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ORIGINAL PAPER

Multiple color signals may reveal multiple messages in male Schreiber's green lizards, *Lacerta schreiberi*

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Abstract Multiple traits may either signal different characteristics of a male or be redundant. These multiple signals may convey different messages if they are intended for different receivers (e.g., male or females) that have different interests. We examined the functions of multiple colorful visual traits of male Schreiber's green lizard (*Lacerta schreiberi*). Results showed that interindividual variation in the characteristics of coloration of males can be related to variation in morphology, health state, dominance status, and pairing status, but that different relationships were found for each color signal. For example, dominant males had brighter "blue" throat and with higher values of ultraviolet (UV) and bluish coloration and darker and greenish dorsal coloration than subordinate males. Health state was also reflected in coloration; males with a higher immune response had "blue" throats with lower amounts of UV coloration, but had "yellow" chests with higher amounts of UV coloration. Males found guarding females also differed in coloration from males found alone. These data suggest that characteristics of coloration of the different multiple signals may reveal different messages for different receivers, either male or female conspecifics. The development of the different signals, based on different morphological and physiological mechanisms and trade-offs, may allow signal reliability of multiple colorful traits in different social contexts.

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Introduction

The evolution of multiple sexual signals is one of the least understood features of sexual selection. Some theoretical models, but not others, have suggested that multiple traits may convey honest information on the genetic and phenotypic quality of males (Møller and Pomiankowski 1993; Johnstone 1995, but see Grafen 1990; Iwasa and Pomiankowski 1994). Traits such as tail length and carotenoid-dependent color badges in widowbirds (*Euplectes ardens*) may be honest signals that function in intra- and intersexual selection, respectively (Andersson et al. 2002). However, another study found that female bowerbirds (*Ptilonorhynchus violaceus*) use both plumage ultraviolet (UV) coloration of males and bower characteristics to choose mates because they signal different aspects of health state of males (Doucet and Montgomerie 2003). Also, in male peacocks, tail feathers and behavioral displays may signal general and current health state, respectively, to females (Loyau et al. 2005). Male tree lizards *Urosaurus ornatus* have two different status signaling color badges: throat badges that are used in short-term encounters for short-distance communication and dorsal badges that are used in long-term encounters for long distance communication (Zucker 1994). Moreover, embedded within the same display of male tree lizards, there are two sexually dimorphic traits that independently act as indicators of functional capacity (belly patch size) and behavioral aggression (dewlap color; Meyers et al. 2006). Furthermore, female mate attraction by male *U.*

ornatus depends on the additive and interactive effects of multiple male traits combined, such as body mass, head size, and body and tail coloration (Hamilton and Sullivan 2005). These results suggest that multiple traits may either signal different characteristics of male condition or be redundant as a way to reinforce the reliability of signals (Møller and Pomiankowski 1993; Sullivan 1994; Rowe 1999).

Multiple signals may convey different messages if they are intended for different receivers that have different interests (i.e., to either male or female conspecifics; Pryke et al. 2001; Andersson et al. 2002). This is because although it is generally assumed that success in male–male competition reflects high quality and that female preference for dominant males should be widespread (Berglund et al. 1996), this is not necessarily so (Qvarnström and Forsgren 1998). Traits reflecting male dominance, such as large body size or status badges, might be expected to be the same traits selected by females because the reliability of these traits is constantly put on trial in male–male contests and cannot be faked without incurring high costs (Berglund et al. 1996; Tarof et al. 2005). However, many studies suggest that traits signaling male dominance are not always attractive to females because they might not be reliable indicators of better paternal care or genetic quality for females, which would lead females to base their mate choice on other male traits (Qvarnström and Forsgren 1998; Andersson et al. 2002; López et al. 2002; Wong and Candolin 2005). Thus, in many cases, the effects of intrasexual selection (i.e., male–male competition) and intersexual selection (i.e., mate choice) may lead to evolution of different coexisting secondary sexual traits.

Many lizards have evolved colorful sexually dimorphic ornaments that are used in intraspecific relationships (reviewed in Cooper and Greenberg 1992). The size and color characteristics of male visual badges may determine success in male–male competition (Thompson and Moore 1991; Olsson 1994a; Zucker 1994; Whiting et al. 2003, 2006) or mate acquisition (Baird et al. 1997; Kwiatkowski and Sullivan 2002; Anderholm et al. 2004; Hamilton and Sullivan 2005; Salvador et al. 2008). Many lizards show multiple colorful signals, but it is not always clear whether these signals have similar or different functions in sexual selection processes. We hypothesized that because different colorful traits are often based on different types of pigments, such as melanins, pteridines, or carotenoids (Cooper and Greenberg 1992), and are regulated by different endocrine pathways (e.g., Calisi and Hews 2007), the elaboration of each type of ornament may involve different physiological trade-offs and thus, the ornaments may convey different messages.

We examined the functions of multiple visual traits of male Schreiber's green lizard (*Lacerta schreiberi*), a large (130 mm maximum snout-to-vent length, SVL) diurnal lacertid lizard found in the northwest, west, and central areas of the Iberian Peninsula (Pérez-Mellado 1998; Marco 2002). For human observers, adult male lizards *L. schreiberi* have predominantly green dorsal coloration with small black spots, yellow chest, and ventral coloration and bright blue head coloration (at least the throat and the mental scales). Coloration is especially intense during the breeding season (Pérez-Mellado 1998; Salvador 1988). Females have brown, or less often, dark green dorsal coloration, with large black spots, pale yellow ventral coloration, and light brown head coloration with black spots. A previous study of the closely related lizard *Lacerta viridis* showed that the saturation of blue throat color in males decreases with increasing level of tick infestation (Václav et al. 2007), which suggests that at least some of these colorful traits are costly and could reveal honest messages about male condition. The occurrence of these multiple colorful and sexually dimorphic traits provides an opportunity to examine whether different visual signals have similar redundant functions or whether each signal has specific messages for either conspecific males or females.

