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Sexual dichromatism and differential conspicuousness in two populations of the common collared lizard (*Crotaphytus collaris*) from Utah and New Mexico, USA

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The common collared lizard (*Crotaphytus collaris*) exhibits considerable geographical colour variation, particularly among males. Populations of this diurnal saxicolous iguanian inhabit patches of rocky habitat throughout the species' broad distribution in North America and are anticipated to experience local differences in selective pressures that influence colouration. Specifically, while social interactions might favour conspicuous colouration, crypsis may be advantageous in interactions with visually orienting predator and prey species. To address the local relationship between lizard and substrate colouration we compared the reflectance spectra of two geographically distant and phenotypically divergent populations of collared lizards with the rocky substrates they inhabit. Our northern study population (*C. c. auriceps* in eastern Utah) occurs on red rocks, where males exhibit boldly coloured turquoise bodies and bright yellow heads. In contrast, our southern study population (*C. c. fuscus* in southern New Mexico) lives on grey and tan rocks, and males in this location exhibit subdued brown and tan dorsal colours. Spectral comparisons revealed that males in the northern population contrasted strongly with their local rocks, whereas males in the southern population matched their rock colours with reasonably good fidelity. This relationship held under a variety of lighting conditions. Females in both populations were less conspicuously coloured than males, although northern females contrasted more with their rocks than did southern females. In addition, sexual dichromatism was pronounced in the northern population but minimal in the southern population. Finally, sexual size and weight dimorphism was strong in the southern population while being virtually absent in the northern population. A comparison of the local predator and prey assemblages suggests that the conspicuous and sexually dichromatic colouration of the northern population may have evolved in response to reduced pressure from visually orienting predators as well as reduced dependence on saurian prey. *Biological Journal of the Linnean Society*, 2002, **77**, 67–85

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INTRODUCTION

Patterns of variation observed in animal colouration across species, populations, seasons and between the sexes have long interested biologists. Although colouration is thought to mediate crucial fitness-altering interactions, colours that are beneficial in one type of interaction can be detrimental in another. Whereas mate choice and intrasexual competition often yield a fitness advantage to individuals with the most conspicuous colour patterns (e.g. Darwin, 1871), this advantage typically is offset by the increased probability of being seen by predators (e.g. Endler, 1992). Research on adaptive colouration in guppies, for

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example, has shown that males are polymorphic for colour pattern elements in which patch colour, brightness, and size represent a local compromise between sexual selection for conspicuous colouration (e.g. Kodric-Brown, 1985; Houde, 1987; Long & Houde, 1989; Houde & Endler, 1990) and natural selection for cryptic colouration (Endler, 1978, 1980, 1991).

Sexual Dichromatism and Adaptive Colouration

It is common for males and females of the same species to exhibit different colour patterns, termed 'sexual dichromatism' (e.g. Gray, 1996; Andersson, Ornborg & Andersson, 1998; Cuthill *et al*., 1999; Badyaev & Hill, 2000). In species that display sexual dichromatism, males usually are the more conspicuously coloured sex: a result arising from the greater competition among males for mating opportunities and from female mate preferences (e.g. Andersson, 1994). Among reptiles, sexual dichromatism in body colouration has been studied in several lizard species (e.g. McCoy *et al*., 1997; LeBas & Marshall, 1999; Wiens, Reeder & De Oca, 1999; see Cooper & Greenberg, 1992 for earlier studies). Although males usually are the more dramatically coloured sex, females in some lizard species also exhibit bright nuptial colouration (reviewed in Cooper & Greenberg, 1992).

In the absence of benefits accruing to conspicuous colouration, natural selection tends to produce colour patterns that render animals inconspicuous against their visual backgrounds (e.g. Endler, 1984; Merilaita, Tuomi & Jormalainen, 1999). Naturally selected protective colouration can reduce predation risk by serving as camouflage (e.g. background matching, countershading, disruptive colouration: Cott, 1940; Endler, 1978, 1981; Edmunds, 1990). Although camouflage often is considered in terms of concealment from predators by prey, predators derive equal benefit, i.e. 'aggressive camouflage' (e.g. Ortolani, 1999). Lizards provide excellent examples of camouflage colouration, and several authors have described species whose dorsal surface reflectance spectra were well matched to their local substrates (e.g. sand, rocks, tree bark: Norris & Lowe, 1964; Gibbons & Lillywhite, 1981). One particularly promising taxon for the study of adaptive colouration in reptiles is *Crotaphytus*, the collared lizards.

Colour Variation in Collared Lizards

Collared lizards comprise one of two iguanian genera in the New World family Crotaphytidae. The nine recognized *Crotaphytus* species are distributed from the mid-western and western United States through northern and western Mexico (McGuire, 1996). These saxicolous (rock dwelling) reptiles are obligate carnivores (Ruppert, 1980), being both insectivorous and saurophagous (lizard eating). Although all species exhibit an increase in the 'vividness' of their colours during the breeding season (whether or not additional nuptial colours are present, e.g. McGuire, 1996), both sexes of most species possess camouflage patterns of spots, bars and reticulations against a relatively drab dorsal colouration. An exception to this trend is the common collared lizard, C. *collaris*, where males are diverse in dorsal colour throughout their distribution. In some *C. collaris* populations males display strikingly conspicuous colouration, whereas in other populations males appear dull, much like females; similarly, populations can differ in the degree of sexual size dimorphism (e.g. McCoy *et al*., 1997). Differences in social organization may account for the variability of male reproductive characters among populations of collared lizards (Baird, Fox & McCoy, 1997).

The social system of *C. collaris* is typical of many iguanians in that adult males are highly territorial, patrolling and defending their territory with conspicuous display behaviours. Typically each male territory overlaps the smaller territories of several females, and to a lesser extent female territories overlap with more than one male. Such a social system facilitates both intrasexual and intersexual competition for mates. Baird *et al*. (1997) argued that the opportunity for collared lizards to engage in territorial and sexual advertising using conspicuous colouration is influenced by population densities and the spatial arrangement of appropriate habitat patches.

Whether colouration appears conspicuous or inconspicuous depends, however, upon the background against which it is viewed and on the visual system of the viewer. Viewers that have the potential to exert selection pressures on the colouration of collared lizards include conspecific individuals, as well as the local array of visually orienting predator and prey species. Moreover, given that (1) stone and earth vary in colouration with geological formations and habitat, that (2) different suites of predator and prey species vary by locality, and that (3) populations vary in the social opportunities for territorial and sexual advertising, it is likely that selective pressures for colour patterns in *C. collaris* vary on a local scale. Spectral analysis of *C. collaris* and of their local visual backgrounds is a starting point for understanding the interactions of selective regimes that produce among-population colour variation.

In this study we describe, spectrally and statistically, the colouration of two geographically discontinuous and phenotypically divergent *C. collaris* populations: the yellow-headed collared lizard (*C. c. auriceps* Fitch & Tanner 1951) of eastern Utah and north-western Colorado, and the Chihuahuan col-

lared lizard (*C. c. fuscus* Ingram & Tanner 1971) of southern New Mexico, extreme western Texas, and northern Mexico. *Crotaphytus c. auriceps* males are boldly coloured with turquoise bodies and yellow heads, whereas *C. c. fuscus* males exhibit brown and tan colour patterns very similar to those of females. We compare these two lizard populations from the perspectives of sexual dichromatism, contrast with their natural backgrounds, sexual size and weight dimorphism, and their local suites of predator and prey species.

MATERIAL AND METHODS

Study Areas and Subjects

We chose our study areas based on sampling by prior researchers (particularly McGuire, 1996). In eastern Utah we concentrated on four sites paralleling the Colorado River, lying from 30 to 50 km north-east of Moab along State Route 128. These locations varied in habitat from boulder fields to eroded cliff faces. Lizard species sympatric with *C. c. auriceps* include *Uta stansburiana*, *Sceloporus undulatus* and *Cnemidophorus tigris*.

In southern New Mexico we focused our efforts on Baylor Canyon Road, a mostly graded dirt road running from Las Cruces, NM approximately 25 km north-east to the town of Organ. We concentrated on the road's northern end, where it bisects an extensive boulder field that spreads out from the base of the Organ Mountains. Sympatric with *C. c. fuscus* at this location are *Cophosaurus texanus*, *Sceloporus magister*, *Phrynosoma cornutum* and *Cnemidophorus* sp.

Lizards at all sites were captured with a pole and noose. Subjects whose spectral measurements were taken outdoors (see below) were kept in cloth bags between capture, data gathering and release.

Spectral Measurements of Collared Lizards and Their Habitats

Lizard Colouration

Reflectance spectra of the lizards were obtained indoors (year 1: June 2000) and outdoors (year 2: May/June 2001) using a reflectance probe (Ocean Optics R200-7) connected to a tungsten-halogen lamp (Ocean Optics LS-1), an Ocean Optics USB2000 portable spectrometer, and a notebook computer running Ocean Optics OOIBASE 32 software. For spectral measurements taken indoors a small black light was positioned near the tungsten-halogen lamp to increase near-UV illumination in a room otherwise dimly lit with incandescent bulbs. Subjects were placed on a flat black rubber mat and reflectance was sampled perpendicular to the target. A white standard (Labsphere Spectralon WS-1) was scanned and dark current removed from the signal immediately prior to scanning a subject, and reflectance spectra were calculated automatically from subject radiance by the software. (Note that reflectance measurements made in years 1 and 2 are not biased by the use of different illumination sources. The purpose of the white standard is to allow calculation of a reflectance spectrum from any illumination source that possesses the wavelengths of interest.)

