

Aggression, color signaling, and performance of the male color morphs of a Brazilian lizard (*Tropidurus semitaeniatus*)

Andre C. Bruinje^{1,2,3} · Felipe E. A. Coelho³ · Tales M. A. Paiva³ · Gabriel C. Costa⁴

Received: 16 October 2018 / Revised: 1 April 2019 / Accepted: 9 April 2019 / Published online: 8 May 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Behavior can help to establish dominance in intrasexual interactions, preventing more costly aggressive interactions and improving access to mates. Distinct color morphs often correlate with behavior, driving differential reproductive success between them. The lizard *Tropidurus semitaeniatus* usually expresses two male color morphs, *Yellow* or *Black*. It is likely that morphs play a role in reproduction, which is still unexplored. Here, we test whether there is morph-related dominance during intrasexual interactions. We used ex situ behavioral trials to test whether a particular morph shows dominance, gathering dominance by attributing scores to aggressive/evasive behaviors. We also tested whether winner individuals show higher performance (sprint speed), and whether spectrophotometric measures of body coloration predict winners of male encounters. Morphs showed differences in behaviors suggesting alternative behavioral tactics: *Black* males behave more aggressively and less evasively while *Yellow* males show the opposite sets of behavior. *Black* males also tend to be dominant, but dominants do not show higher sprint speeds than submissive males. Chest coloration, often displayed during encounters, highly predicts winnings (particularly high yellow chroma and low lightness and UV). Our results show that lizards signal competitive condition by behaviorally exposing their chest. Males displaying more head bobs and with darker chests are more likely to win encounters. Our results suggest that *Yellow* males might undertake a sneaker tactic, preventing aggression costs by evasiveness even though they might perform similarly to *Black* males. Further studies should address whether female preference is biased in relation to male morphs and its colorations, which would suggest selective processes towards costly signals and morph maintenance.

Significance statement

In the struggle for survival and reproduction, often, there is no single best strategy and multiple distinct tactics may evolve. Behavior, color signaling, and performance are frequently correlated with distinct color morphs, which can coexist as alternative mating tactics. However, studies that are able to integrate all these traits are scarce. Here, we test whether different color morphs of the lizard *Tropidurus semitaeniatus* show different behaviors and dominance patterns. We also test whether these color morphs differ in their

Communicated by S. J. Downes

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00265-019-2673-0>) contains supplementary material, which is available to authorized users.

✉ Andre C. Bruinje
abruinje@gmail.com

¹ Graduate Program in Ecology and Conservation Biology, Universidade Federal do Paraná, Curitiba, PR, Brazil

² Department of Physiology, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

³ Laboratory of Biogeography, Macroecology and Evolutionary Biology, Department of Ecology, Universidade Federal do Rio Grande do Norte, Natal, RN, Brazil

⁴ Department of Biology, Auburn University at Montgomery, Montgomery, AL 36124, USA

performances (sprint speed) and visual signaling (behavioral displays and intensity of coloration). We demonstrate that *Black* and *Yellow*-morph males adopt distinct behavioral tactics: an aggressive (*Black*-morph) and an evasive (*Yellow*-morph) tactic. We also show that dominance is highly correlated to chest's intensity of dark yellow colorations and that lizards signal their dominance status through displays of head bob bouts.

Keywords Behavioral display · Animal coloration · Intrasexual competition · Agonistic behavior · Alternative reproductive tactics · Sprint speed

Introduction

Much of biological diversity is produced by processes of sexual selection. An example is the selective pressure for conspicuous

traits that increases signaling in the competition for mate access (Endler 1980). In addition to the selection on morphologies, competition for reproduction can also select for different behavioral tactics (Hurtado-Gonzales and Uy 2010). These multiple tactics are often associated with distinct color morphs (Taborsky et al. 2008). Hence, in many cases, behavior (i.e., either female preference or male behavioral tactics) can drive variation in morphology and coloration. Some examples are male ornaments (e.g., visual, chemical, acoustic, and behavioral signaling) selected by female choice (e.g., Deere et al. 2012; Puechmaile et al. 2014); male armaments and behavioral signals selected by male-male competition (Seddon et al. 2013); and social hierarchy that directly influences mating success (e.g., Hover 1985; Andersson 1994; Berglund et al. 1996). Interestingly, selection on coloration can also influence selection of physiological traits (such as behavior and morphology), an inverse direction of selection driven by pleiotropic effects of some genes that define color expression (e.g., such as *SPR* and *BCO2* in *Podarcis muralis*) (Andrade et al. 2019). Even so, it is still arguable that selection of such colorations can still be driven by behavior through inter- or intrasexual social selection, if animal coloration is used as a signal in these organisms. For instance, mating formation of the lizard *P. muralis* is assorted by color morph (Pérez i De Lanuza et al. 2012). This means that males and females of the same color class will prefer to mate with each other instead of with an individual that expresses another coloration.

In male-male competition, behavioral signals are important because they might convey information on individual fighting ability (Arak 1983). This can help to establish dominance without major costs (Smith and Price 1973). Signals are expected to carry a cost to be honest (Zahavi 1975), and behavioral signals often determine dominance. For instance, in the lizard *Urosaurus ornatus*, dominant males show distinct behaviors (i.e., perform more aggressive behaviors such as biting, chases, lateral compression, dewlap extension, and pushups) and have access to more mates, and hence higher fitness (Robson and Miles 2000). Another example is the males of *Egernia whitii*. In this lizard species, individuals differ in their consistency of behavior: in ex situ male-male trials, individuals that were consistent in always performing aggressively during consecutive trials were usually the winner and dominant (McEvoy et al. 2013). Dominance is often correlated to individual performance. On the beetle *Onthophagus taurus*, physical performance, secondary sexual trait size (horn length), and body mass were all correlated with fighting success in male-male competition trials (McCullough and Simmons 2016). In the teiid lizard *Tupinambis merianae*, physical performance—measured by their bite force—is correlated to aggression levels. In this species, larger and stronger individuals also tend to be more aggressive (Herrel et al. 2009). Dominance was also

shown to correlate with higher locomotor performance. For instance, male *Anolis cristatellus* lizards that won intrasexual encounters also had a better locomotor performance (Perry et al. 2004). Presumably, in lizards, individuals with better locomotor performances might have advantages in defending territories (Garland Jr et al. 1990; Robson and Miles 2000). Interestingly, in this above-mentioned *Anolis* species, winners had higher performance and also executed more behavioral displays than losers, being an excellent example of the relationships among dominance, performance, and behavioral signaling.

Type and intensity of coloration can also signal individual quality. For example, ultraviolet reflection, a highly conspicuous coloration, can inform individual's physiological performance (fighting ability) and aggression, as in *Platysaurus broadleyi* lizards (Stapley and Whiting 2006). Pigment-based coloration, such as from yellow to red chroma, has been also shown to signal quality and predict individual fitness in many species from different taxa such as fish (e.g., *Poecilia reticulata*—Grether 2000; *Oncorhynchus tshawytscha*—Lehnert et al. 2018), birds (e.g., *Cyanistes caeruleus*—García-Navas et al. 2012; *Euplectes ardens*—Pryke et al. 2010), and lizards (e.g., *Zootoca vivipara*—Fitze et al. 2009; *Liolaemus sarmientoi*—Fernández et al. 2018). In addition, morphs with distinct hues are often related to different behavioral tactics (i.e., color morphs—Sinervo and Lively 1996; Moore et al. 1998; Fernández et al. 2018).

