

# Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids

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## Abstract

Sexual selection has been invoked as a major force in the evolution of secondary sexual traits, including sexually dimorphic colorations. For example, previous studies have shown that display complexity and elaborate ornamentation in lizards are associated with variables that reflect the intensity of intrasexual selection. However, these studies have relied on techniques of colour analysis based on human – rather than lizard – visual perception. Here, we use reflectance spectrophotometry and visual modelling to quantify sexual dichromatism considering the overall colour patterns of lacertids, a lizard clade in which visual signalling has traditionally been underrated. These objective methods of colour analysis reveal a large, previously unreported, degree of sexual dichromatism in lacertids. Using a comparative phylogenetic approach, we further demonstrate that sexual dichromatism is positively associated with body size dimorphism (an index of intrasexual selection), suggesting that conspicuous coloration in male lacertids has evolved to improve opponent assessment under conditions of intense male–male competition. Our findings provide the first evidence for the covariation of sexual dichromatism and sexual size dimorphism in lacertids and suggest that the prevalent role of intrasexual selection in the evolution of ornamental coloration is not restricted to the iguanian lineage, but rather may be a general trend common to many diurnal lizards.

## Introduction

Males and females differ along many dimensions, including coloration. In species with conspicuous coloration, males are frequently the most colourful sex, resulting in widespread sexual dichromatism. Populations and species vary widely in the extent and pattern of sexual dichromatism, and this variation is thought to be driven by geographical variation in the strength of sexual and natural selection (Andersson, 1994; Hill & McGraw, 2006). Recent comparative studies have emphasized the role of sexual selection and have tested

the prediction that dichromatism should be greater in species subject to intense sexual selection. This prediction has been confirmed in birds (Owens & Hartley, 1998; Badyaev & Hill, 2000; Figuerola & Green, 2000; Dunn *et al.*, 2001). In contrast, only two studies have addressed the relationship between sexual dichromatism and sexual selection in lizards. Stuart-Fox & Ord (2004) found that, in agamid lizards, the strength of sexual selection is a good predictor of dichromatism in body regions that are concealed from visually oriented predators. Similarly, Chen *et al.* (2012) found that the evolution of colour pattern complexity and colour dichromatism in Australian dragon lizards is strongly influenced by sexual selection.

These and other studies of sexual dichromatism in lizards have relied on photographs and published descriptions of the lizards' coloration (e.g. Stuart-Fox & Owens, 2003; Stuart-Fox & Ord, 2004; Stuart-Fox *et al.*,

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2004; Dolman & Stuart-Fox, 2010; Östman & Stuart-Fox, 2011; Chen *et al.*, 2012). However, it is widely acknowledged that methods of colour quantification based on human colour perception are intrinsically anthropocentric and inadequate to assess the selective pressures that are responsible for the design of chromatic communication systems (e.g. Endler, 1990; Cuthill *et al.*, 1999; Eaton, 2005). The potential for mismeasure is proportional to the differences between our visual system and that of the studied taxon. Diurnal lizards in particular have a tetrachromatic visual system with four types of photopigments, one of them sensitive to near ultraviolet wavelengths (Loew *et al.*, 2002; Fleishman *et al.*, 2011; Pérez i de Lanuza, 2012). In contrast, humans are trichromatic and cannot perceive wavelengths below 400 nm. The differences in visual perception between humans and lizards stress the importance of adopting spectrophotometric objective techniques and visual modelling for studying the design of lizard colour patterns (e.g. Macedonia *et al.*, 2002, 2004, 2009).

Recent advances in the study of animal coloration have produced powerful analytical tools that make it possible to compare entire colour patterns as seen by the signals' primary receivers (Endler & Mielke, 2005; Stoddard & Prum, 2008). These new methods overcome the limitations of previous methodologies that relied on separate pairwise comparisons of different colour patches and allow us to ask questions about differences in overall coloration and pattern complexity among sexes, populations or species. Unfortunately, although the value of these techniques is widely recognized, many find them impractical due to the large effort required for sampling and taking spectrophotometric measurements (e.g. Chen *et al.*, 2012). Here, for the first time to our knowledge, we use visual modelling combined with a comparative approach to assess the role of sexual selection in the evolution of sexual dichromatism, focusing on the Scleroglossan family Lacertidae. Lacertids are an ideal group in which to test hypotheses regarding the evolution of sexually dichromatic coloration because lacertid sexual dichromatism ranges from subtle spectral shape differences (e.g. *Timon lepidus*, Font *et al.*, 2009) to dramatic differences in hue (e.g. *Lacerta agilis*, Pérez i de Lanuza & Font, 2007; Olsson *et al.*, 2011).