Data were displayed with OOIBase32 software (Ocean Optics, Inc.). Twelve body regions were chosen for spectral measurements to obtain a relatively comprehensive profile of body colouration (Table 1). A small ruler attached to the reflectance probe maintained a constant 5 mm distance between the end of the probe and the target. For *C. c. auriceps*, we sampled 12 males (six each year) and six females (three each year). For *C. c. fuscus*, we sampled 12 males (one in year 1, 11 in year 2) and 11 females (two in year 1, nine in year 2).

All spectral readings taken outdoors were obtained during periods of very clear weather, typically under cloudless skies. If subjects felt colder to the touch than ambient air temperature (approx. 32–35 °C) they were warmed under a heat lamp (2000) or placed in direct sunlight in a cloth bag for 10–15 min (2001) before spectral data were gathered.

Table 1. Locations of lizard body regions measured spectrally in this study

Body region	Description of measurement
Crown	Dorsal surface of skull immediately anterior to parietal eye
Collar colour	Dorsal colour bands adjacent to black band(s) in nuchal-cervical region
Dewlap	Centre of gular area
Mandible	Ventral surface of mandible below labial scales
Dorsum background	Background colouration of dorsum (between dorsum bars, if present)
Dorsum bars	Dorsal transverse colour bands overlying background colouration
Side	Skin on side of abdomen immediately ventral to lateral midline
Ventrum	Central area of abdomen
Thigh	Dorsal (outer) surface of mid-thigh
Calf	Dorsal (outer) surface of mid-calf
Foot	Dorsal surface of front toes
Tail	Dorsal surface of tail, several centimeters distal to base

Rocks and Vegetation

Reflectance measurements of rocks, vegetation (e.g. grasses, bushes, cacti, flowers) and soil from the lizards' habitats were gathered in year 2 of the study. These readings were taken at the locations where the objects occurred, and a fibre optic fitted with a collimating lens (Ocean Optics UV-74) was used as the probe with sunlight serving as the illumination source. Soil reflectance spectra were virtually identical in shape to those of local rocks but were slightly darker (5–10%). Given that our soil reflectance sample sizes were small, we elected not to include them in our analyses. Our sample sizes for visual backgrounds in our two study areas were as follows: Utah rocks: $N = 22$, vegetation: $N = 10$; New Mexico rocks: $N = 42$, vegetation: $N = 15$.

Irradiance

A cosine-corrected irradiance probe (Ocean Optics CC-3-UV) and irradiance measurement software (Ocean Optics OOIIrrad) were used to sample habitat light. Prior to obtaining readings the irradiance probe was calibrated with a light source (Ocean Optics LS-1-CAL) designed for this lens. Irradiance data were collected only under clear, cloudless skies. Solar spectra were gathered by orienting the irradiance probe directly toward the sun. Skylight samples were obtained by orienting the probe toward the blue sky but away from the sun, and sunlight was blocked from striking the probe with a small, opaque black object. Irradiance data were used to calculate lizard and background radiance under different lighting conditions with the formula:

$$\text{radiance}\ (\lambda) = \text{reflectance}\ (\lambda) \times \text{irradiance}\ (\lambda)/2\pi$$

where 2π accounts for the hemispheric shape of the irradiance collector (i.e. the volume of a sphere = 4π). Although radiance could have been obtained directly, calculating radiance via reflectance and irradiance allows for the effects of different lighting conditions on animal and substrate colouration to be estimated using the same set of reflectance values. For example, saxicolous lizards inhabiting open areas of the southwestern US generally experience three types of ambient lighting: direct sunlight, desert (or 'blue') shade, and cloudy skies. As cloudy skies result in a largely 'white' light spectrum, this spectrum is roughly similar in the visible wavelengths to the reflectance spectrum of a white standard. Multiplying reflectance by a solar or skylight spectrum approximates the remaining two lighting conditions.

'Colour' Terminology

We use 'hue' in the vernacular sense of 'colour', e.g. red, green, blue, etc. Hue is defined by the shape of the spectral curve, particularly by its peak. 'Chroma' refers to colour saturation or purity, and is a function of the dominant wavelength's slope: the steeper the slope, the higher the chroma. We use brightness, or luminance, to refer to a spectrum's intensity, measured as the area under the curve (e.g. Endler, 1990).

Colour Space

Endler (1990) developed a colour analysis method, termed 'segment classification', that provides a graphical summary of differences in hue and chroma (brightness is equalized for all spectra). Segment classification presumes the presence of a typical opponency system of colour vision that compares the outputs of receptors sensitive to non-adjacent portions of the visible spectrum. Each spectrum from 400 to 700 nm was partitioned into four 75 nm colour segments containing 217 points each. These segments corresponded roughly to the human-perceived colour ranges of violet to blue (400–475 nm), green (475–550 nm), yellow to orange (550–625 nm), and red (625–700 nm). Each colour segment was summed, producing one value per segment, then each of the four values was divided by the sum of the unsegmented spectrum, resulting in four final values. By subtracting non-opposing pairs of these values (i.e. red minus green, yellow minus blue), two 'colour scores' summarizing each spectrum were plotted as a single point in two-dimensional colour space. Hue is determined by the angle of a colour score relative to the top-centre (i.e. 0°) of the graph, and chroma increases with the distance of a colour score from the origin. The further a lizard's colour score falls from the region of colour space occupied by objects in the visual background, the greater the colour contrast and the more conspicuous that body region should appear – irrespective of the visual system viewing it.

For reflectance colour space plots, the reflectance spectra of the lizards, rocks and vegetation were used to create the colour segments and colour scores. To estimate the effects of sunlight and skylight on lizard colouration, two types of radiance colour space plots were also generated, one simulating the effects of direct sunlight and the other of desert shade (i.e. skylight only). For these comparisons an irradiance spectrum (sunlight or skylight) was multiplied by each reflectance spectrum prior to computation of colour scores.

Sex Differences in Brightness and Colour

Several approaches were taken to examine sex differences in body colouration. In our first approach we considered brightness (luminance) and colour (hue and chroma) separately. Sex differences in brightness

('sexual diluminance') were determined in each population by (a) calculating a mean reflectance spectrum for each body region of male and of female subjects, (b) taking the absolute value of the difference between the male and female spectrum, and (c) summing this 'difference spectrum' to produce a single value, which then was divided by 10^3 for numerical convenience.

To determine sex differences in colouration independent of brightness ('sexual dichromatism'), male and female spectra were equalized for total brightness before calculating the male–female difference spectrum. This was achieved by (1) calculating the sum for each spectrum of the pair, (2) calculating the mean of these two sums, (3) dividing this mean value by each sum determined in step 1 to produce an 'equalization factor' for each sex, and finally (4) multiplying this equalization factor times every data point in the original spectrum for each sex. This procedure equalizes the total intensity of the pair of spectra without altering spectral shape (Endler, 1990). Steps (b) and (c) above then were completed to produce a single final value for each body region, which was used as the index of sexual dichromatism.

Multivariate Analysis of Sex and Population Colour Variation

PCA and ANOVA

In a second approach to analysing lizard colour variation, we examined colouration between sexes within each population and for same-sexed individuals between populations. For these analyses spectral data were grouped into 5 nm-wide bins (to meet assumptions for independence of data points), resulting in 75 median values per spectrum from 325 to 700 nm. Principal components analysis (PCA) was used to reduce the 75 values (= 75 variables) to a manageable number. In analyses of spectral data the first PC inevitably represents brightness variation and subsequent PCs represent colour variation (Cuthill *et al*., 1999). Separate PCAs were run on each of the 12 body regions measured, with both sexes and populations being included in each analysis. Following these 12 PCAs, two-way ANOVAs with factors for sex and population were used to test for significant differences in colouration. Where interaction terms were significant, one-way ANOVAs were run on the two opposite-sex/within-population and same-sex/between population combinations (with $\alpha = 0.025$).

DFA

We then sought to determine if a stepwise discriminant function analysis (DFA) could create functions from the PC scores capable of discriminating between the populations and sexes at the 'entire body' level. We wished to generate functions that took into account the spectral data from all 12 body regions simultaneously, but computer memory was insufficient for the required 900 median values (i.e. 75, 5 nm-wide median values × 12 body regions). We therefore broadened the bin size from 5 nm to 20 nm, and a PCA reduced the resulting 216 input variables (18, 20-nm-wide bins from 330 to 700 nm × 12 body regions) to 18 principal components. In the first of two analyses subjects were classified according to population, and in the second they were classified by sex. SPSS (v. 10 for Macintosh) default values were used for variable entry and retention (F-to-enter = 3.4; F-to-remove = 2.7).

Multivariate Analysis of Contrast Between Lizards and Rocks

To test statistically for differences in colour contrast and brightness contrast between the lizards' colouration and that of the local rocks on which they live, the reflectance spectra of rocks first were reduced to medians of 5 nm intervals as was done for lizard colouration. PCAs then were run on data sets that included the reflectance data from males and females of a given population and from rocks in that population's habitat. Next, independent samples t-tests were conducted on each of the first two principal components for each body region of each sex, i.e. 12 tests per sex per principal component. Levene's test was employed to determine whether the P-value associated with equal or unequal variances should be used for significance. Protection against increased Type I error rate from multiple comparisons was made to account for 24 pairwise comparisons within each PC (i.e. 12 body regions × 2 sexes × 1 rock reflectance data set for each population) using the sequential Bonferroni method (Rice, 1989).

