Biological Journal of the Linnean Society, 2009, **97**, 749–765. With 7 figures

Conspicuousness of Dickerson's collared lizard (*Crotaphytus dickersonae*) through the eyes of conspecifics and predators

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Received 27 July 2008; accepted for publication 19 January 2009

Selection should favour coloration in organisms that is more conspicuous to their own visual system than to those of their predators or prey. We tested this prediction in Dickerson's collared lizard (*Crotaphytus dickersonae*), a sexually dichromatic desert reptile that preys on insects and smaller lizard species, and which in turn is prey for birds and snakes. We modelled the spectral sensitivities of the lizards and their avian and snake predators, and compared the conspicuousness of the lizards' entire colour patterns with each class of viewers. Almost all comparisons involving females strongly supported our prediction for greater chromatic and brightness conspicuousness against local terrestrial visual backgrounds to their own modelled visual system than to those of avian and snake predators. Males, in contrast, exhibited far fewer cases of greater conspicuousness to their own visual system than to those of their predators. Our own perception of spectral similarity between blue *C. dickersonae* males and a local nonterrestrial visual background (i.e. the Sea of Cortéz) prompted a further investigation. We compared sea (and sky) radiance with dorsum radiance of *C. dickersonae* males and with males from two distantly-related *Crotaphytus collaris* populations in which males possess blue bodies. In all three visual models, *C. dickersonae* males exhibited significantly lower chromatic contrast with the sea (and sky) than did their noncoastal, blue-bodied congeners. Among potential explanations, the blue body coloration that is unique to male *C. dickersonae* may offset, if only slightly, the cost of visibility to predators (and to prey) through reduced contrast against the extensive, local, nonterrestrial blue backgrounds of the sea and sky. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **97**, 749–765.

ADDITIONAL KEYWORDS: coloration – spectral sensitivity – visual ecology – predation pressure – sensory drive.

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INTRODUCTION

As an exaggerated trait, conspicuous coloration has long been argued to provide advantages for attracting mates and intimidating rivals, and hence to evolve through sexual selection (Darwin, 1871; Andersson, 1994). Yet, with the exception of aposematism (Mappes, Marples & Endler, 2005) conspicuous coloration typically appears disadvantageous for avoiding detection by predators (Endler, 1978; Slagsvold, Dale & Kruszewicz, 1995; Johannesson & Ekendahl, 2002; Godin & McDonough, 2003; Sherratt & Beatty, 2003; Stuart-Fox *et al.*, 2003, 2004; Merilaita & Lind, 2005; Husak *et al.*, 2006; Stuart-Fox, Whiting & Moussalli, 2006; Stuart-Fox, Moussalli & Whiting, 2008; but see also Götmark, 1996) and prey (Grether & Grey, 1996; Baird, 2008). Most animal colour patterns therefore appear to represent a local balance between the social and reproductive advantages of sexually-selected ornamental coloration and the cost of increased visibility to unintended audiences (Endler, 1992; Stuart-Fox & Ord, 2004; Stuart-Fox *et al.*, 2004).

The conspicuousness of an organism's coloration is a relative phenomenon that is influenced by at least four factors (Endler, 1992): (1) contrast among colour elements comprising the pattern ('colour patches'); (2) contrast between the organism's colour pattern and the backgrounds against which it is viewed; (3) light environments that alter signal brightness and spectral contrast; and (4) the spectral sensitivity of the viewer. If predators and prey exhibit different spectral sensitivities, the sensory drive hypothesis (Endler, 1992) predicts that colour signals will evolve in ways that make them more conspicuous to conspecifics than to other viewers.

Predator spectral sensitivity and ornamental colour evolution in prey

Studies of taxonomically diverse animals have examined the competing influences of conspecific and predator spectral sensitivity on the evolution of sexually-selected coloration. Extensive work on Trinidadian guppies (*Poecilia reticulata*) has shown that, in response to predation pressure, male guppies evolve coloration with decreased visibility to the primary predator(s) in a given location. In streams that contain the guppy predator *Macrobrachium crenulatum* (a 'red blind' prawn), but which lack the red-sensitive pike cichlid (*Crenicichla alta*), male guppies display larger and more chromatic orange spots (Endler, 1980, 1987, 1991) that are preferred by females (Kodric-Brown, 1989; Houde & Endler, 1990; Grether, 2000). However, *Macrobrachium* also is the only guppy predator with good ultraviolet sensitivity (Endler, 1991) and, in certain streams containing this predator, male guppies exhibit far fewer and smaller ultraviolet (UV)-bright colour patches (Millar *et al.*, 2006; Kemp, Reznick & Grether, 2008).

In birds, Håstad, Victorsson & Ödeen (2005) showed that colour badges of numerous Swedish songbird species were, on average, more conspicuous to a passerine visual model (UV-sensitive cone) than to an avian predator visual model (violet-sensitive cone). Similarly, Heinsohn, Legge & Endler (2005) found that the green plumage of male *Eclectus roratus* parrots was less detectable to an avian predator visual model than to a conspecific visual model during foraging (i.e. against a background of leaves), where males are likely to be most vulnerable to predation by raptors.

In studies of reptiles and amphibians, Stuart-Fox *et al.* (2003) used a passerine visual model (the blue tit: *Parus caeruleus*) to estimate conspicuousness to avian predators of rock dragon (*Ctenophorus decresii* and *Ctenophorus vadnappa*) plaster models, and found that models having greater contrast with local rocks received the most damage by apparent predators. Interestingly, in the context of aposematism, Siddiqi *et al.* (2004) demonstrated that poison frogs were equally or more conspicuous to an avian visual model than to a poison frog visual model, which follows expectations for warning colour evolution. On the whole, the results of these and other studies of vertebrates imply that conspicuous coloration imparts a substantial survival cost to its bearers due to increased detection by predators and that, when possible, selection should act to reduce conspicuousness to predators relative to that of conspecifics.

Collared lizard coloration and the interaction of natural and sexual selection

Collared lizards (*Crotaphytus* sp.) offer an excellent study system for investigating the complexities of trade-offs between natural and sexual selection in shaping ornamental coloration. Members of this clade are saxicolous (rock-dwelling), insectivorous, and saurophagous (lizard-eating) reptiles from central and western USA and northern Mexico, with coloration that varies along a continuum from inconspicuous to highly conspicuous (McGuire, 1996; Macedonia, Brandt & Clark, 2002; Macedonia *et al.*, 2004). Of the nine *Crotaphytus* species, males in all but two species (*C. dickersonae* and *Crotaphytus collaris*) exhibit brown background coloration overlaid with white reticulations, or white and black bars and spots (McGuire, 1996; McGuire *et al.*, 2007). In short, both sexes of most collared lizard species appear to have experienced substantial selection for crypsis.

Male collared lizards defend territories and advertize their presence by perching on prominent rocks and by displaying when patrolling their territories (McCoy, Baird & Fox, 2003). The tendency for females to defend smaller territories and engage in display behaviour is weaker and varies among populations (Baird, Acree & Sloan, 1996; Husak & Fox, 2003). Collared lizard populations also differ in the opportunities for sexual selection (Baird, Fox & McCoy, 1997) and in predation pressure (Baird *et al.*, 1997; Macedonia *et al.*, 2002; Husak *et al.*, 2006). Regarding predation pressure, in a study of predator attack rates on clay-covered plastic models painted to resemble each of three Oklahoma (USA) collared lizard (*Crotaphytus collaris*) populations, Husak *et al.* (2006) found that the model type exhibiting the strongest colour contrast with local rocks in all three study areas was attacked most frequently by predators.

Recently, Baird (2008) demonstrated that female-coloured yearling male *C. collaris*, painted to resemble more conspicuous adult males, grew significantly more slowly than did control yearling males (painted brown or painted with water). The results showed that the more conspicuously painted young males made fewer attempts to attack prey and that, when they did attack, they were less successful than control males. Baird (2008) attributed the slower growth rates in the experimental males to a reduction in 'aggressive crypsis' (Endler, 1981); that is, being more conspicuous resulted in early detection by prey (Grether & Grey, 1996). Thus, conspicuous ornamental coloration should be particularly costly for collared lizards, which are predators as well as prey.

