



# Behavioral and physiological polymorphism in males of the austral lizard *Liolaemus sarmientoi*

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## Abstract

Integrative behavioral studies show that the interplay between individual physiology and social behavior influences the ecology of the species, ultimately affecting individual fitness. Particularly in lizards, color polymorphism is associated with differential behaviors and reproductive strategies, which are evident in mature males during the mating season. Dominant males generally have greater endurance, higher body temperature, and larger bodies than submissive males, so they can acquire and defend larger territories and have greater access to females for mating. We studied whether the color morphs observed in males of one of the world's southernmost reptiles, *Liolaemus sarmientoi*, are related to behavioral variation during agonistic interactions, thermal physiology, morphology, and/or locomotor stamina. *Liolaemus sarmientoi* males exhibit three color morphs: red (RR), red–yellow (RY), and yellow (YY). These lizards exhibit subtle behavioral displays and we did not observe stamina differences among morphs. However, we found that RR males are more aggressive than YY males during agonistic encounters. In addition, greater body temperature change during trials, higher field body temperatures, and greater head sizes of RR males compared to RY or YY indicate that RR is a dominant morph, which may influence their ability to acquire and defend territory and tactics for achieving reproductive success.

**Keywords** Agonistic behavior · Color morph · Locomotor stamina · Morphology · Thermal physiology

## Introduction

Alternative behavioral strategies in reptiles are often heritable and linked to other traits such as reproductive and hormone cycles, thermal physiology, morphology, immune condition, and locomotor performance. These strategies may also influence individuals' ecological interactions with conspecifics and with other species (Smith and John-Alder 1999; Robson and Miles 2000; Sinervo et al. 2000a, b; Perry et al. 2004; Huyghe et al. 2007; Olsson et al. 2007; Sinervo and Miles 2011). Lizards have been used as models for integrative behavioral studies, which show that individual physiology is closely related to social behavior, which influences the ecology of the species, as well as individual fitness (Miles et al. 2007; Sinervo and Miles 2011; Galeotti et al. 2013; Scali et al. 2016; Lattanzio and Miles 2016). Behavioral studies document that lizards use several types of visual signals to communicate: color patterns, postures, and stereotyped movements (Lombo 1989; Font et al. 2010). Many lizard populations include multiple discrete color morphs that differ in their behaviors and/or reproductive strategies. This

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phenomenon is most common in males (Carpenter 1995; Sinervo and Lively 1996; Huyghe et al. 2007; Miles et al. 2007; Olsson et al. 2007; Bastiaans et al. 2013; Abalos et al. 2016). The behavioral characteristics of each color morph are often expressed through displays with different levels of aggressiveness during the mating season, which, in turn, allow males greater or lesser access to mates (Sinervo and Lively 1996; Olsson et al. 2007; Bastiaans et al. 2013).

The association of color morphs with alternative social strategies has been well-studied in lizards from the northern hemisphere family Phrynosomatidae, especially the lizard *Uta stansburiana* from California (USA). In this species, morphs appear to be controlled by a locus of large effect, which has three alleles with co-dominant effects on throat color (Sinervo et al. 2001, 2006; Corl et al. 2010). Throat color is inherited according to a Mendelian genetic pattern and has a substantial effect on social strategies and behaviors of males and females (Sinervo et al. 2001, 2006). Color morphs in *U. stansburiana* differ in many behavioral and physiological traits, such as territoriality, dispersal, migration, immune function, hormones, and social interactions (in males), as well as egg mass and litter size (in females) (Sinervo and Lively 1996; Sinervo et al. 2000a, b; Svensson et al. 2001; Sinervo and Svensson 2002; Comendant et al. 2003; Mills et al. 2008; Corl et al. 2010; Sinervo and Miles 2011; among other studies). In general, it has been reported that color morphs in lizards differ in locomotor performance (running speed and stamina) and morphology, which appear to influence the outcome of agonistic interactions among males. For example, winners in laboratory trials and/or dominant males and aggressive males in nature usually are faster, have greater stamina and larger head and body than submissive males, so they can acquire and defend large territories and attain more mates (Robson and Miles 2000; Sinervo et al. 2000a; Perry et al. 2004; Calsbeek et al. 2010; Huyghe et al. 2012).

Lizards of the genus *Liolaemus*, belonging to family Liolaemidae from South America, have radiated into a diversity of species with different habits, diets, and modes of reproduction (Cei 1986; Scolaro 2005; Ibagüengoytía 2008; Medina and Ibagüengoytía 2010; Abdala and Quinteros 2014; Fernández et al. 2015, 2017), making it a valuable model for studying behavioral interactions (Martins et al. 2004; Labra et al. 2007; Halloy 2012; Halloy et al. 2013). However, there are no studies in this genus examining the relationship between color polymorphism and behavior or physiology or seeking to explain the emergence and maintenance of population color polymorphism in *Liolaemus* lizards. The study of color polymorphisms linked to behavior in *Liolaemus* could help to shed light on how many times this trait has evolved independently. In particular, it may be possible to take advantage of “replicated natural experiments” in Liolaemidae and Phrynosomatidae, two families

that show substantial parallelism in their life histories (Martins et al. 2004; Fuentes 1976) and are widespread in their respective hemispheres. Herein, we present a starting point for the comprehensive study of social behavior and physiology in Patagonian lizards. Specifically, we studied adult males of *Liolaemus sarmientoi*, which exhibit color polymorphism on the flanks of the body.

*Liolaemus sarmientoi* is a medium sized lizard species (mean snout–vent length,  $SVL_{\text{females}}$ :  $76.90 \pm 1.21$  mm;  $SVL_{\text{males}}$ :  $76.82 \pm 2.02$  mm; Ibagüengoytía et al. 2010), which is omnivorous, saxicolous and viviparous (Cei 1986; Scolaro and Cei 1997). It is distributed between 48°S, 70°W and 52°S, 69°W (Breitman et al. 2014) from central Santa Cruz Province, Argentina, reaching the Strait of Magellan to the South. The distribution makes *L. sarmientoi* and its sympatric congener *Liolaemus magellanicus* the southernmost reptiles of the world (Cei 1986; Scolaro 2005; Breitman et al. 2014). *Liolaemus sarmientoi* is a micro-endemic and specialist species (Abdala et al. 2012) that lives in small populations along rocky outcrops of glaciofluvial deposits or lava spills (from ancient volcanic craters) in the dry Patagonian Magellanic Steppe. *Liolaemus sarmientoi* lives in an unpredictable climate with short daily and seasonal activity periods (5 months), with a mean air temperature of 12 °C during spring and summer. In nature, lizards attain a low mean body temperature of 26 °C during the activity season, even when they prefer a much higher body temperature in the laboratory ( $T_p = 34.4 \pm 0.28$  °C; Ibagüengoytía et al. 2010). These restrictions to attain higher  $T_b$  in nature are probably compensated by their ability to achieve maximum locomotor performance at a wide range of body temperatures (Fernández et al. 2011).

In this study, we explore the existence of color polymorphism in males of *L. sarmientoi* in relation to alternative reproductive tactics, in a lizard that is highly restricted by low environmental temperature and the short duration of the mating season. We test the hypothesis that color polymorphism in adult males is related to different behavioral displays during agonistic interactions, and also relates to thermal ecophysiology, locomotor stamina, and morphology of males. In particular, we test whether color morphs differ in the body temperature ( $T_b$ ) that lizards attain in the natural environment, the  $T_b$  they attain during an agonistic behavioral trial ( $T_b$  change), the  $T_p$ , and the efficiency of thermoregulation ( $E$ , sensu Hertz et al. 1993). Results are discussed in relation to the role of the different morphs in territory acquisition and reproductive success, which could represent an adaptive advantage for species in a changing climate.

