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The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*

Natasha R. LeBas[1][*] **and N. Justin Marshall**[2]

[1]*Department of Zoology, University of Western Australia, Nedlands, WA 6907, Australia*
[2]*Vision Touch and Hearing Research Centre, University of Queensland, Brisbane, QLD 4072, Australia*

Bright coloration and complex visual displays are frequent and well described in many lizard families. Reflectance spectrometry which extends into the ultraviolet (UV) allows measurement of such coloration independent of our visual system. We examined the role of colour in signalling and mate choice in the agamid lizard *Ctenophorus ornatus*. We found that throat reflectance strongly contrasted against the granite background of the lizards' habitat. The throat may act as a signal via the head-bobbing and push-up displays of *C. ornatus*. Dorsal coloration provided camouflage against the granite background, particularly in females. *C. ornatus* was sexually dichromatic for all traits examined including throat UV reflectance which is beyond human visual perception. Female throats were highly variable in spectral reflectance and males preferred females with higher throat chroma between 370 and 400 nm. However, female throat UV chroma is strongly correlated to both throat brightness and chest UV chroma and males may choose females on a combination of these colour variables. There was no evidence that female throat or chest coloration was an indicator of female quality. However, female brightness significantly predicted a female's laying date and, thus, may signal receptivity. One function of visual display in this species appears to be intersexual signalling, resulting in male choice of females.

Keywords: spectral reflectance; sexual dichromatism; UV signalling; male choice; female coloration; *Ctenophorus ornatus*

1. INTRODUCTION

It has been suggested that lizard displays and brightly coloured dewlaps are the functional equivalent of bird song and plumage (West-Eberhard 1983). Many of the lizards in the Iguanidae, Lacertidae and Agamidae families show complex display behaviours and brightly coloured ornaments (Carpenter & Ferguson 1977; Cooper & Greenberg 1992). Australian agamids are no exception with frequent sexual dichromatism (Cooper & Greenberg 1992), territoriality and highly visually orientated behaviour (Geer 1989). The possible functions of lizard displays in communicating information between conspecifics has received considerable attention (Carpenter & Ferguson 1977) and the colours which are frequently emphasized during the display are increasingly being investigated (Fleishman *et al*. 1993). However, the role of lizard displays and coloration in sexual selection has received little attention in comparison to that devoted to bird plumage and display (but see Olsson & Madsen 1998).

Investigating the role of colour in sexual selection is complicated by the difficulties in making an accurate assessment of the signal independent of our visual system (Bennett *et al*. 1994). Recent studies in birds have illustrated the inaccuracies in assuming our visual system is equivalent to that of the species in question (Andersson *et al*. 1998; Hunt *et al*. 1998). For example, many bird species are sensitive to ultraviolet (UV) light (Bennett et al. 1994) and these short wavelengths appear to have a role in sexual signalling (Bennett *et al*. 1997; Hunt *et al*. 1998). As far as we are aware, no agamid retinas have been examined for UV photoreceptors. However, all species which have been investigated in the closely related Iguanids have UV photoreceptors (Fleishman *et al*. 1993). UV-sensitive photoreceptors have also frequently been found in the Gekkonidae (Loew 1994; Ellingson *et al*. 1995; Loew *et al*. 1996) and in a snake (Sillman *et al*. 1997). The wavelength of peak absorption in these UV photoreceptors only ranges across 5 nm in 11 species of lizards (Fleishman *et al*. 1993; Loew 1994; Ellingson *et al*. 1995; Loew *et al*. 1996). Behavioural tests have often found lizards capable of colour discrimination (Cooper & Greenberg 1992). In the absence of species-specific information the most parsimonious assumption for agamids appears to be one of sensitivity to the short (UV) and visible wavelengths.

Ctenophorus ornatus is an agamid lizard which lives exclusively on granite outcrops in southern Western Australia. Males maintain territories exclusive of other males, but typically encompassing a number of female territories (N. R. LeBas, unpublished data). Territories are established at the beginning of spring after lizards emerge from winter hibernation and mating occurs over late spring and early summer (N. R. LeBas, unpublished data). Visual displays such as head bobbing, circumduction and push-ups are common throughout the breeding season and are similar to those in other *Ctenophorus* species (Bradshaw 1965; Carpenter *et al*. 1970) (terminology after Carpenter & Ferguson 1977). The push-up and, to a lesser extent, the head-bobbing displays reveal the chest and throat regions which are usually hidden. *C. ornatus* has a well-developed visual system (Beazley *et al*. 1997) and a retina with sufficient complexity to permit a diet of flying insects. In the exposed, full-sunlight environment which *C. ornatus* inhabits conspecific communication is likely to be by visual cues (Endler 1992; Fleishman 1992).

[*]Author for correspondence (nlebas@cyllene.uwa.edu.au).

