

Sexual Dichromatism and Color Conspicuousness in Three Populations of Collared Lizards (*Crotaphytus collaris*) from Oklahoma¹

JOSEPH M. MACEDONIA,^{2,3} JERRY F. HUSAK,⁴ YONI M. BRANDT,⁵
A. KRISTOPHER LAPPIN,⁶ AND TROY A. BAIRD⁷

²School of Life Sciences, P.O. Box 874501 Arizona State University, Tempe,
Arizona 85287-4501, USA; E-mail: jmacedon@asu.edu

⁴Department of Zoology, Oklahoma State University, Stillwater, Oklahoma 74078, USA

⁵Department of Biology and Center for the Integrative Study of Animal Behavior,
Indiana University, Bloomington, Indiana 47405, USA

⁶Department of Biology, Northern Arizona University, Flagstaff, Arizona 86011, USA

⁷Department of Biology, University of Central Oklahoma, Edmond, Oklahoma 73034, USA

ABSTRACT.—The coloration of animal integuments evolves in response to numerous and often competing selective pressures. Although male-male competition and female mate choice characteristically select for increased color conspicuousness, visibility to predators and to prey often select for decreased conspicuousness. We examined three populations of Common Collared Lizards, *Crotaphytus collaris*, in Oklahoma (Arcadia Lake, Glass Mountains, Wichita Mountains) that have been argued to differ in the intensity of natural and sexual selection acting on their color patterns. Our study had two main objectives. First, reflectance spectra were obtained from the lizards to replicate and extend previous work on differences in sexual dichromatism among these populations. Second, spectra were gathered on components of visual backgrounds at our study sites to explore the possibility that each population may be relatively cryptic within its own habitat. Results showed that most body regions differed significantly in sexual dichromatism among populations, but in contrast to prior work, no one population was more sexually dichromatic than another for all body regions examined. Males exhibited less overlap in coloration with their visual backgrounds than did females (i.e., males were more conspicuous), and females overlapped more in coloration with rocks than with other visual backgrounds. The population estimated previously to experience the strongest predation pressure (Arcadia Lake) was shown in the present study to be the least conspicuous. Some support also was found for the proposition that even the most “colorful” population (Wichita Mountains) may not always be conspicuous when viewed against its typical visual background.

In many sexually reproducing animals, males experience strong competition for mates and greater reproductive variance than females (e.g., Darwin, 1871; Andersson, 1994). Females prefer conspicuously colored males as mates (e.g., Hill 1990; Sætre et al., 1994; Sundberg, 1995; Kwiatkowski and Sullivan, 2002), and such males often achieve greater social dominance or greater access to resources or both (e.g., Evans and Norris, 1996; Gerald, 2001; Pryke et al., 2002; Zamudio and Sinervo, 2003). This differential mating advantage of conspicuous coloration to one sex results in sexual dichromatism. Sexual dichromatism has been examined in numerous species of birds (e.g., Gray, 1996; Andersson et al., 1998; Cuthill et al., 1999; Badyaev and Hill, 2000), and its geographic variation has been studied in several lizards (e.g., McCoy et al., 1997,

2003; Wiens et al., 1999; LeBas and Marshall, 2000; Macedonia et al., 2002).

Although conspicuous coloration can yield reproductive benefits, such benefits may be offset by increased visibility to predators and to prey (e.g., Grether and Grey, 1996; Stuart-Fox et al., 2003). In guppies, for example, among-population differences in local predator guilds drive and constrain local female-preferred color patterns in males across stream systems in Trinidad (e.g., Endler, 1978, 1980, 1991).

The degree to which color conspicuousness varies among populations of a species may provide clues about the intensity of local selective pressures on coloration (e.g., Kwiatkowski, 2003). In western populations of the Common Collared Lizard (*Crotaphytus collaris*) color conspicuousness appears inversely related to species richness/abundance of potential predators of *C. collaris* and their lizard prey (Macedonia et al., 2002; JMM, JFH, YMB, AKL, (unpubl. data)). In some other locations, however, the impact of

¹ G. Smith served as editor for this manuscript.

³ Corresponding Author.

TABLE 1. Snout-vent length (SVL) of study subjects by population and sex.

Population	Sex	(N)	SVL (mm)
			Mean \pm SE
Arcadia Lake	males	11	99.6 \pm 1.8
Arcadia Lake	females	11	87.7 \pm 1.3
Glass Mountains	males	18	94.1 \pm 1.3
Glass Mountains	females	17	92.1 \pm 1.1
Wichita Mountains	males	36	105.9 \pm 1.0
Wichita Mountains	females	25	94.7 \pm 1.4

saurophagy may be inconsequential for selection against conspicuous coloration. One such location is the state of Oklahoma. Stomach contents from well over 200 *C. collaris* sampled throughout Oklahoma produced no evidence of saurophagy (66 subjects: Blair and Blair, 1941; >150 subjects: JMM, JFH, YMB, AKL, (unpubl. data)). Study of Oklahoma *C. collaris*, thus, provides a natural experiment in which saurophagy is essentially removed as a selective agent on adult coloration.

In western populations of *C. collaris*, sexual dichromatism and color conspicuousness are positively correlated (Macedonia et al., 2002), although this relationship may not hold elsewhere. For example, McCoy et al. (1997) used reflectance spectrometry to examine geographic variation in sexual dichromatism in three Oklahoma populations of *C. collaris* (Arcadia Lake: AL, Glass Mountains: GM, Wichita Mountains: WM). These authors found that the population whose males appear most vibrantly colored to humans (WM) was not the most sexually dichromatic population. Further, data on rates of predator sighting and injuries (Baird et al., 1997) led McCoy et al. (1997) to speculate that predation pressure may select for coloration that decreases the conspicuousness of each population against their local rocks. Specifically, it was suggested that strong predation pressure and a homogeneous visual background may maintain comparatively dull coloration in AL males, despite a demonstrated preference by AL females for brightly colored AL males over dull ones, and for WM males over AL males (Baird et al., 1997). In contrast, it was suggested that seemingly conspicuous WM males might actually be cryptic when viewed against the brightly colored lichens and flowering plants present in their habitat (Baird et al., 1997; McCoy et al., 1997). The relationship of body color variation to local visual backgrounds in these populations merits further investigation.

In the present study, we replicate and extend the investigation by McCoy et al. (1997) of sexual dichromatism in the AL, GM, and WM *C. collaris* populations. We compare body coloration among the three study populations and calculate visual

contrast between the lizards and their rocky habitats. In this manner, we investigate the proposition that population-specific coloration may enhance crypsis against local visual backgrounds.

MATERIALS AND METHODS

Subjects and Study Areas.—In June 2002, we collected spectral data from adult lizards in the Arcadia Lake (Oklahoma County), Glass Mountains (Major County), and Wichita Mountains (Comanche County) populations of *C. collaris* at the same study sites used by Baird et al. (1997) and McCoy et al. (1997). The dorsum in adult males of the AL population is brown with greenish (and some yellow) overtones, that of the GM population is dull turquoise to green with brown overtones and yellow bars, and that of the WM population is turquoise with yellow bars. Females in all populations are light brown dorsally (with orange bars and blotches if gravid), although the WM population includes some females whose coloration is male-like to varying degrees.

Lizards were captured by noosing and were held in mesh bags until data were gathered. An identification number was written on two pieces of flagging tape: one piece of tape was placed in each subject's mesh bag and the other marked the capture location. Each subject was released at the exact location of its capture within 30 h of being removed (Table 1).

