

EVOLUTION OF COLOR VARIATION IN DRAGON LIZARDS: QUANTITATIVE TESTS OF THE ROLE OF CRYPSIS AND LOCAL ADAPTATION

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Abstract.—Many animal species display striking color differences with respect to geographic location, sex, and body region. Traditional adaptive explanations for such complex patterns invoke an interaction between selection for conspicuous signals and natural selection for crypsis. Although there is now a substantial body of evidence supporting the role of sexual selection for signaling functions, quantitative studies of crypsis remain comparatively rare. Here, we combine objective measures of coloration with information on predator visual sensitivities to study the role of crypsis in the evolution of color variation in an Australian lizard species complex (*Ctenophorus decresii*). We apply a model that allows us to quantify crypsis in terms of the visual contrast of the lizards against their natural backgrounds, as perceived by potential avian predators. We then use these quantitative estimates of crypsis to answer the following questions. Are there significant differences in crypsis conspicuousness among populations? Are there significant differences in crypsis conspicuousness between the sexes? Are body regions “exposed” to visual predators more cryptic than “hidden” body regions? Is there evidence for local adaptation with respect to crypsis against different substrates? In general, our results confirmed that there are real differences in crypsis conspicuousness both between populations and between sexes; that exposed body regions were significantly more cryptic than hidden ones, particularly in females; and that females, but not males, are more cryptic against their own local background than against the background of other populations. Body regions that varied most in contrast between the sexes and between populations were also most conspicuous and are emphasized by males during social and sexual signaling. However, results varied with respect to the aspect of coloration studied. Results based on chromatic contrast (“hue” of color) provided better support for the crypsis hypothesis than did results based on achromatic contrast (“brightness” of color). Taken together, these results support the view that crypsis plays a substantial role in the evolution of color variation and that color patterns represent a balance between the need for conspicuousness for signaling and the need for crypsis to avoid predation.

Key words.—Color, crypsis, geographic variation, sexual dichromatism, visual contrast.

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Theory predicts that animal color patterns represent a compromise between selection for signaling functions (e.g., sexual signals, status or territorial signals, and species recognition signals) and natural selection for defense against visually oriented predators (Endler 1978; Lythgoe 1979; Andersson 1994; Houde 1997; Espmark et al. 2000). According to this view, differences in coloration between species and populations or between sexes and age classes are the result of subtle differences in the balance between natural and sexual selection (e.g., Endler 1978; 1983; Houde 1997).

Although there is now a large body of empirical and comparative evidence to support the hypothesis that variation in the strength of sexual selection can lead to differences in coloration between the sexes and between populations (e.g., Hill 1994; Endler and Houde 1995; Baird et al. 1997; Bennett and Owens 2002; Kwiatkowski and Sullivan 2002), quantitative studies on the relative role of crypsis are comparatively rare (but see Endler 1984; Merilaita 1998; Storfer et al. 1999). In addition, most previous studies of crypsis have relied on human-oriented indices (e.g., Steward 1977; Gotmark 1993;

Gotmark and Hohlfalt 1995) or estimates of color contrast that do not consider the receiver’s visual system (e.g., Majerus et al. 2000; Macedonia 2001; Macedonia et al. 2002; Heindl and Winkler 2003). However, because both physiological and behavioral experiments have revealed that the visual systems of different groups of animals vary greatly (e.g., Fleishman et al. 1993; Cuthill et al. 2000; Hart 2001a; Marshall 2001; Loew et al. 2002), extrapolation from measures of crypsis based on raw reflectance spectra or the human visual system may be prone to error. As several authors have made clear, crypsis should really be measured from the perspective of the likely predator (Endler and Basolo 1998; Andersson 2000; Endler 2000).

To date, deriving estimates of crypsis or conspicuousness as perceived by nonhuman predators has largely been limited by availability of data on the visual systems of different types of receiver, as well as by our understanding of the neural processing mechanisms contributing to color perception. Fortunately, it is now possible to derive estimates of conspicuousness based on new models of animal color perception, in conjunction with objective measurements of spectral reflectance, ambient light, and increasingly available physiological information on the visual systems of different animal species. For instance, Vorobyev and Osorio (1998; Vorobyev

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et al. 1998) have recently developed a visual model that allows the color discrimination of any animal to be predicted from information on spectral sensitivities and relative numbers of photoreceptors in the retina, while making relatively few additional assumptions. Using this model it is possible to calculate objective measures of chromatic (“hue”) and achromatic (“brightness”) contrast of animal color patterns against natural backgrounds as viewed by the receiver’s visual system under natural illumination (Vorobyev et al. 1998; Stuart-Fox et al. 2003). So far, such receiver-relative measures of contrast have only been used to make qualitative statements about colors appearing more or less conspicuous to a receiver (e.g., Storfer et al. 1999; Marshall 2000; Stuart-Fox et al. 2003). Here, we extend the use of such measures to a quantitative examination of variation in crypsis and conspicuousness, as perceived by a predator.

The overall aim of this study is to use the Vorobyev-Osorio visual model to test quantitatively for evidence of adaptive crypsis and conspicuousness in populations of dragon lizard of the *Ctenophorus decresii* species complex. We ask four specific questions: (1) Are there significant differences in conspicuousness among populations? (2) Are there significant differences in conspicuousness between the sexes? (3) Are body regions “exposed” to visual predators more cryptic than those body regions “hidden” from predators? (4) Is there evidence for local adaptation with respect to crypsis against different substrates?

The *Ctenophorus decresii* species group is ideal for testing for evidence of adaptive crypsis because the species show striking patterns of sexual and geographic variation in coloration, live in a relatively simple visual environment and are subject to predation by visually oriented diurnal birds (Gibbons and Lillywhite 1981). Furthermore, it has already been proposed that geographic variation in both male and female color patterns can be explained by natural selection for background color matching (Houston 1974; Gibbons and Lillywhite 1981). In sympatric populations of *C. decresii* and *C. vadrappa*, there appears to be fine-scale habitat segregation between the species based on rock background color (Gibbons and Lillywhite 1981). Experimental tests showed that both males and females of these species from sympatric populations chose backgrounds against which they were most camouflaged (Gibbons and Lillywhite 1981). Based on this evidence, Gibbons and Lillywhite (1981) proposed that color differentiation, and ultimately speciation in the group, had occurred due to natural selection for background color matching.