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In this study we examined the role of colour as a signal in *C. ornatus*. As the effectiveness of a signal is dependent on the background environment (Endler & Thery 1996), we examined the contrast of the colour signal to the granite background. The camouflage provided by dermal patterning was also investigated; selection favouring contrast for conspecific signalling may be balanced against selection for camouflage in order to avoid predation (Endler & Thery 1996). In *C. ornatus* behavioural displays emphasize the throat and chest areas and we hypothesized that these areas could play a role in signalling sex, female receptivity or mate quality. We tested the hypothesis that the throat region in females, which is emphasized during displays, was subject to male mate choice.

2. METHODS

Lizards were collected from granite outcrops on farmland near Tutanning Nature Reserve, 200 km south-east of Perth, Western Australia. Collection occurred in late spring after lizards had emerged from winter dormancy but prior to oviposition. All females collected had developing follicles or eggs and all males had breeding coloration. The lizards were housed in a controlled temperature room, males in individual cages and females in groups of eight. Prior to the mate choice trials, the lizards were maintained at 20 °C during the day and 13 °C at night in order to slow down female egg development and moulting before the trials. During and following the mate choice trials, the photoperiod and temperature were equivalent to the late spring–summer breeding conditions of a 15 L:9 D cycle and 28 °C during the day and 19 °C at night. Heat lamps were available for basking. Their diet comprised primarily of mealworms dusted in multivitamin and calcium powder and supplementary cockroaches, termites and crickets.

(a) *Reflectance spectrophotometry*

The spectral reflectance of the lizards' skin coloration was measured with a custom-built spectroradiometer ('Sub-Spec', Andor Technology Oriel, Belfast, UK). The area was illuminated with a Xenon flash at 45° to the surface and reflectance measured at 90° to the surface. The measurements were expressed relative to a 99% white barium sulphate standard. Recordings were taken from a 2 mm area and at 1 nm intervals across a spectrum of 300–800 nm wavelength. As the lens of *C. ornatus* filters virtually all light less than 330 nm (see below), analysis was confined to 330–700 nm. The lizards were positioned on black velvet for all measurements. Six regions were measured: the chest, throat, flanks, abdomen, dorsal base colour (two regions for females) and dorsal stripe (figure 1). The chest and throat were measured three times for 24 lizards of each sex and all other regions three times for ten animals of each sex. In total, 990 reflectance spectra were recorded.

The spectra were analysed using principal components (PCs) analysis (Cuthill *et al*. 1999). The data were stripped to 2 nm measurement intervals due to computing limitations. The PCs were based directly on raw data. As is commonly found with reflectance spectra the first PC (PC1) was always nearly perfectly correlated with the mean reflectance, i.e. brightness (Cuthill *et al*. 1999). The remaining PCs (PC2–PC4) describe differences in the shape of the spectra and, hence, potential variation in hue and chroma (Endler 1990; Cuthill *et al*. 1999). Sexual dichromatism was examined using univariate repeated-measures analysis of variance on the PC scores. To examine the
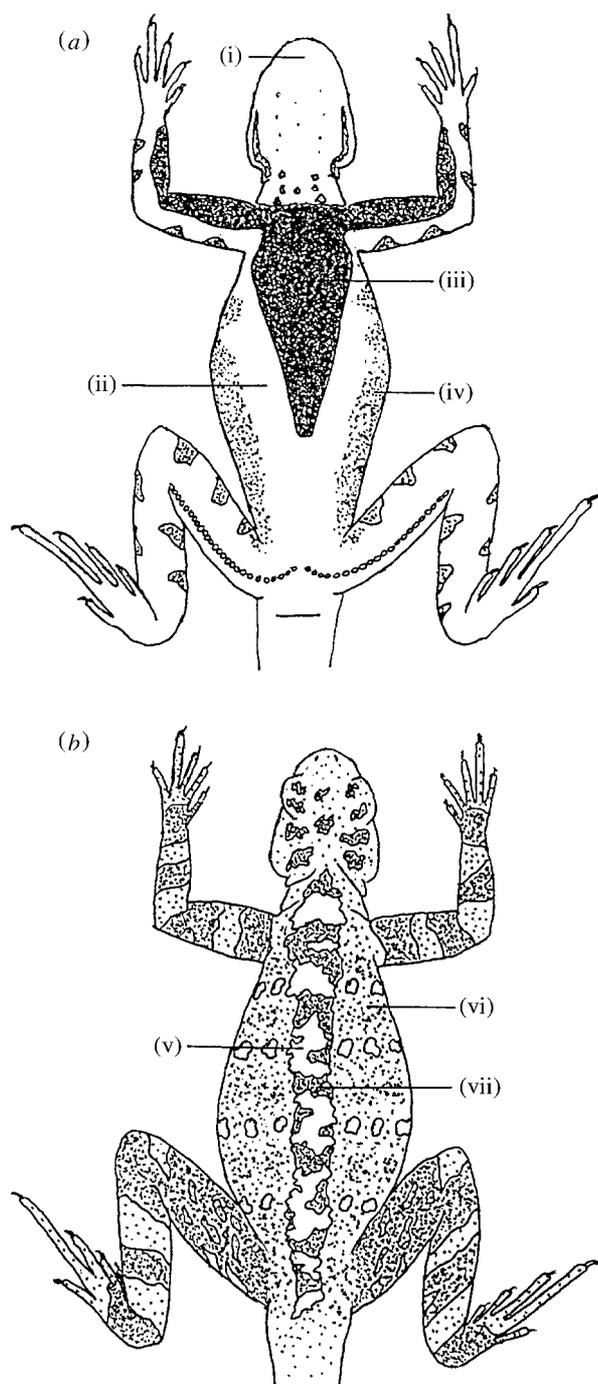

