

## RESEARCH ARTICLE

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

Jair E. Garcia<sup>1,2,\*</sup>, Detlef Rohr<sup>1</sup> and Adrian G. Dyer<sup>2</sup>

<sup>1</sup>School of Applied Sciences, RMIT University, Building 14 Level 6, Bowen Street, Melbourne, VIC 3000, Australia and

<sup>2</sup>School 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 sexes. 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.

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## 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 by 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). However, 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 an indicator of phenotypic quality (Beauleuil 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 many animals in terms of how they interact with their environment (Chittka et al., 1994; Goldsmith, 1994). With the finding of pattern elements reflecting UV radiation between 315 and 400 nm in different vertebrate species including birds (Bennett et al., 1996) and lizards (Fleishman et al., 1993), in addition to evidence for the capability of UV vision in these and other animal groups (Jacobs, 1992; Neumeyer, 1992; Cuthill et al., 2000;

Yokoyama 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 recently been introduced (Endler, 2012), digital photography constitutes a 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, 2011), 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 fordii* (Mallee dragon) was selected as a model species to test for the presence of UV dichromatism as it is regarded as a 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 chromatic monomorphism reported in this species (Olsson, 2001) is somewhat surprising as 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 were 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* (Storr 1965) is a small, ~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 it 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).

A total of 17 individuals, nine males and eight females, were captured by pitfall traps over different days in December 2011 at the Murray Sunset National Park (VIC, Australia). The sex of each individual was determined by the presence of an inverted black ‘V’ mark located on the chest of male individuals (Wilson and Swan, 2008). All lizards were released unharmed 1 m from the trapping line after data recording. Trapping, handling and restraining methods were performed according to RMIT University Animal Ethics Committee application AEC1123.

### UV image recording and camera characterisation

Images corresponding to the dorsal, laterodorsal, dorsolateral and cervical ventrolateral regions were recorded on the RAW native format of a Nikon D70s digital camera (Nikon Corp., Shinjuku, Tokyo, Japan) modified for UV digital recording. The camera was equipped with a Micro Nikkor 105 mm quartz lens (Nikon Corp.)

to ensure free transmission of reflected UV radiation. Samples were placed about 0.7 m from the sensor plane of the camera and irradiated with a Nikon SB-14 Speed light (Nikon Corp.), emitting long-wavelength UV, visible and infrared radiation within a 320–800 nm interval (supplementary material Fig. S1).

Camera modification was performed by a local professional camera technician (Camera Clinic, Melbourne, VIC, Australia). The modification included the replacement of the hot-mirror filter placed by default on top of the camera sensor by a Baader U-filter (Company Seven, Montpelier, MD, USA) and adjustment of the focusing point. The replacement of the hot-mirror filter by the Baader U-filter ensures the transmission of long-wavelength UV radiation whilst cutting off visible and infrared radiation up to 1000 nm (supplementary material Fig. S2). Camera responses corresponding to the red channel are produced by radiation within 325–395 nm to which this channel is highly sensitive (Garcia et al., 2013).

Each lizard sample was photographed against a piece of matt black cardboard including a scale in millimetres and a UV calibration reflectance target reflecting about 86.5% of incident irradiation employed during camera calibration (Dyer et al., 2004). The brightness of the images was standardised on the raw images using nine sampling points located at the centre of the reflectance calibration target. Exposure adjustment was performed by employing the exposure adjustment tool available in Camera Raw version 6.7 for Adobe Photoshop CS5 (Adobe Systems, San Jose, CA, USA). Processed raw images were subsequently encoded into 8-bit, uncompressed TIFF files using the same software package, and subsequently linearised.

Images representing the linear sensor response for the different body regions of each recorded lizard (Fig. 2) were obtained in a two-step process. First, the uncompressed RGB-TIFF images were split into their three component monochrome images, corresponding to the ‘red’, ‘green’ and ‘blue’ colour channels, only retaining those images corresponding to the red channel for further processing (Garcia et al., 2013). Subsequently, the linear sensor response at each pixel location was recovered by inverting, by numerical methods, a biexponential function describing the Opto-Electronic conversion function (OECF) for the red channel of the camera. Curve fitting, inversion and linearisation procedures were done using custom-written codes for MatLab release 2009b (The Mathworks Inc., Natick, MA, USA).

### Visual modelling and data acquisition

Our model accounted for possible differences in the visual appearance of the colour pattern due to the point of view and the visual acuity of two different observers. The model assumes that



Fig. 1. A *Ctenophorus fordi* female recorded with a standard photographic camera (Canon 40D).



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 to 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  $\text{deg}^{-1}$  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  $\text{deg}^{-1}$  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) relative particle size and (iv) UV-reflective area to non-UV-reflective area. The first variable describes the spectral characteristics of the UV-reflective elements

of the pattern as the total amount of UV reflected within a 325–390 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–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 the scale included on each picture as a reference, 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 of a circular element

