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Losing the trait without losing the signal: Evolutionary shifts in communicative colour signalling

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Abstract

Colour signalling traits are often lost over evolutionary time, perhaps because they increase vulnerability to visual predators or lose relevance in terms of sexual selection. Here, we used spectrometric and phylogenetic comparative analyses to ask whether four independent losses of a sexually selected blue patch are spectrally similar, and whether these losses equate to a decrease in conspicuousness or to loss of a signal. We found that patches were lost in two distinct ways: either increasing reflectance primarily at very long or at very short wavelengths, and that species with additional colour elements (UV, green and pink) may be evolutionary intermediates. In addition, we found that patch spectral profiles of all species were closely aligned with visual receptors in the receiver's retina. We found that loss of the blue patch makes males less conspicuous in terms of chromatic conspicuousness, but more conspicuous in terms of achromatic contrast, and that sexual dimorphism often persists regardless of patch loss. Dorsal surfaces were considerably more cryptic than were ventral surfaces, and species in which male bellies were the most similar in conspicuousness to their dorsal surfaces were also the most sexually dimorphic. These results emphasize the consistent importance of sexual selection and its flexible impact on different signal components through evolutionary time.

KEYWORDS
colouration, phylogenetic comparative methods, *Sceloporus* lizard, sexual selection, signal evolution, visual communication

1 | INTRODUCTION

Evolutionary losses of sexual signalling traits are frequent and widespread (Wiens, 2001), leading some to posit that increased predation or relaxed sexual selection are important factors in shaping communicative signals (e.g. Burns, 1998; Kang, Schartl, Walter, & Meyer, 2013; Simpson, Johnson, & Murphy, 2015). Colour traits with signalling functions, such as colour patches, often evolve in response to a complex regime of different natural and sexual selection pressures. On the one hand, many colour ornaments allow individuals to stand out from the background and to be recognized by conspecifics, facilitating courtship and intra-sexual competition, both forms of sexual selection (e.g. Cummings, 2007; Endler, 1983). Relaxed sexual selection may lead to the loss of colour ornaments, as in mallard ducks that have reduced preference for bright plumage (Omland, 1996), or swordtail fish that reduced their preference for male vertical pigment bars (Morris, Moretz, Farley, & Nicoletto, 2005).

On the other hand, background or habitat matching (crypsis) is an effective way to avoid predators and thus being inconspicuous

increases an individual's chances of survival, a process driven by natural selection (Endler, 1983). Colour can also impact thermoregulation and structural properties of the skin that influence resistance to water, pathogens or abrasions (e.g. Smith et al., 2016). Moreover, colour signals co-evolve with the visual system of the receiver. They are often spectrally tuned to match the receiver's photoreceptor spectral sensitivities (Osorio & Vorobyev, 2008); the closer the match, the better the efficacy (i.e. detectability) of the signal (Endler, 1978; Osorio & Vorobyev, 2008). Ultimately, the expressed colour trait is a compromise between responses to sexual and natural selection (Endler, 1978, 1983; Fisher, 1930) potentially operating through multiple pathways (Romero-Diaz, Richner, Granado-Lorencio, Tschirren, & Fitze, 2013) or at different points in time (Ossip-Drahos et al., 2016). Here, we make use of natural evolutionary replication and a comprehensive spectral analysis to explore the patterns exhibited by four independent evolutionary losses of a colourful belly patch in *Sceloporus* lizards.

Because multicomponent and multimodal signals can combine two or more signal components with different functions (Partan & Marler, 2005), the loss of one colour component does not necessarily entail the loss of a signal. For most animals, signalling colour traits are comprised of chromatic (e.g. hue and saturation) and achromatic (e.g. luminance/brightness) components, which can serve very different purposes (Jacot, Romero-Diaz, Tschirren, Richner, & Fitze, 2010; Romero-Diaz et al., 2013; Schaefer, Levey, Schaefer, & Avery, 2006). Colour components do not have to convey information about individual quality to be shaped by selection (Endler & Basolo, 1998; Fisher, 1930), and informative and uninformative (e.g. facilitators of detection) components may be perceived and interpreted as a whole or independently (Johnstone, 1996; Møller & Pomiankowski, 1993). Moreover, colour signals are often associated with other visual components (e.g. motion displays; Hews & Martins, 2013), or with complementary signals from alternative sensory modalities (e.g. acoustic, chemosensory), giving rise to more complex signals (Candolin, 2003; Partan & Marler, 1999). By exploiting distinct channels or aspects of the sensory system of the receiver, redundant signals (*sensu* Johnstone, 1996) help to ensure that crucial information is transferred accurately (Leal & Losos, 2015; Rand & Williams, 1970) and flexibly in a wide range of contexts (Candolin, 2003; Hebets et al., 2016). For example, different colour components may be tuned to match alternative cone pigment optima of the receiver's visual system (Moore et al., 2012; Pérez i de Lanuza & Font, 2007), and chemical signals may be favoured at close range while colouration may be preferred in long-distance communication (López & Martín, 2001).

In addition, an evolutionary switch of a signal from one trait to another or even from one modality to another may occur. Switching could be favoured if the new trait was, for example, more effective, energetically cheaper or less conspicuous to unintended receivers, especially when peak receptor sensitivity of conspecifics and predators match (Wiens, 2001). For example, in three-spine sticklebacks (*Gasterosteus aculeatus*), the red nuptial colouration of males has shifted to black in several populations (Reimchen, 1989; Tinghitella,

Lehto, & Minter, 2015) to increase signal efficacy (McDonald, Reimchen, & Hawryshyn, 1995).