In this paper, we measured the characteristics of coloration of multiple traits of adult male *L. schreiberi* lizards using spectrophotometry. We also measured morphology and health state (i.e., body condition and immune response) of males because these variables may affect dominance status in males and/or be selected by females in potential mates. Additionally, we determined experimentally the dominance status of males by staging encounters between pairs of males and assessed the pairing status of males with females in the field. Finally, we examined the relationships between characteristics of coloration and morphology, health state, dominance status, and pairing status.

Materials and methods

Study species

During the mating season in April 2007, we captured by noosing 23 adult male lizards *L. schreiberi* in rocks and talus close to streams in a Scot's pine (*Pinus sylvestris*) mountain forest in "Valle de la Fuenfria" (Cercedilla, Madrid province, Spain). In this area, lizards are active from March to September, mate in April–May, and produce a single clutch during June (Marco and Pérez-Mellado 1990; Marco 1994). We selected lizards that were clearly reproductively mature (SVL>104 mm and with nuptial coloration). Lizards were individually housed at "El Ventorrillo" Field Station, 5 km from the capture site, in outdoor 80×50 cm polyvinyl chloride terraria with sand substratum, rocks for cover, and water ad libitum. We fed lizards mealworm larvae ad libitum every day. All animals were returned in good condition to their capture sites at the end of trials, 3 weeks after lizards were captured.

Morphological measurements

We measured immediately after capture males' body weight with a digital balance to the nearest 0.1 g ($\overline{X} \pm$ standard error (SE) $= 30.2 \pm 0.8g$; range=25.0–40.8 g) and used a ruler to measure SVL to the nearest 1 mm ($\overline{X} \pm$ SE $= 111 \pm 1$mm; range=104–119 mm) and tail length ($\overline{X} \pm$ SE $= 159 \pm 6$mm; range=112–199 mm). The same person made all measurements. Head size and associated bite force have been identified as an important component in intrasexual agonistic contests of lizards, and this seems to be the cause of sexual dimorphism of head size in many lizards (Anderson and Vitt 1990; Hews 1990; Herrel et al 1999; Lappin et al. 2006). We used digital calipers to make morphological measurements (to the nearest 0.1 mm) of the head of males. Head height ($\overline{X} \pm$ SE $= 12.6 \pm 0.1$mm; range=11.0–13.6 mm) was measured as the greatest vertical distance through the snout from the highest portion of the head to the bottom of the lower jaw. Head length ($\overline{X} \pm$ SE $= 25.4 \pm 0.2$mm; range=23.7–27.4 mm) was the greatest horizontal distance between the tip of the snout and the posterior side of the parietal scales. Head width ($\overline{X} \pm$ SE $= 20.7 \pm 0.3$mm; range=18.7–23.5 mm) was the greatest horizontal distance between the external sides of the parietal scales. We removed the influence of body size on head measurements by regressing each against SVL (all variables ln-transformed) and used the residuals in subsequent analyses.

Color measurements

We measured reflectance of lizards' coloration from 300 to 700 nm using an Ocean Optics USB2000 spectroradiometer with a DT-1000-MINI Deuterium–Halogen light source (Ocean Optics, Inc., Dunedin, FL, USA). This range of wavelengths coincides with the spectral sensitivity measured for other lizard species, which includes visual perception in the UV range (Ellingson et al. 1995; Fleishman et al. 1993, 1997; Loew et al. 2002). To exclude ambient light and standardize measuring distance, a cylindrical metallic tube was mounted on the bifurcated fiber optic probe (Montgomerie 2006). The probe was held at a 90° degree angle to the skin, and reflectance was always measured by the same person (PL). We measured coloration of three visually distinct large patches of coloration ("blue" throat, "yellow" chest, and "green" dorsum) at three standardized spots: the middle of the throat (between the last chin shields and the collar; "throat"), the chest (just anterior to the two forelimbs at the middle of the second row of scales prior to the collar; "chest"), and the dorsum (in the middle point above the two forelimbs; "dorsal"). Reflectance (R) was calculated relative to a white standard (WS-1-SS) with the OOIBase32 software (Ocean Optics, Inc.). Mean reflectance was summarized over 6 nm steps ("binned"; Grill and Rush 2000) before statistical analysis. We measured coloration at three different points at each spot, but because these three measurements were highly repeatable within each spot (intraclass correlation coefficients, $r>0.80$, $P<0.0001$ in all cases), we calculated the mean values of the three measures. Nevertheless, we repeated all statistical analyses using each of these three values. These analyses resulted in the same conclusions, with similar P values, and we therefore present only the results of the analysis based on the mean values.

We mathematically summarized the spectra using principal components analysis (PCA; Endler 1990; Cuthill et al. 1999; Grill and Rush 2000). The PCA summarizes all of the information about the shape of complex reflectance spectra, including bimodal ones like those that we measured in our lizard species (see Fig. 1), into a few PCs that are independent of one another (Montgomerie 2006). In PCA of spectral data, PC1 represents variation in intensity of coloration or brightness, and subsequent PCs represent combinations of hue and chroma (Endler 1990; Cuthill et al. 1999; Grill and Rush 2000). Also, the PCA identifies those sections of the spectrum (wavelength regions) that are contributing to the observed variation, independently of their "importance" in terms of contribution to the total amount of reflectance (Montgomerie 2006). Principal components analyses were performed separately for each part of the body (throat, chest, and dorsal) including spectra for all males.

Body condition and immune response

Individual values of body condition were calculated as the residuals from the regression equation of ln mass (grams) on ln SVL (millimeter), which may represent an index of the relative amount of fat stored and hence an estimation of individual physical condition or nutritional status (Bonnet and Naulleau 1994).