The AL population in central Oklahoma inhabits an uninterrupted tract of gray granite boulders that were imported in 1986 to construct the flood-control spillway for the Arcadia Lake dam (Baird et al., 1996, 2003). In this location, little soil is exposed, vegetation is relatively sparse, and rocks are free of lichens. The GM population in northwestern Oklahoma occupies steep-sided, gypsum-capped buttes, and rocks of the surrounding terrain. Here, highly eroded, exposed red soil is topped with low green vegetation and is dotted with gray gypsum rocks. The habitat of the WM population in southwestern Oklahoma is one of rolling, grassy plains with juniper that is punctuated by large, salmon-colored granite boulders. Most of the soil is vegetated, yellow flowers abound, and the rocks are heavily encrusted with gray, pale bluish-green, chartreuse and, occasionally, golden lichens.

Measurement of Coloration.—Spectral measurements of lizards were gathered using a bifurcating 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 OOIBASE 32 software. Subjects were placed on a nonreflective black rubber mat and radiance scans were taken at a standard angle deviating

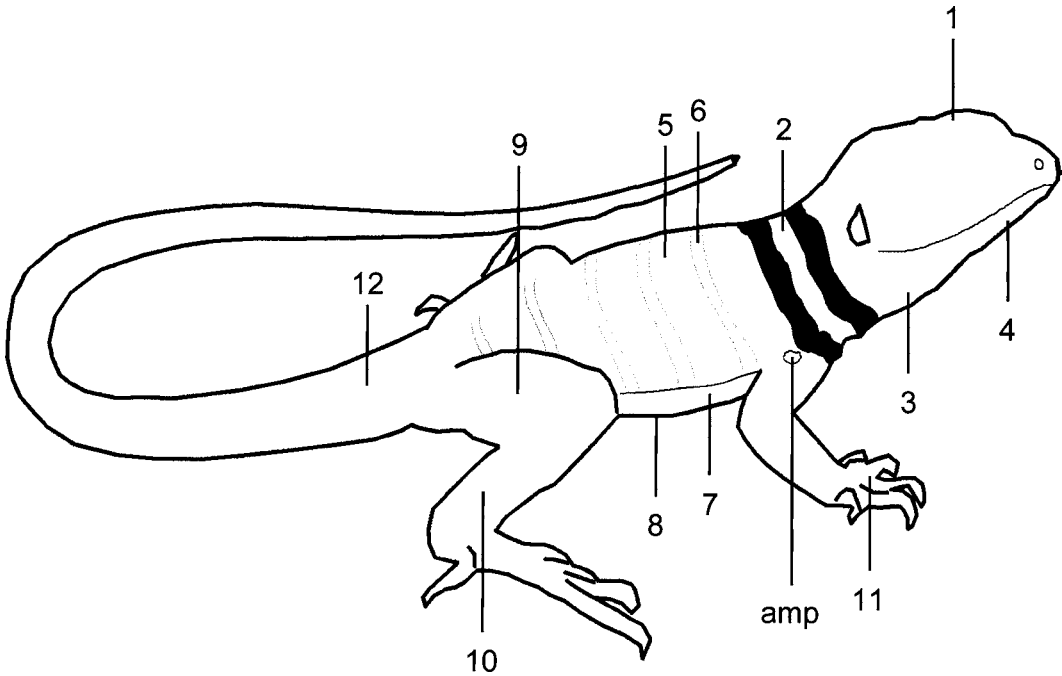


FIG. 1. Body locations on which spectrometric measurements were made. 1: crown, 2: collar color, 3: dewlap, 4: mandible, 5: dorsum background, 6: dorsum bars, 7: side, 8: ventrum, 9: thigh, 10: calf, 11: front foot, 12: tail, AMP: antehumeral mite pocket. (Outline of *Crotaphytus collaris* body and collar traced from painting in Stebbins, 2003.)

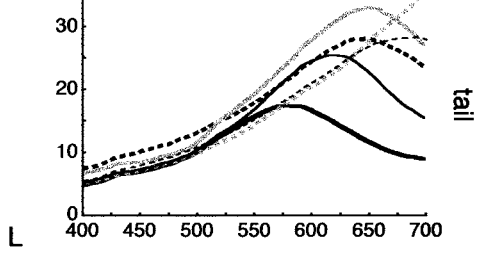
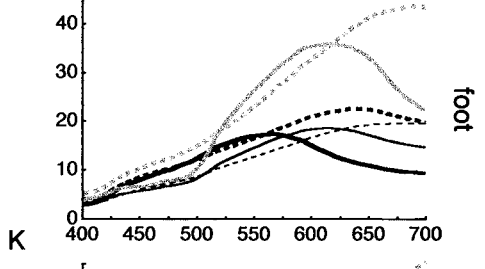
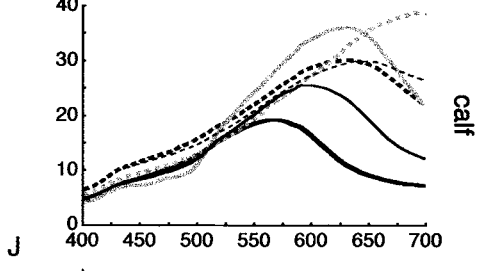
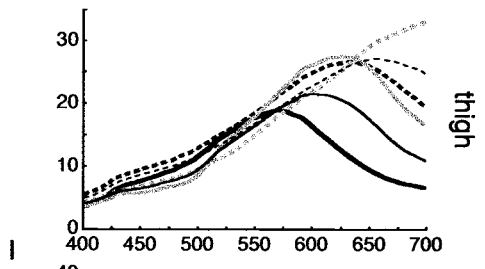
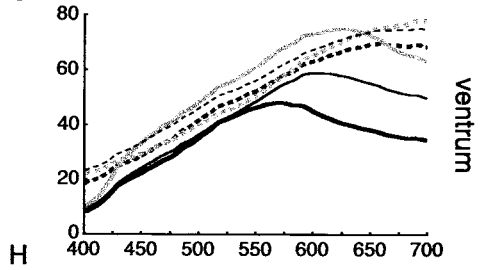
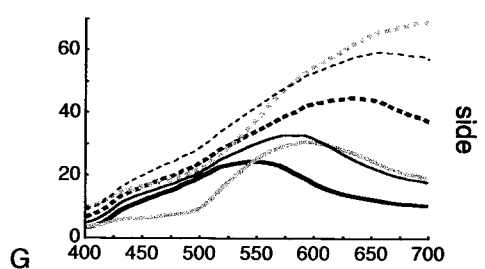
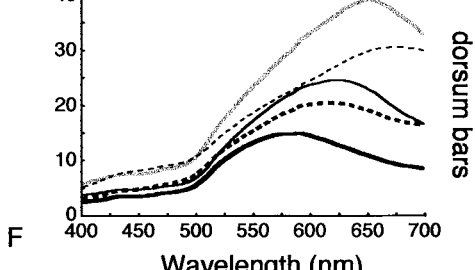
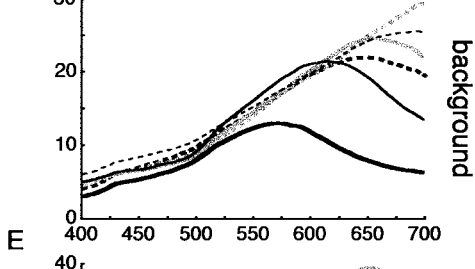
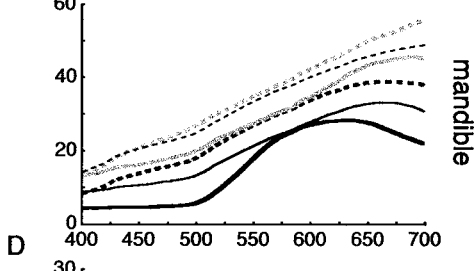
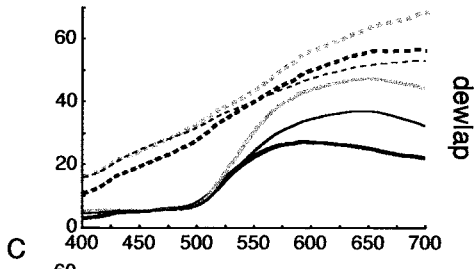
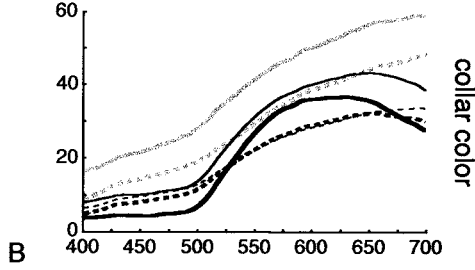
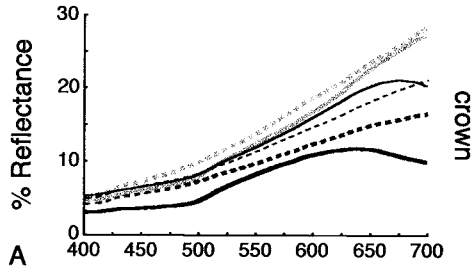
approximately 5° from perpendicular (90°) to the body surface. A white standard (Spectralon WS-1, Labsphere) was scanned and dark current removed from the signal just prior to gathering spectral data from each subject. Reflectance was calculated automatically by the software from each subject's radiance samples using that subject's white standard reading.