To assess the role of sexual selection in the evolution of sexual dichromatism, we looked for patterns of covariation between dichromatism and sexual size dimorphism (SSD), which has been widely used as an indicator of the strength of sexual selection in comparative studies (Stuart-Fox & Ord, 2004; Ord & Martins, 2006; Fairbairn *et al.*, 2007). Particularly in lizards, male–male competition is the main factor driving SSD, which therefore provides an index of the intensity of intrasexual selection (Wikelski & Trillmich, 1997; Ord *et al.*, 2001; Cox *et al.*, 2003, 2007; Corl *et al.*, 2010).

## Materials and methods

### Study animals

We obtained colour measurements from 42 lacertid taxa (a total of 943 individuals belonging to 39 species; three with two subspecies) covering the three main clades of Lacertidae (i.e. Gallotiinae, Lacertini and Eremiadini). See Table S1 for a complete list of species, sample sizes and sample locations.

### Sexual size dimorphism

We calculated standard sexual size dimorphism (SSD) (Cox *et al.*, 2003) using data from published sources and information obtained during field work (Table S1).

### Colour measurements and visual modelling

We took reflectance spectra in the 300–700 nm range of colour patches from multiple body locations (Fig. S1) of each species with a portable USB2000 spectrophotometer and a PX-2 xenon lamp (Ocean Optics, Dunedin, FL, USA) using standard procedures (Font *et al.*, 2009; Pérez i de Lanuza & Font, 2011). Within each sex and species, we averaged all the spectra from a given colour patch, and the resulting spectrum was transformed into coordinates of a single chromatic point located inside a tetrahedral colour space (TCS) (Endler & Mielke, 2005). The distance between different points inside the TCS is proportional to the difference between the corresponding colour patches as perceived by the visual signal receiver. Calculations were performed with TetraColorSpace (Stoddard & Prum, 2008) for Matlab 7 (MathWorks, Natick, MA, USA) taking cone sensitivities of *Platysaurus broadleyi* (Cordylidae, Scleroglossa) (Fleishman *et al.*, 2011). Cone sensitivity spectra, covering the 300–700 nm range of wavelengths, were generously provided by L. Fleishman.

### Sexual dichromatism analyses

We combined two analyses to estimate sexual dichromatism. First, we took average spectra to compare the spectral properties of main colour patches for each species by sex without any visual modelling transformation. Second, we used TCS to obtain overall measures of sexual dichromatism using visual modelling.

#### *Patch-by-patch spectral sexual dichromatism*

The body surface of most lacertids can be divided into three regions based on its coloration. Cryptic dorsal and conspicuous ventral surfaces are present in all the species. The third colour region corresponds to the flanks (lateral and ventrolateral surfaces), where conspicuously coloured outer ventral scales (OVS, Arnold *et al.*, 2007) and/or lateral eyespots are found in many spe-

cies. OVS and eyespots often exhibit ultraviolet reflectance (Molina-Borja *et al.*, 2006; Font *et al.*, 2009; Pérez i de Lanuza & Font, 2011). From spectra of these three surfaces, we extracted conventional variables that describe colour (i.e. brightness, chroma and hue) for each colour patch and compared them by sex using standard ANOVA or Mann–Whitney *U*-tests. Brightness was calculated as the sum of the reflectance of each wavelength over the entire spectrum for all the spectra (Endler, 1990). Chroma measures were different depending on the colour patch. For dorsal surfaces, we used the standard measure described by Endler (1990). For ventral surfaces, we extracted two complementary variables: (i) a measure of medium wavelength chroma calculated by dividing the sum of reflectances within the 400–600 nm range by the sum within the entire range and (ii) a measure of the spectral location of the median reflectance (Marshall *et al.*, 2003; Pérez i de Lanuza *et al.*, 2013). For OVS and eyespots, we calculated the ultraviolet chroma dividing the sum of reflectances within the 300–400 nm range by the sum of reflectances within the 300–700 nm range. Hue was calculated as the spectral location of the maximum (i.e. peak) reflectance.