In some species, two distinct mating tactics can coexist within a sex, commonly within males. In most cases, one of the tactics would be the stereotyped male of the species, showing either conspicuous or colorful signaling, developed armament morphologies, and aggression (i.e., the dominant). The other tactic would be pale and dull, often female-like and evasive (i.e., the sneaker male) (Shuster and Wade 2003). In some species, melanism is shown to correlate with aggression and dominance, with darker coloration being presented in more aggressive and dominant individuals (Osborne 2005; Abalos et al. 2016). Such individuals will also likely have a better reproductive success. Other species can show a more complex mating system, such as the side-blotched lizard. In this species, three co-occurring distinct morphs (yellow, blue, and orange) behaviorally outcompete one another cyclically (Sinervo and Lively 1996). One hypothesis to explain the coexistence of multiple morphotypes is that they are mediated by different behavioral tactics and correlated to distinct physiological performances. In conclusion, several lines of evidence suggest that there is a link among behavior, coloration, and performance.

Here, we use pairwise male competition trials between morphs to test whether the two male color morphs of *Tropidurus semitaeniatus* lizards show distinct behavioral tactics (i.e., more aggressive and less

evasive vs. less aggressive and more evasive). Next, by scoring agonistic behaviors, we test whether one of the two types of male color morphs tends to win more encounters (i.e., being dominant). Male morphs of the lizard *T. semitaeniatus* have different mean body sizes and morph relative frequencies vary greatly among populations (Bruinjé et al. 2018a). So, we expect that they would be socially distinct, presenting different outcomes in between-morph encounters. Because aggression levels and muscular performance are influenced by the same mechanism (testosterone levels) (Regnier and Herrera 1993), we expect that dominant individuals (i.e., winners) would also have better performances (faster sprint speeds). We assess individual performance through sprint speed trials. Next, we assess whether males signal their aggressive condition through visual signals and behavioral displays. We expect that aggression would be signaled as a way of preventing escalating interaction costs. Thus, using spectrophotometric measures of body coloration, we explore whether the lizards' coloration predicts the outcome of encounters. We expect that color traits that are likely to be costly (i.e., conspicuous and pigment-based colorations) would be honest signals of hierarchical status and therefore will predict the outcome of the trials.

Methods

Study species

Tropidurus semitaeniatus is a flat rock-dwelling specialist, endemic, and widespread across Northeast Brazil. Because it is specialized to a saxicolous habit, individuals tend to be aggregated in the landscape within rocky patches. Due to the high density of individuals in rocky outcrops, agonistic interactions play an important role in social hierarchy, and interactions for resources such as basking sites, refuges, food, water, and mates (Martins 1994; Haenel et al. 2003). These small sized lizards (≤ 14 g) are assumed to be territorial and sit-and-wait foragers (Kolodiuk et al. 2009), although its territoriality has not been properly studied. They have a marked reproductive season with the onset at the end of the dry season (around late November) lasting until the beginning of the rainy season (late April) (Ribeiro et al. 2012). Like many lizards, its reproductive behavior is assumed to be polygamous, with males potentially harassing females that remain in their territory. It is therefore likely that intrasexual selection influences reproductive success due to its role in territory acquisition. However, intersexual selection could also play a role as females might choose to remain in territories of dominant males. Females usually deposit clutches of two flat-elongated eggs (Vitt 1981). They often lay eggs in communal

nests and can reproduce more than once within the same breeding season (Vitt and Goldberg 1983; Ribeiro et al. 2012). No parental care was ever reported. Males are larger than females and adult males have a peculiar pattern of colorations: to a human (trichromatic) observer, two classes of colorations can be distinguished at their ventral thighs and cloaca (Fig. 1). Patches can be fully yellow (*Yellow* morph) or have an intense dark color on top of the yellow coloration (*Black* morph). Dorsally however, all lizards seem the same, with a spotted, rocky-looking dorsum and a conspicuous bright longitudinal stripe from the forehead to their middle dorsum (Fig. 1a). Male morphs and female coloration in different body regions are distinguishable by their visual system (Bruinjé et al. 2018b). Male morphs co-occur within populations and can be found occupying the same rocky patch. Morph frequencies, however, can vary among populations (Bruinjé et al. 2018a). Morph differences in body size also vary among populations but, in general, *Black* males tend to have larger body sizes than *Yellow* males (Bruinjé et al. 2018a). With the exception of body size, coloration, and population morph frequencies, differences between color morphs have not yet been investigated. It is thus unknown whether *T. semitaeniatus*' male color morphs correspond to alternative behavioral tactics.

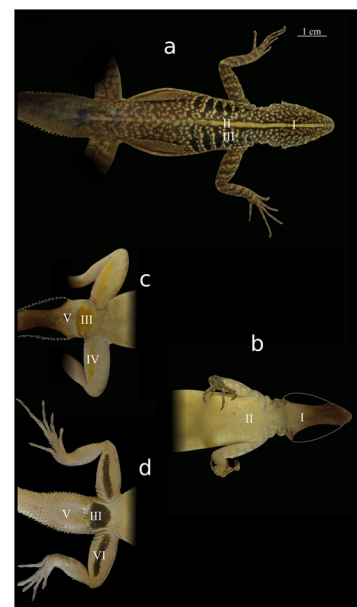


Fig. 1 Dorsal (a) and ventral (b–d) views of male *Tropidurus semitaeniatus* showing the body regions in which spectrophotometric measurements were taken. Dorsal (a) numbering refers to locations of dorsal head stripe (I), dorsal stripe (II), and dorsal side stripe (III). Ventral (b–d) numbering refers to locations of throat (I), chest (II), ventral patch (III), femoral patch (IV), and ventral tail base (V). Adult males of *T. semitaeniatus* express two color morphs that, by a human (tetrachromat) visual system, are differentiable in their ventral color patches (III, IV). Posterior ventral views show a *Yellow* morph male (c) and a *Black* morph male (d). Pictures were taken from live individuals and the hand of the researcher partially covers the lizards (b, c). So, the silhouettes of the lizards are delimited by white dotted lines

Sampling and housing

We conducted male-male interaction trials in March and April of 2015 (within their breeding season, see Ribeiro et al. 2012). We used a noose to collect 240 lizards from a single population in a wild area (João Câmara, RN, Brazil, 05° 32' 15" S, 35° 49' 11" W). We brought the lizards to the laboratory and kept them in individual plastic terrariums (35 × 24 × 12 cm; width × length × height, respectively) fed every other day with three larvae of *Tenebrio molitor*. Terrariums had shelter, ad libitum clean water, and 60-W lamps as heat source timed to natural photoperiod 12:12 h. This study complies with all Brazilian regulations on ethical treatment of wild animal sampling for scientific investigations. Permission to collect and measure the lizards was issued by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio, SISBIO #23164-1).