## Materials and methods

### Captured specimens

Adult males of *L. sarmientoi* ( $n = 36$ ) were caught by hand or noose in the south of Santa Cruz Province, Argentina ( $51^{\circ}\text{S}$ ,  $69^{\circ}\text{O}$ ; 109 m a.s.l.), during the mating season at the end of October 2013. Males used in behavioral trials were drawn from this sample. For morphometric comparisons, we also included data from 14 males captured at the end of November 2011, giving us a total sample size of 50 for morphometric comparisons. GPS coordinates were recorded at all lizard capture sites (GPS GARMIN Map 60Cx). Sex was determined by the presence of pre-cloacal glands in males, and males were considered adult if they had an SVL greater than 63.2 mm according to the size at sexual maturity defined by Fernández et al. (2017).

### Recorded field data

During captures, body temperatures were recorded ( $T_b$ ; TES 1303,  $\pm 0.03$  °C thermometer) using a thermocouple (TES TP-K01, 1.62 mm diameter) inserted approximately 1 cm inside the cloaca. All individuals were captured outside their shelters, carrying out activities related to foraging, social behavior or thermoregulation. The substrate temperature ( $T_s$ ; TES 1303,  $\pm 0.03$  °C thermometer) was also recorded at the capture site. On capture, each male's snout–vent length (SVL) was measured using a digital caliper ( $\pm 0.02$  mm) and mass was measured using a 50 g Pesola© spring scale ( $\pm 0.3$  g).

### Operative temperatures ( $T_e$ ) for lizards' thermoregulation

The operative temperatures ( $T_e$ ) represent the “null” distribution of  $T_b$  that non-regulating animals would achieve in their environment (Hertz et al. 1993).  $T_e$  was measured in a variety of micro-sites, which *L. sarmientoi* inhabit, using grey PVC models ( $1.5 \times 8$  cm) to mimic an *L. sarmientoi* of adult size. Thus, we estimated the temperature that an individual would experience in its environment (such as under the sun, in shadow, on a rock or inside shelter). The model was chosen to represent a living animal and was validated for *Liolaemus* species of similar shape and size to *L. sarmientoi*, showing a strong association between the model temperature and the live animal temperature ( $r^2 > 0.91$ ; Kubisch et al. 2016). Each model was connected to a thermistor and sealed at the end with silicone (Fastix®). To record operative temperatures, 13 thermal models were connected to five data loggers (HOBO Onset

Computer Corporation), which recorded the temperature every 1 min during field work.

### Color morph classification

Color morphs were recorded immediately after capture by taking photos of the ventral, dorsal and lateral view of the body of each male using a VC-03 Nikon camera (D3100) with flash. Photos were also taken after all experiments (see below) in the lab. Thus, the same person identified the color morphs twice: in the field and also with photos taken in the lab.

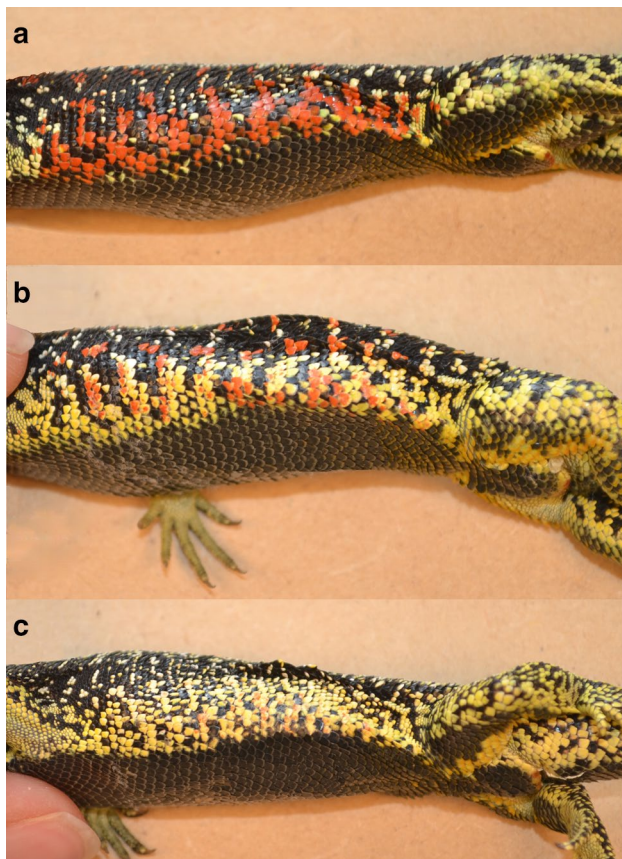
Subsequently, a morph code was assigned using methods previously used with *U. stansburiana* (Sinervo and Lively 1996; Sinervo et al. 2001, 2006), and *Sceloporus grammicus* (Bastiaans et al. 2013). Males were classified by the discrete color observed on the flanks of the animal from the armpit to the hip, and the numbers 1, 0.5 and 0 assigned to each coloration axis (Table 1; Fig. 1). We assigned a score of 1 on a given axis when a color was very intense and not mixed with any other color (pure color, Fig. 1a, c). If two patches of different colors were present on the flank of the lizard (Fig. 1b), we assigned a score of 0.5 on each of those two color axes. All males showed color on the flanks. When one of the colors was absent we assigned 0 for that color on its axis and 1 for the present color.

### Behavioral trials

A subsample of  $n = 34$  males was selected to record, through videos, the behavioral displays between two males interacting in a terrarium to determine the association of agonistic interaction with male color morphs. The day after capture, in the laboratory, we assigned lizards to male–male contests from a sample of individuals chosen taking into account the following premises. Because body size can influence social dominance in lizards (Tokarz 1985; Carpenter 1995; Sacchi et al. 2009; Calsbeek et al. 2010) males in a contest did not differ by more than 4 mm in SVL. In addition, although we do not have data about the home range of *L. sarmientoi*, we attempted to avoid “dear enemy” effects, in which males from neighboring territories exhibit fewer agonistic interactions than males from nonadjacent territories (Whiting

**Table 1** Frequencies assigned to each color morph observed on the flanks of adult males of *L. sarmientoi* and the corresponding photo of Fig. 1

Observed coloration	Red	Yellow	Corresponding photo
Pure red (RR)	1	0	Figure 1a
Red–yellow (RY)	0.5	0.5	Figure 1b
Pure yellow (YY)	0	1	Figure 1c



**Fig. 1** Color morphs observed on the flanks of adult males of *L. sarmientoi*: **a** pure red morphs (RR); **b** red–yellow morphs (RY); **c** pure yellow morphs (YY)

1999). Thus, we ensured that two males used together in a contest had been captured at least 40 m apart from each other, adapting a method used for another territorial lizard species (*Sceloporus grammicus*, Bastiaans et al. 2013). We selected the distance cutoff by recording all the coordinates of all male capture locations and generating a matrix of distances between capture locations, using the program Geographic Distance Matrix Generator (version 1.2.3, American Museum of Natural History 2006). We calculated the average nearest neighbor distance for the population (the mean distance between a focal capture point and the nearest other capture point; approximately 20 m at both sites) and generated the minimum distance between males included in the same trial by doubling that distance (Bastiaans et al. 2013). Thus, 40 m was taken as the minimum distance between males used in the same trial, because it is very unlikely that these males would have had extensive previous interactions.

For the behavioral trials, each male was manipulated with a different latex glove, to prevent mixing scent between individuals before the experiment, and was placed in a chamber measuring 55 cm long  $\times$  35 cm wide  $\times$  24 cm tall, with opaque walls and sand from the sampling site as substrate.