Figure 1. Line diagram of (*a*) the ventral surface of male *C. ornatus* and (*b*) the dorsal surface of female *C. ornatus*. The areas indicated were measured with reflectance spectrophotometry and are (i) the throat, (ii) abdomen, (iii) chest, (iv) flanks, (v) dorsal (stripe and spotting), (vi) dorsal (dark base colour) and (vii) second dorsal (dark colour) in females.

contrast of the throat signal (R_s) against the background of granite (R_g) the signal to background reflectance ratio was calculated ($(R_s - R_g)/R_g$) (Endler & Thery 1996; Andersson *et al*. 1998). The pale and dark granite reflectance spectra were averaged to obtain a single background reflectance value (R_g).

The percentage of light transmitted through the lens and cornea was measured with a spectroradiometer according to the methods of Marshall (1996). Four lenses and corneas were measured from two lizards.
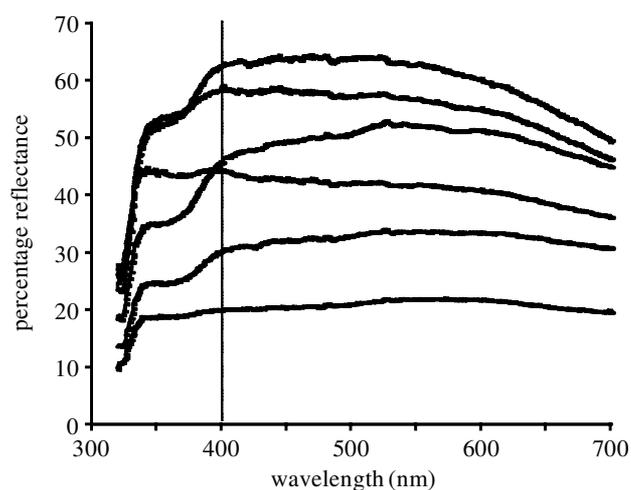
Figure 2. Variation in the female throat spectral reflectance. Each curve represents the reflectance spectra of a different female. The dotted line indicates the lower end of human visual sensitivity.

(b) *Mate choice trials*

Mate choice trials were conducted to determine whether the large amount of variation in female throat reflectance (see below; figure 2) was subject to male mate choice. To summarize the variation in spectral shape in the UV region the percentage reflectance at 370 nm was subtracted from that at 400 nm to obtain a measure of the UV chroma for each female. Females were ranked for their UV chroma score and paired to give high and low UV chroma groups. Each female was used twice, but in a different pairing. Males were used only once. The trials were conducted eight days after the reflectance spectrophotometry. The mate choice trials were conducted using four identical arenas (figure 3). The arenas consisted of a separate compartment for each female (no visual or olfactory contact) and an area in front of both females in which the male could move freely. A partition partially divided the male's compartment so that in choosing the area in front of one female he could not view the other. A line of tape 1.2 m from the edge of the female's cages and in line with the end of the partition indicated the area in which a male was considered to have made a choice of that female. All lizards had identical tiles to sit on and hide under. These tiles were positioned so that there was no difference between each female's tile position in relation to the male and so that males had tiles placed identically in front of each female. The arenas were scrubbed with detergent between trials to remove any chemical or faecal secretions. The arenas were illuminated with True-Lites (Duro-test) which provide full spectrum lighting closely matched to sunlight in the UV region. The females were separated from the males by acrylic beauty glass (Hsinhwa, Kaohsiung, Taiwan) which transmitted long wavelength UV light and had a 100% cut-off at 300 nm.

The lizards were allowed to acclimatize to the arenas overnight and for 1 h the following day. Male position was recorded over two days using a time-lapse video camera which recorded the images directly to a computer. A frame was taken every 20 min resulting in 40 frames a day for a total of 80 frames per trial. This method minimized disturbance to the lizards as the images were downloaded after the lights had gone off at the end of the first day and this was the only time a researcher was present during the trial period. The males were scored as present in either the left or right female section or the middle neutral section for each frame. Trials were discarded if a male
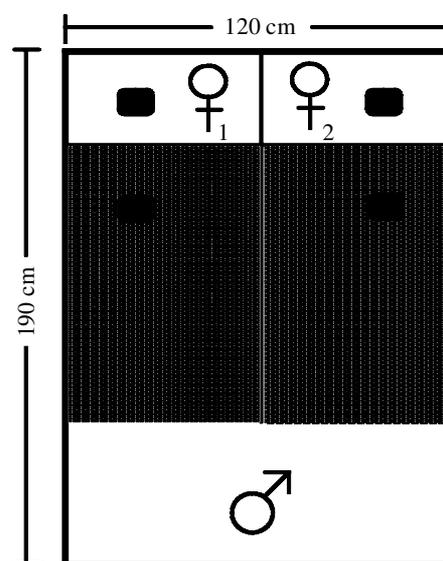

Figure 3. Test arena for the male mate choice trials. The arena is viewed from above and all distances are in centimetres. Dark lines indicate solid walls and the dotted line a clear partition (see the text for details) which separated the females and male throughout the trials. The dark rectangles are the tiles which the lizards could rest on or hide underneath. The shaded areas in front of the female compartments indicate the regions in which a male was considered to have made a choice of the corresponding female.

lizard was not scored at least once in each female's section or if they spent greater than 50% of their time (>40 frames) in the neutral section. Four trials were discarded.

