Current Zoology, 2024, **70**, 59–69
https://doi.org/10.1093/cz/zoac095
Advance access publication 26 November 2022
Original Article

Natural parasites in conjunction with behavioral and color traits explain male agonistic behaviors in a lizard

Rodrigo Megía-Palma[a,b,c,*], **Dhanashree Paranjpe**[d], **Robert D. Cooper**[e], **Pauline Blaimont**[f], and **Barry Sinervo**[g,†]

[a]Department of Biomedicine and Biotechnology, Parasitology Unit, Universidad de Alcalá (UAH), E-28805, Alcalá de Henares, Spain
[b]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, P-4485-661 Vairão, Portugal
[c]BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, P-4485-661 Vairão, Portugal
[d]Rupa Rahul Bajaj Center for Environment and Art, Empress Botanical Gardens, Kavade Mala, Pune, India
[e]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA
[f]Department of Biology, University of Houston Downtown, 1 Main St., Houston, TX 77002, USA
[g]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA

[*]Address correspondence to Rodrigo Megía-Palma. E-mail: rodrigo.megia@uah.es.
[†]Deceased.
Handling editor: Xiang JI

Abstract

Male competition conforms to a cost–benefit model, because while aggression may increase reproductive prospects, it can also increase the risk of injury. We hypothesize that an additional cost in aggressive males would be an increase in parasite load associated with a high energy investment into sexual competition. Some of these infections, in turn, may downmodulate the level of host aggression via energetic trade-offs. We staged dyadic male contests in the lab to investigate the relationships of multiple parasites with the agonistic behavior of lizard hosts, *Sceloporus occidentalis*. We also included both color and behavioral traits from opponents in the analyses because (1) color patches of lizards may serve as intraspecific signals used by conspecifics to assess the quality of opponents, and (2) contests between male lizards fit classical models of escalated aggression, where lizards increase aggression displays in response to an opponent's behavior. The results conform to our hypothesis because male lizards displayed more pushups when they had more ticks. Moreover, some parasites may modulate the levels of aggression because lizards infected by hematic coccidians performed fewer pushups. Interestingly, lizards also displayed fewer pushups when both the chroma and size of the opponent's blue patch were greater. The results thus also supported the role of the blue patch of *S. occidentalis* as a sexual armament, because it contributed to the deterrence of aggression from opponent lizards. We revealed that natural parasitic infections in lizard hosts can contribute to their agonistic behavior. We encourage future studies to account for parasites in behavioral tests with lizards.

Key words: *Ixodes pacificus*, *Lankesterella*, sexual selection, social interactions, ticks.

Males of a multitude of animal species perform behavioral displays that, when combined with color patches and/or fighting structures (e.g., antlers), advertise their quality as mates and competitors (Johnstone 1996). These behavioral traits are interpreted as agonistic (fighting) behavior when they are displayed in the presence of other males and can represent a proxy for their reproductive investment (Deutsch et al. 1990). Among the plethora of behavioral traits performed by males during agonistic contests, pushup and lateral compression displays have evolved as part of the agonistic behavior in squamate species (Cooper and Burns 1987; Cox et al. 2005; Assis et al. 2018). The display of these behaviors may increase the conspicuity of those color patches located on the chest and abdomen (Martins 1994; Calisi and Hews 2007; Baird 2013).

Although cryptic and photoprotective colorations are expected to evolve in ecological contexts of high predation and/or solar radiation (e.g., Reguera et al. 2014; Dunn et al. 2015; Marshall et al. 2015), sexual selection can promote the evolution of conspicuous color patches and complex display behaviors (Emlen and Oring 1977; Andersson 1994; Ord et al. 2001; Stuart-Fox and Ord 2004; Griffith and Pryke 2006; Pérez i de Lanuza et al. 2013). In this sense, color and behavioral traits in lizards may broadcast health status and quality to conspecifics (Swierk and Langkilde 2013; Assis et al. 2018, 2021) because physical displays and color patch production are energetically demanding processes (Martins 1993; Megía-Palma et al. 2018; Lanser et al. 2021). Thus, contest behavior in lizards conforms to a cost–benefit model; fights increase mating opportunities for dominant lizards, but may also result in injuries, energy imbalance, and greater exposure to both predators and some parasites (Christenson and Goist 1979; Lane et al. 2010).

Parasites draw resources from their hosts and some parasitic infections may thus reduce traits contributing to male reproductive success (e.g., Mulvey and Aho 1993), including agonistic behavior (Innocenti et al. 2003; Lanser et al. 2021).

Received 23 July 2022; accepted 19 November 2022

Thus, parasitic infections can have a negative effect on the host physical performance (reviewed in McElroy and Buron 2014). This effect has been more profusely studied in fish hosts; however, the available evidence is mixed (Hamilton and Poulin 1995; Barber 2002; Mikheev et al. 2010). Malarial parasites and ticks can impair the male agonistic behaviors of lizards (Schall and Dearing 1987; Lanser et al. 2021). Nevertheless, positive relationships between parasite load and both pigmentation of color patches and aggression, 2 correlates of reproductive effort in lizards, also suggest that reproductive investment can increase the susceptibility of male lizards to some parasites (Megía-Palma et al. 2021; Payne et al. 2021).

We analyzed male agonistic contests of *Sceloporus occidentalis* (Squamata: Phrynosomatidae), a species with a complex communication system that combines behavioral displays and color patches. Both males and females have blue patches on the venter. The blue coloration has been profusely investigated within the genus *Sceloporus* and different aspects of its reflectance and color patch size have been associated with morphology, physical performance, immune response, parasitization, thermoregulatory and sexual behavior, signal evolution, and hormonal and pigment physiology (e.g., Vinegar 1972; Cooper and Burns 1987; Ressel and Schall 1989; Langkilde and Boronow 2010; Megía-Palma et al. 2018; Robinson and Gifford 2019; Romero-Díaz et al. 2019; Zúñiga-Vega et al. 2021; Assis et al. 2022). For example, the saturation of the blue coloration in sceloporin lizards can be positively associated with testosterone secretion and melanin deposition in the skin (Quinn and Hews 2003; Cox et al. 2005, 2008). These color patches may be fully visible to conspecifics when males perform lateral compressions of the thorax. However, during pushup displays, blue patches may also be partially visible from the front. These 2 behaviors are sequentially performed; with pushups performed first, at a longer distance (Martins 1994). Furthermore, pushups are interpreted as deterrence signals when they are performed in the presence of a male (Martins 1993). Lateral compressions and pushups are displayed by males during both agonistic (e.g., territorial) and courting interactions (females may perform pushups as well) and are part of the visual communication system of *S. occidentalis* (Sheldahl and Martins 2000).

We investigated the importance of color, behavior, and parasites on male agonistic interactions of *S. occidentalis*. The investment that male lizards put into territorial behavior may be influenced by the level of aggression from intruder competitors (i.e., a model of escalated aggression), where opponent behavior would significantly improve our prediction of a focal male's level of aggression (Enquist and Leimar 1983; Bohórquez-Alonso et al. 2018). Thus, we investigated whether opponents' traits (behavior and coloration) can influence the agonistic behavior of focal lizards. Furthermore, we hypothesized that parasite load can be high in aggressive males as a cost associated with their higher activity and the energy allocated to sexual competition. In this sense, testosterone was previously associated with increased tick load in *S. occidentalis* (Pollock et al. 2012) and, given the link between testosterone and aggression in lizards (Moore 1988), we predicted (1) a positive relationship between ectoparasites and agonistic displays (Payne et al. 2021). In opposition, internal parasites endure longer than chronic infections and may induce energetic trade-offs (Holmes and Zohar 1991), which can downmodulate the level of host aggression. Thus, we also predicted (2) that endoparasite infections would be associated with reduced aggression (Schall and Dearing 1987). Lastly, we also predicted (3) color patch characteristics would be important predictors of the agonistic response from opponent lizards, which would support their role as badges of status (e.g., Morris et al. 1995).

