Camouflage and colour change: antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon

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Potential prey are often exposed to multiple predators that vary in their foraging tactics and ability to detect prey. For animals that rely on crypsis to avoid predators, one solution is to alter their behaviour or appearance to maximize crypsis in ways that are specific to different types of predator. We tested whether dwarf chameleons (*Bradypodion transvaalense*) showed different behavioural responses, including colour change, towards multiple predators (bird and snake models) that detect and capture prey in different ways, and whether these antipredator responses varied geographically. Chameleons consistently used the same body postures (lateral compression and flipping to the opposite side of the branch) and displayed similar chromatic (colour) contrast against the natural background in response to both predator types. However, they became significantly more achromatically contrasting (brighter) in the presence of the snake compared to the bird. This relative difference in achromatic contrast towards the two types of predator was consistent among populations. There were also significant differences in both absolute achromatic and chromatic contrast among populations despite very similar light environment, background coloration and habitat structure. Our results highlight facultative crypsis as one type of flexible antipredator tactic and emphasize the importance of visual ecology in understanding prey–predator interactions. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, **88**, 437–446.

ADDITIONAL KEYWORDS: achromatic contrast – antipredator behaviour – chromatic contrast – crypsis – geographical variation.

INTRODUCTION

Potential prey are often exposed to multiple predators that vary in foraging tactics and have different sensory-perception mechanisms. How prey deal with multiple predators and integrate diverse threats, particularly in light of trade-offs resulting from conflicting selection pressures, is a key question in evolutionary ecology (Lima, 1998; Sih *et al.*, 1998; Garcia & Sih, 2003; Templeton & Shriner, 2004). In the longer term, phenotypic plasticity may allow organisms to develop morphological features optimal for their specific environment and suite of predators, especially when they are exposed to varying predation regimes during development (Relyea, 2001a, b; Van Buskirk, 2001). In the immediate term, animals may faculta-

tively adjust behaviour, most commonly their escape behaviour and activity patterns, in response to specific types of predator (Kleindorfer *et al.*, 1996; Hopper, 2001; Manser, 2001; Relyea, 2001b; Van Buskirk, 2001; Cooper, Martin & Lopez, 2003; Templeton & Shriner, 2004).

Colour change is one type of flexible antipredator response that has received relatively little attention because it can be difficult to quantify. However, it can be a particularly effective mechanism, especially for organisms with reduced locomotion, because it allows an animal to rapidly alter its appearance in response to changing environmental conditions. For instance, soft-bodied octopuses rapidly alter their colour pattern (*c.* three times per min) to match the mosaic of substrates during slow foraging, whereas during more rapid movement they mimic fish or use disruptive patterns (Hanlon *et al.*, 1999). Such a rapid change in col-

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oration is rare although relatively rapid colour change has also been anecdotally reported for chameleons. Other taxa, such as the larvae of many frogs and salamanders, have more limited capacity for colour change and have been shown to become lighter or darker to match backgrounds in response to predator cues (Garcia & Sih, 2003). Although there are numerous studies of crypsis (see Stuart-Fox *et al.*, 2004 and references therein) and some quantitative demonstrations that certain species can adjust their coloration to match different backgrounds (e.g. Hanlon *et al.*, 1999; Garcia & Sih, 2003), it is yet to be tested whether animals that do use colour change as an antipredator tactic can adjust coloration in response to specific predators.

Antipredator tactics may vary between populations as a result of geographical variation in predation risk; the major driving force for which is variation in habitat characteristics (Endler, 1980; Houde, 1997). For animals that rely on camouflage to some extent, natural selection to maximize crypsis against different backgrounds can be an important mechanism generating geographical variation in coloration (Endler, 1980; Stuart-Fox *et al.*, 2004). Habitat characteristics can also influence the suite of predators encountered (Hopper, 2001), or predator density, thereby influencing an individual's previous experience with a particular type of predator (Magurran *et al.*, 1993; Houde, 1997). Individuals with different exposures to particular predator types may exhibit different combinations or frequencies of antipredator response (Kelley & Magurran, 2003; Templeton & Shriner, 2004). Despite substantial empirical evidence for population differences in antipredator behaviour, geographical variation in different types of antipredator response (e.g. colour change and other behaviours) has rarely been examined in a multipredator context (one exception is Templeton & Shriner, 2004).

In this study, we examine colour change and other antipredator behaviours (body posturing), in response to two types of predator (a bird and a snake) among four populations of the Transvaal dwarf chameleon, *Bradypodion transvaalense*. Specifically, we asked two questions. First, we asked whether chameleons differentially adjust their coloration and/or body postures in response to the two types of predator. Second, we asked whether the responses to the two types of predator, and/or their relative frequency, vary geographically. To answer these questions, we quantified achromatic contrast (more commonly referred to as brightness) and chromatic contrast (other aspects of coloration, commonly referred to as hue and chroma) of chameleons against the background as well as individual behavioural responses for four populations of *B. transvaalense* when presented with a model bird (fiscal shrike, *Lanius collaris*) and a model snake (boomslang, *Dispholidus typus typus*) in the field. In

addition, we quantified structural habitat characteristics because they may influence geographical variation in coloration and other antipredator behaviours.

