

Male color armaments in lizards and a role for parasites in intrasexual selection

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Abstract

Sexual armaments are usually structures or other traits used during agonistic displays that evolve by intrasexual competition. The role of parasites in their evolution remains obscure. We investigated the relation of infection by three parasites with the agonistic behavior of males *Sceloporus occidentalis* in male contests staged in the lab. The rivals' both behavior and blue patch chroma best predicted the aggression intensity of focal males. Infections by haemococcidians and ticks also contributed to explain the intensity of aggression in focal males. Lizards with fewer ticks engaged in more intense fights, while lizards with more ticks or haemococcidians were less aggressive. Interestingly, males with lower blue chroma were infected by intestinal coccidians and received more aggression. This study reveals direct roles for ticks and haemococcidians in male competition, and an indirect role of intestinal coccidians mediating sexual selection of a color armament in lizards.

(a) Introduction

Sexual armaments are usually structures or color patches displayed during male contests that are either used as weapons (Okada et al. 2006), and/or to signal the hierarchical status or fighting ability (Stapley & Whiting 2006). The latter reduces conflicts with subordinate, less competent males, who avoid the costs associated with fights, but may also increase conflicts with males of similar status (Olsson 1994; Abalos et al. 2016). In either case, these structures afford superior males more frequent access to reproduction (Baird et al. 2013; Morina et al. 2018). Thus, sexual armaments are expected to primarily evolve due to intrasexual selection through male competition, and secondarily due to intersexual selection by female choice preferences (Berglund et al. 1996). This is because these armaments often have a dual role acting simultaneously as sexual ornaments that attract the attention of potential mates (Berglund et al. 1996), although if they evolved first as ornaments or armaments is not always evident (e.g. Morris et al. 2007).

The good-genes hypothesis argues that a females' preference for mating with high quality males exhibits positive selection because it increases the frequency of adaptive genes in the population (Arnold 1993). According to good-genes theory sexual ornaments evolve under intersexual selection for parasite resistance (Hamilton & Zuk 1982). Parasites draw resources from their hosts and undermine their energy budget, which alters the resource allocation to reproduction (Sorci et al. 1996; Webb & Hurd 1999). This may also affect allocation of pigments to sexual coloration, which usually have anti-oxidant activity, and are thus reallocated to the immune system to fight the infection (Hörak et al. 2006; Megía-Palma et al. 2018a). This produces a phenotypic correlation between the severity of the immune insult and the expression of the color ornament

which is interpreted as an honest signal of parasite infection or resistance (Bortolotti et al. 2009; Megía-Palma et al. 2018b). In this context, it is expected that females will evolve a preference towards mating with more colorful males, which would favor the transmission of adaptive genes for parasite resistance (Hamilton & Zuk 1982). Thus, the role of parasites in the evolution of ornaments is clear and multiple studies support it in different taxonomic groups (Houde & Torio 1992; Worden et al. 2000; Del Cerro et al. 2010; but also see Balenger & Zuk 2014). However, the role of parasites in the evolution of secondary sexual characters with dual function is poorly understood.

Male Western fence lizards, *Sceloporus occidentalis* (Squamata: Phrynosomatidae), have complex display behaviors that include the exhibition of their blue and yellow patches. The blue coloration in sceloporine lizards is based on light scattered in micro-structures and underlying (eu-) melanin in the dermis (Quinn & Hews 2003). Blue patches are ventral and are displayed when lizards compress their thorax laterally. Yellow patches are located in the forelimbs in *S. occidentalis* and may be more conspicuously displayed when the lizards perform push-ups. The yellow coloration in this group of lizards is pigment-based (Weiss 2006). Both are displayed during agonistic interactions with other males, and also to court females, which suggests a dual role for these color patches (Carpenter & Ferguson 1977). The behavioral displays of the males are ritualized because their alternative display may depend on the level of escalation in the social conflict or the distance between conspecifics (Sheldahl & Martins 2000). Males displaying these behavioral traits with higher intensity may get more access to females and, hence, more opportunities for reproduction (Schall & Dearing 1987; Schall & Houle 1992). Therefore, any conditions that reduce the intensity of these color displays may result in decreased fitness. Previous studies have shown multiple parasites infecting lizards in a coastal population of California and males infected by intestinal coccidians had blue ventral patches with less spectral chroma (Megía-Palma et al. 2018b). This suggests that the infection limits expression of the male ventral blue patches, which may affect social interactions (Megía-Palma et al. 2018b). We hypothesize that parasites affect male agonistic interactions in this species. To study the potential influence of parasites on male interactions we staged pairwise male contests in the laboratory and recorded their behavioral traits. We predict that infected lizards will perform poorly compared to healthy lizards and that blue patches, used as armaments, will be important predictors that explain the intensity of aggression by rival lizards (Morris et al. 1995). If these predictions are confirmed, our study will demonstrate an influence of parasites on male agonistic interactions and, therefore, define a role for parasites that influence intrasexual selection in *S. occidentalis*.