Material and Methods

Sampling and housing

We used a *lasso* to capture 42 males (SVL range between 53 and 69 mm) of *S. Occidentalis* in May 2014 in a shrubby-400-m transect (from 36.985270º, –122.061440º to 36.985287º, –122.056934º) in the Arboretum of University of California in Santa Cruz (CA, USA) (Megía-Palma et al. 2018). The lizards were housed individually in plastic terraria of 20 cm × 15 cm with a damp substrate of 10-cm depth of peat moss and sand that allowed the lizards to bury themselves (Lane et al. 1995). Water was provided ad libitum, while lizards were fed 2 crickets dusted in a vitamin supplement every 2 days. The terraria were kept in an environmental chamber with a 12L:12D photoperiod provided by natural spectrum fluorescent and ultraviolet lights and a cycling thermal regime (Megía-Palma et al. 2020). During the daytime (7 AM–7 PM) and in the warmest spot of the terraria, mean ± *SE* substrate temperature was 31.5 ± 0.09 ºC (mode = 30.2 ºC; maximum = 39.1 ºC, minimum = 17.6 ºC). In the coolest spot of the terrarium, mean ± SE substrate temperature was 25.6 ± 0.1 ºC (mode = 24.9 ºC; maximum = 38.8 ºC, minimum = 16.8 ºC). Thus, the modal difference between the 2 thermal extremes in the model terrarium evaluated was 4.8 ºC. During the night period (7 PM–7 AM), with no heat source connected, substrate mean ± *SE* temperature was 19.7 ± 0.02 (mode = 19.5 ºC; maximum = 29.3 ºC, minimum = 16.0 ºC) (Megía-Palma et al. 2020). The lizards were released at the end of the study to their exact point of capture.

Diagnosis of parasites

Upon arrival at the lab, we weighed the lizards to the nearest 0.01 g using a digital scale and measured them to the nearest 1 mm from the tip of the snout to the cloacal opening (snout-to-vent length, SVL) using a ruler. We used sterile needles to bleed the tail of lizards, at least 2 cm from the cloaca, carefully avoiding the area of the hemipenes, and collected a small sample of blood (<5 μL) with a heparinized microcapillary tube (BRAND, Wertheim, Germany; 75 mm × 1.1 mm, Na-heparinized). The blood sample was used to make a thin-layer blood smear. The dried blood smears were fixed with methanol and stained for 40 min with Giemsa 1:10 at pH 7.2. A single, trained observed screened 15,000 red blood cells of each lizard at ×1,000 magnification for diagnosing the presence (binary coded yes/no) of any possible types of parasites in the blood (i.e., chronic infections) (Megía-Palma et al. 2017). Fecal samples were collected directly into 1.5-mL micro-centrifuge tubes by briefly massaging the abdomen of the lizards or from individual cages when dropped by the lizards during the following days. These fecal samples were stored in 1 mL potassium dichromate. We applied Sheather's sugar flotation technique to concentrate intestinal parasites. Each sample was screened at 600× magnification and diagnosed for the presence/absence of intestinal coccidians (i.e., chronic infection) (see Megía-Palma et al. 2015). Prior to each dyadic contest, we checked for ectoparasites (i.e., temporary infestation), namely mites (binary coded yes/no) and the number of ticks.

Color patches

Color measurements of all the lizards were performed during the 7 days before the dyadic contest took place. We calculated the area of the blue patches on the right part of the abdomen of the lizards by multiplying its maximum length by maximum width, which was measured with a ruler to the nearest 1 mm. The blue patch area correlated with SVL ($F_{1, 40} = 7.20$, $P = 0.010$; $R^2 = 0.13$), in line with a recent study (Zúñiga-Vega et al. 2021). We calculated a residual patch area variable from the regression of patch area on SVL. Thus, negative values corresponded to lizards with blue patches smaller than average for a given body length. We measured the spectral reflectance of the blue color patches by using an Ocean Optics 2000 spectrophotometer connected to a glass fiber probe with a constant 45° angle and from 400 to 700 nm (Megía-Palma et al. 2018). Our spectral measurements did not include the ultraviolet range because the ultraviolet lamp was not working properly in the spectrophotometer used (see also Megía-Palma et al. 2018). We used a continuous strobe frequency of 10 ms, and a boxcar width of 4 to take 3 consecutive measurements in the color patch. We standardized the spectral measurements by comparing them to a white standard (also provided by Ocean Optics). Spectral measurements were averaged and collapsed into bins of 1 nm that we processed with the software CLR 1.1 (Montgomerie 2008). The chroma of the blue patch was calculated as the light reflected from 400 to 475 nm divided by the total reflectance from 400 to 700 nm (Endler 1990; Grill and Rush 2000). Prior to the spectral measurements and to reduce the potential effects of temperature on their body coloration, the lizards were set at room temperature (~24 °C) waiting for 20 min to ensure that all the lizards were at a similar temperature when color measurements were performed (Megía-Palma et al. 2018).

Neutral arena setup

We staged pairwise dyadic contests 7 days after the lizards were captured (Bohórquez-Alonso et al. 2018). These were staged in a neutral arena in order to remove the effect of residency (Sacchi et al. 2009; Abalos et al. 2016). Contests took place in a room free of noises and with no human presence. We paired the 42 males by similarity in body mass (mean mass difference = 0.64 g) and never exceeded an SVL difference of 2 mm (mean SVL difference = 0.72 mm) (Bastiaans et al. 2013). This pairing strategy minimizes the body size effect (Seddon and Hews 2016), which can be an important predictor of dominance in lizards (e.g., Sacchi et al. 2009). However, these matching criteria forced us to use males in 1 contest only. After the acclimation period in the lab, contestant males were transferred into the neutral arena, which was 60 cm width × 80 cm length × 48 cm height with sandy substrate covering the bottom. The arena was composed of acrylic sheets and covered on 3 sides while the fourth side was left uncovered for behavioral recording using a Flip Video digital camera (Cisco Systems). A 75-W thermal lamp was set up to shine directly above a central rock (14 cm × 12 cm × 12 cm), thus providing an incentive for the lizards to approach the rock and engage in agonistic interactions (Garland et al. 1990). The arena was divided into 3 parts at the beginning of each trial using 2 removable partitions of opaque plastic (Figure 1). The trials took place between 10:00 AM and 6:30 PM for 5 consecutive days between May 30th and June 3rd, 2014. Each lizard was placed at opposite ends of the partitions and allowed 5 min to acclimate to its space (Sheldahl and Martins 2000). After this quick acclimation period, the partitions were removed, allowing the lizards to physically interact (Bastiaans et al. 2013). The behavior of the lizards was filmed for 20 min (Bastiaans et al. 2013). Before each subsequent trial, the sand substrate was changed to avoid the effects of any olfactory cues from the previous trial (Duvall 1979). No lizard suffered injuries.

Behavioral analyses

Social behaviors of *S. occidentalis* are easy to observe and have been thoroughly described by previous authors (Schall and Dearing 1987; Schall and Sarni 1987). Given that we were interested in whether the blue patches can contribute to explain the intensity of the agonistic responses from opponents, we focused on analyzing the data on pushups and lateral compressions, which are associated with the display of the blue patches. Pushups were counted every time a lizard extended 2 or 4 legs and raised its chest from the ground. Lateral compressions were counted every time a lizard compressed its thorax laterally. We analyzed:

(1) The difference in distance between the lizards during the performance of pushups or lateral compressions using a non-parametric Mann–Whitney *U* test for independent groups because the data violated assumptions of parametric tests.

(ii) We calculated a χ^2 to compare the frequencies of aggressive and submissive behaviors (Table S1) displayed by opponents after the performance of pushups and lateral compressions by focal lizards.

(iii) The number of repetitions of pushups and lateral compressions were tested using linear mixed models (LMM) in the R-package "lmer." Log_{10}-transformed number of pushups and cubic-root-transformed number of lateral compressions performed by each lizard best fit LMM with Gaussian distributions. Lizards were tested in dyadic contests; hence, every pair of lizards should be nested in a single contest. This was coded by including the contest pair ID as a random term in the analysis (Millar and Anderson 2004). Fixed predictors included in this LMM were the time of the day and a combination of variables from a focal lizard and its opponent. From focal males, we included the number of ticks and the presence of mites, and the presence of infections by intestinal and hematic coccidians. We also included, as a predictor, the blue chroma of the belly patch of the opponent as a measure of color saturation, which correlated with parasitic infections in a previous study investigating these same individual lizards (Megía-Palma et al. 2018). We also included the (residual) blue patch area of the opponent as covariate. The spectral variables and behavioral traits were *z*-standardized to improve computational stability (R Core Team 2021).