#### Visual modelling and the sexual dichromatism index

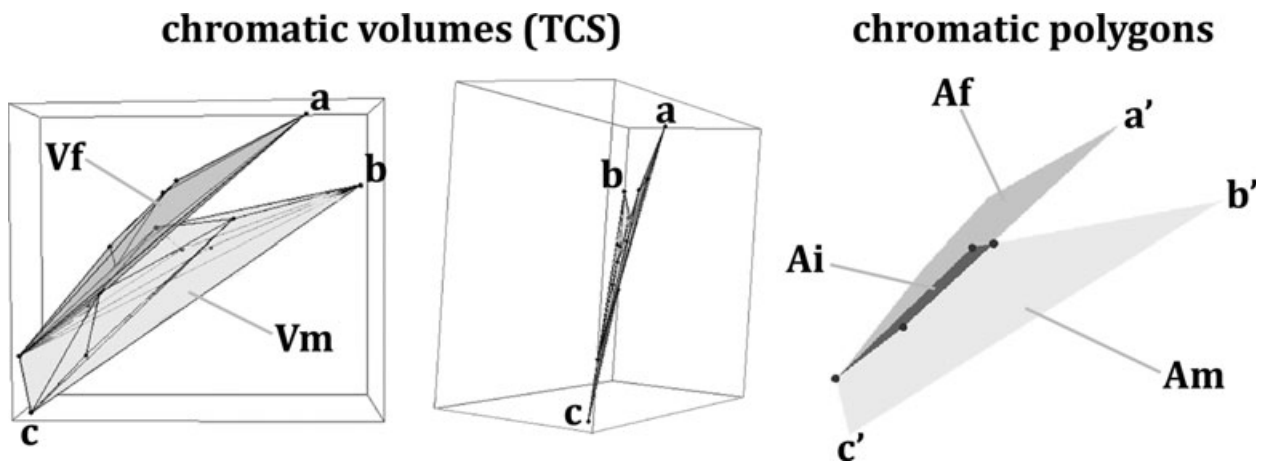
In the TCS, all the chromatic points corresponding to a colour pattern depict a colour volume (Stoddard & Prum, 2008). This volume provides a measure of colour pattern variation within each sex and species and can be used to describe the extent to which different colour patterns overlap by calculating the intersection between

pairs of volumes. Recently, Stoddard & Stevens (2011) used colour overlap to describe how well a cuckoo egg matches a host egg. Due to the geometric complexity of colour volumes (convex polyhedra) included in their sample, Stoddard & Stevens (2011) estimated colour volume overlap of host and cuckoo eggs using Monte Carlo simulations. As lacertid colour volumes are thin wedges with very little volume (Fig. 1), we developed an alternative mathematical methodology to calculate the extent to which colour patterns of males and females overlap. We projected the chromatic points of male and female patterns of a given species to the same plane by a standard linear model fit procedure, obtaining two chromatic polygons. With these polygons, we calculated a sexual dichromatism index (SDI) as follows:

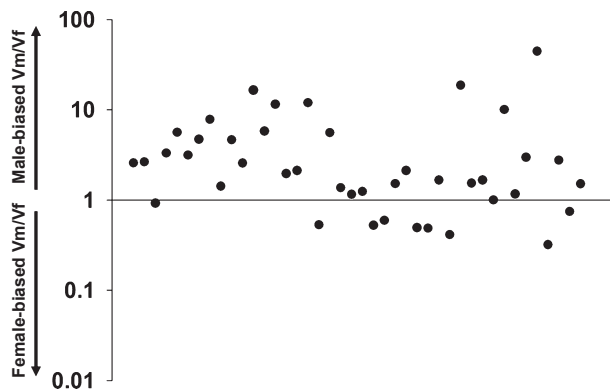
$$SDI = A_i / (A_m + A_f - A_i)$$

where  $A_m$  and  $A_f$  are the areas of the chromatic polygons of males and females, respectively, and  $A_i$  is the intersection area. Low values of SDI represent high levels of sexual dichromatism. Projections, bidimensional convex hulls and calculations were performed in Mathematica 8 (Wolfram, Champaign, IL, USA).

This SDI index is sex independent because the dichromatism can be caused by both males and females having large (or small) chromatic polygons. However, for the majority of species in our sample, the colour volumes of males were larger than those of females. To assess the contribution of males and females to the SDI, we evaluated the relationship between male and female colour variation calculating the ratio between colour volumes of males ( $V_m$ ) and females ( $V_f$ ) (i.e.  $V_m/V_f$ ).