(b) Material and methods

Sampling and housing

The males of *S. occidentalis* used in this study ($N = 42$) are the same as those used in Megía-Palma et al (2018b, 2020). The housing conditions have also been described elsewhere (Megía-Palma et al. 2020). A residual body condition index was calculated as the residuals of the regression between the log-transformed values of body mass and snout-vent length of the lizards (Dunlap & Mathies 1993). A sample of blood ($< 10 \mu\text{L}$) and fecal pellets from the lizards were taken to diagnose infections by both hematic and intestinal coccidians (see Megía-Palma et al. 2018b). The number of ticks and the presence of mites were recorded. We measured the spectral reflectance of the yellow and blue color patches, the throat, and the back with an Ocean Optics 2000 spectrophotometer (for details see Megía-Palma et al. 2018b). In addition, total surface of the blue patches was calculated by multiplying its length by its width. Both were measured with a ruler to the nearest mm. The area of the blue patch was correlated with the SVL of the individual ($F_{1, 40} = 7.19$, $P = 0.010$). We calculated the residuals of blue patch area on SVL to remove this effect. Thus, higher values of (residual) blue patch area indicated lizards with proportionally larger blue patches. The lizards were released at the end of the trials to their original site.

Neutral arena setup

Males were allowed to acclimate in captivity for 7 days prior to staging the pairwise contests (Bohórquez-Alonso et al. 2018). The contests were staged in a neutral arena to remove the effect of residency (Sacchi

et al. 2009; Abalos et al. 2016), and in a small confined room, free of noises and other distractions. The 42 males were paired by similarity in body mass (mean mass difference = 0.64 g) and never exceeding an SVL difference of 2 mm between them (mean SVL difference = 0.72 mm) (Bastiaans et al. 2013). This removes the size effect, which is not an objective of the present study, but is an important predictor of dominance in lizards (e.g. Sacchi et al. 2009). Contestant males were transferred into an artificial arena that was 60 cm width x 80 cm length x 48 cm height which was set up with sandy substrate covering the bottom. The arena was made up of acrylic sheets and covered on three sides while the fourth side was left uncovered for behavioral recording using a digital video camera. A 75W thermal lamp was set up directly above a central rock. The arena was divided into two parts at the beginning of each trial using a removable partition of opaque plastic. The trials took place on 5 consecutive days between the 30th of May and 3rd of June 2014 from 8:00 am to 6:00 pm. Each lizard was placed at opposite ends of the partition and allowed 5 minutes to acclimate to their space. After this acclimation period the partition between the two sides of arena was removed and the behavior of the lizards was filmed for 20 minutes without any human presence in the room. Before each subsequent trial, sand substrate was changed to avoid the effects of any olfactory cues from previous trial (Bastiaans et al. 2013). We visualized the videos and noted every behavior shown by contesting lizards.