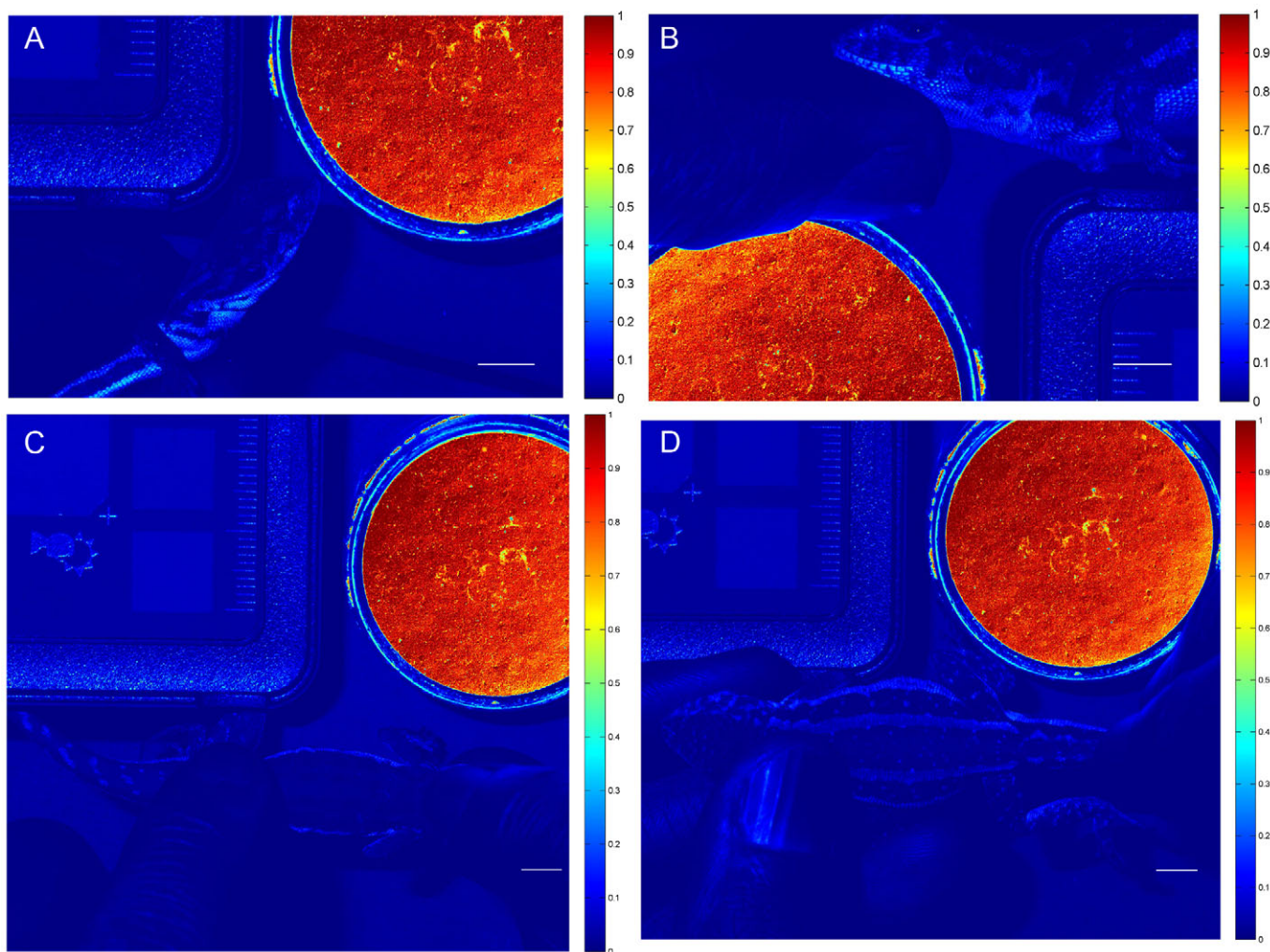


Fig. 2. Pseudocolour representations of linearised UV reflectance digital images corresponding to different body regions of a male and female *C. fordii*. (A,B) Ventrolateral cervical region of a male (A) and female (B). (C,D) Dorsal surface of a male (C) and female (D). Colour bars represent reflectance values, expressed as normalised pixel intensity values, at each pixel location. The vermilion circle corresponds to an ultraviolet calibration standard reflecting up to 87% of total incident irradiation. The scale bars located at the bottom-right corner of each image represent 5 mm.

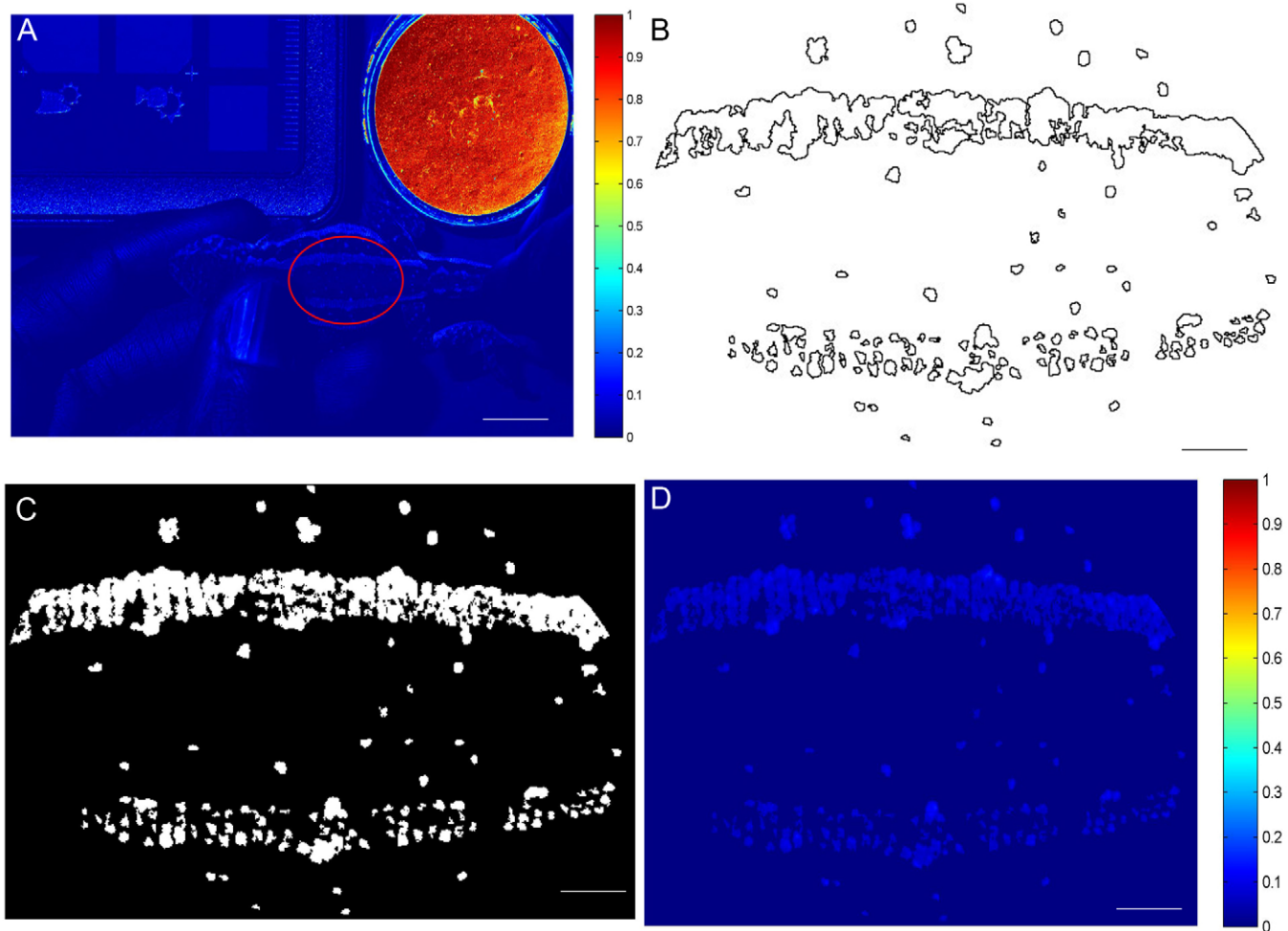


Fig. 3. Pseudocolour representation of images employed for measuring spectral and spatial properties of the UV-reflecting elements in the colour pattern of *C. fordii*. (A) Pseudocolour representation of a linearised UV-reflected digital image where total reflectance matches the pixel intensity level at each pixel location. The colour bar represents different total reflectance amounts. The red ellipse approximately corresponds to the selected sampling area. The vermilion circle located in the upper right corner is a UV reflectance standard reflecting about 87% of the total incident UV radiation. (B) Negative binary mask obtained from the threshold of the sampled area in A. Pixels included in the mask are those reflecting 5–80% of the total incident UV radiation and whose size is equal to or higher than twice the minimum discriminable object as predicted by the visual acuity of a model avian predator. See Materials and methods for details. (C) Particle outlines obtained from B. Particles illustrate the variation in size and number observed among the different UV-reflective elements present in the colour pattern. (D) The median intensity of the UV-reflective patches in the colour pattern, obtained by multiplying the binary mask in B and the sampled area in A. Scale bars on all images represent 10 mm.