Body size and Mass

After completing each subject's series of spectral readings we gathered two additional forms of data. First, we measured each subject's snout–vent length (SVL) to the nearest 0.5 mm, and then weighed each subject to the nearest 0.5 g. These data were examined statistically with the Mann–Whitney U-test.

Sympatric Avian and Ophidian Predator Species and Saurian Prey species

To obtain a rough between-population comparison of bird and snake species that are likely to prey on *Crotaphytus*, as well as the availability of lizard prey, we compiled a list of potential predator and prey species based on distribution maps from published field guides. We do not present data on the array of sympa-

tric mammalian predators, as these are virtually identical for our two populations and thus are unlikely to account for the observed colour differences. Furthermore, many mammalian predators are active at night when collared lizards are asleep within refugia under rocks.

RESULTS

Sex Differences in Brightness and Colour

As anticipated from visual inspection of the lizards, the two study populations differed considerably in their reflectance spectra (Fig. 1). Brightness differences between males and females were greater in more body regions for *C. c. auriceps* than for *C. c. fuscus*, and approached significance ($N = 12$, Wilcoxon $Z = 1.73$, $P = 0.084$; Fig. 2a). When equalizing brightness between the sexes, male and female *C. c. auriceps* differed in colour more than male and female *C. c. fuscus* for all 12 body regions ($N = 12$, Wilcoxon $Z = 3.06$, $P = 0.022$; Fig. 2b).

Colour Space

Reflectance spectra from rocks in our Utah and New Mexico sites differed both in brightness and in chroma (Fig. 3a). Rocks from both study areas had peaks in the 'red' part of the spectrum, but those from New Mexico (rhyolitic volcanic rock with some fine-grained granite) exhibited lower chroma (Fig. 3c) and were brighter than those from Utah (iron oxide-stained Navaho sandstone). The human perceptual difference in colouration was that the rocks in Utah were of a deep salmon-red colour, whereas those in New Mexico were greyish-white with pale pink, orange, and yellow overtones. Vegetation spectra from the two study areas differed as well, with plants in New Mexico being brighter and more yellowish than those in Utah (Fig. 3b).

In comparison to males from their own population, *C. c. auriceps* females exhibited less colour variation and their colour scores overlapped more with the visual background (Fig. 4a). In contrast, male and female *C. c. fuscus* were very similar in extent of colour variation, and most colour scores for both sexes overlapped those of their visual background (Fig. 4b).

Between population colour variation may be best visualized by plotting same-sexed individuals from both populations on the same scale. Variation in male colouration was found to be much larger for *C. c. auriceps* than for *C. c. fuscus* (Fig. 5a). Also, whereas male *C. c. auriceps* colour scores did not overlap those of rocks in their study sites, extensive overlap occurred between the colour scores of male *C. c. fuscus* and their local rocks (Fig. 5a). The comparison for females revealed a similar pattern, but the magnitude of the differences between the populations was smaller (Fig. 5b).

To determine how sunlight and shade would affect colouration of the lizards and their visual backgrounds, colour scores were recalculated after being multiplied by a solar spectrum (Fig. 6a) or a skylight/desert shade spectrum (Fig. 6b). Multiplication by the solar spectrum shifted colour scores toward the yellow region of colour space (Figs 7a,b) whereas multiplication by the skylight spectrum shifted the colour scores toward the blue region (Figs 7c,d). Sunlight had less of an impact than skylight on the colour scores because the solar spectrum is more similar in shape to 'white light' (i.e. reflectance) than is skylight. Interestingly, the skylight spectrum had the overall effect of reducing object chroma, i.e. most colour scores were shifted closer to the colour space origin. This shift was more prominent for *C. c. fuscus* than for *C. c. auriceps* due to the lower chroma of *C. c. fuscus* body colours (Fig. 7).

Multivariate Analysis of Sex and Population Colour Variation

PCA

For the lizard reflectance spectra (Fig. 1), PCA reduced 75, 5 nm-wide spectral medians to three PCs in 11 of the 12 body regions (only two PCs were generated for dewlap reflectance). Most of the variance in the raw spectral data stemmed from brightness variation. Unless brightness is equalized among the spectra prior to conducting a PCA, PC1 is a measure of this property, as evidenced from the 'flat line' appearance of its plotted coefficients (Fig. 8; Cuthill *et al*., 1999). The coefficients for PC2 and PC3 depict the weightings of components representing different aspects of spectral shape (hue + chroma) that are independent of brightness (Fig. 8). Most of the variation in spectral shape (PC2) was accounted for by differences between short- and long-wavelength reflectance (transition around 525 nm), or between very short wavelengths and long wavelengths (transition around 425 nm) (Fig. 8).

ANOVA

In subsequent two-way ANOVAs a significant main effect of sex on brightness (PC1) was revealed for four of the 12 body regions: dewlap, mandible, side, and ventrum (Table 2). Females were brighter than males in all cases (Fig. 1). Six body regions differed between the sexes in spectral shape (PC2 or PC3): dorsum background, dorsum bars, ventrum, thigh, calf, and tail (Table 2). No significant main effects (that lacked a significant interaction term) of population on brightness were revealed, but significant differences in

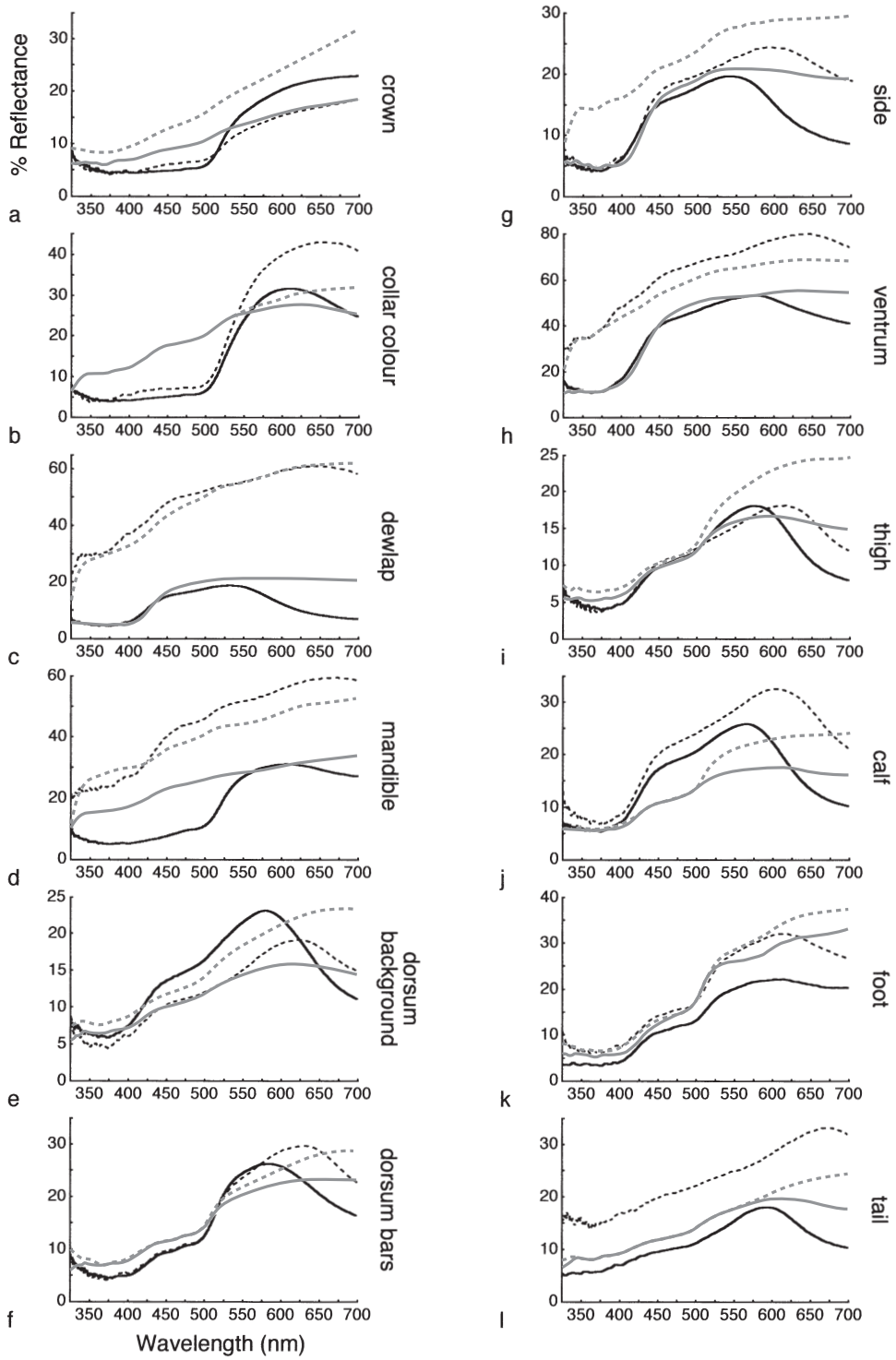

Figure 1. Mean reflectance spectra from 12 body regions measured for *Crotaphytus collaris auriceps* in eastern Utah (males: $N = 12$, solid black lines; females: $N = 6$, dashed black lines) and *C. c. fuscus* in southern New Mexico (males: $N = 12$, solid grey lines; females: $N = 11$, dashed grey lines).