We measured T cell-mediated immune response of lizards in vivo by using the phytohemagglutinin (PHA) injection test (Smits et al. 1999; Belliure et al. 2004). We used a pressure-sensitive spessimeter to measure thickness (to the nearest 0.01 mm) at the same point of the right hindlimb foot pad before and 24 h after injecting 0.04 mg of PHA dissolved in 0.02 ml of phosphate-buffered saline at the marked point. We calculated the immune response as the difference between pre- and postinjection thickness measures (Smits et al. 1999; Belliure et al. 2004). The only appreciable effect of the PHA injection was a slight swelling of the skin, due to the immune response, which disappeared after 48 h. No lizard showed any sign of stress or pain due to this test. Although PHA-induced swelling is related to heightened immune cell activity, it also may involve both innate and adaptive components of the immune system (Martin et al. 2006). Thus, this test might not be an unambiguous index of T cell-mediated immunity per se (but see Tella et al. 2008), but rather a multifaceted index of cutaneous immune activity. We used this test because we were interested in a standardized index of immunocompetence, independent of the type of immune cells involved.

Male dominance status

We staged encounters between pairs of males ($N=23$ males; see "Morphological measurements" section above) during April and beginning of May, coinciding with the mating season, between 1100 and 1300 hours and between 1700 and 1900 hours. We used a neutral arena to avoid the effects of prior residency on the outcome of encounters (Olsson and Shine 2000; López and Martín 2001). The test arenas were outdoor terraria (90×50 cm), each having a sand substrate and divided into two equally sized compartments with a removable opaque partition. To avoid effects of conspecific odors, after each trial, the sand was replaced and cages were cleaned thoroughly with water and dried at the outdoor temperature.

Each male participated in four encounters against four different opponents randomly chosen among those that had been captured in widely separated places (at least 1 km), so that previous familiarity between individual males did not influence the outcome of encounters (Olsson 1994b; López and Martín 2001). The order of encounters and the initial male position on the left and right sides of the arena were randomized. Staged encounters were spaced sufficiently (at least 1 day) to minimize any effects of fatigue and experience resulting from one trial on subsequent trials. All tests were made in outdoor conditions when lizards were fully active.

Males were transferred from their home terraria to the test arena and were given 5 min for acclimation before the partition was removed. Encounters were observed from a hidden point and ended after 5 min. We considered that a male won a single interaction when he approached another individual with an aggressive display and made the other male retreat or run away either without contact, by touching him on the flanks, or, occasionally, by giving quick bites, especially to the snout or head. We noted which male won each interaction and which one was chased and lost. Thereafter, we calculated a sum of aggressive interactions won less interactions lost for each male of each pair and defined the male with the highest positive sum as the dominant individual of the pair (Fox et al. 1981; Martín and Salvador 1993). Typically, males considered as dominants of the pair repeatedly won in a series of interactions in the trial. In a few cases (six out of 46; 13%), it was not possible to determine which male was the dominant of the pair, and we considered it an unknown relationship (i.e., a tie). For each staged encounter, we gave scores of 1 to the dominant and zero to the subordinate, or 0.5 to both males for a tie. A male's overall dominance status score was calculated as the sum of scores obtained among his four encounters (Martín and Salvador 1993; López et al. 2002).

Male pairing status

Both male and female *L. schreiberi* are rather sedentary and occupy optimal microhabitats, with a great overlap between home ranges (Marco 1996). Males do not defend territories, but they often fight with rival males, and some males spend long periods of time guarding females, staying in physical contact with them to prevent matings by other males (Marco 1996; Marco and Pérez-Mellado 1999). Dominant males mate more times, but do not get exclusive access to individual females, which are polyandrous (Marco and Pérez-Mellado 1999). This is because females may easily avoid being guarded by a male by fleeing and hiding. However, females that are paired with a male seem quiet and "accept" being guarded by that particular male for long periods (J. Martín and P. López personal observation). Therefore, we hypothesized that observations of successful mate guarding may reflect female mate preferences. Nevertheless, because some males may also obtain forced matings without guarding, pairing status is not necessarily directly related to mating success. During field observations, we noted whether a captured male was found relatively sedentary and in close proximity (less than 50 cm) to a female, very often in physical contact, or whether the male was found alone whether still or moving. Then, we compared the morphological and color characteristics of paired and unpaired males.

Data analyses

To determine the relationships between dominance status or immune response (dependent variables) and coloration, we used backward stepwise general regression models (GRM) in STATISTICA Software (StatSoft, Inc, Tulsa, OK, USA) with PC scores describing coloration as independent variables. Morphological and coloration (PC scores) characteristics of paired and unpaired males were compared with multivariate analyses of variance (MANOVA), and because we found significant effects in the multivariate analyses (see "Results" section), we performed protected univariate ANOVAs separately on each variable to test which variables explained the significant differences found in the previous MANOVAs models (Scheiner 2001). Variables were log-transformed when required to meet assumptions for parametric analyses.

Results

Male morphology and dominance status

Males' dominance status scores were significantly related to head height (stepwise GRM, model; R^2=0.33, $F_{1,21}$= 10.44, P=0.004; head height: β=0.58, t=3.23, P=0.004), while SVL, tail length, body mass, and other head measurements were not significantly related to dominance and were not included in the final model. Thus, males with taller heads were more dominant.

Immune response, body condition, and dominance status

The males' immune response was significantly and positively correlated with body mass (stepwise GRM, model: R^2=0.50, $F_{1,21}$=21.14, P=0.007; body mass: β=0.71, t= 4.60, P=0.00016) independently of their body length (SVL). Thus, heavier lizards had greater immune responses. Similarly, males with a greater body condition had significantly greater immune responses (GRM model: R^2= 0.20, $F_{1,21}$=5.35, P=0.03; body condition: β=0.45, t=2.31, P=0.03). Dominance status scores were not significantly correlated either with the residuals of the immune response on body weight (R^2=0.07, $F_{1,21}$=1.52, P=0.23) or with body condition (R^2=0.001, $F_{1,21}$=0.02, P=0.88).

