

**Trade-off between camouflage and sexual dimorphism revealed by UV digital imaging: the case of
 Australian Mallee Dragons (*Ctenophorus fordii*)**

Jair E. Garcia^{1,2*}, Detlef Rohr¹, and Adrian G. Dyer²

¹School of Applied Sciences, RMIT University, Building 14 Level 6, Bowen Street, Melbourne, VIC 3000, Australia,

²School of Media and Communication, RMIT University, Building 5 Level 3, Bowen Street, Melbourne, VIC 3000, Australia

Author for correspondence (jirgarci@gmail.com)

SUMMARY

Colour patterns displayed by animals may result from the balance of the opposing requirements of sexual selection through display and natural selection through camouflage. Currently little is known about the possibility of the dual purpose of an animal colour pattern in the UV region of the spectrum, which is potentially perceivable by both predators and conspecifics for detection or communication purposes. Here we implemented linearised digital UV photography to characterise and quantify the colour pattern of an endemic Australian Agamid lizard classically regarded as monomorphic when considering data from the visible region of the spectrum. Our results indicate a widespread presence of UV elements across the entire body of the lizards and these patterns vary significantly in intensity, size, and frequency between genders. These results were modelled considering either lizard or avian visual characteristics revealing that UV reflectance represents a trade-off between the requirements of sexual displaying to conspecifics, and concealment from avian predators.

INTRODUCTION

The trade-off between conspicuousness and concealment and its consequences for the evolution of the colour pattern displayed by many vertebrates is an enduring question in visual ecology and evolution. Sexual dichromatism, ornaments, and conspicuous colour pattern elements displayed by different animal species are shaped by sexual selection (Anderson, 1994; LeBas and Marshall, 2000). Camouflage either by background matching or disruptive coloration is favoured by natural selection to reduce predation (Cuthill et al., 2005; Cuthill et al., 2006; Endler, 2006; Stevens et al., 2006; Stevens and Merilaita, 2009; Troscianko et al., 2009).

Predation studies implementing experiments and models in different animal groups have shown that conspicuous individuals suffer higher predation than their counterparts, thus suggesting that natural selection should favour concealing colour patterns (Stuart-Fox et al., 2003; Husak et al., 2006; Vignieri et al., 2010; Farallo and Forstner, 2012). On the other hand, mate choice experiments with fish, birds and reptiles have demonstrated the importance of visual signals produced by bright and colourful ornaments for mate preference and its role as indicators of phenotypic quality (Beausoleil et al., 2012; Miyagi et al., 2012; Simons et al., 2012; Pérez I De Lanuza et al., 2013).

It has long been appreciated that ultraviolet (UV) vision is important in how many animals interact with their environment (Chittka et al., 1994; Goldsmith, 1994). With the finding of pattern elements reflecting UV radiations between 315 to 400 nm in different vertebrates species including birds (Bennett et al., 1996) and lizards (Fleishman et al., 1993) in addition to evidence for the capability of UV vision by these and other animal groups (Jacobs, 1992; Neumeyer, 1992; Cuthill et al., 2000; Yokohama and Shi, 2000; Yokoyama et al., 2000; Hunt et al., 2001; Loew et al., 2002; Bowmaker et al., 2005; Hart and Hunt, 2007; Fleishman et al., 2011), a potential new trait has to be considered to fully understand the animal coloration puzzle. UV signals are used by

many animals for different purposes including: individual face recognition (Partridge and Cuthill, 2010; Siebeck et al., 2010), mate choice (Bennett et al., 1996; Andersson et al., 1998; LeBas and Marshall, 2000; Eaton, 2005; Ord and Stuart-Fox, 2006; Rick and Bakker, 2008; Olsson et al., 2011) and as indicators of fighting ability (Stapley and Whiting, 2006; Bajer et al., 2011). However the potential trade-off between signalling and concealment in this region of the electromagnetic spectrum remains poorly studied probably due to the difficulty of assessing in a simple manner both the spectral and spatial characteristics of an animal colour pattern from spectrophotometric data (Endler and Mielke, 2005).

Even though new methodologies for analysing the spatial characteristics of animal colour patterns from spectrophotometric readings have been recently introduced (Endler, 2012), digital photography constitutes an time-efficient and effective methodology for simultaneously analysing, in a quantitative and qualitative manner, spectral and spatial components of complex patterns (Stevens et al., 2007). Furthermore, with the recent advent of digital cameras with extended sensitivity into the UV region (Pike, 2010), it is now possible to obtain an objective measurement of the spectral and spatial properties of a colour pattern in this spectral region (Garcia et al., 2013).