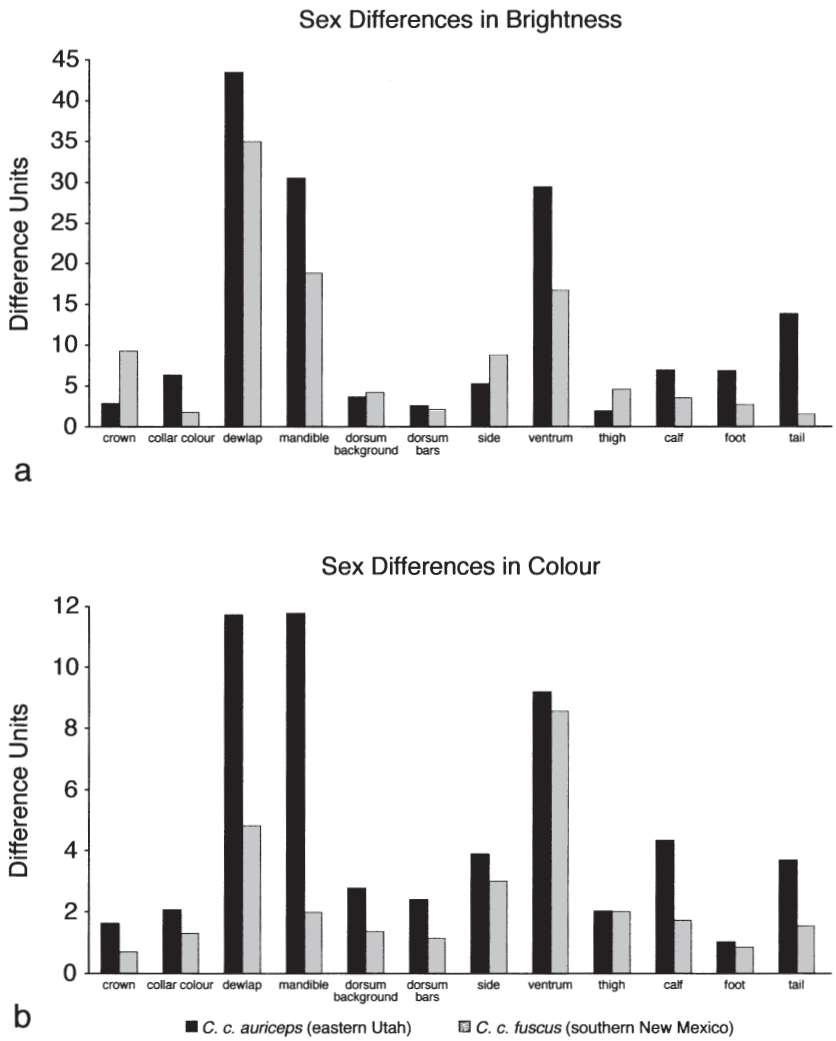

Figure 2. Sex differences in body reflectance: (a) brightness, and (b) colour for males and females from the two study populations. See text for derivation of 'difference units'. Sample sizes as in Fig. 1.

population spectral shape were found for all body regions except side and foot (Table 2).

Significant interaction terms in the two-way ANOVAs were tested for sex and population with one-way ANOVAs. A significant interaction occurred in brightness (PC1) for only one body region: the crown (Table 2). The crown was brighter in males than females in *C. c. auriceps*, but darker in males than females in *C. c. fuscus* (Fig. 1). None of the pairwise comparisons were significant (at $\alpha = 0.025$), however. Interaction terms were significant for spectral shape in four body regions: mandible, dorsum background, side, and ventrum. The mandible was found to differ significantly in spectral shape (PC3) only between males of the two populations ($F_{1,22} = 12.95$, $P = 0.001$). The dorsum background differed significantly in spectral shape (PC2) between the sexes in *C. c. auriceps* ($F_{1,17} = 8.00$, $P = 0.012$), between the sexes in *C. c. fuscus* ($F_{1,21} = 7.97$, $P = 0.010$), and between males in both populations ($F_{1,22} = 12.95$, $P = 0.004$) but not between females of the two populations. The side differed significantly in spectral shape (PC3) between the sexes in *C. c. fuscus* ($F_{1,21} = 14.61$, $P = 0.001$) and between males in the two populations ($F_{1,22} = 15.45$, $P = 0.001$). Last, the ventrum differed significantly in spectral shape (PC3) only between males in the two populations ($F_{1,22} = 15.60$, $P = 0.001$).

DFA

In an analysis of population and sex differences in colouration at the 'entire body' level, stepwise DFA generated a single function from seven (analysis by population) or six (analysis by sex) of the 18 components, which accounted for 59.9% and 53.2%, respec-

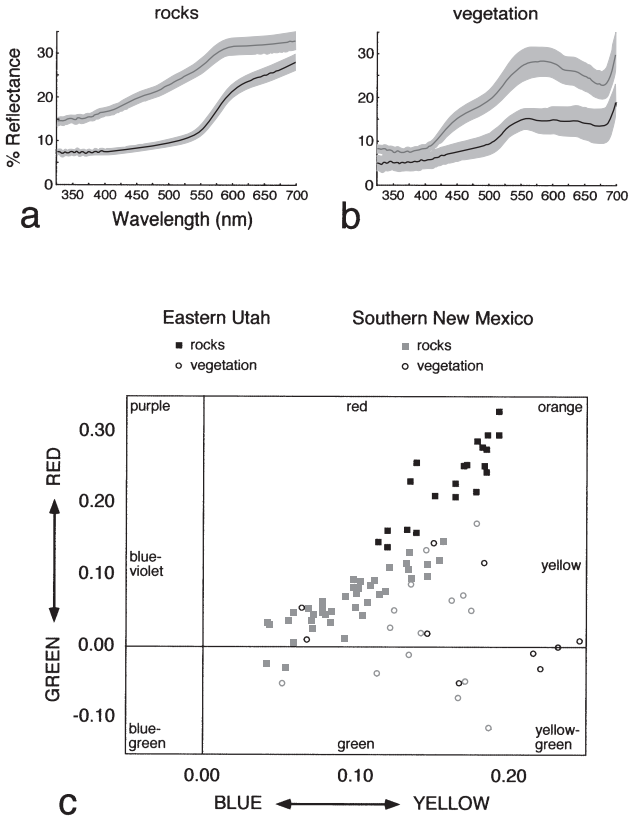

Figure 3. Mean reflectance spectra of (a) rocks, and (b) vegetation from habitats of the two study populations. Black lines: *Crotaphytus c. auriceps*, eastern Utah: rocks ($N = 22$), vegetation ($N = 10$); grey lines: *C. c. fuscus*, southern New Mexico: rocks ($N = 42$), vegetation ($N = 15$). (c) Spectral summaries (colour scores) of representative rock and vegetation samples plotted in the 'colour space' of Endler (1990).

tively, of the variation in the PC scores. In the first DFA the discriminant function classified the 41 subjects to the correct population in 100% of the cases. In the second DFA subjects were classified as males or females with 100% accuracy for *C. c. auriceps*, and 94.1% accuracy for *C. c. fuscus*. The single assignment error was due to classifying a female *C. c. fuscus* as a male.

Multivariate Analysis of Contrast Between Lizards and Rocks

To determine brightness contrast and colour contrast between the lizards and their visual backgrounds, PCAs first were run on reflectance spectra from each body region of both sexes in one population plus the reflectance spectra of rocks in their habitat. Three PCs with eigenvalues >1.0 were produced for 10 of the 12 body regions of *C. c. auriceps* and their local rocks (Table 3), but a third PC was produced from the *C. c. fuscus* data set for only five of the 12 body regions and rocks (Table 4). This difference between populations arises from greater brightness variation (PC1) between *C. c. fuscus* and their rocks (mean percentage variation = 91.4%; Table 4) as compared to *C. c. auriceps* (mean percentage variation = 74.5%; Table 3). Protected *t*-tests (sequential Bonferroni method: Rice, 1989) between lizard and rock reflectance PC scores revealed differences between the two populations in the manner and extent of contrast with their respective rocky visual backgrounds.

Brightness Contrast

Whereas *C. c. auriceps* exhibited few body regions that contrasted significantly in brightness with local rocks (males: one body region; females: three body regions; Table 3), half of the body regions of *C. c. fuscus* (both sexes) exhibited significant brightness contrast with their rocks (Table 4). Only one body region differed significantly from local rocks in brightness contrast across sexes and populations: the ventrum appeared white in females and greyish-white in males (Fig. 1).

Colour Contrast

On PC2 male and female *C. c. auriceps* differed significantly in colour contrast with their rocks for 12 and nine body regions, respectively (Table 2), but male and female *C. c. fuscus* differed significantly in only four and three body regions, respectively. Four of the five body regions that produced a third PC for *C. c. fuscus* exhibited significant lizard/rock colour contrast, but PC3 accounted on the average for less than 2% of the spectral variation between a given body region and that of local rocks (Table 4). Slightly more of the spectral variation was accounted for by PC3 (6.4%) in *C. c. auriceps*, but few body regions showed significant colour contrast with rocks on this variable (two in males and one in females).

In summary, male *C. c. auriceps* exhibited strong colour contrast but virtually no brightness contrast with the rocks on which they live, whereas male *C. c. fuscus* contrasted moderately in brightness but little in colour with their local rocks. Overall, females showed similar patterns of brightness contrast and colour contrast to those of males in their populations, but that contrast typically was weaker (i.e. fewer significant differences).