Before each trial, the chamber had two cardboard barriers to produce three equal sections. Males were assigned randomly to one of the two compartments of the chamber (left or right). The central section was used during experiments to encourage lizards to approach and engage in agonistic interactions, it was composed of a central rock and above it a 40 W incandescent light bulb to light the chamber and also to heat the rock and the central area of the chamber (Bastiaans et al. 2013). In addition, the chamber always received ambient sunlight to guarantee a natural perception of opponents during agonistic trials. After every behavioral trial, the chamber and rock were scrubbed with water and dried, and the substrate was changed to prevent scent cues from influencing future trials. Each individual male was used in only one trial.

We performed trials during the activity hours of the lizards observed during captures (between 11:00 and 18:00 pm). Before the beginning of each trial, males were placed in the 2 outer sections of the chamber for at least 5 min as an acclimation period. Trials commenced when both cardboard dividers were simultaneously lifted and ended after 20 min (Bastiaans et al. 2013). Trials were videotaped using a digital video camera (Sony VC-02) mounted on a tripod above the trial chamber. We measured body temperature of each male with an infrared thermometer (AMPROBE IR-750,  $\pm 0.1$  °C) at the beginning ( $T_{\text{initial}}$ ) and the end of the trial ( $T_{\text{final}}$ ) to calculate the body temperature change during the agonistic behavioral trial (% change in  $T_b$ :  $(T_{\text{final}} - T_{\text{initial}}/T_{\text{initial}}) \times 100$ ).

### Behavioral analyses

For analyses of behavioral displays, we recorded the behaviors detailed in Table 2, which are mostly based on literature descriptions of male agonistic behaviors of the genera *Liolaemus* (Martins et al. 2004; Labra et al. 2007; Halloy 2012; Halloy et al. 2013), *Podarcis* (Sacchi et al. 2009), *Sceloporus* (Bastiaans et al. 2013), and *Anolis* (Lombo 1989).

To avoid pseudoreplication, videos were analyzed with the observer focusing on one male (focal male), and the other male was defined as the opponent (Bastiaans et al. 2013). In choosing focal males, we used equal numbers of males from the left and right acclimation chambers (to which they had been randomly assigned before the trial), to discard a potential effect of the acclimation chamber in the behavior of the focal male, specifically we used 8 males from left and 9 males from right chamber. Videos were analyzed with the program Microsoft Windows Movie Maker version 2012, using the frame-by-frame function, which allows us to count the number of moves made in frames ( $\pm 0.033$  s). We recorded the time that elapsed before the first behavior ( $\text{Latency}_{\text{behavior}}$ ) of the focal male and also tallied the number of movements

**Table 2** Name, description and category of behaviors performed during agonistic behavioral trials. Sources: Martins et al. (2004)<sup>1</sup>, Labra et al. (2007)<sup>2</sup>, Sacchi et al. (2009)<sup>3</sup>, Halloy (2012)<sup>4</sup>, Bastiaans et al.(2013)<sup>5</sup>, Halloy et al. (2013)<sup>6</sup>, Lombo (1989)<sup>7</sup>, and Fernández J.B., personal observation<sup>8</sup>

Name	Description	Source	Category
Push-up	The most common behavior in <i>Liolaemus</i> . Entire body moves up and down vertically due to bending and straightening of front legs. Provides information about the identity of the individual. Common in territorial conflicts, more frequent in the winner	1, 2, 4, 5, 6, 7	Aggression or challenge
Lateral compression	Back arching and trunk compression, displaying lateral and belly color patches	2, 5, 7	Aggression or challenge
Approach	Male moves toward opponent while looking at opponent	3, 5, 7	Aggression or challenge
Touch	Male comes into contact with opponent, but not tongue flicks are made	3, 5	Aggression or challenge
Bask	Male occupies territory to increase his temperature, basking on top of the rock and/or under the lamp	8	Dominance
Tongue flicks to the substrate or air	Male touches substrate or air with their tongue or snout. General exploratory behavior	2, 5, 7	Exploratory behavior
Tongue flicks to the opponent	Male touches opponent with their tongue or snout. General exploratory behavior	2, 5	Exploratory behavior
Retreat	Male approached by his opponent runs away fast without facing him	3, 5, 7	Submission
Scratch	Male scratches the ground or the walls of the chamber with the fore or hind limbs, without facing the opponent	3	Submission
Tail wave	Vigorous tail waves side to side and/or above body	2, 3, 5, 6	Submission
Dorso-ventral flattening	Flattening against ground and eyes close	2, 7	Submission

comprising each behavior (Table 2) performed by the focal male over the course of each 20 min trial. To minimize observer bias, blinded methods were used when all behavioral data were recorded and/or analyzed. Thus, all videos were analyzed by the same observer, without knowledge of the color morphs of the lizards involved in each trial.

### Preferred body temperatures ( $T_p$ )

After behavioral trials, with a minimum of 24 h rest, we recorded preferred body temperatures ( $T_p$ ) for all males ( $n = 35$ ). Lizards were placed individually in an open-top terrarium ( $100 \times 25 \times 15$  cm) with a thermal gradient ( $17\text{--}45$  °C) produced by a 75 W incandescent light bulb in a lamp over one end of the terrarium. The body temperature of each lizard was measured using an ultra-thin (0.08 mm) catheter thermocouple inserted approximately 1 cm inside the cloaca and fastened to the base of the lizard's tail to keep the thermocouple in position during the experiment. Thermocouples were connected to a temperature Data Acquisition Module (USB-TC08, OMEGA), which recorded the body temperature every minute for two hours. For each individual, we estimated the mean  $T_p$ , and these means were compared among color morphs.

### Effectiveness of thermoregulation ( $E$ )

Based on  $T_b$ ,  $T_p$  and the operative temperatures ( $T_e$ ), we obtained the following indices for the three color morphs (sensu Hertz et al. 1993): The index of the mean thermal quality of a habitat from an organism's perspective ( $d_e$ ) was calculated as the mean of the absolute value of the deviations of  $T_e$  from the interquartile of the  $T_p$  of each lizard. The  $d_e$  index ( $\text{mean } |T_e - T_p|$ ) allowed us to estimate the availability of thermal microenvironments that are included in the interquartile of the  $T_p$ . In addition, to measure the average extent to which *L. sarmientoi* experienced  $T_b$  outside the interquartile of the  $T_p$ , the mean of the absolute values of the deviations of  $T_b$  from the interquartile of the  $T_p$  of each lizard was obtained ( $d_b$ ). The  $d_b$  index ( $|T_b - T_p|$ ) allowed us to estimate if the activity body temperatures of the lizard were included in the interquartile of the  $T_p$ . The existence of active selection of the microhabitats by thermoregulation and the effectiveness of the thermoregulation was obtained as  $E = 1 - d_b/d_e$  which integrates the thermal resources that *L. sarmientoi* have in their natural microenvironments and their thermoregulation ability. The  $E$  index allowed us to estimate the existence of thermoregulation, with corresponding  $E$  values close to 1 indicative of an excellent thermoregulator; values of  $E$  close to 0 is indicative of a thermoconformer or a passive thermoregulator; values of

$E$  close to 0.50 is indicative of a moderate thermoregulator (Hertz et al. 1993; Bauwens et al. 1996; Medina et al. 2009; Ibarguengoytia et al. 2010).