We made a priori comparisons between 2-way models (with interactions) and the 1-way model described above to determine the most statistically parsimonious model. We used Akaike's information criterion corrected for a small sample size (i.e., AICc) (Bedrick and Tsai 1994). The 1-way model was the most parsimonious in explaining variation in the number of pushups (it had an ΔAICc_pushup = −11.10, as compared to the 2-way model). However, the model containing the interactions between lateral compressions performed

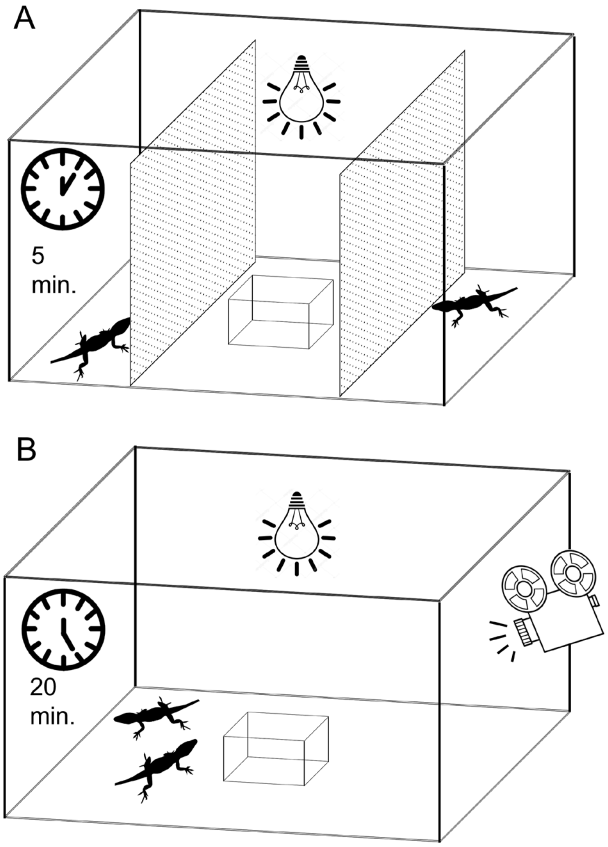

Figure 1 Scheme of the experimental design employed in the laboratory to analyze the agonistic behavior of male *Sceloporus occidentalis* during dyadic contests. (A) Lizards were allowed to acclimate for 5 min to the arena with no visual contact with the opponent lizard prior to the contests. (B) We removed opaque partitions after this first period, which allowed the lizards to physically interact. Their behavior was filmed with no human presence in the room during the next 20 min.

by the opponent and both chroma and area of the opponent's blue patch was the most parsimonious in explaining variation in the number of lateral compressions (ΔAICc_lateral compressions = −16.66, as compared to the 1-way model). Parametric assumptions were tested on the residual distribution of these 2 models and collinearity was assumed to be low based on variance inflation factors (all VIF coefficients <4.1), which were calculated using the R-package "performance" (Lüdecke et al. 2021).

We used multimodel inference and model averaging (Hegyi and Garamszegi 2011; Symonds and Moussalli 2011). This methodology compares all likely models derived from the combination of the variables in the initial model. We included all models in the computation with ΔAICc < 4 relative to the best fit model (Burnham and Anderson 2004). Model selection was performed using the R-package MuMIn (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 *ß* coefficient and adjusted standard error.

(4) We used a 1-way Anova to compare the chroma of the blue ventral patch of the lizards that climbed the central rock on the arena with those that did not. This behavior was also extracted from the observations of the videos and was interpreted as a bold behavior in dominant individuals (Pounds and Jackson 1983; Plavicki et al. 2004; Shanbhag et al. 2006).

Results

Parasitic infections

Ticks *I. pacificus* infested 52% of the lizards with mean ± *SE* abundance of 1.90 ± 0.34 (range = 0–7). Mites *Geckobiella* cf. *texana* infested 35.7% of the lizards. We only found 1 species of blood parasite *Lankesterella occidentalis* and 1 intestinal parasite *Acroeimeria sceloporis* (Megía-Palma et al., 2015, 2017). Prevalence of *L. occidentalis* in the blood was 42.8% and *A. sceloporis* in feces was 38.0%.

Behavioral traits

We registered 1,217 behavioral events in 21 videos (Table S1rial). Pushups were registered in 42.8% (9/21) of the trials. We registered 416 pushups in 39 independent pushup events with a mean ± *SE* 10.67 ± 0.72 pushups per event (range = 1–23). A pushup event is a group of pushups performed close in time and it was considered an independent event when the lizards performed a different behavior between pushup events. Pushup events were performed by the lizards at a mean ± *SE* distance of 26.82 ± 4.58 mm between opponents. 33.3% (13/39) of the pushup events were followed by an aggressive response from the opponent male.

Lateral compressions were registered in 23.8% (5/21) of the tournaments. We registered 88 instances of lateral compression. The mean ± *SE* distance between opponents was 10.61 ± 3 mm. These were considered aggressive interactions because 76.1% (67/88) of the lateral compressions were followed by an aggressive response from the opponent lizard (Table S1).

There were significant differences in the distance between opponents when performing pushups or lateral compressions ($U = 762$, $P < 0.0001$—lateral compressions were displayed at closer distance, see above), and also an individual was significantly more likely to receive an aggressive response after performing a lateral compression than after a pushup ($\chi^2 = 21.24$, $P < 0.0001$).

The multimodel inference approach produced 27 equally likely models (with ΔAICc ≤ 4) explaining the variation in the number of pushups. An averaged model indicated that the number of pushups performed by focal males was best predicted by the opponent's traits such as both blue chroma (estimate ± *SE* = −6.58 ± 2.90), patch area (estimate ± *SE* = −0.02 ± 0.01), and the number of pushups performed by the opponent (estimate ± *SE* = +0.48 ± 0.23) (Table 1). This indicated that males performed more pushups when the opponent lizard also performed more pushups. However, lizards performed less pushups when an opponent male had more intense or proportionally larger blue patches in the abdomen. The males that did climb the central rock under the light source had significantly higher chroma in the blue patch (0.29 ± 0.01 vs. 0.27 ± 0.02) ($\chi^2_{1,40} = 2.15$, $P = 0.038$; Figure 2).

Infections by ticks (estimate = +0.30 ± 0.12) and hematic coccidians (*Lankesterella* sp.) in focal males also entered the final model, although with less importance (Table 1). This indicated that lizards that had more ticks performed more pushups, while those lizards infected by hematic coccidians performed less (Figure 3).

Two equally likely models explained the number of lateral compressions. We found the terms patch size × lateral compressions and chroma × lateral compressions, all from the opponent, important predictors of the number of lateral compressions performed by focal lizards (Table 2). Thus, the display of lateral compressions from opponents elicited more lateral compressions in focal lizards if the former had larger patch areas and lower blue chroma (Figure 4).

Discussion

Pushup and lateral compression displays are fundamental components of the agonistic and courting behavior of *S. occidentalis* (Carpenter and Ferguson 1977; Sheldahl and Martins 2000). The number of these 2 behavioral traits was explained by both the behavioral and color traits of the opponent lizards during staged contests in the lab. This conforms to previous analyses of contest behavior in lizards where behavior and color were important outcome predictors (Bohórquez-Alonso et al. 2018). Males of *S. occidentalis* in our study performed more pushups in the presence of males that displayed more pushups but both the opponent's patch size and blue chroma had a negative effect on the number of pushups displayed by focal lizards. Similarly, the number of pushups displayed by the opponent was also associated with fewer lateral compressions in focal lizards. These relationships suggested that pushup displays, and color traits of blue patches, serve as deterrence signals that would reduce the potential costs of confrontations and thus conform to the definition of a sexual armament (Martins 1993; Morris et al. 1995; Berglund et al. 1996). In support of this interpretation, pushups were performed at a greater distance between contestants and were more frequently followed by nonaggressive responses than lateral compressions.

Interestingly, there were opposing effects of the opponent's blue chroma and patch size on lateral compressions. Focal males responded with more lateral compressions when the opponent males had larger patch areas and lower blue chroma. The results thus suggest that pushups, lateral compressions, as well as the size and spectral properties of the blue patch of *S. occidentalis* can provide complementary visual information to conspecifics at different stages during male agonistic interactions (Carpenter and Ferguson 1977; Martins 1993, 1994). This conforms to the multiple message model, proposed as the best fit for the communication system of *S. occidentalis* (Megía-Palma et al. 2018; Zúñiga-Vega et al. 2021).

