Geographic Variation in Sexual Dichromatism in the Collared Lizard, Crotaphytus collaris
(Sauria: Crotaphytidae)
Author(s): J. Kelly McCoy, H. James Harman, T. A. Baird, Stanley F. Fox
Published by: American Society of Ichthyologists and Herpetologists
Stable URL: http://www.jstor.org/stable/1447560
Accessed: 21/06/2011 07:20

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=asih.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.
Geographic Variation in Sexual Dichromatism in the Collared Lizard, *Crotaphytus collaris* (Sauria: Crotaphytidae)

J. Kelly McCoy, H. James Harmon, T. A. Baird, and Stanley F. Fox

We recorded the color of male and female collared lizards (*Crotaphytus collaris*) from three populations using reflectance spectrophotometry to examine interpopulation differences in sexual dichromatism. The degree of sexual dichromatism within this species varied significantly among local populations. We also examined brightness of coloration and sexual dichromatism in these populations using appraisal by naive observers. Subjective appraisal also showed significant differences among these populations. However, the population appraised as most brightly colored was not appraised as most dichromatic. This study demonstrates that sexual dichromatism may vary significantly among populations of a single species. Although subjective appraisal of sexual dichromatism may yield reliable results when carried out under carefully controlled conditions, assessment of a single pair of individuals or assessment of only male coloration is not sufficient for a study of sexual dichromatism.

COLOR can play important social roles in lizards. Sexual dimorphism in coloration (sexual dichromatism) has been attributed to sexual selection in several lizard species (Vitt and Cooper, 1986; Vial and Stewart, 1989). However, despite the availability of an accurate, objective method for color analysis (reflectance spectrophotometry), most studies of sexual dichromatism in vertebrates, including birds (Read, 1987; Read and Harvey, 1989; Johnson, 1991), fishes (Ward, 1988; Chandler and Cabana, 1991), and lizards (Lefcort and Blaustein, 1991), have relied merely on subjective appraisals of coloration. Usually, the colorations of a number of organisms were ranked by naive observers. These rankings were then used as the basis for analysis of coloration. Furthermore, color appraisal in all of these studies was based on pictures of the animals (or descriptions in Ward, 1988) and not direct observations of the animals. This methodology often relied on appraisal of color in only a single photographed individual and ignored any variation among individuals (although Lefcort and Blaustein used several pictures for species with geographic variation in morphology). Problems associated with subjective appraisal of color may underlie the contradictory conclusions of Hamilton and Zuk (1982) and Read and Harvey (1989) regarding the importance of parasites in the evolution of sexual dichromatism.

In addition to the problematic nature of subjective color appraisals (noted in 1960 by Hutchison and Larimer), several of these studies did not actually consider sexual dichromatism because they ranked species only on the basis of male brightness. Because perception of color is based on several environmental factors including ambient light and background (Lythgoe, 1979), male brightness taken out of context may not reflect the actual brightness of that individual in its own habitat. To assess sexual dichromatism, one must compare male coloration to female coloration. Without the selection pressures encountered by males through sexual selection, females should display the colors that are most effective for predator avoidance and thermoregulation. Only by comparison of male coloration with that of females can we examine the effects of sexual selection on color.

In this study, we used both reflectance spectrophotometry and subjective appraisal of coloration to analyze geographic variation in sexual dichromatism of collared lizards (*Crotaphytus collaris*). This lizard is an ideal species in which to examine intraspecific variation in sexually dimorphic characters. Sexual dimorphism in color and body size is striking in this species (Fitch, 1956). Although only a single subspecies inhabits Oklahoma (*C. collaris collaris*, Webb, 1970), variation among Oklahoma populations rivals that observed throughout the range of the species. We studied three populations of collared lizards in Oklahoma to measure intraspecific differences in sexual dichromatism using reflectance spectrophotometry to document coloration objectively, as well as subjective appraisals of coloration by naive observers. We compared sexual dichromatism among populations using both methods of coloration assessment as a test of the reliability of subjective appraisal for the analysis of color differences. To examine the possibility that brightness of male coloration alone does not reflect sexual dichro-
Materials and Methods

We examined reproductively mature specimens of *C. collaris* from three localities: the Glass Mountains (GM) in northwestern Oklahoma (Major and Woodward Counties, n = 14 males; n = 8 females), the Wichita Mountains National Wildlife Refuge (WM) in southwestern Oklahoma (Comanche County, n = 17 males; n = 14 females), and Arcadia Lake (AL) in central Oklahoma (Oklahoma County, n = 11 males; n = 9 females). During the reproductive season of 1991 (May and June), lizards were captured alive by noosing. Reproductive state was recorded at the time of capture. We used palpation of oviductal eggs as evidence of reproductive maturity in females and the presence of active femoral pores in males. After data on color were collected, lizards were returned to collection sites and released unharmed.