### Locomotor stamina

After the preferred body temperature experiment, we allowed lizards to rest for a minimum of 24 h before the locomotor stamina experiment. We considered 24 h to be enough time for lizards to recover from stress based on the methods and results of previous experiments (Moore et al. 1991; Sinervo et al. 2000a; Langkilde and Shine 2006). We measured the locomotor stamina of  $n = 33$  males (who had previously participated in the contests) on a rubberized belt of a treadmill moving constantly at 0.5 km/h (Sinervo et al. 2000a). Stamina was defined as the time a lizard spent running on the treadmill before becoming exhausted (Sinervo and Huey 1990; Sinervo et al. 2000a). Animals were considered exhausted when they did not show a righting response after being placed on their back. Lizards were motivated to run (when necessary) by gently touching them on their hind legs or tail. Lizards ran at the mean body temperature recorded during captures for this sample of males ( $28.28 \pm 0.77$  °C,  $n = 33$ ), to measure the locomotor stamina at the body temperature that frequently lizards achieved by thermoregulation while are active in nature (Ibarguengoytia et al. 2010). During and after races activity, body temperature of males on the treadmill was maintained with a 75 W incandescent lamp mounted over the track (Sinervo et al. 2000a).

### Morphometric measures

For morphometric measures, we used lizards captured during the mating season ( $n = 36$ ), and also 14 males from the same population captured at the end of November 2011 (total  $n = 50$ ). We measured (using a digital caliper with a precision of 0.02 mm) the head length, head width, head height, inter-limb length (at the insertion to the shoulders and pelvic girdles), distance between knees (measured ventrally with femurs outstretched perpendicularly to body), and distance between elbows (measured dorsally with arms perpendicularly to body). After all experiments, lizards were released at their exact site of capture, using the coordinates we previously recorded (GPS GARMIN Map 60Cx).

### Statistical analyses

We used the statistical software programs Sigma Stat 3.5<sup>®</sup>, SPSS 15.0<sup>®</sup>, JMP 12<sup>®</sup>, and Sigma Plot 10.0<sup>®</sup> for statistical analyses. Discriminant analysis was used to identify the morphometric variables that best explained the differences among color morphs. Principal component analysis (PCA)

was used to develop integrative measures of the behavior of males during agonistic interactions. We used Paired  $t$  Test comparisons to analyze differences between means of the body temperature of focal males at the beginning and the end of the behavioral trial. When we compare means of the three morphs we used one-way analysis of variance (ANOVA) with a Holm–Sidak method as a posteriori test. Assumptions of normality and homogeneity of variance were checked using Kolmogorov–Smirnov and Levene’s tests, respectively. When normality and/or homogeneity of variance failed, we used the equivalent non-parametric test Kruskal–Wallis one-way ANOVA on Ranks for the comparison of the three morphs. Means are given with the standard error ( $\pm$  SE) and when the assumptions of normality failed we present the median. The significance level used for all statistical tests was  $p < 0.05$ .

## Results

### Color morphs

Based on the observations of each male of *L. sarmientoi* ( $n = 50$ ) immediately after capture, the photos taken in the field and the photos taken in the lab, we recorded three color morphs with two pure colors on the flanks of the body. The most common morph in the population was the pure red (RR) color morph with a frequency of 44%, followed by the mixed color morph red–yellow (RY) with a frequency of 40%, and the least common morph was the pure yellow morph (YY), with a frequency of 16%.

### Agonistic behavioral differences among color morphs

We performed a total of 17 agonistic behavioral trials among color morphs: RY–RY ( $n = 4$ ), RY–RR ( $n = 6$ ), RY–YY ( $n = 1$ ), RR–RR ( $n = 3$ ), YY–RR ( $n = 3$ ). Males of different morphs involved in the agonistic behavioral trials ( $n = 34$ ) were not different in SVL (one-way ANOVA:  $F_{2,33} = 0.082$ ;  $p = 0.922$ , Table 4). Regarding the body temperature at the beginning of the trial, there were no differences among the three morphs (ANOVA:  $F_{2,16} = 0.199$ ;  $p = 0.822$ ). Across all morphs, focal males had higher temperatures at the end ( $T_{\text{final}}$ ) than at the beginning ( $T_{\text{initial}}$ ) of the trial (Paired  $t$  test:  $t_{16} = -5.750$ ;  $p < 0.001$ ).

Exploratory analyses revealed that many of the focal male behavioral variables and also the Latency<sub>behavior</sub> and % change in  $T_b$  were correlated with one another, so we used principal component analysis (PCA) to develop integrative measures of behavior. The variables we included in the PCA were the number of incidences of each behavior (Table 2) during the trial, the % change in  $T_b$ , and also the

**Table 3** Loading scores, eigenvalues, and percent variation explained by principal component 1 and 2 (PC1 and PC2) for behaviors exhibited during agonistic trials, time elapsed before the first behavior ( $\text{Latency}_{\text{behavior}}$ ), and also body temperature change during the trials (% change in  $T_b$ ) by focal males of *L. sarmientoi*

Behavior	PC1 loading	PC2 loading
% change in $T_b$	0.253	0.682*
$\text{Latency}_{\text{behavior}}$	-0.460*	0.690*
Bask	0.662*	-0.086
Push-up	0.489*	0.297
Lateral compression	-0.100	0.507*
Approach	0.849*	0.130
Touch	0.841*	-0.050
Tongue flicks to the substrate or air	-0.111	-0.068
Tongue flicks to the opponent	0.828*	0.003
Retreat	0.004	-0.634*
Scratch	0.380	-0.491*
Tail wave	0.151	-0.206
Dorso-ventral flattening	-0.320	-0.776*
Eigenvalue	3.358	2.607
% Variation explained	25.8%	20.1%

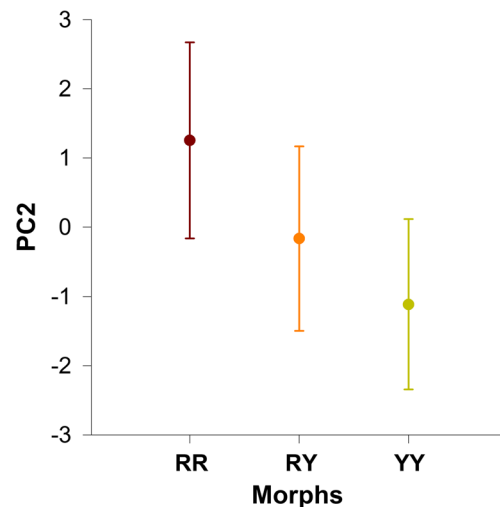
\*Significant scores

$\text{Latency}_{\text{behavior}}$  Principal component 1 (PC1) showed positive loadings from some aggressive and exploratory behaviors (Table 3) but morphs were not significantly different in PC1 (ANOVA:  $F_{2,16} = 1.118$ ;  $p = 0.354$ ).

We considered the principal component 2 (PC2) to be a proxy for male aggression since this axis showed positive loadings (Table 3) from the variables:  $\text{Latency}_{\text{behavior}}$ , % change in  $T_b$ , and also the behavior “lateral compression”, behaviors associated with male aggression or challenge (Lombo 1989; Labra et al. 2007; Bastiaans et al. 2013). In addition, PC2 showed negative loadings from behaviors such as “retreat”, “scratch” and “dorso-ventral flattening”, behaviors associated with male submission (Lombo 1989; Labra et al. 2007; Sacchi et al. 2009; Bastiaans et al. 2013). There were differences among the three morphs in the values of PC2 obtained for each focal male (ANOVA:  $F_{2,16} = 4.823$ ;  $p = 0.026$ ), specifically the males of the RR morph were more aggressive on the PC2 axis than males of the YY morph (Holm-Sidak method:  $t = 3.09$ ,  $p = 0.008$ ; Fig. 2), while RY males were intermediate and not significantly different from either RR or YY (Fig. 2).