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 the inclusion of 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  $\mu$ m UV–visible bifurcated probe and coupled with a xenon PX-2 light source (Ocean Optics, Dunedin, FL, USA) (supplementary material Fig. S3). 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 (Results, Fig. 3B); 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 that 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 codes custom-written for Matlab release 2009b (The Mathworks Inc.).

With the exception of the intensity variable, all variables were normalised to enable a direct comparison. Variable *ii*, describing the number of particles, was normalised by dividing the number of

particles 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 (LSED) distance rather than by ordinary least squares (OLS), implementing linear programming techniques (Kaufman 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, 1999; Mielke and Berry, 2007).

The  $\delta$ -statistic and *P*-values associated with the multivariate LSED-MRPP and univariate LAD-MRPP analyses were obtained by applying 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 described elsewhere (Mielke and Berry, 2007) after applying a reciprocal transformation to the data to ensure homogeneity of variance, the only assumption required by randomisation tests (Berry and Mielke, 1999; Quinn and Keough, 2003). All other statistical analyses were performed in IBM SPSS Statistics v17.0 (IBM Corporation, Armonk, NY, USA).

#### RESULTS

Examples of linear UV images reconstructed for the 'neck' and dorsal regions of a male and a female *C. fordi* are depicted in Fig. 2. Fig. 3 is an example the 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 (supplementary material Fig. S4) indicated a significant positive correlation 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 particle size and UV- to non-UV-reflective ratio ( $\tau=0.834$ ,  $P<0.001$ ). However, the number of particles was not significantly correlated with 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

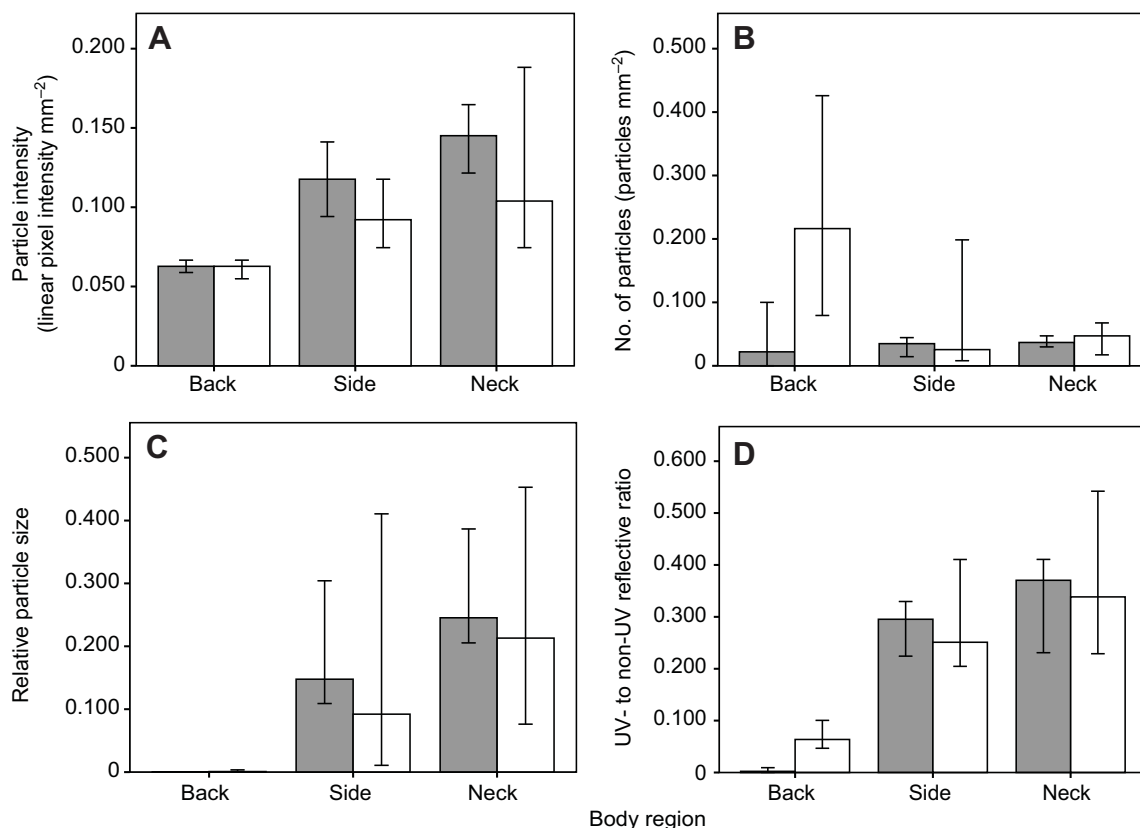


Fig. 4. Median values for (A) particle intensity, (B) number of particles, (C) relative particle size and (D) UV- to non-UV-reflective ratio for males (grey bars) and females (white bars) of *C. fordi*. Error bars represent the 95% confidence interval.



Table 1. Summary of the LSED-MRPP multivariate analysis comparing sex and body region based on the variables median UV intensity and number of particles

Factor	$\delta_o$	<i>P</i> -value	$\eta^2$
Between-subjects: sex	98.8	0.069	0.022
Within-subjects: body region	91.3	0.016*	0.047
Interaction	85.8	0.009**	0.110

$\delta_o$  corresponds to the observed  $\delta$ -statistic.

Reported *P*-values correspond to the probability of obtaining a  $\delta$ -statistic equal to or smaller than  $\delta_o$  after performing 1 million random allocations of the elements into the different groups.

$\eta^2$  is the within-group agreement measure, a measurement of effect size (Endler and Mielke, 2005; Mielke and Berry, 2007).

\**P*<0.05; \*\**P*<0.01.

total observed variation (supplementary material Fig. S5). The first component explains 72.3% of the total variance and is composed of 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 of variable ii, 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 by another lizard. 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 in different ways in males and females. Whilst the number of UV-reflecting elements oscillates across the different body regions in females, males show an almost uniform number of UV elements in the side and neck regions with a significant 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 sexes and a marginal statistical similarity between sexes (Table 1); however, the highly significant interaction suggests that the observed pattern variation across the body region is different for males and females (Table 1).