Spectra of the lizards were recorded with a Varian DMS-100 dual beam spectrophotometer modified to function in the dual wavelength mode (US Patent #4,929,078, H. J. Harmon, 1990, unpubl.). The spectrophotometer was interfaced to a Y-bifurcated optical fiber bundle, the efferent end collecting light from the spectrophotometer chopper and transmitting it to the animal, and the other (afferent) limb of the bifurcation conducting light reflected from the animal to the photomultiplier. The “common” end (16 mm²) transmitted incident light to the animal and collected the reflected light. Spectra were recorded from 400–800 nm with 2 nm resolution; the reference wavelength was set to 400 nm. In dual wavelength mode, the 400 nm “reference” light and the scanned measuring beam are alternated through the same (efferent) limb of the bundle to the lizard. Both reference and measuring sample beam traverse the same optical path and impinge on the same skin area.

Spectrophotometric readings were taken from the gular, dorsolateral, and ventrolateral regions of each lizard. These are all regions that are prominently displayed during the social interactions of collared lizards (Fitch, 1956). Because lizard coloration changes with body temperature (Hutchison and Laimer, 1960; Norris, 1967; Zucker, 1988), all lizards were allowed to bask under sunlamps for approximately 1 h and then held in a lighted incubator maintained at 38 C. The body temperature of each lizard was measured with a cloacal thermometer before spectrophotometric readings were taken. When spectrophotometric readings were taken, all lizards had body temperatures within the optimal range (35–40 C) reported for *C. collaris* by Fitch (1956). The spectral readings analyzed in this study were all taken within 10 days of capture. To make certain that our lizards had not changed color during captivity, as does *Urosaurus ornatus* (Zucker, 1988), we held a small sample (two males from WM and three males from GM) for six weeks while taking spectrophotometric readings after one day, three days, seven days, and at one-week intervals thereafter. Spectral readings showed no significant change with time, indicating that the color of *C. collaris* is stable.

The reflectance spectrum of a “white card” (white paper cardstock) was subtracted from the reflectance spectrum of each animal, removing wavelength-specific characteristics of the instrument from the spectrum of the animal. Thus, the stored spectra analyzed and shown in Figure 1 are reflectance spectra of the animal only. The same white card was used throughout this experiment and was carefully stored between measurements to maintain its reflectance characteristics. Because reflectance characteristics vary among various types of pa-
per cardstock, the expression of reflectance as absolute, or as a percent, would be inappropriate. Although the use of a white card as a reflectance standard precludes us from expressing our measurements as percent reflectance, because this standard was consistently applied, it has no effect on comparisons among spectra collected in the same manner.

Because expression of reflectance as a percent was inappropriate, a linear scale was applied to all spectra collected, and spectrophotometric readings of lizards were expressed as relative reflectance in arbitrary reflectance units (ARU) versus wavelength in nanometers. The area under this curve is a measure of overall brightness in coloration (King et al., 1994). Analysis of spectral data was conducted using the LabCalc (Galactic Industries, Hartford, CT, 1991, unpubl.) program. Before analysis, spectra were smoothed using a fast-Fourier transformation. Sexual dichromatism was calculated for the gular, dorsolateral, and ventrolateral areas separately. Sexual dichromatism was calculated by subtracting the spectrum of a female from the spectrum of a male of the same population and calculating the area of the resulting curve. The magnitude of this area represents the total difference in brightness for that pair of lizards at that location on the body. Sexual dichromatism was calculated for each male paired with each female from the same population. Because this calculation could result in either positive or negative values, the absolute value of each area was used for analysis. This can be seen most clearly in the gular area, where males achieve their brilliant yellow-orange coloration by reflecting less blue and green light than females (Fig. 1).

Means of sexual dichromatism for lizards from each population were compared separately for gular, dorsolateral, ventrolateral, and then the total of all three readings. Levene’s test (Levene, 1960) revealed significant heterogeneity of variances among males for all three readings and the total, so all data were rank transformed (Conover, 1980) before further analysis. Mean sexual dichromatism was compared among sites using one-way analysis of variance with subsampling, adjusted for different numbers of experimental units and different numbers of subsamples (Steel and Torrie, 1980). Each male was considered an experimental unit and the pairings with different females considered as subsamples of that male. Because four tests were conducted on the same set of subjects, probabilities were adjusted using the sequential Bonferroni adjustment (Rice, 1989). All statistical analyses were conducted using the SYSTAT program (I. Wilkinson, SYSTAT, Inc., Evanston, IL, 1990, unpubl.).