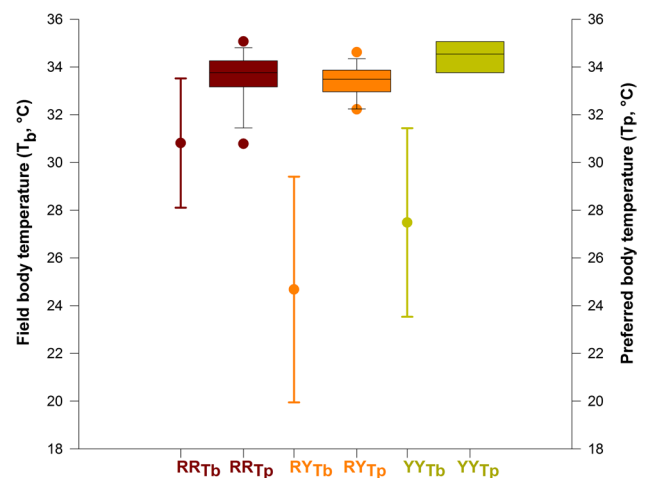
### Field temperatures, preferred body temperature and locomotor stamina differences among color morphs

Field body temperatures recorded during capture differed among color morphs (ANOVA:  $F_{2,34} = 8.81$ ;  $p < 0.001$ ). Specifically, the average temperature of RR males was



**Fig. 2** Mean and standard deviation of the principal component 2 (PC2) values from each focal male of the different morphs (RR pure red, RY red–yellow and YY pure yellow) of *L. sarmientoi*

higher than the average temperature of RY males (Holm-Sidak method:  $t = 4.194$ ;  $p < 0.001$ , Fig. 3; Table 4). The substrate temperatures on which males were captured did not differ among morphs (ANOVAs:  $F_{2,34} = 1.64$ ;  $p = 0.209$ , Table 4). Similarly, we found no differences in mean preferred body temperature among morphs ( $F_{2,34} = 1.85$ ;  $p = 0.173$ , Fig. 3; Table 4), nor in locomotor stamina (Kruskal–Wallis:  $H_2 = 0.46$ ;  $p = 0.792$ ;  $n = 33$ , Table 4).



**Fig. 3** Left axis: Mean and standard deviation of the field body temperature of the different morphs (RR<sub>Tb</sub>: pure red, RY<sub>Tb</sub>: red–yellow and YY<sub>Tb</sub>: pure yellow) of *L. sarmientoi* males. Right axis: Distribution of the preferred body temperatures of morphs of *L. sarmientoi* males (RR<sub>Tp</sub>: pure red, RY<sub>Tp</sub>: red–yellow and YY<sub>Tp</sub>: pure yellow); the 10, 25, 75, and 90% percentiles are indicated for each boxplot

**Table 4** Means ( $\pm$ SEM) and sample size ( $n$ ) of the field body temperature ( $T_b$ ), substrate temperature during capture ( $T_s$ ), preferred body temperature ( $T_p$ ), and locomotor stamina of the different colormorphs of lizards captured during mating season ( $n=35$ ), snout–vent length (SVL) and the significant morphometric variable of the different color morph of all captured lizards ( $n=50$ )

Morphs	$T_b$ ( $^{\circ}$ C)	$T_s$ ( $^{\circ}$ C)	$T_p$ ( $^{\circ}$ C)	Locomotor stamina (min)	SVL (mm)	Head height (mm)
Pure red	30.81 $\pm$ 0.72 (14)*	25.44 $\pm$ 1.11 (14)	33.54 $\pm$ 0.30 (14)	10.08 $\pm$ 0.65 (14)	83.02 $\pm$ 0.85 (22)	9.90 $\pm$ 0.15 (22)*
Red–yellow	24.68 $\pm$ 1.26 (14)*	21.88 $\pm$ 1.87 (14)	33.40 $\pm$ 0.18 (14)	10.90 $\pm$ 1.34 (13)	82.47 $\pm$ 1.33 (20)	9.77 $\pm$ 0.16 (19)*
Pure yellow	27.49 $\pm$ 1.49 (7)	26.81 $\pm$ 3.60 (7)	34.29 $\pm$ 0.52 (7)	11.67 $\pm$ 2.29 (6)	80.06 $\pm$ 2.52 (8)	9.05 $\pm$ 0.27 (8)*

\*Significant differences among means

## Effectiveness of thermoregulation (E)

The effectiveness of thermoregulation was higher in the RR morphs ( $E_{RR} = 0.82$ ) than in RY and YY morphs ( $E_{RY} = 0.55$ ;  $E_{YY} = 0.61$ ). The  $E$  value for RR morphs corresponds to an excellent thermoregulator; while the  $E$  values for RY and YY morphs correspond to moderate thermoregulators.

## Morphology

Considering all males captured ( $n=50$ ), color morphs did not differ in SVL (ANOVA:  $F_{2,49} = 0.89$ ;  $p=0.417$ , Table 4). Among all morphometric variables measured, head height was the only variable that differed among morphs (discriminant analysis:  $\lambda = 0.842$ ;  $p < 0.05$ ; ANOVA:  $F_{2,48} = 4.31$ ;  $p = 0.019$ ; Table 4). Specifically, RR and RY males had greater average head heights than YY males (Holm-Sidak method:  $t_{RRvs.YY} = 2.90$ ;  $p = 0.006$ ;  $t_{RYvs.YY} = 2.40$ ;  $p = 0.025$ , Table 4).

## Discussion

The interplay between discrete color morphs and particular behavioral displays affects life-history strategies (Sinervo and Lively 1996; Sinervo et al. 2001; Miles et al. 2007; Galeotti et al. 2013) and ultimately individual fitness in lizards (Zamudio and Sinervo 2000; Sinervo and Clobert 2003; Miles et al. 2007; Sinervo and Miles 2011; Galeotti et al. 2013). Males of *L. sarmientoi*, one of the southernmost species of reptiles of the world, exhibit color polymorphism on the flanks of the body. We documented the color morphs pure red (RR), red–yellow (RY) and pure yellow (YY) and found that these morphs differed in behavioral displays performed during an agonistic interaction between males. *Liolaemus sarmientoi* males of the RR morph showed higher aggressive behaviors than males of the YY morph. These behaviors included a challenge posture that allows males to display lateral color patches on the body (“lateral compression behavior”), which is also a common behavior in the aggressive morphs of other lizard species (Lombo 1989; Labra et al. 2007; Bastiaans et al. 2013). Additionally,

RR males showed lower numbers of escape and submissive behaviors such as “retreat”, “scratch” and “dorso-ventral flattening” (Lombo 1989; Labra et al. 2007; Sacchi et al. 2009; Bastiaans et al. 2013) than RY and YY males.

It is expected that dominant individuals are capable of monopolizing preferred thermal microhabitats for thermoregulation, and they thus should achieve greater activity body temperatures than submissive individuals (Comendant et al. 2003; Calsbeek and Sinervo 2007). Accordingly, *L. sarmientoi* aggressive males (RR) achieved higher body temperature during the behavioral trials than YY males, and they also took longer to perform their first behavior. Moreover, the RR morph showed higher field body temperatures and were closer to their  $T_p$  than the RY or YY morphs (Fig. 3). The higher effectiveness for thermoregulation of the dominant morph in *L. sarmientoi* (RR) show they can monopolize better quality rocky outcrops than the other morphs, as has also been reported in the dominant morph of *Uta stansburiana* (Calsbeek and Sinervo 2007). In one of the coldest environments for ectotherms in Patagonia, with cold air masses from the Pacific and sub-polar air masses from Antarctica that reach a high mean speed of 37 km/h during spring and summer (Soto and Vázquez 2001), the possibility of a particular morph to occupy the best spots on the rocky outcrop represents a relevant competitive advantage over the rest of the morphs, especially during the mating season, to face the ever-changing weather in the environment that *L. sarmientoi* inhabits.

