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Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards

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Colour pattern variation is a striking and widespread phenomenon. Differential predation risk between individuals is often invoked to explain colour variation, but empirical support for this hypothesis is equivocal. We investigated differential conspicuousness and predation risk in two species of Australian rock dragons, *Ctenophorus decresii* and *C. vadnappa*. To humans, the coloration of males of these species varies between 'bright' and 'dull'. Visual modelling based on objective colour measurements and the spectral sensitivities of avian visual pigments showed that dragon colour variants are differentially conspicuous to the visual system of avian predators when viewed against the natural background. We conducted field experiments to test for differential predation risk, using plaster models of 'bright' and 'dull' males. 'Bright' models were attacked significantly more often than 'dull' models suggesting that differential conspicuousness translates to differential predation risk in the wild. We also examined the influence of natural geographical range on predation risk. Results from 22 localities suggest that predation rates vary according to whether predators are familiar with the prey species. This study is among the first to demonstrate both differential conspicuousness and differential predation risk in the wild using an experimental protocol.

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Colour pattern variation, both within and between populations, is a common and often striking phenomenon found in most animal groups. Well-known examples include guppies, *Poecilia reticulata* (Houde 1997), bivalves (Whiteley et al. 1997), noctuid moths (Bond & Kamil 2002 and references therein) and cichlid fish (Goldschmidt 1996; Deutch 1997; Seehausen et al. 1999). The function and evolution of such colour variation is usually explained by a balance between sexual selection, species recognition and differential predation risk (Endler 1978; Deutch 1997). Under this type of explanation, sexual selection and species recognition are usually thought to favour conspicuous coloration, while

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predation risk favours cryptic coloration (Endler 1978, 1983; Deutch 1997).

Although there is now overwhelming evidence that processes such as sexual selection and species recognition can favour conspicuous coloration (Grant 1965; Williams 1977; Andersson 1994; Houde 1997), empirical evidence for a predation cost associated with conspicuous colours is relatively limited (e.g. Endler 1980, 1983; Götmark 1993; Haskell 1996). In contrast, there is strong empirical and theoretical evidence that seemingly conspicuous coloration does not necessarily result in increased predation risk (Endler 1978; Lythgoe 1979). For example, apparently highly conspicuous patterns can be cryptic in their natural background through disruptive camouflage (Cott 1940; Lythgoe 1979; Merilaita 1998). Conspicuous coloration may also be compensated for by antipredator behaviour (Forsman & Appelqvist 1998; Martin & Lopez 2001) or be avoided by predators because it mimics the coloration of distasteful species (e.g. Brodie 1993; Hinman et al. 1997; Gamberale-Stille 2001; Lindstrom et al. 2001; Riipi et al. 2001) or is unfamiliar (Götmark 1996; Götmark & Olsson 1997; Lindstrom et al. 2000). Experimental evidence using natural systems is therefore

required to establish differential predation risk between colour variants.

A current limitation to the evidence for a relation between differential conspicuousness and differential predation risk is the way in which 'bright' or 'conspicuous' colours are classified. Physiological and behavioural experiments have revealed that the visual systems of many other animal groups differ considerably from that of humans (e.g. Fleishman et al. 1993; Cuthill et al. 2000; Hart 2001b; Marshall 2001). Hence, what may appear conspicuous to a human observer may not be conspicuous to a potential predator, and vice versa. In contrast to recent studies of sexual signalling, most studies of crypsis have not incorporated objective colour measurements or information on the visual system of the predator. In large part, this is because crypsis is difficult to quantify. The way colour is perceived by predators is a function of at least three independent factors: the spectral reflectance of the animal (or particular body regions), the light environment and the visual system of the predator (Endler 1978; Lythgoe 1979). As a result, none of the experimental studies on differential predation risk have determined whether the paints used to create models or manipulate live individuals actually resemble the colour of the prey species, as perceived by predators. This is particularly important given that the great majority of predation experiments have focused on avian predators, which have a very different visual system from that of primates (Cuthill et al. 2000; Hart 2001b).

Our aim in this study was to combine visual modelling with field experiments to test whether different colour variants are differentially conspicuous to the visual system of predators, and whether more conspicuous individuals suffer elevated predation risk in the wild. Australian rock dragons, *Ctenophorus decresii* and *C. vadnappa*, represent a good system for three reasons. First, rock dragons show striking colour pattern variation (Houston 1998). For humans, males of these species vary in throat colour and 'brightness' of the dorsum and flank markings. We refer to males that appear brightly coloured and conspicuous to us as 'bright' and males that appear less colourful (mostly brown) and more cryptic as 'dull'. Second, rock dragon predators are mainly visually oriented avian predators, such as corvids (mainly the little crow, *Corvus bennetti*), kookaburras, *Dacelo novaeguineae*, and the Australian kestrel, *Falco cenchroides*, for which lizards are an important part of the diet (Higgins 1993). Adult dragons have been observed to react to and flee from these predators (Gibbons 1977; Gibbons & Lillywhite 1981). Third, rock dragons inhabit environments that are structurally simple and spend most of their emergent hours basking and displaying on boulders in full sun (Gibbons 1977). Coloration, therefore, is likely to be a factor determining predation risk in these lizards.