The Agamid lizard *Ctenophorus fordi* (Mallee Dragon) was selected as model species to test for the presence of UV dichromatism as it is regarded as monomorphic species in size and colour, with the exception of a characteristic mark located on the ventral surface of the chest in males (Cogger, 2000; Olsson, 2001; Bush et al., 2007). The presence of previously reported chromatic monomorphism in this species (Olsson, 2001) is somewhat surprising since dichromatism is common within the genus (Pianka and Vitt, 2003; Hugall et al., 2008), as exemplified by *Ctenophorus pictus*, a species living sympatrically with *C. fordi* (Cogger, 1978; Healey et al., 2007; Olsson et al., 2009; Olsson et al., 2012). Furthermore even though the presence of dichromatism in the UV region of the spectrum has been reported for other species of the genus (LeBas and Marshall, 2000; Stuart-Fox et al., 2004), the possible occurrence of this characteristic in *C. fordi* remains untested. In the present study digital linearised and quantifiable UV digital images are used to characterise the spectral and spatial properties of pattern elements reflecting UV radiation in this species, testing for a possible dual role of these for camouflage and sexual dichromatism.

MATERIALS AND METHODS

Model species and capture procedures

Ctenophorus fordi is a small, about 5 cm snout-vent length (Cogger, 2000; Wilson and Swan, 2008), endemic Australian lizard common in south-eastern Western Australia through southern South Australia with some populations occupying western Victoria and New South Wales, where is commonly observed near *Triodia scariosa* plant patches (Cogger, 2000; Olsson, 2001). For a human observer, *C. fordi* appears to display a dark reddish-orange coloration with a pale dorso-lateral stripe extending from the posterior region of the neck to the anterior portion of the tail; in turn, the pale stripe is bordered by a thin, black strip (Fig. 1). The dark orange-brown region enclosed by the pale stripe is flecked with small pale spots (Cogger, 2000).

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79 A total of 17 individuals, nine males and eight females, were captured by pitfall over different days in December
80 2011 at the Murray Sunset National Park (Victoria, Australia). The gender of each individual was determined by
81 the presence of and inverted “v” black mark located on the chest of male individuals (Wilson and Swan, 2008).
82 All lizards were released unharmed at 1 m from the trapping line after data recording. Trapping, handling and
83 restraining methods were performed accordingly to RMIT University Animal Ethics Committee application
84 AEC1123.

85 Ultraviolet image recording and camera characterisation

86 Images corresponding to the dorsal, laterodorsal, dorsolateral and cervical ventrolateral regions were recorded
87 on the RAW native format of a Nikon D70s digital camera (Nikon Corp., Shinjuku, Tokyo, Japan) modified for
88 UV digital recording. The camera was equipped with a Micro Nikkor 105 mm quartz lens (Nikon Corp.,
89 Shinjuku, Tokyo, Japan) to ensure free transmission of reflected UV radiation. Samples were placed at about 0.7
90 m from the sensor plane of the camera and irradiated with a Nikon SB-14 Speed light (Nikon Corp., Shinjuku,
91 Tokyo, Japan), emitting long-wavelength UV, visible and infra-red radiation within a 320 to 800 nm interval
92 (Fig. A1 in the Appendix).

93 Camera modification was performed by a local professional camera technician (Camera Clinic, Melbourne,
94 Victoria, Australia). The modification included the replacement of the hot-mirror filter placed by default on top
95 of the camera sensor by a Baader U-filter (Company Seven, Montpelier, Maryland, USA) and adjustment of the
96 focusing point. The replacement of the hot-mirror filter by the Baader U filter ensures the transmission of long-
97 wavelength UV radiation whilst cutting-off visible and infrared radiation up to 1000 nm (Fig. A2 in the
98 Appendix). Camera responses corresponding to the red channel are produced by radiation within 325 to 395 nm
99 to which this channel is highly sensitive (Garcia et al., in press).