Although previous studies failed to find a significant relationship between the blue coloration and male aggression indices in *S. occidentalis* (Seddon and Hews 2016; Lanser et al. 2021), blue chroma in the genus *Sceloporus* increases with increasing melanin in the skin (Quinn and Hews 2003), which in turn, increases with testosterone levels (Cox et al. 2008 but see Zúñiga-Vega et al. 2021). As in other animals, testosterone levels and melanin are positively associated with aggression and physical performance in lizards (Huyghe et al. 2005; Raia et al. 2010; Abalos et al. 2016, but also see Seddon and Hews 2016). The reason why lizards reduced the number of pushups in the presence of males with bigger and more intense blue patches during agonistic interactions will require further investigation. Nonetheless, males that climbed on top of the central, lighted rock in the arena had blue patches with significantly higher chroma. We interpret this fact as a potential behavioral correlate of the dominance status of the lizards, similarly as it occurs in other iguanian lizards (Pounds and Jackson 1983; Plavicki et al. 2004; Shanbhag et al. 2006). Moreover, a previous study showed that spectral components of the blue patches in a similar species correlated with the physical performance of the lizards across different temperatures (Robinson and Gifford 2019). Therefore, males with higher blue chroma might be perceived by opponent lizards as more vigorous rivals.

Nevertheless, the dual function of the blue patch both as an armament and ornament, the latter serving as a visual cue used for sex recognition, is also plausible because several species in this genus may use blue patches for sex discrimination (Vinegar 1972; Cooper and Burns 1987; Lemos-Espinal et al. 1996; Swierk and Langkilde 2013). Furthermore, the degree of sexual dimorphism in a species, that is, a phenotypic difference between sexes, is generally associated with the strength of sexual selection (Stuart-Fox and Ord 2004; Fairbairn et al. 2008; Hoops et al. 2022; Van Niekerk et al. 2022). In support of the sexual discrimination function hypothesis, the males in the population investigated had blue patches that were 94% larger (104.84 ± 6.57 mm^2, n = 42) than those of the females collected for a different study (53.95 ± 5.98 mm^2, n = 21) (Megía-Palma et al. 2018). This sexual dimorphism suggests that this trait might evolve by sexual selection (e.g., Swierk and Langkilde 2013). The functionality of the blue patch in this population as a trait used for sex discrimination, and

Table 1 Linear mixed model based on model averaging analyzing number of pushups performed by males of *S. occidentalis* during dyadic contests

	Importance	Estimate	Adj. *SE*	*z* Value	*P*-value
(Intercept)		1.83	1.20	1.522	0.128
Patch chroma opponent	**1.00**	**−6.58**	**2.90**	**2.265**	**0.024**
Patch area opponent	**0.87**	**−0.02**	**0.01**	**2.870**	**0.004**
Tick abundance	**0.60**	**0.30**	**0.12**	**2.490**	**0.013**
Mite presence	0.59	0.36	0.21	1.735	0.083
Hemococcidian presence	**0.43**	**−0.37**	**0.18**	**1.990**	**0.047**
Time of day	0.31	1.38	1.64	0.842	0.400
Pushups opponent	**0.29**	**0.48**	**0.23**	**2.100**	**0.036**
Lateral comp. Opponent	0.24	0.47	0.26	1.817	0.069
Intestinal coccidian presence	0.06	−0.24	0.22	1.095	0.273

Multimodel inference produced 27 likely models. Important predictors are shown in bold together with estimate ± adjusted standard error.

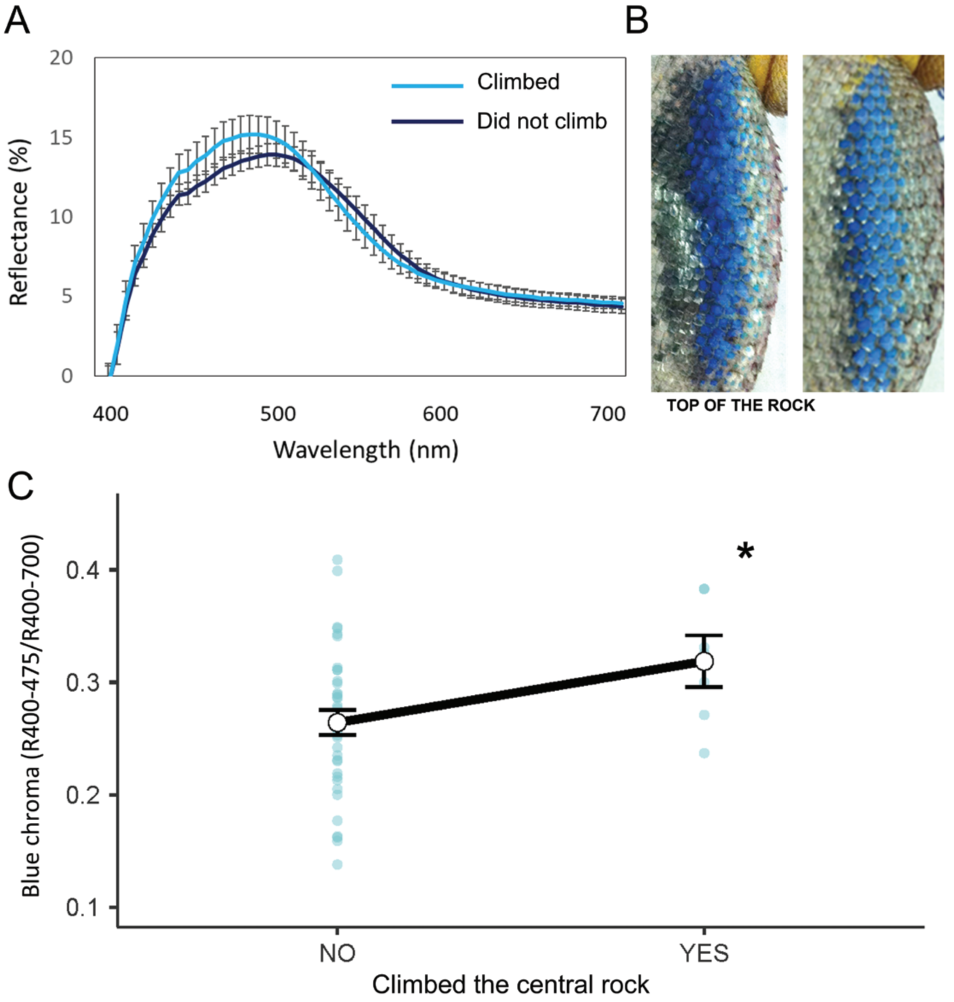

Figure 2 (A) Spectral profiles and (B) examples of the blue patches of lizards that climbed (*n* = 13) and did not climb (*n* = 29) the central rock in the arena during dyadic contests. (C) GLMM plot showing mean ± *SE* chroma of the blue patch of these males. Body size was included as covariate in the analysis. Asterisk indicates significant differences (see Results).

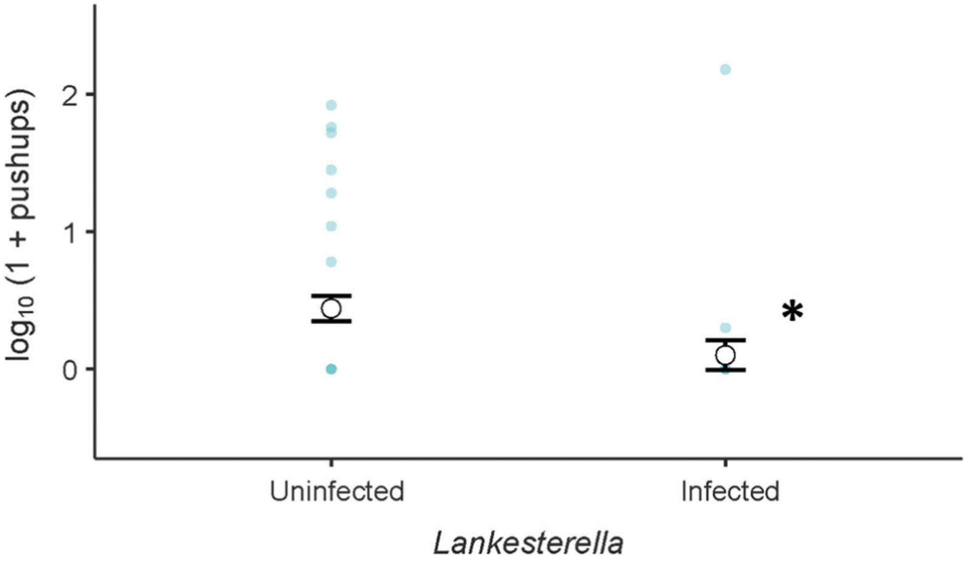

Figure 3 GLMM plot comparing the number of pushups performed by lizards considering the infection by hematic coccidians (genus *Lankesterella*). The observed scores (raw data) are displayed together with the mean ± standard errors. Asterisk indicates significant differences (see Results).