Analysis of behavioral traits

(i) Analysis of push-up and lateral compression behaviors

Since yellow and blue patches are displayed during push-up and lateral compression events, we focused on these two behavioral traits. We recorded 1) the frequency of push-ups (number of push-ups per push-up event and duration in seconds), 2) the distance between opponents when push-ups and lateral compressions occurred. To do this, we used snapshots of the trials to measure the distance between contestants at each of these specific events with the MB-Ruler 5.0 free software (<http://www.markus-bader.de/MB-Ruler/>), and 3) scored whether the immediate response of the opponent to a push-up or a lateral compression event was neutral, submissive or aggressive (Table 1).

(ii) Factor analysis of behavioral traits

We applied factor analysis to reduce the number of behavioral traits recorded and identify factors that may represent correlated behavioral traits (Budaev 2010). We used principal axis factoring and a criterion of minimum eigenvalue > 1 to extract the factors (Fabrigar et al. 1999; Budaev 2010). Factor scores were based on correlations after Varimax (= orthogonal) rotation of the factors. This method allows extraction of orthogonal factors, and more stable and replicable results in case of small sample size (Budaev 2010). Behavioral traits were considered to contribute significantly to the factors when factor loadings were > 0.80 (Table 2), which is above the recommended threshold of 0.5 or 0.7 for behavioral analyses (Budaev et al. 2010).

Statistical analyses

We tested differences in the duration, frequency of push-ups and lateral compressions, as well as the distance between the lizards when these behavioral traits were displayed using non-parametric Mann-Whitney *U* -test for independent groups. The difference in frequency of aggressive *versus* submissive behaviors after each of these focal events was tested with a χ^2 . In addition, to analyze whether self's ("SELF") *versus* rival's ("RIVAL") traits were more informative to explain the behavioral traits summarized with the factor analysis, we used a corrected information criterion (AICc) to compare two general mixed models fitted to a Gaussian distribution, where the trial number was included as random factor. Lower AICc is indicative of a more informative model (Kletting et al. 2009).

The 'SELF' model included SVL, body condition, spectral chroma and area of blue patch –residual value on SVL–, spectral chroma of yellow patch in the forelimbs, spectral luminance of the back, spectral hue of the throat, ectoparasites (presence of mites and number of ticks), and presence of both hematic and intestinal coccidians of focal individuals.

The ‘RIVAL’ model was built with predictors including the behavioral traits displayed by the rival lizard (factors 1 to 5), and also the spectral chroma of the rival’s yellow patch, which correlates with the body length and condition of the males (i.e. Megía-Palma et al. 2018b). We also included the rival’s spectral luminance and chroma of the blue patch because the first correlates with body length and the second is lower in the males infected by intestinal coccidians (Megía-Palma et al. 2018b). These two spectral variables of the blue patch show low auto-correlation ($r^2 = 0.02$, $P = 0.31$). Both models were controlled by the time of the day when the staged contest took place.

We based our analyses on information theory to select the best set of likely models, which is a recommended practice in behavioral ecology (Hegyi & Garamszegi 2011; Symonds & Moussalli 2011). The multimodel inference approach uses a corrected criterion for small sample sizes (i.e. AICc) to estimate the relative importance of each predictor (Bedrick & Tsai 1994). We considered sufficiently informative all the models with $\Delta AICc$ [?] 4 in relation to the best model (the one with the lowest AICc). Model selection was performed using the R-package MuMIn (Burnham & Anderson 2004; Barton 2018). We summed the AICc weights of all the models where the predictor appeared (i.e. conditional average) to calculate the relative importance of each predictor. We calculated the significance of each effect based on the z-standardized β coefficient and standard error. All the analyses were performed in R version 3.4.3 (R Core Team 2017).

(c) Results

Parasitic infections of the lizards tested

There was a 52% prevalence of Western black-legged ticks, *Ixodes pacificus*, in the sample of lizards that were tested in staged pairwise contests with mean \pm SE infestation of 1.90 ± 0.34 ticks per lizard (range = 0-7). Mites infested 35.7% of the lizards. The putative species of mite was *Geckobiella* cf. *texana*. The genera of hematic and intestinal coccidians that infect the lizards were molecularly identified in previous studies (genera *Lankesterella* and *Acroeimeria*, respectively; Megía-Palma et al. 2015, 2017). The prevalence of *Lankesterella* was 42.8% and *Acroeimeria* was 38%.