Male-male competition between color morphs

To test whether color morphs of *T. semitaeniatus* are structured socially in relation to dominance/submissiveness, we staged pairwise encounters between color morphs. We obtained behavioral data by analyzing and quantifying agonistic behaviors from recorded trials. In order to form pairs with a similar body size, we identified male morphs by checking their ventral colored patches (for more information on morph categorization, see Bruinje et al. 2018a), measured snout-vent length (SVL) to the nearest 0.01 mm, and paired unrepeatable lizards of different morphs by size (mean ± SD male size difference: SVL, 1.65 ± 1.31 mm). Even though we allowed little size differences (3.5 mm), we matched lizards by size but allowing *Yellow* males to be the larger ones as much as the *Black* males in order to avoid biasing size difference. Out of our full sample ($N=240$), we managed to pair 42 male lizards with similar body sizes, with a total of 21 trials between male pairs. We excluded four trials that we considered “unresponsive” (individuals did not engage in interaction for more than 50% of the time of the trial). We conducted the trials in a terrarium (70 × 33 × 33 cm) divided into three compartments (Fig. 2). We kept lizards in the lab for 15 days prior to the trials to reduce stress from capture and transportation. We deprived lizards from gathering heat and kept them in room temperature (26 °C) for a period of 24 h prior to the trials. Individuals had 15 min to adjust, each in one side of the terrarium and both separated from each other and from the central area by removable opaque cardboard walls (Fig. 2). We encouraged interactions by heating a natural rock (39 °C ± 2.3SD) with a heat lamp and positioning both rock and heat lamp in the central

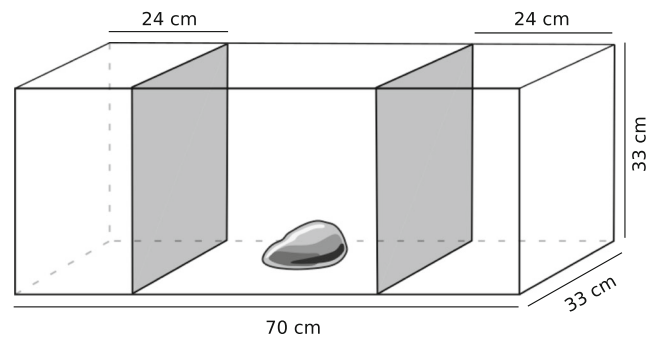


Fig. 2 Scheme of tank used in male-male agonistic trials between male color morphs of *Tropidurus semitaeniatus* lizards with opaque removable walls (in gray). The walls separate visually and physically both subject compartments (left and right compartments) from each other and from natural heated rock (at the center). After 15 min of acclimatization of subjects, the walls are simultaneously removed, allowing subjects to get in contact with each other. Illustrated rock at the center is a natural rock heated with a heat lamp before the trials. Subjects were prevented from thermoregulating for 24 h prior to trials and kept in room temperature (26 °C). The rock is positioned at the center of the tank in order to promote competition between subjects. A heat lamp is also positioned above the rock at the central compartment (not shown)

compartment of the terrarium. Male morphs do not differ in their preferred temperatures (T_{pref}) (ACB et al., unpublished data) so, stimulus for interactions are similar to both morphs. There was no visual contact and access to the rock or lamplight, before the beginning of the 30-min trial (adapted from Schall and Dearing 1987). In order to eliminate potential chemical traces, we thoroughly cleaned the terrarium and replaced sand substrate at the end of each trial. We recorded all trials (120 fps) and used the software VC Griffin for behavior quantification.

We analyzed each video twice, once for each focal male. We defined winners of intrasexual competitions by attributing scores to the agonistic behaviors: each aggressive behavior counted 1 score and each evasive behavior deducted 1 score for each individual. We then used the sum of all displayed behaviors (aggressive and evasive) scores of each individual as the variable *total score*. We categorized agonistic behaviors based on the agonistic ethogram of the species (Coelho et al. 2018). Behaviors displayed by these lizards are easily classifiable: aggressive displays consist of, at least, proactive behaviors towards the opponent while evasive displays are clearly passive and/or towards the opposite direction of the opponent. Also, the majority of these displays are very similar to several species of lizards (e.g., Fernández et al. 2018). Displays that did not fit into any of these classifications (i.e., were not clearly agonistic) were not scored (i.e., had score = 0). Among the zero score, displays were the behaviors that are not clearly a signal of aggression or submissiveness (such as head bobs and head bob bouts) and behaviors that are supposedly exploratory, collecting

information from the environment (e.g., tongue flicks at the substrate). The individual with the higher *total score* of each competition trial is considered winner of the encounter (adapted from Garland Jr et al. 1990). So, each valid pair of competing males resulted in one winner and one loser, individual. To minimize observer bias, we used blinded methods when all behavioral data were recorded and/or analyzed.

Assessment of behavioral visual signaling of male dominance

Apart from agonistic displays, lizards have also a broad diversity of behaviors used in intraspecific social signaling. Among the most common of these behaviors are head bobs, head bob bouts, and tongue flicks, which are all common in *T. semitaeniatus* (Coelho et al. 2018). Head bobs are assumed to play a role in emitting a signal whereas tongue flicks would collect information (chemical) from the environment (Cooper 1994). In order to assess whether individuals make use of behavioral displays to signal their aggressive status, we counted the number of head bob bouts (a sequence of head bobs that usually consists of eight full movements or more) as a visual signaling behavior displayed during the trials to compare with the outcome of the trials.

Performance and male dominance

Aggressiveness is directly influenced by testosterone levels which, in turn, affect muscle development (Regnier and Herrera 1993; Weiss and Moore 2004; Kabelik et al. 2008). Therefore, we expect that more aggressive and dominant individuals would also perform better. To test this hypothesis, we compared the outcome of encounters (“winner” or “loser”) with data on individual maximum sprint speed. To gather sprint speed, we ran each individual in a 2-m long racetrack with sandpaper as substrate for a proper traction (Brandt et al. 2015). Because body temperature (T_b) is known to influence performance in lizards, we allowed individuals to thermoregulate for a period of 90 min prior to the trials. We measured T_b right before the sprint trials with a cloacal thermometer in order to assure that lizards had reached T_b around their T_{Pref} ($37 \pm 2^\circ\text{C}$, ACB et al. unpublished data). Lizards ran three times with a minimum resting period of 24 h between trials. We stimulated the lizards to run with soft touches at the tip of the tail with a feather. The value of maximum sprint was the fastest 25-cm interval of all runs of each individual that we analyzed from 120-fps recordings (for studies with lizards that used similar or lower filming speeds, see Collins et al. 2013; Brandt et al. 2015; Wild and Gienger 2018; Winchell et al. 2018). We made the performance measures 10 days after the behavioral trials.

Color as predictor of male dominance

In order to assess whether color traits are related to aggression (winning/losing trials), we measured coloration in several body parts of each lizard (Fig. 1). We obtained reflectance spectra with an optic fiber (R400-7-UV-VIS, Ocean Optics, Dunedin, FL) attached to a spectrophotometer (USB4000-UV-VIS). We took three measures within eight body regions that might be displayed during encounters: throat (V_{Throat}), chest (V_{Chest}), ventral patch (V_{Patch} , the patch cloacal region), femoral patch ($V_{FemoralPatch}$), ventral tail base ($V_{TailBase}$), head stripe ($D_{HeadStripe}$, measured within the head’s dorsal bright stripe), dorsum stripe (D_{Stripe} , measured within the dorsal bright stripe), and side stripe ($D_{SideStripe}$, measured at the dark stripes directly at the side of D_{Stripe}) (Fig. 1). We derived different color variables (Table S1) from the spectral reflectance curves using the R package pavo (Maia et al. 2013). First, we restricted spectra curves between 300 and 700 nm, the wavelength range perceivable by lizards (Loew et al. 2002), and averaged all three measures taken at each region of each lizard. Ultraviolet reflection, carotenoid, and melanin-based colorations are known to relate with several individual qualities and signaling (Stapley and Whiting 2006; Martín and López 2009; Saenko et al. 2013). So, we derived color variables that represent these different aspects of coloration: segment-specific ultraviolet and yellow saturations (S_{UV} and S_{Yellow} , respectively), hue (*Hue*), and mean lightness ($M_{Lightness}$).