Reflectance was measured from 12 body regions to obtain a reasonably comprehensive profile of adult body coloration (Figs. 1, 2). Female breeding coloration (orange bars, blotches and spots that are most prominent on the dorsolateral body surface) and clusters of red mites in antehumeral mite pockets also were measured when present. A small rule attached to the reflectance probe maintained a 5-mm distance between the end of the probe and the lizard. Before gathering spectral data, subjects in mesh bags were heated in direct sunlight until they felt

as warm to the touch as do lizards that had been basking ($35\text{--}40^\circ\text{C}$; JMM, JFH, YMB, AKL, unpubl.). Spectral scans of rocks, green vegetation (grasses, bushes, and cacti), flowers, lichens, and soil were made in the lizards' habitats using a fiber optic fitted with a collimating lens (Ocean Optics UV-74). For the GM and WM populations, sunlight served as the illumination source; the tungsten-halogen lamp was used for the AL population. Note that the use of different illumination sources to measure reflectance of lizards (tungsten-halogen lamp) and of objects in the visual background (sunlight) did not bias the spectral data in any manner. The white standard facilitates calculation of a reflectance spectrum from any illumination source that possesses the wavelengths of interest.

In contrast to some lizard taxa (e.g., *Anolis*: Fleishman et al., 1993; Macedonia, 2001; Thorpe, 2002; *Carlia*: Blomberg et al., 2001; *Ctenophorus*:

FIG. 2. Mean reflectance spectra of 12 body regions from three *Crotaphytus collaris* populations in Oklahoma: Arcadia Lake, males: thick solid gray lines ($N = 11$), females: thick dashed gray lines ($N = 11$); Glass Mountains, males: thin solid black lines ($N = 18$), female: thin dashed black lines ($N = 17$); Wichita Mountains, males: thick solid black lines ($N = 36$), females: thick dashed black lines ($N = 25$).



Wavelength (nm)

LeBas and Marsall, 2000; *Gallotia*: Thorpe and Richard, 2001), *C. collaris* exhibits little ultraviolet reflectance (Macedonia et al., 2002) aside from the "white" corners of the mouth. Because our tungsten-halogen light source produced strong illumination only down to 400 nm, and because we wished to compare our results directly with those of McCoy et al. (1997), we restrict our spectral analyses to the 400–700 nm range.

Terminology.—Spectral "intensity" (often termed "brightness") is defined here as the sum of individual wavelength amplitudes under the spectral curve over a specified range. "Hue" refers to color in the vernacular sense (e.g., red, green, blue) and is defined by the shape of the spectral curve, particularly its peak wavelength. "Chroma" is color saturation and is a function primarily of the magnitude of the slope between the weakest and strongest parts of the spectrum. The terms "dewlap," "dorsum background," and "side" (Fig. 1) are equivalent, respectively, to "gular," "dorsolateral," and "ventrolateral" in McCoy et al. (1997). We define "sexual dichromatism" in this study as the difference between the sexes in total reflectance intensity for a given body region.

Sexual Dichromatism.—Sexual dichromatism (SD) was determined in the three study populations by first taking the absolute value of the difference at each wavelength between each male's reflectance spectrum and the mean female reflectance spectrum for a given body region. This "difference spectrum" then was summed to produce a single value (divided by 1000 for numerical convenience).

$$SD = \sum |R_{(\lambda)\text{male}} - R_{(\lambda)\text{female}}|/1000 \quad (1)$$

The procedure then was repeated using each female's reflectance spectrum and the mean male reflectance spectrum for each body region. This method is similar to that used by McCoy et al. (1997), who calculated all possible male-female pair permutations in generating sexual dichromatism values. Among-population differences in sexual dichromatism were examined for each body region using the Kruskal-Wallis ANOVA ($\alpha = 0.05$). The Mann-Whitney *U*-Test was used for pairwise comparisons where ANOVAs were significant. Because each population was used twice in the pairwise tests (AL-GM, AL-WM, GM-WM), the α -level for significance was set at 0.025.

Variation in Coloration: Color Space.—To visualize the distributions of lizard colors and those of objects comprising the visual background, reflectance spectra were reduced and plotted in color space using Endler's (1990) segment classification method. Segment classification assumes only the presence of a typical opponency

system of color processing that compares the outputs of receptors sensitive to nonadjacent portions of the visible spectrum.

Spectra were partitioned into four, 75 nm-wide color segments corresponding roughly to violet to blue (400–475 nm; "B" wavelengths segment), blue to green (475–550; "G" wavelengths segment), green to orange (550–625 nm; "Y" wavelengths segment), and orange to red (625–700 nm; "R" wavelengths segment). The sum of each color segment (S_B, S_G, S_Y, S_R) then was divided by the entire spectrum's sum (400–700 nm). These calculations equalize intensity differences among spectra and produce a proportional intensity value for each segment. Subtraction of " S_G " from " S_R " and " S_B " from " S_Y " segment sums results in two values that are plotted as a single color score in two-dimensional color space.

Variation in Coloration: Hue and Chroma.—Hue (H) is depicted as the angle of a color score relative to the top (0°) of the graph's vertical axis and was calculated as (modified from Endler, 1990):

$$H = \frac{\text{ArcCos}(S_R - S_G)(180)}{(C)(\Pi)} \quad (2)$$

Chroma (C) increases as the Euclidian distance from the origin, and was calculated as (modified from Endler, 1990):

$$C = \sqrt{(S_R - S_G)^2 + (S_Y - S_B)^2} \quad (3)$$

Among-population differences in hue and chroma were examined statistically using Kruskal-Wallis ANOVA ($\alpha = 0.05$). *P*-values resulting from ANOVA were subjected to a sequential Bonferroni test (Rice, 1989) to protect against the probability of increased Type I error associated with significant correlations between pairs of body regions in hue or chroma. ANOVAs that remained significant after the sequential Bonferroni test were subjected to Mann-Whitney *U*-Tests for pairwise population comparisons. Each population was used twice in the pairwise tests and the α -level for significance was set at 0.025.