Behavioral traits

Analysis of push-up and lateral compression behaviors

Push-ups were registered in 42.8% (9/21) of the tournaments. We registered 416 push-ups in 39 independent push-up events with a mean \pm SE 10.67 ± 0.72 push-ups per event (range = 1-23). These were performed by the lizards at a mean distance \pm SE of 26.82 ± 4.58 mm between opponents. In push-up events, 33.3% (13/39) were followed by an aggressive response of the opponent male (see a list of behaviors and their classification in Table 1).

Lateral compressions were registered in 23.8% (5/21) of the trials. We registered 88 events of lateral compression with a mean \pm SE duration of 22.12 ± 7.18 seconds. The mean distance \pm SE between opponents was 10.61 ± 3 mm. These took place during aggressive interactions because 76.1% (67/88) of the lateral compressions were followed by an aggressive response from the opponent.

Factor analysis of behavioral traits

We registered 1217 behavioral events. A comprehensive check list of 20 behavioral traits displayed by the lizards during the male tournaments is presented in Table 1.

Statistical analyses revealed that the frequency of these two behaviors in the dyadic trials (i.e. 42.8% vs. 23.8%) in the lab did not significantly differ ($\chi^2 = 1.71$, $P = 0.19$). However, there were significant differences in the distance between opponents ($U = 762$, $P < 0.0001$ – lateral compressions were displayed at closer distance, see above), and in the likelihood of subsequently eliciting an aggressive response from the opponent ($\chi^2 = 21.24$, $P < 0.0001$). Lizards were significantly more likely to receive an aggressive response after performing a lateral compression than after push-ups. In contrast, there was no significant difference in their duration ($U = 471.5$, $P = 0.70$).

The factor analysis performed on the 20 behavioral traits extracted five factors that together explained 62.78% of the variance (Table 2). Factor 1 explained 22.05% of the variance in behavioral traits (eigenvalue = 4.41) and the factor loadings indicated that push-ups, lateral compression, and lunge behaviors were the most important behavioral traits in this factor. Factor 2 explained 18.34% of the variance (eigenvalue = 3.67) and climbing on top of the rock was the most important behavioral traits in this factor. However, tongue flicks (0.77) and rubbing the base of the tail onto the substrate (0.65) also had high correlation coefficients (Table 2). Factor 3 explained 8.68% (eigenvalue = 1.73) with side hop and retreat representing the most important behavioral traits in this factor. Factor 4 explained 7.58% (eigenvalue = 1.51) where tail waving was the most important behavioral traits in this factor. Finally, factor 5 explained 6.11% (eigenvalue = 1.22) where exploring the arena and trying to climb the walls was the most important behavioral trait.

The comparison of the SELF and the RIVAL models explaining Factor 1 suggested that the RIVAL model was more informative (AICc = -22.84) than the SELF model (AICc = 47.12). Opponent's factors 1 (importance = 0.92, β = 0.14, z = 4.79, P < 0.001), 3 (importance = 1.00, β = 0.22, z = 8.26, P < 0.001), and 4 (importance = 0.98, β = 0.07, z = 3.34, P < 0.001) had positive effects on Factor 1 of the focal male (Table 3 and Fig. 1). Thus, the rivals' behaviors summarized in Factors 1, 3, and 4 increased the intensity of the aggressive behavior of the focal males, although the behavioral traits summarized in Factor 4 may contribute very little to explain the variance in Factor 1 of focal lizards (Fig. 1d). Meanwhile rivals' Factor 2 (importance = 0.79, β = -0.05, z = 2.33, P = 0.020) and the chroma of their blue patches (importance = 0.82, β = -0.76, z = 2.08, P = 0.037) were negatively related to Factor 1 (Table 3 and Fig. 2). Thus, rivals' behaviors summarized in Factor 2 and the chroma of their blue patch reduced the aggression intensity of focal males, although these behavioral traits may contribute very little to explain Factor 1 of focal males.

