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Local adaptation and divergence in colour signal conspicuousness between monomorphic and polymorphic lineages in a lizard

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Abstract

Population differences in visual environment can lead to divergence in multiple components of animal coloration including signalling traits and colour patterns important for camouflage. Divergence may reflect selection imposed by different receivers (conspecifics, predators), which depends in turn on the location of the colour patch. We tested for local adaptation of two genetically and phenotypically divergent lineages of a rock-inhabiting lizard, *Ctenophorus decresii*, by comparing the visual contrast of colour patches to different receivers in native and non-native environments. The lineages differ most notably in male throat coloration, which is polymorphic in the northern lineage and monomorphic in the southern lineage, but also differ in dorsal and lateral coloration, which is visible to both conspecifics and potential predators. Using models of animal colour vision, we assessed whether lineage-specific throat, dorsal and lateral coloration enhanced conspicuousness to conspecifics, increased crypsis to birds or both, respectively, when viewed against the predominant backgrounds from each lineage. Throat colours were no more conspicuous against native than non-native rock but contrasted more strongly with native lichen, which occurs patchily on rocks inhabited by *C. decresii*. Conversely, neck coloration (lateral) more closely matched native lichen. Furthermore, although dorsal coloration of southern males was consistently more conspicuous to birds than that of northern males, both lineages had similar absolute conspicuousness against their native backgrounds. Combined, our results are consistent with local adaptation of multiple colour traits in relation to multiple receivers, suggesting that geographic variation in background colour has influenced the evolution of lineage-specific coloration in *C. decresii*.

Introduction

Environmental differences between populations often entail differences in the visual environment, which affects the appearance of colours to conspecifics, predators and prey (Endler, 1993). For signalling traits, this can lead to correlated evolutionary changes in the appearance of the signal, sensory system and mate choice behaviour, a process known as sensory drive (Endler, 1992, 1993). Because the most effective signals will be those which are easy to detect and interpret in their natural setting, the sensory drive hypothesis predicts that population divergence in coloration within species should reflect local adaptation for signal efficacy in different environments (Endler, 1992). However, animal colour patterns have multiple, often conflicting functions (e.g. communication and camouflage), and divergence in coloration is likely to reflect lineage-specific solutions to evolutionary trade-offs between them. Whereas compelling evidence now exists for population divergence in colour signals consistent with sensory drive (reviewed in Dangles *et al.*, 2009; Maan &

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Seehausen, 2011; Servedio *et al.*, 2011; Wilkins *et al.*, 2012; Cole, 2013), few studies have compared the visual contrast of signals in different environments to different receivers (e.g. conspecifics and predators) to understand how interactions between multiple selective pressures may have influenced population divergence in coloration (but see Endler, 1991; Leal & Fleishman, 2004).

Population divergence in coloration often consists of multiple components including signalling traits and colour patterns important for camouflage. Furthermore, individual colour patches may be influenced by a combination of selection for conspicuous signals, selection to maximize crypsis to predators and thermoregulatory requirements, and the relative importance of these selective pressures will vary depending on the location of the colour patch (Endler, 1978; Stuart-Fox & Moussalli, 2011). For example, conspicuous coloration is often restricted to body regions that are minimally exposed to predators whereas dorsal coloration, which is often exposed to visual predators, tends to be cryptic (Stuart-Fox & Ord, 2004; Stuart-Fox *et al.*, 2004). Therefore, population divergence in coloration should reflect optimum conspicuousness of sexual signals to conspecifics, while decreasing the conspicuousness of body regions exposed to predators, in their respective visual environments. In turn, differences in the degree of conspicuousness of different colour patches between populations may provide insight into the strengths of local selective pressures acting on coloration (e.g. Macedonia *et al.*, 2002; Kwiatkowski, 2003).

We assessed how population divergence in male coloration corresponds to visual contrast, as perceived by conspecifics and predators, in the Australian tawny dragon lizard, *Ctenophorus decresii*. The species is sexually dimorphic, with large, brightly coloured males and cryptically coloured females. Adult males exhibit striking throat coloration which differs between two geographically structured genetic lineages (referred to as northern and southern; McLean *et al.*, 2013, 2014). Within the northern lineage, all populations are polymorphic with four discrete colour morphs; pure orange, pure yellow, orange and yellow combined and grey (Teasdale *et al.*, 2013; McLean *et al.*, 2014; Fig. 1a–d). Conversely, populations from the southern lineage are monomorphic, males have blue throats with an ultraviolet (UV) reflectance peak (Fig. S1a), and yellow to orange along the gular fold and dispersed throughout the blue in individuals from Kangaroo Island (McLean *et al.*, 2013, 2014; Fig. 1f,g). This throat coloration, which is fixed at sexual maturity (Osborne, 2004; D. Stuart-Fox, unpublished), is likely to act as a social signal. Males perform courtship and territorial displays in which the head is raised and the gular region is lowered, emphasising the colour of the throat (Gibbons, 1979; Stuart-Fox & Johnston, 2005). Consequently, selection for signal efficacy is likely to be important in *C. decresii*, and divergence in throat coloration between lineages may reflect local adaptation for signal detectability to conspecific lizards in different environments.