Furthermore, some studies have reported the importance of testing whether lizard color patches reflect the ultraviolet (UV) spectrum, because UV coloration plays an important role in communication and mating success in some species (Whiting et al. 2006; Pérez i de Lanuza and Font 2007; Font et al. 2010; Olsson et al. 2011, among others). We suggest that future studies should address the UV relevance in the social behavior of *L. sarmientoi*. In addition, because we do not have the possibility of using a spectrophotometer to test the hypothesis that color in *L. sarmientoi* males may be a continuous trait which appears discrete to the human eye, we have to consider that the yellow and red patches shown by *L. sarmientoi* may not be perceived by conspecifics as categorically independent colors. However, in this study,



the discrete color classification of morphs (by human visual perception) was supported by the findings in the behavioral and physiological differences found among morphs. This eco-physiological differences could suggest that the discrete classification allows us to describe alternative strategies in males of this austral lizard, following the methodology of Sinervo and Lively (1996), Sinervo et al. (2001, 2006), Vercken et al. (2008), Bastiaans et al. (2013), and Yewers et al. (2016), among other studies.

Accordingly, in several polymorphic lizard species, conspicuous, long-wavelength colors (often red or orange) are associated with most aggressive or socially dominant males (e.g., *Uta stansburiana*, Sinervo and Lively 1996; Sinervo et al. 2000a; *Ctenophorus pictus*; Healey et al. 2007; Olsson et al. 2007; *Podarcis melisellensis*; Huyghe et al. 2007; *Chlamydosaurus kingii*; Hamilton et al. 2013; *Ctenophorus decresii*; Yewers et al. 2016; but see Ábalos et al. 2016). In addition, these dominant red or orange males have greater levels of testosterone (Sinervo et al. 2000a; Weiss and Moore 2004; Cox and John-Adler 2005; Olsson et al. 2007; While et al. 2010), which seems to be related to a larger head size. Similarly, RR and RY *L. sarmientoi* males showed greater head height than males of the YY morph. The length and width of the head play important roles in providing a biomechanic advantage in bite force (Vanhooydonck et al. 2010), as does the height (Herrel et al. 2001, 2004; Anderson et al. 2008). This result agrees with the results found in other species of lizards (e.g., *Anolis cristatellus*, Perry et al. 2004; *Podarcis melisellensis*; Huyghe et al. 2007), where head size is a relevant trait to determine the overall outcome of an agonistic interaction between males, even in the absence of obvious aggression, because it is directly related to bite force (Herrel et al. 1998; Huyghe et al. 2009, 2012). However, future studies that relate head morphology to bite force in *L. sarmientoi* males could help confirm this assumption.

In addition, in several species, the dominant morph has greater locomotor performance (Robson and Miles 2000; Sinervo et al. 2000a; Huyghe et al. 2007; Labra et al. 2007; Calsbeek et al. 2010), which allows male lizards to acquire and defend large territories and achieve more matings. However, this correlation between locomotor ability and dominant behavior is not universal among lizards (*Anolis cristatellus*, Perry et al. 2004; *Podarcis melisellensis*; Huyghe et al. 2007 and *Podarcis muralis*; Zajitschek et al. 2012). We also found no correlation between color morph and locomotor stamina, which may be linked with the fact that in *L. sarmientoi* and the other species mentioned above, fighting rarely represents a long-term endurance effort and stamina is not necessarily required to win agonistic encounters. In this sense, the characteristics related to social dominance appear to be influenced by the particular characteristics and environmental and ecological context of each species (Perry et al. 2004). Thus, *L. sarmientoi*, which lives on large

rocky outcrops distributed along the extensive shrub steppe, presents much smaller and subtler behavioral displays than those observed in lizard species of temperate and tropical climates, where generally the population density and the frequency of territorial fighting are much higher. Most likely, males of *L. sarmientoi* rarely need to defend their territories, as their territories are extensive. Instead, it is likely that behavioral displays of dominance are most common during competition for females, which directly affects males' reproductive success and fitness.

The persistence of the YY and RY morphs in *L. sarmientoi*, considering the dominance of RR, suggests there must be other mechanisms that perpetuate the polymorphism in the population. For example, in other species, females of different morphs adjust their clutch size and clutch success in response of population density, morphs frequency, habitat structure, and other environmental parameters (e.g., *Uta stansburiana*, Sinervo et al. 2000b; Sinervo 2001; Sinervo and Zamudio 2001; *Lacerta vivipara*; Vercken et al. 2007, 2010 and *Podarcis muralis*; Galeotti et al. 2013). If alternative reproductive strategies in a polymorphic species have a genetic basis, allelic variation can be maintained if different morphs achieve equal mean fitness in a heterogeneous environment in which phenotypic plasticity is advantageous; or also when there is a negative frequency-dependent selection over the common phenotype (Sinervo 2001; Calsbeek et al. 2001; Vercken et al. 2007). Moreover, genetic variation can also be maintained by over-dominance in fitness traits of heterozygous genotypes over homozygous genotypes, which could also be under frequency-dependent selection (Sinervo and Zamudio 2001; Sinervo and Calsbeek 2006; Vercken et al. 2010).

Although a larger sample size is necessary to strengthen our conclusions about the behavioral and physiological differences among the color morphs of *L. sarmientoi*, this study is a first step to explore the biological and behavioral significance of this polymorphism. In males of *L. sarmientoi*, variation in color morph is associated with head size, body temperature, and aggressive and submissive behaviors displayed during agonistic encounters, which may influence their ability to mate with females and thus have a direct effect on their offspring. Recent studies (Forsman et al. 2008; Pizzatto and Dubey 2012; Takahashi et al. 2014; Bolton et al. 2016; Forsman 2016; Svensson 2017) reveal that some color polymorphic species may be more likely to successfully face present and future environmental changes than monomorphic species, because the increased phenotypic diversity can enhance population persistence. In addition, viviparity in squamates is phylogenetically derived relative to oviparity, and viviparity has evolved many times from oviparity because of biotic and abiotic factors (Shine and Bull 1979; Pizzatto and Dubey 2012). This finding implies that viviparous, polymorphic species such as *L. sarmientoi* have competitive advantages

that may promote their ecological success by allowing them to exploit a wider range of habitat types. These ecological advantages may enhance their resilience, allowing them to better adapt to future climate variations.

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## Compliance with ethical standards

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

**Ethical statement** All applicable international, national and/or institutional guidelines for the care and use of animals were followed. 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. This article does not contain any studies with human participants performed by any of the authors.