Relationships of coloration with dominance, morphology, and immune response

Throat coloration

The PCA on reflectance data of all spectra of throat coloration (Fig. 1a) produced three throat principal components (thPCs) that together accounted for 93.3% of the variation in the original spectra. The first PC (thPC1) accounted for 62.9% of variation (eigenvalue=41.50). Coefficients relating thPC1 to the original reflectance data were all negative and of similar magnitude (Fig. 2a), so thPC1 represented achromatic brightness variation in the original spectra. The second PC (thPC2) accounted for a further 24.1% of the variation (eigenvalue=15.91) in the original spectra. The coefficients relating thPC2 to the original reflectance values below 580 nm were all positive, while above 580 nm, they were negative, with maximum positive values for the 350–500 nm range (Fig. 2a). Thus, thPC2 represented variation in the relative amount of short- to long-wavelength reflectance, with greater thPC2 scores indicating more saturated "bluish" colors. The third PC (thPC3) accounted for 6.3% of the variation (eigenvalue= 4.14), and the pattern of coefficients suggested that negative values represented variation in the relative amounts of medium (420–650 nm) wavelengths and positive values reflect variation in very short (300–420 nm) wavelengths (Fig. 2a).

Male dominance status was significantly correlated with thPC1 and thPC2, negatively with thPC1 and positively with thPC2 (stepwise GRM, model: R^2=0.65, $F_{2,20}$=18.29, P< 0.0001; thPC1: β=−0.69, t=−5.15, P<0.0001; thPC2: β= 0.30, t=2.23, P=0.037). Thus, more dominant males had throat coloration that was brighter (thPC1; Fig. 3a) and had higher values of short-wavelength reflectance (<580 nm, i.e., more saturated UV and "bluish"; thPC2; Fig. 3b). However, the residuals of head height on SVL were also significantly and negatively correlated with thPC1 and positively correlated with thPC2 (stepwise GRM, model: R^2=0.65, $F_{2,20}$= 18.29, P<0.0001; thPC1: β=−0.29, t=−2.20, P=0.039; thPC2: β=0.72, t=5.43, P<0.0001). A similar relationship was also found when we considered absolute head height (stepwise GRM, model; R^2=0.47, $F_{2,20}$=8.72, P=0.002; thPC1: β=−0.51, t=−3.09, P=0.006; thPC2: β=0.42, t= 2.54, P=0.019). Thus, lizards with absolutely or relatively taller heads also had brighter throat coloration (thPC1) with higher values of short-wavelength reflectance (thPC2). Nevertheless, partial regression coefficients showed that thPC1 was significantly correlated with dominance status (r=−0.73, P=0.0001) but was not significantly correlated with residuals of head height on SVL (r=−0.16, P= 0.47), whereas thPC2 was significantly correlated with residuals of head height on SVL (r=0.53, P=0.012) but was not significantly correlated with dominance status (r= 0.16, P=0.46).

Residuals of the immune response on body weight were significantly and negatively correlated with thPC2 (stepwise GRM, model: R^2=0.27, $F_{1,21}$=7.95, P=0.01; thPC2: β=−0.52, t=−2.82, P=0.01). Thus, males with a higher immune response had throat coloration with higher values of long-wavelength (>580 nm, i.e., less saturated UV and "bluish") reflectance (Fig. 3c).

Chest coloration

The PCA on reflectance data of all spectra of chest coloration (Fig. 1b) produced three chest principal components (chPCs) that together accounted for 94.1% of the variation in the original spectra. The first PC (chPC1) accounted for 70.7% of variation (eigenvalue=46.65). The coefficients relating chPC1 to the original reflectance data were all negative and of similar magnitude (Fig. 2b), so

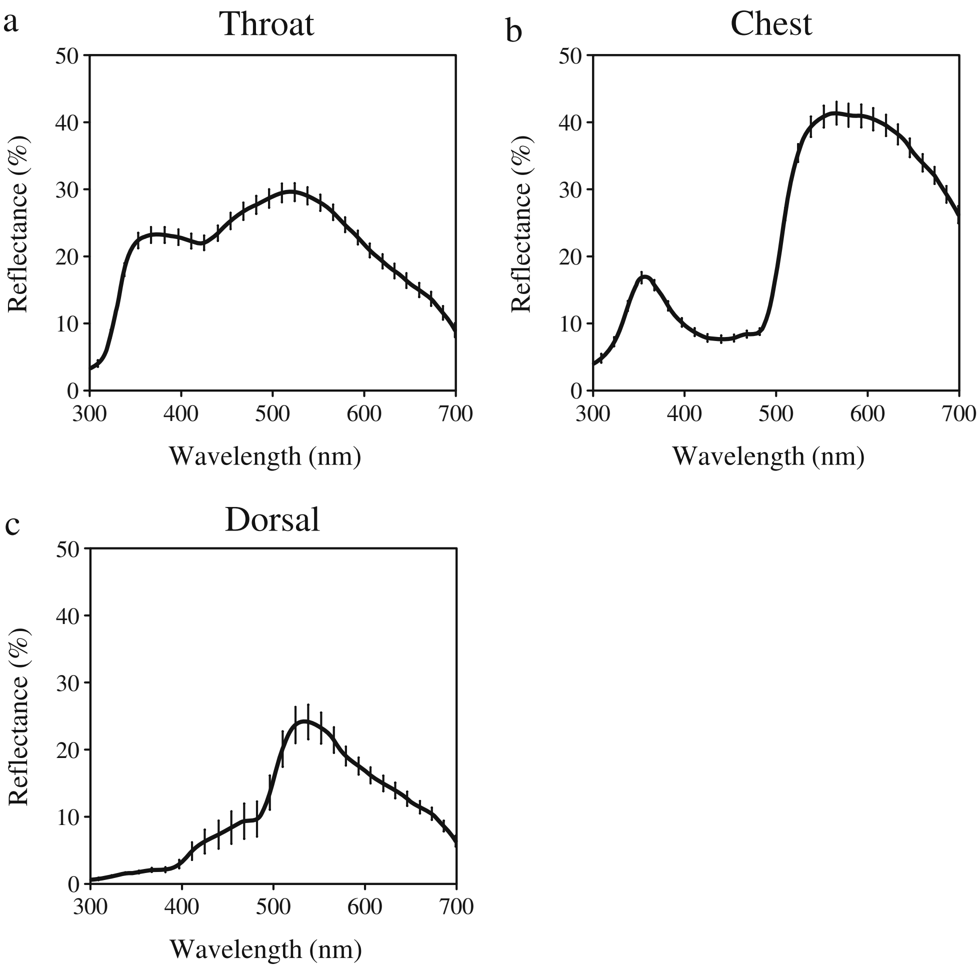

Fig. 1 Mean (± SE showed at 15 nm intervals) reflectance spectra of **a** throat, **b** chest, and **c** dorsal coloration of male lizards *L. schreiberi*