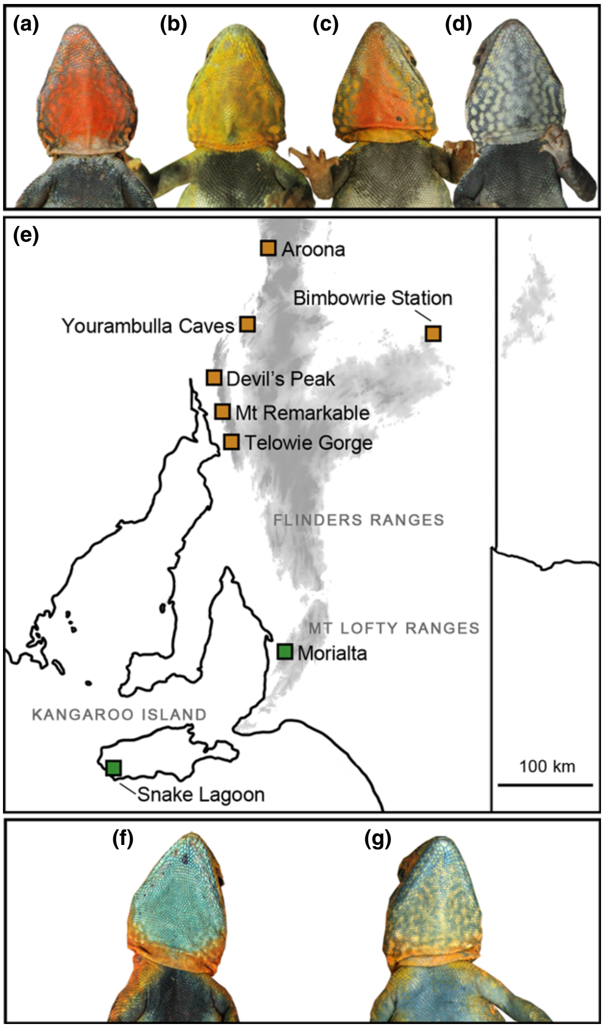

Fig. 1 Map showing the six northern lineage (orange squares) and two southern lineage (green squares) populations of *C. decresii* for which colour data were collected (e). Males from the northern lineage are polymorphic with four discrete throat colour morphs: orange (a), yellow (b), orange-yellow (c) and grey (d), whereas males from the southern lineage have blue throat coloration, which can be distinguished into Mt Lofty Ranges (f) and Kangaroo Island (g) forms.

While throat coloration is highly divergent, northern and southern males have more similar dorsal colour and patterning; however, lateral coloration consisting of a black stripe and yellow-orange coloration around the neck and sides of the head (referred to as neck throughout for brevity) are more extensive and generally more intense in southern individuals (Houston & Hutchinson, 1998; McLean *et al.*, 2013). During behavioural display, males laterally compress their bodies and arch their backs which shows off this coloration, which is absent in females (Gibbons, 1979). Consequently, lateral coloration may be an important social signal; however, due to its location, it is also visible to predators. *C. decresii* inhabits rocky outcrops, perching in prominent positions on the top of boulders, in full sunlight, when basking or displaying and birds are one of the species' primary predators (Gibbons & Lillywhite, 1981; Stuart-Fox *et al.*, 2003). Rock colours vary between the lineages, and the temperate southern region is more heavily vegetated than the semi-arid northern region. Consequently, we expect lateral coloration to reflect a compromise between selection for signalling and crypsis, whereas dorsal coloration should be influenced primarily by selection for crypsis within the local environments. Using objective colour measurements (spectral reflectance) of *C. decresii* males, and models of animal colour vision, we test whether: 1) throat coloration is locally adapted to increase conspicuousness to the visual system of conspecific lizards, 2) dorsal coloration is locally adapted to increase crypsis to the visual system of birds, and 3) lateral coloration is both conspicuous to lizards and cryptic to birds against native backgrounds.

Materials and methods

Study system and reflectance measurements

The tawny dragon, *Ctenophorus decresii*, is a small (≤30 g), agamid lizard endemic to central South Australia and Kangaroo Island. We collected colour data from six sites within the polymorphic northern lineage of *C. decresii* (Aroona, Yourambulla Caves, Devil's Peak, Mt Remarkable, Telowie Gorge and Bimbowrie Station), and two sites in the monomorphic southern lineage (Morialta and Snake Lagoon; Fig. 1e) during late Spring and Summer in 2011 and 2012. Male lizards were captured when active, by hand or by noosing with a loop attached to a telescopic pole, and spectral reflectance measurements were taken within ten minutes of capture to ensure that lizards were at close to optimal body temperatures, as some agamid lizards are darker when cold (Gibbons & Lillywhite, 1981; Cooper & Greenberg, 1992). We measured reflectance of the throat, head, dorsum, neck and lateral stripe (Fig. 2) of 46 males (35 northern, 11 southern) using an Ocean Optics (Dunedin, FL, USA) Jaz portable spectrometer. The probe was held at a constant angle (45°) and distance from the surface of the lizard, and each measurement was expressed relative to a Spectralon 99% white reflectance standard (Labsphere, Inc., North Sutton, NH, USA). Three readings were collected and averaged for each colour patch, and all lizards were released at the site of capture following processing.

To quantify background colour, we measured the reflectance of rocks and lichens on which lizards were observed. We identified different substrate colours (e.g. grey rock, red rock) and again three readings were collected for each patch of colour, which we averaged where appropriate. This resulted in 1–2 samples of each background colour within each site. In the northern lineage rock colours are highly variable, ranging from dark grey to pale yellow; however, the principal rock colours are orange and red-brown scattered with pale green lichen (Fig. 3a,b). Furthermore, red-brown and orange rocks are not present in the southern lineage (Fig. S1b) where the principal rock colours are grey and pink, and the lichen is predominantly orange (Fig. 3c,d). Within each site, lizards were observed on a wide range of rock colours with varying proportions of lichen cover (ranging from 0–90%), and rock colour was variable within an individual's territory (C. A. McLean pers. obs.). A detailed study of microhabitat preference in polymorphic northern populations of *C. decresii* showed that male colour morphs do not differ in microhabitat selection, and choose territories with less vegetation cover and more large rocks relative to available habitat rather than based on substrate colour (Teasdale *et al.*, 2013). Due to these findings, and because we were interested in how differences in the predominant background colours for each lineage may have influenced the evolution of male coloration, we determined the mean reflectance of orange rock ($N = 10$) and green lichen ($N = 6$) across all northern sites, and grey rocks ($N = 7$) and orange lichen ($N = 2$) across all southern sites (Fig. S1b). Additionally, we recorded irradiance in full sun under fine conditions, at approximately 11:00 hours within each site using a dedicated Ocean Optics Jaz-ULM-200 spectrometer with a cosine-corrected probe (Fig. S1c). For analysis, spectral reflectance data were smoothed by averaging over each 5 nm interval within the range 300–700 nm, the approximate visual spectrum of birds and most diurnal lizards (Vorobyev *et al.*, 1998; Loew *et al.*, 2002), and