Statistical analysis

To assess whether male color morphs of *T. semitaeniatus* adopt distinct behavioral tactics we compared the total amount of aggressive and evasive behaviors displayed between morphs. For that, we compared the total amount of aggressive displays between color morphs with a chi-squared test. We also compared the total amount of evasive displays between color morphs with a chi-squared test. Next, to determine whether color morphs differ in winning encounters (i.e., dominance), we performed a paired Wilcoxon signed rank test with the *total score* of individuals as response variable and color morph (*Yellow* vs. *Black*) as fixed factor and paired the test by each male dyad. Because body size is known to correlate with sprint speed performance in lizards, we corrected maximum sprint speed for body size. So, to assess whether color morphs differ in performance, we ran an ANCOVA using color morph as fixed factor, maximum sprint speed as response variable, and SVL as co-variable.

Next, we attributed to each individual a final status of winner (1) or loser (0), producing the binary variable *outcome*, and tested whether there is an association of performance on dominance. For that, we used *outcome* as fixed factor, maximum sprint speed as response variable, and SVL as co-

variable in an ANCOVA. Then, to assess whether coloration predicts *outcome* of encounters, we performed binomial logistic regression analyses with the color variables as predictors of *outcome*. Due to the sample size of trials (17 pairs), we performed separate binomial generalized linear model functions with a logit model using each of the four color variables (*Hue*, $M_{\text{Lightness}}$, S_{UV} , and S_{Yellow}) of each body region (V_{Throat} , V_{Chest} , V_{Patch} , $V_{\text{FemoralPatch}}$, V_{TailBase} , $D_{\text{HeadStripe}}$, D_{Stripe} , and $D_{\text{SideStripe}}$) as predictors. Similarly, to assess whether individuals signal their hierarchical status (dominance) through visual behaviors, we performed a binomial logistic regression analysis with the visual behaviors (number of head bob bouts) as predictor of *outcome*. We ran all statistical analysis in R software (R Core Team 2017).

Data availability

The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Results

Color morphs differed significantly in the types of agonistic behaviors that they displayed during male-male encounters. *Yellow* males performed less aggressive behaviors, $\chi^2_{(1, N=267)} = 5.69$, $P < 0.05$ (Table 1) and more evasive behaviors, $\chi^2_{(1, N=195)} = 14.4$, $P < 0.001$. This resulted in the opposite sets of behavior in *Black* males. Color morphs did also differ in dominance ($V = 153$, $N = 34$, $P < 0.001$), but not in performance after controlling for body size ($F_{1,38} = 2.0944$, $P = 0.156$). Dominant males also have not had higher performances than submissive males when controlling sprint speed for body size ($F_{1,30} = 0.0003$, $P = 0.986$).

Intensity of chest coloration had a strong relationship with dominance (Table 2, Fig. 3a–c). Logistic regression showed

Table 1 Total number of agonistic (aggressive and evasive) behaviors displayed, category of the behavior according to the species agonistic ethogram (Coelho et al. 2018), and relative percentage (in parenthesis), by each male color morph (*Black* and *Yellow*) of *Tropidurus semitaeniatus* lizards during male-male competition encounters

| Behavior | Category | Displayed by | | | |
|----------------------|------------|--------------------|-------|---------------------|-------|
| | | <i>Black</i> males | | <i>Yellow</i> males | |
| Approach | Aggressive | 53 | (24%) | 46 | (19%) |
| Intimidation posture | Aggressive | 38 | (17%) | 22 | (9%) |
| Chase | Aggressive | 14 | (6%) | 13 | (5%) |
| Bite | Aggressive | 31 | (14%) | 28 | (12%) |
| Dorsum show | Aggressive | 17 | (8%) | 5 | (2%) |
| Tail wave | Evasive | 4 | (2%) | 23 | (10%) |
| Retreat | Evasive | 67 | (30%) | 101 | (42%) |

Table 2 Results of logistic regression of color variables on outcome of male-male competition encounters of *Tropidurus semitaeniatus* lizards between their two male color morphs. OR shows the odds ratio of an increase of 10% in the predictor color variable with 95% of confidence interval (CI). Bold indicates models with significant effect of the color variables in predicting the outcome of encounters

| Variable | Estimate | Std. error | OR | 95% CI | <i>P</i> |
|-------------------------|----------|------------|------|-----------|--------------|
| Chest lightness | −0.194 | 0.084 | 0.48 | 0.25–0.92 | 0.028 |
| Chest UV saturation | −38.045 | 17.955 | 0.65 | 0.44–0.98 | 0.042 |
| Chest yellow saturation | 96.605 | 46.016 | 1.55 | 1.01–2.37 | 0.043 |
| Ventral patch hue | 0.035 | 0.015 | 1.36 | 1.05–1.77 | 0.022 |

that low values of $M_{\text{Lightness}}$ and S_{UV} in V_{Chest} were related to a higher winning probability (Table 2, Fig. 3a, b), and also that higher S_{Yellow} values increased winning probability (Table 2, Fig. 3c). At V_{Patch} , hue highly and positively predicted the outcome of encounters (Table 2, Fig. 3d). In addition, logistic regression showed that the number of head bob bouts highly predicted wins (OR = 1.69; 95% CI 1.01–2.85, $N = 34$, $P < 0.05$) (Fig. 4).

Discussion

Color morphs presented significant difference between types of behaviors that they displayed during agonistic intrasexual encounters. *Black* morph males were significantly more aggressive and, in addition, dominated over *Yellow* males more often. These, on the other hand, behaved more evasively (and less aggressively) and tended to end the trial as submissive. Among the agonistic displays categorized as submissive and evasive is tail waving, which *Yellow* males displayed more often. Tail displays are usually described as anti-predatory behaviors, but it is also observed in subordinate individuals within social interactions, as in *Chalcidius viridianus* after being chased by a rival (Machado et al. 2007; Alonso et al. 2010; Sánchez-Hernández et al. 2012). Different behavioral tactics are known to occur in some polymorphic species, enabling morph coexistence (Dijkstra et al. 2009). In *Podarcis muralis* for instance, a species of lizard that may express up to five color morphs, morph distribution and their relative frequencies vary among populations. Recent evidence suggests that these morphs, that differ in several physiological traits (e.g., temperature-dependent locomotor performance; Zajitschek et al. 2012), compensate physiological and occurrence differences through their behavior, mediating habitat use (Pérez de Lanuza and Carretero 2018). In these lizards, success in dyadic agonistic encounters also vary depending on which morphs are competing (Abalos et al. 2016). In *Tropidurus semitaeniatus*, *Yellow* males displayed higher number of tail wave (and all evasive behaviors), fewer displays of aggressive behaviors, and tended to be submissive. These results suggest