Using this system, we sought to answer the following questions. (1) Are 'bright' males more conspicuous to avian predators? (2) Are 'bright' males more likely to suffer predator attacks? (3) Does natural geographical range play a role in differential predation risk? Our goal was to assess the role of natural selection for crypsis, through variation in predation risk, in the evolution of

colour pattern differences within and between *C. decresii* and *C. vadnappa*. If crypsis is important in the distribution and maintenance of colour variation, one prediction is that each species should be most cryptic in its own habitat (Endler 1978, 1983). Predation risk, however, may be influenced by geographical variation in the type and abundance of potential predators (Endler 1980; Downes & Adams 2001). For these reasons, we used data from 11 independent localities within the natural ranges of each species.

METHODS

Study Species

The *C. decresii* species group (rock dragons) comprises five closely related species (*C. decresii*, *C. fionni*, *C. rufescens*, *C. tjantjalka* and *C. vadnappa*) that differ markedly in coloration, especially males (Houston 1998). While female colour patterns resemble the colour and texture of their respective substrates, males vary in their apparent degree of crypsis both within and between populations and species (Houston 1998). Most populations have both bright and dull males, with intermediate gradations. Brighter males of *C. vadnappa* and *C. decresii* have an aqua-blue or grey-blue dorsum and bright orange and black flank markings. Duller males have a brown dorsum and dull orange and black markings. *Ctenophorus vadnappa* is more strikingly coloured with numerous vertical stripes, while *C. decresii* has single dorsolateral orange stripes that extend only partway along the body. The flank markings on both species extend well on to the dorsal surface of the lizard and are clearly visible from above.

To determine how variation in lizard coloration is perceived by birds, we used a bright and dull male *C. decresii* from Telowie Gorge in the southern Flinders Ranges and a bright and dull male *C. vadnappa* from Blinman Creek in the northern Flinders Ranges. We created lizard replicas to match these individuals as closely as possible by visual comparison of reflectance spectra. We selected representative bright and dull males from a group of 40 males of each species that had been captured by noose and retained in captivity for behavioural studies. Males were housed individually in outdoor enclosures (50×80 cm) containing a stack of bricks or tiles at either end for basking and shelter. All lizards were maintained on a diet of mealworms (*Tenebrio* spp.) dusted with multivitamin and calcium powder, supplemented with crickets, maggots, cockroaches and locusts, and provided with water ad libitum. Lizards used for this study remain in captivity and will ultimately be lodged with the South Australian Museum. We had permits for the study from the South Australian National Parks, University of Queensland and Queensland National Parks.

Spectrophotometry

To measure lizard spectral reflectance we used an Ocean Optics S2000 spectrophotometer. We measured reflectance normal to the surface and, for illumination, we held

a deuterium–tungsten DT1000 light source at a 45° angle following established protocols (Endler 1990; Cuthill et al. 1999). Measurements were expressed relative to a 'labsphere' certified 99% white reflectance standard. Lizards were measured after they had been allowed to reach their preferred body temperature (35–40°C), because agamid lizards are generally darker when cold (Cooper & Greenberg 1992). Lizards that showed signs of an opaque film characteristic of being close to shedding were not used. We measured three body regions: dorsum, orange flank markings (Fig. 1a, b) and black flank markings. Measurements were taken at three locations for each body region and the mean was used as the representative spectrum. All spectral reflectance measurements were taken within a month of the lizards being in captivity.

Backgrounds were sampled from rocks near or upon which lizards were first sighted and rocks were returned to the laboratory for reflectance measurement. Measurement of background spectral reflectance followed the same protocol as that used for lizard reflectance spectra. We took the average of three measurements for each background colour and then averaged reflectance spectra for each background colour for each locality to give a mean background rock reflectance (Fig. 1a, b). All spectral data (lizards and backgrounds) were averaged over each 5-nm interval to facilitate data manipulation.

To measure irradiance we used an Ocean Optics S2000 spectrophotometer and an Ocean Optics cosine adaptor head, using standard protocols (Endler & Thery 1996). Irradiance was measured in full sun, under a cloudless sky (Fig. 1c).

Visual Modelling

Visual systems encode contrast signals, that is, a colour relative to a background (Vorobyev et al. 1998). We calculated 'contrast' of the colour of each lizard body region relative to its natural background, as perceived by potential avian predators. Chromatic 'contrasts' were calculated following Vorobyev et al.'s (1998) model, which describes the discriminability of two colours against a chromatic background by their 'distance', ΔS, in perceptual space, where perceptual space is defined by quantum catches of receptors. This model can be modified to calculate discriminability of a single colour against a chromatic background. We used this model because it accurately predicts behavioural data for a broad range of animal taxa, including birds, while making minimal assumptions (Vorobyev & Osorio 1998). It allows colour discrimination to be predicted in any animal provided spectral sensitivities and relative numbers of photoreceptors are known (Vorobyev & Osorio 1998).

