Winner raised-body displays increase the odds of winner bites by a factor of 3.4 while loser foot shakes decrease the odds by a factor of 3.2. D) Forest plot showing the odd ratios for predictors of winner chases in the logistic model. Loser foot-shake decrease the odds of winner chase by a factor of 2.8. Winner bite increases the baseline odds by a factor of 7.26 and the odds are multiplied by a factor of 1.87 for each 1 SD increase in winner black area.

Figure 3. Predictors of contest outcome and male socio-spatial dominance. A) Forest plot comparing the estimated effect size and sign (probabilities ± CI_{95} obtained from the logit-scale coefficients) for each of the significant predictors in the B-T model M2 (Table 2). B) Relationship between relative fighting ability ± CI_{95}, probability of winning, and proportion of black coloration (in z-scores) according to the B-T model M2. Model coefficients in BT models correspond to the logarithm of odd ratios, from which fighting ability and probability of winning can be calculated. Fighting ability is expressed in odd ratios, so that the odds of male A beating male

B is ability A/ability B. The horizontal dotted line represents ability = 1 and probability = 0.5, even odds. A male 2 SD above the mean for black coloration will have exp(2*0.84) = 5.37 odds (i.e. probability = 0.84) of defeating a rival whose black coloration is at the mean. C) Effect plot showing the positive relationship between RHP (i.e. obtained by fitting a BT model on the matrix of contests without specifying predictors) and the proportion of black area in the OVS. D) Effect plot of the logistic model showing the positive relationship between the probability of occupying a HQ site and RHP. Blue lines and shaded areas represent partial regression and CI_{95}. Lines in magenta are a loess nonparametric-regression smooth of the partial residuals (magenta circles).

Figure 4. Predictors of contest intensity. A) Forest plot showing multiplicative effects (exponentiated model β ± CI_{95}) for individual predictors on the number of interactions between pairs of potential rivals (i.e. contest duration). Blue and purple asterisks indicate significant coefficients for the different opponents. The inset at the lower left corner shows a schematic diagram of the theoretical predictions for the sign of the relationship between opponent traits and contest duration according to pure self-assessment (SA), cumulative assessment (CAM) or mutual-assessment (MA). B) Forest plot showing multiplicative effects for mean individual predictors on the duration of contests between matched rivals (i.e. excluding pair combinations showing a differences larger than 1 SD for the focal predictor). Any CI_{95} within the orange shaded area support SA. Black asterisks indicate significant coefficients. C) Density plots (shaded area) and mean ± CI_{95} (vertical solid and dotted lines) for the effect of site quality combination on the number of interactions. Red letters summarize clustering according to Tukey contrasts. Ratios ± CI_{95} from Tukey contrasts (red dots and lines) are shown in the upper right corner. Red asterisks indicate significant contrasts. D) Forest plot showing multiplicative effects ± CI_{95} for individual predictors on contest escalation. E) Forest plot showing multiplicative effects for winner-loser differences in individual predictors on contest escalation. Any CI_{95} within the orange green area support MA against SA and CAM. F) Density plots and mean ± CI_{95} for the effect of site quality combination on contest score. Red letters summarize clustering according to Tukey contrasts. Ratios ± CI_{95} from Tukey contrasts (red dots and lines) are shown in the upper right corner. Red asterisks indicate significant contrasts.