Interestingly, the SELF model suggested that there was a significant effect of haemococcidians and tick load on Factor 1. The effect of the infection by the haemococcidian genus *Lankesterella* was negative (importance = 0.88, β = 0.08, z = 2.70, P = 0.007); infected lizards displayed less push-ups, lateral compressions, and lunge behaviors (Fig. 3a). The number of ticks had a positive effect on Factor 1 (importance = 0.73, β = 0.05, z = 2.18, P = 0.028) (Table 3). However, this positive relationship was only at low levels of infestation (< 4) and not when lizards had more ticks (> 6) (Fig. 3b).

(d) Discussion

Our data support previous observations on the function of push-ups in *S. occidentalis*. This may be a visual signal displayed towards conspecifics from longer distances and reduces the escalation of conflicts between males differing in status (Sheldahl & Martins 2000). The chromatic properties of the yellow patch significantly differ between the sexes in this population and, specifically, its spectral chroma correlates with the body length of the males (see Megía-Palma et al. 2018b). However, it was not an important predictor of the behavioral traits tested here, suggesting that intrasexual male competition does not influence evolution of the yellow patches in this species. Conversely, an intersexual signal of quality based on the display of yellow patches was previously described in *Sceloporus virgatus* (Weiss 2006), a closely related species. This suggests that yellow patches in *S. occidentalis* might also signal individual quality (body size) to conspecifics of both sexes in this population (Megía-Palma et al. 2018b), but not necessarily as an agonistic signal of male aggression (Martins 1993).

The factor analysis of the behavioral traits indicated that Factor 1 correlates with push-ups, lateral compressions, and lunge behavior; three behavioral traits displayed during male agonistic interactions in *S. occidentalis*. Indeed, the blue ventral patches are displayed towards opponents during the performance of lateral compressions, at a short distance of 1.6 cm between contestants in this study, and this behavior frequently (76.1%) elicited aggressive responses from rivals. Thus, factor 1 will be hereafter referred to as 'aggressive behavior'.

The comparison of the SELF versus the RIVAL models provided us with a comprehensive view of the relative importance of behavioral traits, color, and infection as predictors of male aggressive behavior during pairwise contests in *S. occidentalis*. The behaviors summarized in factors 1 (i.e. aggressive behavior) and

3 (i.e. submissive behavior; Table 1) of rival lizards were important predictors, with similar magnitudes, of the aggressive behavior of focal males (see Figs. 1a and 1c). Thus, our analyses suggest that behavioral traits from rivals have an important influence on the aggressive response of focal male lizards, supporting the escalated model of aggression (i.e. Enquist & Leimar 1983) previously proposed for this species (Sheldahl & Martins 2000). However, these relationships were non-linear. Strikingly, this may follow a quadratic pattern with a maximum intensity of escalation at intermediate aggression levels from both contestants, deescalating if the aggression of the rival increases (Fig. 1a). This suggests that push-ups, lateral compression, and lunge behaviors may not necessarily imply physical altercation, but performing these aggressive behaviors is exhausting for the lizards and has likely physiological costs (Schall & Dearing 1987; Marler & Moore 1988). Similarly, an intriguing result is the behavioral pattern observed for focal lizards receiving submissive responses from their opponents; these ‘bully’ males performed the highest intensity of aggressive display with no sign of de-escalation (Fig. 1c). Tail waving (i.e. Factor 4) was also an important predictor of aggression in the RIVAL model, but its relationship with the aggressive behavior from focal males suggested a neutral effect on it (Fig. 1d). This behavior might have a deflective function as proposed for other lizards with similar behavior (Telemeco et al. 2011).