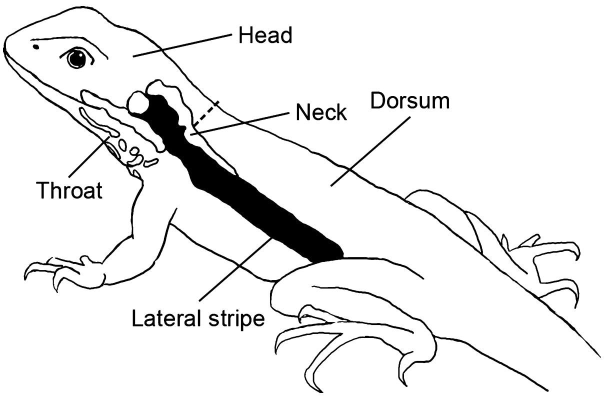

Fig. 2 Male *C. decresii* body regions for which spectral reflectance measurements were taken. When calculating dorsal colour patch proportions, we considered the head region to end in line with the forelimbs (dotted line).

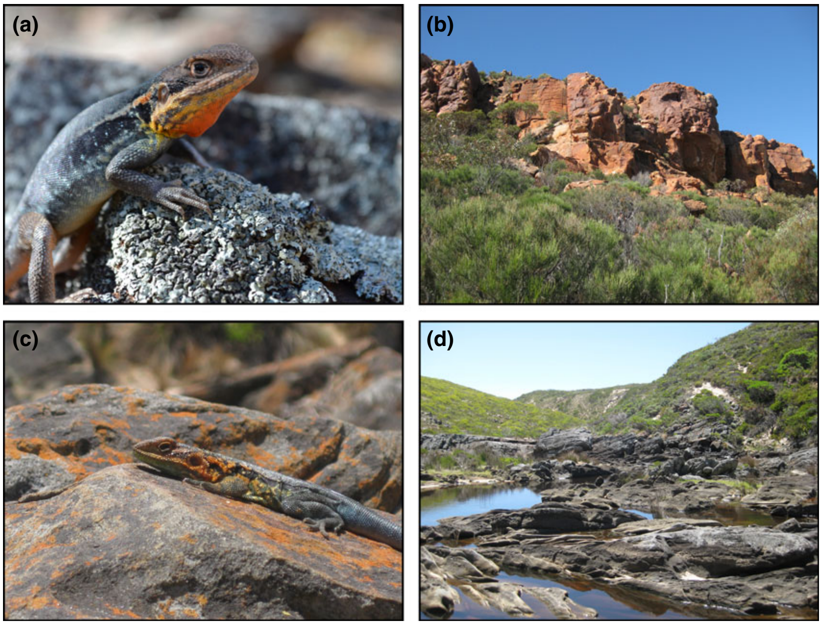

Fig. 3 A northern lineage male (orange-yellow morph; Aroona) against a rock with green lichen (a), northern orange rock (Flinders Ranges; b), a southern lineage male (Snake Lagoon) against a rock with orange lichen (c) and southern grey rock (Kangaroo Island; d).

the mean irradiance across all sites was normalized to a maximum of one.

Visual models

We evaluated the contrast of throats and lateral coloration (neck and stripe) against backgrounds, and the internal contrast between throat colours, as perceived by a conspecific lizard. We also assessed the conspicuousness of dorsal coloration (head and dorsum) and lateral coloration (neck and stripe) against backgrounds as perceived by potential avian predators. We applied the model of Vorobyev & Osorio (1998), using calculations detailed in Siddiqi *et al.* (2004), to determine the 'distance' between two colours in units of just noticeable differences (JND), where one JND is the threshold of discrimination and the greater the value, the more discriminable the colours. Accordingly, a JND value of greater than one indicates that two colours can be discriminated, whereas colours are indistinguishable if they have a contrast value of less than one JND (based on the visual system of the receiver and the light environment). In general, JND values between one and three mean that two colours are unlikely to be discriminated, but values below six JNDs may also be difficult to discriminate in complex visual environments (Siddiqi *et al.*, 2004). Lighting conditions are incorporated into calculations of JNDs and changes in ambient lighting will affect estimated values; however, the relative differences in JNDs of lizard colours against backgrounds are very unlikely to change with the relatively minor changes in the shape of irradiance spectra in terrestrial environments.