Body Size and Mass

Size and mass data revealed strong differences in sexual dimorphism between the two populations. Although male and female *C. c. auriceps* did not differ

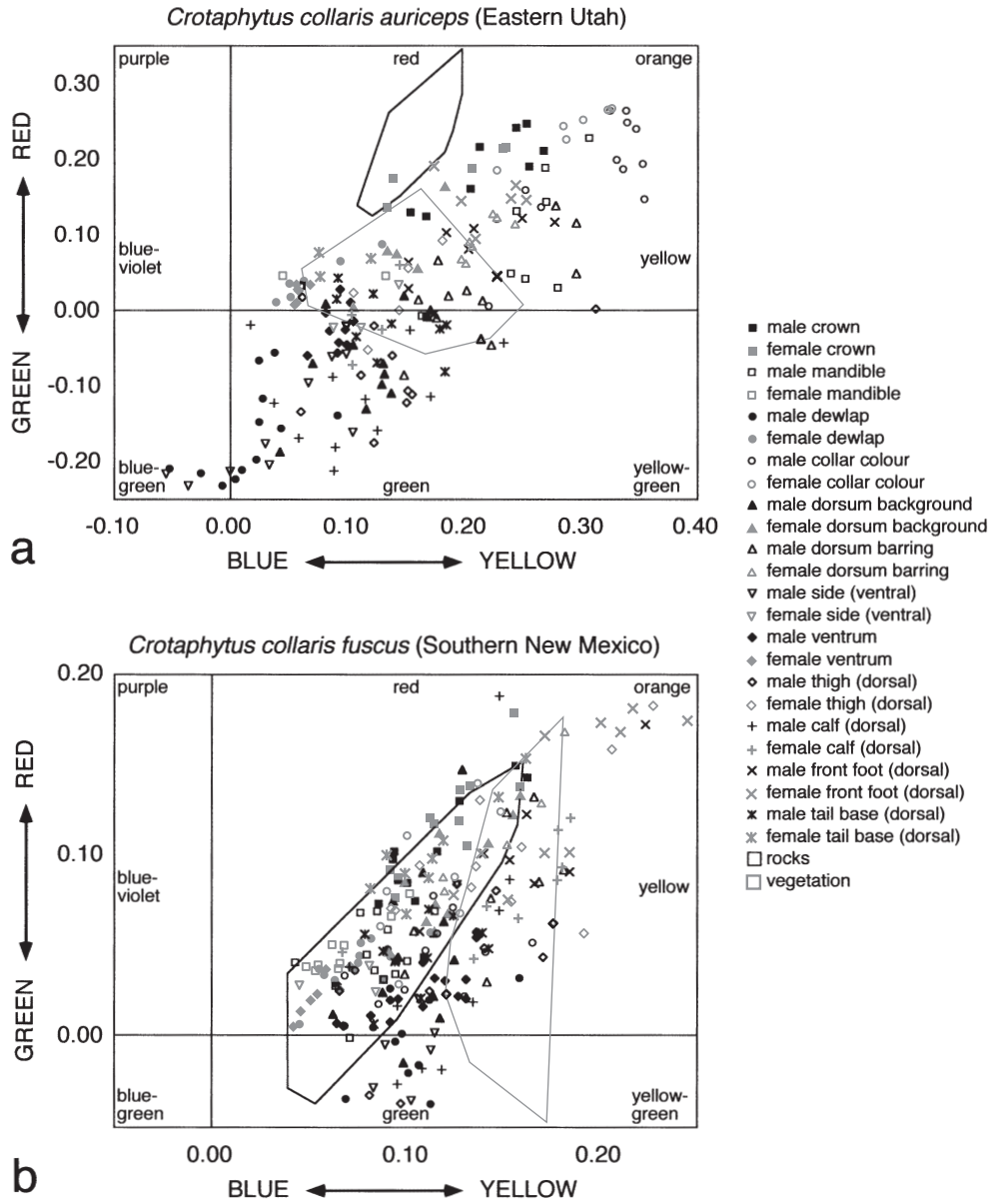

Figure 4. Plots of reflectance colour scores for (a) *Crotaphytus c. auriceps* (black symbols; males, $N = 12$; females, $N = 6$) and (b) *C. c. fuscus* (grey symbols; males, $N = 12$; females, $N = 11$) against the visual backgrounds of their natural habitats. Legend as in Fig. 3.

in size or mass ($N_1 = 13$, $N_2 = 6$; SVL: males = 92.3 ± 0.9 mm, females = 88.0 ± 2.1 mm, $U = 19.5$, $P = 0.085$; mass: males = 30.5 ± 1.0 g, females = 29.7 ± 1.5 g, $U = 33.5$, $P = 0.629$), *C. c. fuscus* males and females differed significantly on both measures ($N_1 = 12$, $N_2 = 10$; SVL: males = 107.5 ± 1.6 mm, females = 92.0 ± 2.1 mm, $U = 10$, $P = 0.001$; mass: males = 54.8 ± 2.5 g, females = 30.6 ± 2.9 g, $U = 5.5$, $P = 0.0003$). Likewise, males from the two populations differed significantly both in size and mass ($N_1 = 13$, $N_2 = 12$; SVL: $U = 1$, $P = 0.0001$; mass: $U = 0$, $P = 0.0001$) but females differed on neither measure ($N_1 = 6$, $N_2 = 10$; SVL: $U = 21.5$, $P = 0.355$; mass: $U = 28.5$, $P = 0.870$).

Sympatric Avian and Ophidian Predator Species and Saurian Prey Species

Lists compiled from distribution maps in field guides indicated that potential avian predators of adult col-

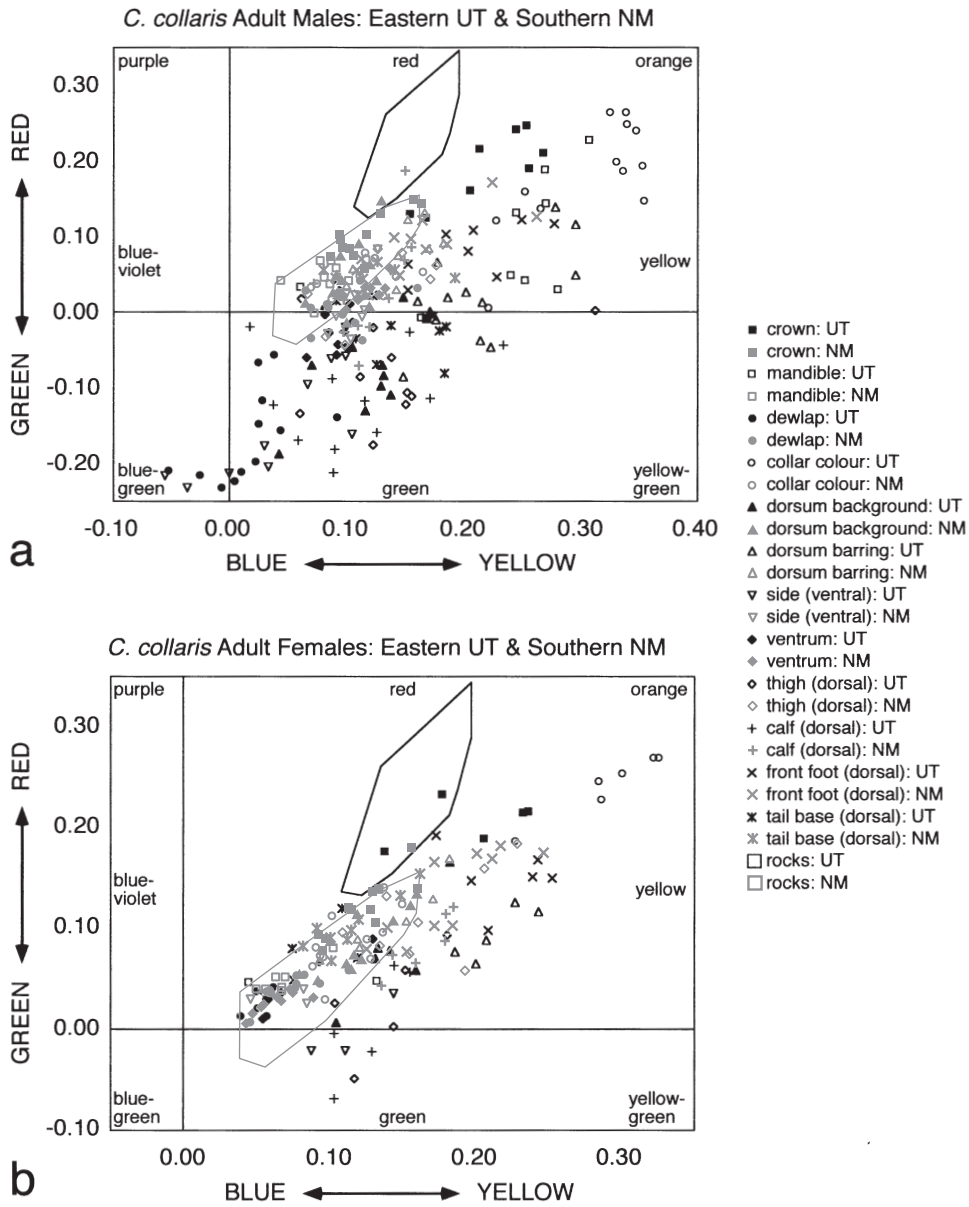

Figure 5. Plots of reflectance colour scores for (a) males, and (b) females against rocks in their natural habitats. Legend as in Figs 3 and 4.

lared lizards, including various raptors, are mostly shared between the two study populations (Table 5a). A notable exception to this pattern is the roadrunner (*Geococcyx californianus*), which is absent from our Utah population. A rich snake fauna of 19 species occurs at our New Mexico study site, while in Utah a depauperate array of up to five species occurs (Table 5b). Similarly, at 17 species, saurian prey richness is considerably higher in southern New Mexico compared with only seven species in eastern Utah (Table 5c).