(c) *Female reproductive condition*

The females used in the mate choice trials all had palpable eggs or follicles. We hypothesized that the large variation in female throat spectral reflectance (see below; figure 2) could indicate either reproductive state or female quality. Reproductive state was measured by the time taken for the females to lay and female quality was measured by egg number and weight. The females were separated to a laying cage when they had oviductal eggs and the date of laying and number (one to five) and weight of eggs recorded. Unusually, some females retained one or more eggs and laid these up to eight days later. In these cases the date of laying was recorded as the day on which the first egg was laid. As the wet weight of retained eggs could have been inflated due to the increased time in the oviduct, dry weights were used. Initially we had planned to measure female quality by offspring size and viability; however, only five out of the 50 eggs laid were fertilized. As the fertilized eggs were amongst the first to be laid the unfertilized eggs were initially discarded and, hence, the sample sizes for the dry egg weight analyses are smaller than those for the egg number analyses (nine and 16, respectively).

3. RESULTS

(a) *Sexual dichromatism*

Three measures from each region of skin were used in a repeated-measures analysis of variance with sex as a factor. All measures were highly repeatable (mean repeatability $= 0.80$, range $= 0.65–0.91$ and p-range $= 0.002–0.0001$). The spectral reflectance patterns differed with sex in either brightness or spectral shape for all
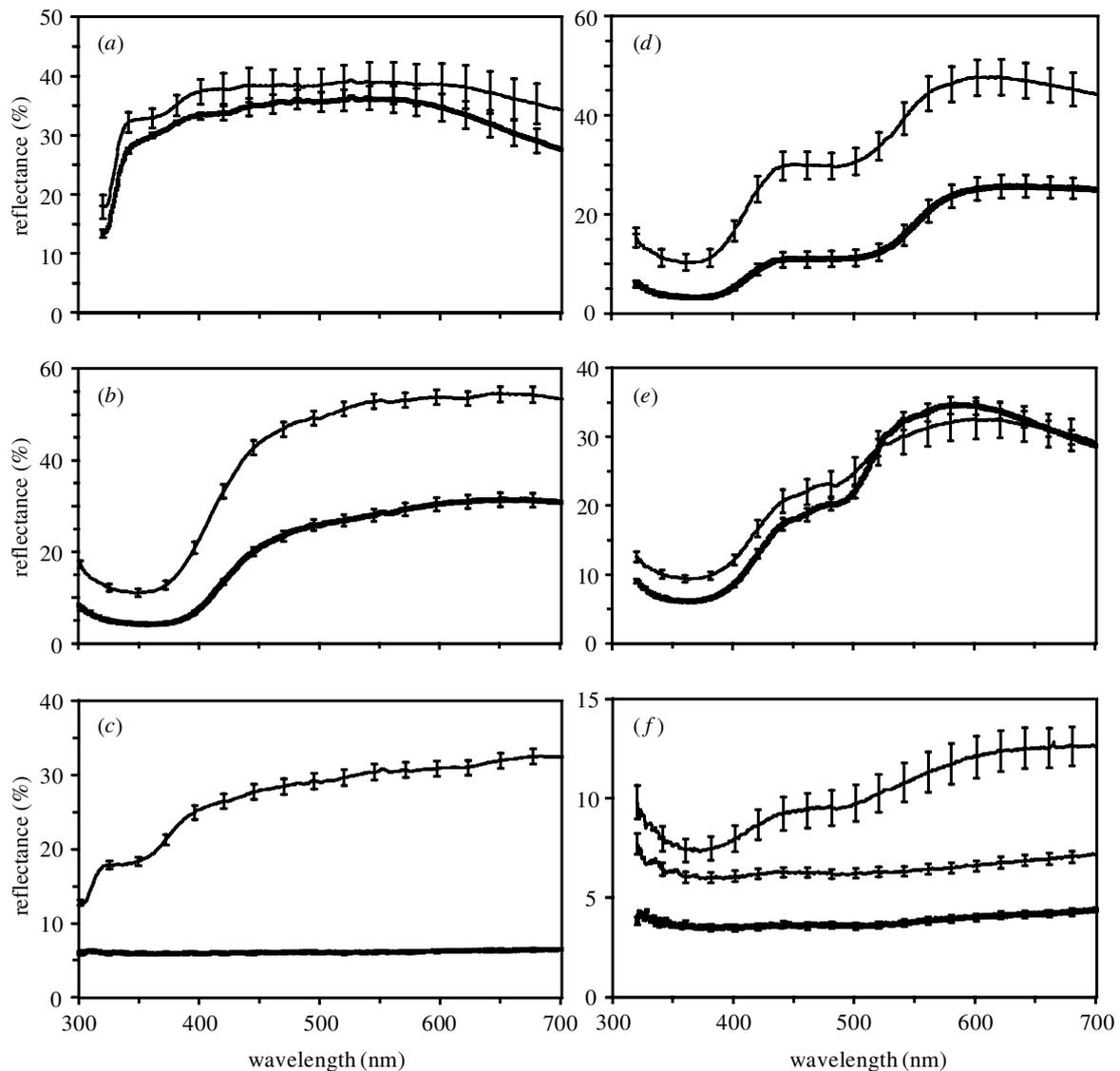
Figure 4. The reflectance spectra (± s.e.) of *C. ornatus* body regions. (*a*) Throat, (*b*) abdomen, (*c*) chest, (*d*) flanks, (*e*) dorsal (stripe) and (*f*) dorsal (dark) regions. The spectra in regions (*a,c,d*) are the average from 24 lizards of each sex which in turn were averaged from three repeated measures for each lizard. For regions (*b*) and (*f*) $n = 10$ and for (*e*) $n = 9$ and 8 for males and females, respectively. (*f*) Females have two dorsal dark colours: a 'brown' base colour and 'black' spots. The females are denoted by a thin line and the males by a thick line. Standard error bars have been stripped and are only plotted at 10 nm intervals for clarity.