The *Ctenophorus decresii* species complex is a monophyletic group comprising five closely related species (*C. decresii*, *C. fionni*, *C. rufescens*, *C. tjantjalka*, and *C. vadrappa*) that differ primarily in coloration (Houston 1974, 1998; Melville et al. 2001). All members of the group are territorial and use complex displays for social and sexual signaling. These displays emphasize the coloration of the throat, chest, and flank regions through head bobs, and front and hind leg pushups performed in lateral presentation with the body laterally compressed (Gibbons 1979). Most of the time, only the head, dorsum, and flank (lateral and dorso-lateral) body regions are visible to avian predators. Thus, selection for crypsis is likely to influence the coloration of these body

regions more than ventral regions exposed only during interactions, for which selection for other signaling functions may be more important. We therefore examine conspicuousness of ‘hidden’ and exposed body regions in order to compare the roles of selection for crypsis and selection for signaling.

To answer our four questions, we examine relative background color matching in males and females using six populations belonging to the three species that display the most color variation within the group, *C. decresii*, *C. fionni* and *C. vadrappa*. We use measures of chromatic and achromatic contrast of lizards against their natural backgrounds as viewed by potential avian predators under natural illumination. For simplicity, we focus on background color matching and degree of crypsis is defined as being inversely proportional to the visual contrast between a color and the background. Experimental work has shown that this index of background color matching is an accurate measure of real avian predation risk in natural populations of rock dragons (Stuart-Fox et al. 2003).

MATERIALS AND METHODS

Study Sites and Species

We examined variation in background color matching between six populations of rock dragon belonging to three species, *C. decresii* (southern and northern), *C. fionni* (southern, central, and northern), and *C. vadrappa*. The geographic distribution of these populations, and the sample sizes we obtained from each population, are given in Figure 1 and Table 1, respectively. Rock dragons occupy rock outcrops and spend most of their emergent hours basking or displaying in full sun. Populations occur on substrates of diverse geological origin reflecting the complex geological history of rock formations in South Australia (Parker et al. 1985; Lemon 1996). Across populations substrates vary greatly but at any one site the background is typically relatively uniform in terms of both rock type and coloration.

Lizards’ color patterns were classified into six body regions: chest, head, throat, dorsum, dark flank region, and flank markings (Fig. 2). The “dorsum” refers to a narrow strip along the center of the back, whereas “flank” refers to both the dorso-lateral and lateral parts of the lizard. Because both flank regions extend onto the dorsal surface of the lizard, they are likely to be clearly visible to avian predators. Both the dark flank regions and flank markings vary in pattern between taxa. Dark flank areas are arranged in vertical bars in *C. vadrappa*, a single thick dorsolateral stripe in *C. decresii*, and cover most of the flank in *C. fionni*. These dark patches vary from almost pure black in *C. vadrappa*, *C. decresii*, and central *C. fionni* to pale gray in southern *C. fionni*. The flank markings of males consist of bright orange vertical bars in male *C. vadrappa*; cream spots tending to pale orange bars in northern *C. fionni*; white and pale gray spots in central and southern *C. fionni*, respectively; and cream, yellow, or orange markings extending from the nape partway along the upper flank in *C. decresii* (Fig. 2). Equivalent body regions were measured in females, except for *C. fionni* north and south females which have both dark and light dorsal colors but do not have flank markings equivalent to those in males.

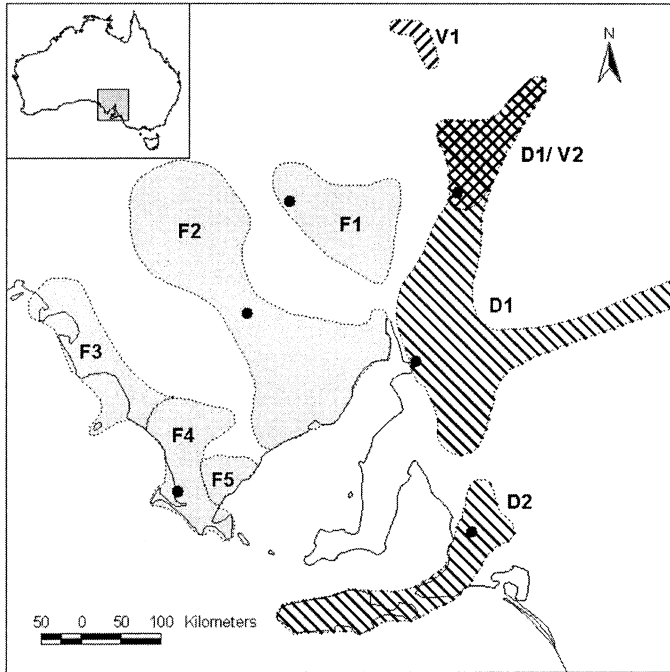


FIG. 1. Distribution of major color forms for three species of the *Ctenophorus decresii* species group: *C. decresii* (hatched left to right), D1 northern and D2 southern; *C. fionni* (F1 to F5, shaded gray), F1 northern, F2 central, F3 western F4 southern, F5 Port Lincoln; and *C. vahnappa* (hatched right to left), V1 northern and V2 main (Flinders Ranges). The region with both D1 and V2 (cross hatched) represents an area where these two species occur in broad sympatry. Color forms are those described by Houston 1974 with modifications by Gibbons and Lillywhite 1981. Sampling locations for this study are marked by black dots.

TABLE 1. Sample sizes for six color forms belonging to three species.