100 Each lizard sample was photographed against a black matte cardboard including a scale in millimetres and the
101 ultraviolet calibration reflectance target reflecting about 86.5% of incident irradiation employed during camera
102 calibration (Dyer et al., 2004). Brightness of the images was standardized on the RAW images using nine
103 sampling points located at the centre of the reflectance calibration target. Exposure adjustment was performed
104 employing the exposure adjustment tool available in Camera Raw version 6.7 for Adobe Photoshop CS5 (Adobe
105 Systems, San Jose, California, USA). Processed raw images were subsequently encoded into 8-bit,
106 uncompressed TIFF files employing the same software package, and subsequently linearised.

107 Images representing the linear sensor response for the different body regions of each recorded lizard (Fig. 3A)
108 were obtained in a two-step process. First the uncompressed RGB-TIFF images were split into their three
109 monochrome composing images, corresponding to the ‘red’, ‘green’ and ‘blue’ colour channels, only retaining
110 those images corresponding to the red channel for further processing (Garcia et al., 2013). Following, the linear
111 sensor response at each pixel location was recovered inverting by numerical methods a biexponential function
112 describing the Opto-Electronic conversion function (OECF) for the red channel of the camera. Curve fitting,
113 inversion and linearisation procedures were done employing custom-written codes for Matlab release 2009b
114 (The Mathworks Inc., Natick, Massachusetts, USA).

Our model accounted for possible differences in the visual appearance of the pattern due to point of view and the visual acuity of two different observers. The model assumes that the lateral and ventrolateral regions are mainly observed by conspecifics, *i.e.* a lizard observer (Font et al., 2009), whilst the dorsal surface is observable by an avian predator (Stuart-Fox et al., 2004). Consequently it was assumed that an observable UV reflective pattern element should have a size equal or higher than twice the minimum discriminable object size (practical object size), predicted from the visual acuity of the two model observers (Gaffney and Hodos, 2003). The minimum object size detectable by a lizard observer was calculated as 0.9 mm from a visual acuity of 13.6 cycles/degree reported for *Anolis carolinensis* (Fleishman, 1992; New and Bull, 2011); whilst, the minimum object size detectable by an avian predator was calculated as 0.17 mm from a visual acuity of 73 cycles/degree corresponding to *Falco berigora* (Reymond, 1987), a common predator of the target species (Marchant et al., 1990). Predicted object sizes for both observers were calculated for a distance equal to 0.7 m.

Four variables were selected to characterise the pattern of those regions visible to the modelled observers: (i) median particle intensity, (ii) number of particles, (iii) UV reflective area to non-UV reflective area and (iv) relative particle size. The first variable describes the spectral characteristic of the UV reflective elements of the pattern as the total amount of UV reflected within a 325 to 390 nm spectral interval, expressed as linear pixel intensity values, corresponding to the spectral sensitivity of the red channel of the modified Nikon D70s camera (Garcia et al., 2013). Variables ii to iv measure different aspects of the spatial characteristics of the UV reflecting elements of the pattern in terms of size and number.

Data corresponding to the variables describing spatial characteristics were obtained from linearised images after applying image segmentation processing techniques using the threshold and ‘particle analysis’ tools available in ImageJ version 1.46r (Schneider et al., 2012). The implemented image processing protocol is a modification of a published methodology for the study of animal patterns using image segmentation (Young et al., 2011). Prior to image segmentation, individual linearised images were calibrated in millimetres using as reference the scale included on each picture then sample areas were delimited using the elliptical selection tool (Fig. 3A), and saved as individual, uncompressed TIFF image files. Sample images were subsequently segmented using intensity and size threshold values.

The size threshold was expressed in area units assuming that each segmented image region (‘particle’) consists in a circular element circumscribed in a square whose sides equal the practical object size. Two intensity threshold values were set at pixel intensity levels corresponding to between 5 and 80% of the total reflected irradiation. The lower threshold value selected prevents including camera responses with a low signal-to-noise ratio whilst the upper limit excludes extremely high camera responses that may have lost information due to clipping (Stevens et al., 2007). The intensity interval delimited by the upper and lower intensity threshold values includes reflectance values observed for the selected body regions from spectral reflectance readings. Spectrophotometric readings were obtained using an Ocean Optics USB2000 spectrophotometer equipped with a 200 μ m UV-visible bifurcated probe and coupled with a xenon PX-2 light source (Ocean Optics, Dunedin, Florida, USA) (Fig. A3 in the Appendix). Measurements were recorded as part of a parallel study along with measurements of different background elements.