Variation in Conspicuousness: Contrast with the Visual Background.—Contrast between each body region and the background of local rocks was determined independently for each population and sex. Intensity contrast (IC) was calculated as the mathematical difference between the total reflectance of a given lizard body region for a given subject ($Q_T[L]$) and the total mean reflectance of local rocks ($Q_T[R]\bar{x}$), divided by the sum of these two quantities:

$$IC = \frac{Q_T[L] - Q_T[R]\bar{x}}{Q_T[L] + Q_T[R]\bar{x}} \quad (4)$$

Positive values result when a lizard body region is brighter than the rock background; negative

TABLE 2. Sexual dichromatism in *Crotaphytus collaris* from Arcadia Lake (AL), Glass Mountains (GM), and Wichita Mountains (WM) populations, Oklahoma. Degrees of freedom = 2, except for dorsum bars (where $df = 1$). Chi^2 is the Kruskal-Wallis ANOVA test statistic. See text for derivation of dichromatism scores. NS = not significant in ANOVA. α -level for significance in posthoc Mann-Whitney U -Tests = 0.025. * = $P \leq 0.025$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

Body Region	AL	GM	WM	Chi^2	P	Significant population pairs in posthoc comparisons
crown	3.064	2.758	2.705	1.345	0.510	NS
collar color	11.595	8.032	6.172	9.765	0.008	AL-GM*, AL-WM**
dewlap	16.078	15.908	19.540	1.0363	0.006	GM-WM***
mandible	6.753	11.584	9.807	13.503	0.001	AL-GM***, AL-WM**
dorsum background	2.870	4.426	5.927	36.708	0.000	AL-GM**, AL-WM***, GM-WM***
dorsum bars	—	5.246	4.199	3.615	0.057	NS
side	20.187	17.030	14.687	11.660	0.003	AL-WM***
ventrum	9.462	13.133	15.030	13.222	0.001	AL-WM***
thigh	4.470	6.186	7.223	24.103	0.000	AL-WM***, GM-WM**
calf	5.756	6.288	8.905	23.810	0.000	AL-WM***, GM-WM**
foot	5.927	4.553	5.965	11.776	0.003	AL-GM*, GM-WM***
tail	5.237	5.081	7.468	19.890	0.000	AL-WM**, GM-WM***

values indicate that the lizard body region is darker than the rock background (e.g., Fleishman and Persons, 2001).

To determine contrast in spectral shape independent of intensity, that is, color contrast (CC), the total reflectance for each body region of each subject first was equalized in intensity with the mean total reflectance of the local rock background. This equalization was achieved by (1) calculating the sum (area under the curve) of the lizard spectrum and of the mean local rock spectrum, (2) calculating the mean of these two sums, (3) dividing this mean by each sum determined in step 1 to produce an "equalization factor" for each spectrum, and finally (4) multiplying the lizard (or rock) equalization factor times every datapoint in the lizard (or rock) spectrum (e.g., Endler, 1990). Percent color contrast between the intensity-equalized pair of spectra then was calculated as (modified from Schultz, 2001)

$$CC = \frac{\sum |Q_L(\lambda) - Q_R(\lambda)\bar{x}|}{2Q_T}, \quad (5)$$

where the difference between intensity-equalized lizard and rock mean spectra at each wavelength is summed over the entire spectrum and divided by twice the total spectral intensity. This provides a proportional value varying between zero and one. Among population differences in IC and CC were examined statistically with Kruskal-Wallis ANOVA ($\alpha = 0.05$). P -values resulting from these ANOVAs were subjected to a sequential Bonferroni test to protect against increased Type I error associated with significant correlations between pairs of body regions in intensity contrast and

color contrast. ANOVAs that remained significant after the sequential Bonferroni test were subjected to Mann-Whitney U -Tests for pairwise population comparisons. The α -level for significance was set at 0.025 because each population was used twice in the pairwise tests. All statistical tests were run using SPSS (Macintosh v.10).

RESULTS

Sexual Dichromatism.—Sexual dichromatism differed significantly across the study populations in 10 of 12 body regions. No single population, however, was consistently the most or least sexually dichromatic across the body regions measured (Table 2).

Variation in Coloration: Color Space.—Plots of color score means in color space revealed several differences among the study populations. In the AL population, most color score means of both sexes overlapped rock color scores, whereas only a few female color score means in the GM population overlapped their rock color scores, and no color score means in the WM population overlapped their rock color scores (Fig. 3). The two measures that exhibited the most extreme mean values in color space (i.e., distance from the origin) were orange female gravid coloration and the reddish-orange mites in antehumeral mite pockets (Fig. 3). Only flowers in the GM and WM populations were equally or more chromatic than these two body regions.

Plots of individual color scores (Fig. 4) revealed several relationships between the sexes and with respect to objects in the visual background. Male color scores were distributed across a larger area of color space than were female color scores, and

female color scores overlapped those of local rocks far more frequently than did male color scores (Fig. 4).

Variation in Coloration: Hue and Chroma.—In all pairwise comparisons of body regions that differed significantly among populations, both sexes exhibited the highest hue angles (i.e., more blue and less brown) in the WM population, lowest hue angles in the AL population, and intermediate hue angles in the GM population (Fig. 5). Males were more extreme than females in the expression of high hue angles, especially on the trunk and limbs. Chroma (saturation) frequently exhibited the opposite pattern, with the AL population most often exhibiting the strongest chroma, and the WM population the weakest, in significant comparisons of trunk and limb body regions (Fig. 6).

Variation in Conspicuousness: Color Space.—Examining each population independently, color scores from a number of male body regions in the AL population overlapped those of rocks (Fig. 4A). Female color scores in this population overlapped those of rocks to an even greater extent; more female color scores fell within than outside the polygon enclosing rock color scores (Fig. 4B). Interestingly, no color scores of either sex overlapped those of local vegetation (see Discussion).

In the GM population, few male color scores overlapped those of rocks and none overlapped soil, but color scores from several body regions (especially the side) overlapped those of vegetation (Fig. 4C). Females in this population differed from males in having more color scores (especially the dewlap and ventrum) overlap those of rocks, and in having virtually no scores (i.e., a single calf score) overlap those of vegetation (Fig. 4D).

The WM population exhibited the broadest distribution of color scores in color space. This population was similar to the GM population in that more female than male color scores overlapped those of rocks, and many male but few female scores overlapped those of vegetation

(Fig. 4E, F). Lichens comprised as much a part of rock coloration as did the rocks themselves, and color scores of several body regions fell within the polygons enclosing lichen color scores.

Variation in Conspicuousness: Contrast with the Visual Background.—In the GM and WM populations, all male body regions except the ventrum and collar (WM only) were darker than local rocks. AL males exhibited the weakest intensity contrast with rocks in seven of the 12 body regions and differed from the GM and WM populations in being brighter than rocks for the dewlap, mandible, and dorsum bars (Fig. 7). For those male body regions that showed significant lizard-rock intensity contrast across populations, all body regions (except the side) differed between AL and WM, whereas no body regions differed between GM and WM (Fig. 7). No similar general trends were evident for females, where pairs of populations differing in intensity contrast were body region-specific (Fig. 7). Across the 12 body regions, neither sex consistently exhibited stronger intensity contrast with rocks.