To determine how conspicuous the different male colorations appear to potential avian predators, we used spectral sensitivity data from Hart et al. (2000) for the blue tit, *Parus caeruleus* (Fig. 1d), which incorporates both the spectral absorption of the cone and the transmission properties of the associated oil droplet. Blue tit spectral sensitivities were used to approximate those of avian predators. There is no complete published spectral sensitivity data for the main predators of rock dragons
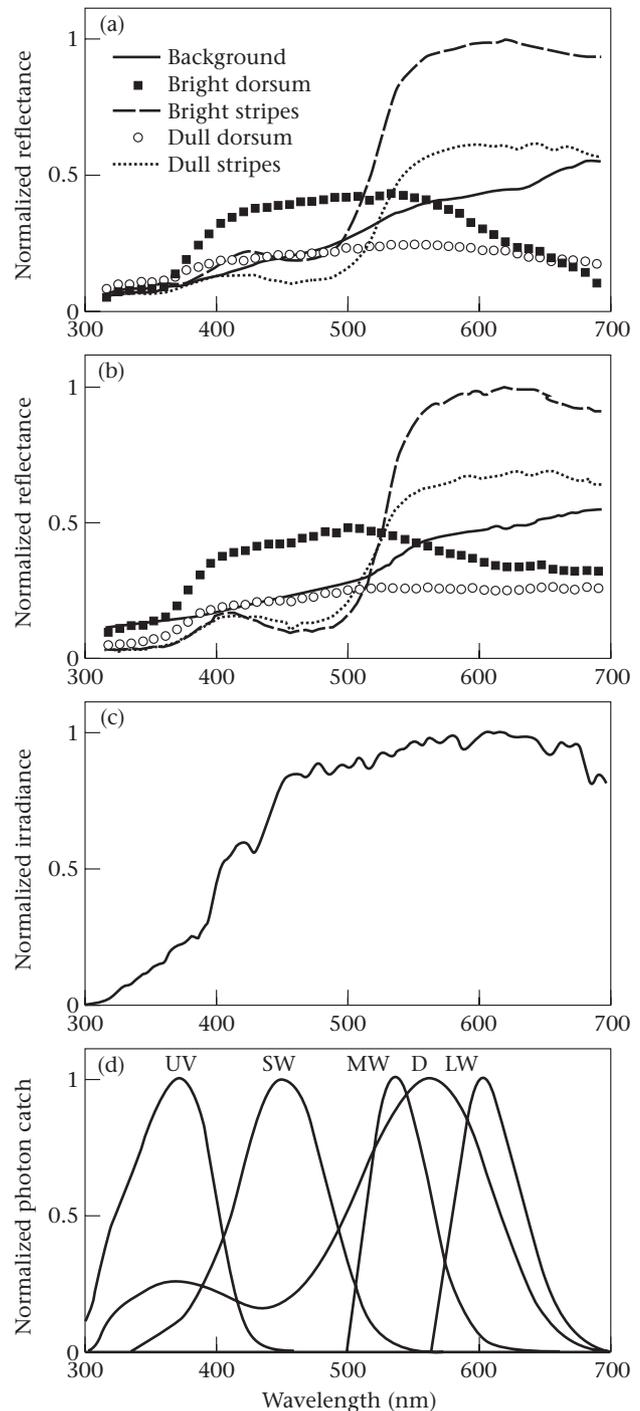

Figure 1. Reflectance spectra used to calculate achromatic and chromatic contrasts (see Figs 3 and 4). Mean background, bright and dull male dorsal surfaces, and orange flank markings normalized to 'bright orange' for (a) *C. decresii* and (b) *C. vadnappa*. (c) Irradiance under sunny conditions. (d) Spectral sensitivities of the four single cones: ultraviolet sensitive (UV), short wavelength sensitive (SW), medium wavelength sensitive (MW) and long wavelength sensitive (LW), and the double cone (D) for the blue tit, (data from Hart et al. 2000) used in contrast calculations.

(corvids, raptors or kingfishers). However, birds are highly conserved in their visual pigment characteristics (reviewed in Hart 2001b), so the spectral sensitivities of

blue tits are likely to be a good approximation of those of any avian predator. The greatest interspecific variation in avian cone sensitivities is in the ultraviolet- or violet-sensitive cone (Hart 2001b). Because the dorsal and flank markings of rock dragons have very low reflectance over these wavelengths (Fig. 1a, b), any small discrepancy in the spectral sensitivities of blue tits and avian lizard predators should have little effect on the results.

Model calculations were as follows. First, we calculated the total output (receptor quantum catches) for each avian cone type i for each lizard and background colour by the following equation, which corresponds to equation (1) in Vorobyev et al. (1998):

$$Q_i = \int R_i(\lambda)S(\lambda)I(\lambda)\mathrm{d}\lambda \tag{1}$$

where λ represents wavelength, R_i is the spectral sensitivity of cone type i, $S(\lambda)$ is the fraction of incident photons reflected from the colour patch, integrated over the visual spectrum (in this case 320–700 nm) and $I(\lambda)$ is the spectrum of light entering the eye (irradiance on the colour patch). Irradiance (I) and spectral sensitivities for each cone R_i were normalized to one. This calculation was done for the lizard colour patch to obtain Q_i^t (receptor quantum catches for the target, t), as well as for the background colour patch, to obtain Q_i^b (receptor quantum catches for the background, b), for each cone type i. Receptor quantum catches for the target were then normalized to the background to give the value $q_i = Q_i^t/Q_i^b$.