chPC1 represented achromatic brightness variation in the original spectra. The second PC (chPC2) accounted for a further 13.0% of the variation (eigenvalue=8.61) in the original spectra. The coefficients relating chPC2 to the original reflectance values below 500 nm were all negative, while above 500 nm, they were positive (Fig. 2b). Thus, chPC2 represented variation in the relative amount of short- to long-wavelength reflectance, with greater chPC2 scores indicating more saturated “yellowish” colors. The third PC (chPC3) accounted for 10.3% of the variation (eigenvalue=6.82), and the pattern of coefficients suggested that it represented variation in the relative amounts of medium (340–620 nm) wavelengths in the negative side to both very short (300–340 nm) and very long (620–700 nm) wavelengths in the positive side (Fig. 2b).

Males’ dominance status was not significantly correlated with any chPC describing chest coloration. Thus, chest coloration characteristics seemed independent of the dominance status of a male.

Residuals of the immune response on body weight were significantly and negatively correlated with chPC2 (stepwise GRM, model; $R^{2=}0.50$, $F_{1,21}=21.47$, $P=0.00014$; chPC2: $\beta=-0.71$, $t=-4.13$, $P=0.00014$). Thus, males with a higher immune response had chest colorations with higher values of short-wavelength reflectance (<500 nm, i.e., more saturated “yellowish”; Fig. 4).

Dorsal coloration

The PCA on reflectance data of all spectra of dorsal coloration (Fig. 1c) produced three dorsal principal components (dPCs) that together accounted for 96.0% of the variation in the original spectra. The first PC (dPC1) accounted for 76.2% of variation (eigenvalue=50.27). The coefficients relating dPC1 to the original reflectance data were all negative and of similar magnitude (Fig. 2c), so dPC1 represented achromatic brightness variation in the original spectra. The second PC (dPC2) accounted for a further 12.3% of the variation (eigenvalue=8.13) in the original spectra. The pattern of coefficients suggested it represented variation in the relative amounts of very short (300–410 nm) wavelengths in the positive side to very long (650–700 nm) wavelengths in the negative side (Fig. 2c). The third PC (dPC3) accounted for 7.5% of the variation

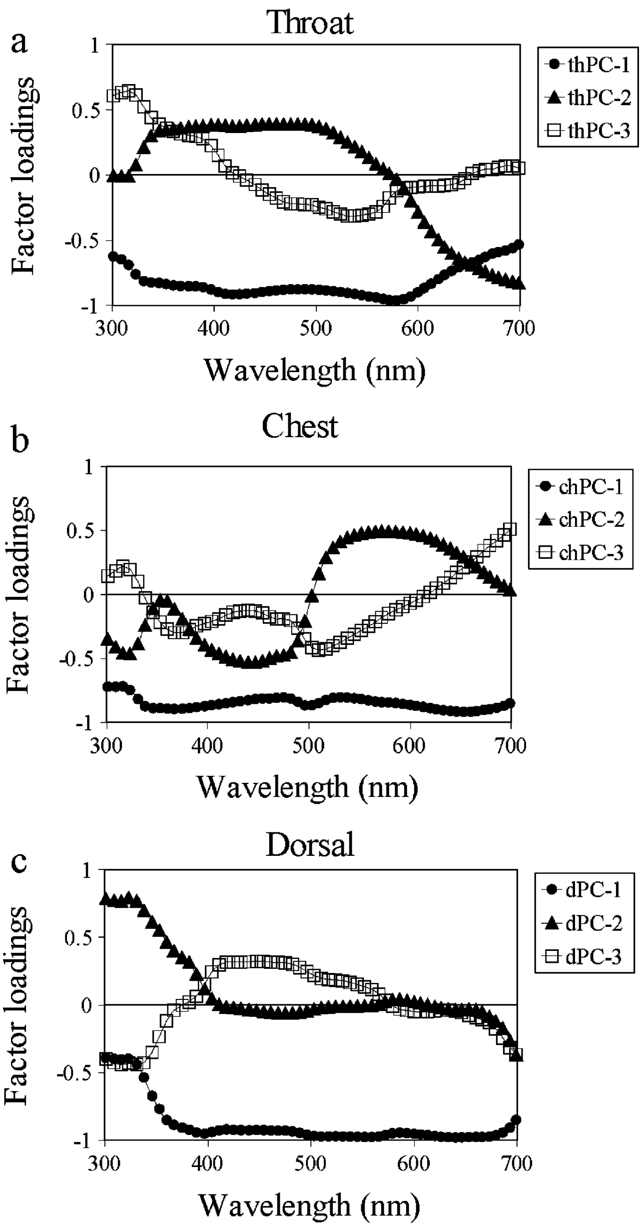

Fig. 2 Coefficients of the first three principal components from PCAs on reflectance spectra that characterize **a** throat, **b** chest, and **c** dorsal coloration of male lizards *L. schreiberi*

(eigenvalue=4.95), and the pattern of coefficients suggested that it represented variation in the relative amounts of medium (380–580 nm) wavelengths in the positive side to both very short (300–380 nm) and very long (580–700 nm) wavelengths in the negative side (Fig. 2c), with greater dPC3 scores indicating more saturated "greenish" colors.