**Fig. 1** Colour volumes and corresponding chromatic polygons. Chromatic volumes (TCS): two views of the colour volumes of *Podarcis melisellensis* calculated with TetraColorSpace.  $V_f$  and  $V_m$  are the colour volumes of females and males, respectively.  $a$ ,  $b$  and  $c$  indicate three representative chromatic points that define these colour volumes in both views. Chromatic polygons: projection of chromatic points onto a two-dimensional plane ( $a'$ ,  $b'$  and  $c'$  are the two-dimensional projections of  $a$ ,  $b$  and  $c$ ).  $A_m$  and  $A_f$  are the areas of chromatic polygons of males and females, respectively, and  $A_i$  is the intersection area.  $A_m$ ,  $A_f$  and  $A_i$  are used in the calculation of sexual dichromatism index (SDI).



**Fig. 2** Values of the  $V_m/V_f$  ratio for all the taxa in the sample. The y-axis has a decimal logarithmic scale. Values above 1 indicate males with more complex colour pattern than females (i.e. males with a larger colour volume than females). Values below 1 indicate females with more complex colour pattern than males (i.e. males with a smaller colour volume than females).

Large values of this ratio represent species in which males show a more chromatically diverse colour pattern than females (Fig. 2).

### Comparative phylogenetic analyses

We analysed the relationship between SDI and SSD performing phylogenetic generalized least squares (PGLS; Martins & Hansen, 1997). We used two complementary evolutionary models: a model of Brownian motion (BM) and, because our premise is that sexual dichromatism evolves under directional sexual selection, an Ornstein–Uhlenbeck (OU) model with a single global optimum. As no single published source included all the species of interest, we compiled a phylogenetic hypothesis from several partial phylogenies (Appendix S1). Analyses were performed twice, that is, including data from all available taxa and excluding *Podarcis lilfordi* subspecies. This was done to prevent possible distortions caused by peculiarities of insular evolution in these subspecies that inhabit small islets and show extravagant colorations (Pérez i de Lanuza & Font, 2011). Previously to the analyses, SSD and SDI were log-transformed. The analyses were performed using the *ape* (Paradis *et al.*, 2004) and *geiger* packages (Harmon *et al.*, 2007) in R (<http://cran.r-project.org>).

### Contribution of different colour patches to overall sexual dichromatism

As in other lizards, body coloration in lacertids is the result of multiple selection pressures. Whereas efficient communication often favours conspicuous colorations, the need to remain concealed from both prey and

predators selects for cryptic colorations (Bradbury & Vehrencamp, 2011). In lacertids, the trade-off between these conflicting selective regimes results in animals that are relatively cryptic dorsally, but that possess conspicuous ventral and ventrolateral colorations that function as chromatic signals (Pérez i de Lanuza & Font, 2011; Pérez i de Lanuza, 2012).