Color form	No. of males	No. of females
Northern <i>C. decresii</i>	9	7
Southern <i>C. decresii</i>	3	4
Northern <i>C. fionni</i>	6	5
Central <i>C. fionni</i>	4	5
Southern <i>C. fionni</i>	5	3
<i>C. vahnappa</i>	14	5

Spectroradiometry

Lizard spectral reflectance was measured using a bifurcated fiber optic probe connected to an Ocean Optics (Dunedin, FL) S2000 spectrometer at one end and an Ocean Optics deuterium-tungsten DT1000 light source at the other. The probe was mounted within a probe holder that allowed readings to be taken from an oval area 3.5×5 mm, at a constant distance of 1 cm from the surface. The end of the tubular probe holder was cut at a 45 degree angle such that illumination was at 45 degrees relative to the surface, and reflectance measured at the same angle following established protocols (Endler 1990; Arnold et al. 2002; McNaught and Owens 2002; Hausmann et al. 2003; Stuart-Fox et al. 2003). Measurements were expressed relative to a certified 99% diffuse white reflectance standard. Dark current and white standard measurements were taken before measuring each lizard. Lizards were returned to the laboratory for reflectance measurements in a darkened room. Lizards were placed in a tank with a basking area under a heat lamp for at least 15 min prior measurement. Reflectance was measured after lizards had attained their preferred body temperature ($35\text{--}40^\circ\text{C}$, Gibbons 1977), determined using a thermocouple. Each spectrum taken was an average of three readings. Measurements were taken at three different locations for each body region and

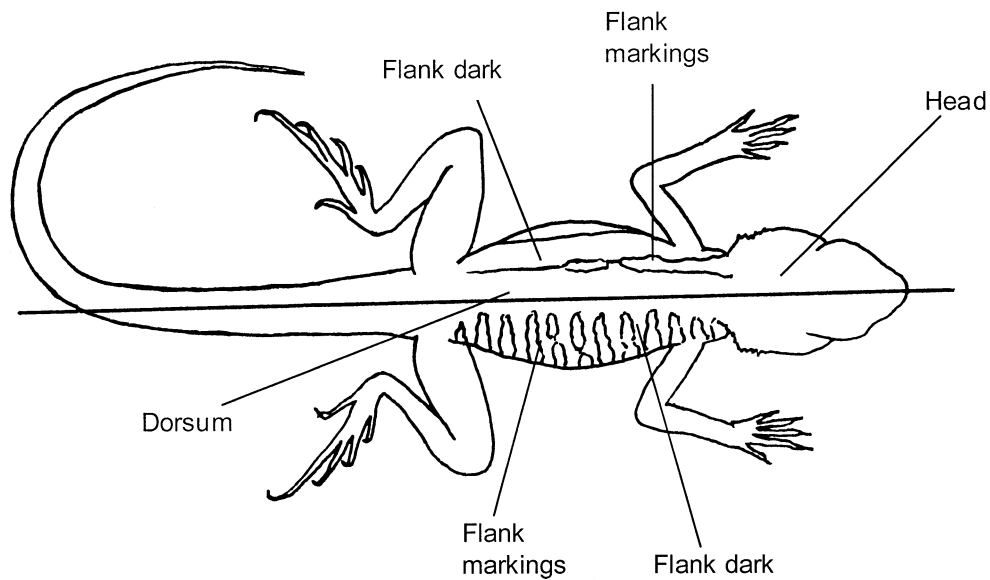


FIG. 2. Diagram of lizard body regions, showing *C. decresii* patterns above horizontal line, and *C. vahnappa* patterns below. *Ctenophorus fionni* north patterning is similar to *C. vahnappa*, but barring is less marked. In *C. fionni* central, vertical barring is replaced by rows of pale spots and in *C. fionni* south, vertical barring is replaced by irregular pale patches.