The visual model estimates chromatic (colour) contrast (ΔS) based on the four single cones (ultraviolet/violet sensitive (UVS/VS), short wavelength sensitive (SWS), medium wavelength sensitive (MWS), and long wavelength sensitive (LWS)) and achromatic (luminance) contrast (f_D) based on the double cone, which is thought to be responsible for detecting differences in signal luminance for both lizards and birds (Campenhausen & Kirschfeld, 1998; Hart, 2001a; Osorio & Vorobyev, 2005). Full details of model calculations for *C. decresii* based on spectral sensitivities of the closely related ornate dragon, *Ctenophorus ornatus* (Barbour *et al.*, 2002), and for *C. decresii*'s main bird predators, are detailed in Teasdale *et al.* (2013; see also Fig. S1). Preliminary data on spectral sensitivities from microspectrophotometry for both the northern and southern lineages of *C. decresii* show no differences between lineages (supported by opsin gene expression data), and confirm that spectral sensitivities are nearly identical to those of *C. ornatus* (M. Yewers, B. Knott, C. McLean, A. Moussalli, A. T. D. Bennet and D. Stuart-Fox, unpublished data). This is consistent with the phylogenetic conservatism of visual systems evident within lizard families (Olsson *et al.*, 2013). Consequently, we assumed that the two lineages of *C. decresii* shared the same visual system. Common predators of *C. decresii* include the little crow, *Corvus bennetti*, and the grey butcherbird, *Cracticus torquatus*, which have ultraviolet sensitive (UVS) visual systems, and the Australian kestrel, *Falco cenchroides*, and the laughing kookaburra, *Dacelo novaeguineae*, which have violet sensitive (VS) visual systems (Gibbons & Lillywhite, 1981; Stuart-Fox *et al.*, 2003; Hart & Hunt, 2007). Therefore, we performed analyses based on the spectral sensitivities of both avian visual systems, including the effects of coloured oil droplets associated with the different cones (Endler & Mielke, 2005). Results were qualitatively the same for both avian visual systems so we only report UVS results here.

Statistical analysis

We calculated the visual contrasts (ΔS and f_D) of each male colour patch (throat, head, dorsum, neck and stripe) against lineage-specific mean backgrounds (southern grey rock and orange lichen, northern orange rock and green lichen), and the visual contrasts between throat colours. For statistical analysis, we used the contrasts of blue, orange and yellow throat colours as these occur in discrete colour patches, and combined cream and grey contrasts (in 50 : 50 proportions) to account for the fine patterning consistently observed in individuals of the grey morph (Teasdale *et al.*, 2013; Fig. 1d). A measure of dorsal conspicuousness was derived by combining contrasts of the head and dorsum for each individual, weighted by the proportion of the total dorsal surface that each patch occupied, which were 30% head and 70% dorsum (excluding limbs and tail; Fig. 2).

We used generalized linear models (GLMs, SAS 9.3; PROC GLM) to compare the conspicuousness of southern and northern males against native and non-native backgrounds, and the internal contrasts between constituent throat colour patches of each morph. Chromatic and achromatic contrast values were the dependent variables, and throat colour or lineage (for dorsal and lateral coloration) and background, and their interaction, were the independent variables in the model. We performed *post hoc* pairwise comparisons and applied false discovery rate (FDR) correction for multiple tests to assess differences between morphs/lineages and backgrounds.

Results

Conspicuousness of throat coloration to conspecific lizards

From the perspective of a lizard, throat colours differed significantly in their chromatic and achromatic contrast against rock and lichen backgrounds, and there was a significant interaction between throat colour and background (Table 1). Not all possible pairwise comparisons (between all morphs on all backgrounds) were considered as only those assessing whether there are differences in conspicuousness for each colour morph on their native versus non-native background were of relevance to the initial hypotheses. With the exception of the grey morph, these comparisons revealed that throats were more chromatically conspicuous against native than non-native lichen backgrounds but less chromatically conspicuous against native than non-native rock backgrounds (Fig. 4a,b, respectively; Table S1). Specifically, northern orange and yellow throats were more chromatically conspicuous against green lichen (native) than orange lichen (non-native; $P < 0.0001$ and $P = 0.008$, respectively; Fig. 4a; Table S1), and southern blue throats were more chromatically conspicuous against orange lichen (native) than green lichen (non-native; $P < 0.0001$; Fig. 4a; Table S1). Conversely, northern orange and yellow throats were less conspicuous against orange rock (native) than grey rock (non-native; $P < 0.0001$; Fig. 4b; Table S1), and southern blue throats were less chromatically conspicuous against grey rock (native) than orange rock (non-native; $P = 0.001$; Fig. 4b; Table S1). All throat colours, irrespective of lineage, had a greater achromatic contrast against southern backgrounds than against northern backgrounds ($P < 0.01$ for all pairwise comparisons; Fig. 4c,d; Table S1); however, there was no significant difference in the achromatic contrast of southern blue throats against lichen backgrounds (Fig. 4c; Table S1).

Table 1 Results of general linear models (GLMs) testing for significant differences in chromatic and achromatic contrast of throat colours against rock and lichen backgrounds from the perspective of a conspecific lizard. Throat colours are blue (southern), grey, orange and yellow (northern), and backgrounds are grey rock, orange lichen (southern), orange rock and green lichen (northern). Contrasts are in units of just noticeable differences (JND).

Contrast	Source	SS	$F_{\text{d.f.}}$	P
Chromatic	Throat colour	370.791	$28.54_{3,232}$	<0.0001
	Background	74.740	$5.75_{3,232}$	<0.001
	Throat colour × Background	907.855	$23.30_{9,232}$	<0.0001
Achromatic	Throat colour	647.920	$12.81_{3,232}$	<0.0001
	Background	4199.702	$83.04_{3,232}$	<0.0001
	Throat colour × Background	660.284	$4.35_{9,232}$	<0.0001

SS, Type III sum of squares.

Throat colour morphs differed significantly in the internal contrast between constituent throat colour patches (chromatic: $F_{4,\ 77} = 15.33$, $P < 0.0001$, achromatic: $F_{4,\ 77} = 10.87$, $P < 0.0001$). The chromatic contrasts between the primary and secondary colours of southern males (blue and yellow) and the orange morph (orange and cream) were significantly greater than the orange-yellow, yellow and grey morphs, whereas the achromatic contrast between the two colours of the grey morph (grey and cream) was significantly greater than all other morphs ($P < 0.01$ for all pairwise comparisons; Fig. 5).