Males' dominance status was significantly and positively correlated with dPC1 and with dPC3 (stepwise GRM, model: $R^2=0.50$, $F_{2,20}=9.93$, $P=0.001$; dPC1: $\beta=0.60$, $t=3.45$, $P=0.002$; dPC3: $\beta=0.47$, $t=2.33$, $P=0.03$). Thus, more dominant males had darker dorsal coloration (dPC1; Fig. 5a) and with higher values of medium-wavelength reflectance (380–580 nm, i.e., more saturated "greenish"; dPC3; Fig. 5b).

Residuals of the immune response on body weight were significantly and positively correlated with dPC1 (stepwise GRM, model: $R^2=0.51$, $F_{1,21}=21.91$, $P=0.00013$; dPC1: $\beta=0.71$, $t=4.68$, $P=0.00013$). Thus, males with a higher immune response had darker dorsal coloration (Fig. 5c).

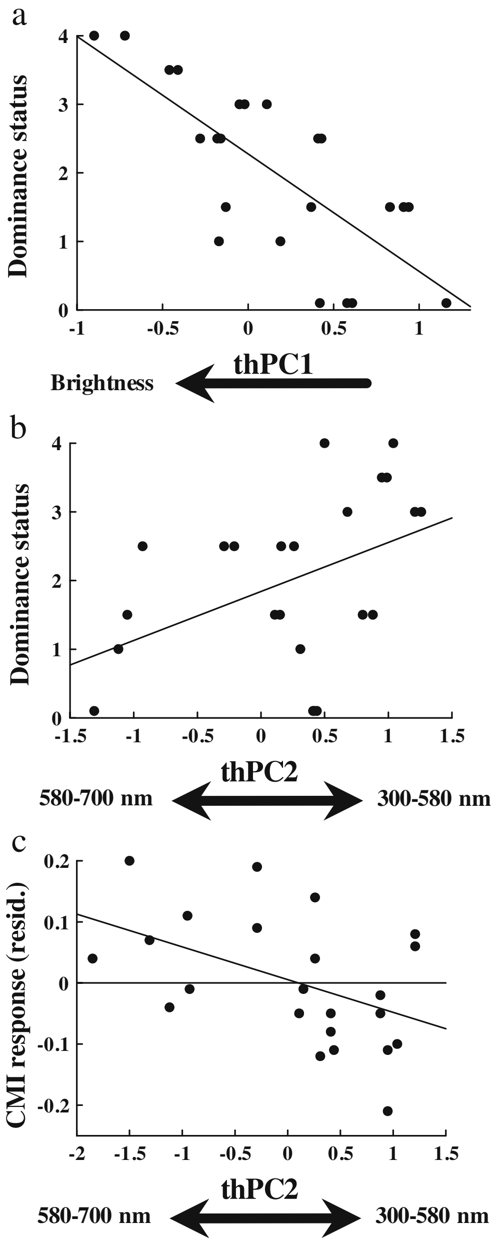

Fig. 3 Relationships between **a**, **b** dominance status or **c** residuals of the cell-mediated immune (*CMI*) response on body weight with the thPC scores describing characteristics of throat coloration of male lizards *L. schreiberi*. *Arrows* indicate the variables or wavelengths correlated with each PC

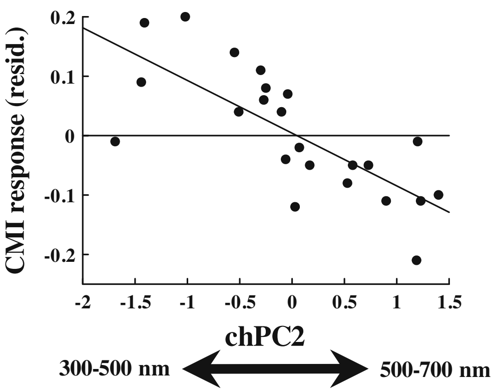

Fig. 4 Relationships between residuals of the cell-mediated immune (*CMI*) response on body weight with the chPC scores describing characteristics of chest coloration of male lizards *L. schreiberi*. *Arrows* indicate the wavelengths correlated with each PC

Morphology, coloration, and pairing status

Males found guarding a female (paired males) had significantly different overall morphological characteristics than males found alone (unpaired males; MANOVA; Wilk's λ= 0.36, $F_{6,16}$=4.78, P=0.006). Univariate protected ANOVAs showed that paired males had significantly shorter SVL and significantly longer tails than unpaired males, but they did not significantly differ in body weight or head size (Table 1).

Paired males also had significantly different overall characteristics of coloration than unpaired males (MANOVA; Wilk's λ=0.15, $F_{9,13}$=8.30, P=0.0004; Table 1). Univariate protected ANOVAs showed that paired males had throats significantly darker (thPC1) and with significantly higher values of short (<580 nm; thPC2) and very short (300–420 nm; thPC3) wavelength reflectances. Also, paired males had chest coloration with significantly higher values of long (>500 nm; chPC2) and medium (340–620 nm; chPC3) wavelength reflectances. Paired and unpaired males did not significantly differ in brightness of chest coloration (chPC1) or in any aspect of dorsal coloration (dPCs; Table 1). Thus, paired males had darker and more saturated UV and "bluish" throats and more saturated "yellowish" chests. Paired males had significantly lower dominance status scores (1.3±0.4) than unpaired ones (2.5±0.3; $F_{1,21}$=6.74, P=0.017), but they did not significantly differ in relative head height ($F_{1,21}$= 0.43, P=0.52), nor in the residuals of the immune response on body weight ($F_{1,21}$=0.07, P=0.79) nor in body condition ($F_{1,21}$=0.01, P=0.99).

Discussion

Our results showed that interindividual variation in the characteristics of coloration of multiple sexual signals of male lizards *L. schreiberi* can be related to variation in morphology, immune response, dominance status, and pairing status, but that different relationships are found for each color signal. These data suggest that characteristics of coloration of the different signals may reveal different messages to conspecifics.