Dwarf chameleons are good models for studying colour change in response to predators for three reasons. First, due to morphological specialization of chameleons (strong lateral compression, sets of two or three fingers and toes fused on each foot), they have very limited ability to flee a predator and rely on crypsis to avoid predation (Necas, 2001). Second, although there is more than one way of being cryptic (Endler, 1978), chameleons are likely to use simple crypsis, whereby an organism's colour pattern closely matches that of the background (Endler, 1978; Osorio & Srinivasan, 1991). Third, dwarf chameleons are susceptible to a range of predator types, chief among which are birds and snakes (Branch, 1998). The boomslang and fiscal shrike are among the most important predators of dwarf chameleons (Wager, 1986; Branch, 1998). The boomslang is a diurnal, arboreal, venomous colubrid snake with very large, forward facing eyes (Branch, 1998). As the boomslang actively and rapidly pursues its prey (Wager, 1986; Branch, 1998), it is likely to rely on visual cues, including coloration, for prey detection. Similarly, the fiscal shrike is an aggressive hunter of chameleons which often impales dwarf chameleons on thorns (Wager, 1986) and is a common and very widespread species in southern Africa. These predators are likely to exert strong selection on chameleon antipredator responses, providing an ideal opportunity to examine variation in both behavioural and phenotypic antipredator responses to multiple predators.

METHODS

STUDY SITES AND SPECIES

Bradypodion transvaalense is a small [mean snout-vent length (SVL) = 60 mm], viviparous dwarf chameleon, endemic to South Africa. Recent phylogeographical work suggests that at least four main lineages can be recognized with 2.5–4% divergence between lineages based on the mitochondrial ND2 gene (T. Townsend, unpubl data). We chose four populations that represent the four main lineages: Barberton (25°51′32″S, 31°2′9″E) near the north-west border of Swaziland; Tullach Mohr Nature Reserve in the Elands Valley (25°33′35″S, 30°34′58″E); forest in the immediate surrounds of Graskop (24°58′4″S, 30°47′49″E); and Woodbush Nature Reserve in the north (23°49′55″S, 29°58′37″E). The four lineages vary in coloration, especially male display coloration (D. Stuart-Fox, unpubl. data). Individuals from Barberton vary from grey-brown to combinations of blue, black and white; those from Elands Valley vary from grey-brown to combinations of green, black and white;

those from Graskop vary from grey-brown to combinations of blue, green, yellow, black and white; and those from Woodbushvary from grey-brown to combinations of orange, yellow and black.

FIELD EXPERIMENTS

Dwarf chameleons were captured at night during February 2004. For each population, eight adults of each sex were caught, except for Barberton and the Elands Valley populations for which we caught five adult males. Specimens were kept in cloth bags with branches. Only sexually mature adults (minimum male SVL = 61 mm, minimum female SVL = 67 mm) were captured.

Behavioural trials were performed within the natural habitat, between 10:00 h and 15:00 h when chameleons are naturally active. Chameleons were placed on a perch (a natural branch) and presented with the two model predators. The fiscal shrike was stuffed and mounted with its wings slightly open (Fig. 1) and the

Figure 1. Fiscal shrike model and chameleon (Graskop) in typical antipredator response posture. The chameleon is on the opposite side of the branch from the predator, its body laterally compressed.

model boomslang snake was made of resin from a cast of a dead boomslang and painted by a professional model maker to resemble an adult male . To control for variation in the signalling environment, the same branch (and location) was used for all trials. The boomslang model was mounted so that the majority of the body was along a 1 m branch, while the shrike was mounted at the end of a 1 m dowel stick. The order of presentation of the snake and bird were randomised, to account for possible effects of presentation order. Both types of predators were presented from multiple angles (lower or higher than the focal animal) to ensure that differences in predator response coloration were not simply due to difference in angle of presentation. Thus, each chameleon was presented with the bird and snake predator under similar viewing conditions (constant irradiance and background, and a range of angles of presentation of the predator).

We only observed three types of behavioural response, which we recorded for each individual in response to the two predators: (1) lateral compression of body, legs vertically under the body, concealing the chameleon behind the branch; (2) flipping to the opposite side of the branch from the predator; and (3) dropping to the ground in a tight ball (akinesis). Chameleons rarely exhibited the final behaviour (10 out of 116 trials). To test whether observed behaviours were an artefact of being presented with a moving object, we presented chameleons from one population (Woodbush) with a moving branch with leaves. In these trials, the order of presentation of the branch, shrike and boomslang, were randomised. None of the 16 chameleons presented with a branch reacted with any of the above three antipredator behaviours.

We took reflectance measurements as soon as the chameleon showed a clear behavioural response to the predator. Measurements were taken using a probe at the end of a 1.2 m bifurcated fibre-optic cable, connected to a spectrometer (SD2000, Ocean Optics, Florida, USA) and light source (PX2, Ocean Optics). Readings were taken from an oval area 3.5×5 mm, at a constant distance of 1 cm from the surface. Illumination was at 45° relative to the surface, and reflectance was measured at the same angle following established protocols (Endler, 1990; 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. Reflectance measurements of chameleon coloration were taken for four body regions [top, middle and bottom flank and casque (side of the head)]. The order in which the four body regions were measured was randomised to prevent any systematic bias in colour measurements due to handling. Usually, measurements for only two body regions could be taken before the chameleon would

start to change colour. The chameleon would then be returned to the perch, allowed to settle, and then presented with the model predator again until it showed clear behavioural reaction. Readings for the remaining two body regions were then taken.