Univariate *post hoc* analyses were performed following the multivariate analysis to examine variation in colour pattern across body region in males and females within each individual variable

(Table 2). LAD-MRPP analyses revealed a significant difference in the total amount of reflected UV by the two sexes, but failed to reject the null hypothesis of equality in the total number of particles present in the different body regions of males and females at a significance level  $\alpha=0.05$ . Differences among body regions show an interesting pattern (supplementary material Fig. S6), with a significant difference in the total amount of UV reflected by each region (variable i) but the analyses marginally failed to reject the null hypothesis for the total number of UV-reflective elements (variable ii) at  $\alpha=0.05$ , with a highly significant interaction between body region and sex.

A total of three unplanned (pairwise) comparisons were performed for each variable to identify significant differences between the sexes 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 sex. Comparisons failed to reject the null hypothesis of equality in the amount of UV reflected by the cervical ventrolateral region of males and females at a significance level  $\alpha=0.05$  (Table 3).

## 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 have shown 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 preying on *C. 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 the evolution of different signal–receiver relationships, which in turn may shape the appearance of lizard patterns in complex environments.

Microhabitat specialisation has been proposed as one reason underlying the great lizard diversity present in Australian arid

Table 2. Summary of *post hoc* LSED-MRPP univariate analysis comparing sex and body region based on the variables median UV intensity and number of particles

Factor	Variable	$\delta_o$	<i>P</i> -value	$\eta^2$
Between-subjects: sex	Median intensity	1.94	0.0096**	0.056
	Number of particles	98.46	0.074	0.022
Within-subjects: body region	Median intensity	2.26	<0.001**	0.460
	Number of particles	90.50	0.079	0.370
Interaction	Median intensity	1.07	0.006**	0.110
	Number of particles	85.56	0.009**	0.110

$\delta_o$ , *P*-values and  $\eta^2$  as for Table 1.

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

	Back		Side		Neck	
	$\delta_o$	<i>P</i> -value	$\delta_o$	<i>P</i> -value	$\delta_o$	<i>P</i> -value
Median UV intensity	1.22	0.830	1.95	0.022*	2.33	0.071
Number of particles	215.0	0.007**	32.6	0.600	14.9	0.570

$\delta_o$  corresponds to the observed  $\delta$ -statistic.  
Reported *P*-values correspond to the exact probability of obtaining a  $\delta$ -statistic equal to or smaller than  $\delta_o$ .  
Comparisons were made implementing a MRPP analysis on two groups, each one representing either male or female.  
\**P*<0.05; \*\**P*<0.01.

ecosystems (Pianka, 1986; Pianka, 1989; Vitt et al., 2003). Ecological and phylogenetic structure studies have provided evidence supporting this hypothesis based on diet and habitat utilisation (Daly et al., 2008; Rabosky et al., 2011). Microhabitat specialisation has also been proposed as an underlying cause of the convergence of the species belonging to genus *Ctenophorus* into three morphologically distinct, albeit phylogenetically unrelated ecomorphs: burrowers, rock dwellers and spinifex/sand specialists (Greer, 1989; Melville et al., 2001; Hugall et al., 2008). Our data suggest 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 such as the one occupied by *C. fordi*, it is hypothesised that there is an increase in predation risk due to the 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 range 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 con-specifics 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* comes from 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 which the lizards are observed (supplementary material Fig. S7). Interestingly, females are characterised by presenting small, contrasting UV elements in this region that 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 with their local background (Fig. 2D, Fig. 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 to 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, which show a 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 that are potentially capable of UV vision, it would be advantageous to possess a colour pattern that also provides 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 females 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 lead to a plausible hypothesis that perhaps males move more than females, and motion would tend to break this sort of disruptive coloration crypsis. There exists some supporting evidence for future testing of this motion–vision-related hypothesis. Indeed females may benefit from displaying a disruptive coloration that is expected to be more effective when the animal is still, as females of *C. fordi* are not typically active in mate choice (Olsson, 2001), and males approach females for mating (Cogger, 1978; Olsson, 2001).

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

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

## CONCLUSION

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

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## AUTHOR CONTRIBUTIONS

J.E.G. contributed to the conception, design and execution of the study, interpretation of the findings, and drafting and revision of the manuscript. D.R. contributed to the conception of the study, interpretation of the findings and revision of the document. A.G.D. contributed to the conception and design of the study, interpretation of the findings, and drafting and revision of the manuscript.

## COMPETING INTERESTS

No competing interests declared.