Image regions satisfying the size and intensity threshold conditions are referred as ‘particles’ and regarded as UV-reflective patches potentially perceivable by either the model lizard or avian observer. Once the particles of a given image were obtained, their size and number were measured using the particle analysis tool available in the same software package (Fig. 3B under the Results section); then, a binary negative mask was created from the outcome image from the particle analysis (Fig. 3C) and subsequently multiplied by the sample image.

The image resulting from multiplying the mask and linearised image (Fig. 3D) contains zeroes on all those pixel locations which do not correspond to a particle and the original linear pixel intensity values elsewhere. The magnitude of the intensity variable represents the median linear pixel intensity value from all non-zero pixel locations. Image multiplication and calculation of the median intensity were performed using custom codes written for Matlab release 2009b (The Mathworks Inc., Natick, Massachusetts, USA).

Excepting the intensity variable all variables were normalised to enable a direct comparison. Variable ii, describing the number of particles, was normalized by dividing the number of particle in the sample by the total sampled area. Variable iii, describing particle size, is a unit-less variable representing the ratio of average particle size to the sampled area and therefore is already normalised. Finally variable iv, describing the UV to non-UV reflective ratio, was obtained by dividing the total area of the UV reflective particles of each individual sample by its corresponding sampled area.

Experimental design and statistical analysis

Data collected from the processed images were arranged in a partly nested (split-plot) ANOVA design and expressed as a linear model (Montgomery, 2009). We tested for differences in the spectral and spatial characteristics of the UV reflective pattern elements displayed by females and males of *C. fordi* on the selected body regions based on the magnitudes of the four selected variables.

The coefficients required by the linear model were obtained by least sum of absolute (LAD) or, Euclidean distances (LSED) rather than by ordinary least squares (OLS) implementing linear programming techniques (Kaufman Jr et al., 2002). The residuals obtained after fitting the regression model were analysed implementing multiresponse permutation procedures (MRPP) to test for group differences examining differences among the medians of the different groups (Berry and Mielke Jr, 1999; Mielke and Berry, 2007).

The δ -statistic and P-values associated with the multivariate LSED-MRPP and univariate LAD-MRPP analyses were obtained implementing a Monte Carlo resampling approximation based on 1 million simulations, whilst the within-group agreement measure (\mathfrak{R}), a measure of effect size, was calculated from Pearson type III approximations (Mielke and Berry, 2007). Univariate analyses were followed-up by unplanned (pairwise) comparisons implementing MRPP analysis. LSED, LAD, and MRPP calculations were performed using algorithms by Mielke and Berry (2007) after applying a reciprocal transformation to the data to ensure homogeneity of variance, the only assumption required by randomization tests (Berry and Mielke Jr, 1999; Quinn and Keough, 2003). All other statistical analyses were performed in IBM SPSS Statistics v17.0 (IBM Corporation, Armonk, New York, USA).

RESULTS

Examples of linear UV images reconstructed for the ‘neck’ and dorsal regions of a male and a female individual of *C. fordi* are depicted in Fig. 2. Fig. 3 exemplifies different images obtained during the processing of one of the images in Fig. 2. A graphical summary of the obtained measurements for all the 51 image samples is presented in Fig. 4.

Bivariate correlation analyses performed on the four variables (Fig. A4 in the Appendix) indicated a significant positive correlations between particle size and median intensity ($\tau = 0.722$, $P < 0.001$), UV to non-UV reflective ratio and median intensity ($\tau = 0.678$, $P < 0.001$); and, between particle size and UV to non-UV reflective ratio ($\tau = 0.834$, $P < 0.001$). On the other hand the number of particles was not significantly correlated with either median intensity ($\tau = -0.010$, $P = 0.312$), particle size ($\tau = -0.104$, $P = 0.280$), or UV to non-UV reflective ratio ($\tau = -0.020$, $P = 0.839$).

A principal component analysis (PCA) performed on the correlation matrix of the four variables suggested the presence of two factors (principal components) explaining up to 92.5% of the total observed variation (Fig. A5 in the Appendix). The first component explains 72.3% of the total variance and is composed by variables i, iii and iv describing the median particle intensity, particle size and UV to non-UV reflective ratio. The second component explains 20.2% of the total variation and is exclusively composed by variable ii measuring the number of particles. Therefore the remaining analyses were focused on just variables i and ii: median intensity and number of particles, describing the spectral and spatial characteristics of the pattern respectively. This was done to avoid including highly correlated, redundant variables in the multivariate analysis which reduces the power of the multivariate tests (Tabachnick and Fidell, 2007).