Subjective appraisals of coloration were made using color photographic slides of lizards taken at the time spectrophotometric readings were taken. Conditions for these photographs were carefully controlled. All lizards were photographed using the same camera, lens, aperture, and shutter speed. Lizards were photographed in an unlighted, windowless room using a quartz halogen light for illumination. A booth was constructed which held all lizards at the same distance from the camera and used the same background. Lizards were photographed on three rolls of Kodachrome 64 from the same lot and processed at the same time. Photographs of some lizards were not used in the subjective appraisals of coloration because the positions of these lizards were sufficiently contorted that we felt accurate comparisons of coloration would be impossible. This reduced the sample sizes for these analyses slightly (GM: n = 12 males, n = 8 females; AL: n = 9 males, n = 8 females; WM: n = 11 males, n = 9 females). These precautions ensure that comparisons based on photographic slides reflect actual differences in the coloration of the lizards.

Coloration was appraised subjectively by 10 naive observers. Differences in male coloration were assessed by presenting each observer with slides of all 32 male lizards. Slides were presented to observers on a large slide viewer (38 × 50 cm); thus, all lizards were visible at the same time. Observers were asked to arrange the slides from most brightly colored to least brightly colored, considering overall coloration. Ranks were then assigned from the ordered slides. The same procedure was used to assess differences in female coloration using slides of all 25 female lizards. For the comparison of sexual dichromatism among populations, observers were presented with 24 pairs of slides (eight pairs of slides from each population). Pairs of slides (one slide of a male lizard and one slide of a female from the same site) were held together in cardboard mounts, and observers were asked to arrange the paired slides from most different to least different in terms of the brightness of overall coloration. Ranks were then assigned from the ordered pairs. The pairs of lizards were drawn at random from all of the slides used for subjective appraisal of coloration, and a new set of random pairings was used for each observer.

Differences in overall brightness among sites for both males and females were examined using the same procedure. First, for each lizard used in this analysis we calculated the average
Table 1. Comparison of Mean Sexual Dichromatism Measured by Reflectance Spectrophotometry Expressed as the Area Between Reflectance Spectra for Males and Females (ARU × nm) in Three Areas of the Body and Their Total Among Populations of Collared Lizards (Crotaphytus collaris) from Arcadia Lake (AL), the Glass Mountains (GM), and the Wichita Mountains (WM). Comparisons made by one-way analysis of variance with subsampling, adjusted for different numbers of experimental units and subsamples (Steel and Torrie, 1980).

<table>
<thead>
<tr>
<th>Area of body</th>
<th>WM</th>
<th>GM</th>
<th>AL</th>
<th>F</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gular</td>
<td>65.65</td>
<td>68.20</td>
<td>44.30</td>
<td>3.002</td>
<td>2, 37.01</td>
<td>0.0619</td>
</tr>
<tr>
<td>Dorsolateral</td>
<td>86.37</td>
<td>124.22</td>
<td>94.84</td>
<td>10.955</td>
<td>2, 37.26</td>
<td>&lt;0.0001*</td>
</tr>
<tr>
<td>Ventrolateral</td>
<td>68.63</td>
<td>78.11</td>
<td>58.96</td>
<td>0.364</td>
<td>2, 37.29</td>
<td>0.6971</td>
</tr>
<tr>
<td>Total</td>
<td>220.65</td>
<td>270.53</td>
<td>198.45</td>
<td>12.547</td>
<td>2, 37.52</td>
<td>&lt;0.0001*</td>
</tr>
</tbody>
</table>

* Indicates significant difference at overall P < 0.05 after sequential Bonferroni adjustment for multiple related tests.

The three populations of lizards displayed significant differences in mean sexual dichromatism. Analysis of coloration using reflectance spectrophotometry revealed that these populations were significantly different in the degree of sexual dichromatism in the dorsolateral area, and in total sexual dichromatism (Table 1). There were no significant differences in the degree of sexual dichromatism in the gular or ventrolateral regions. The GM population was consistently the most dichromatic. The AL population was the least dichromatic, except in the dorsolateral area, whereas the WM population generally displayed sexual dichromatism intermediate between the other two populations.