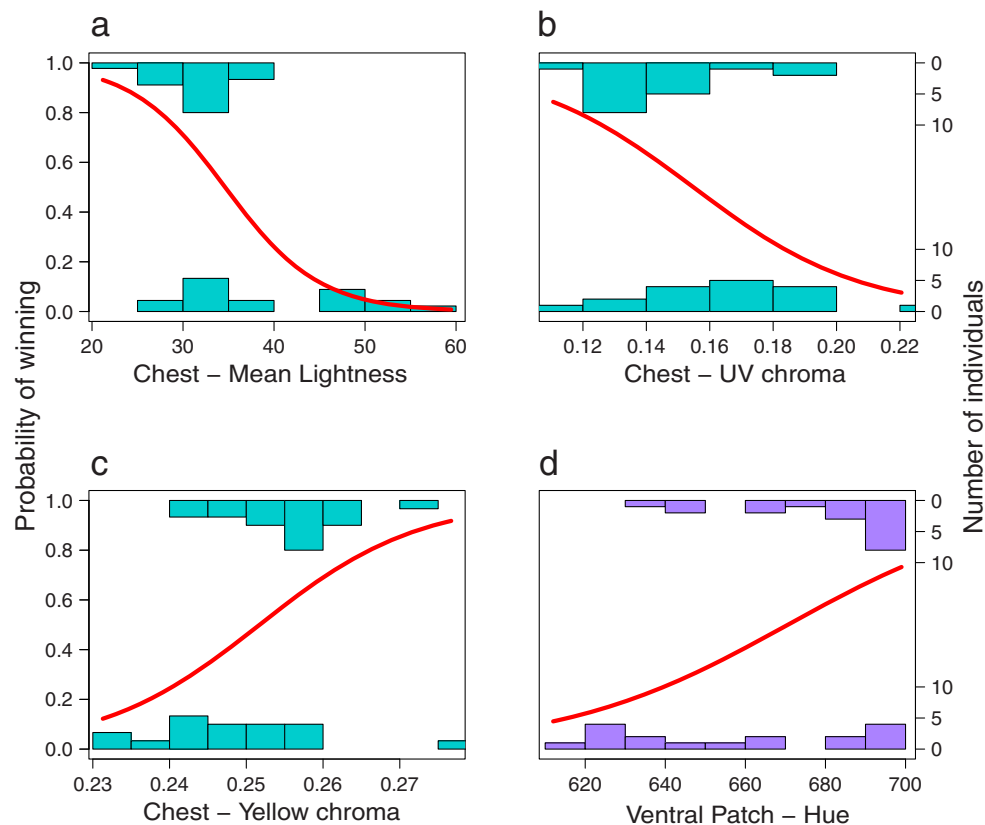


Fig. 3 Plots of logistic regression models of color variables on the outcome of encounters between males of the lizard *Tropidurus semitaeniatus*. Red continuous lines show logistic model of the probability of winning encounters (Y left axis) in relation to trait value (X axis). Bar plots show the number of individuals (Y right axis) that won (upper bars) and lost (lower bars) encounters distributed according to their

trait value (X axis). Bar plot colors relate to the body regions chest (green; a–c) and ventral patch (purple; d). Significant (that yielded P values < 0.05) models are plotted by color variables in body regions: mean lightness at the chest (a); ultraviolet chroma at the chest (b); yellow chroma at the chest (c); and hue at ventral patch (d)

an occurrence of alternative behavioral tactics in the species, with *Yellow* males showing an evasive and submissive tactic while *Black* males, a dominant and aggressive tactic. Further studies should explore whether male color morphs of *T. semitaeniatus* also differ in behaviors in other contexts such as testing them for boldness, which could characterize male morphs within a proactive-reactive axis of a behavioral syndrome (Sih et al. 2004). In such situation, aggression and boldness are correlated, and a selected increase in one trait drives the other. This correlation could buffer the selection towards aggressiveness since extremely aggressive individuals would also be extremely bold. Exacerbated boldness would increase natural selection by predation of such individuals, buffering the selection towards aggressiveness.

Color morphs differed in dominance with *Black* males winning more encounters. Dominants did not, however, differ in body size-controlled sprint speed. Dominant males also did not differ in performance from submissive males. Namely, sprint speed performance is not related to agonistic dominance in intrasexual interactions in *T. semitaeniatus*. Interestingly, this result goes against our expectations based on studies of

other lizard species in which performance was found to be correlated to dominance. For instance, dominance is highly associated with sprint speed and stamina performances in *Urosaurus ornatus* (Robson and Miles 2000). Likewise, sprint speed is significantly higher in winner males of *Sceloporus occidentalis*. However, stamina does not relate with wins in this species (Garland Jr et al. 1990). Although maximum sprint speed is commonly used as a proxy for performance in lizards, it is possible that it does not capture whole organism performance and is influenced by ecological habits of the species. *Tropidurus semitaeniatus* lizards are sit-and-wait foragers that tend to remain in the same rock outcrops for long periods of time during the day, moving short distances intermittently to capture prey, and thermoregulate and hide in rock crevices nearby (Kolodiuk et al. 2009). Sprint speed might play a role in retreating from threats and patrolling and defending a territory, but may not capture a performance measure related to intrasexual dominance mediated by agonistic interactions in this species. As an alternative in these lizards, it would be interesting to explore other physiological variables as a proxy of performance and its relationship with

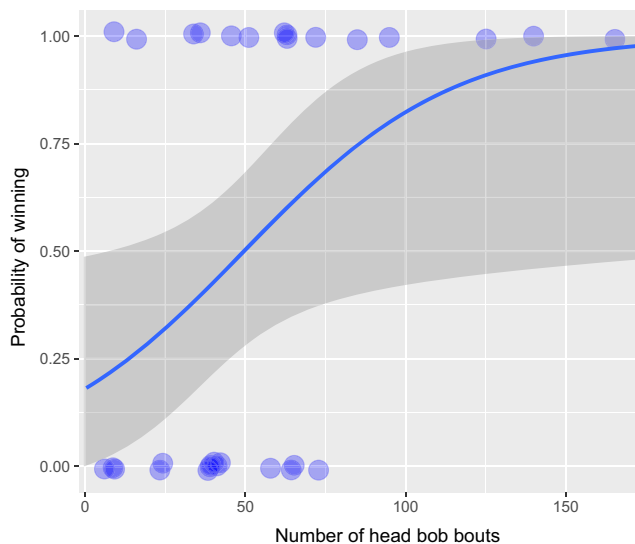


Fig. 4 Logistic regression model of the number of head bob bouts on the outcome of encounters between male morphs of *Tropidurus semitaeniatus*. Blue continuous line shows logistic function. The increment on the probability of winning encounters increases with number of displays of head bob bouts. Purple circles at the top indicate number of bouts displayed by each winner lizards whereas circles at the bottom indicate number of bouts displayed by loser lizards

dominance. Bite force would be a good example, as the behavior bite was very common in the trials (Table 1) and it is discussed to be a better physiological performance predictor of dominance due to its direct influence on agonistic interactions (Herrel et al. 2009).

The intensity of coloration at the chest of the lizards had a strong relationship with dominance. Low values of lightness predicted greater probability of winning encounters and, in addition, higher values of yellow saturation also increased winning probability. For instance, an increase in 10% of chest yellow saturation increases the chances of winning by 55% (Table 2). In other words, lizards with darker and more intense yellow saturation in their chests were more likely to win. This is an interesting finding since the expression of both dark and yellow colors are often related to pigment-based coloration (e.g., melanin and carotenoid) (Steffen and McGraw 2009), being both costly and indicative of individual quality (Grether 2000; Martín and López 2009). In addition, ventral yellow coloration was also found to correlate with increased aggression in *Zootoca vivipara* (Vercken and Clobert 2008). The underlying mechanisms of the expression of darker-yellow coloration in *T. semitaeniatus* were not yet studied. However, it is known that melanism is often correlated to testosterone-mediated aggression (McGraw et al. 2003; Osborne 2005), dominance status (Evans et al. 2000), and to configure cost to the bearer in several contexts (Evans et al. 2000; Jawor and Breitwisch 2003; Tanaka 2009; Qi et al. 2011).