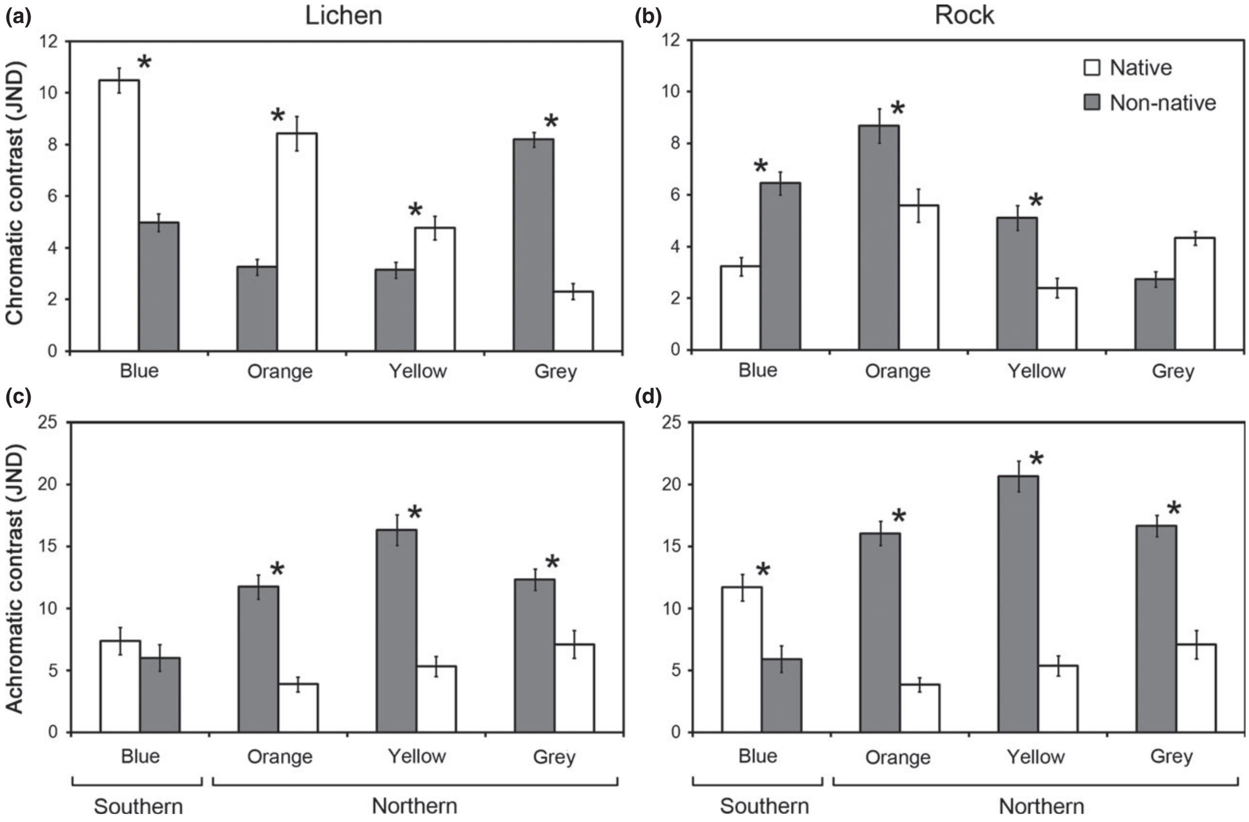

Fig. 4 Mean (± SE) chromatic (a) and achromatic (c) contrasts of southern (blue) and northern (orange, yellow and grey) throat colours against orange lichen (southern) and green lichen (northern), and chromatic (b) and achromatic (d) contrasts against grey rock (southern) and orange rock (northern) from the perspective of a lizard. In each case, paired bars show contrasts against southern backgrounds on the left and northern backgrounds on the right, and shading indicates whether backgrounds are native or non-native. Contrasts are in units of just noticeable differences (JND), and asterisks indicate statistically significant comparisons ($P < 0.05$).

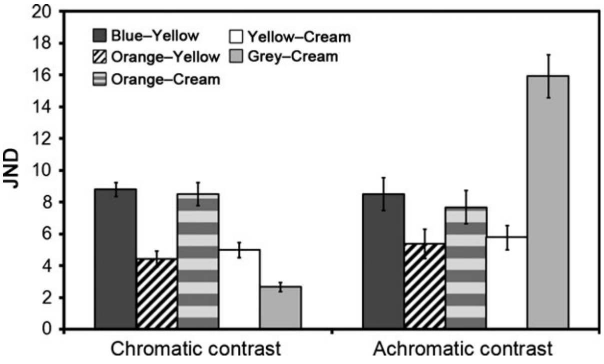

Fig. 5 Internal chromatic and achromatic contrasts (mean just noticeable differences (JND) ± SE) between constituent throat colour patches for the blue (southern), orange-yellow, orange, yellow and grey (northern) morphs, respectively.

Conspicuousness of lateral coloration to lizards and birds

Neck coloration of the two lineages differed significantly in chromatic and achromatic contrast against rock and lichen backgrounds (Table 2). There was a significant interaction between lineage and background, as perceived by both lizards and birds (Table 2), with the neck coloration of both lineages matching native lichen more closely than non-native lichen (Fig. 6a,c; Table S2). Specifically, the neck coloration of northern males was significantly less chromatically (bird: $P < 0.006$) and achromatically (bird: $P < 0.0001$, lizard: $P < 0.0001$) conspicuous against native green lichen than against non-native orange lichen (Table S2), whereas the neck coloration of southern males was less chromatically conspicuous against native orange lichen than non-native green lichen (bird: $P = 0.0004$, lizard: $P < 0.0001$; Table S2).