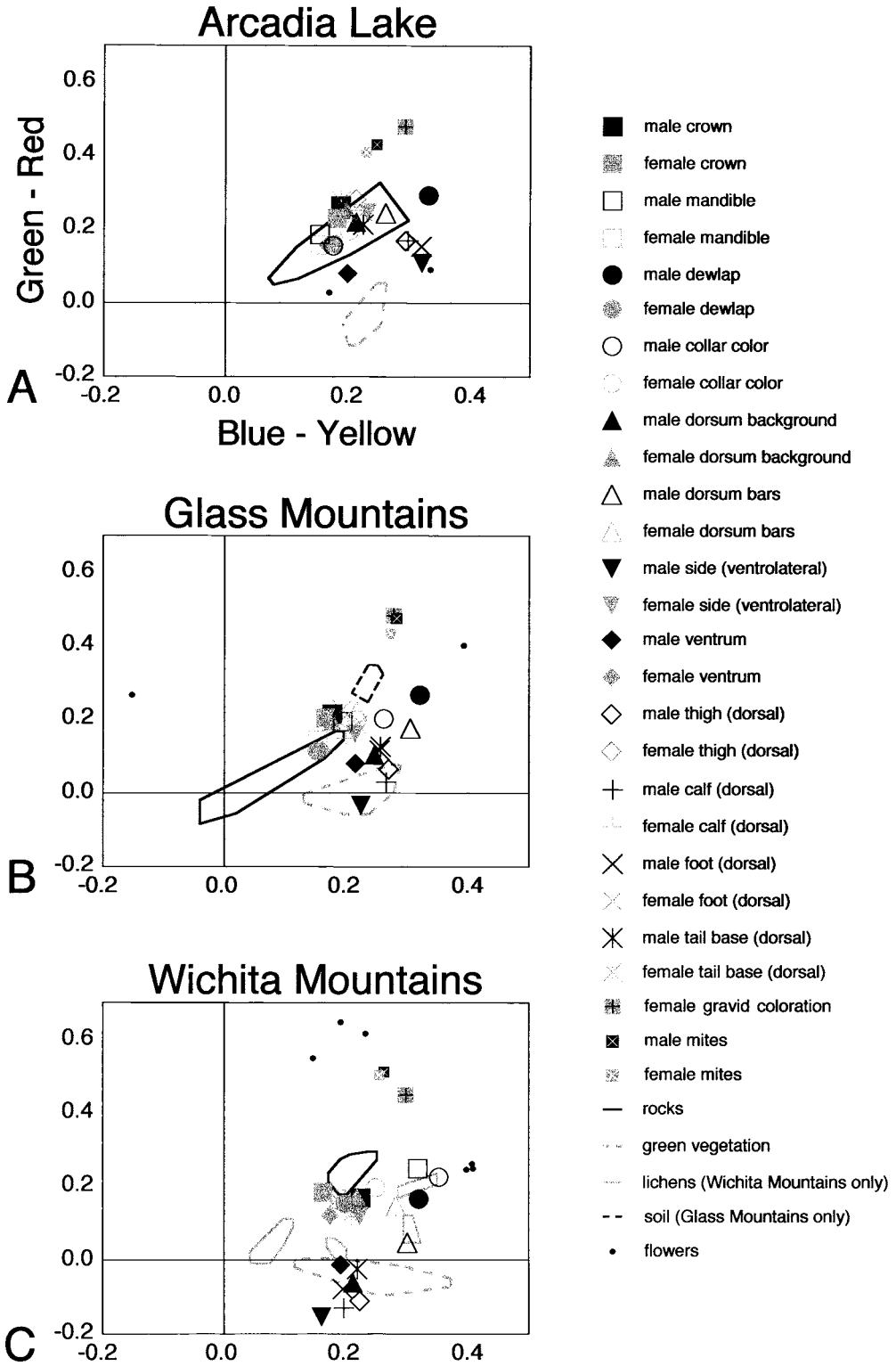
For males, the population that exhibited the strongest color contrast with local rocks for a given body region was divided about evenly between the GM and WM populations (Fig. 8). Last, GM females consistently exhibited the strongest color contrast with rocks and differed significantly in contrast magnitude from the other two populations on all body regions (Fig. 8).

DISCUSSION

Sexual Dichromatism.—The results of our sexual dichromatism analysis differ from those of McCoy et al. (1997) at the same study sites. We found sexual dichromatism to be greatest for the dewlap and dorsum background in the WM population, and greatest for the side in the AL population. By comparison, McCoy et al. (1997) found sexual dichromatism in these same body regions to be greatest in the GM population. Comparing the mean reflectance of these body regions between the two studies revealed considerable differences in the spectral curves,

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FIG. 3. Mean reflectance color scores for the three study populations plotted in the color space of Endler (1990). Polygons with solid black lines enclose rock color score distributions, those with dashed, gray lines enclose vegetation color score distributions, those with solid gray lines enclose lichen color score distributions, and those with dashed black lines enclose soil color score distributions. Individual color scores for flowers shown, but other visual background color scores omitted for clarity. Only the portion of color space containing color scores is shown (on the vertical axis red = 1.0 and green = -1.0; on the horizontal axis yellow = 1.0 and blue = -1.0). Color space plots scales to same dimensions for comparison among populations. For the Wichita Mountains population, lichens fell into four groups: gray (left center: $N = 9$); pale blue-green (center; $N = 3$); chartreuse (right: $N = 5$); gold (upper right: $N = 2$). Female orange gravid coloration: Arcadia Lake, $N = 11$; Glass Mountains, $N = 16$; Wichita Mountains, $N = 20$. Mites: Arcadia Lake males: $N = 2$, females: $N = 2$; Glass Mountains males: $N = 7$, females: $N = 1$; Wichita Mountains males: $N = 32$, females: $N = 11$. Lizard sample sizes as in Figure 2.



especially for the dorsum background (dorsolateral) and side (ventrolateral). These differences are particularly prominent in wavelengths from 400–500 nm, which may be due in part to the use of white card stock by McCoy et al. (1997) as a reflectance standard. Conspicuous differences also occur in the relative amplitudes of male and female spectra for a given body region, however, and we cannot rule out the possibility of population-level changes in coloration over the 11 years between data collection in the two studies.

Coloration and Contrast with the Local Visual Background.—Males exhibited distributions of color scores that were broader and more population-specific than those of females. Males also differed considerably among populations in overlap of their color scores with prominent components of their visual backgrounds, whereas overlap of female body regions with backgrounds was restricted largely to rocks (for a similar finding in chuckwallas, see Kwiatkowski, 2003). Despite WM males exhibiting the greatest Euclidian distance between color score means from several body regions (Fig. 3), and thus strong “internal” color contrast, they did not always exhibit strong color contrast with their visual backgrounds. Although WM females were relatively inconspicuous against the salmon-coloration of their rocks, the abundance of colorful lichens masked to some degree the chromatic turquoise and gold coloration of WM males. By comparison, GM males exhibited the greatest color contrast for five body regions, and GM females exhibited greater color contrast than AL and WM females for all body regions. This result stems from the fact that green males and brown females both stand out against the achromatic gray gypsum that characterizes GM habitat.

Potential Sources of Color Variation among the Study Populations.—The diversity of animal color patterns observed in nature arises from compromises, on a local scale, among the multiple functions that color must serve (e.g., Endler, 1992). Such functions may include conspecific intimidation, mate attraction, sex identification, predator avoidance, thermoregulation, and others. Prior research on the AL, GM, and WM populations provides a context with which to view the results of the work presented here.

Assessment of female mate preferences, as gauged by time spent in proximity to sized-matched males varying in color “brightness,” showed that AL females preferred “brighter” males from their own population to “duller” ones and preferred the “more colorful” WM males to their own males (Baird et al., 1997). In contrast, WM females showed no preference of bright over dull males from their own population, nor did they prefer their own males over the duller AL

males (Baird et al., 1997). This result is consistent with the greater opportunity of AL females (which, unlike GM and WM females, are not territorial) to choose a mate among numerous males in their high-density habitat (Baird et al., 1996). The somewhat muted, brownish hues of AL males, therefore, cannot be explained by an absence of female preference for more vivid male coloration.

The dearth of other lizard species that would constitute prey for *C. collaris* in Oklahoma also rules out saurophagy as a force that could provide selective advantages for inconspicuous coloration. For example, only three instances of saurophagy (all cannibalism) have been documented in the seasonally monitored AL population since 1990 (TAB, pers. obs.). Despite being less conspicuous than GM or WM males, AL males still are more conspicuous than males in highly saurophagous populations of *C. collaris* in the desert southwest (e.g., Macedonia et al., 2002; JMM, JFH, YMB, AKL, unpubl. data).

Predator sighting rates and the incidence of tail breaks suggest that predation pressure is greater in the AL population than in the GM and WM populations (Baird et al., 1997). The extensive overlap of AL body color scores with rocks but not vegetation is interesting in light of the habitat, that is, densely packed rocks of similar size with scant vegetation and the estimated predator pressure on this population.