Male lizards *L. schreiberi* with taller heads were more dominant in staged agonistic encounters with other males. As in many other lizard species, head size may confer

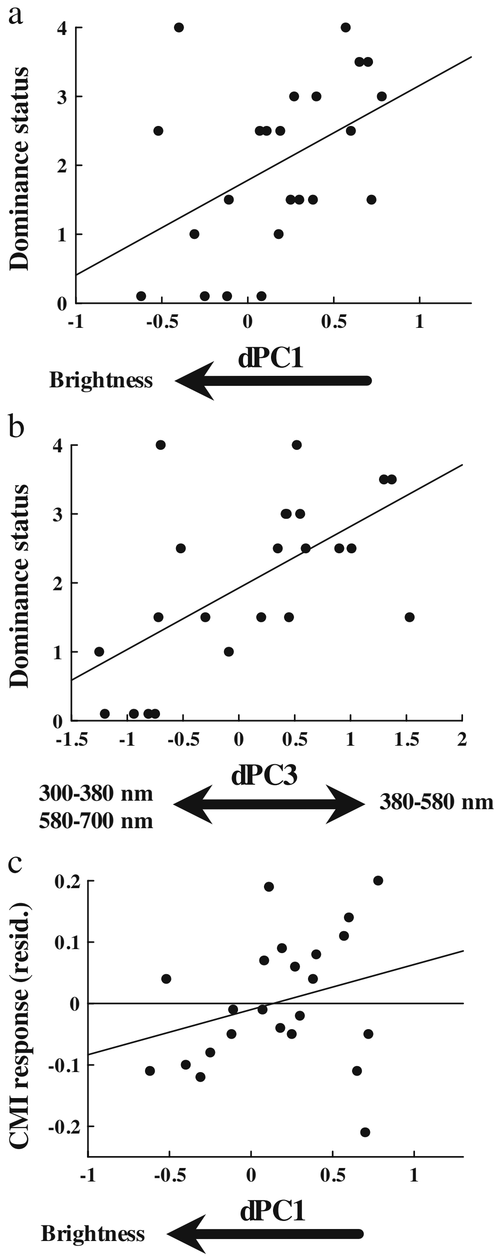

Fig. 5 Relationships between **a**, **b** dominance status or **c** residuals of the cell-mediated immune (*CMI*) response on body weight with the dPC scores describing characteristics of dorsal coloration of male lizards *L. schreiberi*. *Arrows* indicate the variables or wavelengths correlated with each PC

Table 1 Characteristics (mean ± SE) of morphological variables and coloration (PC scores) of paired and unpaired male lizards *L. schreiberi*

	Paired males	Unpaired males	$F_{1,21}$	*P*
Morphology				
SVL (mm)	108±1	113±1	7.92	**0.01**
Tail length (mm)	175±9	149±7	5.03	**0.04**
Weight (g)	28.5±0.9	31.2±1.1	3.03	0.10
Head height (mm)	12.5±0.2	12.7±0.2	0.73	0.40
Head length (mm)	25.1±0.3	25.6±0.3	1.45	0.24
Head width (mm)	20.7±0.4	20.8±0.4	0.02	0.88
Coloration				
Throat				
thPC1	0.46±0.16	−0.04±0.13	5.70	**0.026**
thPC2	0.70±0.12	−0.04±0.22	6.55	**0.018**
thPC3	0.52±0.19	−0.35±0.18	10.41	**0.004**
Chest				
chPC1	0.56±0.30	0.03±0.23	1.97	0.17
chPC2	0.97±0.23	−0.11±0.26	8.16	**0.009**
chPC3	−0.10±0.27	0.59±0.20	4.36	**0.049**
Dorsal				
dPC1	0.11±0.13	0.14±0.12	0.03	0.86
dPC2	0.58±0.30	−0.09±0.22	3.42	0.08
dPC3	−0.13±0.22	0.27±0.24	1.32	0.26

Results (*F*, *P*) from protected one-way analyses of variance comparing paired and unpaired males are showed. Significant differences are marked in bold

dominance because males with larger heads can bite harder during fights (e.g., Herrel et al. 1999; Huyghe et al. 2005; Lappin et al. 2006) and thus can have advantages in intrasexual agonistic contests if an escalation occurs (Huyghe et al. 2005). In contrast, body size per se did not convey status within the small range of sizes considered in this experiment (i.e., all males were large and adult individuals, while younger/smaller individuals were not considered). In other lizard species, bite performance, rather than size per se, confers dominance and fitness advantages (Lappin and Husak 2005). Further study using a larger size range of male *L. schreiberi* is needed to assess the role of body size.

Dominant male *L. schreiberi* also had throats (and lateral sides of the head) with “blue” coloration that was brighter and saturated more in UV and blue wavelengths and dorsal coloration that was darker and greener (medium wavelength). The evolution of social dominance requires phenotypic traits that convey honest information about an individual’s status (Berglund et al. 1996). In *L. schreiberi*, the relationship between throat coloration and status was not independent of head height, which showed a similar correlation with coloration. Most agonistic interactions consisted of displays in which the dominant male approached with head lowered and the neck and throat inflated (Marco and Pérez-Mellado 1999). This display would allow a male to judge in advance the fighting ability of an opponent not only from coloration characteristics but also from his actual head size and to retreat before a fight occurred. In this sense, UV and blue coloration of the throat may act as an amplifier of the head size, which would facilitate the estimation of head size and associated dominance status at long distance. Some aspects of head coloration may signal status per se (i.e., brightness), but the maintenance of the honesty of the signal might be dependent on the relationship between coloration and actual head size and associated bite performance, which could not be faked. Males with small heads would not be able to deceptively signal a superior status because the reliability of this color signal indicating head size is constantly put on trial in male–male contests and could be subjected to social control by genuinely dominant males (Rohwer 1982; Martín and Forsman 1999; Whiting et al. 2003). This is in accordance with the field observation that larger male *L. schreiberi* develop blue head coloration earlier in their lives than smaller males, which maintain white-brown head subadult coloration until they grow and are large enough (Marco 1994, 1995). Similarly, in the lizard *Platysaurus broadleyi*, throat UV, not body size or residency, acts as a as a primary signal in fighting ability assessment. However, throat UV is only used during the initial stage of opponent assessment; when UV coloration is experimentally manipulated, it does not influence contest outcome (Stapley and Whiting 2006). The actual body or head size may be the final determinant if the color signal is incongruent with the actual fighting ability, which would allow maintaining the honesty of the signal by genuinely dominant males.