Within the genus *Crotaphytus*, Dickerson's collared lizard (*C. dickersonae*) is the most visually striking and sexually dichromatic species. Male background body colour ranges from aquamarine to sky blue, with the trunk and top of the head being infused with deep cobalt blue. Female background colour is largely brown, tan, and grey (sometimes with blue–grey overtones), with the tail and hind limbs ranging in colour from straw to lemon yellow. This species is restricted geographically to Isla Tiburón in the Sea of Cortéz and the adjacent coastal mountains of Sonora, Mexico (McGuire, 1996). Strong sexual dichromatism, which implies the presence of substantial sexual selection, is of particular interest because *C. dickersonae* also is expected to be subject to heightened natural selection for crypsis due to a latitudinal gradient of increasing predator and lizard prey species richness and abundance (Macedonia *et al.*, 2002). The possibility that an antagonism between sexual and natural selection has resulted in highly colourful male lizards leads us to question what roles spectral sensitivities and viewing backgrounds may have played in the evolution of this colourful sexual ornamentation.

In the present study, we investigated sexual dichromatism and colour conspicuousness in *C. dickersonae* from the visual system perspectives of (1) conspecifics; (2) a sympatric, diurnal, visually hunting snake (the coachwhip: *Masticophis flagellum*); and (3) an avian predator model. The coachwhip is a relatively large, aggressive, and actively foraging snake that captures sedentary as well as active prey (Secor & Nagy, 1994). In a metabolic study, Secor & Nagy (1994) found that approximately half of the diet of *M. flagellum* consisted of lizards, and this snake is considered the most dangerous ophidian predator of collared lizards (Husak *et al.*, 2006). Diurnal avian predators that are sympatric with *C. dickersonae* and that might pose a lethal threat include large hawks such as Swainson's hawk (*Buteo swainsoni*) and the red-tailed (*Buteo jamaicensis*). However, the terrestrial roadrunner (*Geococcyx californianus*) is commonly known to favour lizards and snakes in the diet and likely represents the most dangerous avian predator of collared lizards (J. Husak, pers. comm.). Given that spectral sensitivity data are unavailable for the roadrunner or for any diurnal raptor, our avian predator visual model utilizes visual system data from another terrestrial bird of open habitats, the peafowl, *Pavo cristata* (Hart, 2002).

We created visual models based on retinal cone pigments (and oil droplets, if present) and then employed a statistical procedure known as 'compositional analysis' (Endler & Mielke, 2005), which can be used to determine the overall disparity between the colour patterns of animals and their visual backgrounds. This approach allowed us to estimate potential differences in perceived conspicuousness of our study subjects to different viewers, and to test the prediction of the sensory drive hypothesis that the coloration of these lizards should be more conspicuous to their own visual system than to those of their predators.

MATERIAL AND METHODS

Study area and subjects

The distribution of *C. dickersonae* is limited to Isla Tiburón, in the midriff islands region of the Sea of Cortéz (Gulf of California), and to the mountains of the adjacent Sonoran coastline from Bahia Kino north to Punta Cirio (McGuire, 1996). In July 2003, May 2004, and May 2005, we collected data on the mainland population of *C. dickersonae*, concentrating on the coastal range between the towns of Kino Nuevo and Punta Chueca.

Lizard capture

Lizards were captured with a pole and noose. Body temperature was taken immediately upon capture

using a Miller & Weber T6000 cloacal thermometer. Subjects were assigned unique numbers, and flagging tape was used to mark capture locations. Subjects were held in mesh bags and kept in an insulated cooler until data were collected from them. Each subject was released at its marked location within 48 h of capture.

Reflectance measures of lizards and terrestrial visual backgrounds

Reflectance spectra of lizard body regions and representative terrestrial visual backgrounds were obtained with a reflectance probe (Ocean Optics R200-7) connected to a xenon lamp (Ocean Optics PX-2), a portable spectrometer (Ocean Optics USB-2000), and a notebook computer running Ocean Optics OOIBASE32 software. Samples of rocks that were closely similar in colour to (but much smaller than) adjacent larger rocks on which the lizards perched were collected for reflectance measurements, as were samples of vegetation and soil occurring in the vicinity of these rocks. Lizards and background objects were placed on a dull black rubber mat for spectral measurements. A small ruler, covered in black tape and attached to the reflectance probe, maintained a constant 5-mm distance between the end of the probe and the target. Spectra of lizards and background objects were obtained in a dimly lit room at a 75° angle relative to the target to reduce the possibility of specular effects (i.e. glare). Subjects (in mesh bags) were monitored closely using a cloacal thermometer while being warmed in the sun until reaching basking temperatures (36–38 °C; see Results), at which time reflectance of their coloration was obtained. Reflectance spectra from ten body regions of both sexes (plus two additional body regions of females) were gathered to create a relatively comprehensive profile of body coloration (Fig. 1). A Whiteport Optolon 2 matte white standard (> 97% reflectance in the range 300–1100 nm; ANCAL, Inc.) was scanned and dark current was removed from the signal immediately prior to obtaining a subject's reflectance readings.

Irradiance and radiance measurements

Downwelling irradiance (μmol m^{-2} s^{-1} nm^{-1}) was measured using a fiber optic and a cosine-correcting probe (Ocean Optics CC-3-UV) that was held overhead and oriented upward. Downwelling irradiance samples were averaged to produce a mean that was used to transform reflectance of lizard body regions and terrestrial visual backgrounds to radiance (see below). For comparison, sidewelling irradiance also was measured by orienting the irradiance probe parallel to the ground and taking readings from each cardinal direction (North, East, South, West); these readings were later averaged. Sea of Cortéz radiance and skylight radiance (μmol m^{-2} s^{-1} nm^{-1} sr^{-1}) were measured using a fibre optic fitted with a collimating lens (Ocean Optics 74-UV) adjusted to a small acceptance angle (≈3°). Skylight radiance was obtained by aiming the fibre/collimating lens overhead at a cloudless sky 60–75° away from the sun. Sea radiance was measured by pointing the same lens toward the sea from the shoreline and from cliff banks. The response of the spectrometer was calibrated with a calibration lamp (Ocean Optics LS1-CAL) prior to taking irradiance measurements, and was recalibrated prior to taking direct radiance (sea and sky) measurements. Habitat light measurements were taken between 10.00 h and 16.00 h under a clear and cloudless desert sky, which is the typical light environment for the study animals during their hours of greatest activity.

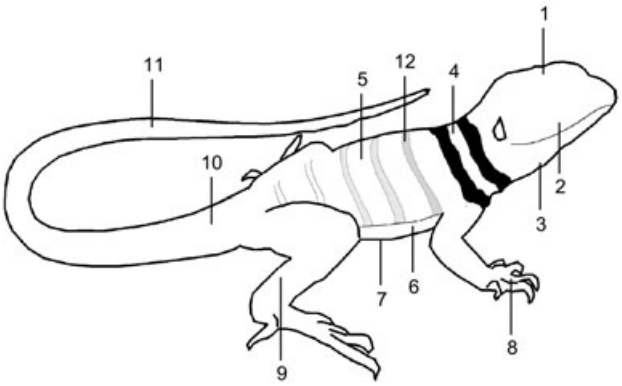

Figure 1. Body regions from which spectrophotometric data were obtained. 1, crown; 2, maxilla; 3, dewlap; 4, collar colour; 5, dorsum; 6, side; 7, ventrum; 8, front toes; 9, calf; 10, tail base; 11, female tail (medial); 12, female gravid coloration. Modified from Macedonia *et al.* (2004).

Microspectrophotometry of visual pigments and oil droplets

Microspectrophotometriy (MSP) was conducted on *Crotaphytus dickersonae* (3 adults) and *Masticophis flagellum* (2 adults) by one of us (E.R.L.). Subjects were dark adapted for a minimum of 2 h, after which they were deeply anesthetized with halothane and decapitated with sharp shears (in accordance with Cornell University IACUC protocol #2001-0115). Further preparations and measurements were carried out under infrared light (> 800 nm; Kodak safelight No. 11) using image converters. Eyes were hemisected and retinas were teased from the pigment epithelium under buffer solution (cold Ca^{2+}/Mg^{2+}-free Ringer's

solution, pH 7.4, supplemented with 6% sucrose). Pieces of retina were macerated, sandwiched between cover slips edged with silicone grease, and placed on the stage of a computer-controlled, single-beam MSP (Loew, 1994). Spectra were recorded at 1-nm intervals in the range 750–350 nm, and back again from 350–750 nm. The selection criteria used for including data into the λ_{max} analysis pool were the same as described in Loew (1994). Additional details (e.g. spectral smoothing and template fitting procedures) are provided elsewhere (Siddiqi *et al.*, 2004). Oil droplet/inner segment absorbances also were determined at 1-nm intervals over the same wavelength range.