DISCUSSION

In this study we have shown that our two selected populations differ in colouration, sexual dichromatism, contrast with their visual backgrounds, and sexual size/weight dimorphism. Four general trends observed in the lizards' reflectance spectra can be summarized as follows.

First, females typically were brighter than males, especially ventrally and in the longer wavelengths. When perched on rock piles and viewed from below

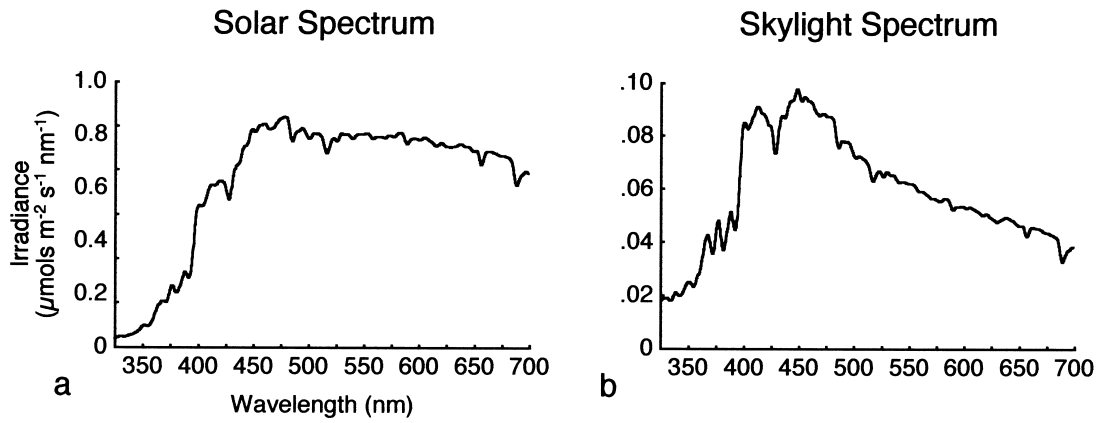

Figure 6. Representative (a) solar, and (b) skylight spectra used in calculation of lizard and visual background radiance from reflectance. Both irradiance spectra were obtained under exceptionally clear, cloudless skies. The skylight spectrum contains no direct sunlight. Irradiance samples were identical in spectral shape and range of intensities in the eastern Utah and southern New Mexico study areas.

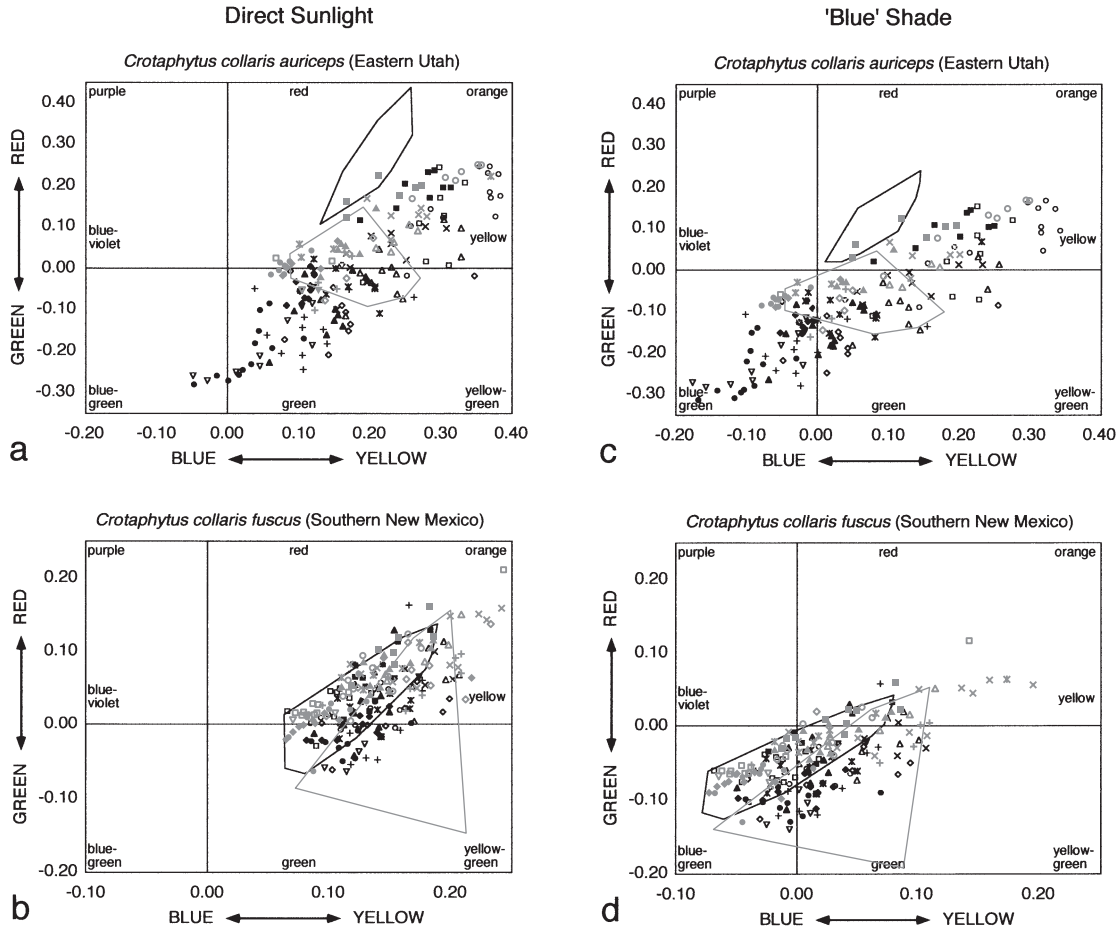

Figure 7. Plots of radiance colour scores that illustrate how different illumination sources affect light reflected from the lizards and from their visual backgrounds. Two ambient spectral conditions commonly experienced by the lizards in this study are shown: illumination by (a,b) direct sunlight, and by (c,d) skylight (as occurs in the shade of a rock under a blue sky). Sample sizes of males and females as in Fig. 1. Sample sizes of rocks and vegetation as in Fig. 3.

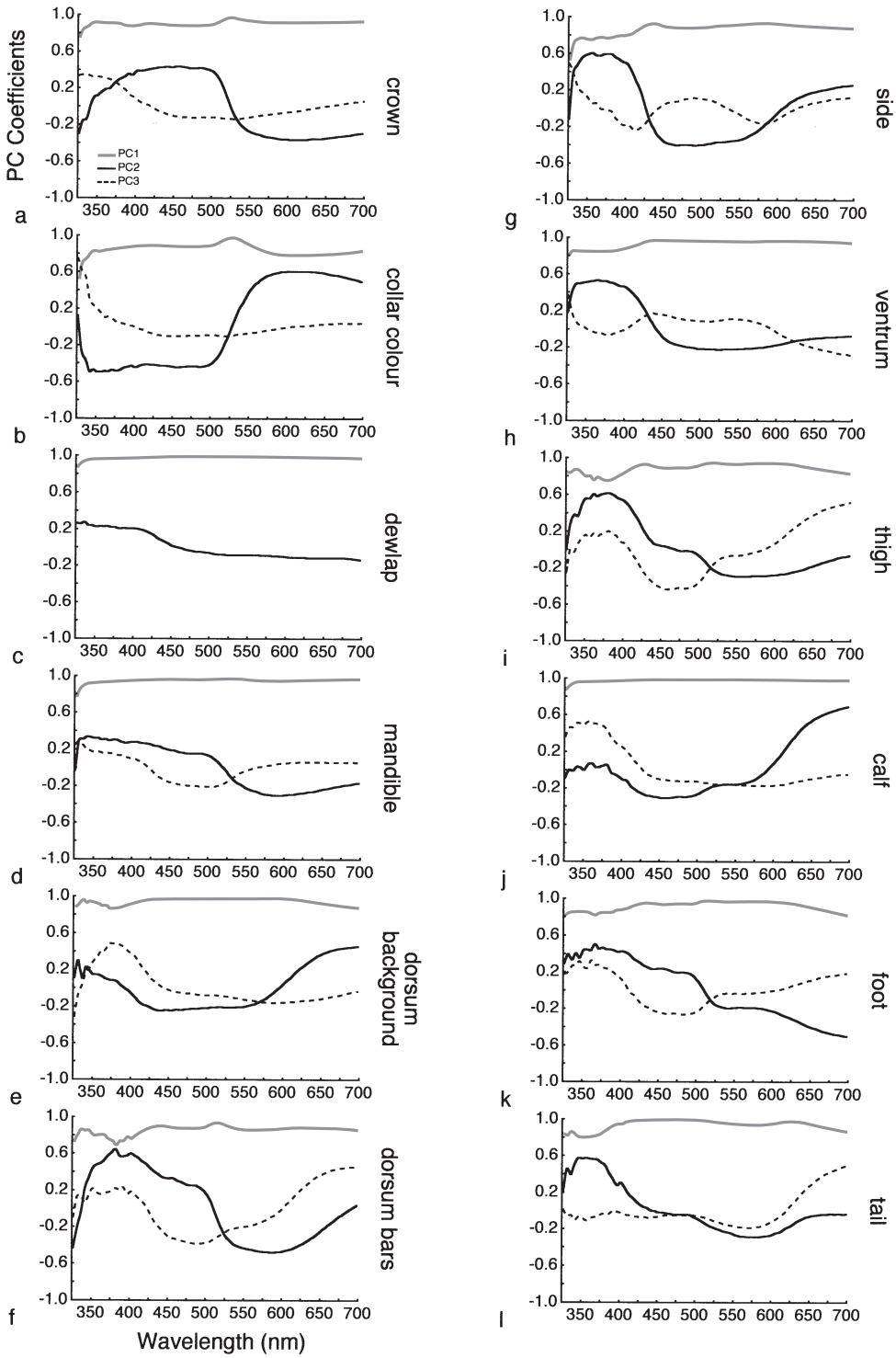

Figure 8. Principal component coefficients (or, 'loadings') showing the weightings of the three PCs as they relate to the original 12 body regions. PC1: grey lines, PC2: black lines, PC3: dashed lines. Among-subject variation is greatest where PC coefficients exhibit different signs. For example, in the crown (8a) individual variation in colour (PC2) is greatest between the reflectance strength of wavelengths from 350 to 500 (UV to bluish-green) and that of wavelengths from 550 to 700 (yellowish-green to red). Lizard sample sizes as in Fig. 1.