With the exception of the chromatic contrast against grey rock, the black lateral stripe contrasted highly against all other backgrounds (chromatic contrast JNDs > 3; achromatic contrast JNDs > 10). There was no difference between lineages in the chromatic contrast of the lateral stripe (Table 2; Fig. S2a). However, the darker black lateral stripe of southern males had higher achromatic contrast against all backgrounds than the lateral stripe of northern males (Table 2; Fig. S2b).

Table 2 Results of general linear models testing for significant differences between lineages (southern and northern) and backgrounds in the chromatic and achromatic contrast of lateral coloration (neck and stripe) against grey rock, orange lichen (southern), orange rock and green lichen (northern). Results are only shown from the perspective of a bird (UVS), as results were qualitatively the same for birds and lizards, and contrasts are in units of just noticeable differences (JND).

Region	Contrast	Source	SS	$F_{\mathrm{d.f.}}$	P
Neck	Chromatic	Lineage	27.198	$9.07_{1,156}$	0.003
		Background	93.228	$10.36_{3,156}$	<0.0001
		Lineage × Background	74.347	$8.26_{3,156}$	<0.0001
	Achromatic	Lineage	170.536	$7.15_{1,156}$	0.008
		Background	1973.085	$27.56_{3,156}$	<0.0001
		Lineage × Background	536.816	$7.50_{3,156}$	0.0001
Stripe	Chromatic	Lineage	0.548	$0.82_{1,148}$	0.366
		Background	866.421	$434.36_{3,148}$	<0.0001
		Lineage × Background	0.128	$0.06_{3,148}$	0.979
	Achromatic	Lineage	322.663	$9.96_{1,148}$	0.002
		Background	7714.685	$79.36_{3,148}$	<0.0001
		Lineage × Background	0.000	$0.00_{3,148}$	1.000

SS, Type III sum of squares.

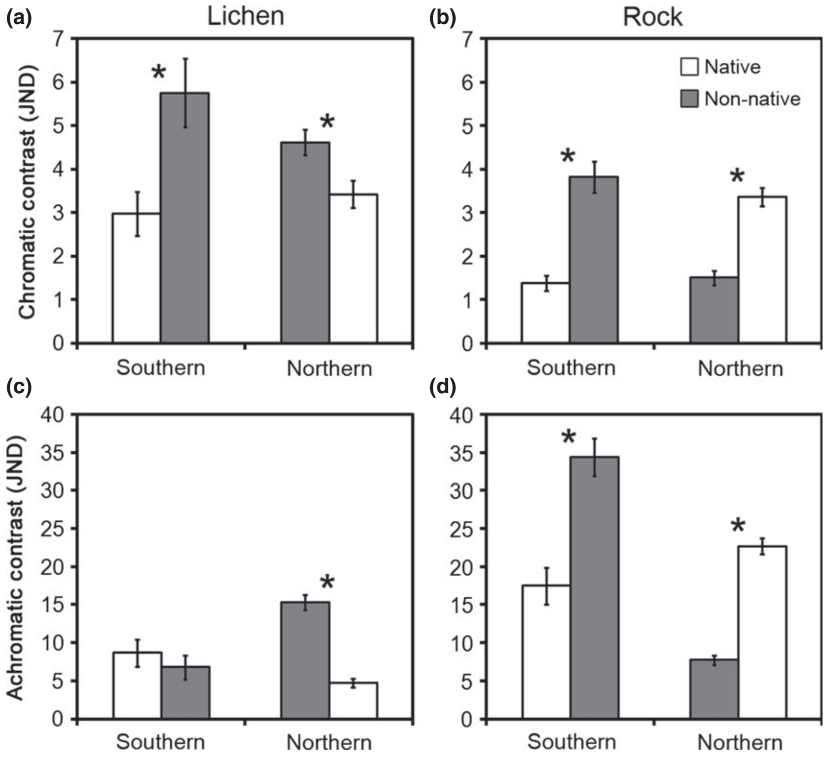

Fig. 6 Mean (± SE) chromatic (a) and achromatic (c) contrasts of southern and northern bright neck coloration against orange lichen (southern) and green lichen (northern), and chromatic (b) and achromatic (d) overall contrasts of southern and northern dorsal coloration against grey rock (southern) and orange rock (northern) from the perspective of a bird with an UVS visual system. In each case, paired bars show contrasts against southern backgrounds on the left and northern backgrounds on the right, and shading indicates whether backgrounds are native or non-native. Contrasts are in units of just noticeable differences (JND), and asterisks indicate statistically significant comparisons ($P < 0.05$).

Furthermore, the lateral stripe of both lineages was more chromatically contrasting against orange lichen (Fig. S2a) and more achromatically contrasting against northern backgrounds (green lichen and orange rock) than against southern backgrounds (orange lichen and grey rock; $P < 0.0001$ for all pairwise comparisons; Fig. S2b).

Dorsal conspicuousness to avian predators

To the visual system of a bird, there was no difference in the chromatic contrast of dorsal coloration between lineages (Table 3), although both lineages contrasted more against orange lichen than other backgrounds (Fig. S3a). Southern males had higher achromatic contrast (i.e. were more conspicuous) against all backgrounds than northern males (Table 3; $P < 0.0001$ for all pairwise comparisons; Fig. S3b) but both lineages were more achromatically contrasting against northern backgrounds (green lichen and orange rock) than against southern backgrounds (orange lichen and grey rock; $P < 0.0001$ for all pairwise comparisons; Table S3). Consequently, both southern and northern males

Table 3 Results of general linear models testing for significant differences between lineages (southern and northern) and backgrounds in the chromatic and achromatic contrast of dorsal coloration against grey rock (southern) and orange rock (northern) backgrounds from the perspective of a bird (UVS). Contrasts were in units of just noticeable differences (JND).