The signal of the receptor channel f_i is proportional to the natural logarithm of the quantum catch (equation 4 of Vorobyev et al. 1998: $f_i = \ln q_i$). For the background b, $q_i^b = 1$, so $f_i^b = 0$. Therefore, for a model of discriminability of a single target against a background, the difference in the signal of the receptor channels for target and background, Δf_i, is equal to f_i^t, which can be substituted directly into equation (8) of Vorobyev et al. (1998) giving:

$$\Delta S^2 = (\omega_1 q_2)^2(f_4^t - f_3^t)^2 + (\omega_1 q_3)^2(f_4^t - f_2^t)^2$$
$$+ (\omega_1 q_4)^2(f_3^t - f_2^t)^2 + (\omega_2 q_3)^2(f_4^t - f_1^t)^2 \tag{2}$$
$$+ (\omega_2 q_4)^2(f_3^t - f_1^t)^2 + (\omega_3 q_4)^2(f_2^t - f_1^t)^2$$
$$/((\omega_1 q_2 q_3)^2 + (\omega_1 q_2 q_4)^2 + (\omega_1 q_3 q_4)^2 + (\omega_2 q_3 q_4)^2)$$

where ΔS is the 'distance' between two colours (in this case target and background) for tetrachromatic vision and ω_i is the noise-to-signal ratio (Weber fraction) for the colour channel i. The Weber fraction was calculated using equation (10) of Vorobyev et al. (1998), valid for bright illumination conditions:

$$\omega_i = v_i/\sqrt{\eta_i} \tag{3}$$

where v_i is the noise-to-signal ratio of a single cone and η_i is the number of receptor cells of type i within the receptor field. We used Vorobyev et al.'s (1998) estimate of ω_i for the long-wavelength-sensitive cone (LWS) of the Pekin robin, *Leiothrix lutea* ($\omega_4 = 0.05$) and estimates of η_i from anatomical data (Hart 2001a) to derive ω_i for the remaining receptor classes. The estimate of $\omega_4 = 0.05$ for the Pekin robin is an empirical estimate based on behavioural data (see Appendix 1 in Vorobyev et al. 1998).

Because relative values of ω_i are defined by the relative proportions of cone types, our assumption that $\omega_4 = 0.05$ does not affect the qualitative results of our model.

The ratio of photoreceptor classes (values of η_i) varies greatly between birds (Hart 2001a) and is currently not available for the predators of rock dragons. Relative proportions of photoreceptor types in birds are a function of both phylogeny and ecology (Hart 2001a). We used available values of η_i for the European blackbird, *Turdus merula*, which resembles one of the main predators of rock dragons, the little crow (Hart 2001a) in both phylogeny and ecology (η_i for the ultraviolet-sensitive (UVS) cone=1; short-wavelength-sensitive (SWS) cone=1.71; medium-wavelength-sensitive (MWS) cone=2.14; long-wavelength-sensitive (LWS) cone=1.89). To check how sensitive the results are to the choice of η_i, we also performed the calculations with the η_i of the sacred kingfisher, *Todiramphus sanctus*, and the blue tit. It appeared that model calculations are dependent on the value of Weber fractions to a limited extent, such that the choice of η_i does not affect qualitative results.

The above model of chromatic contrast disregards achromatic signal, which is likely to be important for prey detection (Osorio et al. 1999; Hart 2001b). Neural processes coding achromatic signals may be additive or by a single receptor type (Osorio et al. 1999). In birds, double cones have been implicated in the perception of luminosity (Campenhausen & Kirschfeld 1998; Hart 2001b). Although the mechanisms coding achromatic signals in birds are still poorly understood (Osorio et al. 1999; Hart 2001b), evidence suggests they are primarily a function of double cones rather than an additive function of single cones (Campenhausen & Kirschfeld 1998). We therefore estimated achromatic (luminosity) contrast as f_D/ω_D where the subscript D represents the blue tit double cone (M. Vorobyev, personal communication). Because ω_D is the same for all targets, it does not affect relative achromatic contrasts and can be disregarded for the purposes of comparing relative achromatic contrasts, represented by the value f_D.