To quantify background colours, we took reflectance readings for two types of background: branches and leaves. Background coloration was measured as the mean reflectance of the leaves or branches on which chameleons were caught and the leaves and branches in the immediate vicinity of the perch where experiments were conducted (Fig. 2). Leaf or branch backgrounds for each population were means of 17–40 measurements (Fig. 2). Irradiance was measured with a SD2000 spectrometer and a calibrated, cosine-corrected irradiance probe (CC-3-DA, Ocean Optics), under fine conditions in the shade at the forest edge, which were the same conditions as those under which the behavioural experiments were conducted (Fig. 2).

CONTRAST CALCULATIONS

As perceived crypsis is a function of the contrast of the animal against the background (Endler, 1978), we derived measures of achromatic and chromatic contrast of the chameleons relative to the natural background. The achromatic (total light reflected, analogous to brightness) and chromatic (principal colour and its purity, analogous to hue and chroma combined) components together summarize variation in raw reflectance spectra and represent the two aspects in which a colour may be conspicuous. The contrast measures we used are simple measures of contrast in radiance (Endler, 1990; Macedonia, 2001; Heindl & Winkler, 2003). We first converted background and chameleon reflectance spectra to radiance spectra by multiplying each reflectance spectrum by the irradiance spectrum (normalized to a maximum of 1) for the corresponding population. Achromatic contrast was calculated using $(R^t - R^b)/(R^t + R^b)$, where R^t and R^b are the radiance of the target (chameleon) and background, respectively, integrated over 320–700 nm. To calculate chromatic contrast, all radiance spectra of the chameleons and backgrounds were standardized for brightness (area under the curve 320–700 nm = 1). Chromatic contrast was then calculated as the Euclidean distance (D_s) between the radiance spectrum of the chameleon vs. background (Endler, 1990; Macedonia, 2001; Heindl & Winkler, 2003), using:

$$D_S = \sqrt{\sum [Q^t(\lambda) - Q^b(\lambda)]^2},$$

where $Q^t(\lambda)$ and $Q^b(\lambda)$ is the radiance at a given wavelength and summation is over each 5 nm interval from 320 to 700 nm.
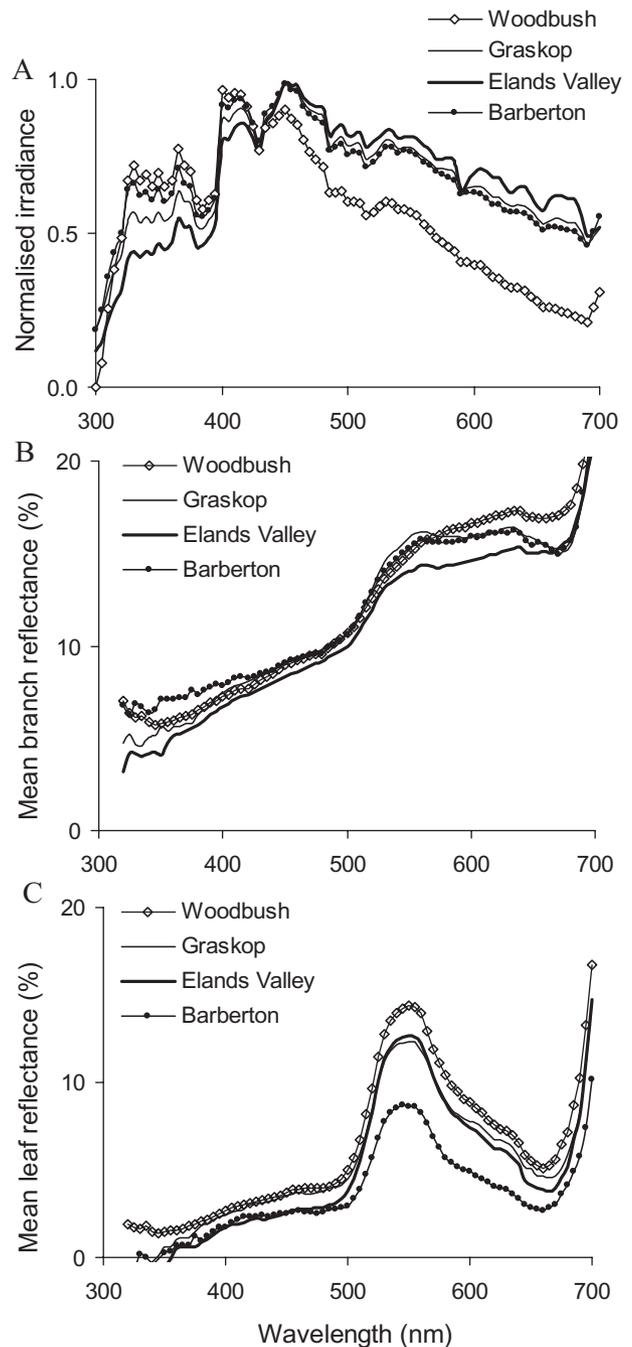

Figure 2. Population variation in background reflectance and irradiance spectra. A, irradiance; B, mean branch reflectance; C, mean leaf reflectance.