Health state of male lizards was also reflected in some characteristics of coloration. Males with a relatively higher immune response had "blue" throats with lower amounts of UV coloration, but had "yellow" chests with higher amounts of UV coloration. Thus, the UV component of coloration seems to have dual and opposite messages depending on the body position of the signal. This might be explained by the different morphological structures on which coloration of these two signals are based. The "blue" head may be based on structural coloration and melanin pigments (Macedonia et al. 2000; Quinn and Hews 2003), whereas the "yellow" chest is probably based on carotenoid pigments. Thus, there might exist different trade-offs between the production of each signal and the maintenance of the immune system. This is consistent with the fact that different aspects of coloration patterns and performance traits of lizards may be regulated by different hormones or endocrine pathways (e.g., Sinervo et al. 2000; Calisi and Hews 2007).

On the one hand, increasing UV and blue coloration in the throat might require higher testosterone circulating levels (which will also increase head size, bite force, aggressiveness, and dominance; Whiting et al. 2006). Testosterone plays an important role in modulating the allocation of resources to reproductive physiology and behavior (Moore and Lindzey 1992), but increasing testosterone may have immunosuppressive effects (Belliure et al. 2004). Therefore, dominant males with more UV head coloration might have the cost of a lower immune response. Similarly, in males of the lizard *Psammodromus algirus*, high testosterone levels increase the development of nuptial coloration but render males more susceptible to parasites (Salvador et al. 1996a) and decrease their immune response (Belliure et al. 2004). Similar trade-offs among testosterone, signaling, and parasites have been suggested in other lizard species (Olsson et al. 2000; Klukowski and Nelson 2001; Uller and Olsson 2003; Václav et al. 2007; but see Schall and Staats 1997). On the other hand, allocating more yellow carotenoids to the chest, which consequently might decrease structural UV coloration, may be costly because there is a trade-off with the role of these pigments in the maintenance of the immune function (López et al. 2009). Thus, lizards with more UV coloration in the chest might allocate less carotenoids to coloration and maintain a greater immune response.

The relationships between coloration and pairing status suggest that male dominance is not the single factor that determines pairing success in this lizard. This suggests that female *L. schreiberi* do not always prefer dominant males, as occurs in other lizards (López et al. 2002; Stapley 2008). Males with throats with more UV and bluish coloration, presumably more dominant, had higher pairing status. However, paired males had lower dominance status, darker head coloration, and even had smaller body length than unpaired males. Their tails were longer than those of unpaired males, but their head sizes did not differ from those of unpaired males. Interindividual variation in tail length could arise from previous tail loss events, which may affect dominance status of male lizards (Fox and Rotsker 1982; Martín and Salvador 1993) and have long-term effects on their mating success (Salvador et al. 1996b; Hofmann and Henle 2006).

These contradictory results may be explained if the final mating success of a male results from the balance between two opposite selective forces (Andersson 1994). High dominance status would decrease intrasexual competition for accessing females, but if females exhibit preferences and accept guarding males, preferences may be based on other male traits not related to dominance (e.g., López et al. 2002; Lailvaux and Irschick 2006; Stapley 2008). Accordingly, field observations show that dominant male *L. schreiberi* mate more times, but these males do not get exclusive access to individual females, which are polyandrous (Marco and Pérez-Mellado 1999). Thus, paired males had chests with more yellow carotenoid-dependent coloration. Since animals may suffer a trade-off between allocation of pigments to physiological functions and ornamentation (Faivre et al. 2003; López et al. 2009), the expression of carotenoid-dependent coloration may often serve as an honest signal of individual quality (Blount et al. 2003). For example, less parasitized male lizards *Podarcis muralis* had brighter and more yellowish ventral colorations (Martín et al. 2008). In chuckwalla lizards, *Sauromalus obesus*, male color likely functions as an indicator of food resources to females (Kwiatkowski and Sullivan 2002). Further experimental work is needed to test whether female lizards *L. schreiberi* may use chest coloration of males as a signal of condition or genetic quality. Finally, it is possible that mating success also depends on male behavior during courtship rather than on morphological or coloration traits per se as it occurs in other lizards (Baird et al. 2007; Stapley 2008).

Nevertheless, paired and unpaired male *L. schreiberi* did not differ in immune response or body condition. Thus, it is likely that the pairing success of a male is not only determined by the female mate preferences but also by the male's ability to displace other males and to subdue females (Anderson 1994; Wong and Candolin 2005; Fitze et al. 2008). In some species, males that otherwise would be rejected by females may be still able to get matings by fighting with other "preferred" males and forcing matings with females (Wong and Candolin 2005). In the agamid lizard, *Ctenophorus ornatus*, male chest patch size predicts territory size and the number of females in the territory, but does not predict reproductive success (LeBas 2001). Instead, on the one hand, males with larger heads also have a higher number of females in their territories and higher reproductive success, but males with larger body size do not have a greater number of females in their territories yet get higher mating success from extraterritorial copulations (LeBas 2001). Therefore, the mating success of a male would result from a balance between his intrasexual success in agonistic contests (dominance) and his attractiveness (health state, courtship behavior) to females (Anderson 1994; Fitze et al. 2008). Because increasing dominance to maximize intrasexual success may decrease health state and success in intersexual selection, a male should trade off investments among multiple traits to optimize his mating success.

We conclude that the multiple colorful signals of male *L. schreiberi* may carry different messages for different receivers, either male or female conspecifics, which have different interests. The development of the different signals, based on different morphological and physiological mechanisms and trade-offs, might allow the reliability of multiple colorful traits in different social contexts. Further experimental work that manipulates the expression of the signals is needed to verify whether our correlative results can be explained by these hypotheses.

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