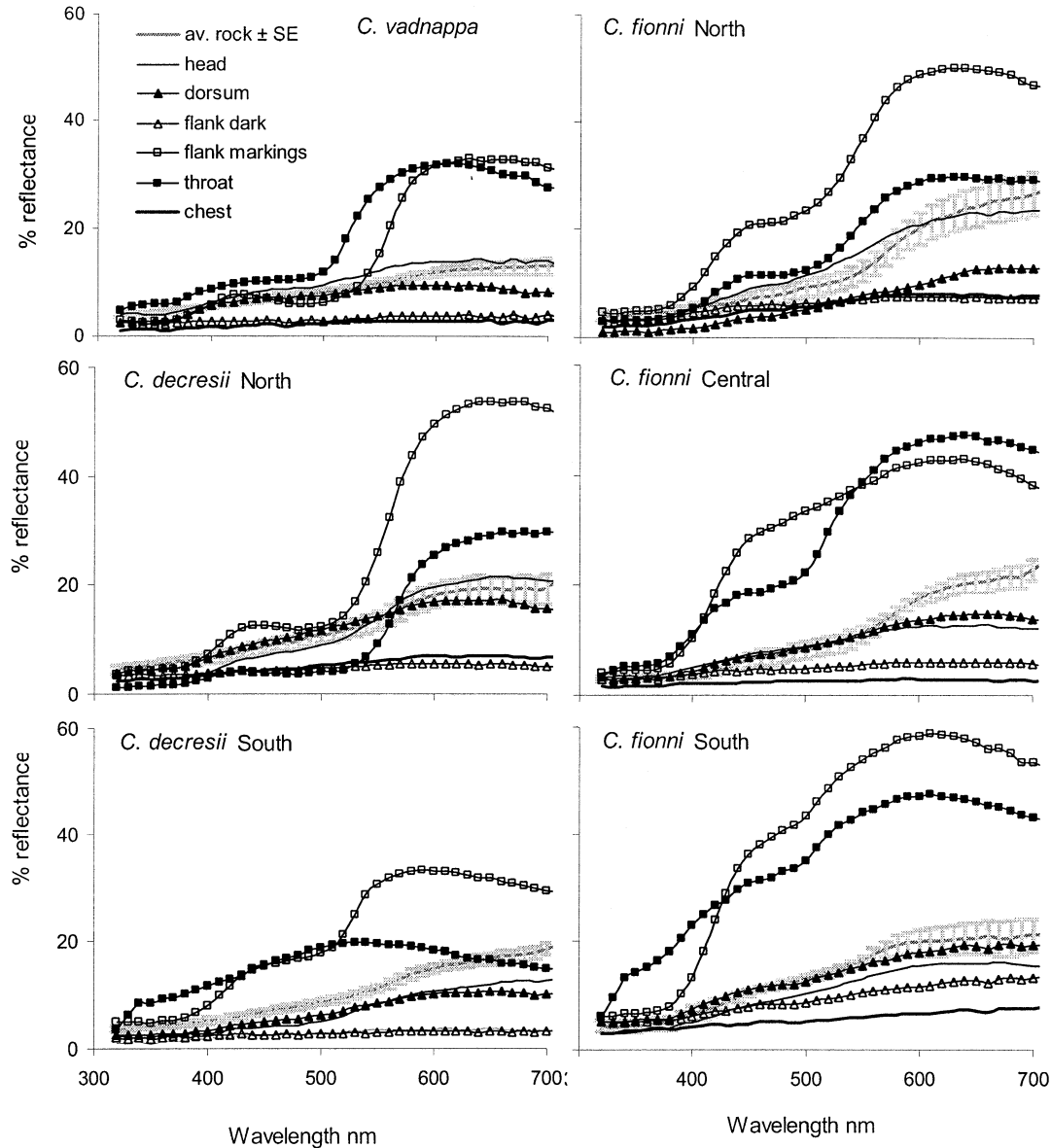


FIG. 3. Reflectance spectra of backgrounds and body regions of a representative male from each population. The shaded gray curve represents the mean background color used in contrast calculations \pm the standard error. Reflectance spectra of the six body regions of a male from each population are also shown for comparison.

the mean used as the representative spectrum (see Fig. 3 for representative reflectance spectra of males from each population).

For background colors, we sampled rocks near or upon which lizards were first sighted. Thus, we collected rock samples that were representative of the background color of habitat used by rock dragons at any given site. Rock samples were returned to the laboratory for reflectance measurement, for which we followed the same protocol as that used for measurement of lizard reflectance spectra. The average of three measurements was taken for each rock sample. Background measurements were then averaged to obtain a mean background color for each population (Fig. 3). We used a mean background color, rather than individual rock samples, because rock type and coloration were typically relatively

consistent within each population, as shown by the narrow standard errors on the background spectra (Fig. 3). Mean background color therefore provided a biologically realistic description of the typical reflectance properties of the rocks upon which the dragons live.

Irradiance was measured using an Ocean Optics S2000 spectrometer and an Ocean Optics cosine adaptor head. Irradiance was measured in full sun, under a cloudless sky. All spectral data (lizards, backgrounds, and irradiance) were averaged over each 5 nm wavelength interval to facilitate data manipulation.

Calculation of Contrasts

Visual systems encode contrast signals, that is, a color relative to a background (Vorobyev et al. 1998). Therefore,

we calculated “contrast” of the color of each lizard body region relative to its natural background, as perceived by potential avian predators. We based our models on an avian visual system because the main predators of rock dragons are birds, such as corvids, kookaburras (*Dacelo novaeguineae*), and the Australian kestrel (*Falco cenchroides*), for which lizards are an important part of the diet (Gibbons and Lillywhite 1981; Higgins 1993). Contrasts were calculated for each of the six body regions of each individual against the mean rock background color of its own population as well as against the background of every other population. We calculated both chromatic (hue) and achromatic (brightness) contrasts because they represent the two aspects in which a color may be conspicuous.

Contrasts were calculated following the model of Vorobyev et al. (1998). The model describes the discriminability of two colors against a chromatic background by their distance, ΔS , in perceptual space, where perceptual space is defined by quantum catches of photoreceptors. This model has been shown to accurately predict behavioral data (Vorobyev and Osorio 1998) and can be modified to calculate discriminability of a single color against a chromatic background (see Stuart-Fox et al. 2003). Chromatic contrast calculations were as follows. First, we calculated the total output (receptor quantum catches) for each avian cone type i for each lizard and background color by the following equation, which corresponds to equation (1) in Vorobyev et al. (1998):

$$Q_i = \int R_i(\lambda)S(\lambda)I(\lambda) d\lambda \quad (1)$$

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 color 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 color patch). Irradiance (I) and spectral sensitivities for each cone R_i were normalized to one. This calculation was done for the lizard color patch to obtain Q_i^t (receptor quantum catches for the target, t), as well as for the background color 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 normalised to the background to give the value $q_i = Q_i^t/Q_i^b$. Modification of the Vorobyev et al. (1998) model to give discriminability, ΔS , of a color against a chromatic background for tetrachromatic vision gives the following equation (Stuart-Fox et al. 2003):

$$\begin{aligned} \Delta S^2 = & (\omega_1\omega_2)^2(f_4^t - f_3^t)^2 + (\omega_1\omega_3)^2(f_4^t - f_2^t)^2 \\ & + (\omega_1\omega_4)^2(f_3^t - f_2^t)^2 + (\omega_2\omega_3)^2(f_4^t - f_1^t)^2 \\ & + (\omega_2\omega_4)^2(f_3^t - f_1^t)^2 + (\omega_3\omega_4)^2(f_2^t - f_1^t)^2 \\ & \div [(\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 \\ & + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2] \end{aligned} \quad (2)$$

where $f_i^t = \ln q_i$ and ω_i is the noise-to-signal ratio (Weber fraction) for the color channel i . Data for the Weber fraction was derived from Vorobyev et al. (1998) and Hart (2001b); for full details see Stuart-Fox et al. (2003).

For calculations of achromatic contrasts, we assumed that

perception of luminosity in birds is a function of double cones only. Although the mechanisms coding achromatic signals in birds are still poorly understood (Osorio et al. 1999; Hart 2001a), current evidence suggests they are primarily a function of double cones rather than an additive function of single cones (Campenhausen and Kirschfeld 1998). Achromatic (luminosity) contrast was therefore estimated as f_D/ω_D where D represents the blue-tit double cone (M. Vorobyev, pers. comm. 2002). 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 . Calculations of achromatic contrasts also assume that the reflection geometry of the rock and lizard surface is the same. If this assumption does not hold, then achromatic contrast will depend on the sun and/or viewer angle, a possibility which we discuss in more detail in the Discussion.