In addition to visual communication by the expression of coloration, we showed that visual behavioral displays also play a role in the outcome of agonistic interactions in this

species. The number of head bob bouts displayed during the encounters highly predicted wins. With an increase in 10% of head bob bouts, for instance, the chances of winning are increased by 69%; thus, meaning that individuals signaled their fighting ability through head bobbing, making use of this behavior to reinforce dominance status. Head bob bouts are sequences of rapid up-and-down movements of the head. While performing it, the lizard extends its neck and often stretches its forearms in a way that the head is positioned as high as possible (Coelho et al. 2018). During such a display to conspecifics, it is likely that its opponent visually assesses both throat and chest areas of the behaving individual. Therefore, together with a high correlation between darker-yellowish colors and wins, it suggests that lizards tend to expose these colorations during contests. Although our results are not a proof of a costly signal of chest coloration, they suggest that the ventral parts of the body play a role in conspecific communication. In addition, the increased head bob bouts related to aggression also supports this suggestion.

It is likely that both behavior and color function as signals of male quality (Osborne 2005). Different signals may convey the same, or supplementary, information, thus reinforcing each other (e.g., back-up hypothesis; Johnstone 1996). Further studies should explore physiological mechanisms of the production of structural and pigment-based coloration in these lizards. Both ultraviolet reflectance and lightness—types of coloration linked to signal cost by conspicuousness—had a negative effect on the probability of winning (Fig. 3a, b). So, notably, individuals with lower ultraviolet reflectance at their chest tended to win encounters (Fig. 3b). This finding is contrary to our expectations based on previous studies: intrasexually, UV reflection is known to correlate with (*Lacerta viridis*, Bajer et al. 2011), and inform (*Platysaurus broadleyi*, Stapley and Whiting 2006), fighting skills in lizards; whereas intersexually, males choose females with high ventral UV (*Ctenophorus ornatus*, LeBas and Marshall 2000) and UV-deprived males are also less likely to be chosen by females (*Ameivula ocellifera*, Lisboa et al. 2017). Therefore, although there is evidence that *T. semitaeniatus* lizards reflect UV at their throats (Bruinjé et al. 2018b), UV signaling does not appear to determine male social dominance. Hence, with the conjoined results of UV and lightness on winnings, we conclude that dominance is signaled through the expression of darker chests. Further, at the ventral patches—a colored patch common to several *Tropidurus* species—hue highly predicted the outcome of agonistic interactions (Fig. 3d). Although behaviors that exhibit the patches are not displayed very often (Coelho et al. 2018), it appears that coloration at the patches plays a role in the probability of winning, as darker yellow-to-greenish color is expressed at the patch (Fig. 1; Bruinjé et al. 2018b).

We did find a strict social status relationship of dominance/submissiveness between *T. semitaeniatus* color morphs, in

which *Black* morph males tended to dominate over *Yellow* males. In addition, we found a higher proportion of aggressive against evasive displays in *Black* males, while the opposite was found in *Yellow* males. Together, these results suggest that morphs behave consistently as alternative behavioral tactics in this species. In addition, we found that chest coloration plays a significant role on dominance in intrasexual context. We found strong association of low lightness and yellow coloration to dominance, which suggests that individuals signal their intrinsic quality—fighting ability—through their coloration. Future steps would be to explore the physiological mechanisms responsible for the production of color of the chest and ventral patch areas. Coloration of ventral patches in *Tropidurus* species is supposed to be linked to the occurrence of glandular scales (Carvalho et al. 2016), which was not studied yet. Hormone levels might be responsible for mediating high melanin in the tissue. Thus, pigment-based coloration promoted by hormone levels could characterize these patches as multi-modal signaling badges. Also, this information would allow inferences on the costs of this signal and its function in social interactions. In addition, it would be interesting to manipulate coloration at the chest during female choice experiments. Here, we show that chest coloration is a strong predictor of male dominance and such experiments could reveal whether this trait also influences reproductive success through differential female preference for alternatives as mates.

Acknowledgments We thank the Universidade Federal do Rio Grande do Norte for the structure in which measurements and trials were performed. We also thank TC Bruinjé for assistance with analysis, and three anonymous reviewers which contributions significantly improved the paper.

Funding We thank CAPES – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior for AB's PhD scholarship and PDSE fellowship (88881.135775/2016-01). This work was supported by CNPq – Conselho Nacional de Desenvolvimento Científico e Tecnológico (grant 474392/2013-9). GC thanks CNPq productivity grant (302297/2015-4).

Compliance with ethical standards

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Ethical approval was granted through the Ethics committee to the use of animals—CEUA (Protocol No. 040/2013). This study complies with all Brazilian regulations on ethical treatment of wild animal sampling under scientific investigations.

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

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. <https://doi.org/10.1163/1568539X-00003366>
- Alonso MLB, Cotrina JM, Pardo DA, Font E, Molina-Borja M (2010) Sex differences in antipredator tail-waving displays of the diurnal yellow-headed gecko *Gonatodes albogularis* from tropical forests of Colombia. *J Ethol* 28:305–311. <https://doi.org/10.1007/s10164-009-0186-4>
- Andersson MB (1994) Sexual selection. Princeton University Press, Princeton
- Andrade P, Pinho C, Pérez G et al (2019) Regulatory changes in pterin and carotenoid genes underlie balanced color polymorphisms in the wall lizard. *P Natl Acad Sci* 116:5633–5642
- Arak A (1983) Sexual selection by male-male competition in natterjack toad choruses. *Nature* 306:261–262. <https://doi.org/10.1038/306261a0>
- 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. <https://doi.org/10.1098/rsbl.2011.0520/r10.1111/j.1095-8312.2000.tb00221.x>
- 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. <https://doi.org/10.1006/bjil.1996.0043>
- Brandt R, Galvani F, Kohlsdorf T (2015) Sprint performance of a generalist lizard running on different substrates: grip matters. *J Zool* 297: 15–21. <https://doi.org/10.1111/jzo.12253>
- Bruinjé AC, Leivas PT, Costa GC (2018a) Characterisation of sexual dimorphism and male colour morphs of *Tropidurus semitaeniatus* (Spix, 1825) in three populations from northeast of Brazil. *Herpetol Notes* 11:755–760
- Bruinjé AC, Moura MO, Maggi BS, São-Pedro VA, Pessoa DMA, Costa GC (2018b) Conspecifics of the Striped Lava Lizard are able to distinguish sex and male colour morphs in apparently homogeneous dull dorsal coloration. *Amphibia-Reptilia* published online. <https://doi.org/10.1163/15685381-20181048>
- Carvalho ALG, Sena MA, Peloso PLV, Machado FA, Montesinos R, Silva HR, Campbell G, Rodrigues MT (2016) A new *Tropidurus* (Tropiduridae) from the semiarid Brazilian Caatinga: evidence for conflicting signal between mitochondrial and nuclear loci affecting the phylogenetic reconstruction of South American collared lizards. *Am Museum Novit* 3852:66–68. <https://doi.org/10.1206/3852.1>
- Coelho FEA, Bruinjé AC, Costa GC (2018) Ethogram with the description of a new behavioral display for the striped lava lizard, *Tropidurus semitaeniatus*. *S Am J Herpetol* 13:96–101. <https://doi.org/10.2994/SAJH-D-17-00101.1>
- Collins CE, Self JD, Anderson RA, McBrayer LD (2013) Rock-dwelling lizards exhibit less sensitivity of sprint speed to increases in substrate rugosity. *Zoology* 116:151–158. <https://doi.org/10.1016/j.zool.2013.01.001>
- Cooper WE (1994) Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. *J Chem Ecol* 20:439–487. <https://doi.org/10.1007/BF02064449>
- Deere KA, Grether GF, Sun A, Sinsheimer JS (2012) Female mate preference explains countergradient variation in the sexual coloration of guppies (*Poecilia reticulata*). *Proc R Soc Lond B* 279:1684–1690. <https://doi.org/10.1098/rspb.2011.2132>
- Dijkstra PD, Hemelrijk C, Seehausen O, Groothuis TGG (2009) Color polymorphism and intrasexual competition in assemblages of cichlid fish. *Behav Ecol* 20:138–144. <https://doi.org/10.1093/beheco/arn125>
- Endler J (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 34:76–91. <https://doi.org/10.2307/2408316>
- Evans MR, Goldsmith AR, Norris SRA (2000) The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). *Behav Ecol Sociobiol* 47:156–163