## FUNDING

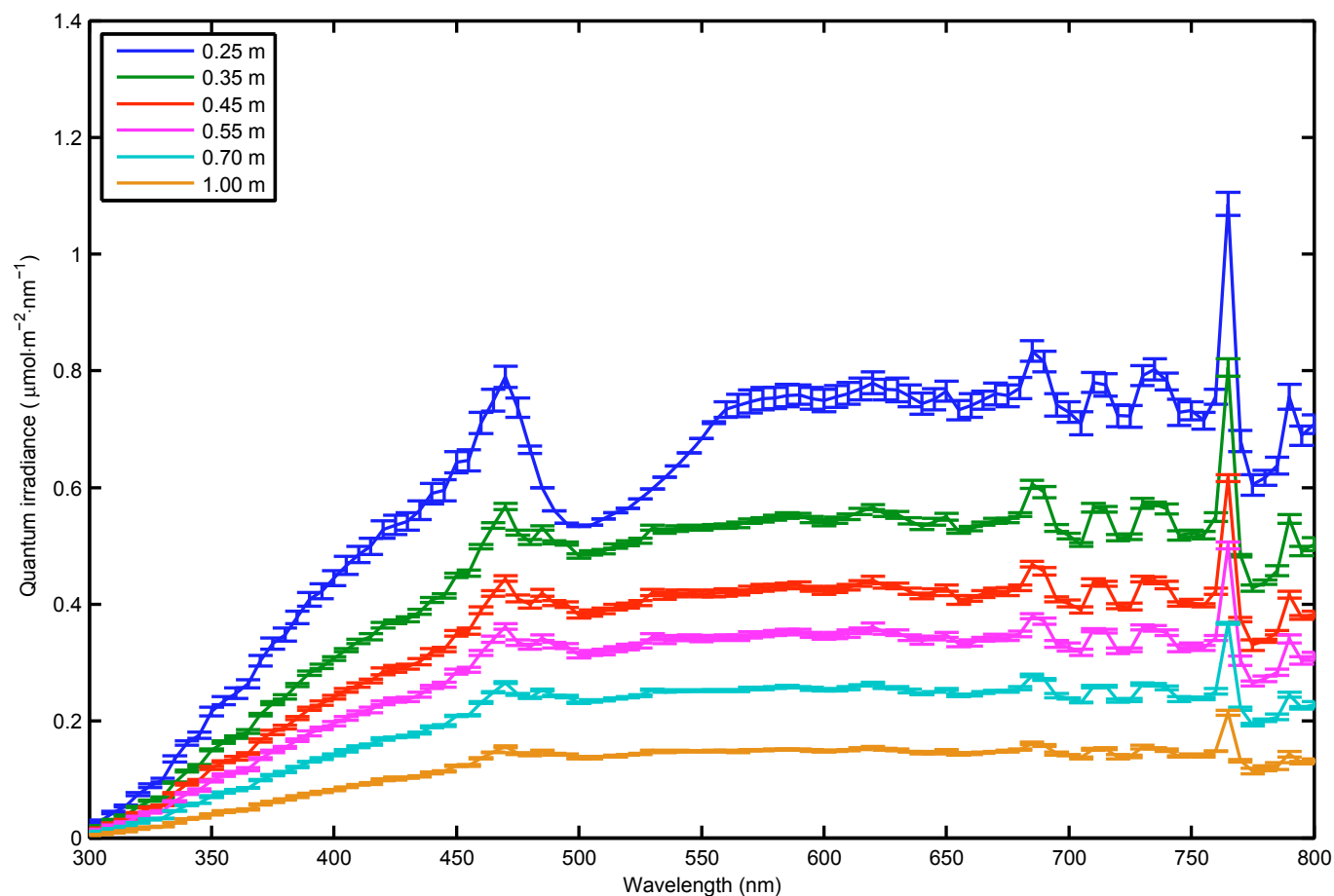
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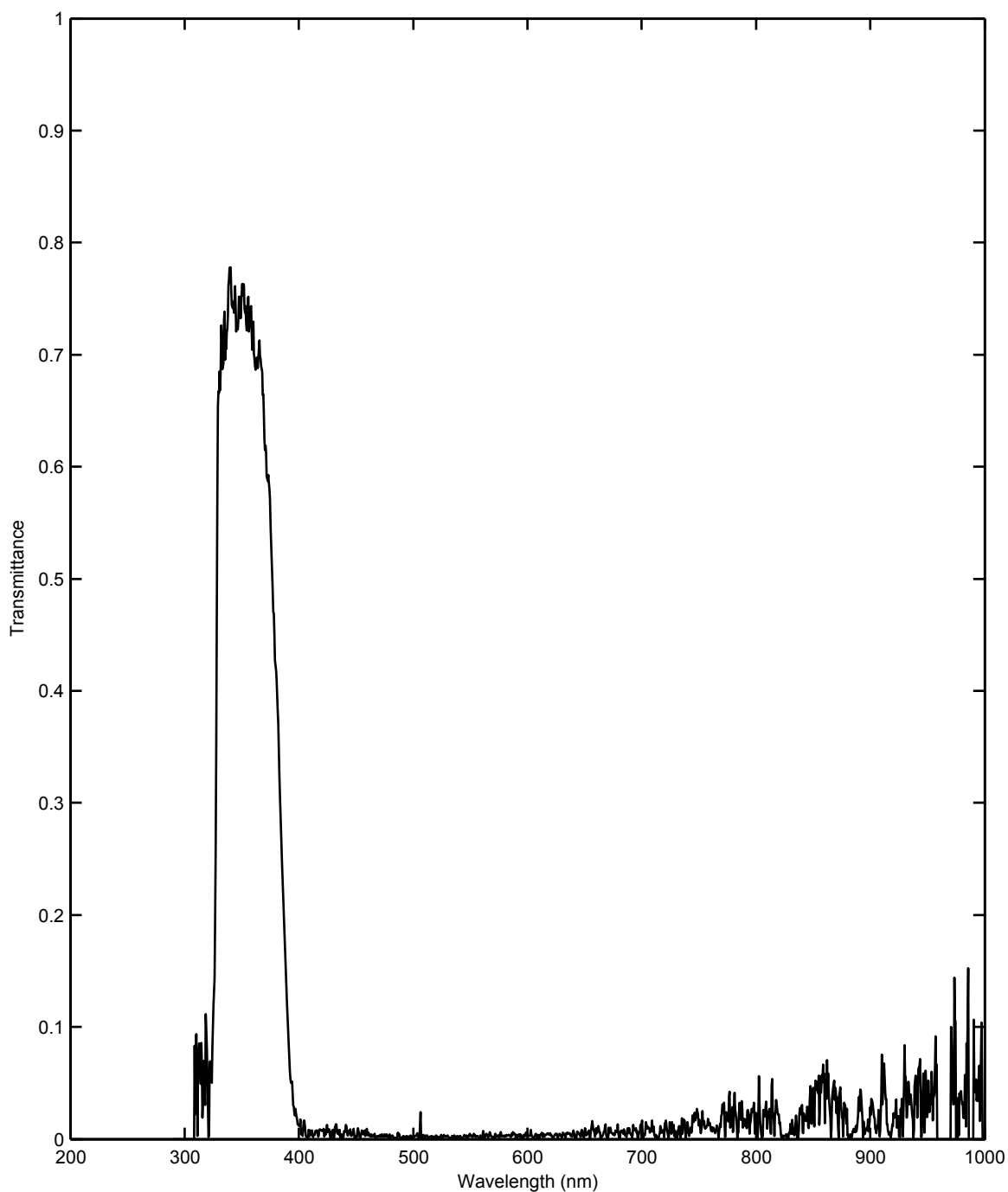
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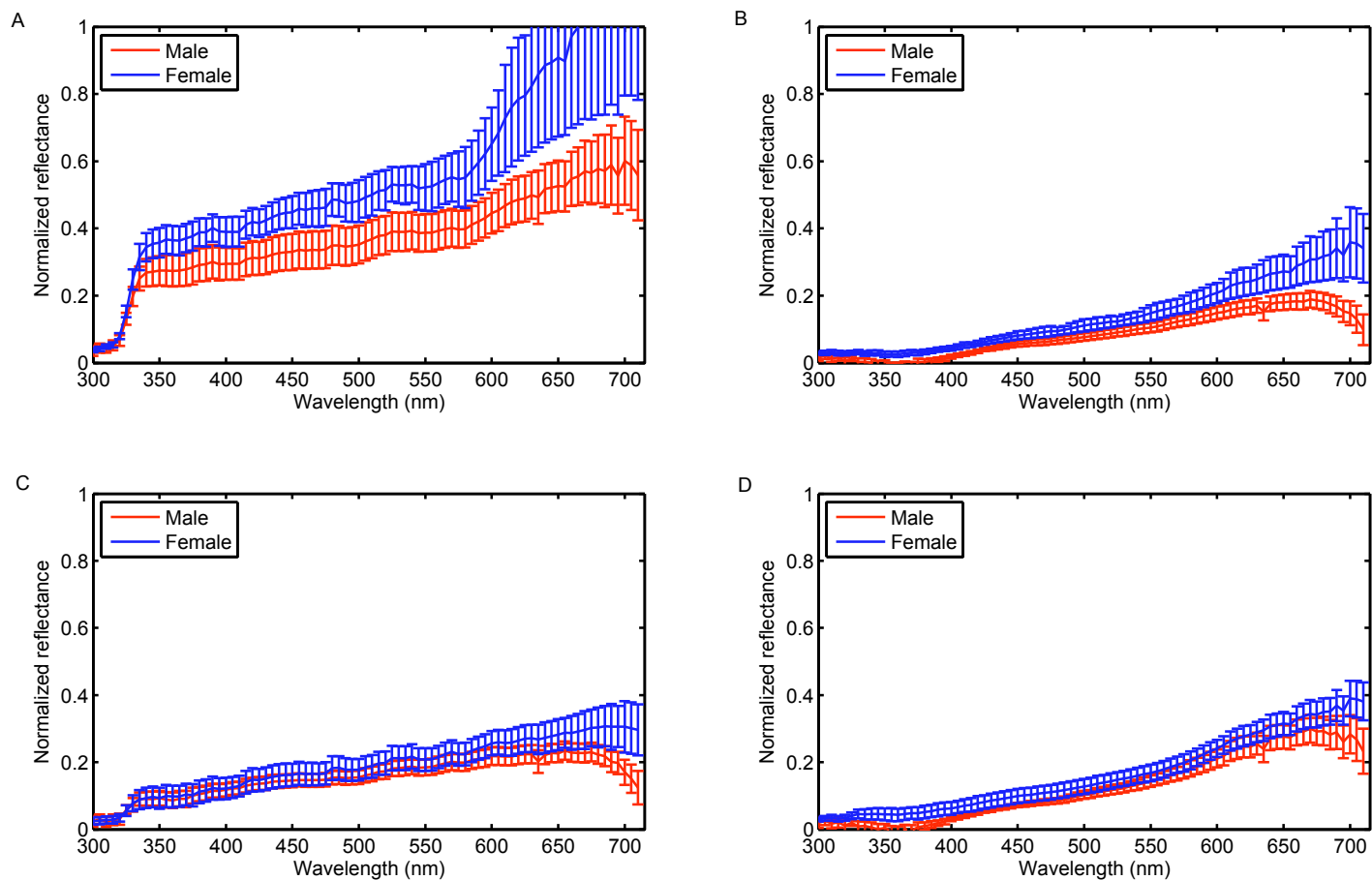