Lizard Models

We made lizard models from dental stone (plaster) using latex moulds of four naturally deceased *C. decresii* males with snout–vent lengths to within 2 mm of each other (76–78 mm), to create 200 almost identical casts. Male *C. decresii* and *C. vadnappa* do not differ in any morphological trait apart from coloration and minor head scalation characters (Houston 1974; Gibbons 1977), so the use of *C. decresii* males to make moulds for both species should not affect our results. Casts from the four moulds were randomized with respect to the colours they were painted. Although plasticine is often used for predation experiments so that predators can be identified from the indentations they leave (Brodie 1993; Castilla & Labra 1998), we used plaster because it provided a paintable medium that would not melt on rocks that may reach temperatures of over 60°C. Models were realistic enough that wild lizards approached and head-bobbed to them and on several occasions a female was found basking next
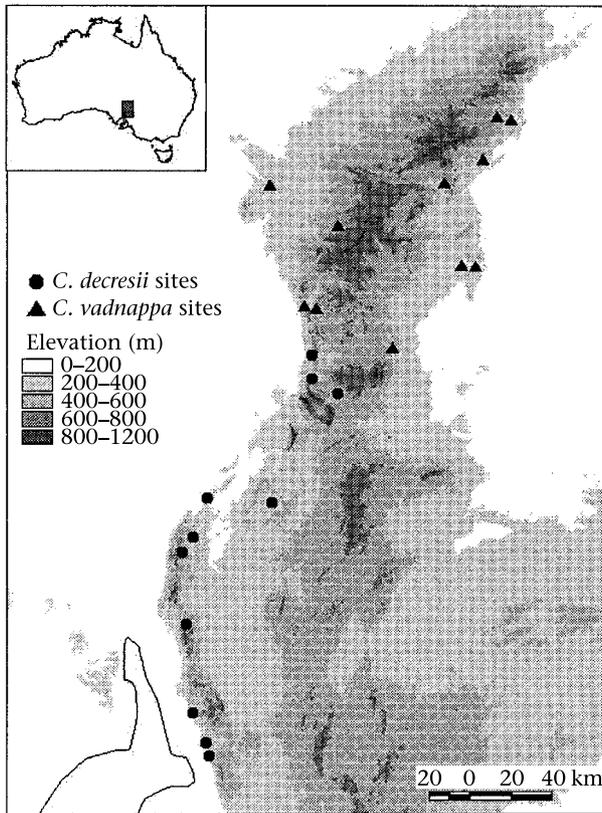
Figure 2. Sites chosen for predation experiments, Flinders Ranges, South Australia. Eleven sites, at least 5 km apart, were chosen for each species.

to a male model. An attack by a little crow was observed on one occasion. Attacks by Australian kestrels have also been observed on similar models of these species (Gibbons & Lillywhite 1981).

To paint models we used acrylic paints that matched as closely as possible the colour of the animals. We matched colours by measuring the spectral reflectance of paints and adjusting the paints to match the reflectance spectra of lizards as closely as possible. We calculated avian adapted cone responses to model colours against natural backgrounds using the same methods as above. Four types of models were created: bright and dull males of both *C. vadnappa* and *C. decresii*.

Experimental Design

We used a complete randomized block design: 100 models (25 of each colour type) were placed in random order on top of boulders about 5 m apart. We standardized sites by placing models along the mid-slope of gorges (2–4 m above the creek bed) because predation risk may differ according to topographical position. Models were exposed to predators for 1 day per site (put out at 0800 and collected at 1600 hours). A total of 22 sites were chosen, 11 occupied by *C. vadnappa* and 11 by *C. decresii* (Fig. 2). Sites were separated by at least 5 km. Although some of the sites were in a region where both species occur in broad sympatry, the two species rarely occur in

fine scale sympatry (Gibbons & Lillywhite 1981). Sites were chosen that were inhabited by one species only as indicated by both locality records from the South Australian Museum and personal observation.

We anchored models to boulders with a tent peg attached to fishing line and a chalk mark was placed beneath each model. Attacks, defined as unambiguous movements, that is, a movement of at least 5 cm from the original chalk mark, were counted at the end of each day. On most occasions, models that were moved had been flipped over, crushed, broken or knocked off the rocks and on one occasion a model was found hanging from a nearby tree. To check that models could not be moved in this way by other rock dragons, we placed one model in each of 80 enclosures, each containing one male dragon (40 *C. decresii* and 40 *C. vadnappa*). Enclosures represented artificially small territories (50 × 80 cm) to maximize the chances of a dragon moving a model. Five models (6%) were moved perceptibly, but all of these movements were slight, none of the models having been flipped over or damaged. Given this evidence, and the weight and density of the dental stone models, we believe it is unlikely that any of our cases of putative predator attack were due to the action of other dragons.

Cases of predator attack are also unlikely to be caused by any other disturbance. The study sites were in a remote, semiarid region of Australia, with many of the sites accessible only by four-wheel drive. During our field work, we rarely encountered another human being at the study sites. Snakes, the other predator of rock dragons, hunt using olfactory and temperature cues rather than visual cues and would be unlikely to move plaster models. Finally, aggressive interspecific interactions with other lizard species and nonpredators have not, to our knowledge, been observed and are therefore unlikely to account for the attack rates reported here.

Proportions of each model type attacked per site were arcsine transformed and analysed with a three-factorial ANOVA with brightness (bright or dull), species (*C. decresii* or *C. vadnappa*) and range (*C. decresii* range or *C. vadnappa* range) as factors. Range was tested against sites nested within range as the error term.

RESULTS

Are Bright Males More Conspicuous?