Although it is preferable to measure contrast as perceived by the potential predators, by incorporating information on the visual system of the receiver (e.g. Storfer *et al*., 1999; Stuart-Fox *et al*., 2003, 2004), not enough is known about diurnal snake visual systems to enable comparison to birds. Snake visual systems

vary greatly depending on the species' visual ecology (Sillman *et al.*, 1997, 1999; Sillman, Johnson & Loew, 2001). For instance, the retinas of some primarily nocturnal snakes only contain rods whereas those of some diurnal snakes living in bright light environments contain only cones (Sillman *et al.*, 1997). As a result, calculations of receiver-relative contrast (particularly achromatic contrast) based on a semiaquatic garter snake or nocturnal python model (the only systems for which there exists comprehensive spectral sensitivity data) are unlikely to be realistic for a boomslang. For this reason, we chose measures of achromatic and chromatic contrast that were independent of the receiver visual system.

HABITAT VARIATION

For each population, we measured seven structural habitat variables within five representative 10×10 m plots in which chameleons had been found. The variables were as follows: (1) canopy height; (2) percentage canopy cover; (3) percentage vine cover; (4) number of trees over 5 m tall; (5) number of shrubs (between 1 and 5 m tall); (6) number of perches at 0.5–1 m within a 50×50 cm cube, and (7) number of perches at 1.5–2 m within a 50×50 cm cube. Canopy height was visually estimated as 0–5, 5–10, 10–15 m or > 15 m. Percentage canopy cover was measured with a spherical densiometer and percentage vine cover was approximated as one of four categories: 0–25%, 25–50%, 50–75% and 75–80% of the trees or shrubs in the plot that were covered with vines or lianas. The number of perches at 0.5–1 m or 1.5–2 m was measured as the mean number of stems within five 50×50 cm cubes placed randomly within the plot at those heights.

STATISTICAL ANALYSES

First, we tested for differences in the frequencies of antipredator behaviours towards birds and snakes using repeat measures ANOVA for categorical data. Predator type was the repeated measure and the response variables were presence or absence of each antipredator behaviour. We tested for effects of sex and population and their interaction with predator type. Second, we tested for differential colour responses to the two predators using repeat measures ANOVA. The contrast values were the dependent variables and predator type was the repeated measure on the individual chameleons (subjects). Sex, population, body region and order of presentation (and their interaction with predator type) were included in the models as between-subject effects. We tested for an effect of presentation order despite randomising presentation of the bird and snake to the chameleons to test whether prior handling affected subsequent reflectance measures. Third, we assessed whether populations could be discriminated based on their habitat characteristics using discriminant function analysis. Analyses were performed in SAS version 9.1.

RESULTS

VARIATION IN RESPONSE TO PREDATOR TYPE

Although chameleons consistently reacted behaviourally to both the bird and snake models, frequencies of the three types of antipredator body posture (flattening themselves, flipping to the opposite side of the branch and dropping) did not differ significantly in response to the two types of predator (Table 1). This appears to be primarily because antipredator body postures did not vary greatly; on the great majority of occasions (88% of trials), chameleons flattened themselves and flipped to the opposite side of the branch (Fig. 1).

Chameleon coloration in response to predators varied among individuals from uniform pale grey-brown to grey-brown with a pale patch in the mid-flank (Fig. 1). There were significant differences in achromatic contrast, but not chromatic contrast, of chameleons against both backgrounds when presented with a snake compared to a bird (Table 2). Under identical viewing conditions (constant background and irradi-

Table 1. Effects of predator type (predator), sex and population on chameleon behavioural responses (repeat measures analysis of variance for categorical data)

Dependent variable (behaviour)	Factor	Statistical analyses	
		$X^2_{d.f.}$*	P
Flattened	Predator	0.01_1	0.965
	Population	3.26_3	0.354
	Sex	2.09_1	0.148
	Predator*Sex	0.33_1	0.569
	Predator*Population	0.53_3	0.912
Opposite	Predator	0.08_1	0.778
	Population	1.3_3	0.728
	Sex	0.01_1	0.998
	Predator*Sex	1.95_1	0.163
	Predator*Population	1.4_3	0.786
Drop	Predator	0.01_1	0.965
	Population	1.13_3	0.771
	Sex	1.75_1	0.186
	Predator*Sex	0.62_1	0.203
	Predator*Population	2.92_3	0.404

*d.f., degrees of freedom.

Table 2. Effects of predator type (predator), presentation order (order), sex, population and body region on chameleon colours (repeat measures ANOVAs)