regions measured, including those which appeared mono-morphic to humans (figure 4 and table 1). The spectral shape differences in the throat were most marked in the UV region (table 1) where the female throats dropped off sharply at 400 nm before plateauing to 350 nm, whereas the male throats showed a steadily declining curve in the UV region (figure 4*a*). The female throat reflectance was also maintained in the red end of the spectrum, whereas the male throat reflectance declined after 600 nm (figure 4*a*). The females had brighter flanks, abdomens and dorsal dark colour than the males, but did not differ from the males in spectral shape (figure 3*b*,*d*,*f* and table 1). The dorsal stripe differed in spectral shape between the sexes (table 1) with greater reflectance in the short wavelengths for females and the long wavelengths for males (figure 4*e*). The chest spectra were not analysed using PC analysis scores as this region clearly varied across the whole spectrum (figure 4*c*).

(b) *Colour contrast and signalling*

The spectral reflectance of the granite and female dorsal surface revealed a close match between the mottled patterns of the female and those of the granite (figure 5*a*). The female throat reflectance spectra differed greatly from that of granite particularly in the UV region (figure 5*a*). The contrast of the throat and dorsal back pattern against the granite highlights the strength of the throat as a potential signal and the extent of the camouflage provided by the dorsal pattern of females (figure 5*b*) and, to a lesser extent, males (figure 5*c*). The wavelength of maximum contrast of the throat against the granite did not differ between males (369 ± 4.4 nm) and females (361 ± 4.8 nm) (unpaired $t_{44} = 1.176$ and $p = 0.25$). For the sexes combined the average wavelength of peak contrast was 365 ± 3.3 nm.

Female chest reflectance was similar to the throat in the decline at the beginning of the UV region before

Table 1. *Sexual dichromatism in the reflectance spectra of* C. ornatus

(PC1–PC4, which correspond to the brightness and spectral shape of the reflectance spectra, were analysed for five colour traits in a univariate repeated-measures ANOVA with sex as a factor. The values listed are F-ratios. All tests were done separately and are significant after sequential Bonferroni adjustment for the number of tests.)

		brightness	spectral shape			
region	d.f.	PC1	PC2	PC3	PC4	difference
throat	1,46	0.002	0.005	3.923	25.194*	females steeper curve in the UV and flatter curve in the red region
throat: UV only	1,46	1.834	21.481*	0.000	18.756*	females steeper curve in the UV region
flanks	1,46	59.821*	0.883	1.452	0.205	females brighter
abdomen	1,18	30.128*	0.001	2.696	0.071	females brighter
dorsal: stripe	1,15	0.485	59.026*	0.513	0.085	males more reflective in long wave, females more in short wave
dorsal: dark	1,18	27.561*	0.058	0.066	0.621	females brighter

* Significant sex difference $p = 0.0001$.

levelling off (figure 5a,c). Females which had high throat UV chroma also had a low PC2 score for the chest (Pearson's correlation $n = 22$, $r = -0.64$ and $p = 0.001$). Inspection of the eigenvectors for the chest PCs revealed that low PC2 scores were indicative of low UV reflectance relative to the visible reflectance, i.e. high UV chroma. The similarity between the throat and chest UV chroma may indicate that these areas are part of the same signal; however, there were significant differences between these areas in their brightness (chest mean ± s.e. $= -4.54 \pm 2.9$ and throat mean ± s.e. $= 4.96 \pm 3.04$) (unpaired t-test $t_{44} = -2.25$ and $p = 0.03$) and spectral shape (combined chest and throat PC2 chest mean ± s.e. $= -2.05 \pm 0.41$ and throat mean s.e. $= 2.24 \pm 0.43$) (unpaired t-test $t_{44} = -7.29$ and $p = 0.0001$). Inspection of the eigenvectors for the combined PC2 revealed that the significant difference between these regions was due to the throat reflecting more in the UV region and the chest reflecting more in the visible region.