Raw reflectance spectra of male lizards and their backgrounds show qualitatively that dull males are more closely matched to their background than bright males are (Fig. 1a, b) for both species. The visual models confirm that to birds, the dorsum and orange markings of dull individuals resemble the background more closely than those of bright individuals (Figs 3, 4).

The magnitude of chromatic contrast values was consistently greater for bright than dull males in both species, although the degree of difference was less for *C. decresii* than for *C. vadnappa* (Fig. 3). Chromatic contrasts of the orange flank markings of bright males were 30% greater in *C. decresii* and 40% greater in *C. vadnappa* than those of dull males. Chromatic contrasts of the
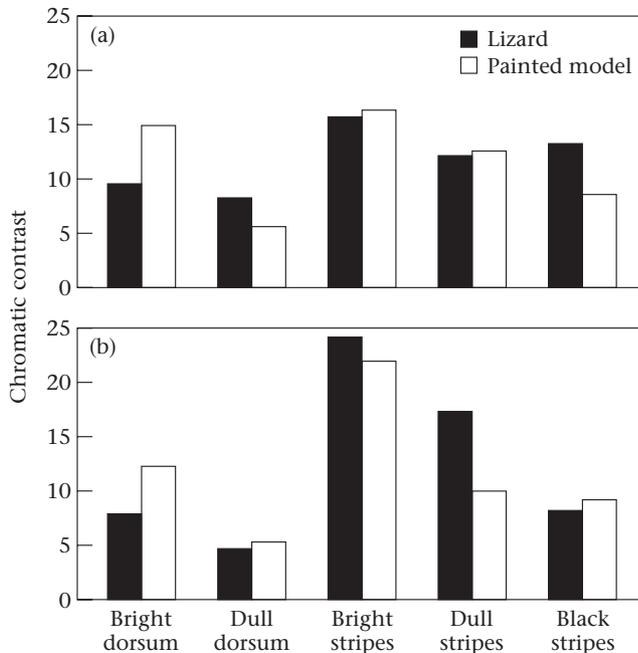
Figure 3. Chromatic contrast (ΔS) of representative bright and dull male lizards and painted models against natural background measured in receptor quantum catches for (a) *C. decresii* and (b) *C. vadnappa*.
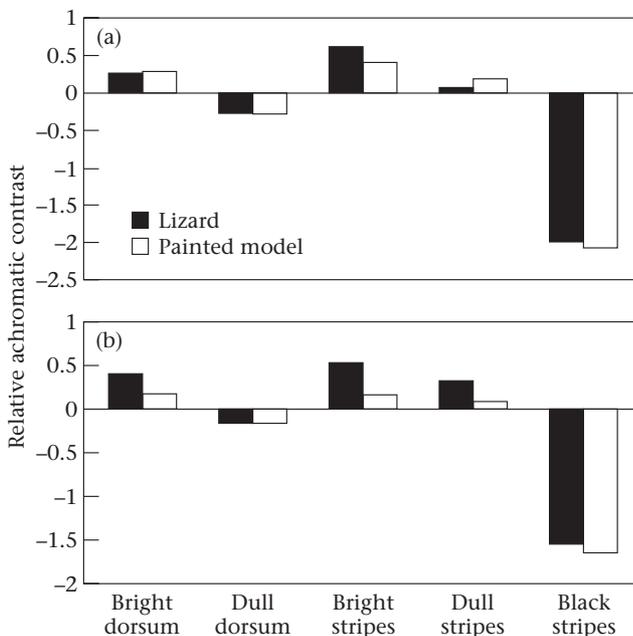

Figure 4. Relative achromatic contrast (f_D) of representative bright and dull male lizards and painted models against natural background measured in receptor quantum catches for (a) *C. decresii* and (b) *C. vadnappa*.

dorsum of bright males were 15% greater in *C. decresii* and 75% greater in *C. vadnappa* than those of dull males. Chromatic contrasts for the orange flank markings of both bright and dull *C. vadnappa* were much greater than those of *C. decresii* against their own backgrounds (Fig. 3). For the dorsum, however, chromatic contrasts were

slightly greater for *C. decresii* than *C. vadnappa* against their own backgrounds (Fig. 3).

In *C. decresii*, relative achromatic contrast for the orange markings of bright males was more than seven times that of dull males (0.6 and 0.08, respectively; Fig. 4a). However, achromatic contrasts for the dorsum of bright and dull males were similar. The dorsum of bright males had higher luminosity than the background (positive contrast) and the dorsum of dull males had lower luminosity than the background (negative contrast; Fig. 4). For *C. vadnappa*, achromatic contrasts for both the orange flank markings and the dorsum of bright males were approximately double the magnitude of those of dull males (Fig. 4b). For both species, the black markings common to both bright and dull males showed the greatest achromatic contrast, with values of −2.0 for *C. decresii* and −1.56 for *C. vadnappa* (Fig. 4). Hence, these models of achromatic and chromatic contrast predict that both bright and dull males appear conspicuous to birds to some extent, because dull males are not perfectly matched to their backgrounds. However, the models also predict that bright males should be relatively more conspicuous to birds than dull males.