Table 2 Linear mixed model based on model averaging analyzing number of lateral compressions performed by males of *S. occidentalis* during dyadic contests

	Importance	Estimate	Adj. *SE*	*z* value	*P*-value
(Intercept)		0.45	0.17	2.600	0.009
Lateral compressions opponent	**1.00**	**1.41**	**0.15**	**9.574**	**<0.001**
Pushups opponent	**1.00**	**–0.33**	**0.08**	**4.196**	**<0.001**
Patch area opponent: Lateral comp. opponent	**1.00**	**–0.25**	**0.03**	**8.121**	**<0.001**
Patch chroma opponent: Lateral comp. opponent	**1.00**	**–0.35**	**0.13**	**2.688**	**0.007**
Patch area opponent	0.00	–0.08	0.06	1.235	0.217
Time of the day	0.31	0.48	0.45	1.088	0.277
Patch chroma opponent	0.00	–0.12	0.07	1.703	0.089
Tick abundance	0.00	0.03	0.05	0.499	0.618
Mite presence	0.00	–0.02	0.05	0.397	0.691
Hemococcidian presence	0.00	–0.03	0.04	0.686	0.493
Intestinal coccidian presence	0.00	–0.01	0.05	0.099	0.921

Multimodel inference produced 2 likely models. Important predictors are shown in bold together with estimate ± adjusted standard error.

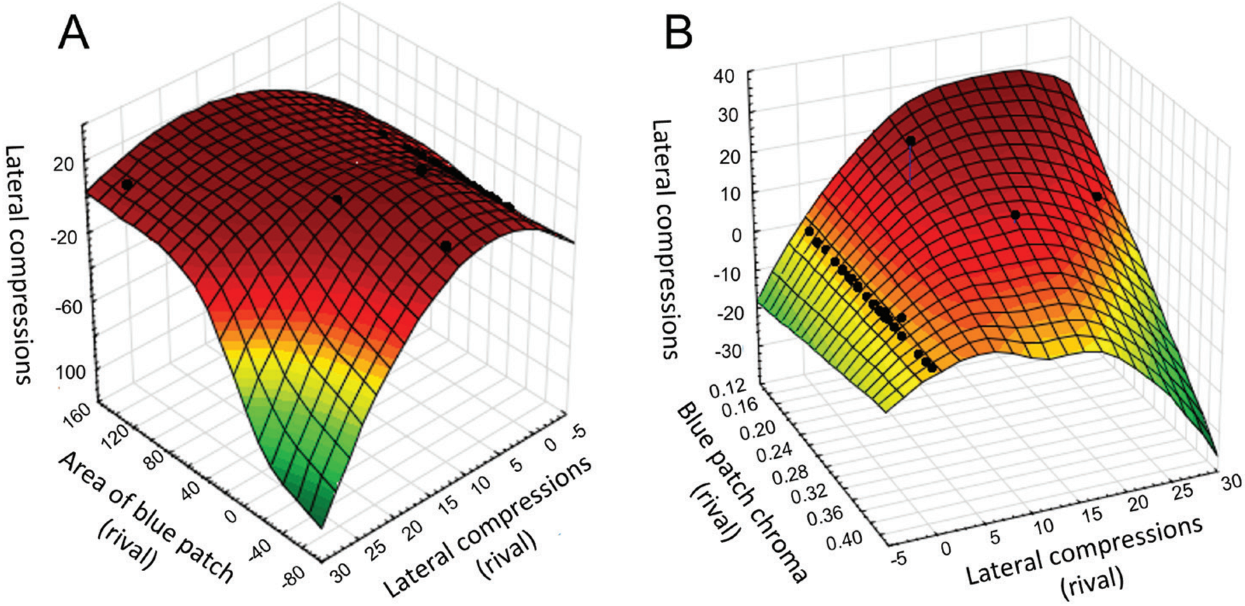

Figure 4 Relationship between the number of lateral compressions performed by male lizards and (A) the size and (B) chroma of the ventral blue patch of opponents. The models predict that males responded with more lateral compressions to those opponents (A) with relatively larger blue patches and that performed few lateral compressions, and (B) with less intense blue patches that performed more lateral compressions. Dots represent raw data.

hence involved in mate choice, will require further research because we did not conduct any behavioral trials with females. Nevertheless, our results suggest that the blue patch of *S. occidentalis* can act as a visual signal during male contests.

Our study faced a limitation because, as commented, the spectral measurements of the blue coloration only included the electromagnetic range of the human visual spectrum (400–700 nm) (Endler 1990). The ultraviolet (UV) region of the visual spectrum seems to play an important role in the communication system of lizards in the families Lacertidae and Cordylidae (Whiting et al. 2006; Martín and López 2009; Bajer et al. 2011). However, this has not yet been demonstrated in phrynosomatids. Moreover, previous studies on the blue coloration of lizards from taxonomic families other than Phrynosomatidae suggest that the "blue" coloration is actually UV, only looking blue to the human eye (e.g., Font and Molina-Borja 2004). It peaks within the UV wavelength range (i.e., 300–400 nm) and has a spectral tail that enters the human visible spectrum above 400 nm (Pérez i de Lanuza and Font 2010; Megía-Palma et al. 2016a, 2016b). In contrast, the available spectral evidence of the blue coloration in species of the genus *Sceloporus* (fam. Phrynosomatidae) peaks between 400 and 500 nm and, hence, has a low influence of the UV spectrum range (Stoehr and McGraw 2001; Ossip-Drahos et al. 2018; Goodlett and Stephenson 2019; Zúñiga-Vega et al. 2021). In support of this argument, a recent comparative study showed a low influence of the UV spectral range in the male blue ventral coloration in 11 out of 12 species of the genus *Sceloporus* (including *S. occidentalis*), all of which having spectral peaks between 400 and 500 nm—that is, non-UV reflectance (see fig. 2 in Romero-Díaz et al. 2019).

Lizards infested by ticks performed more pushups. Moderate to severe infestations by black-legged ticks can impair physiological and behavioral traits of *S. occidentalis* (Dunlap and Mathies 1993; Megía-Palma et al. 2020; Lanser et al. 2021). However, infestations of 5–7 nymphal ticks may have only a moderate impact on the lizards (Dunlap and Mathies 1993; Megía-Palma et al. 2020). Nonetheless, lizards performing more aggressively may not necessarily gain greater access to reproduction. For example, those males of the rainbow trout (Actinopterygii: Salmonidae) experimentally infected by eye flukes were more aggressive but they also lost contests more often than uninfected males (Mikheev et al. 2010). In this sense, natural infestation by black-legged ticks can explain an average reduction in body mass of 11.61% in the lizards from our sampled population (Megía-Palma et al. 2020), and it has been shown that an experimental increase in tick load significantly reduces the hematocrit of *S. occidentalis* as well as impair male fighting performance (Lanser et al. 2021). However, the positive relationship found in our study between unmanipulated tick load and aggression might mirror a component of the male reproductive strategy. More active males increase exposure to parasites during seasonal peaks of ectoparasite abundance (e.g., Moore 1988; Barrientos and Megía-Palma 2021). However, male lizards may also maximize access to females via increased activity (Marler and Moore 1988). Moreover, the positive relationship found here between aggression and ticks conforms to predictions of the ecological immunology theory (EIT) (Sheldon and Verhulst 1996). EIT posits that males would suffer an increase in parasites in response to increased reproductive effort (e.g., Salvador et al. 1996). This reproductive strategy can increase the fitness of those males in better physical condition, at least in the short term because the net fitness of parasitism on hosts should be evaluated throughout the host's life (Sorci et al. 1996; Bower et al. 2019).