Dependent variable (contrast)	Factor	Leaf background		Branch background	
		F_{dfs}	P	F_{dfs}	P
Achromatic contrast	Predator	$15.38_{1,46}$	< 0.001*	$17.04_{1,46}$	< 0.001*
	Population	$17.71_{3,58}$	< 0.0001*	$7.11_{3,58}$	< 0.001*
	Sex	$0.05_{1,58}$	0.82	$0.26_{1,58}$	0.61
	Body region	$80.35_{3,166}$	< 0.0001*	$91.35_{3,166}$	< 0.0001*
	Order	$3.55_{1,50}$	0.065	$4.43_{1,50}$	0.04
	Predator*Body region	$1.07_{3,134}$	0.98	$1.19_{3,134}$	0.9
	Predator*Sex	$0.13_{1,46}$	0.72	$0.05_{1,46}$	0.82
	Predator*Population	$0.64_{3,46}$	0.59	$0.87_{3,46}$	0.46
Chromatic contrast	Predator	$1.49_{1,46}$	0.23	$0.01_{1,46}$	0.95
	Population	$44_{3,58}$	< 0.0001*	$8.11_{3,58}$	0.0001*
	Sex	$26.83_{1,58}$	< 0.0001*	$0.01_{1,58}$	0.92
	Body region	$34.2_{3,166}$	< 0.0001*	$6.28_{3,166}$	0.0005*
	Order	$1.5_{1,50}$	0.23	$0.18_{1,50}$	0.67
	Predator*Body region	$0.2_{3,134}$	0.89	$0.25_{3,134}$	0.86
	Predator*Sex	$1.4_{1,46}$	0.24	$1.25_{1,46}$	0.27
	Predator*Population	$0.15_{3,46}$	0.93	$0.14_{3,46}$	0.93

*Significant ($P < 0.05$) after Bonferroni correction for multiple non-independent tests (four tests: achromatic and chromatic contrast for each of two backgrounds).
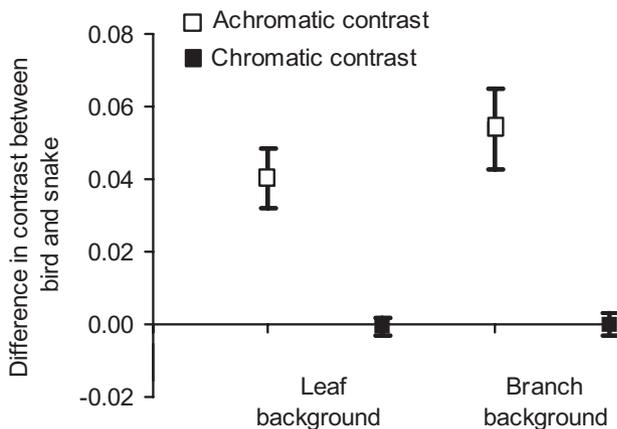

Figure 3. Mean difference between contrasts of individual chameleon coloration in response to snake relative to bird. Positive difference (> 0) indicates individuals were consistently more contrasting in response to the snake than bird predator. Bars show SE.

ance), chameleons became significantly more achromatically contrasting when presented with a snake compared to a bird (Fig. 3). None of the interactions with predator type were significant, therefore this relative difference held true across the sexes and across populations (Table 2). Order had a marginally significant effect (Table 2) although this effect was non-significant with Bonferroni correction. Chameleons tended to be less bright when measured the second time, but we identified a significant effect of predator type despite the weak order effect, which would tend to mask an effect of predator type.

GEOGRAPHIC VARIATION IN ANTIPREDATOR RESPONSE

The frequency of behavioural responses between populations did not differ significantly (Table 1). However, there were significant differences in both absolute achromatic and chromatic contrast between populations (Table 2). Relative differences in contrast varied depending on whether achromatic or chromatic contrast against leaf or branch backgrounds were being considered (Figs 4A, B). That is, no single population was consistently more or less contrasting. In general, chameleons were brighter than both backgrounds (positive contrast) and were less contrasting against branches than leaves (Fig. 4). In addition, both achromatic and chromatic contrast differed between body regions (Table 2). Chromatic contrast against the leaf background also differed between the sexes (Table 2), with males more chromatically contrasting than females (mean ± SE = 0.062 ± < 0.001 for males and 0.059 ± < 0.001 for females).

Despite geographical variation in contrast, there was only weak evidence for differentiation amongst the four sites based on the seven habitat variables
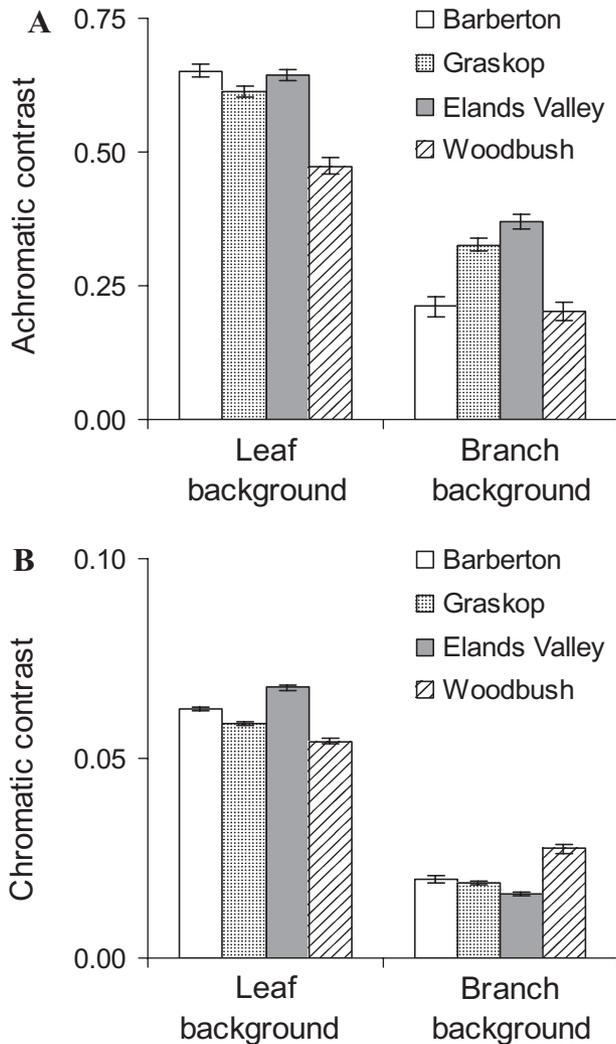
Figure 4. Mean contrasts ± SE against leaf and branch backgrounds for the four populations. A, achromatic contrasts in response to bird and snake predators; B, chromatic contrast in response to bird and snake predators.
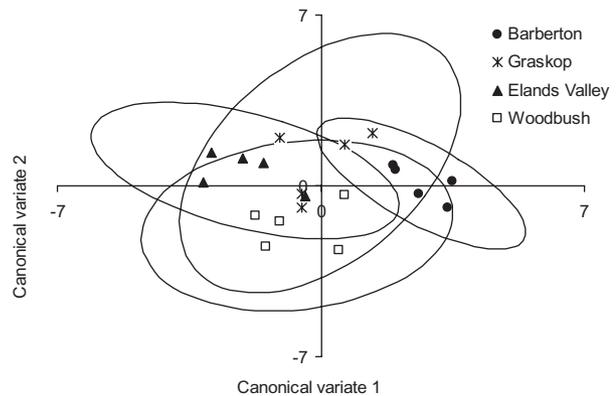