There was a moderately close correspondence between the chromatic contrasts of real lizards and the models (Figs 3, 4). The models should therefore be adequate approximations of what an avian predator would perceive on viewing a typical bright and dull lizard. The difference in achromatic contrast between bright and dull painted models was generally less than the difference between bright and dull real lizards. However, the opposite was true for chromatic contrast. The difference between bright and dull painted models was greater than for real lizards, particularly for the dorsum. Considering both chromatic and achromatic contrasts, results of predation experiments should be adequate approximations of the relative predation cost of conspicuous coloration in rock dragons.

Do Bright Males Suffer More Attacks?

Of 113 unambiguous attacks, 47 were on bright *C. vadnappa* models, 24 on dull *C. vadnappa*, 28 on bright *C. decresii* and 14 on dull *C. decresii* models. There were no predator attacks at one site (9 km north-northeast of Wipena Pound), so statistical tests were performed for 21 sites, 10 within the range of *C. decresii* and 11 within the range of *C. vadnappa*. Overall, bright models were attacked significantly more often than dull models (Table 1). 'Brightness' was a main effect so this pattern holds true over both geographical ranges and for both species.

Is Range Important?

Because there was a significant range × species interaction (Table 1), we carried out a Tukey–Kramer multiple comparison (Sokal & Rohlf 1995). In the range of *C. vadnappa*, *C. vadnappa* models were attacked significantly more often than *C. decresii* models ($t_{57}=3.24$, $P=0.01$; Fig. 5), but in the range of *C. decresii* there was no significant

Table 1. ANOVA comparing patterns of predator attacks on different lizard model types in the Flinders Ranges, Australia

Factor	Sum of squares	df	F	P
Range*	97.83	1	0.92	0.35
Species	191.51	1	3.07	0.08
Range×species	459.39	1	7.37	0.009
Brightness	440.45	1	7.07	0.01
Range×brightness	20.09	1	0.32	0.57
Species×brightness	17.36	1	0.28	0.6
Range×species×brightness	16.66	1	0.27	0.61
Site (range)	2022.02	19	1.71	0.06
Error	3551.18	57		

*Range was tested against site nested within range as the error term.

difference in attack rate on the two species ($t_{57}=0.66$, $P=0.91$; Fig. 5). Furthermore, *C. vadnappa* models were attacked significantly more often in their own range (northern Flinders Ranges; $t_{57}=2.81$, $P=0.03$) than in the southern Flinders Ranges, whereas *C. decresii* was attacked at a similar rate in both regions (Fig. 5).

DISCUSSION

Our first aim in this study was to test whether male dragons that varied in coloration were differentially conspicuous to avian predators. Results of the visual models predict that the dorsum and orange markings of bright males are more conspicuous to an avian predator than those of dull individuals. This is because bright males contrast more in terms of both achromatic and chromatic signals than dull males against the natural rock background. The difference between bright and dull males is also evident to the human observer because there is almost no UV component to the dorsal and flank markings of these dragons.

Estimates of relative conspicuousness based on the visual modelling presented here have two types of limitation. First, the model makes several assumptions about

Figure 5. Mean arcsine transformed percentages±SE of models attacked per site for each species in each geographical range.

how birds perceive colour, the most important of which are that colour-coding mechanisms in birds are by unspecified opponent mechanisms (that is, by comparison of the outputs of all possible combinations of photoreceptor types) and colour discrimination is limited by photoreceptor noise. Models of colour discrimination based on these assumptions accurately predict behavioural performance of colour vision in a variety of animal groups, including birds (Vorobyev & Osorio 1998). The other important assumption is that neural processes coding achromatic signals are a function of double cones only. This assumption fits best with what is currently known about avian visual systems. Furthermore, alterations to the model are unlikely to change our results qualitatively because of the relatively large differences between bright and dull males.

The second type of limitation of the model is that it extrapolates from passerine species to all avian predators, although raptors and passerines are known to differ in their visual acuities (Reymond 1987). Whether they also differ in their colour discrimination abilities is not known, although spectral sensitivities of passerine and nonpasserine species are similar (Hart 2001b). In general, the visual systems of different bird species will be adapted to different visual tasks (Hart 2001b). For these reasons, it is important to test empirically the predictions of visual models.

Our second aim was to test whether the greater conspicuousness of bright males leads to higher predation risk. This was necessary for the reasons already mentioned and because it does not automatically follow that differential conspicuousness results in differential predation risk in the wild, particularly where species are aposematic, mimic noxious prey, or where colour plays a minor role in prey detection relative to other factors such as movement. We found that the conspicuous bright models of both species suffered significantly more predator attacks than the dull models. Although we cannot be certain that attacks were by avian predators, the evidence suggests that attacks by other predators or conspecifics are so unlikely as to be safely disregarded (see Methods).