The average spectrophotometric traces from each body area for lizards from each population (Fig. 1) show a striking correspondence to the perceived coloration of the lizards. Male lizards from the GM and WM populations display blue-green coloration in the ventrolateral region, which can be seen in the strong reflectance of light in wavelengths from 450–500 nm. Males from AL, however, display much more green coloration in the ventrolateral region and most strongly reflect light from 550–600 nm in wavelength. In all three populations, the dorsolateral region of male lizards is generally green, and the spectrophotometric traces from this region of the body show that the greatest amount of light is reflected in wavelengths from about 500–600 nm. The bright yellow-orange coloration which is found in the gular region of males from all three populations is a result of strong reflection of light in wavelengths from 600–700 nm and reduced reflectance of light in the blue and green wavelengths. The spectrophotometric traces show that the differences in coloration between males and females result from more uniform reflectance of all wavelengths of light by females. This lack of a distinct peak in reflectance produces colors that are perceived as less intense. The coloration of females generally ranges from tan in the gular and ventrolateral regions to brown or olive-green in the dorsolateral region.

The spectrophotometric traces revealed that the AL population was noticeably less bright in color than the lizards from the other populations. Both males and females from AL reflected less light in most wavelengths. This was especially noticeable in the dorsolateral and ventrolateral areas where AL lizards reflected much less light in the blue wavelengths (425–475 nm). These spectra also show that females from the WM population were brighter in color than females from the GM population. In the readings from the dorsolateral area, male lizards from
McCOY ET AL.—SEXUAL DICHROMATISM IN CROTAPHYTUS

Table 2. Average Rankings by Naive Observers of Brightness of Coloration and Sexual Dichromatism of Collared Lizards (Crotaphytus collaris) from Three Oklahoma Populations and Results of Kruskal-Wallis Comparisons among Sites. Lower ranks are brightest (for dichromatism, most different).

<table>
<thead>
<tr>
<th>Site</th>
<th>Male coloration</th>
<th>Female coloration</th>
<th>Sexual dichromatism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arcadia Lake</td>
<td>25.09</td>
<td>18.31</td>
<td>16.71</td>
</tr>
<tr>
<td>Glass Mountains</td>
<td>15.57</td>
<td>13.40</td>
<td>9.09</td>
</tr>
<tr>
<td>Wichita Mountains</td>
<td>10.36</td>
<td>7.77</td>
<td>11.70</td>
</tr>
<tr>
<td>P</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

the GM and WM populations were similar in color, but because of the differences in female coloration, the GM population displays greater dichromatism. Although the males from the WM population displayed a striking turquoise to aqua blue color in the ventrolateral area, this coloration is achieved through high reflectance in a narrow band of wavelengths (450-475 nm), and in total they reflected less light than males from the GM population.

Results of the subjective appraisals of coloration agreed closely with the results of the spectrophotometric analysis. For both male and female lizards, there was significant agreement in rankings among observers (males: $W = 0.605$, $P < 0.001$; females: $W = 0.460$, $P < 0.001$). The analysis of coloration by naive observers also demonstrated that there were significant differences in brightness among sites for both males and females (Table 2). Observers consistently judged lizards (both male and female) from WM as brightest and AL lizards as least bright. Sexual dimorphism, appraised by naive observers, also varied significantly among sites (Table 2). Consistent with our spectrophotometric analysis, the brightest lizards (WM) were not the most dimorphic. Rather, the greatest degree of sexual dichromatism was displayed by lizards from GM, which were intermediate in brightness.

Discussion

Populations of collared lizards at three different locations in Oklahoma display significant differences in the degree of sexual dichromatism. These same populations also display significant differences in body size and shape (McCoy et al., 1994). From these analyses, it is reasonable to hypothesize that sexual dimorphism in color, body size, and body shape is subject to different selective pressures in these three populations. From previous studies of lizard coloration, it is also reasonable to hypothesize that the color of males in each population is a compromise between crypsis, thermoregulation, and sexual selection.

Numerous studies have shown that coloration affects the thermoregulation of lizards (Norris, 1967; Pearson, 1977; Porter and Tracy, 1983). Although Talbot and Livezy (1963) used reflectance spectrophotometry to document geographic variation in the coloration of Sceloporus occidentalis that they attributed to differences in thermoregulatory requirements at different locations, our three populations are separated by a maximum distance of only 200 km, making it unlikely that differences in insolation or climate result in selection for radically different coloration for thermoregulatory purposes. There may also exist differences in absorption of light in wavelengths greater than 800 nm, which contains substantial energy but was not considered in this study.