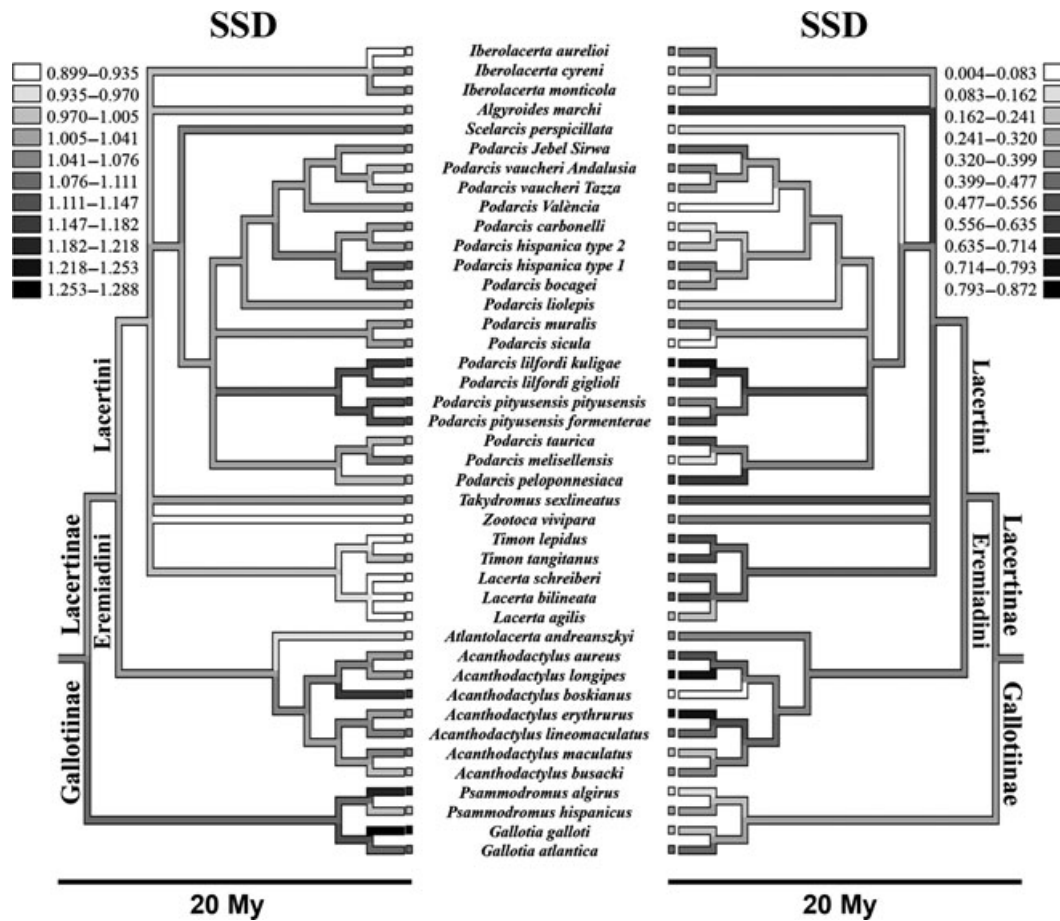
To identify the relative contribution of these three body regions to sexual dichromatism, for each taxon studied we measured sexual dichromatism separately in (i) the dorsal surface, (ii) the ventral surface and (iii) OVS and/or eyespots. For each coloration, sexual dichromatism was calculated as the Euclidian distance between the corresponding male and female chromatic points. For each taxon, the three values of sexual dichromatism were normalized by the highest value. Then, using these three values as coordinates of sexual dichromatic points, we plotted together the data of all the taxa in the sample to identify graphically which colorations contribute more to the overall dichromatism.

## Results

Examples of the reflectance spectra of males and females are shown in Fig. S2. Table S2 shows the values of each colour variable and statistics of sexual dichromatism in the spectral patch-by-patch comparisons. In our sample, 25 of 42 taxa show sexual dichromatism in the lateral conspicuous OVS and/or eyespots, 15 taxa are sexually dichromatic for the ventral surface, and 14 for the dorsal surface. Overall, 31 taxa have some kind of spectral sexual dichromatism (73% of the taxa in our sample).

Figure 3 shows historical reconstructions of SSD and SDI evolution, and Table S1 shows SDD and SDI data for each taxon included in the sample. The PGLS analysis reveals a significant relationship between the two variables irrespective of whether *Podarcis lilfordi* subspecies are included (BM: AIC = -178.28, coefficient = -0.025,  $P = 0.0055$ ; OU: AIC = -176.28, coefficient = -0.025,  $P = 0.0055$ ) or not (BM: AIC = -168.64, coefficient = -0.027,  $P = 0.0027$ ; OU: AIC = -166.64, coefficient = -0.027,  $P = 0.0027$ ). In short, these results indicate that more sexually dimorphic lacertid species tend to also be more sexually dichromatic.

Table S1 shows colour volumes for males and females and the  $V_m/V_f$  ratio for each species. In general, colour volumes are strongly male-biased. In fact, colour volumes of males are larger than those of females in 32 taxa (i.e. 74%), and in one species (*Takydromus sexlineatus*), males and females have colour volumes of the same size (Table S1). In species in which males have larger volumes than females, the mean  $V_m/V_f$  ratio is 5.86 ( $N = 32$ ; range: 1.15–44.48). In species in which females have larger volumes than males, the mean  $V_m/V_f$



**Fig. 3** Historical character reconstructions of sexual dichromatism index (SDI; species with more intense male-biased body size dimorphism are darker) and sexual size dimorphism (SSD; species with a higher sexual dichromatism are lighter) in lacertid lizards. My = millions of years. Reconstructions were performed with a squared parsimony model (Brownian motion) in Mesquite 2.74 (Maddison & Maddison, 2011).