Visual modelling

Three visual models were constructed using MSP data gathered for the present study (*C. dickersonae* and *M. flagellum*) or provided by Nathan Hart for the Indian peafowl (*Pavo cristatus*). Regarding birds, very short-wavelength perception in diurnal birds can be partitioned into those species possessing a UV-sensitive (UVS) photoreceptor (higher passerines, parrots, gulls, and the rhea), and those having a violet-sensitive (VS) photoreceptor (all other species; Endler & Mielke, 2005; Hart & Vorobyev, 2005). Birds with a VS visual pigment (e.g. *P. cristatus*: $\lambda_{max} = 424$ nm; Hart & Vorobyev, 2005) can perceive UV wavelengths, but they are less sensitive to UV than birds that possess a UVS visual pigment. The peafowl has a VS rather than a UVS visual pigment, and therefore represents a reasonable approximation for an avian predator visual model. Although MSP data are not available for the lizard-hunting roadrunner (*G. californianus*, Cuculidae) or for any member of its order (Cuculiformes), opsin gene sequence data strongly suggest that all Cuculiformes, as well as all Falconiformes (hawks and falcons), are VS species (Ödeen & Håstad, 2003). Thus, *sensu* Håstad *et al.* (2005) we used MSP data from a bird of open plains and scrubland that possesses a VS photopigment as our avian predator model.

Gaussian visual pigment absorbance curves were generated from λ_{max} values obtained via MSP, *sensu* Govardovskii *et al.* (2000). For *C. dickersonae*, the absorbance spectrum for each photoreceptor class was multiplied by its associated normalized oil droplet transmittance spectrum. The long-wavelength-sensitive (LWS) visual pigment was associated approximately equally with two types of oil droplet, so for this photoreceptor a mean oil droplet transmission spectrum was generated and multiplied by the LWS visual pigment absorbance spectrum. The resulting visual pigment × oil droplet curves were normalized to the curve with the highest peak. Because snakes do not possess oil droplets (Sillman *et al.*, 1997), no modification of the *M. flagellum* visual pigment absorption spectra was carried out.

Photoreceptor absorbance data for *P. cristatus* (Hart, 2002) include the modifying effects of oil droplets as well as those of various ocular media (cornea, lens, and humors). Data are not available for transmission effects of ocular media in *C. dickersonae* and *M. flagellum*; thus, our visual models for these two species do not include this information. Nevertheless, in avian species that possess a UVS cone, reduction of short-wavelength transmission typically is minor (finches: Hart *et al.*, 2000) compared to species that possess a VS cone (peafowl: Hart, 2002; turkey: Hart, Partridge & Cuthill, 1999). Data on ocular transmission in a chameleon species (*Chameleo dilepis*: Bowmaker, Loew & Ott, 2005), which possess a UVS cone, exhibit minor transmission reduction at short wavelengths, just like those of avian species with UVS cones. Our inability to account for these transmission effects in our reptilian visual models therefore is likely to be of comparatively minor consequence. We did not create visual models for lizard species on which *C. dickersonae* preys (Garcia & Whalen, 2003) because visual pigments and oil droplets in these iguanians are closely similar to those of collared lizards (E. R. Loew, unpubl. data).

In the present study, the quantum catch of a photoreceptor, Q_i, is given by the formula:

$$Q_i = \int_{\lambda_{min}}^{\lambda_{max}} R(\lambda) I(\lambda) SS(\lambda) d\lambda \quad (1)$$

where $R(\lambda)$ is the reflectance spectrum of the object being viewed, $I(\lambda)$ is the irradiance spectrum illuminating the object, and $SS(\lambda)$ is the spectral sensitivity of a given photoreceptor class integrated over the wavelength range of interest, $d(\lambda)$. For skylight and sea surface spectra, $R(\lambda)$ is direct radiance and $I(\lambda)$ is removed from the equation. Except where noted, $\lambda_{min} = 330$ nm and $\lambda_{max} = 700$ nm.

To estimate the response of a model visual system to a given radiance spectrum, the spectral sensitivity of each cone class was multiplied by that radiance spectrum and the resulting cone outputs (i.e. four in the case of a tetrachromat) were individually summed. Each sum then was multiplied by the reciprocal of the area under each spectral sensitivity curve to satisfy the assumption that the neural stimulation of each cone class is equal in response to a 'white' stimulus (Fleishman & Persons, 2001). The relative stimulation of each cone class then was calculated by dividing the corrected sum for each cone class output by the combined sum of all cone class outputs (see Fleishman & Persons, 2001, for additional details). We refer to these relative stimulation (S) values as: S_{UVS} (ultraviolet wavelengths-sensitive pigment), S_{SWS}

(short wavelengths-sensitive pigment), S_{MWS} (middle wavelengths-sensitive pigment), and S_{LWS} (long wavelengths-sensitive pigment).

Our visual modelling makes some simplifying assumptions, such as the prospect that all cone classes contribute equally to colour perception. In addition, these models do not account for 'photoreceptor noise' (Vorobyev & Osorio, 1998) in predicting the differential chromatic and brightness discrimination abilities of the three taxa considered here. Receptor noise-based visual models predict spectral sensitivity well, but they require information about the relative proportions of different cone classes in the retina. Cone class ratios have not been determined for *Crotaphytus* or *Masticophis*. We also are unaware of published cone class ratios for any diurnal lizards, and we have no reason to consider that these ratios in the garter snake (Sillman *et al.*, 1997) may approximate those of *Masticophis*. Thus, similar to some other studies of lizards (Fleishman & Persons, 2001; Stuart-Fox & Moussalli, 2008), we acknowledge that failing to take receptor noise into account might reduce precision in estimates of perceived contrast, especially where the comparison involves spectrally similar colours.

Modelling colour perception

Sensu Endler & Mielke (2005), perception of a colour pattern element or background in our lizard and avian predator visual models is defined by values $\{S\} = \{S_{UVS}$ or S_{VS}, S_{SWS}, S_{MWS}, and $S_{LWS}\}$, and in our snake visual model by $\{S\} = \{S_{UVS}$, S_{SWS}, and $S_{LWS}\}$. Here, a colour pattern with N elements comprises an $N \times 4$ (or $N \times 3$ in the snake) matrix, **S**, with the $\{S\}$ as rows. The **S** matrix is transformed to a compositional matrix, $\mathbf{S_c}$, by dividing each cell value by the row total. The non-independence of matrix columns is removed by transforming the points ($\mathbf{S_c}$ rows) into coordinates $\{S_T\} = \{x, y, z\}$ that lie within the boundaries of a tetrahedral colour space having a height equal to 1. The formulae required to transform the **S** matrix to a tetrahedral coordinate matrix, $\mathbf{S_T}$, are presented as eqn. 20 in Endler & Mielke (2005). Given that *M. flagellum* is a trichromat with UVS, SWS, and LWS cones, we modelled its perception of *C. dickersonae* colour pattern elements in tetrahedral colour space using a zero value for the MWS cone when converting the **S** matrix to the $\mathbf{S_T}$ matrix. Trichromat colour scores plotted in tetrahedral colour space are restricted to one face of the tetrahedron (Endler & Mielke, 2005).

Modelling brightness perception

Given their broad sensitivity and abundance in the avian retina, double cones (which contain the LWS pigment) are thought to be responsible for brightness perception (Maier & Bowmaker, 1993; Vorobyev *et al.*, 1998; Osorio, Miklosi & Gonda, 1999a; Osorio, Vorobyev & Jones, 1999b; Hart, 2001). The same assumption has been made for frogs (Siddiqi *et al.*, 2004). Data from electroretinography and behavioural experiments have ruled out contributions of the UVS and SWS cones in the achromatic vision of *Anolis* (Fleishman & Persons, 2001), and the limitation of longer wavelengths to perception of achromatic contrast suggests that double cones are used for this purpose in lizards as well.