Contrast	Source	SS	$F_{\mathrm{d.f.}}$	*P*
Chromatic	Lineage	2.520	$2.74_{1,158}$	0.100
	Background	710.957	$257.27_{3,158}$	<0.0001
	Lineage × Background	2.061	$0.75_{3,158}$	0.526
Achromatic	Lineage	3522.602	$104.91_{1,158}$	<0.0001
	Background	2379.664	$70.87_{3,158}$	<0.0001
	Lineage × Background	18.225	$6.075_{3,158}$	0.909

SS, Type III sum of squares.

had similar absolute achromatic contrast against their native backgrounds (Fig. 6d, S3b).

Discussion

We hypothesized that differences in throat and dorsal coloration between the two main genetic lineages of *C. decresii* should reflect local adaptation to enhance conspicuousness to conspecific lizards and reduce conspicuousness to predators, respectively. The results revealed a more complex pattern than we had expected. Although throat colours were more chromatically conspicuous against native than non-native lichen backgrounds (with the exception of the grey morph), this was not the case for primary rock colours. Indeed, northern orange and yellow, and southern blue throats were less conspicuous against their native rock backgrounds. The markings on the neck and side of the head matched native lichens more closely than non-native lichens (to both lizards and birds) but contrasted strongly with the black lateral stripe, which was highly conspicuous against all backgrounds. In terms of dorsal coloration, southern males were more achromatically conspicuous to birds than northern males against all backgrounds; however, the lineages had similar absolute contrasts against their native backgrounds. These results suggest interesting interactions between background coloration and local selective pressures, which we discuss below.

Conspicuousness of social signals

Lineage-specific throat coloration was generally very conspicuous (high JND values) to lizards, particularly against native lichens which grow patchily on rocks throughout the region. The highest chromatic contrast was between southern blue throats and their native orange lichen, which can be extensive on rocks in southern populations (Fig. 3c), and is almost absent in northern populations. By contrast, the orange and yellow throat coloration present in northern males may be difficult to distinguish from southern backgrounds because they more closely resemble the colour of orange lichen, even though they are conspicuous against southern grey rock. Additionally, southern throat coloration had a large internal chromatic contrast (between blue and yellow), which can increase conspicuousness at short viewing distances (e.g. Marshall, 2000; Bohlin *et al.*, 2008), and conspecifics are expected to view each other at relatively close range. Yellow also had the greatest achromatic contrast with both grey rock and orange lichen. Therefore, blue and yellow together, which constitute southern throat coloration, may provide the most effective overall throat colour signal (compared to northern throat colours) against the combination of background colours present in southern sites.

Given that the northern lineage of *C. decresii* is polymorphic, selection for conspicuous throat signals may vary among morph types in association with correlated behavioural, morphological or life-history traits. In the northern lineage of *C. decresii*, orange males display higher aggression towards model intruders than the three other morphs (M. Yewers & D. Stuart-Fox, unpublished data). Therefore, this dominant behavioural strategy may necessitate a more conspicuous throat colour signal. Consistent with this hypothesis, of the northern throat colours, orange was the most chromatically conspicuous against the predominant native orange rock, but was also very conspicuous against southern grey rocks. Rock colour is particularly variable in the northern lineage and includes grey rocks as well as yellow, orange and reddish-brown. Consequently, orange may be the most conspicuous throat colour against the full spectrum of rock colours observed in northern populations, as well as against the native pale green lichen that finely speckles many of the northern rocks (Fig. 3a).

The relative conspicuousness of *C. decresii* signals is dependent on the background against which they are viewed (particularly rock *versus* lichen). Here, we focused on the most abundant rock colours in the two lineages: grey rock in the south and orange rock in the north (which also happened to be unique to the northern lineage); however, there are other rock colours present in these lineages. Therefore, males could potentially select substrates that maximize colour contrast during courtship and territory defence and maximize crypsis at other times (e.g. when basking). Sophisticated choice of display location, or modification of visual backgrounds to maximize conspicuousness has been demonstrated in multiple species (e.g. Endler & Théry, 1996; Heindl & Winkler, 2006). For example, golden-collared manikins, *Manacus vitellinus*, remove leaf litter and perform courtship displays on cleared earth to increase plumage conspicuousness (Uy & Endler, 2004). In *C. decresii,* however, throat colour morphs of the northern lineage do not differ in microhabitat preferences (Teasdale *et al.*, 2013; M. Yewers & D. Stuart-Fox, unpublished data). Extensive field observations suggest that perching rocks are selected according to their size, presence of a suitable crevice and position (e.g. in relation to other territories and obscuring vegetation; C. McLean pers. obs.; Teasdale *et al.*, 2013) rather than by colour; suggesting that choice of display location to maximize colour contrast is unlikely in this species. Additionally, *C. decresii* colour signals may be viewed from different angles, which will alter the background against which they are viewed (e.g. green vegetation or blue sky). Despite this, *C. decresii* is a rocky habitat specialist and will thus be predominately viewed adjacent to (if not directly against) rock and lichen backgrounds. Consequently, comparing the contrasts of lizards against the most abundant substrate colours seems appropriate in this system.