Vf ratio is 0.60 ( $N = 10$ ; range: 0.32–0.96). Figure 2 shows values of the  $V_m/V_f$  ratio for all the taxa included in the sample.

Figure 4 shows the relative contribution to sexual dichromatism of the dorsal, ventral and lateral body surfaces. The conspicuous lateral colour patches (i.e. OVS and eyespots) show the most dichromatic coloration in 28 of the 42 taxa, whereas the ventral and dorsal surfaces are the main source of dichromatism only in a few taxa (seven for both colorations).

## Discussion

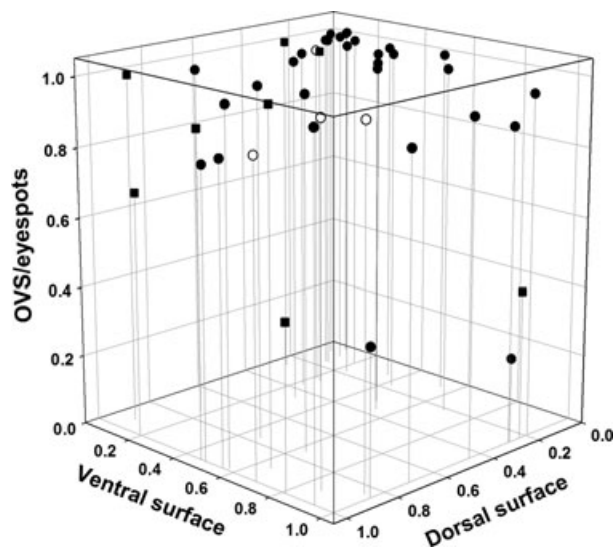
To our knowledge, this is the first study that uses the comparative method to investigate the evolution of sexual dichromatism of overall colour patterns considering the visual sensibility of signal receivers. We used visual modelling to develop a methodology that would allow us to examine sexual dichromatism using objective measurements of colour while considering overall

coloration patterns. Our results suggest that sexual dichromatism in lacertids, which we show to be much more widespread than previously reported, evolves under the same general selection pressures as in other lizard families.

## Evolution of sexual dichromatism in lacertids

Our results show that male-biased sexual dimorphism in body size is a good predictor of sexual dichromatism in the family Lacertidae. Those species in which males are larger than females tend to be more sexually dichromatic (male-biased), suggesting that sexual dichromatism in lacertids is driven by sexual selection. This agrees with previous results obtained with other lizard clades (Stuart-Fox & Ord, 2004; Chen *et al.*, 2012).

As female mate choice is relatively rare in lizards (Olsson & Madsen, 1995, 1998; Tokarz, 1995; LeBas & Marshall, 2001; Olsson, 2001; Wikelski *et al.*, 2001; Font *et al.*, 2012), SSD is often assumed to be mainly driven by intrasexual selection (Wikelski & Trillmich,



**Fig. 4** Contribution of the dorsal, ventral and lateral surfaces of lacertids to sexual dichromatism. Each axis represents the degree of sexual dichromatism in one of the three surfaces: ventral surface, dorsal surface, and outer ventral scales (OVS) and/or eyespots. In all axes, large values represent increased sexual dichromatism. Each point corresponds to a species, and its coordinates are described by the values of sexual dichromatism in the three axes. Open circles, filled circles and squares represent species of Gallotiinae, Lacertini and Eremiadini clades, respectively. Note how dichromatic points cluster near the corner representing high levels of sexual dichromatism in OVS and/or eyespots and relatively low levels of ventral and dorsal sexual dichromatism.

1997; Cox *et al.*, 2003, 2007; Corl *et al.*, 2010). Social dominance is strongly influenced by body size, which confers an advantage in male agonistic encounters (e.g. Wikelski & Trillmich, 1997; Abell, 1998; LeBas, 2001; Huyghe *et al.*, 2005; Osborne, 2005; Karsten *et al.*, 2009). Although some colour patches have been shown to act as intersexual signals (e.g. Bajer *et al.*, 2010), the finding of a relationship between SSD and sexual dichromatism suggests a crucial role of colour patterns in male–male competition in lacertids. Body coloration may provide valuable clues to a male’s intrinsic quality or condition and may improve opponent assessment during agonistic interactions. In fact, many displays used by fighting males, such as gular depression, lateral body compression and broadside presentation, seem to be designed to reveal male coloration to rivals (e.g. Stuart-Fox *et al.*, 2009; Bajer *et al.*, 2011). Moreover, sexual differences in colour volume size reveal that males often have more complex and diverse colorations than females.