Selection for crypsis may also play a major role in the evolution of lizard coloration (Norris and Lowe, 1964; Lillywhite et al., 1977; Gibbons and Lillywhite, 1981). Differential selection for cryptic coloration may have significant effects on our populations. Differences in predation pressure among the three populations may result in selection for greater or lesser crypsis. Sightings of potential predators and estimates of injury rates among lizards from these populations indicate that predation pressure is substantially greater at AL (T. A. Baird, S. F. Fox, and J. K. McCoy, unpubl.). Also, the most common background colors appear subjectively to differ greatly among these three localities. Lizards in the WM population live on large granitic outcrops. The rocks in this area are dark red with numerous patches of bright green and yellow lichens. The lizards at GM live on gypsum outcrops which are almost uniformly very light grey. The rocks available to the AL population are a uniform medium grey. Different colored backgrounds will result in different colors being most effective for predator avoidance. This points out the importance of considering sexual dichromatism, not just brightness of males. The brightest colored population might actually be highly cryptic in its own habitat because of differences in background coloration, and the
brightest population is not necessarily the most dichromatic. We suggest that future work on habitat-specific crypsis in these three populations of lizards would be valuable.

Our comparison of the use of spectrophotometric measurements and subjective appraisal of color demonstrates that, at least under carefully controlled conditions, subjective appraisal may represent a viable method for analyzing differences in coloration. Similar results were obtained with each method although the range of wavelengths examined differs slightly (400–800 nm for spectrophotometry and 400–700 nm for human vision). However, this comparison also underscores certain deficiencies in other applications of subjective appraisal as a means of analyzing differences in coloration. Most obviously, male brightness is not the same as sexual dichromatism. If sexual dichromatism is the phenomenon under consideration, it is imperative to examine the color of both males and females. Our comparison also suggests that a single individual (e.g., a picture from a field guide) may not be sufficient for analysis of sexual dichromatism. Some pairs of individuals from GM (overall the most dichromatic population) were ranked very weak in sexual dichromatism; also some pairs of lizards from AL (the least dichromatic population overall) were ranked very dichromatic. That we found good agreement between these two methods is certainly not a blanket endorsement of all studies which rely on subjective appraisal to analyze differences in coloration.

A combination of selective forces acting on coloration is also indicated by the patterns of difference and similarity among populations in sexual dichromatism in various regions of the body. All three populations are similar in sexual dichromatism in regions that are less visible to potential predators (gular and ventrolateral) but that can be displayed to prospective mates or rivals. The region of the body that is most visible to predators (dorsolateral) is also the region in which these populations displayed significant differences.

The measurable variation in sexual dichromatism suggests that there are differences in sexual selection among these three populations, but without further evidence, it is impossible to determine the exact level of sexual selection acting on each population. Because coloration is also subject to selection resulting from thermoregulatory considerations and predation, which might act as counterselection to the bright coloration promoted by sexual selection, it is impossible to draw conclusions about sexual selection without information on these other selective processes. As pointed out by Hutchison and Larimer (1960), the coloration of a lizard will be the net result of all selective pressures acting on that trait.

ACKNOWLEDGMENTS

We thank J. Gosney and R. Parker for access to collecting sites in the Glass Mountains, the US Army Corps of Engineers for access to the Arcadia Lake dam area, and the US Fish and Wildlife Service for access to the Wichita Mountains National Wildlife Refuge. S. S. Fox and M. Acree assisted with fieldwork. We thank 10 naive observers for their subjective rankings of lizard color. This study was funded by a grant to JKM from the Payne County Audubon Society and in part by grants from Oklahoma State University and the University of Central Oklahoma.

LITERATURE CITED

McCOY ET AL.—SEXUAL DICHROMATISM IN CROTAPHYTUS 571


(JKM, SFF) DEPARTMENT OF ZOOLOGY, OKLAHOMA STATE UNIVERSITY, STILLWATER, OKLAHOMA 74078; (HJH) DEPARTMENT OF MICROBIOLOGY AND MOLECULAR GENETICS, OKLAHOMA STATE UNIVERSITY, STILLWATER, OKLAHOMA 74078; and (TAB) DEPARTMENT OF BIOLOGY, UNIVERSITY OF CENTRAL OKLAHOMA, EDMOND, OKLAHOMA 73034. Present address: (JKM) DEPARTMENT OF BIOLOGY, ANGELO STATE UNIVERSITY, SAN ANGELO, TEXAS 76909. E-mail: (JKM) kelly.mccoy@angelo.edu. Submitted: 11 Sept. 1995. Accepted: 10 Dec. 1996. Section editors: D. Cundall and F. Irish.