To estimate brightness perception, we modelled the sensitivity of double cones in the range 400–700 nm. For the *C. dickersonae* visual model, a mean was calculated between the transmittance of the LWS cone oil droplet and the dispersed pigment in the accessory member of the double cone pair (see Results); this quantity then was multiplied by the absorbance of the LWS pigment to create the brightness parameter. Because the double cones of *M. flagellum* do not possess oil droplets, the absorbance of the LWS cone pigment alone was used to estimate brightness perception for this predator. Finally, *P. cristata* (our avian predator visual model) uses the LWS pigment in both members of the double cone, but the oil droplet characteristics differ for the two members (Hart, 2002). Thus, a mean absorption curve of the primary and secondary oil droplets was calculated and multiplied by the LWS pigment to estimate brightness perception for this species.

Analysis of colour patterns and visual backgrounds

Similar to some other recent studies (Endler *et al.*, 2005; Heinsohn *et al.*, 2005; Wilson, Heinsohn & Endler, 2007; Kemp *et al.*, 2008), we used a distribution-free statistical method, LSED-MRPP (Endler & Mielke, 2005), to examine differences in entire colour patterns of *C. dickersonae* males and females against their primary terrestrial visual backgrounds. The analysis provides an effect size value termed 'disparity' (K), which increases in magnitude with increased divergence between groups in any attribute of their distributions (Endler & Mielke, 2005). We used LSED-MRPP to calculate disparity values for each lizard against each type of terrestrial background (rocks, vegetation) in each visual model (lizard, bird, and snake). For the vegetation background, a summary spectrum created from a 40% contribution of the green vegetation sample mean and a 60% contribution of the brown vegetation sample mean was used to represent the actual mix of vegetation colours in the environment. This estimate was based on careful examination of numerous photos of

our study area. For significance tests, we used the generalized linear model procedure in SAS, with sex and visual model as independent variables and individual as a random factor nested within sex. The Tukey–Kramer method was used for post-hoc pairwise comparisons of all sex × visual model combinations.

Because colour pattern elements are represented in the LSED-MRPP data matrix in proportion to the area they contribute to the colour pattern, we obtained these proportions from a set of digital photo close-ups of undisturbed subjects in a typical 'basking' position under natural field conditions. The mountainous terrain of *C. dickersonae* habitat provides the potential for conspecifics, prey, and all predator classes to detect these lizards from virtually any visual angle. We therefore used the same set of 12 photos, taken at a number of visual angles, for all three visual models.

For each sex, the *C. dickersonae* body outline was traced twice in each photo using Adobe Photoshop (version 7.0 for Macintosh) and the two measurements were averaged. Each body region/colour pattern element then was traced twice and averaged. Finally, the number of pixels contained in each body region was divided by the number of pixels contained in the entire body, which provided a proportional area occupied by that colour pattern element in that photograph. Except for female gravid coloration, the proportional area coverage for each colour pattern element was closely similar for the two sexes. The body region proportional areas thus were averaged across all photographs (i.e. sexes were combined), producing a final set of colour pattern element proportions (Table 1).

Table 1. Percent area occupied by each body region (relative to total body area) as estimated from photos of subjects in a typical basking position

Body region	Percent body area (mean ± SE)
Crown	1.78 ± 0.59
Collar	1.12 ± 0.17
Dewlap	2.95 ± 0.47
Maxilla	2.62 ± 0.39
Dorsum background	15.00 ± 1.39
Side	2.39 ± 0.56
Ventrum	2.11 ± 0.96
Calf	5.44 ± 0.64
Front toes	1.69 ± 0.45
Tail	17.96 ± 3.07
Gravid orange*	4.75 ± 2.35

*Females only; 12 of 22 females exhibited gravid orange coloration and were coded as such; the remaining ten females were coded without this coloration.
Mean percent area averages of body areas in photographs were rounded to the nearest integer to weight the number of spectral samples used for each body region in calculating entire colour pattern contrasts. For details, see text.
Means are from photographs of seven males and five females.

Calculating colour contrast with nonterrestrial visual backgrounds

From the ridges and western slopes of the coastal mountains, and from the sea-facing slopes on Isla Tiburón, the Sea of Cortéz constitutes a substantial nonterrestrial visual background in addition to the blue desert sky (see Supporting information). A striking similarity (apparent to human viewers) between the unusual blue coloration of adult male *C. dickersonae* and the hues of the sea led us to speculate that the costs of visibility to predators and to prey against terrestrial backgrounds may be offset to some degree through reduced contrast against the extensive nonterrestrial blue backgrounds of the sea and sky. As a preliminary exploration of this possibility, we examined three collared lizard populations: male *C. dickersonae* and males from two phylogenetically distant clades of *C. collaris* (Orange, Riddle & Nickle, unpubl. data; McGuire *et al.*, 2007) in which blue coloration appears to have evolved independently. Neither *C. collaris* population occurs near a large body of water: one is located in eastern Utah and western Colorado (Macedonia *et al.*, 2002) and the other is restricted to southwest Oklahoma (Macedonia *et al.*, 2004). To determine how population differences in blue coloration appeared to our visual models relative to the Sea of Cortéz and a Sonoran Desert sky, chromatic contrast was calculated as the Euclidian distance (Δ_T) between dorsum and sea radiance colour scores in tetrahedral colour space (Endler & Mielke, 2005), as:

$$\Delta_T = \sqrt{(x_a - x_b)^2 + (y_a - y_b)^2 + (z_a - z_b)^2}$$

where x, y, and z are the three dimensions of the colour tetrahedron. One-way analyses of variance (ANOVA) tested for collared lizard population differences in dorsum-sea and dorsum-sky Euclidian distances in each of the three visual models.

RESULTS

Sexual dichromatism

For most body regions, females exhibited greater reflectance intensity (larger area under the curve) but males were more chromatic (steeper curve slopes; Fig. 2). Some exceptions include a brighter white collar and tail base in males, and the strongly