The pattern displayed by *C. fordi* is characterised by reflecting a lower amount of incident UV radiation on the dorsal region, visible to aerial predators, than either the lateral or the neck region, which are observable to a lizard observer. Among the different body regions, the anterior ventrolateral surface (‘neck’) reflects the highest amount of UV radiation (Fig. 4A).

The number of UV reflecting elements varies on different ways in males and females. Whilst the number of UV reflecting elements oscillates across the different body regions on females, males show an almost uniform amount of UV elements in the side and neck regions with a notorious absence of such elements on the dorsal surface (Fig. 4B).

The multivariate analysis, taking into account the joint effect of the two selected variables, suggests the presence of significant differences among the different body regions in both genders and a marginal statistical similarity between genders (Table 1); however, the highly significant interaction suggests that the observed variation pattern across the body region differs for males and females (Table 1).

223 **Table 1: Summary of the LSED-MRPP multivariate analysis comparing genders and body regions based on median**
 224 **UV intensity and number of particles variables.**

Factor	Observed statistic (δ_o)	P-value	\mathfrak{R}
<i>Between-subjects</i>			
Gender	98.8	0.69×10^{-1}	0.22×10^{-1}
<i>Within-subjects</i>			
Body region	91.3	$0.16 \times 10^{-1} *$	0.47×10^{-1}
Interaction	85.8	$0.91 \times 10^{-2} **$	0.11

δ_o corresponds to the observed δ -statistic. Reported P-values corresponds to the probability of obtaining a δ -statistic equal or smaller than δ_o after performing 1 million random allocations of the elements into the different groups. \mathfrak{R} is the within-group agreement measure, a measurement of effect size (Endler and Mielke, 2005; Mielke and Berry, 2007)

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226 Univariate *post-hoc* analyses were performed following the multivariate analysis to examine variation in the
 227 pattern across body region in males and females within each individual variable (Table 2). LAD-MRPP analyses
 228 revealed a significant difference in the total amount of reflected UV by the two genders, but failed to reject the
 229 null hypothesis of equality in the total number of particles present in the different body regions of males and
 230 females at a significance level $\alpha = 0.05$. Differences among body regions show an interesting pattern (Fig. A6 in
 231 the Appendix), significantly differing in the total amount of UV reflected by each region (variable i) but failing
 232 to reject marginally the null hypothesis for the total number of UV reflective elements (variable ii) at a $\alpha = 0.05$,
 233 with a highly significant interaction between body region and gender.

234 **Table 2: Summary of *post-hoc* LSED-MRPP univariate analysis comparing genders and body regions based on**
 235 **median UV intensity and number of particles variables.**

Factor	Variable	Observed statistic (δ_o)	P-value	\mathfrak{R}
<i>Between-subjects</i>				
Gender	Median intensity	1.94	$0.96 \times 10^{-2} **$	0.56×10^{-1}
	Number of particles	98.46	0.74×10^{-1}	0.22×10^{-1}
<i>Within-subjects</i>				
Body region	Median intensity	2.26	$< 0.001 **$	0.46
	Number of particles	90.50	0.79×10^{-1}	0.37
Interaction	Median intensity	1.07	$0.55 \times 10^{-2} **$	0.11
	Number of particles	85.56	$0.89 \times 10^{-2} **$	0.11

δ_o , P-values and \mathfrak{R} as for Table 1.

A total of three unplanned (pairwise) comparisons were performed for each variable to identify significant differences between genders at each level of the body region factor. Comparisons revealed a significant difference in the number of particles present in the dorsal region of males and females and in the amount of UV reflected by the laterodorsal and dorsolateral regions of each gender. Comparisons failed to reject the null hypothesis of equality in the amount of UV reflected by the cervical ventrolateral region of the two genders at a significance level $\alpha = 0.05$ (Table 3).

Table 3: Summary of unplanned (pairwise) comparisons between males and females performed at each body region for the UV intensity and number of particles variables.

	Back		Side		Neck	
	Observed statistic (δ_o)	P-value	Observed statistic (δ_o)	P-value	Observed statistic (δ_o)	P-value
Median						
UV intensity	1.22	0.83	1.95	0.22×10^{-1} *	2.33	0.71×10^{-1}
Number of particles	215.0	0.70×10^{-2} **	32.6	0.60	14.9	0.57

δ_o corresponds to the observed δ -statistic. Reported P-values correspond to the exact probability of obtaining a δ -statistic equal or smaller than δ_o . Comparisons were made implementing a MRPP analysis on two groups, each one representing one of the two genders.