In spiny lizards (genus *Sceloporus*), recent behavioural and comparative studies identified a potential evolutionary trade-off between colour and chemical (Pruett et al., 2016), colour and motion (Martins et al., 2015), and motion and chemical signals (Ossip-Klein, Fuentes, Hews, & Martins, 2013), suggesting that compensation via increased reliance on alternative signal modalities is possible. This compensation scenario is congruent with the back-up or redundant signal hypothesis (see above) and suggests that the loss of one signal component may not affect the integrity of the message. For example, in pied flycatchers (*Ficedula hypoleuca*), territory quality is positively correlated with colour traits (Siitari & Huhta, 2002; Sirkiä & Laaksonen, 2009). Even though females choose males based primarily on territory quality (Alatalo, Lundberg, & Glynn, 1986), in the absence of territory cues, they still prefer to mate with males that have brighter black and white patches (Sætre, Dale, & Slagsvold, 1994), suggesting that colour traits serve as back-up signals of territory quality. Environmental conditions (e.g. habitat luminosity, vegetation type, social context) may determine in which cases a trait loss implies a signal loss and in which cases it does not (Endler, 1992). Thus, it is unclear whether the loss of a colour trait always implies the loss of signal and little evidence exists about the processes that might account for these losses.

Here, we test for evolutionary changes in conspicuousness and sexual dimorphism that would indicate whether loss of the belly patches typical of *Sceloporus* lizards also reflect signal loss. In *Sceloporus*, coloured belly patches (usually blue) are used primarily during male territorial disputes to signal aggression (Cooper & Burns, 1987; Martins, 1993b; Martins, Ord, & Davenport, 2005; Ossip-Drahos, Berry, King, & Martins, 2018). When present, belly patches typically occur only in males, or at a minimum, more prominently in males. In males, a portion of the abdomen (whether colourful or plain white) can be seen from the side when the lizard is at rest, and abdominal exposure is enhanced during aggressive interactions by use of "full-show" displays in which the lizard extends all four legs while arching the back and compressing the abdomen laterally (e.g. Hews & Benard, 2001; Martins et al., 2015). Belly colour is related to the probability of winning in staged male–male encounters in *S. virgatus* (Quinn & Hews, 2000), and patch size conveys information on body size, condition, fighting ability and parasite load in *S. undulatus* and *S. jarrovii* (Halliday, Paterson, Patterson, Cooke, & Blouin-Demers, 2014; Langkilde & Boronow, 2010; Ossip-Drahos et al., 2018). Coloured belly patches have been lost independently within the genus at least seven times (Ossip-Drahos et al., 2016; Wiens, 1999), giving rise to white-bellied species in which sexual dimorphism for ventral colouration is apparently absent. We now focus on four of these evolutionary losses spread across the *Sceloporus* genus and ask: (1) Are the spectral properties of the four losses similar, suggesting that they are examples of a similar phenotypic evolutionary phenomenon? (2) Does loss of colour patches decrease conspicuousness? and (3) Does loss of colour patches lead to a loss of signal (i.e. actual loss of sexual dimorphism from a receiver's perspective)?
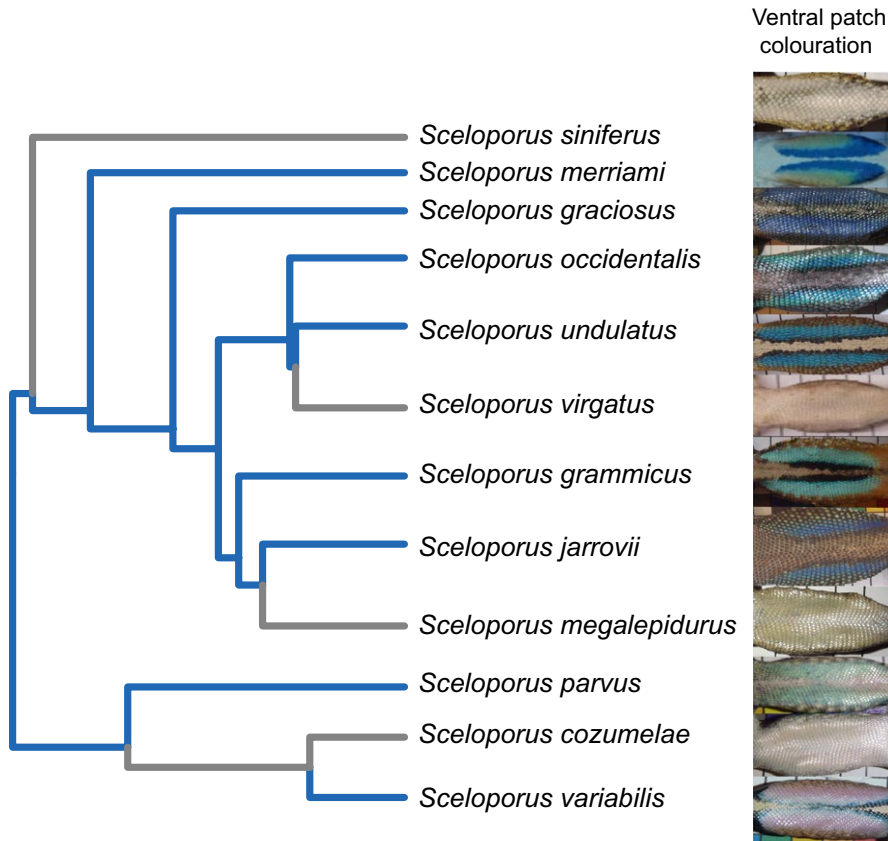
Ventral patch
colouration

FIGURE 1 A phylogeny of the 12 *Sceloporus* species studied and modified from Wiens et al. (2013). The 12 target species are scattered across the full range of a phylogeny of more than 80 *Sceloporus* taxa. Grey branches indicate episodes in which the male ventral blue patches were lost, as inferred by Ossip-Drahos et al. (2016). Also, depicted are photos of the ventral surface (head is to the left) of a typical male of each species

2 | MATERIALS AND METHODS

2.1 | Study species

We collected spectral reflectance measures from each of 12 species of *Sceloporus* lizards representing four independent evolutionary losses of the colourful belly patches (Figure 1). For three of the four losses, we identified one species that had lost the belly patch and two closely related congeners with colourful bellies, choosing individual species that were relatively abundant and accessible in the wild. The fourth loss is represented by a clade of four extant species that do not have colourful belly patches nor close sister taxa. To represent this loss, we chose one of the extant species (*S. siniferus*) and two more distantly related *Sceloporus* species (*S. merriami* and *S. graciosus*) with colourful bellies (see Ossip-Drahos et al., 2016 for complete ancestral reconstruction of 81 species). In most colourful species, patch colour is predominantly blue with black edges; however, we include two species that have multiple colour elements in their patches: *S. merriami*, which has a pale green oval edged by a blue J-shaped patch; and *S. variabilis*, which exhibits pink patches with blue and black borders (Figure 1). Two of the belly patch losses occurred relatively recently (< 12 Mya; *S. virgatus* and *S. megalepidurus*), whereas the other two are more ancient (40–18 Mya; *S. siniferus* and *S. cozumelae*) (Ossip-Drahos et al., 2016).