Lateral coloration (cream-orange neck and black stripe; Fig. 2) may also be a social signal as it is displayed during contests and courtship and is more pronounced in males than in females. Therefore, we expected lineage-specific lateral coloration to be shaped by both sexual selection and predation as it is a social signal which is located on a body region visible to predators. We found that neck coloration was conspicuous against rocks to both lizards and birds, but not against native lichen. Furthermore, lateral coloration is more extensive in southern males than in northern males (McLean *et al.*, 2013). This may be because sexual selection on male traits (including coloration) can vary geographically. For example, females favour bright male dorsal coloration in some populations of the chuckwalla, *Sauromalus obesus*, but not in others (Kwiatkowski & Sullivan, 2002). In the polymorphic northern lineage of *C. decresii*, sexual selection may vary in relation to throat coloration and/or alternative behavioural strategies adopted by the different colour morphs (e.g. Thompson & Moore, 1991; Sinervo & Lively, 1996; Huyghe *et al.*, 2009; Olsson *et al.*, 2009, M. Yewers & D. Stuart-Fox, unpublished). Conversely, given that the southern lineage is not variable for throat coloration (i.e. is monomorphic), selection for more intense and extensive lateral coloration may be stronger than in the northern lineage.

Although cream-orange neck coloration more closely matched native than non-native lichen, it contrasted highly with the conspicuous black lateral stripe. Therefore, an interesting possibility is that lateral coloration is both a sexually selected signal and contributes to disruptive camouflage, by breaking up the lizard's outline. Disruptive camouflage is most effective when colours are highly contrasting, located at the body's margins and when one of the colours matches elements of the background (Stevens & Merilaita, 2009). In accordance with this, when viewed from above, the high-contrast black lateral stripe and cream-orange neck coloration of *C. decresii* occur at the body's margins, and the neck coloration is a relatively close match to the native lichen.

Dorsal conspicuousness to avian predators

Dorsal coloration (head and dorsum; Fig. 2) was chromatically similar between lineages and closely matched grey rock (low JNDs). Southern males were more achromatically conspicuous against all backgrounds than northern males; however, the dorsal coloration of both lineages contrasted more against northern background colours (orange rock and green lichen). Consequently, the absolute achromatic contrast of southern and northern males was comparable. In other words, divergence between the lineages has resulted in similar conspicuousness of dorsal coloration against the native background in each lineage (Fig. S3). Given that luminance (achromatic) signals can be particularly important for prey detection (Osorio *et al.*, 1999; Hart, 2001b), our results suggest local background coloration has constrained the evolution of dorsal coloration in *C. decresii*. Nevertheless, the dorsal coloration of southern males did not maximize crypsis as they were more conspicuous than northern males against southern backgrounds (grey rock and orange lichen). Therefore, factors other than predation risk may affect dorsal coloration, in particular, dorsal coloration may also be influenced by sexual selection (e.g. due to correlated evolution with sexual signals) or by geographic variation in predator assemblages and/or abundance (e.g. Macedonia *et al.*, 2002; Kwiatkowski, 2003). Furthermore, conspicuousness does not necessarily equate to higher predation risk, as individuals can compensate for increased detectability by altering their behaviour (e.g. Hedrick, 2000; Cabido *et al.*, 2009; Fowler-Finn & Hebets, 2011), and it is currently not known whether the lineages differ in their response to predators.

Conclusions

We found clear differences between lineages in conspicuousness of sexual signals to conspecifics when viewed against native versus non-native backgrounds. Our results suggest that the contrast of both throat and lateral coloration against patchily distributed lichens may be an important, but heretofore unrecognized driver of signal divergence in this species, and potentially other rock-dwelling taxa. Furthermore, our results suggest that background coloration has constrained the evolution of dorsal coloration, for which both lineages were similarly conspicuous to birds (despite differences in the colour of both the lizards and their backgrounds). This study provides evidence that geographic variation in multiple colour traits reflects local adaptation to variable background colours, in relation to multiple receivers. Further research should focus on how spatial variation in predation risk and/or sexual selection in *C. decresii* interact with lineage-specific differences in the visual environment (and potentially neutral processes) to influence geographic colour variation.

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Supporting information

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

Figure S1 The average reflectance of *C. decresii* throat colours (a), and visual modelling data used to quantify lizard conspicuousness including: background spectra, with the shaded area showing the full range of rock colours recorded for sites in the southern lineage (from dark grey to light pink), while rock colours in the northern lineage also include red, yellow and orange (from bottom of shaded area to broken line; b), normalized irradiance (c), and the spectral sensitivities of lizard (d), ultraviolet sensitive (UVS) bird (e) and violet sensitive (VS) bird (f) photoreceptors (UVS, ultraviolet sensitive; VS, violet sensitive; SWS, short wavelength sensitive; MWS, medium wavelength sensitive; LWS, long wavelength sensitive single cones; D, double cone).

Figure S2 Comparison of mean (± SE) chromatic (a) and achromatic (b) contrast of southern and northern lateral stripes against grey rock (southern), orange rock (northern), orange lichen (southern) and green lichen (northern) from the perspective of a bird with an UVS visual system.

Figure S3 Comparison of mean (± SE) chromatic (a) and achromatic (b) contrast of southern and northern dorsal coloration against grey rock (southern), orange rock (northern), orange lichen (southern) and green lichen (northern) from the perspective of a bird with an UVS visual system.

Table S1 Pairwise comparisons of chromatic (ΔS) and achromatic (FD) contrast values of throat colours against native and non-native rock and lichen backgrounds from the perspective of a lizard.

Table S2 Pairwise comparisons of chromatic (ΔS) and achromatic (FD) contrast values of southern and northern lateral coloration (neck) against native and non-native rock and lichen backgrounds as perceived by UVS birds and lizards respectively.

Table S3 Pairwise comparisons of chromatic (ΔS) and achromatic (FD) contrast values of southern and northern dorsal coloration against native and non-native rock backgrounds as perceived by an UVS bird.

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