Figure 5. Plot of canonical variates 1 and 2 from the discriminant function analysis on habitat variables showing the relative position of each habitat plot for the four populations. Ellipses represent 95% confidence ellipses. CV1 explained 66% of the variation and discriminates populations based on the number of perches at 0.5 m (correlation between this variable and CV1 = 0.83), shrub density (correlation = 0.6) and canopy height (correlation = –0.57), while CV 2 explained 22% of the variation and discriminates between populations very poorly, but primarily on the number of perches at 0.5 m (correlation = 0.5).

(Wilks' $\lambda_{3,1.5,4} = 0.057$, $F_{21,29.3} = 2.37$, $P = 0.016$). Although the multivariate discrimination was significant, classification success was very poor (classification success: Barberton 80%; Tullach 0%; Graskop 60%; and Woodbush 40%) and there was considerable overlap between sites (Fig. 5). Stem density at 0.5–1 m was responsible for the significant discrimination among sites, with Barberton having more under-story vegetation than Elands Valley (Fig. 5).

DISCUSSION

VARIATION IN RESPONSE TO PREDATOR TYPE

Dwarf chameleons exhibited consistent differential colour responses to snake and bird predators. Specifically, chameleons from all four populations became significantly more achromatically contrasting when presented with a snake than when presented with a bird. Other antipredator behaviours (flattening themselves, flipping to the opposite side of the branch and dropping) were similar in response to the two predators. Thus, chameleons facultatively adjust their brightness, but not body postures, in response to two different types of predator. The change in brightness was consistent across body regions and chameleon predator-response coloration was generally uniform, supporting the view that chameleons employ simple crypsis rather than other forms of crypsis such as disruptive coloration (Endler, 1978). The only other empirical demonstrations of colour change in response to predators among vertebrates are for amphibian larvae. Frog and salamander larvae often change colour (especially brightness) to better match a given background (Garcia & Sih, 2003). However, background matching is often imperfect and these larvae rely on a combination of antipredator tactics including predator-specific escape behaviours (Van Buskirk, 2001; Garcia & Sih, 2003).

There are two possible, but not mutually exclusive, explanations for the observed difference in achromatic contrast in response to birds and snakes. First, typical prey approach angles and viewing conditions may differ for the two predators. Although we presented chameleons with both types of model predator from multiple angles under identical viewing conditions,

chameleon colour changes may be stereotypical responses to particular predators that vary in their mode of prey location. For instance, if snakes typically approach the chameleon from below, being very pale may maximize crypsis against a background of relatively high illumination and contrast (e.g. backlit, mottled forest shade with pale lower leaf surfaces), whereas a bird typically approaching a chameleon from above may perceive the chameleon against a background of lower luminance and contrast (e.g. frontlit, dark forest floor). Perceived achromatic contrast will depend greatly on illumination angle and the angle at which the chameleon is approached, especially as chameleons flatten themselves and position themselves on the opposite side of the branch in response to predators. How the interaction between body posture and brightness affects absolute perceived contrast and crypsis is difficult to quantify and is best examined in controlled behavioural trials on bird and snake responses to different visual stimuli (Osorio *et al.*, 1999). For this reason, measures of achromatic contrast are best interpreted in a relative, rather than absolute sense (Stuart-Fox *et al.*, 2004).

The second explanation for the observed predator-specific colour change is that chameleons adjust their brightness according to the properties of the predator's visual system. Both snakes and birds may be more reliant on achromatic contrast (in addition to movement) than chromatic contrast for prey detection. For instance, birds use chromatic signals to distinguish large targets whereas they require achromatic contrast to discriminate small targets and visual textures (Osorio *et al.*, 1999). However, birds and snakes would need to have sufficiently different visual ecology, especially in terms of achromatic contrast sensitivity, to warrant a predator specific response by the chameleon. Such differences in visual ecology are likely as birds and snakes differ in their means of prey location. Most snakes use olfactory cues in addition to visual cues for prey detection (Schwenk, 1995) whereas birds rely exclusively on visual cues (Kassarov, 2003).