The colours of these lizards occur against a wide variety of visual backgrounds at our study sites, including white sand (*S. cozumelae*), red and grey rocks (*S. jarrovii*, *S. merriami*, *S. parvus*, *S. variabilis*,

S. virgatus), brown trees and logs (*S. graciosus*, *S. occidentalis*, *S. undulatus*), and green leaves and cactus pads (*S. grammicus*, *S. megalepidurus*, *S. siniferus*). We measured 42–82 individual lizards from each species, including 22–56 males and 18–31 females (Supporting Information Table S1). Ossip-Drahos et al. (2016) reported earlier on belly measures of four of these species (*S. merriami*, *S. siniferus*, *S. undulatus* and *S. virgatus*). Here, we present new data on eight additional species, and on the dorsal surfaces of all 12 species.

2.2 | Measuring reflectance & conspicuousness

We captured animals in the wild and used a spectrometer (USB2000 + , Ocean Optics Inc., Dudedin, FL) to measure their spectral reflectance relative to a white Spectralon reflectance standard (WS-1-SL, Ocean Optics), with a xenon lamp (Ocean Optics PX-2) and reflectance probe (Ocean Optics R200-7) fitted with a black tip housing cut at a 45° angle. For each lizard, we took three measures of the coloured patch (or where the coloured patch would typically occur) from the left side of the belly, and three measures from the dorsal surface (from the centre of the right side of the back) regardless of any dorsal patterning. Correlations between measures taken from the same individual were on average > 0.96 across species. We averaged the three measures for each animal for further analyses. For *S. merriami* and *S. variabilis* males, we report only on measures of the predominant colour elements of their patches. For each species, we also took three measures of the spectral reflectance of each of

the predominant substrate types (e.g. rocks, logs, cactus pads) on which we found lizards during hours of peak activity.

We estimated conspicuousness using the Vorobyev and Osorio (1998) visual model, employing AVICOL (Gomez, 2006) to implement the model and relying on standard measures of daylight irradiance (Wyszecki & Stiles, 1982). This estimation procedure required that we also specify information on the retinal cone sensitivities of the putative viewer of the colour. Since this information is not yet available for *Sceloporus* lizards, we used Macedonia et al.'s (2009) measures of *Crotaphytus dickersonae*, a closely related (in a sister family), diurnal lizard with a visual system that is likely to be similar to that of a *Sceloporus* receiver, but which is also an occasional *Sceloporus* predator (Ossip-Drahos et al., 2016). Lizard visual pigments appear to be quite conserved (Fleishman, Loew, & Whiting, 2011; Loew, Fleishman, Foster, & Provencio, 2002); for example, although *Crotaphytus* diverged from *Anolis* lizards much earlier than they did from *Sceloporus*, *Crotaphytus* and *Anolis* cone pigments differ in their mean peak spectral sensitivities by only 7.5 nm. Using this visual model, we transformed the raw spectral data into two measures, chromatic contrast ("CC") and achromatic contrast ("AC") that describe the difference between each colour and a specified background from the perspective of that receiver, measured in Just Noticeable Differences (JNDs). JNDs higher than 1 indicate detectable differences, with CC values emphasizing conspicuousness differences between two colours in terms of hue and chroma, whereas AC values describe conspicuousness differences in terms of luminance or brightness.

2.3 | Statistical analyses

Because species share an evolutionary history and cannot be treated as independent data points for standard analyses (Felsenstein, 1985), we took a phylogenetic comparative approach to analyse these data. We extracted information for our 12 species from the time-calibrated phylogeny described in Wiens, Kozak, and Silva (2013), which used fossils to anchor the node times (Figure 1). We started with a general descriptive analysis of the reflectance profiles, comparing averages of males and females, ventral and dorsal surfaces, for each species. To summarize these and to evaluate similarities, we also calculated the relative area of each spectral profile from 300 to 700 nm in 50 nm bins and averaged within each of the 12 species. We then used a phylogenetic Principal Components Analysis (pPCA; Revell, 2009) to reduce those relative reflectance measures at 50 nm intervals into composite variables that summarized the reflectance profiles across the spectrum. We implemented the pPCAs using the phyl.pca function of the phytools package v0.6-44 (Revell, 2012) in R (R Development Core Team, 2015).

Next, we asked whether loss of colour patches led to a loss of conspicuousness by comparing the conspicuousness of males from species with versus without colourful belly patches. To do this, we calculated species averages of the measures of conspicuousness we obtained for each spectral profile (CCs and ACs calculated separately for male belly patches and dorsal surfaces) and then used

phylogenetic comparative methods. Specifically, we fit Hansen's (1997) adaptation-inertia model to ask how much the total amount of time spent in each evolutionary context (in colourful- vs. white-bellied species) predicts interspecific variation in male conspicuousness. In general terms, the adaptation-inertia model is based on an Ornstein-Uhlenbeck (OU) process, and incorporates stasis and selection explicitly, as opposed to a random process of Brownian motion (BM). We estimated model parameters using SLOUCH v2.0 (Kopperud, Pienaar, Voje, Orzack, & Hansen, 2017) and OUCH v2.11-1 (King & Butler, 2009) scripts in R, incorporating within-species measures in the SLOUCH analysis. Both implementations require estimates of ancestral states, so we used the ancestral reconstruction of Ossip-Drahos et al. (2016, Figure 1). Both models estimate optimal values of the response measure (conspicuousness) in each of the specified evolutionary contexts (while evolving as colourful- vs. white-bellied species). Although the underlying mathematics of the two versions of the adaptation-inertia model are similar, the approaches implemented in the two programs might yield slightly different results (Hansen, Pienaar, & Orzack, 2008). Here, we present results from both models for cross-validation purposes only. Lastly, we simulated our data over 10,000 trees to determine how often each model (OU vs. BM) was chosen, bootstrapped model parameter estimates 10,000 times to obtain confidence intervals as *per* Cressler, Butler, and King (2015) and confirmed the results also with Blomberg's K (Blomberg, Garland, & Ives, 2003), which is less sensitive to sample size than Pagel's λ (Münkemüller et al., 2012). Because we found little evidence of phylogenetic signal, we also report the results of non-phylogenetic ANOVAs comparing species with and without colourful belly patches.