Table 2. Sex and population comparisons of *Crotaphytus collaris* reflectance spectra. Values shown are *F*-ratios of two-way ANOVAs on principal component scores derived from medians of 5-nm wide bins between 325 and 700 nm. Values in parentheses are the percent variance explained by that component. Each body region analysed separately. All PCs had eigenvalues >1.0. Degrees of freedom: 1, 40. Main effects: $*P = 0.05$, $**P = 0.01$, $***P = 0.001$. See text for results of significant interactions tested with one-way ANOVAs

	Sex			Population			Interaction		
	Brightness	Spectral shape		Brightness	Spectral shape		Brightness	Spectral shape	
Body region	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Crown	1.703 (84.7%)	1.630 (11.0%)	0.179 (2.2%)	7.134** (same as at left)	27.085***	0.000	4.417* (same as at left)	4.047	0.138
Collar colour	0.608 (73.2%)	2.084 (22.3%)	0.013 (2.3%)	4.655	45.467***	0.726	0.089	0.723	0.593
Dewlap	79.521*** (96.4%)	1.499 (1.9%)	–	0.097	10.665**	–	0.191	0.950	–
Mandible	18.430*** (91.4%)	0.280 (5.7%)	0.027 (1.6%)	1.505	11.301***	2.416	0.040	1.672	5.716*
Dorsum background	1.127 (89.1%)	15.681*** (5.7%)	0.775 (4.0%)	0.560	3.132	15.165***	0.024	4.684*	0.935
Dorsum bars	0.224 (73.4%)	0.581 (14.7%)	4.172* (7.2%)	1.431	21.461***	2.904	0.001	0.181	1.108
Side	4.195* (78.0%)	2.093 (12.4%)	0.678 (6.6%)	2.322	3.151	1.265	0.014	0.769	19.055***
Ventrum	12.802*** (89.2%)	23.755*** (7.6%)	2.607 (2.0%)	0.140	0.358	6.929*	0.007	1.395	7.410**
Thigh	1.201 (79.8%)	0.233 (9.5%)	6.191* (7.9%)	1.918	1.752	13.216***	0.542	0.001	0.667
Calf	1.855 (83.3%)	13.995*** (9.5%)	0.854 (5.4%)	1.964	12.264***	0.602	0.261	1.757	0.571
Foot	2.232 (84.4%)	0.140 (10.4%)	2.784 (2.9%)	1.011	1.562	3.404	0.200	0.315	0.461
Tail	1.227 (87.9%)	0.696 (6.8%)	22.193*** (3.5%)	0.107	0.258	5.887*	0.463	0.898	0.669

these features would tend to make females' ventral surfaces contrast less against a bright sky than those of males. This strong ventral brightness may be considered an example of adaptive countershading (e.g. Cott, 1940). The greater brightness in longer wavelengths (ventrally and dorsally) contributed to their brown appearance, which likewise made them contrast less with rocks, dirt, and dead vegetation.

Second, in many body regions (although not all) males exhibited stronger chroma than females. For most animals with colour vision, colours with strong chroma should be more detectable against most natural backgrounds than colours that are chromatically weak (Endler, 1990).

Third, *C. c. fuscus* exhibited weaker chroma than *C. c. auriceps*. As low-chroma colours exhibit 'flatter' reflectance spectra than do high-chroma colours, the former reflect the ambient light spectrum more faithfully (Endler, 1990). Animals with low-chroma colours can potentially benefit from a sort of 'dynamic crypsis', where the animals and their visual backgrounds will track changing light conditions in synchrony and along similar spectral trajectories (e.g. Endler, 1997, fig. 14.3). Thus, *C. c. fuscus* should be inherently less conspicuous than *C. c. auriceps* in their respective habitats.

Fourth, body regions of male and female *C. c. auriceps* differed more from each other in brightness and in colour than did those of male and female *C. c. fuscus*. Calculation of 'difference units' showed that *C. c. auriceps* is more sexually dichromatic than *C. c. fuscus*.

The most striking result of the colour space analysis was that most colour scores of *C. c. fuscus* males overlapped those of their rocks, but no colour scores of male *C. c. auriceps* overlapped those of their rocks.

Table 3. Contrast between reflectance spectra of *Crotaphytus collaris auriceps* body regions and that of local rocks. Values shown are *t*-statistics from pairwise tests of principal component scores derived from medians of 5-nm wide bins between 325 and 700 nm. Values in parentheses are the percent variance explained by that component. Each body region analysed separately. All PCs had eigenvalues >1.0. Degrees of freedom: males = 34; females = 28. $^{**}P = 0.01$, $^{***}P = 0.001$. All tests 2-tailed. *P*-values adjusted for 12 pairwise comparisons per sex using the sequential Bonferroni method (Rice, 1989)

	Males			Females		
	Brightness contrast	Colour contrast		Brightness contrast	Colour contrast	
Body region	PC1	PC2	PC3	PC1	PC2	PC3
Crown	−1.866	3.786***	4.036***	−3.436**	0.831	3.164***
	(75.5%)	(16.3%)	(4.9%)	(same as at left)		
Collar colour	−0.984	−6.937***	4.414***	0.522	−6.457***	−0.016
	(59.3%)	(33.4%)	(3.5%)			
Dewlap	−1.749	−12.763***	–	4.348**	−4.844***	–
	(92.0%)	(6.7%)				
Mandible	1.704	−3.964***	−2.429	1.835	−0.582	−1.997
	(81.3%)	(11.6%)	(4.9%)			
Dorsum background	0.435	−10.240***	−0.463	0.643	−3.692***	−2.121
	(81.2%)	(13.4%)	(4.1%)			
Dorsum bars	0.033	−10.496***	−0.979	0.277	−7.860***	0.764
	(67.5%)	(19.2%)	(10.2%)			
Side	−0.592	8.127***	−0.135	1.014	4.883**	1.600
	(50.4%)	(40.0%)	(7.4%)			
Ventrum	6.909***	−6.057***	–	4.216**	1.732	–
	(93.1%)	(4.9%)				
Thigh	−1.573	−7.541***	0.193	−0.906	−4.715**	0.650
	(66.6%)	(23.8%)	(6.8%)			
Calf	0.503	−9.436***	−0.404	0.999	−4.584***	1.134
	(74.3%)	(19.2%)	(5.1%)			
Foot	−0.639	−5.898***	1.027	0.785	−5.765***	0.905
	(78.8%)	(11.4%)	(7.9%)			
Tail	0.436	−6.747***	−1.306	1.978	−3.477**	0.200
	(73.6%)	(15.4%)	(8.8%)			

This finding reinforced our visual impression that male *C. c. auriceps* stand out from the background, whereas male *C. c. fuscus* are inconspicuous. In both populations, however, male body regions that were most distant in colour space from rocks and vegetation (and which also were the most chromatic) were the dewlap, side, calf and thigh. These body regions would have low visibility to raptors on the wing, but also to the eyes of potential prey being stalked when using rocks to obscure the hunter's body below the eyes. Note that the distance in colour space of these body regions from that of local rocks was far greater in male *C. c. auriceps* than in *C. c. fuscus*, and only *C. c. auriceps* males exhibited additional body areas (e.g. mandible, collar colour) that fell well outside their visual backgrounds. Adult females showed similar patterns to those of males in their populations, except that colour score variability and distance between body and visual background colour scores were much reduced in *C. c. auriceps* females compared to those of males.