**Fig. S1.** Average spectral power distributions (SPD) of the Nikon SB-14 electronic flash unit employed as a UV-source for image recording. SPDs were recorded at six different distances from the sensor of an NIST traceable ILT-900 spectroradiometer (International Light Technologies) equipped with an irradiance collector. Each SPD consists on the average of five independent measurements. Error bars represent 95% confidence intervals.

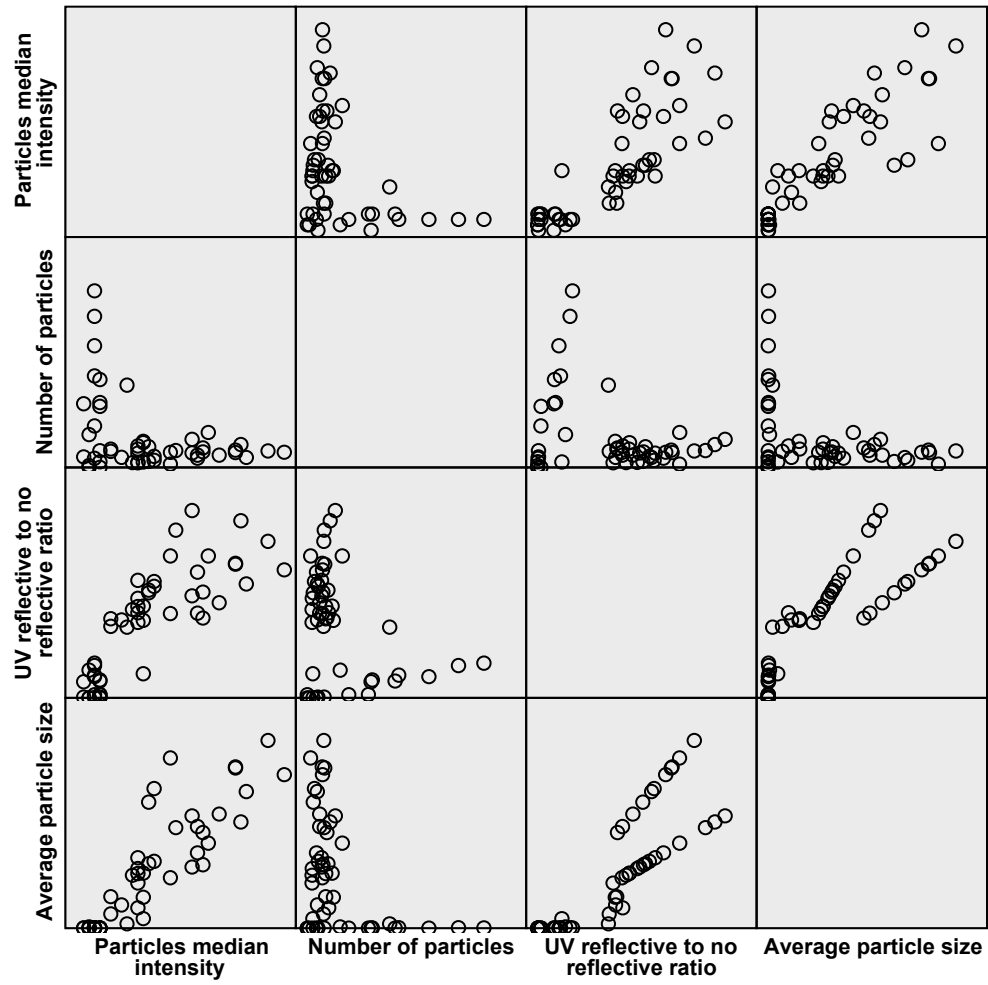


**Fig. S2.** Spectral transmittance of a Baader U-filter (Company Seven), which replaced the hot-mirror filter on the modified Nikon D70s digital camera. Spectral transmittance curve was calculated from spectral irradiance data recorded with a NIST traceable ILT-900 spectroradiometer (International Light Technologies) equipped with an irradiance collector.