**Informed consent** Informed consent was not required.

## 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
- Abdala CS, Quinteros AS (2014) Los últimos 30 años de estudios de la familia de lagartijas más diversa de Argentina. Actualización taxonómica y sistemática de Liolaemidae. *Cuadernos de Herpetología* 28:55–82
- Abdala CS, Acosta JL, Acosta JC et al (2012) Categorización del estado de conservación de los lagartos de la República Argentina. *Cuadernos de Herpetología* 26:215–248
- Anderson RA, McBrayer LD, Herrel A (2008) Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biol J Linn Soc* 98:709–720
- Bastiaans E, Morinaga G, Gamaliel Castañeda Gaytán J, Marshall JC, Sinervo B (2013) Male aggression varies with throat color in 2 distinct population of the mesquite lizard. *Behav Ecol* 24(4):968–981
- Bauwens D, Hertz PE, Castilla AM (1996) Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* 77:1818–1830
- Bolton PE, Rollins LE, Griffith SC (2016) Colour polymorphism is likely to be disadvantageous to some populations and species due to genetic architecture and morph interactions. *Mol Ecol* 25:2713–2718
- Breitman MF, Minoli I, Avila LJ, Medina CD, Sites JW Jr, Morando M (2014) Lagartijas de la provincia de Santa Cruz, Argentina: distribución geográfica, diversidad genética y estado de conservación. *Cuadernos de Herpetología* 28(2):83–110
- Calsbeek R, Sinervo B (2007) Correlational selection on lay date and life history traits: experimental manipulations of territory and nest site quality. *Evolution* 61(5):1071–1083
- Calsbeek R, Alonzo SH, Zamudio K, Sinervo B (2001) Sexual selection and alternative mating behaviours generate demographic stochasticity in small populations. *Proc R Soc B Biol Sci* 269:157–164
- Calsbeek B, Hasselquist D, Clobert J (2010) Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard (*Podarcis muralis*) ventral colour morphs. *J Evolutionary Biol* 23(6):1138–1147
- Carpenter GC (1995) Modeling dominance: the influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetol Monogr* 9:88–101
- Cei JM (1986) Reptiles del Centro-oeste y Sur de la Argentina. *Herpetofauna de las Zonas Áridas y Semiáridas*, 1st edn. Museo Regionale di Scienze Naturali, Torino
- Comendant T, Sinervo B, Svensson EI, Wingfield J (2003) Social competition, corticosterone and survival in female lizard morphs. *J Evol Biol* 16(5):948–955
- Corl A, Davis AR, Kuchta SR, Comendant T, Sinervo B (2010) Alternative mating strategies and the evolution of sexual size dimorphism in the side-blotched lizard, *Uta stansburiana*: a population-level comparative analysis. *Evolution* 64:79–96
- Cox RM, John-Adler HB (2005) Testosterone has opposite effects on male growth in lizards (*Sceloporus* spp.) with opposite patterns of sexual size dimorphism. *J Exp Biol* 208:4679–4687
- Fernández JB, Smith J Jr, Scolaro A, Ibagüengoytía NR (2011) Performance and thermal sensitivity of the southernmost lizards in the world, *Liolaemus sarmiento* and *Liolaemus magellanicus*. *J Therm Biol* 36:15–22
- Fernández JB, Medina SM, Kubisch EL, Manero AA, Scolaro JA, Ibagüengoytía NR (2015) Female reproductive biology of the lizards *Liolaemus sarmiento* and *L. magellanicus* from the southern end of the world. *Herpetol J* 25:101–108
- Fernández JB, Medina SM, Kubisch EL, Scolaro JA, Ibagüengoytía NR (2017) Reproductive strategies in males of the world's southernmost lizards. *Integr Zool*. <https://doi.org/10.1111/1749-4877.12224>
- Font E, Carazo P, Pérez i de Lanuza G, Barbosa D (2010) Comportamiento y comunicación animal: ¿Qué nos enseñan los lagartos? *Acta Zool Lilloana* 54(12):11–34
- Forsman A (2016) Is colour polymorphism advantageous to populations and species? *Mol Ecol* 25(12):2693–2698
- Forsman A, Ahnesjö J, Caesar S, Karlsson M (2008) A model of ecological and evolutionary consequences of color polymorphism. *Ecology* 89(1):34–40
- Fuentes ER (1976) Ecological convergence of lizard communities in Chile and California. *Ecology* 57:3–17
- Galeotti P, Sacchi R, Pellitteri-Rosa D, Bellati A, Cocca W, Gentili A, Scali S, Fasola M (2013) Colour polymorphism and alternative breeding strategies: effects of parent's colour morph on fitness traits in the common wall lizard. *Evol Biol* 40(3):385–394
- Halloy M (2012) Visual display variations in neotropical lizards, *Liolaemus quilmes* (Iguania: Liolaemidae): relation to sex and season. *Herpetol J* 22:265–268
- Halloy M, Robles C, Salica MJ, Semhan R, Juárez Heredia V, Vicente N (2013) Estudios de comportamiento y ecología de lagartijas de los géneros *Liolaemus* y *Phymaturus*. (Iguania: Liolaemini). *Cuadernos de Herpetología* 27(1):15–26
- Hamilton DG, Whiting MJ, Pryke SR (2013) Fiery frills: carotenoid-based coloration predicts contest success in frillneck lizards. *Behav Ecol* 24(5):1138–1149