We found a positive relationship between SSD and sexual dichromatism for overall coloration patterns in lacertids, including both exposed and concealed body regions. However, sexual dichromatism is to a large

extent due to colour patches located along the lizard’s flanks (i.e. OVS, lateral eyespots), in relatively concealed locations. These patches make a disproportionate contribution to sexual dichromatism because they are present in males but lacking in females or, when present in both sexes, show chromatic differences between males and females. Given their location, these male-biased colour patches seem ideally suited to function as chromatic signals. Furthermore, they show reflectance maxima in the ultraviolet range, which could provide a ‘private’ communication channel inaccessible to potential eavesdroppers lacking ultraviolet vision (Font *et al.*, 2009; Pérez i de Lanuza & Font, 2011). These results agree with those obtained with agamid lizards, in which SSD correlates with sexual dichromatism in concealed body regions (but not in exposed regions) that are assumed to have a primarily signalling function, such as the throat, chest and ventrum (Stuart-Fox & Ord, 2004).

Our results highlight the complex nature of visual communication in lacertids and suggest that the differences between squamate lineages are unlikely to fit neatly into simple dichotomies, such as that characterizing iguanians as visual and scleroglossans as chemosensory (e.g. Vitt & Pianka, 2005; Mason & Parker, 2010). Based on our results, we surmise that the processes responsible for the evolution of body coloration are similar in lacertids, agamids and iguanids and are probably shared by most lineages of diurnal lizards. Interestingly, this general trend differs from that found in birds, in which sexual dichromatism is often driven by intersexual (i.e. female mate choice) rather than intrasexual selection (Andersson, 1994; Owens & Hartley, 1998; Figuerola & Green, 2000; Dunn *et al.*, 2001; Badyaev & Hill, 2003; Toomey & McGraw, 2012).

Sexual selection resulting from male to male competition is a major driver of SSD in lizards (Stuart-Fox & Ord, 2004; Ord & Martins, 2006; Cox *et al.*, 2007). However, other (not mutually exclusive) selective forces may also influence SSD evolution in this group, such as fecundity selection (which favours large females when number of offspring increases with maternal size) or natural selection to reduce resource competition between sexes (Cox *et al.*, 2007). Although Cox *et al.* (2007) concluded that fecundity selection and natural selection hypotheses have weak empirical support generally, a comparative study performed on eight species of lacertids (all included in our sample) found a strong relationship between fecundity and SSD (Braña, 1996). These results suggest that fecundity selection favours female-biased SSD and acts against male-biased SSD, at least in species in which large females were selected to increase fecundity. Therefore, in some lacertids, the relationship between sexual dichromatism and SSD may be obscured because selection on males (i.e. intrasexual selection) and females (i.e. fecundity selection) acts on SSD in opposite directions.

*Lacerta agilis* provides an example of a species in which fecundity selection acting on females may be an important evolutionary force. This species shows intense male-biased sexual dichromatism (see results; Pérez i de Lanuza & Font, 2007; Olsson *et al.*, 2011), male conspicuous breeding coloration mediates male–male contests (e.g. Olsson, 1994; Olsson & Silverin, 1997; Olsson *et al.*, 2011), and contest success is related to male size (Olsson, 1992). However, in some subspecies, females are often larger than males (Roitberg, 2007). The available evidence shows that female size and clutch size (i.e. egg number) are correlated (Olsson, 1993; Amat *et al.*, 2000), suggesting that fecundity selection in this species is strong (Roitberg, 2007) and may cause the SSD female-biased pattern. That some species, such as *L. agilis*, in which fecundity selection may be strong, show male-biased sexual dichromatism reinforces our main conclusion that male–male intrasexual selection is the most important selective pressure driving the evolution of sexual dichromatism in lacertids. In fact, as our sample includes species that evolved under different selective regimes, the finding of a significant relationship between SSD and sexual dichromatism highlights the overwhelming role of intrasexual selection as a driver of sexual dichromatism.