- Fernández JB, Bastiaans E, Medina M, Mendéz De la Cruz FR, Sinervo BR, Ibarguengoytia NR (2018) Behavioral and physiological polymorphism in males of the austral lizard *Liolaemus sarmientoi*. *J Comp Physiol A* 204:219–230. <https://doi.org/10.1007/s00359-017-1233-1>
- Fitzze PS, Cote J, San-Jose LM, Meylan S, Isaksson C, Andersson S, Rossi JM, Clobert J (2009) Carotenoid-based colours reflect the stress response in the common lizard. *PLoS One* 4:e5111. <https://doi.org/10.1371/journal.pone.0005111>
- García-Navas V, Ferrer ES, Sanz JJ (2012) Plumage yellowness predicts foraging ability in the blue tit *Cyanistes caeruleus*. *Biol J Linn Soc* 106:418–429. <https://doi.org/10.1111/j.1095-8312.2012.01865.x>
- Garland T Jr, Hankins E, Huey RB (1990) Locomotor capacity and social dominance in male lizards. *Funct Ecol* 4:243–250. <https://doi.org/10.2307/2389343>
- Grether GF (2000) Carotenoid limitation and mate preference evolution: a test of the indicator hypothesis in guppies (*Poecilia reticulata*). *Evolution* 54:1712–1724. <https://doi.org/10.1111/j.0014-3820.2000.tb00715.x>
- Haenel GJ, Smith LC, John-Alder HB (2003) Home-range analysis in *Sceloporus undulatus* (Eastern fence lizard). I. Spacing patterns and the context of territorial behavior. *Copeia* 2003:99–112. [https://doi.org/10.1643/0045-8511\(2003\)003\[0099:HRAISU\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2003)003[0099:HRAISU]2.0.CO;2)
- Herrel A, Andrade DV, de Carvalho JE, Brito A, Abe A, Navas C (2009) Aggressive behavior and performance in the Tegu lizard *Tupinambis merianae*. *Physiol Biochem Zool* 82:680–685. <https://doi.org/10.1086/605935>
- Hover EL (1985) Differences in aggressive behavior between two throat color morphs in a lizard, *Urosaurus ornatus*. *Copeia* 1985:933–940. <https://doi.org/10.2307/1445244>
- Hurtado-Gonzales JL, Uy JAC (2010) Intrasexual competition facilitates the evolution of alternative mating strategies in a colour polymorphic fish. *BMC Evol Biol* 10:391. <https://doi.org/10.1186/1471-2148-10-391>
- Jawor JM, Breitwisch R (2003) Melanin ornaments, honesty, and sexual selection. *Auk* 120:249–265. [https://doi.org/10.1642/0004-8038\(2003\)120\[0249:MOHASS\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2003)120[0249:MOHASS]2.0.CO;2)
- Johnstone RA (1996) Multiple displays in animal communication: 'back-up signals' and 'multiple messages'. *Phil Trans R Soc B* 351:329–338. <https://doi.org/10.1098/rsta.1892.0001>
- Kabelik D, Weiss SL, Moore MC (2008) Steroid hormones alter neuroanatomy and aggression independently in the tree lizard. *Physiol Behav* 93:492–501. <https://doi.org/10.1016/j.physbeh.2007.10.008>
- Kolodiuk MF, Ribeiro LB, Freire EMX (2009) The effects of seasonality on the foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata: Tropiduridae) living in sympatry in the Caatinga of northeastern Brazil. *Zoologia* 26:581–585. <https://doi.org/10.1590/S1984-46702009000300026>
- LeBas N, Marshall N (2000) The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. *Proc R Soc Lond B* 267:445–452. <https://doi.org/10.1098/rspb.2000.1020>
- Lehnert SJ, Garver KA, Richard J, Devlin RH, Lajoie C, Pticher TE, Heath DD (2018) Significant differences in maternal carotenoid provisioning and effects on offspring fitness in Chinook salmon colour morphs. *J Evol Biol* 31:1876–1893
- Lisboa CMCA, Bajer K, Pessoa DMA, Huber M, Costa GC (2017) Female Brazilian whiptail lizards (*Cnemidophorus ocellifer*) prefer males with high ultraviolet ornament reflectance. *Behav Process* 142:33–39. <https://doi.org/10.1016/j.beproc.2017.05.009>
- Loew ER, Fleishman LJ, Foster RG, Provencio I (2002) Visual pigments and oil droplets in diurnal lizards: a comparative study of Caribbean anoles. *J Exp Biol* 205:927–938
- Machado LL, Galdino CAB, Sousa BM (2007) Defensive behavior of the lizard *Tropidurus montanus* (Tropiduridae): effects of sex, body size and social context. *S Am J Herpetol* 2:136–140. [https://doi.org/10.2994/1808-9798\(2007\)2\[136:DBOTLT\]2.0.CO;2](https://doi.org/10.2994/1808-9798(2007)2[136:DBOTLT]2.0.CO;2)
- Maia R, Eliason CM, Bitton PP, Doucet SM, Shawkey MD (2013) Pavo: an R package for the analysis, visualization and organization of spectral data. *Methods Ecol Evol* 4:906–913. <https://doi.org/10.1111/2041-210X.12069>
- 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. <https://doi.org/10.1007/s00265-009-0794-6>
- Martins EP (1994) Phylogenetic perspectives on the evolution of lizard territoriality. In: Vitt L, Pianka ER (eds) *Lizard ecology: historical and experimental perspectives*. Princeton University Press, Princeton, pp 117–144
- McCullough EL, Simmons LW (2016) Selection on male physical performance during male–male competition and female choice. *Behav Ecol* 27:1288–1295. <https://doi.org/10.1093/beheco/arw033>
- McEvoy J, While GM, Sinn DL, Wapstra E (2013) The role of size and aggression in intrasexual male competition in a social lizard species, *Egernia whitii*. *Behav Ecol Sociobiol* 67:79–90. <https://doi.org/10.1007/s00265-012-1427-z>
- McGraw KJ, Dale J, Mackillop EA (2003) Social environment during molt and the expression of melanin-based plumage pigmentation in male house sparrows (*Passer domesticus*). *Behav Ecol Sociobiol* 53: 116–122
- Moore MC, Hewsf DK, Knapp R (1998) Hormonal control and evolution of alternative male phenotypes: generalizations of models for sexual differentiation. *Am Zool* 38:133–151. <https://doi.org/10.1093/icb/38.1.133>
- Osborne L (2005) Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decresii*). *J Ethol* 23:189–197. <https://doi.org/10.1007/s10164-005-0151-9>
- Pérez i De Lanuza G, Carretero MA (2018) Partial divergence in microhabitat use suggests environmental-dependent selection on a colour polymorphic lizard. *Behav Ecol Sociobiol* 72:138. <https://doi.org/10.1007/s00265-018-2550-2>
- Pérez i De Lanuza G, Font E, Carazo P (2012) Color-assortative mating in a color-polymorphic lacertid lizard. *Behav Ecol* 24:273–279. <https://doi.org/10.1093/beheco/ars164>
- Perry G, Levering K, Girard I, Garland T Jr (2004) Locomotor performance and social dominance in male *Anolis cristatellus*. *Anim Behav* 67:37–47. <https://doi.org/10.1016/j.anbehav.2003.02.003>
- Pryke SR, Andersson S, Lawes MJ (2010) Sexual selection of multiple handicaps in the red-collared widowbird: female choice of tail length but not carotenoid display. *Evolution* 55:1452–1463
- Puechmaile SJ, Borissov IM, Zsebok S, Allegrini B, Hizem M, Kuenzel S, Schuchmann M, Teeling EC, Siemers BM (2014) Female mate choice can drive the evolution of high frequency echolocation in bats: a case study with *Rhinolophus mehelyi*. *PLoS One* 9: e103452. <https://doi.org/10.1371/journal.pone.0103452>
- Qi Y, Wan H, Gu H, Wang Y (2011) Do displays and badges function in establishing the social structure of male toad-headed lizards, *Phrynocephalus vlangalii*? *J Ethol* 29:381–387. <https://doi.org/10.1007/s10164-010-0252-y>
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>
- Regnier M, Herrera AA (1993) Changes in contractile properties by androgen hormones in sexually dimorphic muscles of male frogs (*Xenopus laevis*). *J Physiol* 461:565–581. <https://doi.org/10.1113/jphysiol.1993.sp019529>
- Ribeiro LB, Silva NB, Freire EMX (2012) Reproductive and fat body cycles of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a caatinga area of northeastern Brazil. *Rev Chil Hist Nat* 85:307–320. <https://doi.org/10.1590/S0073-47212011000200010>