Not all the traits that significantly explained the aggressive behaviors of focal males (i.e. Factor 1) had a positive feedback effect; some behavioral traits likely related with dominance and correlated with Factor 2, such as climbing on top of the rock, licking an opponent’s body, or rubbing the cloaca on the substrate (i.e. marking), reduced the level of aggression of the focal males. This suggests that males may use other cues to assess fighting ability of rivals prior to confrontations, avoiding the costs of fighting with males of higher status (Briffa 2014; Abalos et al. 2016). Chemical scrutiny of the opponent’s scents might be one discrimination mechanism used by the lizards because 40% (487/1217) of the behaviors registered were tongue flicking, which was either performed towards the ground, walls and air, or towards different parts of the opponent’s body (Duvall 1982). This hypothesis is supported by the fact that *S. occidentalis* can discriminate different individuals by their odor (Duvall 1979). Furthermore, femoral secretions of lizards convey cues of individual quality that may be used by conspecifics to assess the fighting ability of rivals (Moreira et al. 2006; Martín et al. 2007; Martín & López 2007).

In addition, the spectral chroma of the rival’s blue patch had a negative feedback effect on the aggressive escalation of focal males. This suggests that the visual scrutiny of the rival’s blue patches can also dissuade focal males from fighting, confirming that the ventral blue patches of *S. occidentalis* play the dual role of ornaments and of armaments during social interactions (e.g. Cooper & Burns 1987). This is an interesting finding because when these males were infected by intestinal coccidians of the genus *Acrooimeria* they exhibited blue patches with lower spectral chroma (Megía-Palma et al. 2018b) and in the present study the males that engaged in fights with lower spectral chroma in their blue patches elicited more intense aggressive behaviors from opponents. Thus, this relationship suggests that intestinal coccidians may ultimately reduce the fitness of infected males through intrasexual competition because infected lizards that receive more aggression may also suffer higher costs of fights, hindering their access to reproduction (Marler & Moore 1989).

Although less informative than behavioral and color traits of the rival, parasites of focal lizards were also important predictors of their own aggressive behavior. Lizards infected by haemococcidians displayed significantly fewer push-ups, lateral compressions, and lunges. In this population, larger males were shown to have a greater prevalence of infection by this parasite (Megía-Palma et al. 2018b). However, the observed effect of this parasite on the behavioral display of the males was independent of lizard body size. The infection by *Lankesterella* might reduce the males’ competitive ability and ultimately hinder their access to reproduction (Schall & Dearing 1987; Schall & Houle 1992). A similar effect was also suggested for *Plasmodium mexicanum*, a virulent haemosporidian parasite that infects *S. occidentalis* in other localities (Schall & Dearing 1987). Interestingly, *Lankesterella* is a parasite that is significantly more frequent in males (Megía-Palma et al. 2018b). In a previous study in this population, we failed to find a significant relationship between color expression in males and *Lankesterella* infection ($P = 0.06$ with the spectral luminance of the blue patch; Megía-Palma et al. 2018b). This does not discard the possibility that females still perceived a difference,

because if parasites of the genus *Lankesterella* hinder the fighting ability of the males, we expect that females could discriminate healthy males, likely based on males winning fights (Schall & Dearing 1987). This might allow for the vertical transmission of genes for parasite resistance into their male offspring (Hamilton & Zuk 1982). These new findings suggest that *Lankesterella* may be a virulent parasite that plays an important role promoting both inter- and intrasexual selection in this population through its influence on males' aggressive behavior.

Similarly, males with the higher tick load (> 6 ticks) displayed less push-ups and lateral compressions, and performed fewer lunges. However, this relationship was non-linear. Lizards tended to perform more of these behaviors at low levels of infestation (Fig. 3b). Testosterone may positively influence the aggressive behavior of this lizard species, similar to other closely-related species of the family Phrynosomatidae (Moore 1988; Weiss & Moore 2004), and tick load can co-vary with the concentration of this androgen in *S. occidentalis* (Pollock et al. 2012). Taken together, this suggests that testosterone may link the aggressive behavior of males to low intensities of tick infestation. However, as commented previously, the opposite was observed at higher intensities of infestation. Ticks draw blood from the lizards and significantly reduce their hematocrit at moderate infestations (> 5 ticks according to Dunlap & Mathies, 1993). As estimated in a previous study in this population, an infestation of only 5 to 7 ticks may provoke, on average, a 10% reduction of hematocrit in the lizards (Megía-Palma et al. 2020). This may impair the rapid oxygen demands of the muscles involved in the sudden movements displayed by the males during agonistic encounters (Schall & Dearing 1987). Lizards with moderate tick infestations, which likely impair the oxygen carrying capacity of the lizards' blood, may not be able to keep up the displays for an extended duration (Dunlap & Mathies 1993). Thus, our results suggest that moderate infestations by ticks reduce intensity of behavioral display during intrasexual aggressive interactions in this species, supporting that aggressive displays are exhausting for males. This, together with previous results in this population, reaffirms that ticks exert an important selective pressure on the lizards. Tick prevalence and mean intensity of infestation are very high in April, reducing the body mass of some lizards and potentially leading to their death (Megía-Palma et al. 2020), while later in May and June tick abundance is reduced but they affect the behavior of the lizards during male agonistic interactions (this study). This suggests that ticks may exert a selective pressure on this population during April, when massive infestations of up to 61 nymphal ticks per lizard occur (Megía-Palma et al. 2020), and here we revealed a similar pattern that may also contribute to the positive selection of superior competitors or more resistant lizards during the mating season.