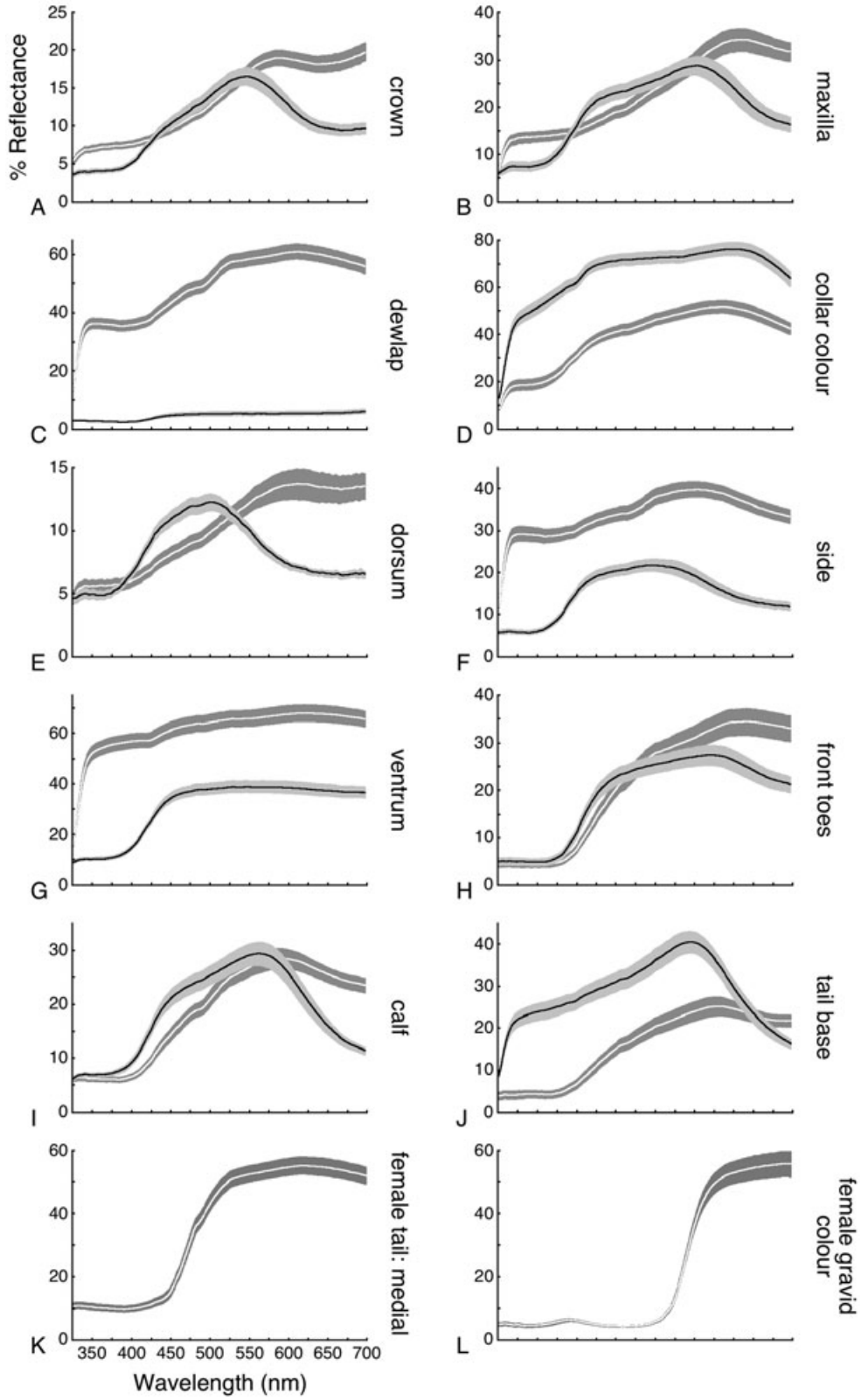

Figure 2. Reflectance of body regions sampled spectrally for 27 adult male and 22 adult female *Crotaphytus dickersonae*. Plots show the mean (solid lines) ± SE (grey surrounds). Males, black lines with light grey standard errors; females, white lines with dark grey standard errors.

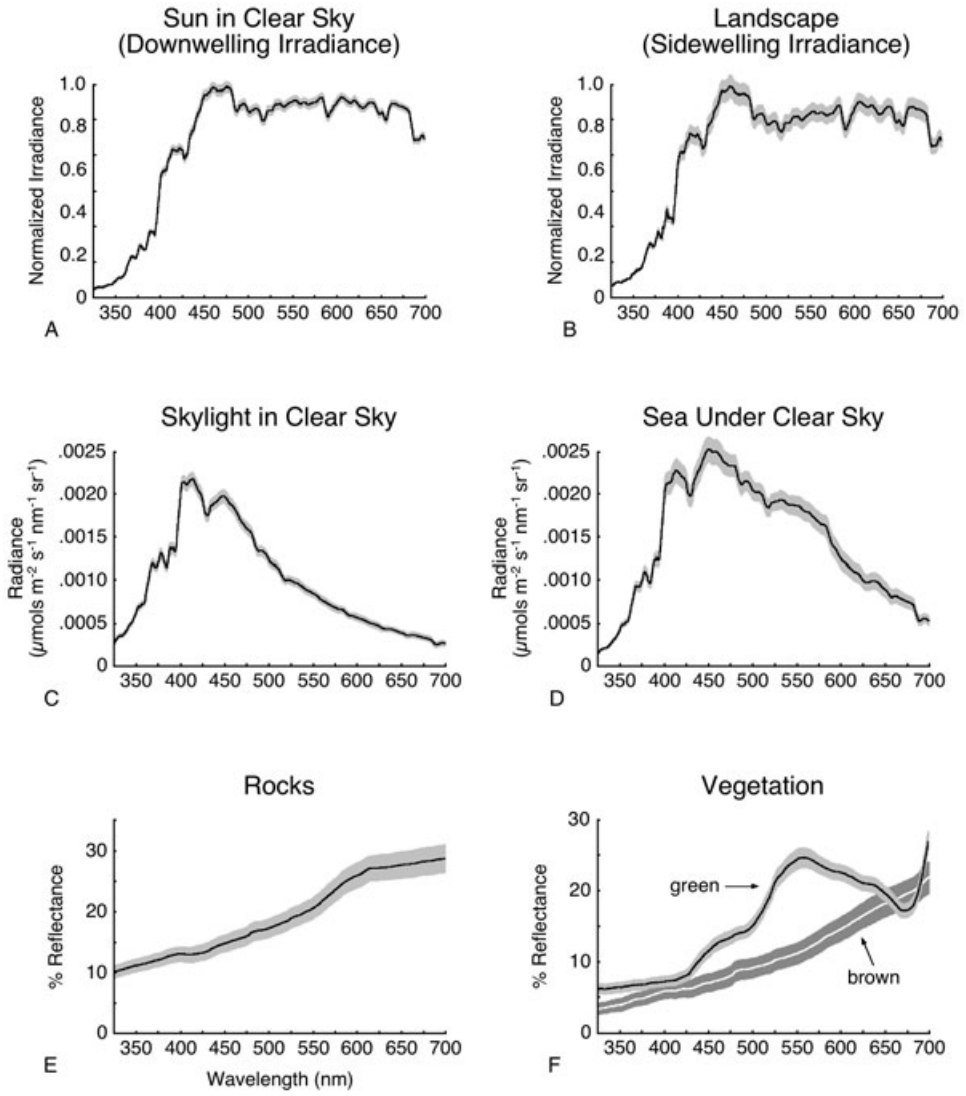

Figure 3. Spectra of habitat light and visual backgrounds used in this study. Plots show the mean (solid lines) ± SE (grey surrounds). Sample sizes: (A) $N = 3$, (B) $N = 6$, (C) $N = 12$, (D) $N = 12$, (E) $N = 30$, (F) green: $N = 9$; brown: $N = 7$.

chromatic yellow medial and distal tail region of females, as well as highly chromatic orange gravid coloration (Fig. 2).

Habitat light and visual backgrounds

The mean downwelling irradiance of the sun in a clear blue sky (Fig. 3A) was virtually identical in spectral shape with mean sidewelling (lateral) irradiance of the landscape (Fig. 3B), although the landscape samples were more variable. Skylight radiance in a clear sky exhibited a strong peak around 450 nm ('blue'), but wavelengths in the deep 'violet' (just above 400 nm) were stronger (Fig. 3C). Sea radiance was similar to skylight radiance in spectral shape up to approximately 475 nm (although 'blue' wavelengths were stronger than 'violet'), but exhibited greater energy in middle (green/yellow) wavelengths (500–600 nm) and, to a lesser degree, long wavelengths (600–700 nm; Fig. 3D). Reflectance spectra of terrestrial backgrounds are shown in Figure 3E, F.

Microspectrophotometry

Crotaphytus dickersonae possesses a pure-cone retina; neither rods, nor rod-specific (RH1 opsin) pigment were found. All visual pigments were vitamin A1-based, as determined from their similarity to rhodopsin visual pigment templates. The retina contained four classes of single-cone photoreceptors (Fig. 4A) as well as a double cone; no sex differences were observed. The details provided in Table 2 origi-