### Objective assessment of sexual dichromatism in overall colour patterns

For both theoretical and practical reasons, we strongly advocate the use of techniques allowing the objective comparison of entire colour patterns. Had our methodology not included objective measurements of colours and lizard-based visual modelling, we might have overlooked an important portion of sexual dichromatism in lacertids. As evidenced by our results, spectral differences in ultraviolet-reflecting patches (often associated with signalling functions in lacertids and other lizards, e.g. Fleishman *et al.*, 1993, 2009, 2011; Fleishman & Persons, 2001; Leal & Fleishman, 2004; Lappin *et al.*, 2006; Stapley & Whiting, 2006; Whiting *et al.*, 2006; Stuart-Fox *et al.*, 2009; Bajer *et al.*, 2010, 2011; Olsson *et al.*, 2011) are the cause for much of the sexual dichromatism observed within the Lacertidae clade. In Cooper & Greenberg's (1992) classic review of lizard coloration, only 38% of lacertid species were considered sexually dichromatic using a classification based on human visual perception. In contrast, our simple patch-by-patch spectral analysis reveals that 73% of the species in our sample show some kind of sexual dichromatism, at least in the spectral properties of their main colour patches. Clearly, objective colour measurements and visual modelling are necessary to prevent such underestimates and to reach conclusions that take into account how the receivers of chromatic signals (i.e. lacertids, not humans) perceive their own

body colorations (Kelber *et al.*, 2003; Endler & Mielke, 2005; Andersson & Prager, 2006).

Our methodology also allows us to consider the effects of two sources of variation in sexual dichromatism: chromatic innovation and chromatic elaboration (Endler *et al.*, 2005). Thus, a modification of the spectral properties of a colour patch (i.e. elaboration) resulting in a displacement of a chromatic point located in a vertex of the chromatic polygon may cause an increase (or decrease) in the overlap between the chromatic polygons of males and females, thereby increasing (or decreasing) the amount of sexual dichromatism. For example, we found that *Acanthodactylus boskianus* and *A. longipes* are more and less sexually dichromatic, respectively, than the Eremiadini basal group (*Atlantolacerta andreanszki*) without the addition or disappearance of any colour patch. In this case, the derived condition is achieved exclusively through elaboration of previously existing colour patches. A more pronounced departure from ancestral conditions may be caused by the addition of chromatic characters with novel spectral properties (i.e. chromatic innovation) in one of the sexes. This would introduce a new vertex in the chromatic polygon, decreasing the overlap between polygons from both sexes and thus increasing sexual dichromatism (e.g. the presence of ultraviolet OVS and eyespots of *Iberolacerta cyreni* and *I. monticola* compared with their absence in *Iberolacerta aurelioi*). Other changes quantified by our methodology may act in the opposite direction. For example, the adoption of a colour typical of one sex by individuals of the other sex (e.g. conspicuous ultraviolet yellow patches in *Acanthodactylus erythrurus*), or the elimination of colour patches that are only present in one sex (e.g. *Takydromus sexlineatus* or *Zootoca vivipara* lack ultraviolet patches, but probably evolved from a Lacertini ancestor with ultraviolet patches; Pérez i de Lanuza, 2012), results in less sexually dichromatic species.

We are aware that more sophisticated methods of visual modelling that incorporate psychophysical information about neural processes of colour discrimination may provide more resolution than the methods used here (Vorobyev & Osorio, 1998). In our analyses, we necessarily obviated this information because it is not currently available for lacertids. However, the sexual dichromatism index developed here is easily adapted to other, more complex, visual models that include psychophysical information, such as the perceptual distances model proposed by Pike (2012).

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Lacertid phylogeny.

**Appendix S2** Acknowledgments for assistance in sampling.

**Figure S1** Body locations in which spectrometric measurements were made.

**Figure S2** Reflectance spectra from representative coloration of head or dorsum (a, b), throat (c), belly (d), outer ventral scales (e), and dorsolateral surfaces with rare colorations from some species (f).

**Table S1** Species included in this study. Sample sizes (*N*) correspond to those used for colour analyses.

**Table S2** Values for hue ( $\lambda_{\max}$  = spectral location of maximum reflectance), chroma ( $C_{UV}$  = ultraviolet chroma,  $\lambda_{0.5}$  = spectral location of the median reflectance; MC = medium wavelength chroma, C = standard Endler's chroma), and brightness (Q) measured from lateral conspicuous patches, ventral and dorsal surfaces.

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