DISCUSSION

Lizards constitute a group of highly visually-driven animals potentially capable of UV vision and in many cases possessing colour patterns reflecting energy in this spectral range (Fleishman et al., 1993; Fleishman et al., 1997; Loew et al., 2002; Fleishman et al., 2011). In this study we show that the UV coloration displayed by *C. fordi* can be explained as a trade-off between the opposing requirements for sexual selection and camouflage based on the spectral and spatial characteristics of the pattern.

We acknowledge that other spectral channels (wavelengths > 400 nm) in either conspecifics or predators may drive different behaviours or, interact with the UV channel (Kevan et al., 2001). However it is valid to investigate the UV spectral region as this waveband is used for communication in some signal-receiver relationships by animals, particularly at close range (Heiling et al., 2003; Losey, 2003; Siebeck et al., 2010), including lizards (Fleishman et al., 2009; Fleishman et al., 2011), and is known to be potentially visible to some avian species including those commonly predating on *Ctenophorus fordi* (Marchant et al., 1990; Hart and Vorobyev, 2005; Hart and Hunt, 2007; Ödeen and Håstad, 2009). Moreover, variability in the spectral tuning of avian SW1 photoreceptors allows for the classification of birds into two distinct groups: UV sensitive (UVS) and violet sensitive (VS) birds (Hart, 2001; Håstad et al., 2005; Hart and Hunt, 2007; Hunt et al., 2009), thus allowing for the evolution of different signal-receiver relationships which in turn may shape the appearance of lizard patterns in complex environments.

Microhabitat specialization has been proposed as a reason underlying the great lizard diversity present in Australian arid ecosystems (Pianka, 1986, 1989; Vitt et al., 2003). Ecological and phylogenetic structure studies have provided evidence supporting this hypothesis based on diet and habitat utilization (Daly et al., 2008; Rabosky et al., 2011). Microhabitat specialization has also been proposed as an underlying cause for the convergence of the species belonging to genus *Ctenophours* into three morphologically distinct, albeit phylogenetically unrelated eco-morphs: burrowers, rock dwellers and spinifex/sand specialists (Greer, 1989; Melville et al., 2001; Hugall et al., 2008). Our data suggests that the colour pattern displayed by *C. fordi* may also represent another example of microhabitat adaptation, which increases concealment through background matching, and is possibly reinforced by disruptive coloration in the case of female lizards

In open habitats as the one occupied by *C. fordi*, it is hypothesised that there is an increase in predation risk due to an easier detection of the lizard by its aerial predators (Ord and Stuart-Fox, 2006). Therefore natural selection should favour the evolution of inconspicuous colour patterns, providing camouflage across the entire spectral region perceivable by the lizard's predators, leading to a reduction in dichromatism thus presenting a classic example of opposing requirements by natural and sexual selection. Then the characteristics of the colour pattern displayed by *C. fordi* in the UV may be interpreted as a trade-off between these opposing requirements, where concealment is maximised in those regions visible to predators (dorsum), whilst limiting dichromatism to those body parts easily visible by conspecifics during social interactions, as previously proposed for other species of the genus *Ctenophorus* living in rocky environments (Gibbons and Lillywhite, 1981; Stuart-Fox et al., 2003). Our results are consistent with this hypothesis and provide novel insights for a species occupying open environments dominated by sand and *Spinifex* grass.

Specifically, evidence for the presence of camouflage in the UV spectral region in *C. fordi*, is the low amount of UV radiation being reflected by the dorsal region by both males and females; which, matches the low UV reflectance of most elements making up the visual background against the lizards are observed (Fig. A7 in the Appendix). Interestingly, females are characterised by presenting small, contrasting UV elements in this region which are not present in males. The size and distribution of these elements touching the body outline at several points, in addition to their relatively higher UV reflectance compared to their local background (Figs 2D, 4B.), are consistent with the required characteristics for a disruptive colour pattern (Stevens et al., 2006; Stevens and Merilaita, 2009).