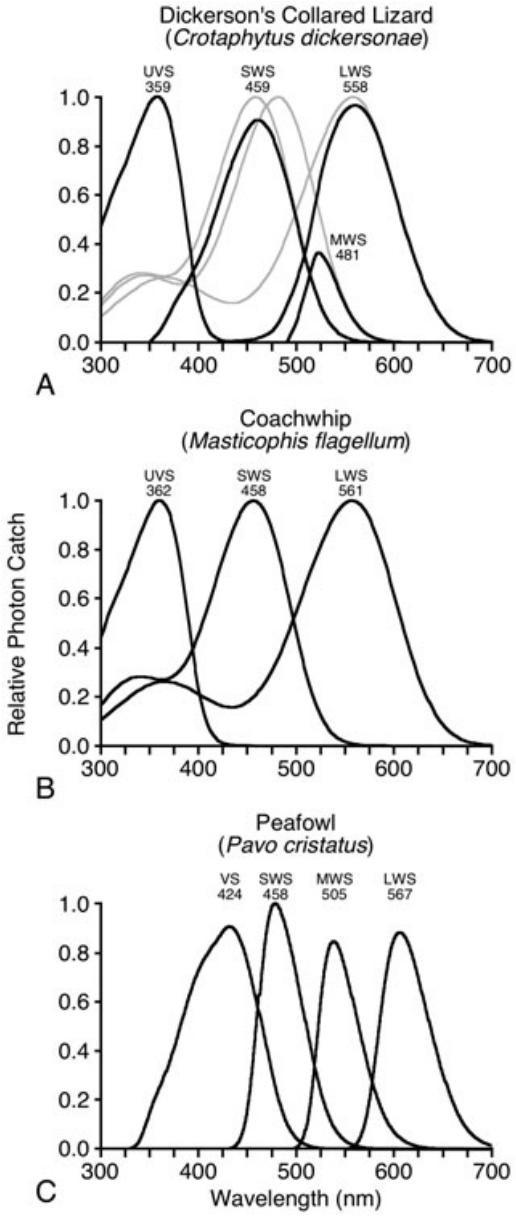

Figure 4. Relative photon catches for each cone class in (A) the study species, *Crotaphytus dickersonae* ($N = 3$); (B) a snake predator of collared lizards, *Masticophis flagellum* ($N = 2$); and (C) the bird *Pavo cristata* (data from Hart, 2002) serving as a violet-sensitive (VS)-cone visual model for an avian predator. The thick black-lined curves depict spectral sensitivity for each cone class after oil droplet filtering (the coachwhip in 'B' has no oil droplets). The thin grey-lined curves in 'A' (*C. dickersonae*) represent the short- (SWS), middle- (MWS), and long- (LWS) wavelength-sensitive visual pigments prior to oil droplet filtering (the ultraviolet-senstive cone oil droplet is transparent and has no effect on spectral curve shape). Numbers above each curve indicate peak wavelength absorbance for each visual pigment in the absence of filtering by oil droplets.

nate only from cells that met selection criteria for noise and bandwidth, and that were attached to an inner segment with a droplet. Many other records of all pigment/droplet classes were obtained and used qualitatively to ensure that no classes were missed. *Masticophis flagellum*, similar to other diurnal snakes (Sillman *et al.*, 1997) possesses an all-cone retina in which neither rods, nor oil droplets were detected. Three types of single cones were identified in two adult specimens examined (Fig. 4B, Table 2). Hart (2002) provided visual pigment, oil droplet, and ocular media data for *P. cristata*. The photoreceptor absorbance curves recreated from Hart's data are shown in Figure 4C.

Disparity of lizards and terrestrial backgrounds

The results of a two-way ANOVA conducted on disparity *K*-values from LSED-MRPP analysis of individual lizard and rock tetrahedral coordinates showed significant main effects of sex ($F_{2,94} = 73.13$, $P < 0.0001$) and visual model ($F_{2,94} = 100.86$, $P < 0.0001$), and a significant sex × visual model interaction ($F_{2,94} = 87.22$, $P < 0.0001$). Protected post-hoc pairwise comparisons (Tukey–Kramer) revealed that, within each visual model, *C. dickersonae* males were more conspicuous against rocks than were females ($P < 0.0001$ for all comparisons). Disparity between male colour pattern and rocks differed significantly for all visual model pairwise comparisons: conspicuousness was greatest for the avian visual model, intermediate for the lizard visual model, and least for the snake visual model (Fig. 5, top). By comparison, *C. dickersonae* females were more conspicuous to their own visual model than to the bird and snake visual models (Fig. 5, top).

A similar analysis with vegetation as the visual background revealed significant main effects of sex ($F_{2,94} = 269.07$, $P < 0.0001$) and visual model ($F_{2,94} = 16.24$, $P < 0.0001$), as well as a significant sex × visual model interaction ($F_{2,94} = 12.70$, $P < 0.0001$). Male colour pattern conspicuousness was significantly greater against vegetation for the conspecific and snake visual models than for the avian visual model, whereas females were significantly more conspicuous to the conspecific visual system than to the snake and bird visual systems (Fig. 5, bottom).

The results of a two-way ANOVA on brightness disparity *K*-values of individual lizards and rocks showed a significant main effect for visual model ($F_{2,94} = 26.46$, $P < 0.0001$) but not for sex ($F_{2,94} = 1.87$, $P > 0.05$), and also showed a significant sex × visual model interaction ($F_{2,94} = 17.52$, $P < 0.0001$). Post-hoc tests revealed that females were more conspicuous than males in brightness against rocks to the conspe-

Table 2. Single cone visual pigment and oil droplet values obtained by microspectrophotometry

	Visual pigments				Oil droplets		
Species	UVS	SWS	MWS	LWS	C	G	Y
Crotaphytus dickersonae	359 ± 0.8 (8)	459 ± 0.7 (6)	481 ± 0.8 (9)	558 ± 1.1 (6)	373 ± 1.2 (3)	521 ± 1.0 (16)	489 ± 0.7 (13)
Masticophis flagellum	362 ± 1.4 (10)	457 ± 0.9 (12)	–	558 ± 0.8 (21)	–	–	–

Values for each cone class visual pigment (UVS, ultraviolet-wavelength-sensitive; SWS, short-wavelength-sensitive; MWS, medium-wavelength sensitive; LWS, long-wavelength-sensitive) are the mean λ_{max} values (nm) obtained by template-fitting ± SD; the corresponding sample sizes (N) are in parentheses. Oil droplets associated with UVS cones are transparent to wavelengths within the visual range of terrestrial vertebrates. The clear (C) oil droplet is associated with SWS cones, the green (G) oil droplet is associated with MWS cones, and the yellow (Y) oil droplet is associated with LWS cones. The oil droplet values are the 50% of peak cut-off wavelengths (Loew *et al.*, 2002). In *Crotaphytus dickersonae*, some LWS cones possessed a yellow oil droplet and others possessed a green oil droplet. The principal member of the *C. dickersonae* double cone exhibited a peak absorbance of 557 ± 0.8 nm ($N = 11$) and always was associated with the yellow oil droplet. The accessory member of the double cone possessed the same peak absorbance (556 ± 1.1, $N = 9$), but lacked an oil droplet, and instead contained a dispersed yellowish pigment in the ellipsoid with the three-peaked shape typical of carotenoids. *Masticophis flagellum* possesses neither an MWS cone class, nor oil droplets. Double cones containing the LWS pigment were observed, but these separated in preparation.

cific ($P < 0.0001$) and avian ($P < 0.05$) visual systems, but not to the snake visual system ($P > 0.05$). Within sexes, although males were equally conspicuous in brightness against rocks to all three visual systems, females were more conspicuous to their own visual system than to the snake or bird visual systems (Fig. 6, bottom).

A similar analysis with vegetation as the visual background revealed a significant main effect for visual model ($F_{2,94} = 9.87$, $P < 0.0005$) but not for sex ($F_{2,94} = 1.58$, $P > 0.05$), and there was a significant sex × visual model interaction ($F_{2,94} = 8.77$, $P < 0.0005$). Post-hoc tests revealed that females were more conspicuous than males against vegetation in brightness to the conspecific ($P < 0.0001$) and the avian ($P < 0.0001$) visual systems, but not to the snake visual system ($P > 0.05$). Within sexes, males were equally conspicuous in brightness against vegetation to all three visual systems, whereas females were equally conspicuous to their own and the avian visual system, but less conspicuous to the snake visual system (Fig. 6, bottom).

Male coloration and nonterrestrial visual backgrounds

Euclidian distance between male dorsum radiance and sea radiance tetrahedral coordinates (Fig. 7) differed significantly among the three collared lizard populations in each visual model (lizard: $F_{2,64} = 108.6$; snake: $F_{2,64} = 127.6$; bird: $F_{2,64} = 106.0$; $P < 0.001$ in each case). A similar result occurred between male lizard and blue desert sky tetrahedral coordinates (lizard: $F_{2,64} = 114.0$; snake: $F_{2,64} = 122.9$; bird: $F_{2,64} = 117.4$; $P < 0.001$ in each case).