For both chromatic and achromatic contrast calculations, blue tit *Parus caeruleus* spectral sensitivities were used to approximate those of avian predators (data from Hart et al. 2000). There is no complete published spectral sensitivity data for the main predators of rock dragons (corvids, raptors, and kingfishers). However, birds are highly conserved in their visual pigment characteristics (reviewed in Hart 2001a). Of the 31 species from nine orders of birds whose visual pigments have been examined using microspectrophotometry, the range of peak sensitivities for each type of visual pigment are as follows: Long wavelength (LWS $\lambda_{\max} = 543$ –571 nm, blue tit = 563 nm); medium wavelength (MWS $\lambda_{\max} = 497$ –510 nm, blue tit = 503 nm); short wavelength (SWS $\lambda_{\max} = 430$ –463 nm, blue tit = 448 nm); extreme short wavelengths (UVS/VS $\lambda_{\max} = 362$ –426 nm, blue tit = 371 nm) (Hart 2001b). Because blue tit spectral sensitivities fall approximately in the middle of the known ranges for birds, they are likely to be an adequate approximation of those of any avian predator. The greatest interspecific variation in avian cone sensitivities is in the ultra violet or violet sensitive cone (Hart 2001a). Because rock dragons have very low reflectance over these wavelengths, any small discrepancy in the spectral sensitivities of the blue tit versus those of the species that actually predate these dragons should have little effect on the results (see Stuart-Fox et al. 2003).

Statistical Analyses

To test whether sexes and populations differed in relative crypsis, two-way MANOVAs were used to test for global effects of sex and population on multiple dependent variables, in this case, absolute contrasts for each body region: head, dorsum, flank dark, flank markings, chest, and throat. Only where MANOVA results were significant did we proceed to two-way ANOVAs testing for effects of sex and population on each body region separately. Bonferroni adjustment to P -values was applied due to multiple tests (Rice 1989). Where interaction terms from the two-way ANOVAs were significant, we proceeded to one-way ANOVAs on each sex and population separately, again adjusting significance levels for multiple tests.

Second, we tested whether body regions exposed to avian predators were more closely matched to the background than

TABLE 2. Results of MANOVAs testing for significant differences between sexes and among populations in chromatic and achromatic contrast against the rock background.

	Factor	Wilk's lambda	df	F	P
Chromatic contrast	Sex	0.27	6	18.54	<0.0001
	Population	0.12	24	5.02	<0.0001
	Sex × Population	0.37	18	2.78	0.0005
Achromatic contrast	Sex	0.38	6	11.45	<0.0001
	Population	0.29	24	2.63	0.0002
	Sex × Population	0.41	18	2.46	0.002

body regions hidden from predators. Three-way ANOVAs were used to test for an effect of body region (exposed vs. hidden), with sex and population as the other two factors. The head, dorsum, dark flank regions, and flank markings were classed as “exposed” body regions while the chest and throat were classed as “hidden.”

Third, to test whether each population was locally adapted to its own background, we compared contrasts against the local background versus contrasts against the backgrounds of every other population, again using three-way ANOVA with background (own vs. other), sex, and population as the factors. For this analysis, we pooled the four body regions visible to avian predators as these body regions are all expected to be under natural selection for crypsis.

All statistical analyses were performed using the PROC GLM procedure in the statistical package SAS version 8.02.

RESULTS

Do Populations Differ in Crypsis?

MANOVAs testing for differences in crypsis between populations across all exposed body regions were significant for both chromatic and achromatic contrast (Table 2). We therefore proceeded to analyze each body region separately.

When we performed analyses separately for each body region we found that population differences in crypsis varied depending on body region and whether chromatic or achromatic contrast was being considered (Table 3). Populations differed significantly in the chromatic contrast of the dark flank regions, flank markings, and chest, but did not differ

significantly for the head or dorsum. When we explored interactions, we found that the throat region differed significantly between populations for both males ($F_4 = 6.53, P = 0.0007$) and females ($F_3 = 10.71, P = 0.0003$). However, the only body regions that were significantly different among populations in achromatic contrast were the throat in males ($F_4 = 9.48, P < 0.0001$) and the flank markings in females ($F_3 = 6.32, P = 0.0005$). In sum, the greatest variation in crypsis/conspicuousness among populations was found in the chest, throat, and flank regions. There were no significant differences among populations in contrasts of the head or dorsum.

Do Males and Females Differ in Crypsis?

Using MANOVAs to test for differences in crypsis between sexes for all body regions, we found that there was significant sexual dichromatism for both chromatic and achromatic contrast (Table 2). We therefore proceeded to analyze each body region separately.

Analyses based on individual body regions revealed that chromatic contrast of males was significantly greater than that of females for the dorsum, both flank regions, and the chest (Table 3). In addition, achromatic contrast of males was significantly greater than that of females for the flank dark body region (Table 3). When we explored interactions, we found that in *C. vadrappa*, males were also significantly more chromatically contrasting than females for the throat ($F_1 = 29.34, P < 0.0001$) and significantly more achromatically contrasting than females for the flank markings ($F_1 = 13.68,$

TABLE 3. Results of two-way ANOVAs testing for significant differences between the sexes and among populations in chromatic and achromatic contrasts for each body region. Values that are significant at $P < 0.05$ and $P < 0.01$ after Bonferroni adjustment are denoted by single and double asterisks, respectively.