Available data on bird and snake visual systems suggest that birds and snakes generally differ in their visual acuity (the spatial frequency resolvable at maximum contrast) and capacity for colour discrimination. Birds have greater cone density and therefore greater visual acuity than snakes (Sillman *et al.*, 1997, 1999, 2001; Osorio *et al.*, 1999;) and possess four visual pigments (Hart, 2001) rather than the three visual pigments of most snakes studied to date (Sillman *et al.*, 1997, 1999, 2001). Acuity interacts with achromatic contrast sensitivity (and colour discrimination) in prey detection. For instance, a predator with good acuity but poor contrast sensitivity may be unable to detect relatively large prey under low light and low contrast conditions such as forest shade. Although birds have excellent visual acuity, they have relatively poor discrimination of achromatic contrast (Hodos, 1993; Kassarov, 2003). The extent to which birds and snakes differ in sensitivity to achromatic signal and the interaction between contrast discrimination and visual acuity in prey detection is not known. It is clear, however, that birds and snakes do differ in their visual ecology. Therefore, it is possible that chameleons fine tune their colour response to maximize crypsis according to predator type.

GEOGRAPHIC VARIATION IN ANTIPREDATOR RESPONSE

Although the relative difference in brightness in response to the snake and bird was consistent, populations differed in absolute chromatic and achromatic contrast against the background. There are two primary explanations for the observed geographical variation in absolute contrast. First, the absolute abundance of predators, and thus the strength of natural selection for crypsis, may differ between populations (Endler, 1980). Unfortunately, data on the abundance of the boomslang and fiscal shrike for these populations are not available. However, no single population was consistently more or less contrasting in both chromatic and achromatic contrast against both backgrounds, as expected if the strength of natural selection for crypsis was stronger for some populations than others. In addition, habitat structural characteristics varied little between the populations except in terms of stem density at 0.5–1 m. Given that habitat variation is limited and that the boomslang and fiscal shrike are generally widespread and abundant, it seems unlikely that absolute predator density is sufficiently variable among the populations to explain the marked differences in contrast observed.

The second explanation for geographical variation in achromatic and chromatic contrast is that there may be variation between populations in sexual selection for signalling. Populations of dwarf chameleons are currently isolated and exhibit moderate levels of genetic differentiation and marked variation in display coloration (D. Stuart-Fox, unpubl. data). Thus, divergent sexual selection in isolated populations may have lead to the observed differentiation in display coloration. Population differences in the contrast of colours adopted in response to predators (against similar backgrounds) may reflect divergent sexual selection for signalling in conjunction with limits to capacity for colour change. Although chameleons can exhibit some dramatic changes in coloration, such changes are nevertheless limited to within a certain range, determined by the position, density and type of chromatophores within the dermis and their associated pigments or structural features (Cooper & Greenberg, 1992; Necas, 2001). It is probable that the range

of colours available to a chameleon varies between populations and is partially dictated by selection for signalling. As a result, populations exhibiting very different display coloration may also differ in their predator response coloration.

CONCLUSIONS

In this study, we examined relative changes in contrast in response to two types of predator, rather than change in coloration relative to the initial coloration of the chameleon, for two reasons. First, it is not obvious what a measure of a chameleon's initial or 'neutral' colour might represent within the complex natural setting in which the experiments were conducted, making biological interpretation difficult. Second, the number of colour measurements that can be taken without the chameleon becoming stressed is limited. Even with two treatments (bird vs. snake), there was indication of an order effect, although we nevertheless detected a highly significant effect of predator type. As a consequence of only measuring relative colour change, we do not know the degree to which chameleons actively reduced contrast to the background in response to each predator. However, the predator-specific responses were consistent across populations despite variation in absolute contrast, providing strong evidence that the change in brightness (evident to the human eye) is an antipredator response. Also, we cannot conclude that chameleons adjust their brightness to appear equally cryptic to birds and snakes because we could not derive realistic measures of receiver-relative contrast. Nonetheless, we suggest that the predator-specific brightness change in dwarf chameleons is likely adaptive, given that predation is a strong selective force and that this response was consistent among populations that differ in other aspects of their coloration. Accordingly, we have discussed the possible differences in the visual ecology of birds and snakes that could explain the predator-specific brightness change observed in dwarf chameleons.

Overall, this study demonstrates that animals that use colour change as an antipredator tactic may change colour in response to specific predators, and not just in response to specific backgrounds, and also suggests that dwarf chameleons have a remarkable ability to facultatively adjust crypsis. Furthermore, our results suggest that achromatic signal may be more important than chromatic signal for effective camouflage and highlight the importance of predator visual ecology in understanding predator–prey interactions.

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REFERENCES

Branch WR. 1998. *Field guide to snakes and other reptiles of southern Africa.* Sanibel Island, Florida: Ralph Curtis Books.

Cooper WE, Greenberg N. 1992. Reptilian coloration and behavior. In: Gans C, Crews D, eds. *Biology of the Reptilia.* Chicago: Chicago University Press, 298–422.