In opposition, lizards chronically infected by hematic coccidians, *L. occidentalis*, performed fewer pushups. Interestingly, Lanser et al. (2021) did not find any significant effect of *L. occidentalis* on the contest behavior of males of *S. occidentalis*. Chronic infections by blood parasites have been previously associated with physiological and behavioral alteration in lizard hosts (e.g., Schall et al. 1982; Dunlap and Schall 1995; Oppliger et al. 1996; Žagar et al. 2022). These effects included that male lizards infected by malarial parasites (gen. *Plasmodium*) did not dominate agonistic interactions as often (Schall and Dearing 1987). As indicated in Lanser et al. (2021), the prevalence of *L. occidentalis* in their study population was low (12%) compared to the population studied here (42.8%). This suggests that (1) the higher prevalence of *L. occidentalis* afforded us greater statistical power; (2) the results reflect differences across populations in the vulnerability of the lizards to the effects of infection by this parasite (Piecyk et al. 2019); (3) and/or the effect of the experimental manipulation of the tick load performed by Lanser et al. (2021) accounted for most of the variance of the behavioral traits quantified in the lizards. The parasite genus *Lankesterella* infects hosts of various taxa and regions of the world (lizards: Megía-Palma et al. 2017; birds: Merino et al. 2006; Martínez et al. 2018; and amphibians: Netherlands 2019). However, its pathogenic effect is poorly described as compared to other parasites (Chagas et al. 2021). Here, the lower behavioral performance of infected lizards suggests a negative effect of *Lankesterella* on the agonistic behavior of *S. occidentalis* and partially supports the initial prediction of energetic trade-offs between aggression and infections by endoparasites. However, intestinal coccidians and mites had no effect on the behavioral traits evaluated. The number of mites per lizard host was low in the sample (Megía-Palma, pers. obs). The lower volume of blood drawn by mites as compared to ticks might also explain their lack of effect (but see Klukowski and Nelson 2001). Intestinal coccidians also had no effect on the behavior of the lizards despite the expected negative effect (Megía-Palma et al. 2018, 2020). This suggests that some parasites may interfere in physiological processes leading to specific trade-offs but not others (Xu et al. 2010).

In conclusion, the role of male blue patches as a badge of status was supported because the size and chroma of the opponents' blue patches were negatively associated with the number of pushups and lateral compressions performed by focal males during pairwise contests. Our results also revealed a comparatively smaller influence of some parasites on lizard agonistic behavior and thus a rather limited support for a parasite-mediated cost–benefit model of aggression. The lower number of pushups performed by lizards infected by *Lankesterella* partially supports the prediction that parasitic infections can contribute to explain host contest behavior in lizards (Lanser et al. 2021). Interestingly, the results also showed that the relationship between tick abundance and aggression can be positive in unmanipulated lizards (but see Lanser et al. 2021), suggesting that more aggressive lizards can incur higher costs in terms of increased ticks (Payne et al. 2021). This may occur via a higher exposure to parasites of more aggressive (dominant) males moving more in a territory (Moore 1988; Bouma et al. 2007) and/or via energetic trade-offs between aggression and immunity (Pryke et al. 2007). This is a clear indication that further experimental testing of the mediation of parasites in the cost–benefit hypothesis is still needed in agonistic contests.

Acknowledgments

To B, a constant inspiration. S. Reguera helped to capture lizards. C. Wertin, N. Bunn, and K. Pauling assisted housing the lizards and with male contests.

Funding

American National Science Foundation and Spanish Ministerio de Economía y Competitividad provided financial support (EEBB-I-14-08326 to RM-P and EF-1241848 to BS). RM-P enjoys a postdoctoral contract (CEECIND/04084/2017) by ICETA – Instituto de Ciências, Tecnologias e Agroambiente da Universidade do Porto and Fundação da Ciência e Tecnologia. Authors declare no conflict of interest.

Conflict of Interest

Authors declare no conflict of interest.

Ethical Statement

UCSC ethics committee (IACUC) and CDFG provided permits for carrying out this investigation.

Author Contributions

BS: supervision. RM-P, DP, PB: data collection. RMP: formal analysis. RM-P, PB, RC: writing.

Data Availability

Data was provided as supplementary file for the review process and will also be accessible after an embargo period from Mendeley Data. DOI: 10.17632/td73sj9wxm.1

Informed Consent

Not applicable.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

References

Abalos J, Pérez i de Lanuza G, Carazo P, Font E, 2016. The role of male coloration in the outcome of staged contests in the European common wall lizard *Podarcis muralis*. *Behaviour* **153**:607–631.

Andersson M, 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Assis BA, Avery JD, Earley RL, Langkilde T, 2022. Masculinized sexual ornaments in female lizards correlate with ornament-enhancing thermoregulatory behavior. *Integr Org Biol* **4**:obac029.

Assis BA, Avery JD, Tylan C, Engler HI, Earley RL et al., 2021. Honest signals and sexual conflict: female lizards carry undesirable indicators of quality. *Ecol Evol* **11**:7647–7659.

Assis BA, Swierk L, Langkilde T, 2018. Performance, behavior and offspring morphology may offset reproductive costs of male-typical ornamentation for female lizards. *J Zool* **306**:235–242.

Baird T, 2013. Lizards and other reptiles as model systems for the study of contest behaviour. In: Hardy I, Briffa M, editors. *Animal Contests*. Cambridge: Cambridge University Press, 258–286.

Bajer K, Molnár O, Török J, Herczeg G, 2011. Ultraviolet nuptial colour determines fight success in male European green lizards *Lacerta viridis*. *Biol Lett* **7**:866–868.

Barber I, 2002. Parasites, male-male competition and female mate choice in the sand goby. *J Fish Biol* **61**:185–198.

Barrientos R, Megía-Palma R, 2021. Associated costs of mitigation-driven translocation in small lizards. *Amphib-Reptilia* **42**:275–282.

Barton K, 2018. MuMIn: Multi-Model Inference. R package version 1.40.4. Available from: https://CRAN.R-project.org/ package=MuMIn.

Bastiaans E, Morinaga G, Castañeda-Gaytán JG, Marshall JC, Sinervo B, 2013. Male aggression varies with throat color in 2 distinct populations of the mesquite lizard. *Behav Ecol* **24**:968–981.

Bedrick EJ, Tsai CL, 1994. Model selection for multivariate regression in small samples. *Biometrics* **50**:226–231.

Berglund A, Bisazza A, Pilastro A, 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol J Linn Soc* **58**:385–399.

Bohórquez-Alonso ML, Mesa-Avila G, Suárez-Rancel M, Font E, Molina-Borja M, 2018. Predictors of contest outcome in males of two subspecies of *Gallotia galloti* (Squamata: Lacertidae). *Behav Ecol Sociobiol* **72**:63.

Bouma MJ, Smallridge CJ, Bull CM, Komdeur J, 2007. Susceptibility to infection by a haemogregarine parasite and the impact of infection in the Australian sleepy lizard *Tiliqua rugosa*. *Parasitol Res* **100**:949–954.

Bower DS, Brannelly LA, McDonald CA, Webb RJ, Greenspan SE et al., 2019. A review of the role of parasites in the ecology of reptiles and amphibians. *Austral Ecol* **44**:433–448.

Burnham KP, Anderson DR, 2004. Multimodel inference, understanding AIC and BIC in model selection. *Sociol Method Res* **33**:261–304.

Calisi RM, Hews DK, 2007. Steroid correlates of multiple color traits in the spiny lizard *Sceloporus pyrocephalus*. *J Comp Physiol B* **177**:641–654.

Carpenter CC, Ferguson GW, 1977. Variation and evolution of stereotyped behavior in reptiles. In: Gans S, Tinkle DW, editors. *Biology of the Reptilia. Vol. 7: Ecology and Behavior*. New York: Academic Press, 335–554.

Chagas CRF, Harl J, Preikša V, Bukauskaitė D, Ilgūnas M et al., 2021. *Lankesterella* (Apicomplexa, Lankesterellidae) blood parasites of passeriform birds: prevalence, molecular and morphological characterization, with notes on sporozoite persistence *in vivo* and development *in vitro*. *Animals* **11:** 1451.

Christenson TE, Goist Jr KC, 1979. Costs and benefits of male: male competition in the orb weaving spider *Nephila clavipes*. *Behav Ecol Sociobiol* **5**:87–92.

Cooper Jr WE, Burns N, 1987. Social significance of ventrolateral coloration in the fence lizard *Sceloporus undulatus*. *Anim Behav* **35**:526–532.

Cox RM, Skelly SL, Leo A, John-Alder HB, 2005. Testosterone regulates sexually dimorphic coloration in the eastern fence lizard *Sceloporus undulatus*. *Copeia* **2005**:597–608.