DISCUSSION

Darwin (1871) conceived sexual selection theory to explain the presence of extravagant male secondary sexual traits that should be rigorously opposed by natural selection. Given that it is costly for predators and prey to be detected by each other, inconspicuous coloration should prevail unless benefits accrued through sexual selection outweigh the costs imposed by natural selection. In the present study, we have attempted to account for the influences of spectral sensitivities and visual backgrounds on conspicuous sexual coloration in male *C. dickersonae*. This species is of particular interest because, although natural selection for crypsis should be relatively high (as inferred from geographic patterns of species richness in potential predators and lizard prey of collared lizards), *C. dickersonae* exhibits the most striking sexual dichromatism in the genus *Crotaphytus*. We therefore looked beyond a simple objective classification of colour to ask what roles vision and viewing backgrounds may have played in the evolution of this ornamentation.

As anticipated, males exhibited dramatically greater chromatic disparity with rocks and vegetation than did females. Although females did show greater brightness disparity with these backgrounds than males, the magnitude of this difference between the

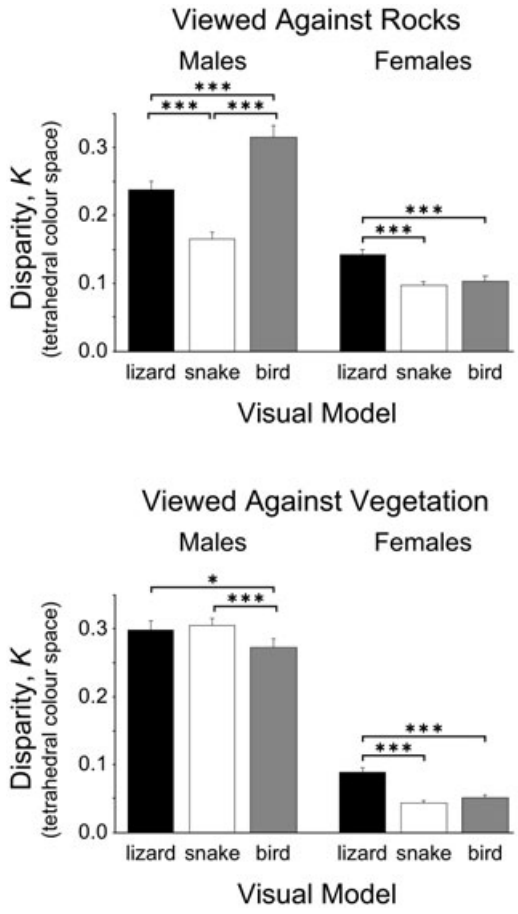

Figure 5. Disparity (K) between *Crotaphytus dickersonae* colour patterns and visual backgrounds in tetrahedral colour space from the perspective of conspecific and model predator systems. For significant ($P < 0.0001$) two-way analyses of variance (sex and visual model: fixed factors, individuals nested within sex as a random factor), Tukey–Kramer post-hoc tests were used to compare results for each visual model within each sex. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

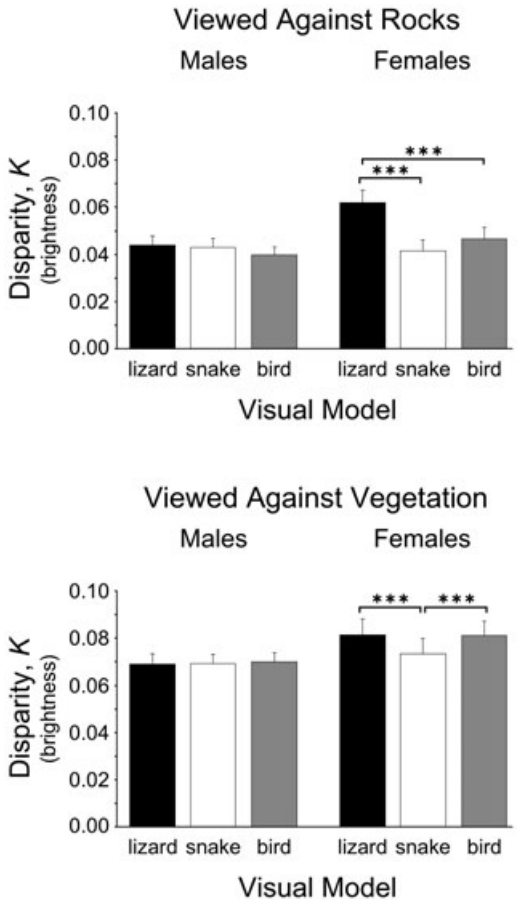

Figure 6. Disparity (K) in brightness between *Crotaphytus dickersonae* colour patterns and visual backgrounds. Symbols as in Fig. 5.

sexes was small and seems unlikely to be consequential for detection by predators and prey in a bright desert environment.

Females always were less conspicuous chromatically to the modelled predator visual systems than to their own modelled visual system, and were equally or more conspicuous in brightness contrast to their own visual system than to those of their predators. Because females do not often experience the advantages accrued by males from conspicuous coloration, natural selection is expected to favour inconspicuous coloration in females of many species (Darwin, 1871; Andersson, 1994). Our results suggest that *C. dickersonae* females are inconspicuous not only in the sense of matching their terrestrial visual backgrounds more closely than do males (i.e. lower disparity values), but also that they use colours that make them more conspicuous to conspecifics than to their predators.

Disparity between female coloration and terrestrial backgrounds always was greater in the avian than in the snake visual model in our results, although the differences were not often statistically significant. Similarly, Stuart-Fox *et al.* (2008) showed that, although dwarf chameleons (*Bradypodion taeniabronchum*) exhibited better background colour matching to a taxonomic mount of a shrike than to a resin replica of a boomslang, the chameleons were more conspicuous chromatically to their avian visual model (a tetrachromat with oil droplets) due to poorer colour discrimination by their snake visual model (a trichromat lacking oil droplets).

The results obtained in the present study provide mixed support for our prediction that selection should favour colour patterns in prey that are more conspicuous to their own visual systems than to those of their