The lens and cornea transmitted wavelengths down to 327.5 ± 1.44 nm with a 50% cut-off at 343.5 ± 0.87 nm.

(c) *Male choice and female reproductive status*

Female throat reflectance varied considerably between individuals in both spectral shape and brightness (figure 2). The coefficients of variation for the female throat UV chroma and brightness were very high (UV chroma = 92.7 and brightness = 35.8).

The males spent significantly more time (number of frames) in the sections closest to the females than in the neutral section (one group t-test on arcsine-transformed data with expected value arcsine (66.66%), $t = 3.48$, d.f. = 21 and $p = 0.002$). The males spent more time with females with high UV chroma (mean s.e. $= 43.6 \pm 5.08$ frames) than with females with low UV chroma (mean time ± s.e. $= 24.1 \pm 4.44$ frames) (Wilcoxon signed-rank test, $n = 18$, $\mathcal{Z} = -1.96$ and $p = 0.05$). Post-hoc tests revealed that the males also spent more time with females with high chest UV chroma (mean ± s.e. $= 46.5 \pm 4.71$ frames) than with females with low chest UV chroma (mean s.e. $= 21.11 \pm 3.94$ frames) (Wilcoxon signed-rank test, $n = 18$, $\mathcal{Z} = -2.57$ and $p = 0.01$).

Females with high throat UV chroma showed a tendency to lay earlier than females with low throat UV

chroma (Spearman's rank correlation, $n = 13$, $r = -0.52$ and $p = 0.07$). However, PC1, which is equivalent to female brightness, significantly predicted a female's days to laying (least-squares regression, $F_{12} = 9.5$, $r^2 = 0.47$ and $p = 0.01$). The UV chroma measure incorporates the variation in the reflectance brightness as well as the spectral shape, which is indicated by the significant correlation between these two measures (Pearson's correlation, $n = 22$, $r = 0.81$ and $p = 0.001$). In contrast, the second PC for the UV region (UV-PC2) summarizes the variation in the reflectance curve with the variation due to brightness removed. There was no significant relationship between UV-PC2 and days to laying (least-squares regression $F_{12} = 1.3$, $r^2 = 0.11$ and $p = 0.28$). This lack of relationship indicates that the trend for females with high UV chroma to lay earlier is most likely due to the brightness component of this measure. The female chest UV chroma was not related to days to laying (Spearman's rank correlation, $n = 13$, $r = 0.11$ and $p = 0.7$). It is the brightness of the female's throat then which indicated their time to laying, with brighter females laying earlier than dull females.

A post-hoc test on male preference for brighter females revealed no significant difference in the time males spent with the bright (mean ± s.e. $= 42.3 \pm 5.22$ frames) and dull females (mean time ± s.e. $= 25.3 \pm 4.57$ frames) (Wilcoxon signed-rank test, $n = 18$, $\mathcal{Z} = -1.70$ and $p = 0.09$).

There was no relationship between egg number and any of the following variables: throat UV chroma (Spearman's rank correlation, $n = 16$, $r = -0.17$ and $p = 0.86$), throat brightness ($n = 16$, $r = 0.10$ and $p = 0.71$) or chest UV chroma ($n = 16$, $r = 0.02$ and $p = 0.93$). Neither was there a relationship between the average dry egg weight and the following variables: throat UV chroma ($n = 9$, $r = -0.45$ and $p = 0.2$), throat brightness ($n = 9$, $r = 0.13$ and $p = 0.71$) or chest UV chroma ($n = 9$, $r = 0.47$ and $p = 0.19$). The low sample sizes for the egg weight tests prevent a conclusive rejection of the null hypotheses.