Body region	Sex		Population		Sex × Population		
	$F_{(df = 1)}$	P	$F_{(df = 4)}$	P	$F_{(df = 3)}$	P	
Chromatic contrast	Head	5.0	0.03	1.51	0.21	1.05	0.38
	Dorsum	8.99	0.004*	2.61	0.05	0.99	0.4
	Flank dark	31.77	<0.0001**	7.75	<0.0001**	3.19	0.03
	Flank markings	50.25	<0.0001**	16.53	<0.0001**	3.33	0.03
	Chest	26.65	<0.0001**	10.31	<0.0001**	1.2	0.32
	Throat	18.2	<0.0001**	2.5	0.05	9.11	<0.0001**
Achromatic contrast	Head	0.2	0.66	0.81	0.52	0.73	0.54
	Dorsum	3.85	0.06	0.55	0.7	0.59	0.62
	Flank dark	12.58	<0.0001**	2.22	0.08	0.55	0.65
	Flank markings	9.6	0.003*	3.37	0.02	5.18	0.004*
	Chest	1.17	0.29	0.14	0.17	2.03	0.12
	Throat	26.34	<0.0001**	4.82	0.002*	6.28	0.001**

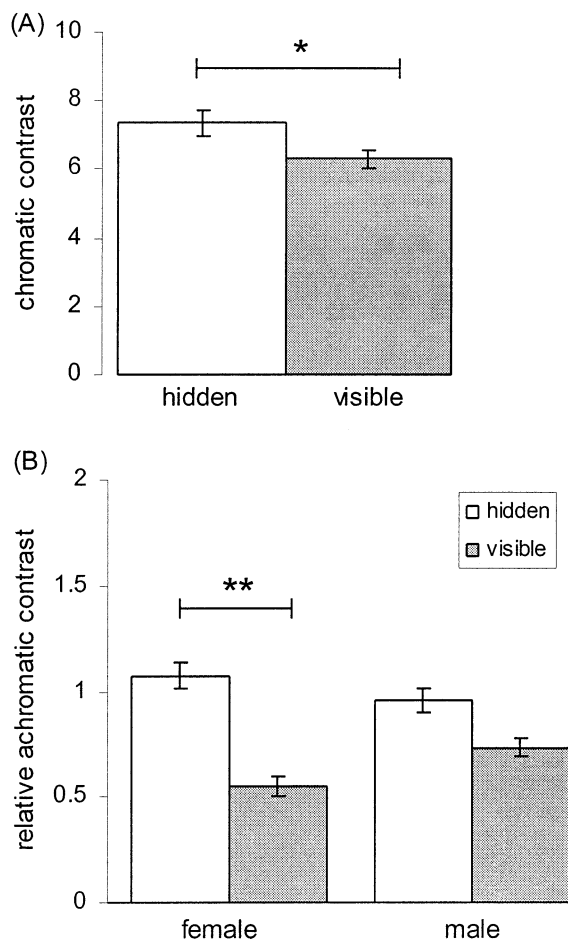


FIG. 4. Mean contrasts of body regions hidden from predators (throat, chest) and exposed to predators (head, dorsum, flank dark, flank markings) against rock background (A) chromatic contrast in receptor quantum catches (ΔS); (B) relative achromatic contrast in receptor quantum catches (f_D), for males and females. Error bars are standard errors around the mean.

$P = 0.002$). However, the throats of females were significantly more achromatically contrasting than the throats of males in three populations: northern *C. decresii* ($F_1 = 14.8$, $P = 0.002$), southern *C. decresii* ($F_1 = 30.88$, $P = 0.003$), and northern *C. fionni* ($F_1 = 21.56$, $P = 0.001$). Only the head showed no significant difference in conspicuousness between the sexes for any population.

Are "Exposed" Body Regions More Cryptic?

Body regions hidden from avian predators were significantly more chromatically contrasting against the background than body regions exposed to avian predators (Fig. 4a). For achromatic contrast, there was an interaction between type of body region and sex (Table 4). Male body regions hidden from avian predators were not significantly more conspicuous than body regions visible to avian predators (Fig. 4b). This is because both types of body region are conspicuous in males, not because they are both cryptic. On the other hand, females were significantly more conspicuous for hidden than visible body regions in terms of achromatic contrast (Fig. 4b).

Evidence for Local Adaptation?

There was an interaction between background type and sex for chromatic contrast (Table 5). Females, but not males, were significantly more cryptic against their local backgrounds than against the backgrounds of other populations (Fig. 5a). For achromatic contrast, there was an interaction between background type and population. Examination of contrasts for each population separately revealed that only *C. vadrappa* was significantly more cryptic against the local background than against the background of other populations (Fig. 5b).

Although many of our results were highly significant, the scale of this analysis is relatively coarse and sample sizes are small for some populations. Nonsignificant results with low P -values should therefore be interpreted with caution. In the majority of cases, however, P -values for nonsignificant

TABLE 4. Results of three-way ANOVAs testing for an effect of body region (exposed vs. hidden).

Factor		Sum of squares	df	F	P
Chromatic contrast	Body region	84.22	1	5.6	0.02
	Sex	1101.33	1	73.18	<0.0001
	Population	379.56	5	5.04	0.0002
	Body region \times Sex	7.56	1	0.5	0.48
	Body region \times Population	108.7	5	1.44	0.21
	Sex \times Population	192.65	5	2.56	0.03
	Body region \times Sex \times Population	123.7	5	1.64	0.15
	Error	5733.98	38		
Achromatic contrast	Body region	10.65	1	50.53	<0.0001
	Sex	0.08	1	0.4	0.53
	Population	0.65	5	0.81	0.54
	Body region \times Sex	1.68	1	7.97	0.005
	Body region \times Population	1.87	5	1.78	0.12
	Sex \times Population	2.06	5	1.95	0.09
	Body region \times Sex \times Population	1.66	5	1.58	0.16
	Error	80.5	38		

TABLE 5. Results of three-way ANOVAs testing for an effect of background (own vs. other).

Factor		Sum of squares	df	F	P
Chromatic contrast	Background	48.12	1	11.02	0.001
	Sex	565.73	1	129.57	<0.0001
	Population	124.05	5	5.68	<0.0001
	Background × Sex	26.63	1	6.1	0.01
	Background × Population	21.61	5	0.99	0.42
	Sex × Population	164.84	5	6.18	<0.0001
	Background × Sex × Population	28.31	5	1.3	0.26
	Error	3609.23	419		
Achromatic contrast	Background	0.01	1	0.39	0.53
	Sex	1.65	1	51.95	<0.0001
	Population	1.28	5	8.06	<0.0001
	Background × Sex	0.0	1	0.0	0.95
	Background × Population	0.42	5	2.63	0.02
	Sex × Population	0.89	5	5.63	<0.0001
	Background × Sex × Population	0.06	5	0.36	0.88
	Error	20.74	419		