It may be argued that UV coloration is not effective as a disruptive mechanism because texture discrimination in birds is thought to be mainly mediated by achromatic signals detected by the double cone photoreceptor which is tuned at longer wavelengths in avian species (Jones and Osorio, 2004; Hart and Hunt, 2007). However there is also experimental evidence that UV cues are important for foraging and motion detection in birds, with the latter showing preference for UV-reflecting targets such as fruits (Church et al., 1998; Siitari et al., 1999; Rubene et al., 2010; Werner et al., 2012). Therefore, for a common prey of birds which are potentially capable of UV vision, it would be advantageous possessing a colour pattern also providing camouflage in this spectral region; especially, in open environments where UV radiation is available (Endler, 1993). The reinforcement of background matching camouflage by disruptive coloration in females would make the latter less conspicuous than males as observed in other lizard and bird species displaying dichromatism in the visible and the UV spectral regions (Stuart-Fox et al., 2003; Eaton, 2005). Our data thus leads to a plausible hypothesis that perhaps

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301 males move more than females, and motion would tend to break this sort of disruptive coloration crypsis. There
 302 exists some supporting evidence for future testing of this motion vision related hypothesis. Indeed females may
 303 benefit from displaying a disruptive coloration that is expected to be more effective when the animal is still,
 304 since females of *C.fordi* are not typically active in mate choice (Olsson, 2001), and males approach females for
 305 mating (Cogger, 1978; Olsson, 2001).

306 The presence of UV-dichromatism limited to those regions exposed to conspecifics, in addition to the size of
 307 UV-reflecting patches which are easily discriminable by the visual acuity of a lizard observer (Fig. 4C),
 308 provides further support for the hypothesis of a reduced dichromatism as a response to higher predation risk
 309 (Ord and Stuart-Fox, 2006). However, it is also possible that UV-reflective elements also play a role in visual
 310 communication at short distances as suggested by data from studies in some aquatic species (Losey, 2003;
 311 Siebeck et al., 2010). The significant difference in intensity observed between males and females for the lateral
 312 region and the marginally non-significant difference in UV brightness for the ventrolateral cervical region,
 313 suggest that dichromatism is present in the species as expected from the phylogenetic relationships within the
 314 *Ctenophorus* genus (Hugall et al., 2008). As such we suggest discarding the description of *Ctenophorus fordi* as
 315 a monomorphic species in colour, even though differences between males and females are hardly detectable in
 316 other spectral intervals including the human visible range of the spectrum.

317 Although most of the current understanding of the role of an animal colour pattern for signalling is based on the
 318 analysis of data describing its spectral properties, variations in the spatial component of the pattern may explain
 319 an important amount of the variation observed within individuals and between genders as here reported for
 320 *Ctenophorus fordi*. For this reason we suggest including spatial information as part of the characterisation of
 321 animal colour patterns, a task simplified by employing characterised digital cameras, particularly when the
 322 presence of UV coloration is suspected or revealed by the implementation of spectrophotometric techniques.

323 **CONCLUSION**

324 The complex UV coloration displayed by *C. fordi* constitutes an excellent example of a trade-off between the
 325 requirements for visual communication and camouflage in open habitats where predation risk is high. In this
 326 species a compromise between these two opposing needs is likely to be achieved by reducing the presence of
 327 conspicuous traits in males to regions only observable by conspecifics whilst minimising exposure thorough
 328 background matching and disruptive coloration on surfaces visible by aerial predators. The trade-off only
 329 became apparent when considering simultaneously the spatial and spectral properties of a colour pattern, task
 330 simplified by implementing photographic techniques with characterised cameras in addition to standard
 331 spectrophotometric techniques.

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524 **FIGURE LEGENDS**

525 **Figure 1: Female individual of *Ctenophorus fordi* recorded with a standard photographic camera (Canon**
 526 **40D).**

527 **Figure 2: Pseudocolor representations of linearised UV reflectance digital images corresponding to**
 528 **different body regions of a male and a female individual of *Ctenophorus fordi*.** A) Ventrolateral cervical
 529 region of a male and B) female. C) Dorsal surface of a male and D) female. Colour bars represent reflectance
 530 values, expressed as normalised pixel intensity values, at each pixel location. Vermillion semicircle corresponds
 531 to an ultraviolet calibration standard reflecting up to 87% of total incident irradiation. The scale bars located at
 532 the bottom-right corner of each image represent 5 mm.