4. DISCUSSION

Many functions have been proposed for lizard displays, such as conspecific communication (Fleishman 1992), species and sex recognition (Cooper & Greenberg 1992)
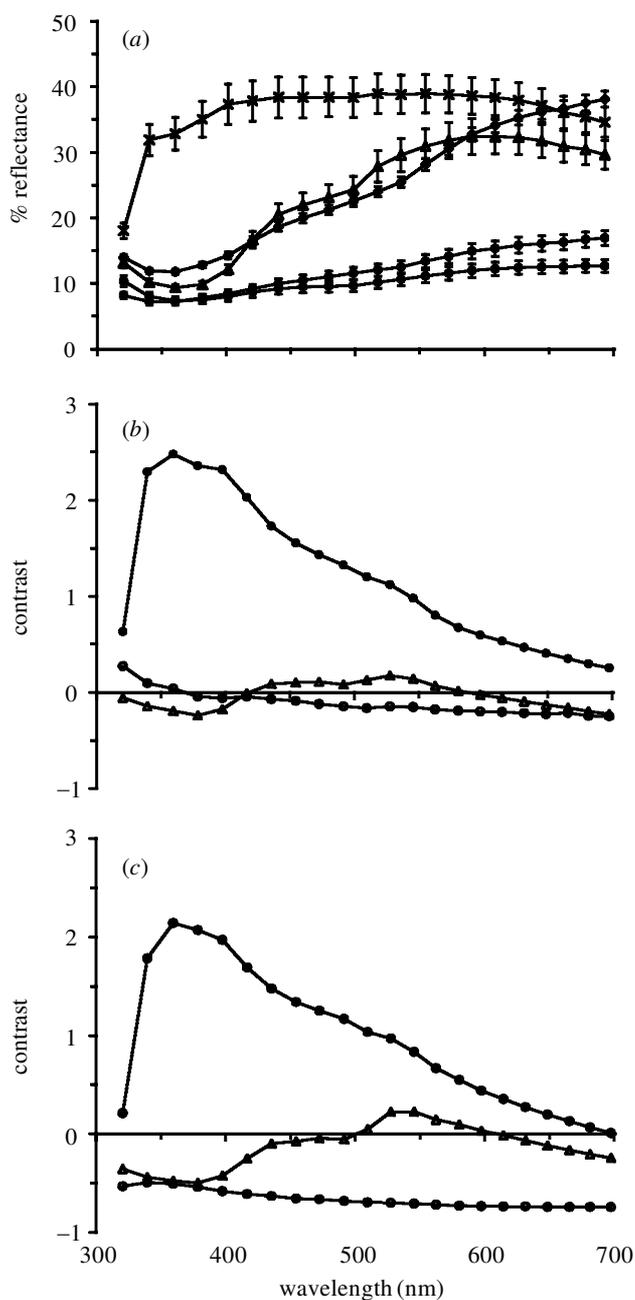
Figure 5. The reflectance spectra and their contrasts against a granite background in *C. ornatus*. (*a*) Reflectance spectra (± s.e.) of the female throat (crosses), dark dorsal colour (filled circles) and light dorsal stripe (open triangles) and reflectance spectra of the granite background, light (filled diamonds) and dark sections (open circles). (*b*) Contrast of the female throat (filled circles) and light (open triangles) and dark (open circles) dorsal patterns against the granite background (for the throat contrast an average of the light and dark granite). The contrast is a measure of the signal to background ratio (see § 2(a)). (*c*) Contrast of male throat (filled circles) and light (open triangles) and dark (open circles) dorsal patterns against the granite background.

and predator–prey signalling (Leal 1999). This study provides evidence that the areas of colour associated with the displayed regions in *C. ornatus* are effective visual signals to conspecifics. In female *C. ornatus* the signal appears to convey information on reproductive state which may explain male choice of females.

(a) *Visual signalling*

The reflectance spectrophotometry revealed evidence for dorsal camouflage and ventral signalling in *C. ornatus*. The mottled appearance of the female dorsal pattern is well camouflaged against the granite surface as was evidenced by the lack of contrast between the two. *C. ornatus* is attacked by birds of prey (N. R. LeBas, personal observation) whose likely UV vision corresponds to the dorsal camouflage of *C. ornatus* extending into the UV region. The homogeneous granite outcrops and high light environment of the habitat of *C. ornatus* means that signals and camouflage are set against a simple background and do not have to be interpreted across a range of light environments.

The spectral reflectance of male and female throats could be a signal for conspecific communication. Throat reflectance, unlike that of the other 'white' regions in *C. ornatus*, continued into the UV region at levels comparable to the rest of the spectrum. Both the 'white' abdomen and dorsal stripe dropped off in reflectance after 430 nm. The drop-off in reflectance in the UV region for the dorsal stripe is consistent with the corresponding decline for the pale patches of the granite. The difference in UV reflectance between the abdomen and throat suggests that high UV reflectance is not typical of all ventral white colours in *C. ornatus*. It is unlikely that the difference in UV reflectance between these ventral regions is due to selection on the abdomen as this area is not visible to conspecifics or predators. Moreover, throat coloration is displayed during the frequent head-bobbing displays of *C. ornatus* (N. R. LeBas, personal observation). Rapid head elevations would generate throat flashes which contrast strongly against the background. Research on sticklebacks has found that preferences for a signal were more likely to be a function of its efficiency at generating a visual contrast than a feature of its intrinsic spectral characteristics (McDonald *et al.* 1995). It is likely that the high UV reflectance in the throat is a consequence of selection for a signal with high contrast against a granite background.

The peak contrast of the throat against the granite is in the UV region at precisely the wavelength of peak absorption in the Iguanid UV photoreceptor (Fleishman *et al.* 1993). The wavelength of peak absorption for UV photoreceptors found within the lizards (11 species) only ranges across 5 nm (Fleishman *et al.* 1993; Loew 1994; Ellingson *et al.* 1995; Loew *et al.* 1996). The conservative nature of this photoreceptor in the lizards suggests that a UV photoreceptor in *C. ornatus* is likely to be in this range and will be stimulated by the wavelength of peak contrast of the throat. The transmission by the lens of these UV wavelengths further supports such a photoreceptor.