- Robson MA, Miles DB (2000) Locomotor performance and dominance in male Tree Lizards, *Urosaurus ornatus*. *Funct Ecol* 14:338–344. <https://doi.org/10.1046/j.1365-2435.2000.00427.x>
- Saenko SV, Teyssier J, van der Marel D, Milinkovitch MC (2013) Precise colocalization of interacting structural and pigmentary elements generates extensive color pattern variation in *Phelsuma* lizards. *BMC Biol* 11:105. <https://doi.org/10.1186/1741-7007-11-105>
- Sánchez-Hernández P, Ramírez-Pinilla MP, Molina-Borja M (2012) Agonistic and courtship behaviour patterns in the skink *Chalcides viridanus* (Fam. Scincidae) from Tenerife. *Acta Ethol* 15:65–71. <https://doi.org/10.1007/s10211-011-0109-6>
- Schall JJ, Dearing MD (1987) Malarial parasitism and male competition for mates in the western fence lizard, *Sceloporus occidentalis*. *Oecologia* 73:389–392. <https://doi.org/10.1007/BF00385255>
- Seddon N, Botero CA, Tobias JA, Dunn PO, MacGregor HEA, Rubenstein DR, Uy JAC, Weir JT, Whittingham LA, Safran RJ (2013) Sexual selection accelerates signal evolution during speciation in birds. *Proc R Soc B* 280:20131065. <https://doi.org/10.1098/rspb.2013.1065>
- Shuster SM, Wade MJ (2003) Mating systems and strategies. Princeton University Press, Princeton
- Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19:372–378. <https://doi.org/10.1016/j.tree.2004.04.009>
- Sinervo B, Lively CM (1996) The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380:240–243. <https://doi.org/10.1038/380240a0>
- Smith JM, Price GR (1973) The logic of animal conflict. *Nature* 246:15–18. <https://doi.org/10.1038/246015a0>
- Stapley J, Whiting MJ (2006) Ultraviolet signals fighting ability in a lizard. *Biol Lett* 2:169–172. <https://doi.org/10.1098/rsbl.2005.0419>
- Steffen JE, McGraw KJ (2009) How dewlap color reflects its carotenoid and pterin content in male and female brown anoles (*Norops sagrei*). *Comp Biochem Physiol B* 154:334–340. <https://doi.org/10.1016/j.cbpb.2009.07.009>
- Taborsky M, Oliveira RF, Brockmann HJ (2008) The evolution of alternative reproductive tactics: concepts and questions. In: Oliveira RF, Taborsky M, Brockmann HJ (eds) *Alternative reproductive tactics: an integrative approach*. Cambridge University Press, Cambridge, pp 1–21
- Tanaka K (2009) Does the thermal advantage of melanism produce size differences in color-dimorphic snakes? *Zool Sci* 26:698–703. <https://doi.org/10.2108/zsj.26.698>
- Vercken E, Clobert J (2008) Ventral colour polymorphism correlates with alternative behavioural patterns in female common lizards (*Lacerta vivipara*). *Ecoscience* 15:320–326. <https://doi.org/10.2980/15-3-3135>
- Vitt LJ (1981) Lizard reproduction: habitat specificity and constraints on relative clutch mass. *Am Nat* 117:506–514. <https://doi.org/10.1086/283731>
- Vitt LJ, Goldberg SR (1983) Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. *Copeia* 1983:131–141
- Weiss SL, Moore MC (2004) Activation of aggressive behavior by progesterone and testosterone in male tree lizards, *Urosaurus ornatus*. *Gen Comp Endocrinol* 136:282–288. <https://doi.org/10.1016/j.ygcen.2004.01.001>
- Wild KH, Gienger CM (2018) Fire-disturbed landscapes induce phenotypic plasticity in lizard locomotor performance. *J Zool* 305:96–105. <https://doi.org/10.1111/jzo.12545>
- Winchell KM, Maayan I, Fredette JR, Revell LJ (2018) Linking locomotor performance to morphological shifts in urban lizards. *Proc R Soc B* 285:20180229. <https://doi.org/10.1098/rspb.2018.0229>
- Zahavi A (1975) Mate selection—a selection for a handicap. *J Theor Biol* 53:205–214. [https://doi.org/10.1016/0022-5193\(75\)90111-3](https://doi.org/10.1016/0022-5193(75)90111-3)
- Zajitschek SRK, Zajitschek F, Miles DB, Clobert J (2012) The effect of coloration and temperature on sprint performance in male and female wall lizards. *Biol J Linn Soc* 107:573–582. <https://doi.org/10.1111/j.1095-8312.2012.01963.x>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.