- Healey M, Uller T, Olsson M (2007) Seeing red: morph-specific contest success and survival rates in a colour-polymorphic agamid lizard. *Anim Behav* 74(2):337–341
- Herrel A, Aerts P, De Vree F (1998) Ecomorphology of the lizard feeding apparatus: a modeling approach. *Neth J Zool* 48:1–25
- Herrel A, De Grauw E, Lemos-Espinal JA (2001) Head shape and bite performance in Xenosaurid lizards. *J Exp Zool* 290:101–107
- Herrel A, Vanhooydonck B, Van Damme R (2004) Omnivory in lacertid lizards: adaptive evolution or constraint? *J Evol Biol* 17:974–984
- Hertz PE, Huey R, Stevenson RD (1993) Evaluating Temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am Nat* 142:796–818
- Huyghe K, Vanhooydonck B, Herrel A, Tadić Z, Van Damme R (2007) Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. *Integr Comp Biol* 47(2):211–220
- Huyghe K, Husak JF, Herrel A, Tadić Z, Moore IT, Van Damme R, Vanhooydonck B (2009) Relationships between hormones, physiological performance and immunocompetence in a color-polymorphic lizard species, *Podarcis melisellensis*. *Horm Behav* 55(4):488–494
- Huyghe K, Vanhooydonck B, Herrel A, Tadić Z, Van Damme R (2012) Female lizards ignore the sweet scent of success: male characteristics implicated in female mate preference. *Zoology* 115(4):217–222
- Ibargüengoytía NR (2008) Estrategias reproductivas en reptiles. In: Vidal MA, Labra A (eds) *Herpetología de Chile*. Science, Santiago de Chile, pp 392–425
- Ibargüengoytía NR, Medina SM, Fernández JB, Gutiérrez JA, Tappari F, Scolaro A (2010) Thermal biology of the southernmost lizards in the world: *Liolaemus sarmientoi* and *Liolaemus magellanicus* from Patagonia, Argentina. *J Therm Biol* 35:21–27
- Kubisch EL, Corbalán V, Ibargüengoytía NR, Sinervo B (2016) Local extinction risk of three species of lizard from Patagonia as a result of global warming. *Can J Zool* 94:49–59
- Labra A, Carazo P, Desfilis E, Font E (2007) Agonistic interactions in a *Liolaemus* lizard: structure of head bob displays. *Herpetologica* 63(1):11–18
- Langkilde T, Shine R (2006) How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. *J Exp Biol* 209:1035–1043
- Lattanzio MS, Miles DB (2016) Trophic niche divergence among color morphs that exhibit alternative mating tactics. *R Soc Open Sci* 3:150531
- Lombo JG (1989) Caracterización de los patrones de conducta agresiva territorial del lagarto de la sabana de Bogotá *Phenacosaurus heterodermus* (Sauria: Iguanidae). *Caldasia* 16(76):112–118
- Martins EP, Labra A, Halloy M, Thompson JT (2004) Large-scale patterns of signal evolution: an interspecific study of *Liolaemus* lizard headbob displays. *Anim Behav* 68(3):453–463
- Medina M, Ibargüengoytía NR (2010) How do viviparous and oviparous lizards reproduce in Patagonia? A comparative study of three species of *Liolaemus*. *J Arid Environ* 74:1024–1032
- Medina M, Gutierrez J, Scolaro A, Ibargüengoytía NR (2009) Thermal responses to environmental constraints in two populations of the oviparous lizard *Liolaemus bibronii* in Patagonia, Argentina. *J Therm Biol* 37:579–586
- Miles DB, Sinervo B, Hazard LC, Svensson EI, Costa D (2007) Relating endocrinology, physiology and behaviour using species with alternative mating strategies. *Funct Ecol* 21(4):653–665
- Mills SC, Hazard L, Lancaster L, Mappes T, Miles D, Oksanen TA, Sinervo B (2008) Gonadotropin hormone modulation of testosterone, immune function, performance, and behavioral trade-offs among male morphs of the lizard *Uta stansburiana*. *Am Nat* 171:339–357
- Moore MC, Thompson CW, Marler CA (1991) Reciprocal changes in corticosterone and testosterone levels following acute and chronic handling stress in the tree lizard *Urosaurus ornatus*. *Gen Comp Endocr* 81:217–226
- Olsson M, Healey M, Astheimer L (2007) Afternoon T: testosterone level is higher in red than yellow male polychromatic lizards. *Physiol Behav* 91(5):531–534
- Olsson M, Andersson S, Wapstra E (2011) UV-Deprived coloration reduces success in mate acquisition in male sand lizards (*Lacerta agilis*). *Plos One* 6(5):e19360
- Pérez i de Lanuza G, Font E (2007) Ultraviolet reflectance of male nuptial coloration in sand lizards (*Lacerta agilis*) from the Pyrenees. *Amphibia Reptil* 28(3):438–443
- Perry G, LeVering K, Girard I, Garland T (2004) Locomotor performance and social dominance in male *Anolis cristatellus*. *Anim Behav* 67(1):37–47
- Pizzatto L, Dubey S (2012) Colour-polymorphic snake species are older. *Biol J Linn Soc* 107(1):210–218
- Robson MA, Miles DB (2000) Locomotor performance and dominance in male tree lizards, *Urosaurus ornatus*. *Funct Ecol* 14(3):338–344
- Sacchi R, Pupin F, Gentilli A, Rubolini D, Scali S, Fasola M, Galeotti P (2009) Male–male combats in a polymorphic lizard: residency and size, but not color, affect fighting rules and contest outcome. *Aggress Behav* 35(3):274–283
- Scali S, Sacchi R, Mangiacotti M, Pupin F, Gentilli A, Zucchi C, Sannolo M, Pavesi M, Zuffi MA (2016) Does a polymorphic species have a ‘polymorphic’ diet? A case study from a lacertid lizard. *Biol J Linn Soc* 117(3):492–502
- Scolaro A (2005) *Reptiles Patagónicos: Sur. Guía de Campo*. Universidad Nacional de la Patagonia, Trelew
- Scolaro JA, Cei JM (1997) Systematic status and relationships of *Liolaemus* species of the *archeforus* and *kingii* groups: morphological and taxonumerical approach (Reptilia: Tropicuridae). *Bolletín del Museo Regionale di Scienze Naturali Torino* 15(2):369–406
- Shine R, Bull JJ (1979) The evolution of live-bearing in lizards and snakes. *Am Nat* 1979:905–923
- Sinervo B (2001) Runway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. *Genetica* 112:417–434
- Sinervo B, Calsbeek R (2006) The developmental, physiological, neural, and genetical causes and consequences of frequency-dependent selection in the wild. *Annu Rev Ecol Evol Syst* 37:581–610
- Sinervo B, Clobert J (2003) Morphs, dispersal, genetic similarity and the evolution of cooperation. *Science* 300:1949–1951
- Sinervo B, Huey RB (1990) Allometric engineering: an experimental test of the causes of interpopulational differences in performance. *Science* 248(4959):1106–1110
- Sinervo B, Lively CM (1996) The rock-paper-scissors game and the evolution of alternative male reproductive strategies. *Nature* 380:240–243
- Sinervo B, Miles DB (2011) Hormones and behavior of reptiles. In: Norris DO, Lopez KH (eds) *Hormones and reproduction of vertebrates*. Academic, London, pp 215–246
- Sinervo B, Svensson E (2002) Correlational selection and the evolution of genomic architecture. *Heredity* 89:329–338
- Sinervo B, Zamudio KR (2001) The evolution of alternative reproductive strategies: fitness differential, heritability, and genetic correlation between the sexes. *J Hered* 92(2):198–205
- Sinervo B, Miles DB, Frankino WA, Klukowski M, De Nardo DF (2000a) Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Horm Behav* 38:222–233
- Sinervo B, Svensson E, Comendant T (2000b) Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* 406:985–988

- Sinervo B, Bleay C, Adamopoulou C (2001) Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. *Evolution* 55(10):2040–2052
- Sinervo B, Chainé A, Clobert J, Calsbeek R, Hazard L, Lancaster L, McAam AG, Alonzo S, Corrigan G, Hochberg ME (2006) Self-recognition, color signals, and cycles of greenbeard mutualism and altruism. *Proc Natl Acad Sci USA* 103(19):7372–7377
- Smith LC, John-Alder HB (1999) Seasonal specificity of hormonal, behavioral, and coloration responses to within-and between-sex encounters in male lizards (*Sceloporus undulatus*). *Horm Behav* 36(1):39–52
- Soto J, Vázquez M (2001) Las condiciones climáticas de la provincia de Santa Cruz. In: Soto J, Vázquez M (eds) *El gran libro de la provincia de Santa Cruz*. Ed. Oriente-Alfa Centro literario, Madrid, p. 651
- Svensson EI (2017) Back to basics: using colour polymorphisms to study evolutionary processes. *Molec Ecol*. <https://doi.org/10.1111/mec.14025>
- Svensson E, Sinervo B, Comendant T (2001) Condition, genotype-by-environment interaction, and correlational selection in lizard life-history morphs. *Evolution* 55:2053–2069
- Takahashi Y, Kagawa K, Svensson EI, Kawata M (2014) Evolution of increased phenotypic diversity enhances population performance by reducing sexual harassment in damselflies. *Nature Commun* 5:4468
- Tokarz RR (1985) Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). *Anim Behav* 33(3):746–753
- Vanhooydonck B, Cruz FB, Abdala CS, Moreno Azócar DL, Bonino MF, Herrel A (2010) Sex-specific evolution of bite performance in *Liolaemus* lizards (Iguania: Liolaemidae): the battle of the sexes. *Bio J Linn Soc* 101:461–475
- Vercken E, Massot M, Sinervo B, Clobert J (2007) Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. *J Evol Biol* 20(1):221–232
- Vercken E, Sinervo B, Clobert J (2008) Colour variation in female common lizards: why we should speak of morphs, a reply to Cote et al. *J Evol Biol* 21(4):1160–1164
- Vercken E, Clobert J, Sinervo B (2010) Frequency-dependent reproductive success in female common lizards: a real-life hawk–dove–bully game? *Oecologia* 162(1):49–58
- Weiss SL, Moore MC (2004) Activation of aggressive behavior by progesterone and testosterone in male tree lizards, *Urosaurus ornatus*. *Gen Comp Endocr* 136(2):282–288
- While GM, Isaksson C, McEvoy J, Sinn DL, Komdeur J, Wapstra E, Groothuis TG (2010) Repeatable intra-individual variation in plasma testosterone concentration and its sex-specific link to aggression in a social lizard. *Horm Behav* 58(2):208–213
- Whiting MJ (1999) When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*. *Behav Ecol Sociobiol* 46(3):210–214
- Whiting MJ, Stuart-Fox DM, O'Connor D, Firth D, Bennett NC, Blomberg SP (2006) Ultraviolet signals ultra-aggression in a lizard. *Anim Behav* 72(2):353–363
- Yewers MSC, Pryke S, Stuart-Fox D (2016) Behavioural differences across contexts may indicate morph-specific strategies in the lizard *Ctenophorus decresii*. *Anim Behav* 111:329–339
- Zajitschek SR, 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(3):573–582
- Zamudio KR, Sinervo B (2000) Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. *Proc Natl Acad Sci* 97(26):14427–14432