(b) *Sexual dichromatism*

The spectral reflectance patterns differed with sex in either brightness or spectral shape for all regions measured, including those monomorphic to humans. However, the biological significance of these differences or whether they are perceived cannot be discerned by spectral reflectance alone (Cuthill *et al.* 1999). The brighter dorsal coloration in females results in a better match with the granite background, as does the spectral shape difference in the dorsal white stripe. The significance of the brighter flanks and abdomen in

females is unknown. The difference between the sexes in the shape of the curve for the throat in the UV region is potentially a difference in hue and chroma. If *C. ornatus* has UV and blue photoreceptors similar to those in the Iguanids (Fleishman *et al.* 1993) this variation between the sexes could theoretically also be perceived.

To the human visual system, male *C. ornatus* have a black chest patch and females typically have no patch distinguishable from the white abdomen. The reflectance spectrophotometry revealed that female *C. ornatus* have a chest patch; it is duller than the abdomen in the visible region and brighter in the UV region. This is in keeping with observations that some females occasionally appear to have a chest patch which is darker than the abdomen. In these cases the human visual system is perceiving the higher visible brightness of the abdomen without perceiving the higher UV brightness in the patch. The strong correlation in females between the UV chroma of the throat and that of the chest suggests these areas may be part of the same signal. However, analysis of PCs indicated these areas differ in brightness and their relative amount of UV reflectance. Female throats are more reflective than chests in the UV region. Higher UV reflectance in the throat generates the contrast peak of the throat against the granite in the UV region. Moreover, as the chest patch is surrounded by the white of the abdomen it is less important for it to contrast against the granite. The chest patch may be more important in short distance interactions.

(c) Mate choice and bright female coloration

The tendency of males to associate with females with a high throat UV chroma is indicative of a sensitivity to this trait. The relationships between the throat UV chroma and throat brightness and chest UV chroma warranted post-hoc tests into the importance of these variables in male choice of females. Males showed the strongest preference for females with a high chest UV chroma, though whether males assess the chest and throat UV chromas separately is unknown. Post-hoc tests also revealed that males showed a stronger preference for high UV chroma than for brightness. However, brightness and chroma as measures of a colour are so tightly linked that they are difficult to consider separately (Endler 1990) and are likely to have the most biological significance when considered together. In non-role-reversed species examples of male choice of female traits are rare (Andersson 1994). In *C. ornatus* the interpretation of male choice is complicated as it may arise from two different adaptive scenarios. Female traits can indicate receptivity (as in primates; Dixson 1983) and/or act as ornaments or honest signals. There was no evidence that the female throat reflectance was an indicator of female quality. Instead male sensitivity to throat reflectance may be advantageous in determining female reproductive state.

The relationship between UV chroma and a female's laying date appears to be mainly a consequence of the brightness component of this measure. The relationship between brightness and female laying date could be a consequence either of females changing brightness with reproductive condition or, if female brightness is a consistent trait over time, brighter females developing eggs sooner. *C. ornatus* females moult during the breeding season and dermal surfaces following moulting are brighter to human vision. It seems unlikely therefore that female brightness is a consistent trait within a female over time, particularly as temporal variation in female brightness has been documented in other lizards (Cooper & Greenberg 1992). Rather, moulting in females may occur at a particular reproductive stage, resulting in an advertisement of their state.

Many female lizards develop bright colours during the breeding season (Olsson & Madsen 1998). The function of this coloration is currently unclear, but is usually interpreted as a method of male rejection and an indication of the end of female receptivity (Olsson & Madsen 1998). Whilst this has been shown most conclusively for the closely related *Ctenophorus maculosus* (Olsson 1995), for many other species the timing of the colour changes relative to ovulation and copulation is unclear (Cooper & Greenberg 1992). Whilst bright coloration may often peak after ovulation, its onset frequently begins during vitellogenesis and will increase with increasing female receptivity (Turner *et al.* 1969; Vinegar 1972; Ferguson 1976; Werner 1978; Zucker & Boecklen 1990). Determining whether bright female coloration indicates increasing or decreasing receptivity appears to depend largely on interpretation. Is the increasing coloration prior to ovulation or the colour peak once gravid the most important? If bright coloration does generally signal unreceptivity it seems problematic that females require sperm over the period in which they are signalling increasing unreceptivity.

In *C. ornatus* the advantages to indicating approaching receptivity would seem to outweigh those of signalling unreceptivity. The relationship between female brightness and laying date suggests an increase in throat brightness with approaching ovulation. Whether this brightness continues to increase after ovulation and egg laying is unknown. The tendency for males to associate with brighter as well as high UV chroma females suggests that brightness may be attractive to males. It is unknown whether females mate multiply; however, they are unable to store sperm between breeding seasons (N. R. LeBas, unpublished data). Typically, many females reside within a male's territory; the ability to flash the brightest signal when most receptive could increase opportunities for female mate choice or copulations with males other than the territory holder. The benefits to signalling rejection once gravid are less obvious as forced copulation or similar male aggression has not been observed despite 700 h of observation of this species. The role of colour signalling and bright female coloration in lizards warrants further attention.

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