The habitat of the GM population is more complex than that of the AL population. The lichen-free boulders, stones, and gypsum shards that are scattered across and permeate the soil typically range from white to light gray (although medium and dark gray fragments also are present). This pale, achromatic rock creates considerable visual contrast with the rich red soil and patchy green vegetation that dominate the landscape. Only a trivial number of GM male color scores fell within the polygon enclosing their rock color scores, and none fell within the polygon enclosing soil color scores. Thus, when viewed from above, GM males should be relatively conspicuous against the light gray rock and red soil to most vertebrate color vision systems.

However, overlap did occur in color space between GM male color scores and green vegetation. Although their greenish limbs/tails and yellow dorsum bars/collars contrast with local rock and soil color, the abundance of green vegetation clusters, some with yellow flowers, might provide a modicum of camouflage for GM males at lateral visual angles, particularly when predators or prey are at a distance from the lizards. By comparison, the relative scarcity of vegetation in the habitat of the AL population would make green body coloration more con-

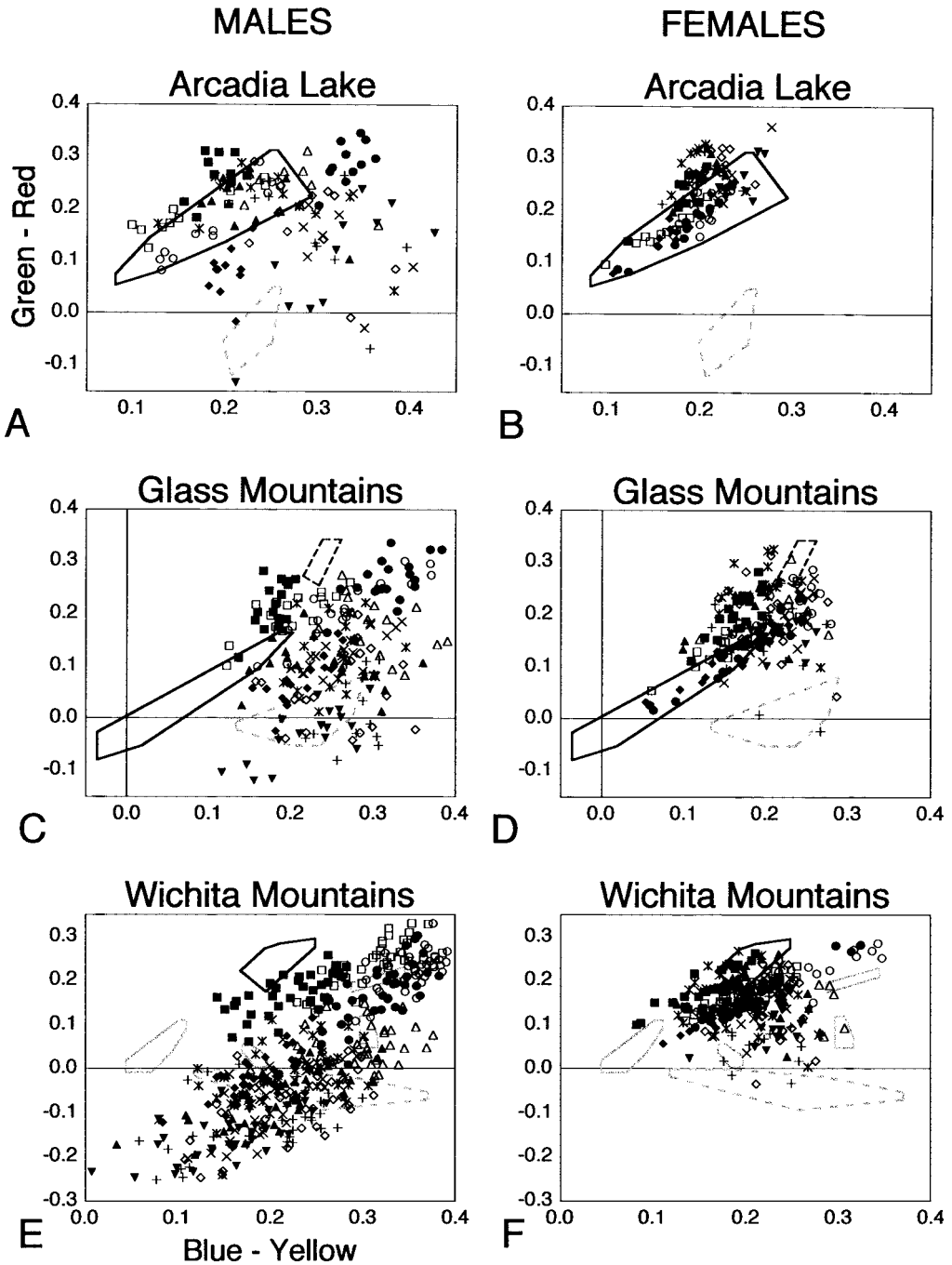


FIG. 4. Reflectance color scores of 12 body regions for the three study populations plotted in the color space of Endler (1990) showing color scores for individual males and females. Portion of color space shown for each population varies according to distribution of their color scores. Symbols as in Figure 3, except females symbols shown here in black, and color scores for flowers, mites, and female gravid coloration are not shown. Legend as in Figure 3.