In addition, we asked whether loss of colour patches has led to a loss of signal by comparing colourful and white-bellied species and conspicuousness differences between males and females. We ran t tests (Welch t tests assuming different variances with a Bonferroni correction for multiple testing) to test for sex differences in conspicuousness within each species, using the base package of R. If the loss of the blue patch entailed a loss of signal, intersexual differences in CC and AC in white-bellied species would not be significant, in contrast to colourful species, where conspicuousness differences would be high.

3 | RESULTS

3.1 | White and blue spectral profiles are highly diverse

Overall, we found that *Sceloporus* species differ remarkably in terms of their belly patch spectral reflectance (Figure 2). Ventral colour patches that appear essentially white to the human eye exhibited very different spectral profiles, as can be seen by comparing the ventral spectral curves for males of the four white-bellied species (Figure 2, blue lines in top row) with the ventral spectral curves of most female *Sceloporus* (Figure 2, red lines in all panels). Similarly, the blue bellies of males from colourful species (Figure 2, blue lines in
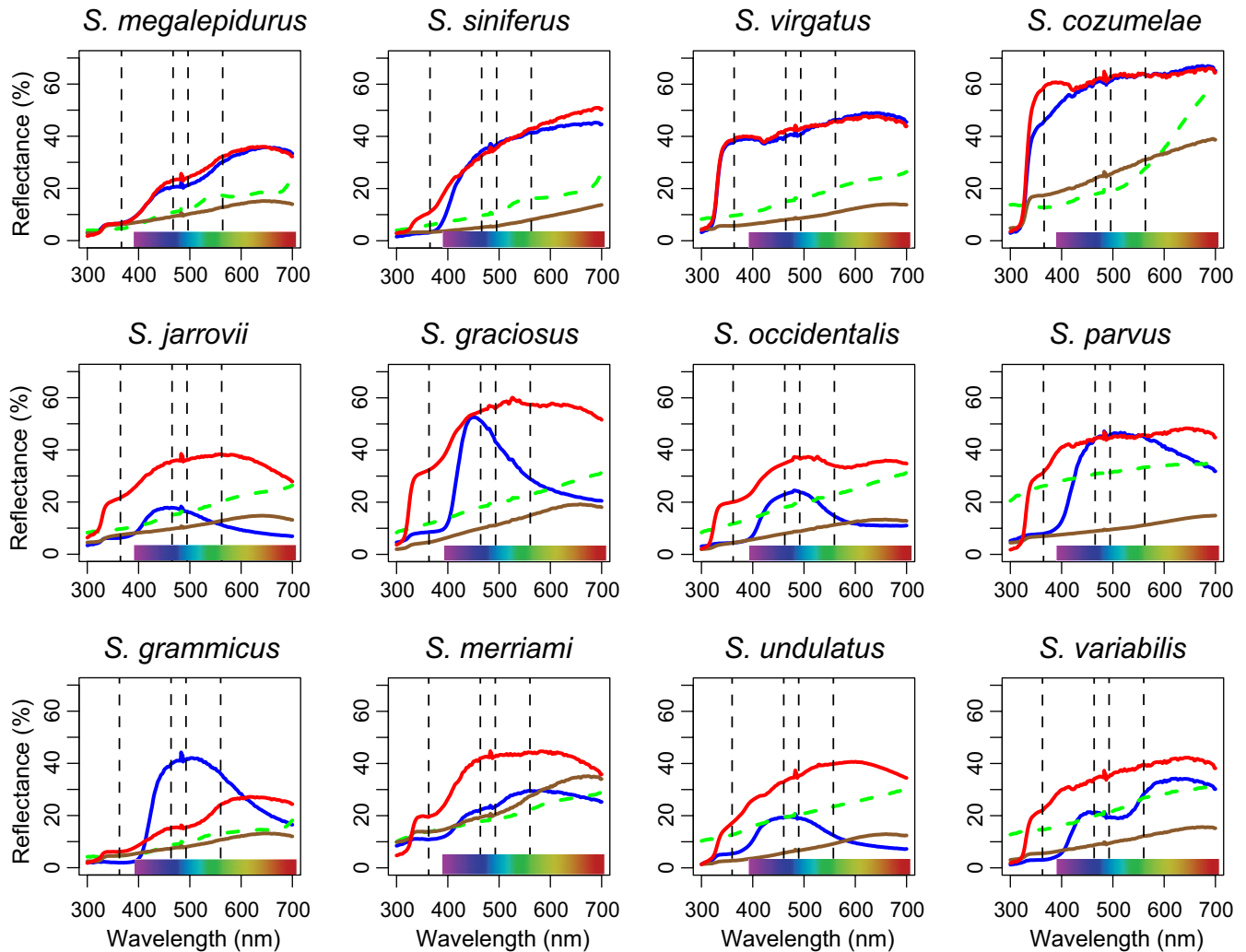
FIGURE 2 Mean spectral reflectance for male ventral patches (blue lines), female ventral surfaces (red lines), male dorsal surfaces (brown lines) and habitat (green dashed lines) for 12 species of *Sceloporus* lizards. Vertical dashed lines indicate peak receptor sensitivities of a representative lizard, *Crotaphytus dickersonae* (UVS: 359 nm; SWS: 459 nm; MWS: 481 nm; LWS: 558 nm; Macedonia et al., 2009). Plots are grouped vertically by clade such that the top row depicts measures of white-bellied species, with plots for two closely related species below. Note that the standard errors for each point on these spectral profiles are small, such that they are well-represented by the width of the lines