Cooper WE, Martin J, Lopez P. 2003. Simultaneous risks and differences among individual predators affect refuge use by a lizard, *Lacerta monticola. Behaviour* **140:** 27–41.

Endler JA. 1978. A predator's view of animal color patterns. *Evolutionary Biology* **11:** 319–364.

Endler JA. 1980. Natural selection on color patterns in *Poecilia reticulata. Evolution* **34:** 76–91.

Endler JA. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* **41:** 315–352.

Garcia TS, Sih A. 2003. Color change and color-dependent behavior in response to predation risk in the salamander sister species *Ambystoma barbouri* and *Ambystoma texanum. Oecologia* **137:** 131–139.

Hanlon RT, Forsythe JW, Joneschild DE. 1999. Crypsis, conspicuousness, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biological Journal of the Linnean Society* **66:** 1–22.

Hart NS. 2001. The visual ecology of avian photoreceptors. *Progress in Retinal and Eye Research* **20:** 675–703.

Heindl M, Winkler H. 2003. Interacting effects of ambient light and plumage color patterns in displaying Wire-tailed Manakins (Aves, Pipridae). *Behavioral Ecology and Sociobiology* **53:** 153–162.

Hodos W. 1993. The visual capabilities of birds. In: Zeigler HP, Bishop HJ, eds. *Vision, Brain and Behaviour in Birds.* London: MIT Press, 63–75.

Hopper KR. 2001. Flexible antipredator behavior in a dragonfly species that coexists with different predator types. *Oikos* **93:** 470–476.

Houde AE. 1997. *Sex, Color and Mate-Choice in Guppies.* Princeton: Princeton University Press.

Kassarov L. 2003. Are birds the primary selective force leading to evolution of mimicry and aposematism in butterflies? An opposing point of view. *Behaviour* **140:** 433–451.

Kelley JL, Magurran AE. 2003. Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries* **4:** 216–226.

Kleindorfer S, Hoi H, Fessl B. 1996. Alarm calls and chick reactions in the moustached warbler, *Acrocephalus melanopogon*. *Animal Behaviour* **51:** 1199–1206.

Lima SL. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advanced Studies in Behaviour* **27:** 215–290.

Macedonia JM. 2001. Habitat light, colour variation, and ultraviolet reflectance in the Grand Cayman anole, *Anolis conspersus*. *Biological Journal of the Linnean Society* **73:** 299–320.

Magurran AE, Seghers BH, Carvalho GR, Shaw PW. 1993. Evolution of adaptive variation in antipredator behavior. *Marine Behaviour and Physiology* **23:** 29–44.

Manser MB. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268:** 2315–2324.

Necas P. 2001. *Chameleons: Nature's Hidden Jewels*. Malabar: Krieger Publishing.

Osorio D, Miklosi A, Gonda Z. 1999. Visual ecology and perception of coloration patterns by domestic chicks. *Evolutionary Ecology* **13:** 673–689.

Osorio D, Srinivasan MV. 1991. Camouflage by edge enhancement in animal coloration patterns and its implications for visual mechanisms. *Proceedings of the Royal Society of London Series B-Biological Sciences* **244:** 81–85.

Relyea RA. 2001a. Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* **82:** 523–540.

Relyea RA. 2001b. The relationship between predation risk and antipredator responses in larval anurans. *Ecology* **82:** 541–554.

Schwenk K. 1995. Of tongues and noses – chemoreception in lizards and snakes. *Trends in Ecology and Evolution* **10:** 7–12.

Sih A, Englund G, Wooster D. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* **13:** 350–355.

Sillman AJ, Carver JK, Loew ER. 1999. The photoreceptors and visual pigments in the retina of a boid snake, the ball python (*Python regius*). *Journal of Experimental Biology* **202:** 1931–1938.

Sillman AJ, Govardovskii VI, Rohlich P, Southard JA, Loew ER. 1997. The photoreceptors and visual pigments of the garter snake (Thamnophis sirtalis): a microspectrophotometric, scanning electron microscopic and immunocytochemical study. *Journal of Comparative Physiology A-Sensory Neural and Behavioral Physiology* **181:** 89–101.

Sillman AJ, Johnson JL, Loew ER. 2001. Retinal photoreceptors and visual pigments in Boa constrictor imperator. *Journal of Experimental Zoology* **290:** 359–365.

Storfer A, Cross J, Rush V, Caruso J. 1999. Adaptive coloration and gene flow as a constraint to local adaptation in the streamside salamander, *Ambystoma barbouri*. *Evolution* **53:** 889–898.

Stuart-Fox DM, Moussalli A, Johnston GR, Owens IPF. 2004. Evolution of colour variation in dragon lizards: quantitative tests of the role of crypsis and local adaptation. *Evolution* **58:** 1549–1559.

Stuart-Fox DM, Moussalli A, Marshall NJ, Owens IPF. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Animal Behaviour* **66:** 541–550.

Templeton CN, Shriner WM. 2004. Multiple selection pressures influence Trinidadian guppy (*Poecilia reticulata*) antipredator behavior. *Behavioral Ecology* **15:** 673–678.

Van Buskirk J. 2001. Specific induced responses to different predator species in anuran larvae. *Journal of Evolutionary Biology* **14:** 482–489.

Wager VA. 1986. *The Life of the Chameleon*. Durban: Wildlife Society.