Our results confirm the role of the male ventral blue patches as armaments in *S. occidentalis*, given that its spectral chroma deterred aggressive responses from rivals during pairwise contests. Conversely, males with less chroma received higher intensity of aggression. This suggests that intestinal coccidians affect male agonistic interactions because the males infected by these parasites had less blue chroma (Megía-Palma et al. 2018b). In addition, the negative relationships between infection by haemococcidians and ticks at moderate intensities (> 6), with the aggressive behavior of the males indicate that these parasites reduce the lizards' ability to fight. This, altogether, suggests a role of parasites in male-male interactions, and in the intrasexual selection of lizards. Parasite resistance might be under selection in this population because the least parasitized males are also the most competitive ones. Mate choice is likely based on males' behavioral display. Therefore, most aggressive males likely achieve more frequent access to females (Schall & Dearing 1987). We propose here a mechanism mediated by parasites to explain how parasites and male intrasexual competition contribute to the evolution of a structural-based blue patch with dual function in *S. occidentalis*.

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Table 1. Description and classification of the behavioral traits displayed by *S. occidentalis* during pairwise staged contests that were performed in the laboratory.

Behavioral trait	Description	Classification
Approach	Moving toward opponent directly	Dominant/Aggressive
Femoral pore rub	Rubbing the underside of tail on the substrate	
Foot on opponent's head	Stepping a foot on the other lizard	
Head bobs	Moving the head rapidly up and down	
Lateral compression	Blue ventral patches are displayed in the sides	
Lick opponent's body	Tasting the rival's body with the tongue	
Lunge	Sudden intense motion toward opponent	
On top of rock	Climbs onto rock	
Push-ups	Moving the body up and down by bending forelimbs	
Touch	Physical contact occurs	
Basking	Flattening the body on the ground under the lamp	Exploratory/Neutral
Digging	Displacing sand with head or forelimbs	
Exploring	Walks around the arena	
First movement	First lizard moving in the video	
Tail vibration	End of tail vibrates, and is not raised	
Tail wave	Tail is raised and waves from side to side	
Tongue flick/lick	Tasting the ground or air with the tongue	
Trying to climb walls	Jump on walls	
Retreat	Walking away from opponent	Submissive
Side hop	A retreat movement in which lizard hops away	

Table 2. Factor loadings extracted from behavioral traits of male *Sceloporus occidentalis* during staged contests in the lab. In brackets is shown the percentage of explained variance. Behavioral traits with factor loadings over 0.80 based on principal axis factoring and varimax normalized rotation of the factors are shown in bold.