bottom two rows) varied considerably, with the lighter blue patches of *S. graciosus*, *S. grammicus* and *S. parvus* showing quite different spectral patterns compared to the much darker blue patches of *S. jarrovii*, *S. occidentalis* and *S. undulatus*. Surprisingly, the peak hue of colourful male patches (highest point of blue lines in the eight lower panels) was similar to the background habitat (dashed green lines) in five of eight species, with the exception of *S. graciosus*, *S. grammicus* and *S. parvus*. Peak hues of colourful male bellies were also remarkably close to the wavelengths best perceived by two of the lizard retinal receptors (SWS λ = 459 and MWS λ = 481 nm). All species but *S. virgatus*, and *S. megalepidurus* also showed a secondary sex difference near the UV-sensitive receptor (λ = 359 nm), caused by UV-absorbing male ventral patches.

Using a phylogenetic Principal Components Analysis to summarize the relative areas under 50 nm segments of the spectrum, we found that there are two distinct types of white bellies (Figure 3). The

first PC axis, accounting for 61% of the variation, was a general measure of the brightness of the human-visible spectrum (i.e. 380–700), correlating positively with the longer wavelengths (550–700 nm: yellows, oranges, and reds) and negatively with shorter wavelengths (400–500 nm: violet and blue). The second PC axis (32% of variance) better described variation in the UV (300–400 nm), although it also negatively correlated with blue and green (450-550 nm) (Figure 3). In males of two of the four white-bellied species (*S. megalepidurus* and *S. siniferus*), male patches had a yellowish sheen (relatively high PC1). Males of the other two white-bellied species (*S. virgatus* and *S. cozumelae*) had instead high UV reflectance (high PC2) and neither higher short- nor long-wavelength reflectance (PC1; Figure 3).

Intriguingly, the spectral profiles for males of the two species that have added other colours to their blue belly patches were similar to those for white-bellied species, albeit in different ways. Male *S. variabilis* have evolved a novel pink component to their
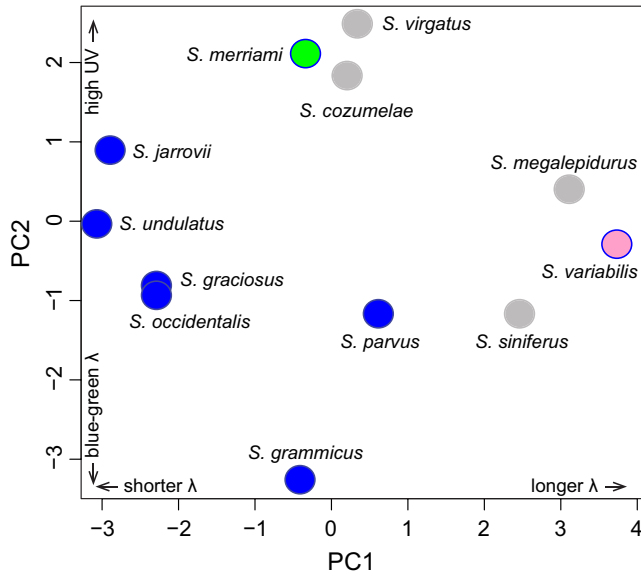
FIGURE 3 Results from a phylogenetically corrected Principal Components Analysis. PC1 roughly describes the human-visible spectrum, with positive values corresponding to longer wavelengths (λ; yellows, oranges and reds) and negative values corresponding to shorter wavelengths (violets and blues). PC2 describes UV reflectance, correlating positively with high UV reflectance (300–400 nm) and negatively with blue–green wavelengths. Point colours indicate the predominant colour of male belly patches. For *S. merriami* and *S. variabilis*, the point and border colours indicate the two main colours present on the male belly, although the PC values are for spectral measures of the predominant colour component only

belly patches, and the spectral profile of their colour patches was bimodal with both pink and blue elements (Figure 2). As shown in the pPCA, *S. variabilis* spectral profiles were similar to those for white-bellied male *S. megalepidurus* and *S. siniferus*, with strong reflectance in the longer wavelengths (high PC1) and only moderate levels of UV reflectance (PC2; Figure 3). Similarly, *S. merriami* males have evolved a novel pale green component to their belly patches, and the spectral profiles for their colour components was most similar to that of the white-bellied *S. virgatus* and *S. cozumelae* in that they were all highly reflective in the UV (PC2), and only slightly more reflective at longer wavelengths (PC1; Figure 3). The blue bellies of other species that retain colourful belly patches were generally dark in terms of the human-visible spectrum (low PC1; except *S. grammicus* and *S. parvus*) and exhibited intermediate values of UV reflectance (PC2; except *S. grammicus* males, which were very dark in the UV) (Figure 3).

3.2 | Loss of colour patches does not significantly decrease conspicuousness against the background

Using the Vorobyev & Osorio (1998) visual model to consider how differences in different aspects of these spectral profiles would be perceived by a receiver, we found that males of all 12 species had conspicuous bellies (Figure 4). Males of species with colourful

bellies were more ventrally conspicuous in terms of chromatic contrast ("CC") than were males of species lacking ventral patches (non-phylogenetic ANOVA: $F_{1, 409} = 79.0$, $P < 0.001$, Figure 4a). However, there were dramatic exceptions. For example, white bellies of *S. siniferus* were very conspicuous with high CC, whereas the blue bellies of *S. jarrovii*, *S. merriami* and *S. undulatus* were not (Figure 4a). In addition, males of species with colourful belly patches were considerably less conspicuous than were males of white-bellied species in terms of achromatic contrast ("AC") (non-phylogenetic ANOVA: $F_{1, 409} = 82.7$, $P < 0.001$, Figure 4b). Again, there were some exceptions. Although three of the four white-bellied species were very conspicuous in terms of AC, the white-bellied *S. megalepidurus* males were relatively inconspicuous ventrally, and the very bright blue of male *S. grammicus* bellies were quite conspicuous in this sense (Figure 4b).