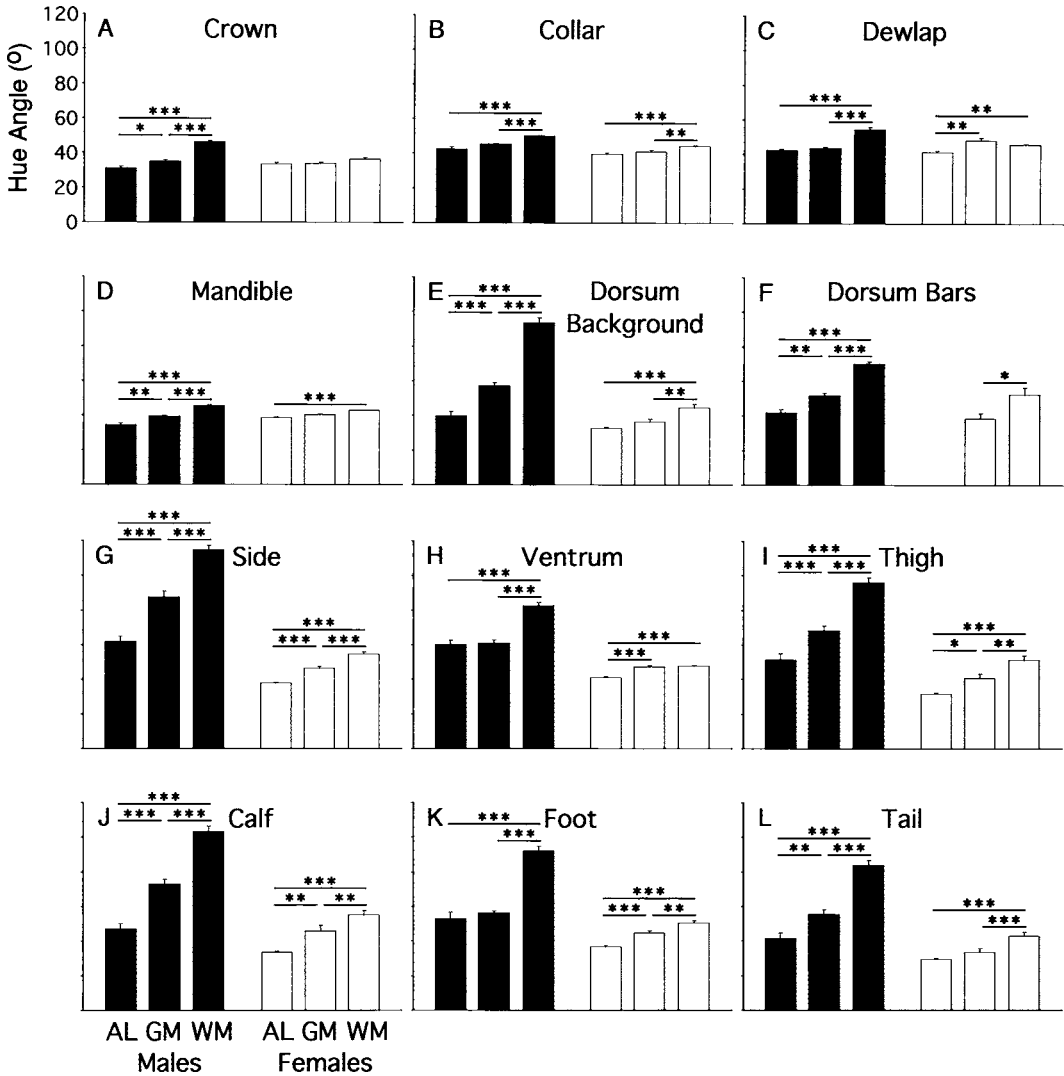


FIG. 5. Pairwise population comparisons of hue angle for the 12 body regions measured. Pairwise tests were run only on variables (body regions) that passed a sequential Bonferonni test on *P*-values from the 12 ANOVA results for each sex. Asterisks indicate levels of significance: * = *P* < 0.025, ** = *P* < 0.01, *** = *P* < 0.001. See text for calculation of hue. Note: A line spanning the bars of all three populations indicates results of a test between the AL and WM populations.

spicuous there, and AL males were less green (i.e., lower hue angle) than GM (or WM) males on all body regions.

Baird et al. (1997) and McCoy et al. (1997) speculated that the abundance of lichens and flowering plants in the WM habitat comprise a visual background that may render WM males cryptic. Results of our color space analyses provide some support for this proposition. Numerous WM male color scores fell within or adjacent to polygons containing lichen color

scores; the ventrum overlapped pale bluish-green lichens, dorsum bars overlapped chartreuse lichens, and the mandible, collar color, and dewlap all fell in the same region of color space as golden lichens. In addition, the golden-yellow hue of the mandible, collar color, and dewlap in WM males was quite similar to that of yellow flowers common in the visual background.

A number of WM male color scores likewise overlapped those of green vegetation, particularly the dorsum background, tail, and ventrum

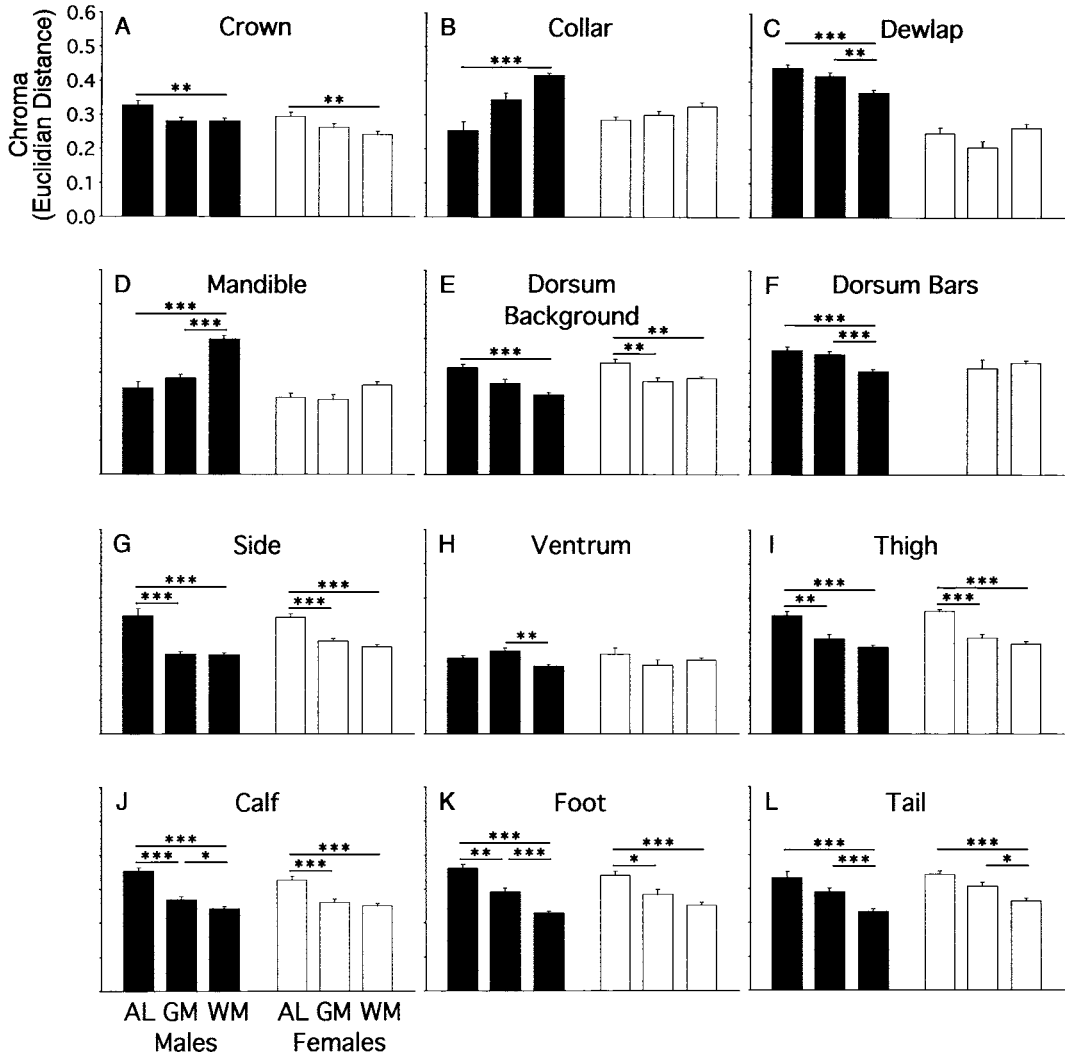


FIG. 6. Pairwise population comparisons of chroma for the 12 body regions measured. See text for calculation of chroma. Legend as in Figure 5.

(but also the thigh and calf). In most males, however, these body regions were far more blue-green than the yellowish-green of vegetation.

Summary.—In this study, we examined two principal aspects of geographic color variation—sexual dichromatism and color conspicuousness—in three populations of *C. collaris* from Oklahoma. Results of our sexual dichromatism analysis revealed no single population to be the most (or least) sexually dichromatic across the 12 body regions measured. This result differs from McCoy et al. (1997), who found the GM population to be most sexually dichromatic for the three body regions they analyzed.

We also addressed in a preliminary fashion McCoy et al.'s (1997) hypothesis that natural

selection, via predation pressure, has produced body coloration that results in each population being somewhat inconspicuous against its own visual backgrounds. Notwithstanding the potential influence of genetic forces like founder effects and drift, our results are consistent with this hypothesis for the AL population but are less clear for the GM and WM populations. For example, although WM males exhibited virtually no color overlap with local rocks, the boulders in their habitat have much of their surfaces cloaked in lichens. WM male body coloration overlaps extensively in hue and chroma with most of these lichens, and this overlap might reduce their visibility to avian predators. Likewise, the abundance of yellow flowers in this grassland habitat