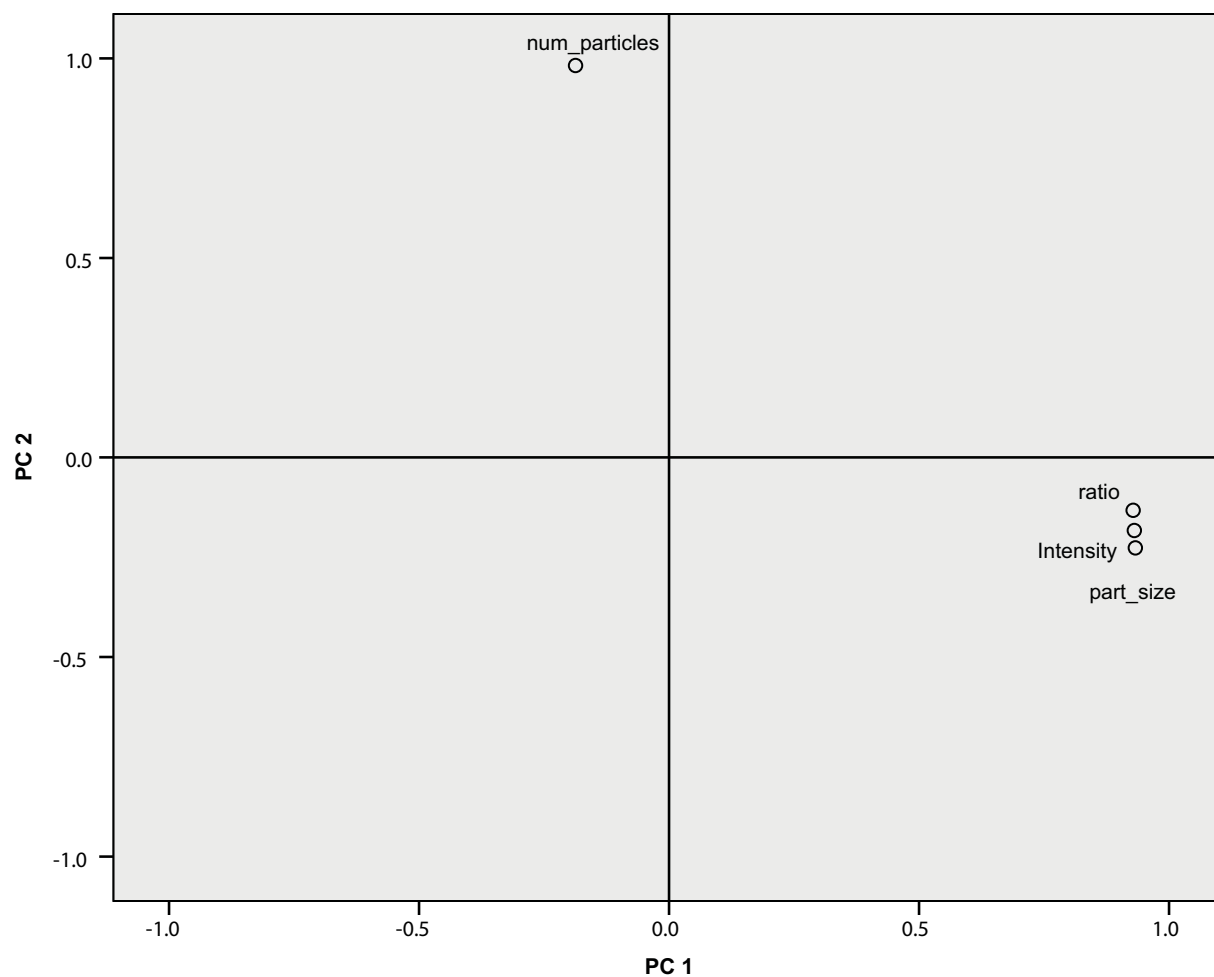




**Fig. S3.** Average reflectance spectra for ( $N=11$ ) males (red line) and ( $N=13$ ) females (blue) of *Ctenophorus fordi* measured at four body locations: (A) cervical ventrolateral region ('neck'), (B) dorsal thoracic surface, (C) dorsolateral surface and (D) anterior dorsal region ('head'). Reflectance readings were recorded with an Ocean Optics USB2000 spectrophotometer equipped with a bifurcated 400  $\mu\text{m}$  UV-visible probe and using a PX-2 xenon lamp (Ocean Optics) as the irradiation source. A Spectralon (LabSphere) was used as a calibration standard. Error bars represent 95% confidence intervals.