Given that our results almost certainly reflect the actions of avian predators, these predation experiments
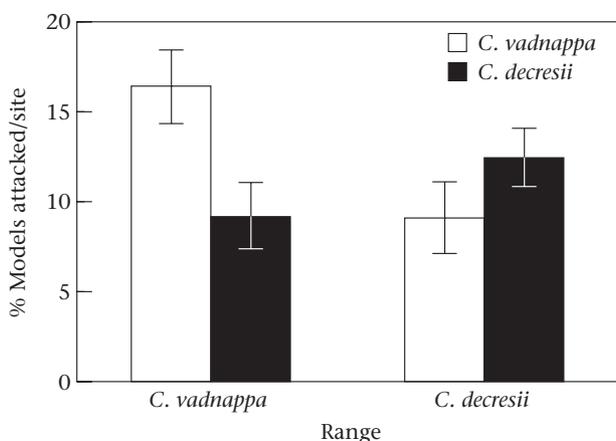
suggest that coloration per se is an important cue used by avian predators in prey detection. Experimental evidence from at least one lizard species suggests that predation risk is influenced primarily by the probability of detection by predators, rather than the probability of capture after detection (Schwarzkopf & Shine 1992). Our results, therefore, strongly suggest that there is a cost associated with being 'bright', in terms of increased risk of predation by avian predators.

Our third aim was to test whether geographical variation in predation rates could explain the evolution of colour pattern differences between *C. vadnappa* and *C. decresii*. Overall predation rates did not differ between the ranges of the two species, suggesting that geographical variation in the abundance of predators cannot account for colour pattern differences between *C. vadnappa* and *C. decresii*. However, our results also indicate that the role of natural geographical range may be more complex than expected. *Ctenophorus vadnappa* suffered higher predation risk than *C. decresii* in its own range, contrary to initial predictions that each species should be more cryptic in its own habitat. Furthermore, for *C. vadnappa*, predation risk was significantly higher in its own range than within the neighbouring species' range. A possible explanation for why predation risk for *C. vadnappa* was low in the southern Flinders Ranges (range of *C. decresii*) is dietary conservatism or a form of frequency-dependent predation. *Ctenophorus decresii* occurs at relatively low densities in broad-scale sympatry with *C. vadnappa* over much of the northern Flinders Ranges. Thus, predators in the northern Flinders Ranges may have had exposure to both species and attacked *C. vadnappa* models at greater frequencies because they are more conspicuous. In the southern Flinders Ranges, however, where *C. vadnappa* is absent and *C. decresii* is common, predators would not have had exposure to *C. vadnappa* and would therefore not have formed a search image for this species. Thus, in the southern Flinders Ranges, predators confronted with an unfamiliar species may have avoided them or preferentially chosen the familiar *C. decresii*. This hypothesis is supported by substantial experimental evidence for avian predators avoiding novel prey (Götmark 1996; Götmark & Olsson 1997; Marples et al. 1998; Lindstrom et al. 2000). Furthermore, recent theoretical work supports the importance of frequency-dependent predation in generating and maintaining colour polymorphism (Bond & Kamil 2002).

Two factors that may be important in determining predation rates but were not considered in this study are behaviour and pattern. First, the likelihood of being detected and attacked by a predator will depend on both conspicuous coloration and behaviour (Forsman & Appelqvist 1998). Differences in conspicuousness may be compensated for behaviourally by variation in predator avoidance behaviours, or by microhabitat selection to maximize crypsis, resulting in equal predation rates on different colour variants (Forsman & Appelqvist 1998; Martin & Lopez 2001). However, predator avoidance behaviours used to compensate for elevated predation risk, such as extra vigilance, altered foraging movements or reduced basking, are likely to be costly (Martin & Lopez

2001). Therefore, increased predation risk may exert selection pressure on conspicuous coloration through indirect, rather than direct costs, as has been shown empirically for another lizard species (Martin & Lopez 2001). Microhabitat selection can also compensate for apparently conspicuous coloration and warrants further investigation in this system (Endler 1993). Our results showing differential conspicuousness and predation risk of colour variants in the absence of microhabitat selection provide the basis for further studies examining the role of natural selection in maintaining intrapopulation colour variation.

The second factor that was not incorporated into this study, but may affect relative conspicuousness, is pattern. Pattern can enhance crypsis either by mimicking the pattern of the background or, in the case of disruptive coloration, by breaking up body lines when one or more of the colours matches the background (Cott 1940; Marshall 2000). Neither of these, however, adequately explains pattern in *C. vadnappa* and *C. decresii* males. Flank patterns are striped rather than granular like the rock background. Furthermore, neither flank colour matches the background in bright males, although in dull males, the dull orange flank markings can be a similar colour to orange-brown rocks. Pattern can also enhance crypsis if patches of an animal's colour pattern appear to merge at a distance, and the intermediate colour matches the background. Nevertheless, our results show that colour per se is an important determinant of predation risk: for each species, bright models were attacked significantly more often than dull models despite sharing the same pattern.

Although the fitness costs and benefits associated with each colour variant are not known, our results suggest that, unlike some cases of colour polymorphism (Bond & Kamil 2002), crypsis alone cannot explain the evolution and maintenance of colour variation in these species. Our results show that rock dragon colour variants are differentially conspicuous to their avian predators and that this translates to differential predation risk. It remains to be discovered, in this system, whether the cost associated with conspicuous coloration is offset by an advantage in terms of female choice or social dominance.

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