533 **Figure 3: Pseudocolor representation of images employed for measuring spectral and spatial properties of**
 534 **the UV reflecting elements in the colour pattern of *Ctenophorus fordi*.** A) Pseudocolour representation of a
 535 linearised UV reflected digital image where total reflectance matches the pixel intensity level at each pixel
 536 location. Colour bar represents different total reflectance amounts. Red ellipse approximately corresponds to the
 537 selected sampling area. The vermillion circle located on the upper right corner is a UV reflectance standard
 538 reflecting about 87% of the total incident UV radiation. B) Negative binary mask obtained by the threshold of
 539 the sampled area in A. Pixels included in the mask are those reflecting 5 to 80% of the total incident UV
 540 radiation and whose size is equal or higher to twice the minimum discriminable object as predicted by the visual
 541 acuity of a model avian predator. See text for details. C) Particle outlines obtained from B). Particles illustrate
 542 the variation in size and number observed among the different UV reflective elements present in the colour
 543 pattern. D) Result of multiplying the binary mask in B) and the sampled area in A) used to calculate the median
 544 intensity of the UV reflective patches in the colour pattern. Scale bars on all images represent 10 mm.

545 **Figure 4: Median values for A) particle intensity, B) number of particles, C) relative particle size and, D)**
 546 **UV to non-UV reflective ratio for males (grey bars) and females (white bars) of *Ctenophorus fordi*.** Error
 547 bars represent a 95% confidence interval.

548 **APPENDIX**

549 **Figure A1: Average spectral power distributions (SPD) of the Nikon SB-14 electronic flash unit employed**
 550 **as UV-source for image recording.** SPDs were recorded at six different distances from the sensor of an NIST
 551 traceable ILT-900 spectroradiometer (International Light Technologies, USA) equipped with an irradiance
 552 collector. Each SPD consist on the average of five independent measurements. Error bars represent 95%
 553 confidence intervals.

554 **Figure A2: Spectral transmittance of a Baader U-filter (Company Seven, USA) as the one replacing the**
 555 **hot-mirror filter on the modified Nikon D70s digital camera.** Spectral transmittance curve was calculated
 556 from spectral irradiance data recorded with a NIST traceable ILT-900 spectroradiometer (International Light
 557 Technologies, USA) equipped with an irradiance collector.

558 **Figure A3: Average reflectance spectra for ($n = 11$) males (red line) and ($n = 13$) females (blue) of**
 559 ***Ctenophorus fordi* measured at four body locations: A) cervical ventrolateral region ('neck'), B) dorsal**
 560 **thoracic surface, C) dorsolateral surface and D) anterior dorsal region ('head').** Reflectance readings were
 561 recorded with an Ocean Optics USB2000 spectrophotometer (Ocean Optics, USA) equipped with a bifurcated
 562 400 μm ultraviolet-visible probe and using a PX-2 xenon lamp (Ocean Optics, USA) as irradiation source. A
 563 Spectralon (LabSphere, USA) was used as calibration standard. Error bars represent 95% confidence intervals.

564 **Figure A4: Bivariate scatter plot corresponding to the four variables selected for characterising the**
 565 **spectral and spatial characteristics of the UV reflective elements present in the colour pattern of**
 566 ***Ctenophorus fordi*.**

567 **Figure A5: Factor (component) plot showing the loadings for the two components extracted from a PCA**
568 **analysis with a Varimax factor rotation performed on the four original variables: median intensity**
569 **(Intensity), number of particles (num_particles), relative particle size (part_size) and, UV to non-UV ratio**
570 **(ratio).**

571 **Figure A6: Interaction plots of the cells medians for gender (between-subjects factor) and body region**
572 **(within-subjects) factor.** Median values and confidence intervals are those reported in Fig. 3; therefore, errors
573 bars were omitted to facilitate visual interpretation.

574 **Figure A7: Average reflectance spectra from different elements constituting the visual background of**
575 ***Ctenophorus fordi*.** A) Hardened sand/clay cores, B) loose sand/clay granules, C) dry *Triodia* leaves, D) fresh
576 *Triodia* leaves and E) plant debris. Reflectance readings were recorded with an Ocean Optics USB2000
577 spectrophotometer (Ocean Optics, USA), equipped with a bifurcated 400 µm ultraviolet-visible probe and using
578 a PX-2 xenon lamp (Ocean Optics, USA) as irradiation source. A Spectralon (LabSphere, USA) was used as
579 calibration standard. Error bars represent 95% confidence intervals.