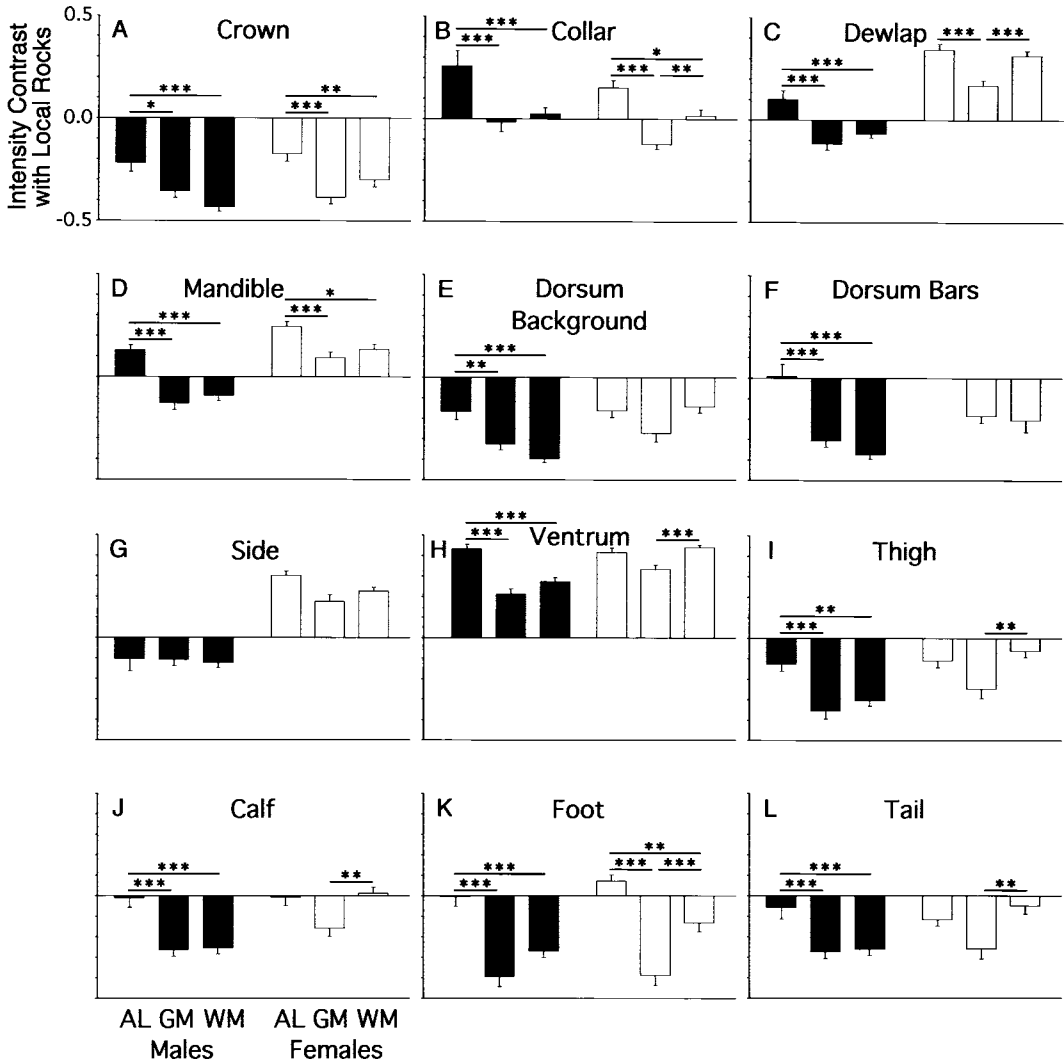


FIG. 7. Pairwise population comparisons of intensity contrast between lizard body regions and rocks. Values computed from mean reflectance spectra for each body region in each lizard population and their local rocks. Values above the zero line indicate body reflectance brighter than rocks; values below the zero line indicate body reflectance darker than rocks. See text for calculation of intensity contrast. Legend as in Figure 5.

might reduce color contrast with WM males' chromatic yellow mandibles, dewlaps, and collars to terrestrial predators. However, we have no evidence to suggest that predation pressure has selected for coloration in WM males to match that of lichens and flowers. Indeed, the conspicuous and complementary color pattern of a blue body and yellow head has evolved in other lizards (e.g., rock agamids), including other *C. collaris* populations that lack potentially crypsis-enhancing lichens on their rocks (e.g., Macedonia et al., 2002). Nevertheless, it seems possible that WM males could possess an advantage over AL and

GM males in being able to exploit a range of chromatic colors that make them very conspicuous once detected, but which provide a degree of camouflage when immobile.

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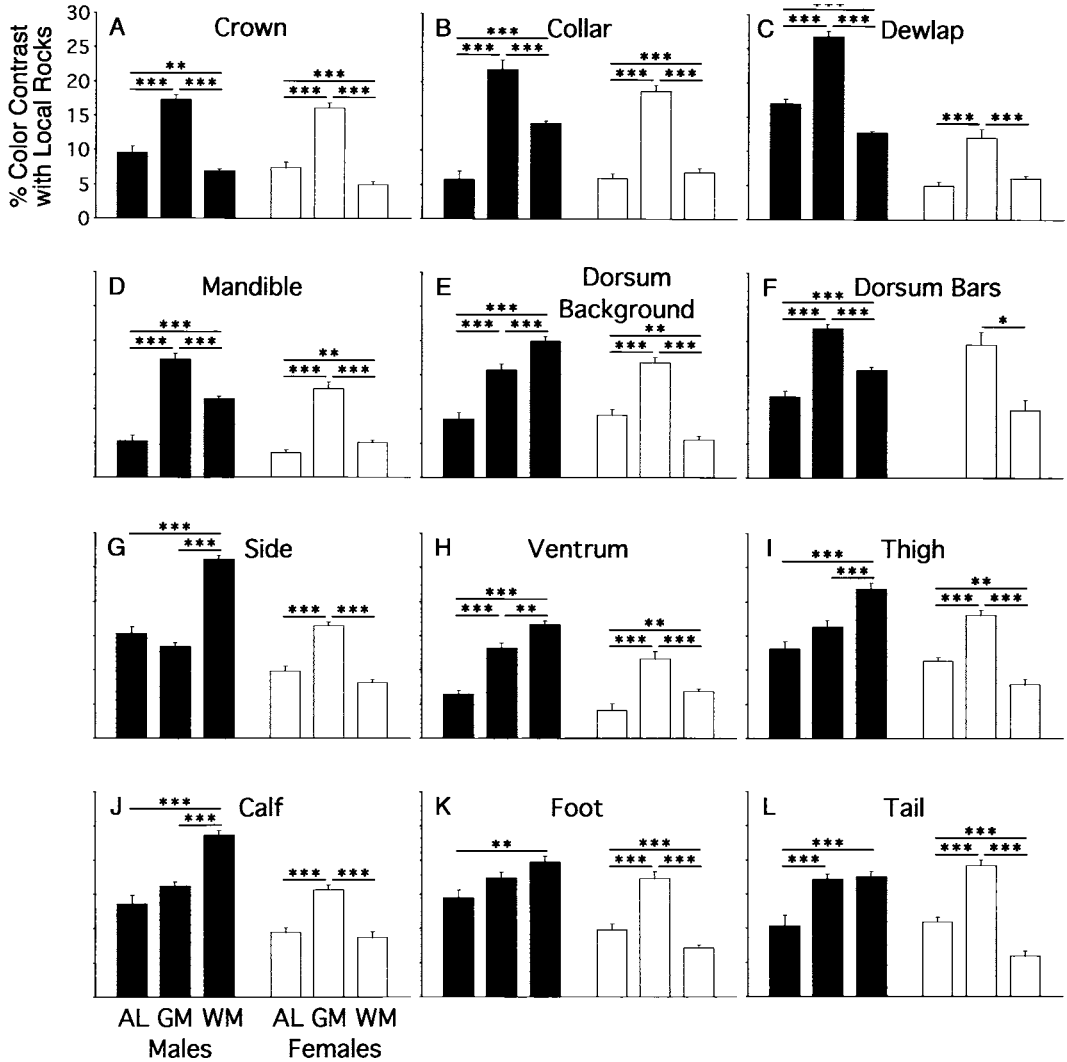


FIG. 8. Pairwise population comparisons of color contrast between lizard body regions and local rocks. See text for calculation of color contrast. Legend as in Figure 5.

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