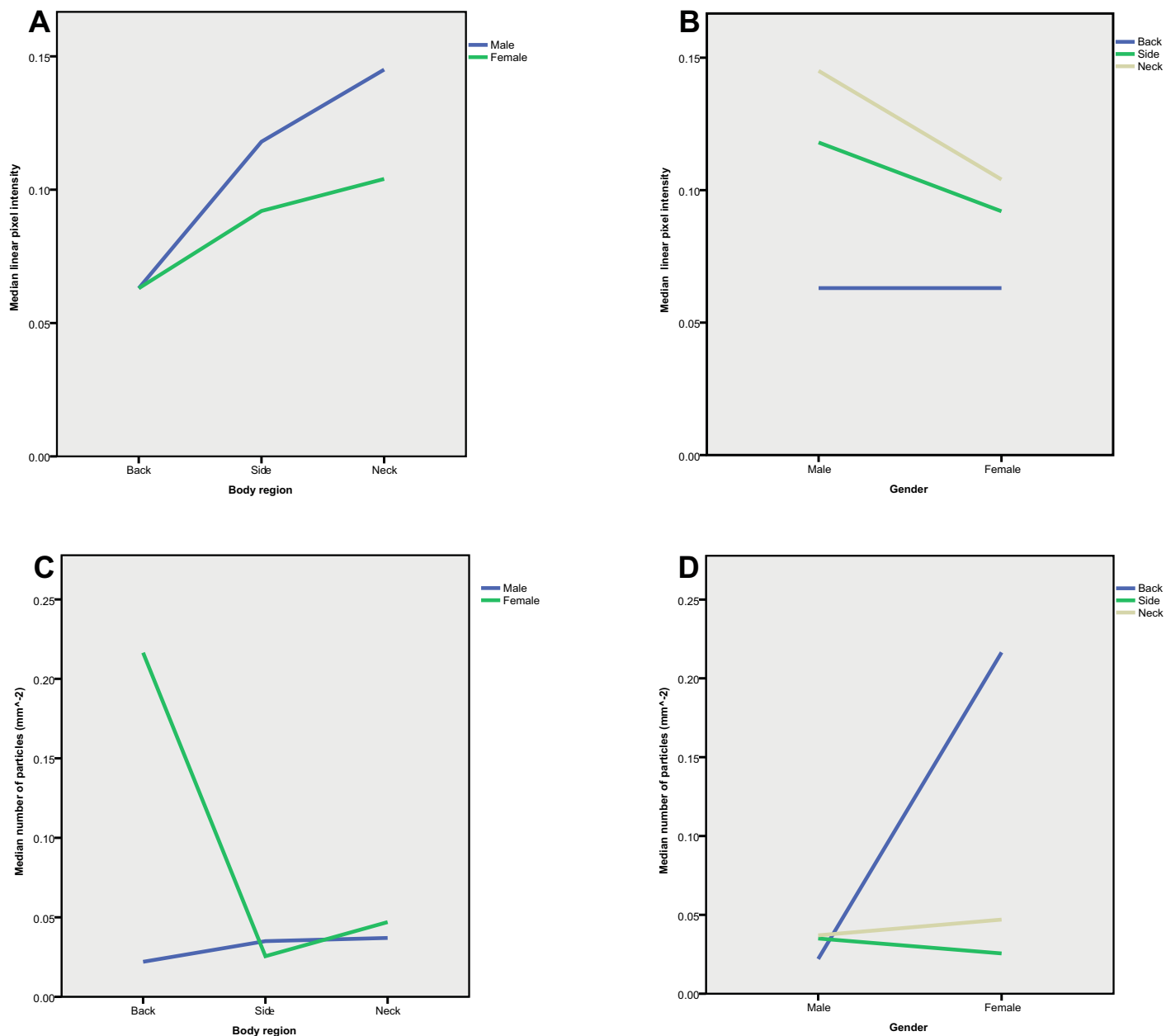


**Fig. S4.** Bivariate scatter plot corresponding to the four variables selected for characterising the spectral and spatial characteristics of the UV-reflective elements present in the colour pattern of *Ctenophorus fordii*.

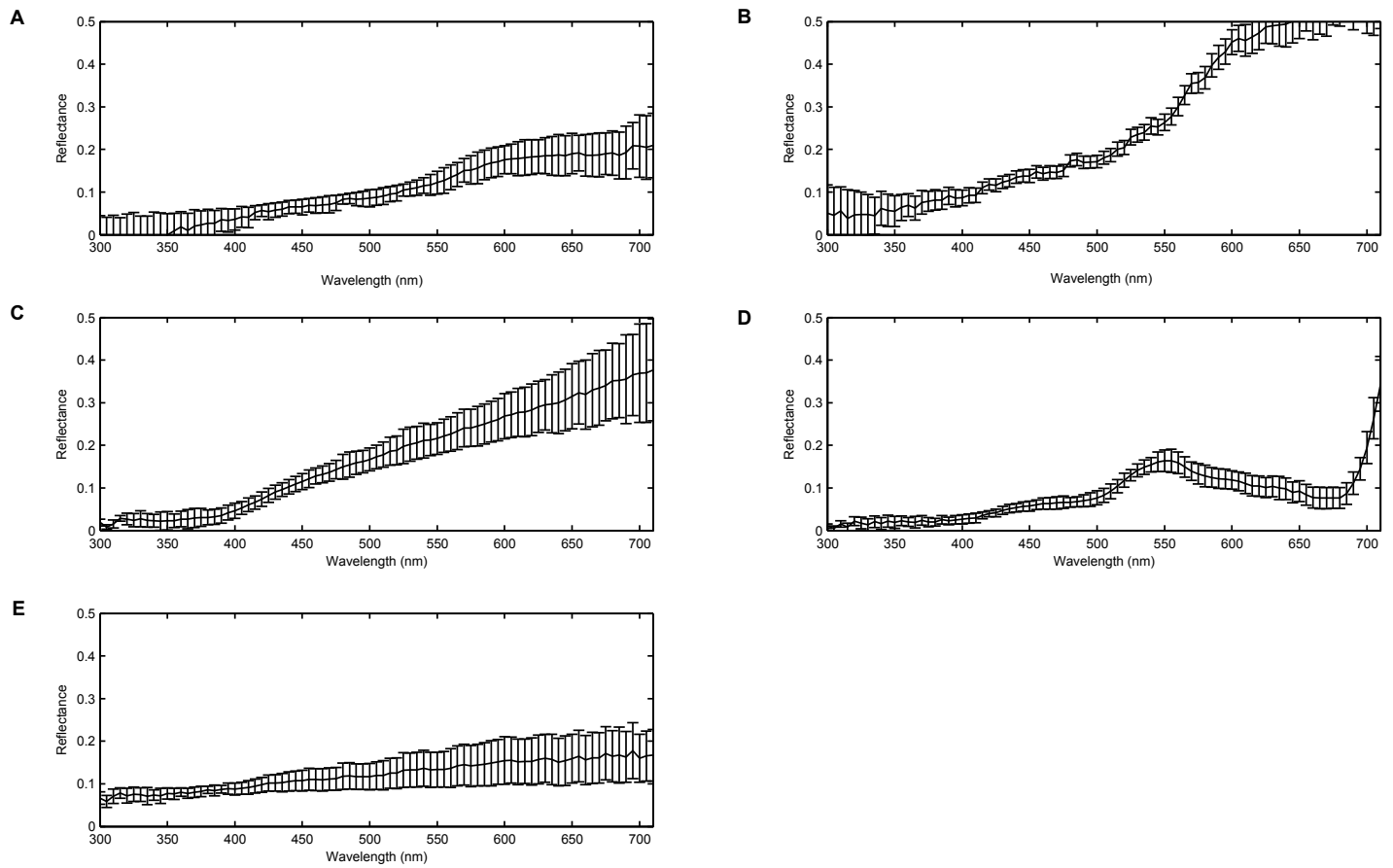


**Fig. S5.** Factor (component) plot showing the loadings for the two components extracted from a PCA analysis with a Varimax factor rotation performed on the four original variables: median intensity (Intensity), number of particles (num\_particles), relative particle size (part\_size) and UV to non-UV ratio (ratio).





**Fig. S6.** Interaction plots of the cell medians for gender (between-subjects factor) and body region (within-subjects) factor. Median values and confidence intervals are those reported in Fig. 3; therefore, errors bars were omitted to facilitate visual interpretation.



**Fig. S7.** Average reflectance spectra from different elements constituting the visual background of *Ctenophorus fordi*. (A) Hardened sand/clay cores, (B) loose sand/clay granules, (C) dry *Triodia* leaves, (D) fresh *Triodia* leaves and (E) plant debris. Reflectance readings were recorded with an Ocean Optics USB2000 spectrophotometer equipped with a bifurcated 400  $\mu\text{m}$  UV-visible probe and using a PX-2 xenon lamp (Ocean Optics) as the irradiation source. A Spectralon (LabSphere) was used as a calibration standard. Error bars represent 95% confidence intervals.