Phylogenetic analyses confirmed that differences in average ventral conspicuousness between colourful- and white-bellied species were large. Both OUCH and SLOUCH estimated large differences between the optimal values of ventral conspicuousness for species evolving with colourful belly patches (e.g. SLOUCH optimal ventral CC = 24.2 [20.4, 28.2]) and those with white bellies (SLOUCH optimal CC = 17.3 [16.2, 18.9]). The SLOUCH model explained 29% of the interspecific variation and models that included belly colour as a factor (OU) were favoured over BM in our simulation procedure (Supporting Information Table S2; Figure S2). Differences between estimated optima for ventral AC were also large (Supporting Information Table S2), with the SLOUCH model explaining nearly 28% and, again, our simulations most strongly supported an OU model of evolution (Supporting Information Table S2). We found little evidence that phylogeny was an important predictor of conspicuousness (Pagel's $\lambda = 0$, Blomberg's K < 1; Supporting Information Table S2), suggesting that the non-phylogenetic ANOVAs above offer an appropriate hypothesis test for these data.

Males of all 12 *Sceloporus* species were much less conspicuous in terms of CC of their dorsal (Supporting Information Figure S1a; median CC = 5) compared to ventral surfaces (median CC = 17). In contrast, measures of dorsal AC were comparable (Supporting Information Figure S1b; median AC = 14) to those for ventral surfaces (median AC = 13). The difference between dorsal and ventral conspicuousness was negatively correlated with the sex difference in ventral conspicuousness (r = −0.9 for CC; r = −0.4 for AC). Males of species with colourful belly patches were dorsally less conspicuous in chromatic terms than were males of species that lack those belly patches (Supporting Information Figure S1a; non-phylogenetic ANOVA: $F_{1, 409} = 113.9$, $P < 0.001$), but more conspicuous in terms of AC (Supporting Information Figure S1b; non-phylogenetic ANOVA: $F_{1, 409} = 56.14$, $P < 0.001$). The differences between estimated optima were again large and the SLOUCH model explained 20% and 21% of the variation, respectively (Supporting Information Table S2). OUCH and SLOUCH found little impact of phylogeny on dorsal CC while dorsal AC showed higher phylogenetic signal. The latter suggests that the
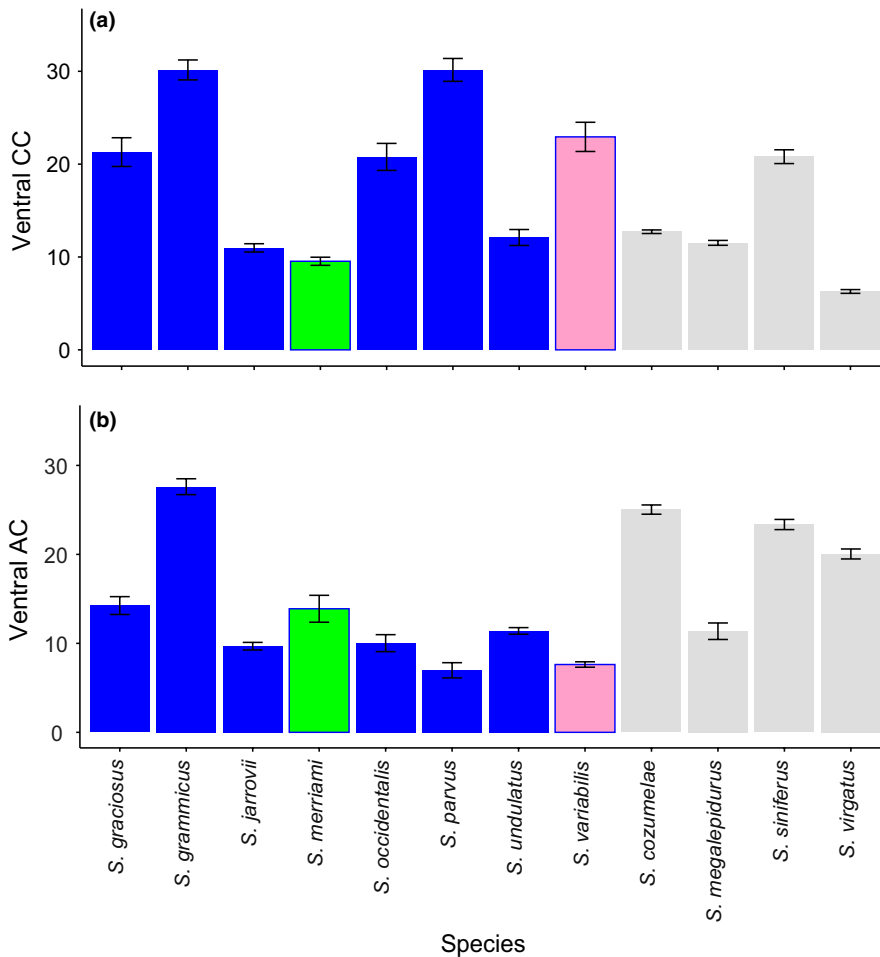
FIGURE 4 Average conspicuousness, measured in Just Noticeable Differences, in chromatic contrast (a), and achromatic contrast (b) for male *Sceloporus* bellies. Bars indicate ± 1 *SE* and colours are as in Figure 3

results of the non-phylogenetic ANOVA should be interpreted cautiously for dorsal AC.

3.3 | Loss of colour patch, not of signal: Sex differences persist in most white-bellied species

We found large sex differences in ventral conspicuousness in most species with colourful belly patches (Figure 5). In general, males with colourful bellies were more conspicuous than were females of the same species in terms of ventral CC (Figure 5a; t tests: *P* < 0.05) and less conspicuous than females in terms of ventral AC (Figure 5b; t tests: *P* < 0.05). The exceptions were *S. merriami*, which showed little sex difference in ventral CC and AC, and *S. parvus* and *S. undulatus*, which showed little sex difference in ventral AC (all *P* > 0.05). In contrast, we found almost no evidence of sex differences in dorsal conspicuousness for species with colourful male belly patches (*P* > 0.05). The exceptions were female *S. merriami*, which were more dorsally conspicuous than *S. merriami* males in terms of CC ($t_{82.5} = 3.9$, *P* < 0.001), and male *S. occidentalis*, which were more dorsally conspicuous than female *S. occidentalis* in terms of AC ($t_{50.6} = 3.2$, *P* = 0.04).