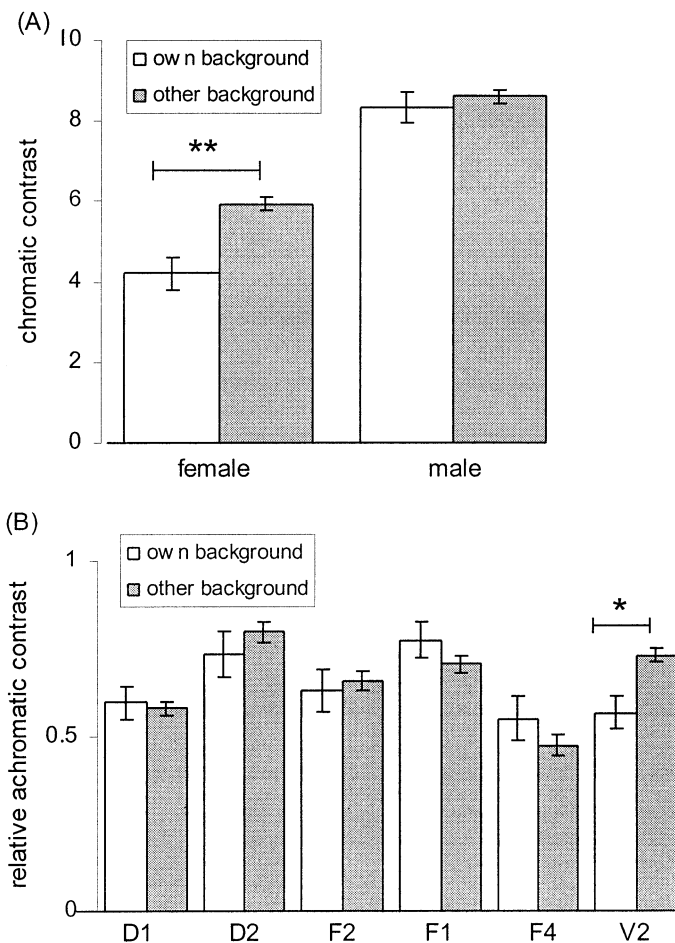


FIG. 5. Mean contrasts of body regions exposed to predators against the local background and backgrounds of other populations. (A) chromatic contrast in receptor quantum catches (ΔS) for males and females; (B) relative achromatic contrast in receptor quantum catches (f_D) for each population. Population names on the X-axis refer to populations delineated in Figure 1. *Ctenophorus decresii*, D1 northern and D2 southern; *C. fionni*, F1 northern, F2 central, F4 southern; and *C. vadrappa*, V2. Error bars are standard errors around the mean.

results are relatively large, particularly after correction for multiple tests.

DISCUSSION

Geographic Color Variation

Our study of rock dragons provides support for the hypothesis that natural selection for crypsis plays an important role in the evolution of color variation. First, although there were significant differences in crypsis across populations for some body regions, we found no evidence for population differences in either achromatic or chromatic contrast for the head and dorsum. Given the relatively low contrast of these body regions, this suggests that all populations may be highly cryptic against their respective backgrounds for these body regions, which are most vulnerable to predators. Second, body regions that are exposed to avian predators were significantly more cryptic than hidden body regions for both sexes in terms of chromatic contrast and for females in achromatic contrast, providing additional support for the role of natural selection. Finally, we found evidence for local adaptation, with females showing significantly less chromatic contrast against their local background than against the backgrounds of other populations, and both sexes of *C. vadrappa* being more cryptic against the local background in achromatic contrast.

Although our results broadly support the importance of natural selection for crypsis, some of the results conflict with expectations based on background matching alone, suggesting that the evolution of geographic color variation in rock dragons may be more complex than previously thought. First, there were population differences in crypsis for the flank body regions, which are visible to avian predators. Chromatic contrast for the flank body regions differed among populations in both sexes, and populations also differed in the achromatic contrast of female flank markings. For these body regions, some populations displayed highly contrasting coloration, most notably *C. vadrappa* and *C. fionni* central and northern males as well as *C. decresii* northern and southern females. Second, although females were significantly more cryptic in terms of ‘hue’ against the local background than against

other backgrounds, males were not. In addition, only *C. vadrapp* individuals were significantly more cryptic against their own background in terms of "brightness." Although our analysis may not have the sensitivity to detect subtle variation in degree of local adaptation, taken together, these results strongly suggest that background color matching and the action of natural selection alone cannot explain geographic color variation, particularly for males.

There are several possible explanations for geographic variation in crypsis and the variation in the extent of local adaptation observed. Gene flow can constrain local adaptation in crypsis, as has been shown empirically for the streamside salamander (*Ambystoma barbouri*, Storfer et al. 1999). Apart from northern and central *C. fionni*, populations of the *C. decresii* species complex examined here are separated by relatively large mitochondrial genetic distances (Grant 2000; Melville et al. 2001). However, even in the absence of current gene flow, there may be evolutionary lag in adaptive morphological change since population separation. Alternatively, variation in crypsis and the extent of local adaptation may have an adaptive explanation. Natural selection may vary geographically due to differences in the density and species composition of avian predators (Endler 1983; Macedonia et al. 2002). For example, the Australian kestrel (*Falco cenchroides*) is likely to be a more important predator relative to other species in the arid northern regions than in the range of the southern *C. decresii* and *C. fionni* populations. However, experimental tests of predation risk for males belonging to two of the color forms, *C. decresii* north and *C. vadrapp*, found no evidence for differences in predation pressure between the geographic ranges of these two populations (southern and northern Flinders Ranges, respectively, Stuart-Fox et al. 2003). Even if predation pressure varies little across the geographic regions, the relative strength of selection for signaling functions could account for differences between populations.

Sexual Selection and Dichromatism

For sexually dichromatic species, males and females may differ in their relative conspicuousness. In many vertebrate species, competition over mates, and thus sexual selection, is likely to be stronger in males (reviewed in Andersson 1994). This is particularly true for species in which there is no male parental care, such as lizards (Olsson and Madsen 1998). For such systems, signal investment is generally male biased and female color patterns are more cryptic than those of males. Therefore, it might be expected that female color patterns would show stronger evidence that color differentiation is driven by geographic variation in the requirements for crypsis. The results of this study largely support this view. Females were consistently more cryptic than males for the chest, flank regions, and even the dorsum. In addition, in terms of crypsis, females tended to be locally adapted to the background whereas no such pattern was apparent for males.