Cox RM, Zilberman V, John-Alder HB, 2008. Testosterone stimulates the expression of a social color signal in yarrow's spiny lizard *Sceloporus jarrovii*. *J Exp Zool A* **309**:505–514.

Deutsch CJ, Haley MP, Le Boeuf BJ, 1990. Reproductive effort of male northern elephant seals: estimates from mass loss. *Can J Zool* **68**:2580–2593.

Dunlap KD, Mathies T, 1993. Effects of nymphal ticks and their interaction with malaria on the physiology of male fence lizards. *Copeia* **1993**:1045–1048.

Dunlap KD, Schall JJ, 1995. Hormonal alterations and reproductive inhibition in male fence lizards *Sceloporus occidentalis* infected with the malarial parasite *Plasmodium mexicanum*. *Physiol Zool* **68**:608–621.

Dunn PO, Armenta JK, Whittingham LA, 2015. Natural and sexual selection act on different axes of variation in avian plumage color. *Sci Adv* **1**:e1400155.

Duvall D, 1979. Western fence lizard *Sceloporus occidentalis* chemical signals. I. Conspecific discriminations and release of a species-typical visual display. *J Exp Zool* **210**:321–325.

Emlen ST, Oring LW, 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* **197**(4300):215–223.

Endler JA, 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biol J Linn Soc* **41**:315–352.

Enquist M, Leimar O, 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *J Theor Biol* **102**:387–410.

Fairbairn DJ, Blanckenhorn WU, Szekely T, 2008. *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford: Oxford University Press.

Font E, Molina-Borja M, 2004. Ultraviolet reflectance of color patches in *Gallotia galloti* from Tenerife, Canary Islands. In: Pérez-Mellado V, Riera N, Perera A, editors. *The Biology of Lacertid Lizards*, Vol. 8. Recerca: Institut Menorquí d'Estudis. 201–221.

Garland Jr T, Hankins E, Huey RB, Huey RB, 1990. Locomotor capacity and social dominance in male lizards. *Funct Ecol* **4**:243–250.

Goodlett C, Stephenson BP, 2019. Body color and morphological correlates of fitness in eastern fence lizards *Sceloporus undulatus*: a spectrophotometric approach. *Herpetologica* **75**:69–78.

Griffith SC, Pryke SR, 2006. Benefits to females of assessing color displays. In: Hill GE, McGraw K, editors. *Bird Coloration: Function and Evolution*. New Haven: Harvard University Press, 233–279.

Grill CP, Rush VN, 2000. Analysing spectral data: comparison and application of two techniques. *Biol J Linn Soc* **69**:121–138.

Hamilton WJ, Poulin R, 1995. Parasites, aggression and dominance in male upland bullies. *J Fish Biol* **47**:302–307.

Hegyi G, Garamszegi LZ, 2011. Using information theory as a substitute for stepwise regression in ecology and behavior. *Behav Ecol Sociobiol* **65**:69–76.

Holmes JC, Zohar S, 1991. Pathology and host behaviour. In: Barnard CJ, Behnke JM, editors. *Parasitism and Host Behaviour*. London: Taylor and Francis, 34–63.

Hoops D, Whiting MJ, Keogh JS, 2022. A smaller habenula is associated with increasing intensity of sexual selection. *Brain Behav Evol* **97**:265–273.

Huyghe K, Vanhooydonck B, Scheers H, Molina-Borja M, Van Damme R, 2005. Morphology, performance and fighting capacity in male lizards *Gallotia galloti*. *Funct Ecol* **19**:800–807.

Innocenti G, Pinter N, Galil BS, 2003. Observations on the agonistic behavior of the swimming crab *Charybdis longicollis* Leene infected by the rhizocephalan barnacle *Heterosaccus dollfusi* Boschma. *Can J Zool* **81**:173–176.

Johnstone RA, 1996. Multiple displays in animal communication: ‘backup signals’ and ‘multiple messages’. *Philos T R Soc B* **351**:329–338.

Klukowski M, Nelson CE, 2001. Ectoparasite loads in free-ranging northern fence lizards *Sceloporus undulatus hyacinthinus*: effects of testosterone and sex. *Behav Ecol Sociobiol* **49**:289–295.

Lane JE, Boutin S, Speakman JR, Humphries MM, 2010. Energetic costs of male reproduction in a scramble competition mating system. *J Anim Ecol* **79**:27–34.

Lane RS, Kleinjan JE, Schoeler GB, 1995. Diel activity of nymphal *Dermacentor occidentalis* and *Ixodes pacificus* (Acari: Ixodidae) in relation to meteorological factors and host activity periods. *J Med Entomol* **32**:290–299.

Langkilde T, Boronow KE, 2010. Color as a signal: the relationship between coloration and morphology in male eastern fence lizards *Sceloporus undulatus*. *J Herpetol* **44**:261–271.

Lanser DM, Vredevoe LK, Kolluru GR, 2021. Tick parasitism impairs contest behavior in the western fence lizard *Sceloporus occidentalis*. *Behav Ecol Sociobiol* **75**:1–15.

Lemos-Espinal JA, Smith GR, Ballinger RE, 1996. Ventral blue coloration and sexual maturation in male *Sceloporus gadoviae* lizards. *J Herpetol* **30**:546–548.

Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D, 2021. Performance: an R Package for assessment, comparison and testing of statistical models. *J Open Source Softw* **6**:3139. doi:10.21105/joss.03139.

Marler CA, Moore MC, 1988. Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behav Ecol Sociobiol* **23**:21–26.

Marshall KL, Philpot KE, Damas-Moreira I, Stevens M, 2015. Intraspecific colour variation among lizards in distinct island environments enhances local camouflage. *PLoS ONE* **10**:e0135241.

Martín J, López P, 2009. Multiple color signals may reveal multiple messages in male Schreiber’s green lizards *Lacerta schreiberi*. *Behav Ecol Sociobiol* **63**:1743–1755.

Martínez J, Merino S, Badás EP, Almazán L, Moksnes A et al., 2018. Hemoparasites and immunological parameters in snow bunting *Plectrophenax nivalis* nestlings. *Polar Biol* **41**: 1855–1866.

Martins EP, 1993. Contextual use of the pushup display by the sagebrush lizard *Sceloporus graciosus*. *Anim Behav* **45**:25–36.

Martins EP, 1994. Structural complexity in a lizard communication system: the *Sceloporus graciosus* “Push-Up” display. *Copeia* **1994**:944–955.

McElroy EJ, de Buron I, 2014. Host performance as a target of manipulation by parasites: a meta-analysis. *J Parasitol* **100**:399–410.

Megía-Palma R, Barrientos R, Gallardo M, Martínez J, Merino S, 2021. Brighter is darker: the Hamilton–Zuk hypothesis revisited in lizards. *Biol J Linn Soc* **134**:461–473.

Megía-Palma R, Martínez J, Acevedo I, Martín J, García-Roa R et al., 2015. Phylogeny of the reptilian *Eimeria*: are *Choleoeimeria* and *Acroeimeria* valid generic names? *Zool Scr* **44**:684–692.

Megía-Palma R, Martínez J, Paranjpe D, D’Amico V, Aguilar R et al., 2017. Phylogenetic analyses reveal that *Schellackia* parasites (Apicomplexa) detected in American lizards are closely related to the genus *Lankesterella*: is the range of *Schellackia* restricted to the Old World? *Parasite Vector* **10**:470.

Megía-Palma R, Martínez J, Merino S, 2016a. Structural- and carotenoid-based throat colour patches in males of *Lacerta schreiberi* reflect different parasitic diseases. *Behav Ecol Sociobiol* **70**:2017–2025.

Megía-Palma R, Martínez J, Merino S, 2016b. A structural colour ornament correlates positively with parasite load and body condition in an insular lizard species. *Sci Nat* **103**:1–10.

Megía-Palma R, Paranjpe D, Reguera S, Martínez J, Cooper RD et al., 2018. Multiple color patches and parasites in *Sceloporus occidentalis*: differential relationships by sex and infection. *Curr Zool* **64**:703–711.

Megía-Palma R, Paranjpe D, Blaimont P, Cooper R, Sinervo B, 2020. To cool or not to cool? Intestinal coccidians disrupt the behavioral hypothermia of lizards in response to tick infestation. *Ticks Tick Borne Dis* **11**:101275.