We also found detectable sex differences in ventral or dorsal colours of all white-bellied species except *S. virgatus* (Figure 5). The most dramatic pattern was for male *S. siniferus* bellies, which were

much more conspicuous than female *S. siniferus* bellies in terms of CC (Figure 5a; $t_{60.4} = 12.1$, *P* < 0.001) due to a marked darkness in very short (UV) and very long wavelengths (Figure 2). Although there was no detectable sex difference in *S. siniferus* ventral AC (Figure 5b; $t_{60} = 0.6$, *P* < 0.60), female *S. siniferus* dorsal surfaces were more conspicuous than those of *S. siniferus* males in both CC ($t_{76.7} = 3.3$, *P* < 0.01) and AC ($t_{78.5} = 4.1$, *P* < 0.01).

Female *S. cozumelae* were slightly more conspicuous than male *S. cozumelae* in terms of ventral CC (Figure 5a: $t_{41} = 4.4$, *P* < 0.001), but not AC (Figure 5b: $t_{33} = 0.9$, *P* = 0.40), and female *S. megalepidurus* were more conspicuous than male *S. megalepidurus* in terms of ventral AC (Figure 5b: $t_{68} = 2.4$, *P* = 0.02), but not CC (Figure 5a: $t_{49} = 0.4$, *P* = 0.70). We found no detectable sex differences in dorsal conspicuousness for either species in terms of CC or AC (*P* > 0.05 in all cases). The only white-bellied species that did not exhibit sex differences in ventral colouration was *S. virgatus* (Figure 5; *P* > 0.05 for both CC and AC). Intriguingly, male *S. virgatus* had more conspicuous dorsal surfaces than did female *S. virgatus* in terms of both CC ($t_{49} = 2.1$, *P* = 0.04) and AC ($t_{62.6} = 3.0$, *P* < 0.01).

Sexual dimorphism was relatively smaller in white-bellied species compared to blue-bellied species but so was the intra-sexual variance of the trait (e.g. S.E. in Figure 4), especially in ventral CC, allowing for a narrower discrimination.
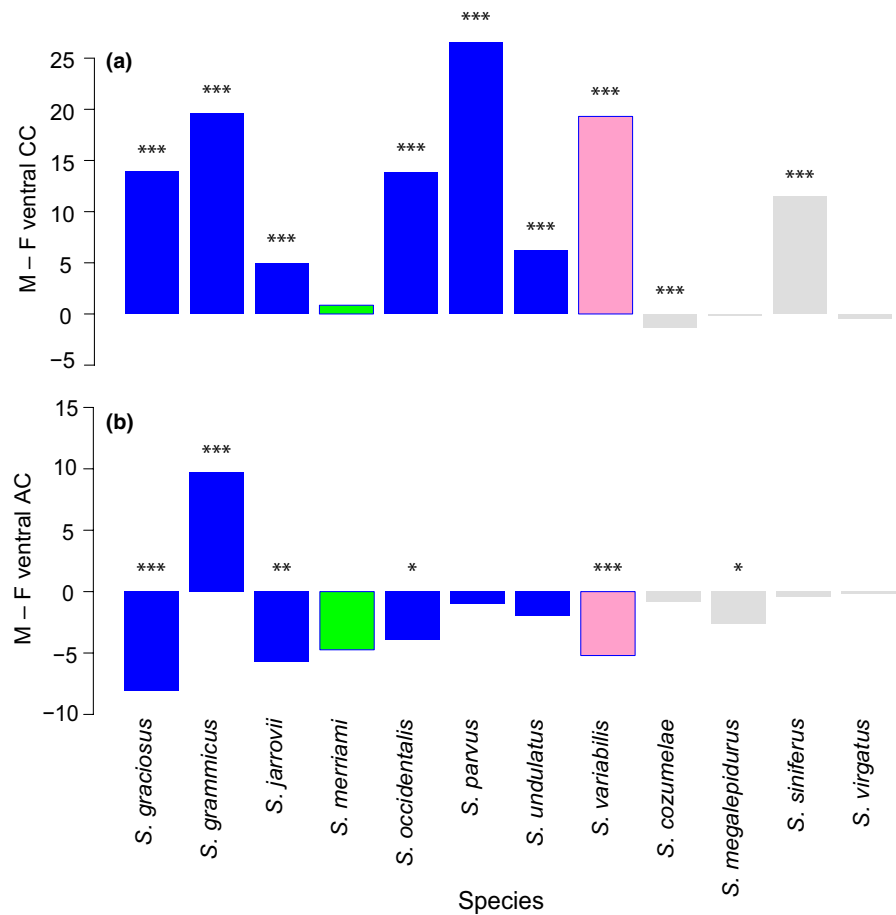
FIGURE 5 Average differences in Just Noticeable Differences between the conspicuousness of male and female *Sceloporus* in ventral chromatic contrast (a) and achromatic contrast (b). Bars above the zero-line indicate more conspicuous males, whereas bars below the zero-line indicate more conspicuous females. Colours are as in Figure 3, and asterisks denote the level of significance: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$ with Bonferroni correction

4 | DISCUSSION

Colour signalling traits are widespread in the animal kingdom and frequently used to attract mates, maintain territories and minimize predation (Endler, 1992), and their loss may be an important indicator of predator pressure or relaxed sexual selection (Wiens, 2001). Here, looking at four independent evolutionary loses, we found that blue patches have been lost in two main ways: (1) by increasing reflectance in the longer wavelengths to create a yellowish sheen or (2) by increasing reflectance in the UV wavelengths, and that both may facilitate evolutionary shifts to secondary colours such as green or pink. Further, although to the human eye white-bellied species are less conspicuous than their coloured congeners and appear less sexually dimorphic, our results suggest that rather than lost, these signal attributes have been modified. Male *Sceloporus* were less conspicuous on their dorsal than on their ventral surfaces, and white bellies were just as conspicuous as blue bellies. White-bellied species also exhibited comparable sexual dimorphism, albeit in different wavelengths.