Behavioral traits	F1 (22.05%)	F2 (18.34%)	F3 (8.68%)	F4 (7.58%)	F5 (6.11%)
Approach	0.779	0.110	0.140	-0.044	0.106
Basking	0.017	0.353	0.113	-0.136	0.472
Digging	0.057	-0.062	-0.178	0.041	0.052
Exploring	-0.107	0.454	0.052	-0.004	0.841
Femoral pore rub	-0.116	0.654	-0.034	-0.032	-0.006
First movement	-0.140	0.379	0.116	-0.315	0.247
Foot on opponent's head	0.186	0.509	0.206	0.092	0.011
Head bobs	0.369	-0.068	-0.095	0.197	-0.103
Lateral compression	0.855	-0.087	0.304	-0.078	0.016
Lick opponent's body	0.232	0.610	0.157	0.413	0.228
Lunge	0.943	-0.030	0.061	0.054	-0.033
On top of rock	-0.126	0.833	-0.013	-0.070	0.013
Push-ups	0.911	-0.022	-0.192	0.116	-0.084
Retreat	0.214	0.091	0.956	0.032	0.103
Side hope	0.224	-0.104	0.898	0.122	0.083
Tail Vibration	-0.093	0.006	0.010	0.636	-0.016

Behavioral traits	F1 (22.05%)	F2 (18.34%)	F3 (8.68%)	F4 (7.58%)	F5 (6.11%)
Tail wave	0.258	0.006	0.034	0.860	-0.085
Tongue flick/lick	0.018	0.769	-0.065	-0.038	0.426
Touch	0.717	0.009	0.128	0.059	-0.042
Trying to climb walls	-0.044	-0.106	-0.091	-0.026	0.887

Table 3. Results of multimodel inference approached by model averaging that show the importance of self and rival's traits as predictors of the aggressive behaviours (Factor 1) of males *Sceloporus occidentalis* during staged contest filmed in the laboratory. Predictors with significant coefficients are shown in bold.

SELF model	Importance	Estimate	Adj. SE	z value	Pr(> z)
(Intercept)		0.49	0.54	0.92	0.359
Haemococcidians	0.88	0.08	0.03	2.70	0.007
Tick intensity	0.73	0.05	0.02	2.19	0.029
Chroma of the blue patch	0.31	0.71	0.56	1.25	0.210
Intestinal coccidians	0.30	-0.05	0.04	1.10	0.273
Area of blue patch	0.26	0.00	0.00	1.00	0.317
Throat hue	0.25	-0.05	0.06	0.93	0.352
Body condition	0.24	0.49	0.53	0.93	0.350
Time of the day	0.22	0.36	0.48	0.75	0.451
back luminance	0.19	0.00	0.00	0.49	0.622
Yellow chroma	0.19	0.13	1.76	0.07	0.941
Mites	0.18	0.00	0.04	0.09	0.932
SVL	0.17	-0.02	0.15	0.13	0.899
RIVAL model	Importance	Estimate	Adj. SE	z value	Pr(> z)
(Intercept)		0.90	0.41	2.21	0.027
FA3 (rival)	1.00	0.22	0.03	8.26	< 0.001
FA4 (rival)	0.98	0.07	0.02	3.34	0.001
FA1 (rival)	0.92	0.14	0.03	4.79	0.000
Blue patch chroma (rival)	0.82	-0.76	0.37	2.08	0.037
FA2 (rival)	0.79	-0.05	0.02	2.33	0.020
Yellow chroma (rival)	0.30	-1.09	1.10	0.99	0.322
FA5 (rival)	0.27	0.02	0.02	1.14	0.253
Area of blue patch (rival)	0.24	0.00	0.00	1.05	0.296
Time of the day	0.20	0.20	0.25	0.81	0.419
Blue patch luminance (rival)	0.17	0.00	0.00	0.37	0.709

Figure Captions.

Figure 1. Relationships between the behavioral traits of male lizards summarized in Factor 1 and the behavioral traits of rival males summarized in the Factors 1, 2, 3, and 4 (see Table 2 for the behavioral traits correlated with each one of the factors).

Figure 2. Relationship between the behavioral traits of male lizards summarized in Factor 1 and the spectral chroma of their rivals' blue patches.

Figure 3. (a) Mean \pm SE display of aggressive behavioral traits (i.e. Factor 1) in *Sceloporus occidentalis* between males infected by haemococcidians of the genus *Lankesterella* and uninfected males. (b) The aggressive behavior of the males increased at low to moderate levels of infestation by ticks, while decreased with higher intensities of infestation.