Merino S, Martínez J, Martínez-de la Puente J, Criado-Fornelio A, Tomás G et al., 2006. Molecular characterization of the *18S* rDNA gene of an avian *Hepatozoon* reveals that it is closely related to *Lankesterella*. *J Parasitol* **92**:1330–1335.

Mikheev VN, Pasternak AF, Taskinen J, Valtonen ET, 2010. Parasite-induced aggression and impaired contest ability in a fish host. *Parasite Vector* **3**:1–8.

Millar RB, Anderson MJ, 2004. Remedies for pseudoreplication. *Fish Res* **70**:397–407.

Montgomerie R, 2008. CLR 1.1 Software. Analyzing Colours. [Last Accessed 2021 February 01]. Available from: https://bobmontgomerie.wordpress.com/resources/analyzing-colours/.

Moore MC, 1988. Testosterone control of territorial behavior: Tonic-release implants fully restore seasonal and short-term aggressive responses in free-living castrated lizards. *Gen Comp Endocr* **70**:450–459.

Morris MR, Mussel M, Ryan MJ, 1995. Vertical bars on male *Xiphophorus multilineatus*: A signal that deters rival males and attracts females. *Behav Ecol* **6**:274–279.

Mulvey M, Aho JM, 1993. Parasitism and mate competition: Liver flukes in white-tailed deer. *Oikos* **66**:187–192.

Netherlands EC, 2019. *Ecology, Systematics and Evolutionary Biology of Frog Blood Parasites in Northern KwaZulu-Natal, 109*. PhD thesis, North-West University (South Africa) and KU Leuven (Belgium).

Oppliger A, Celerier ML, Clobert J, 1996. Physiological and behaviour changes in common lizards parasitized by haemogregarines. *Parasitology* **113**:433–438.

Ord TJ, Blumstein DT, Evans CS, 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. *Proc R Soc Lond B* **268**:737–744.

Ossip-Drahos AG, Berry NJ, King CM, Martins EP, 2018. Information-gathering as a response to manipulated signals in the eastern fence lizard *Sceloporus undulatus*. *Ethology* **124**:684–690.

Payne E, Sinn DL, Spiegel O, Leu ST, Gardner MG et al., 2021. Consistent after all: Behavioral repeatability in a long-lived lizard across a 6-year field study. *Anim Behav* **174**:263–277.

Pérez i de Lanuza G, Font E, 2010. Lizard blues: blue body coloration and ultraviolet polychromatism in lacertids. *Rev Española Herpetol* **24**:67–84.

Pérez i de Lanuza G, Font E, Monterde JL, 2013. Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids. *J Evol Biol* **26**:1826–1835.

Piecyk A, Roth O, Kalbe M, 2019. Specificity of resistance and geographic patterns of virulence in a vertebrate host-parasite system. *BMC Evol Biol* **19**:1–14.

Plavicki J, Yang EJ, Wilczynski W, 2004. Dominance status predicts response to nonsocial forced movement stress in the green anole lizard *Anolis carolinensis*. *Physiol Behav* **80**:547–555.

Pollock NB, Vredevoe LK, Taylor EN, 2012. The effect of exogenous testosterone on ectoparasite loads in free-ranging western fence lizards. *J Exp Zool Part A* **317**:447–454.

Pounds JA, Jackson JF, 1983. Utilization of perch sites by sex and size classes of *Sceloporus undulatus undulatus*. *J Herpetol* **17**:287–289.

Pryke SR, Astheimer LB, Buttemer WA, Griffith SC, 2007. Frequency-dependent physiological trade-offs between competing colour morphs. *Biol Lett* **3**:494–497.

Quinn VS, Hews DK, 2003. Positive relationship between abdominal coloration and dermal melanin density in phrynosomatid lizards. *Copeia* **2003**:858–864.

R Core Team., 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available from: https://www.R-project.org/.

Raia P, Guarino FM, Turano M, Polese G, Rippa D et al., 2010. The blue lizard spandrel and the island syndrome. *BMC Evol Biol* **10**:1–16.

Reguera S, Zamora-Camacho FJ, Moreno-Rueda G, 2014. The lizard *Psammodromus algirus* (Squamata: Lacertidae) is darker at high altitudes. *Biol J Linn Soc* **112**:132–141.

Ressel S, Schall JJ, 1989. Parasites and showy males: Malarial infection and color variation in fence lizards. *Oecologia* **78**:158–164.

Robinson CD, Gifford ME, 2019. Intraseasonal changes of patch color in prairie lizards *Sceloporus consobrinus*. *Herpetologica* **75**:79–84.

Romero-Díaz C, Rivera JA, Ossip-Drahos AG, Zúñiga-Vega JJ, Vital-García C et al., 2019. Losing the trait without losing the signal: Evolutionary shifts in communicative colour signalling. *J Evol Biol* **32**:320–330.

Sacchi R, Pupin F, Gentilli A, Rubolini D, Scali S et al., 2009. Male-male combats in a polymorphic lizard: residency and size, but not color, affect fighting rules and contest outcome. *Aggress Behav* **35**:274–283.

Salvador A, Veiga JP, Martin J, Lopez P, Abelenda M et al., 1996. The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation. *Behav Ecol* **7**:145–150.

Schall J, Bennett AF, Putnam RW, 1982. Lizards infected with malaria: physiological and behavioral consequences. *Science* **217**:1057–1059.

Schall JJ, Dearing MD, 1987. Malarial parasitism and male competition for mates in the western fence lizard *Sceloporus occidentalis*. *Oecologia* **73**:389–392.

Schall JJ, Sarni GA, 1987. Malarial parasitism and the behavior of the lizard *Sceloporus occidentalis*. *Copeia* **1987**:84–93.

Seddon RJ, Hews DK, 2016. Phenotypic correlates of melanization in two *Sceloporus occidentalis* (Phrynosomatidae) populations: behavior, androgens, stress reactivity, and ectoparasites. *Physiol Behav* **163**:70–80.

Shanbhag B, Saidapur S, Radder R, 2006. Big boys on top: Effects of body size, sex and reproductive state on perching behaviour in the tropical rock dragon *Psammophilus dorsalis*. *Anim Biol* **56**:311–321.

Sheldahl LA, Martins EP, 2000. The territorial behavior of the western fence lizard *Sceloporus occidentalis*. *Herpetologica* **56**:469–479.

Sheldon BC, Verhulst S, 1996. Ecological immunology: Costly parasite defences and trade-offs in evolutionary ecology. *Trends Ecol Evol* **11**:317–321.

Sorci G, Clobert J, Michalakis Y, 1996. Cost of reproduction and cost of parasitism in the common lizard *Lacerta vivipara*. *Oikos* **76**:121–130.

Stoehr AM, McGraw KJ, 2001. Ultraviolet reflectance of color patches in male *Sceloporus undulatus* and *Anolis carolinensis*. *J Herpetol* **35**:168–171.

Stuart-Fox DM, Ord TJ, 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proc R Soc Lond* **271**:2249–2255.

Swierk L, Langkilde T, 2013. Bearded ladies: females suffer fitness consequences when bearing male traits. *Biol Lett* **9**:20130644.

Symonds MR, Moussalli A, 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol* **65**:13–21.

Van Niekerk JH, Megía-Palma R, Forcina G, 2022. Thermoregulatory function and sexual dimorphism of the throat sack in Helmeted Guineafowl *Numida meleagris* across Africa. *Avian Res* **13**:100047.

Vinegar MB, 1972. The function of breeding coloration in the lizard *Sceloporus virgatus*. *Copeia* **1972**:660–664.

Whiting MJ, Stuart-Fox DM, O'Connor D, Firth D, Bennett NC et al., 2006. Ultraviolet signals ultra-aggression in a lizard. *Anim Behav* **72**:353–363.

Xu T, Ping J, Yu Y, Yu F, Yu Y et al., 2010. Revealing parasite influence in metabolic pathways in Apicomplexa infected patients. *BMC Bioinform* **11**:1–9.

Žagar A, Simčič T, Dajčman U, Megía-Palma R, 2022. Parasitemia and elevation as predictors of hemoglobin concentration and antioxidant capacity in two sympatric lizards. *Comp Biochem Phys A* **270**:111233. doi:10.1016/j.cbpa.2022.111233.

Zúñiga-Vega JJ, Pruett JA, Ossip-Drahos AG, Campos SM, Seddon RJ et al., 2021. Information out of the blue: phenotypic correlates of abdominal color patches in *Sceloporus* lizards. *Zoology* **149**:125961.