By multiplying the reflectance spectra of the lizards and their rocks by a solar spectrum or a skylight/shade spectrum, we simulated the appearance of the lizards and their substrates under these primary lighting conditions. Application of the solar spectrum increased lizard and rock chroma (shifted colour scores away from the colour space origin), whereas the skylight/shade spectrum reduced chroma (shifted colour scores toward the origin). The correlation between relatively weak chroma in body and rock colouration in *C. c. fuscus*, and relatively strong chroma in body and rock colouration in *C. c. auriceps*, resulted in a greater shift in colour space in the former

Table 4. Contrast between reflectance spectra of *Crotaphytus collaris fuscus* body regions and that of local rocks

	Males			Females		
	Brightness contrast	Colour contrast		Brightness contrast	Colour contrast	
Body Region	PC1	PC2	PC3	PC1	PC2	PC3
Crown	−8.327*** (93.2%)	2.205 (5.8%)	–	−2.556 (same as at left)	3.502***	–
Collar colour	−1.517 (91.8%)	−1.681 (5.9%)	−5.707*** (1.8%)	−0.976	−2.759	−1.619
Dewlap	−2.698 (93.1%)	−4.852*** (4.4%)	−5.543*** (1.8%)	4.506***	−1.647	−5.471**
Mandible	−0.663 (93.7%)	−0.941 (3.9%)	−6.511*** (1.7%)	2.657	0.793	−5.873**
Dorsum background	−4.952*** (94.3%)	−1.074 (4.8%)	–	−3.395***	−2.229	–
Dorsum bars	−2.681 (91.5%)	−3.162** (7.2%)	–	−1.744	−2.143	–
Side	−2.273 (90.3%)	−2.751 (6.2%)	−2.669 (3.1%)	−0.735	−0.633	2.094
Ventrum	4.602*** (88.3%)	−7.392*** (9.4%)	−3.043** (1.5%)	9.157***	1.410	−1.929
Thigh	−4.331*** (91.7%)	−1.817 (6.9%)	–	−3.196**	−3.436***	–
Calf	−4.094*** (92.2%)	−1.715 (6.3%)	–	−2.927**	−2.872	–
Foot	−1.714 (82.5%)	−4.846*** (15.7%)	–	−1.446	−5.212***	–
Tail	−3.403*** (94.1%)	−0.976 (5.0%)	–	−2.957**	−2.181	–

Degrees of freedom: males: 52; females: 51. Legend as in Table 3.

than the latter. This finding suggests that *C. c. fuscus* should appear relatively inconspicuous, and *C. c. auriceps* (males) should appear relatively conspicuous, regardless of ambient lighting conditions.

Stepwise DFA revealed that the sexes and populations could be discriminated statistically with virtually 100% accuracy. The only assignment error was the misclassification of a female *C. c. fuscus* as a male. The classification success of the sexes in *C. c. fuscus* was unexpected, given the significantly weaker sexual dichromatism in that population than in *C. c. auriceps*. Evidently, subtle yet consistent sex differences in brightness and colour occur in *C. c. fuscus*.

Selection and Adaptive Colouration in *C. collaris*

Inconspicuous colouration, weak sexual dichromatism, and strong male-biased sexual size dimorphism (SSD) are considered ancestral character states for the Crotaphytidae (*Crotaphytus* and *Gambelia*) (McGuire, 1996). The polarity of these character states, together with geographical distribution, suggests that *C. c. auriceps* is a much younger population of C. *collaris* than is *C. c. fuscus* (Ingram & Tanner, 1971). Our interest now lies in determining the factors responsible for maintaining such strong differences in colouration and in sexual size and weight dimorphism between these two populations.

Our results showed that males from New Mexico are considerably larger than females, and exhibit female-like colouration, while males from Utah are similar in size to females, but conspicuously coloured. This pattern of variation cannot simply be accounted for by differences in the intensity of sexual selection, which would predict a concordant pattern of variation. As suggested by Baird *et al*. (1997), social opportunities to utilize conspicuous colouration in territorial and in sexual advertising, and large body size in aggressive interactions, may vary substantially between populations.

Table 5. (a) Potential avian predators of *C. collaris* (b) potential snake predators of *C. collaris*, and (c) lizard species that may be preyed upon by *Crotaphytus collaris* in our study areas

Species	Common Name	Moab. UT[1]	*Las Cruces, NM*[2]
(a) Avian predators			
Circus cyaneus[3]	Northern harrier	yes	yes
Falco sparverius[3]	American kestrel	yes	yes
Falco mexicanus[3]	Prairie falcon	yes	yes
Geococcyx californianus[4]	Roadrunner	no	yes
Ictinia mississippiensis[3]	Mississippi kite	no	yes
Totals		3	5
(b) Snake predators			
Arizona elegans	Glossy snake	no	yes
Bogertophis subocularis	Trans-Pecos rat snake	no	yes
Crotalus atrox	Western diamondback rattler	no	yes
Crotalus lepidus	Rock rattlesnake	no	yes
Crotalus molossus	Blacktail rattlesnake	no	yes
Crotalus viridis	Western rattlesnake	yes	yes
Elaphe gutata	Corn snake	no	yes
Heterodon nasicus	Western hognose snake	no	yes
Hypsiglena torquata	Night snake	yes	yes
Lampropeltis getula	Common kingsnake	no	yes
Lampropeltis triangulum	Milk snake	no	yes
Masticophis flagellum	Coachwhip	no	yes
Masticophis taeniatus	Striped whipsnake	yes	yes
Pituophis melanoleucus	Bullsnake, gopher snake	yes	yes
Rhinocheilus lecontei	Long-nosed snake	?	yes
Salvadora deserticola	Big Bend patch-nosed snake	no	yes
Salvadora grahamiae	Mountain patch-nosed snake	no	yes
Sistrurus catenatus	Massasauga	no	yes
Trimorphodon biscutatus	Lyre snake	no	yes
Total		4–5	19
(c) Lizard prey			
Cnemidophorus exsanguis	Chihuahuan whiptail	no	yes
Cnemidophorus grahamii	Checkered whiptail	no	yes
Cnemidophorus inornatus	Little striped whiptail	no	yes
Cnemidophorus neomexicanus	New Mexico whiptail	no	yes
Cnemidophorus tigris	Western whiptail	yes	yes
Cnemidophorus uniparens	Desert grassland whiptail	no	yes
Cophosaurus texanus	Greater earless lizard	no	yes
Eumeces obsoletus	Great Plains skink	no	yes
Gambelia wislizenii	Leopard lizard	yes	yes
Holbrookia maculata	Lesser earless lizard	no	yes
Phrynosoma cornutum	Texas horned lizard	no	yes
Phrynosoma douglassii	Short-horned lizard	yes	no
Phrynosoma modestum	Round-tailed horned lizard	no	yes
Sceloporus graciosus	Sagebrush lizard	yes	no
Sceloporus magister	Desert spiny lizard	no	yes
Sceloporus poinsetti	Crevice spiny lizard	no	yes
Sceloporus undulatus	Prairie lizard	yes	yes
Urosaurus ornatus	Tree lizard	yes	yes
Uta stansburiana	Side-blotched lizard	yes	yes
Totals		7	17

Snakes and lizards: [1]species from range maps in Stebbins (1985); [2]species from range maps in Degenhardt *et al*. (1996). Avian: species from range maps in [3]Clark & Wheeler (1987) and [4]Peterson (1998). Rare species not included.

In addition, the derived character states in *C. c. auriceps* may have arisen from relaxation of selective pressures operating on *C. c. fuscus*. Specifically, the derived traits could have been facilitated by a reduction in pressure by visually orienting predators and by consumption of lizard prey. These two possibilities may be mutually reinforcing, and we currently lack the data required to assess their relative contributions. Nevertheless, data from stomach contents and bite force studies of C. *collaris* in Utah and New Mexico, coupled with information on the geographical distribution of potential predators and saurian prey, provide a starting point.

Stomach Contents, Bite Force, and Saurophagy in *C. collaris*

In a sample of 145 *C. c. baileyi* from western New Mexico, eight lizards were contained in seven stomachs, one stomach contained a snake, and another a bird nestling (Best & Pfaffenberger, 1987). Although this quantity is small, by comparison not a single stomach in 98 *C. c. baileyi* from north-western Utah contained a vertebrate of any kind (Knowlton, 1938). Moreover, these populations are not as extreme in expression of conspicuous and inconspicuous colouration as observed in our study populations. It seems plausible that *C. c. fuscus*, being both the southernmost representative of C. *collaris* and coinciding with the greatest diversity and abundance of lizard species (see below), may be more saurophagous than other C. *collaris* populations.

Lappin (1999) constructed a transducer to measure bite force performance in live crotaphytids and found that peak bite force increased with absolute increases in cranial size and cranial robustness. Of the *C. collaris* males examined, the top 20% exhibiting the strongest bite force came from the southern reaches of the species' distribution, half of which were *C. c. fuscus* males. It likewise has been our subjective impression during the present study that *C. c. auriceps* males are much more gracile in cranial elements than are *C. c. fuscus* males. We currently are conducting a study of stomach contents, cranial morphology and bite force in our study populations, and to date we have observed saurophagy in *C. c. fuscus* but not in *C. c. auriceps*.

Species Richness and Abundance of *Crotaphytus* Predators and Lizard Prey

Our two study populations appear to differ in the presence of several important diurnal, visually orienting predator species. Of primary importance is the absence from our Utah study area of the roadrunners, a cursorial bird that preys on large numbers of lizards. An additional lizard specialist absent in Utah is the coachwhip, *Masticophis flagellum*. This snake is known to prey so heavily on collared lizards in some areas of Oklahoma that *Crotaphytus* and *Masticophis* densities appear to cycle together (J. Husak, pers. comm.).

The number of lizard species that could serve as collared lizard prey increases from Utah to New Mexico. This latitudinal gradient in lizard diversity, as well as abundance, has been noted by other authors (e.g. Pianka, 1967, 1968; Kiester, 1971). Thus, the conspicuous sexual dichromatism in our northern population may have arisen as a response to relaxed selection for crypsis, stemming from the absence of important visually orienting predators such as roadrunners and coachwhips as well as the decreased availability of saurian prey.

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