We found tremendous diversity in the spectral profiles of blue belly patches, including green and pink shades (on *S. merriami* and *S. variabilis*) that more closely resembled those of white bellies than they did those of other colourful species (Figure 3). Although many of these colourful belly patches were very conspicuous in terms of hue (CC), so was the white belly, for example, of *S. siniferus*. White

bellies also differed significantly from the background in terms of achromatic contrast (AC). Ventral colour patches are a conspicuous signal to conspecifics and allow individuals to stand out from their habitats (Leal & Fleishman, 2002). Our results are reminiscent of Noble's (1934) finding that male *S. undulatus* respond similarly to experimentally altered belly patches of different hues (e.g. gold, silver, yellow), suggesting that brightness and/or contrast may be the more relevant stimulus, over hue. From this perspective, our example is also similar to the vertical bars of swordtails and nuptial coloration of sticklebacks in which contrast, rather than hue, seems to be the primary signalling element (McDonald et al., 1995; Morris et al., 2005). Species lacking ventral patches may be seen as brighter in their habitats and potentially more readily visible by conspecifics owing to their higher AC. For example, *S. cozumelae*, which lives in white sand beaches, reflects more light than their already bright habitat in certain wavelengths (Figure 2), which causes them to stand out. We need additional studies to parse the functional difference between CC and AC from the perspectives of both conspecifics and predators.

We also found that white bellies in both sexes exhibited considerable UV reflectance, but that white-bellied males in some species also showed "anti-UV" patches (i.e. UV-absorbing patches), which will increase conspicuousness against UV-reflecting surfaces. UV wavelengths are potentially important to the visual system of many lizards, such as *Anolis* (Leal & Fleishman, 2004), *Lacerta* (Pérez i de

Lanuza & Font, 2014) and *Crotaphytus* (Macedonia et al., 2009), and may also serve as signals. Males of most species in our study exhibited dips in spectral reflectance near the 359 nm UV-sensitive cone visual pigments (Figure 2). From the perspective of a lizard, these UV-absorbing areas would appear as dark patches, similar to the blue belly patch typical of the genus. In part because of these UV-absorbing patches of males, we also found significant sexual dimorphism in white-bellied species (Figure 5). The match between ventral reflectance curves and lizard peak cone sensitivities in the blue, green and pink wavelengths (Figure 2) further supports that colouration has an important role in signalling and that colour signals co-evolve with the visual system of the receiver (Osorio & Vorobyev, 2008).

In addition, white-bellied species may compensate for lack of blue patches or reduced dimorphism by increasing reliance on alternative sensory channels to maintain communication. For example, males of white-bellied *Sceloporus* species tend to give more aggressive headbob displays (i.e. more headbobs per display and longer displays) than do those with colourful belly patches, perhaps shifting the aggressive function of the colour patch (used primarily in direct combat) to dynamic motion displays over evolutionary time (Martins et al., 2015). Similarly, lizard chemical cues can serve as reliable signals for sex identification and fighting ability or aggression (Hews & Martins, 2013). *Sceloporus* species use femoral pore secretions for chemical signalling (e.g. Campos, Strauss, & Martins, 2017; Pruett et al., 2016), which may provide redundant information to belly colour patches. Chemical signals may also be used more often in species without coloured belly patches, as in *S. virgatus*, which seems to rely heavily on chemical signals (Hews & Benard, 2001; Hews, Date, Hara, & Castellano, 2011). Trade-offs between signal modalities have been suggested in other taxa, including birds, where song elaboration is negatively correlated with plumage colouration (Badyaev, Hill, & Weckworth, 2002), but these hypotheses require more study.

Our phylogenetic analyses were consistent in finding differences in conspicuousness between white and colourful *Sceloporus* species. Both OUCH and SLOUCH analyses found stronger support for OU than BM models to describe the evolution of ventral colours, as shown by our simulations (Supporting Information Table S2), and we found virtually no evidence for phylogenetic signal in these cases. However, the relatively small number of species (12) and evolutionary transitions (4) in this study may not be sufficient to detect phylogenetic effects and these comparative analyses should be interpreted with caution. Nevertheless, our current results, as well as previous evidence, are congruent with some form of selection being involved in the evolution of *Sceloporus* colours (Ossip-Drahos et al., 2016; Ossip-Klein et al., 2013). Selection should favour any improvement of signal detection by conspecifics in a particular habitat (Leal & Fleishman, 2002; Wiens, 2001), whether this is accomplished by relying on alternative colour components, or alternative signal modalities. However, studies have found stronger evolutionary links between belly patch colouration and habitat (e.g. arboreality), and belly patch colouration and reproductive physiology

(i.e. viviparity) than between belly colours and other types of communicative signals (motion and chemical) (Martins, 1993a; Ossip-Klein et al., 2013). Among the former, the physical context, which is importantly determined by habitat type, is a strong shaping force of multimodal or multicomponent signals in other lizards (e.g. Anolis; Leal & Fleishman, 2004; Ord, Stamps, & Losos, 2013). Thus, the physical context may also play a key role in the diversification of colour signals in *Sceloporus* species, which are occupying very distinct habitats (see methods) with different spectral properties (Figure 2, green dashed lines).

In summary, we have shown that colour patch losses have occurred in different ways, and that loss of a colour trait does not necessarily translate into a loss of signal. By using alternative colour components, such as areas of high or low UV reflectance or increasing contrast, lizards may remain conspicuous to conspecifics despite not exhibiting colourful patches. In addition, our results show how changing the evenness of reflectance across the spectrum may be an intermediate step facilitating evolutionary shifts between white and secondary colours (e.g. green or pink) without requiring major shifts in the peak colour (hue) or the visual receptors that may be tightly focused on that peak. Finally, our study emphasizes the consistent importance of natural and/or sexual selection and its flexible impact on different signal components through evolutionary time.

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