Male body regions that varied most among populations were also those most variable and divergent in conspicuousness between the sexes. For some body regions visible to predators, namely the dorsum and flank regions, the sexes differed in chromatic or achromatic contrast. In each case,

the males were more conspicuous. Body regions on the ventral surface were more chromatically conspicuous than body regions exposed to avian predators in both sexes. However, for males, both types of body region were equally conspicuous in terms of achromatic contrast. The chests of males are almost black and therefore just as achromatically contrasting as the dark flank regions. The throat colors of males are a combination of gray, blue, black, yellow, or orange in all populations. All these colors are also evident in male flank markings, resulting in significant differences between the sexes for these body regions. The throat, chest, and flanks are all used in territorial and sexual signaling (Gibbons 1979). Rock dragon display behaviors include lowering of the dewlap, head bobs, and front and hind leg push-ups performed in lateral presentation with the body laterally compressed (Gibbons 1979). These behaviors emphasize the throat, chest, and flank regions. These regions were the most variable and divergent in degree of conspicuousness between sexes and are thus the most likely candidates as targets of sexual selection in males. That flank regions used in social and sexual displays are conspicuous in males, despite being visible to avian predators, argues strongly for the influence of sexual selection in the evolution of male flank coloration.

Assumptions of the Visual Models

Throughout this study we have assumed that our measures of variation in background color matching provide an accurate estimation of how cryptic or conspicuous lizards appear to avian predators. Indeed, we have defined "crypsis" as being inversely proportional to the visual contrast between the color of the lizards and their backgrounds. It is therefore important to remember that there are limitations to this approach. For instance, the visual models that we have used make assumptions regarding how birds perceive color. The most important assumptions in calculation of chromatic contrasts are that color-coding mechanisms in birds are by unspecified opponency mechanisms (comparison of outputs of all combinations of cone types) and color discrimination is limited by photoreceptor noise. At present, very little information is available on how birds actually process information received from the different cone types, whether individuals can facultatively adjust the way in which information is processed, or whether there is substantial variation between individuals, sexes, or species in the method of processing. It seems likely that, like other animals with color vision, birds may have specific opponency whereby they selectively compare the input from particular pairs of cones, rather than using all possible cone-contrast combinations (Kelber et al. 2003). Nevertheless, we anticipate that our results will prove relatively robust to such refinements because the models of color discrimination that we have used, which are based on unspecified opponency, have already been shown to accurately predict performance of color vision in a variety of animal groups, including birds (Vorobyev and Osorio 1998).

For calculation of achromatic contrasts, we assumed 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 (Campenhausen and Kirschfeld 1998). Perhaps more importantly, however,

our measures of achromatic contrast also assume that the surface of the lizard and rock background have the same reflection geometry. Of course, in reality they are likely to differ such that perceived achromatic contrast will depend on both the sun and viewer angles (see Wyszecki and Stiles 1982; Endler 1990). Lizards may thus appear relatively brighter or duller against the background than suggested by our estimates of achromatic contrast, depending on viewing conditions. Therefore, such differences in geometry may explain why results for chromatic and achromatic contrasts were not entirely consistent and why results for chromatic contrasts were more consistent with expectations of the background matching hypothesis than those for achromatic contrasts.

Finally, the visual models extrapolate from passerine species to all avian predators. Raptors and passerines are known to differ in their visual acuities (Reymond 1987). Whether they also differ in their photoreceptor spectral sensitivities and relative number of photoreceptors of different classes is not yet known. The evidence to date suggests that spectral sensitivities of passerine and nonpasserine species examined so far are highly conserved (reviewed in Hart 2001a). Nevertheless, it would be interesting to repeat these analyses of crypsis using the visual sensitivities of an avian raptor should such data becomes available.

Another type of limitation of our study is that the estimates of background matching do not incorporate information on pattern and the relative area that color patches occupy on the lizard and the background. Pattern can influence the degree of crypsis in a number of ways. Pattern may enhance crypsis when the grain and geometry, as well as color of the animal, represent random samples of those of the background (Endler 1978). Alternatively, an animal may appear cryptic if the scale of the pattern is smaller than the visual acuity of the predator, even where the color or pattern are not random samples of the background (Endler 1978). For example, the conspicuous blue and yellow stripes of some reef fish merge to appear the same green as the algae background when viewed by predators from a distance (Marshall 2000). Finally, particular patterns may result in disruptive camouflage, whereby body lines are broken or disrupted when one or more colors at the body margins matches the color of the background (Cott 1940; Lythgoe 1979; Merilaita 1998). As a result of the many possible combinations of color and pattern, different animal color patterns may represent different, but equally effective, adaptive solutions to the problem of maximizing crypsis (Endler 1978). Again, the analysis of pattern is beyond the scope of the current study, but we do not wish to suggest that it is unimportant in the evolution of either coloration or crypsis.

Despite these limitations, we have used visual models as the framework for this study because they are an advance on human-oriented measures of crypsis or the analysis of spectral data without reference to the receiver's visual system. Also, in the case of these particular visual models and this particular group of lizards, our experimental work suggests that measures of background contrast do provide biologically meaningful estimates of relative crypsis in rock dragons (Stuart-Fox et al. 2003; but see Merilaita 2003). Predation experiments demonstrated that differences in both chromatic and achromatic contrast between bright and dull males within

populations result in differential predation risk from avian predators in the wild (Stuart-Fox et al. 2003). Thus, it seems likely that even without considering such potentially important features as pattern, the differences in chromatic and achromatic contrast between the sexes and between populations would also translate to differential conspicuousness and associated predation costs. Furthermore, the approach presented here can be extended to examining conspicuousness of body regions used for signaling, as perceived by conspecific receivers. Quantifying the receiver-relative contrast of animals against their natural backgrounds is therefore a useful way of examining the interaction between natural and sexual selection in the evolution of animal color patterns.

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