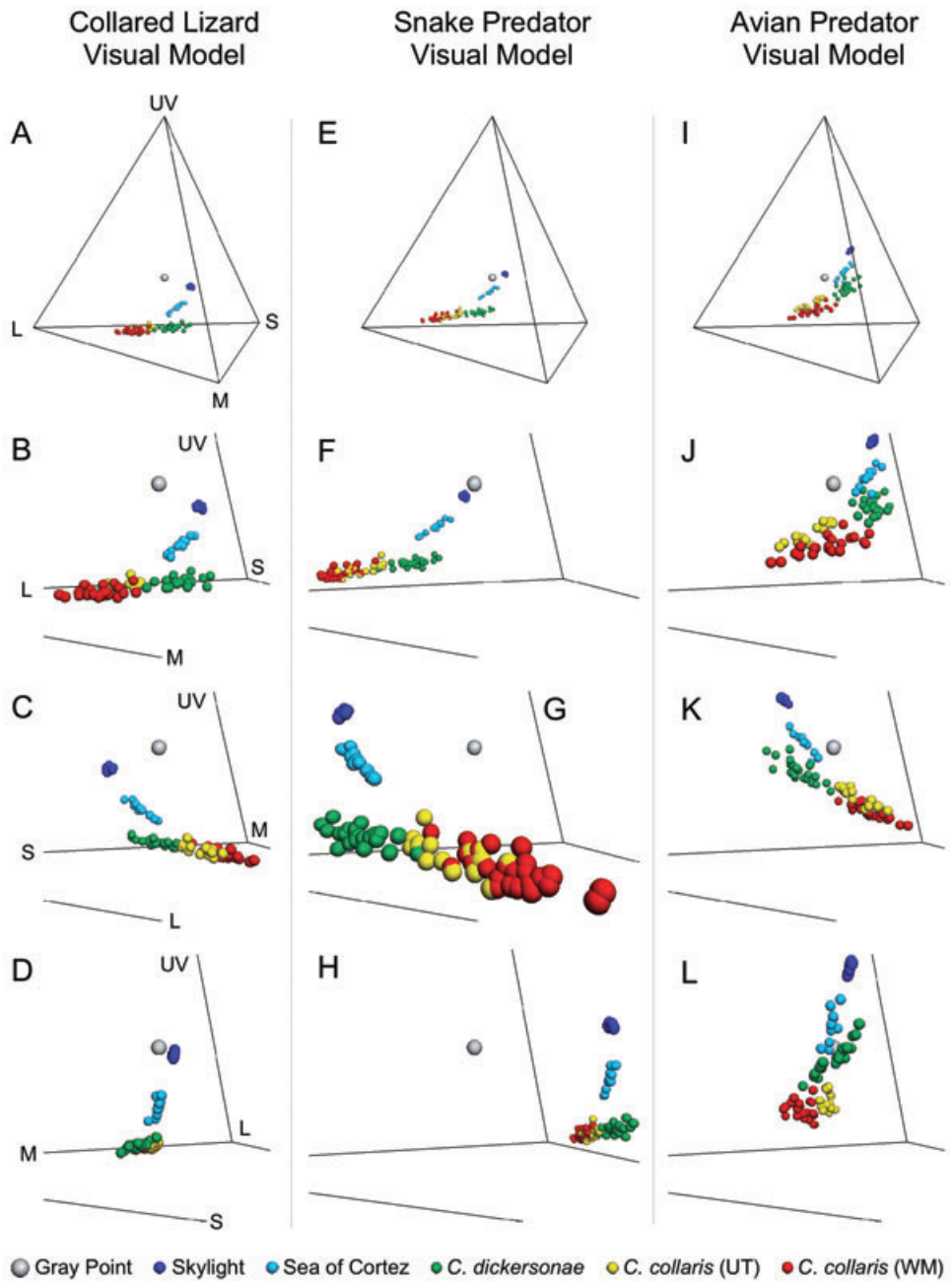

Figure 7. Radiance colour scores of males from three collared lizard populations in which males exhibit blue dorsal coloration, plotted together with Sea of Cortéz and skylight radiance in tetrahedral colour space for three visual models. Row two of each column presents the same orientation of the tetrahedron as shown in row one, but magnified for clarity. Rows three and four illustrate the tetrahedrons rotated 120° and 240° from their orientation in row two. The vertices of the tetrahedron represent the locations where only a single cone class (ultraviolet, short, medium, long) is stimulated. Each sphere represents an individual spectrum, and sphere colours designate different backgrounds and lizard populations: dark blue, skylight radiance ($N = 12$); turquoise, Sea of Cortéz radiance ($N = 12$); green, dorsum radiance male *Crotaphytus dickersonae* ($N = 27$); yellow, dorsum radiance of male *Crotaphytus collaris 'auriceps'* from eastern Utah (UT: $N = 17$); red, dorsum radiance of *C. collaris* from the Wichita Mountains (WM: $N = 25$) of southwestern Oklahoma. The light grey sphere (grey point) represents the achromatic centre point of the tetrahedron; the colours increase in chromaticity as one moves from the grey point to each vertex of the tetrahedron. Skylight radiance and sea radiance were obtained by direct measurement, whereas lizard radiance was calculated from reflectance multiplied by downwelling irradiance. Radiance and irradiance spectra were obtained under clear and cloudless skies, typical for this Sonoran Desert habitat.

predators. In some cases (especially brightness disparity in males), there was no difference in conspicuousness between lizard- and predator-modelled visual systems. Although female *C. dickersonae* were consistently more conspicuous to the conspecific visual model than to those of avian and snake predators, this was rarely the case for males. One consequence of this outcome is that elaboration of male coloration is likely to carry increasingly greater predation risk, which may add to the 'handicap' value of this coloration in a manner consistent with the viability indicator model of sexual selection (Zahavi, 1975).

The probability of selection producing coloration that always is more perceptible to conspecifics than to other audiences must become increasingly unlikely as the number of visual systems and visual backgrounds being considered increases. Indeed, in all studies performed to date where predator and prey visual system modelling has been combined with disparity analysis, prey visual systems were not consistently better at target-background discrimination than were those of predators (Heinsohn *et al.*, 2005; Wilson *et al.*, 2007; Kemp *et al.*, 2008). Moreover, in a study of ontogenetic colour change in the green python (*Morelia viridis*), the results obtained indicated that avian predator vision always was superior to that of the pythons in discriminating the snakes from their backgrounds (Wilson *et al.*, 2007).

At present, we know little about actual predation pressure on our study species. We attempted to determine whether avian or snake predators pose a greater threat by tethering clay-covered plastic replicas of *C. dickersonae* males (blue) and females (brown) to rocks throughout our study area. Although this technique proved successful in a prior study of predation pressure on *C. collaris* (Husak *et al.*, 2006), most of our *C. dickersonae* replicas were quickly dispatched from their rock perches and chewed extensively by the locally abundant ground squirrels (Harris' antelope squirrel, *Ammospermophilus harrisii*), leaving this question unanswered. Behavioural assays (e.g. the distance at which a lizard flees an approaching observer) and opportunistic sightings of potential predators suggest, however, that current predation pressure on *C. dickersonae* is not strong (Plasman, Duchateau & Macedonia, 2007).

Finally, in our analysis of chromatic contrast between blue-bodied collared lizards and nonterrestrial visual backgrounds, in all visual models, male *C. dickersonae* tetrahedral coordinates fell significantly more closely to those of the sea and sky than was observed for blue males in either *C. collaris* population that we tested. Although no males were closely similar in colour to blue skylight, male *C. dickersonae* tetrahedral coordinates clustered in colour space nearer to those of the Sea of Cortéz than did the blue *C. collaris* males, and this was particularly evident in the avian predator visual model. Interestingly, the only context in which male *C. dickersonae* were more visible chromatically to a predator than to conspecifics was when viewed against rocks in the avian predator model (Fig. 7). Realistically, the frequency must be quite low when male *C. dickersonae* are in the line of sight of predators or prey and are framed against the background of the sea, although they may be visually juxtaposed against the blue sky with greater frequency. In any case, increased chromatic similarity to these nonterrestrial backgrounds holds the potential to offset, if only slightly, the probability of being detected by predators and by prey (e.g. including smaller lizard species).

It is reasonable to assume that ornamental blue male body coloration has evolved in *C. dickersonae* and in some *C. collaris* populations through sexual selection, via male–male competition and/or female mate choice (Baird *et al.*, 1997). Although female-like coloration would render male *C. dickersonae* less conspicuous to all viewers against terrestrial backgrounds, such coloration would negate the very social and reproductive advantages that conspicuous ornamental blue coloration may provide them. A reduction in chromatic contrast with nonterrestrial visual backgrounds therefore may represent something of a selective compromise, however small, in helping to offset the social benefits of male conspicuousness with the cost of increased detection by predators and prey.

ACKNOWLEDGEMENTS

We are grateful to J. Husak for supplying the specimens of *M. flagellum* to E.R.L. for microspectrophotometry, to J. Merry for statistical help with SAS, and to M. Hollenshead for field assistance. We also thank N. Hart for providing visual pigment, oil droplet, and ocular media data for *P. cristata*. We are grateful to W. Wells and B. Oldfield for allowing us to use their photographs of *C. dickersonae* in the Supporting information. Permits required to conduct this research were obtained from the Secretaria del Medio Ambiente y Recursos Naturales (SEMARNAT). This research was conducted under IACUC protocol numbers #05-821R (ASU), #00-014 (NAU), and #2001-0115 (Cornell). D.J.K. was supported by the Australian Research Council grant #DP-0557190.

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SUPPORTING INFORMATION

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

Photo 1. Dickerson's collared lizard (*Crotaphytus dickersonae*; female above, male below) basking in the mountains northeast of Bahia Kino, Sonora, Mexico. Note the strong colour contrast of the male's blue coloration against the reddish rocks. The equally striking chromatic orange barring on the female is present only when gravid. Photo by William Wells.
Photo 2. Illustration of the chromatic yellow tail often seen in female *Crotaphytus dickersonae* irrespective of reproductive state. Photo by William Wells.
Photo 3. Adult male *Crotaphytus dickersonae* on coastal rocks near Kino Nuevo. Note not only the extent of blue backgrounds comprising sea and sky, but also the bluish veiling light effect of their radiance on the appearance of Isla Tiburon in the background. Photo by Paul S. Hamilton.
Photo 4. Adult male *Crotaphytus dickersonae* in its natural habitat on Isla Tiburón. Photo by Barney Oldfield.
Photo 5. *Crotaphytus dickersonae* habitat in the hills northeast of Bahia Kino, Sonora, Mexico. Photo by Barney Oldfield.

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Photo 1

Photo 2

Photo 3

Photo 4

Photo 5