MECHANISMS OF SELECTION FOR THE EVOLUTION

OF SEXUAL DIMORPHISM IN THE COLLARED

LIZARD (<u>CROTAPHYTUS</u> <u>COLLARIS</u>)

By

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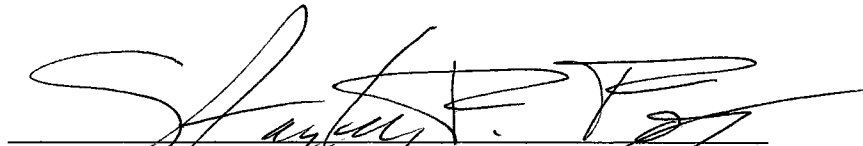
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has been immensely enjoyable, as well as scientifically profitable, and I owe much of my success to him.

I must also mention the support of my family, especially my wife, Therese. Despite the trials of life with a field biologist, she has been unwavering in her support and her confidence in me.

Although his untimely death prevented him from seeing the end of this project, I want to acknowledge the contributions of my father, Dr. C.J. McCoy. Not only through my graduate education, but through my entire life, his unflinching support of my decisions (even when he knew they were bad decisions) has been in large measure the foundation of my life. His advice on matters scientific had great influence on my choice of careers and on my research interests. It was largely through his advice that I embarked on this study. He not only provided advice, but also helped in the field. Indeed, the last time we spent together was in the field at my study site in the Glass Mountains. Even since his passing, memory of what he would (and would not) approve provides considerable guidance. I wish he could have seen the end of this project, I think he would have been proud.

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Chapter VI.

INTRODUCTION

This project was designed to simultaneously test several hypotheses regarding the evolution of sexual dimorphism. The basic design of the project involves a comparison of two populations of collared lizards (<u>Crotaphytus</u> <u>collaris</u>) which display significant differences in sexual dimorphism. This research is presented as a series of related papers, each in correct format for submission to an appropriate scientific journal. Chapters 2, 3, 4, and 5, are in correct format for submission to <u>Herpetologica</u>. Chapter 6 is in correct format for submission to <u>The</u> <u>American</u> <u>Naturalist</u>.

GROWTH, ALLOMETRY, AND SEXUAL DIMORPHISM IN THE COLLARED LIZARD, CROTAPHYTUS COLLARIS (SAURIA: CROTAPHYTIDAE).

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Abstract: Possible proximate causes of sexual dimorphism, i.e., sexual differences in growth, allometry, and age distribution, were compared between two populations of collared lizards (Crotaphytus collaris) exhibiting significant differences in sexual dimorphism. There were slight differences between populations in growth and asymptotic size. The pattern of sexual differences in the allometry of various morphological characters also varied between sites. In most years at both sites there were no significant differences in age distribution between males and females, thus sexual size dimorphism in these populations is not simply due to sexual differences in mortality. At least some of the proximate mechanisms producing sexual dimorphism are genetically controlled and are subject to selection. This in turn suggests that differences in sexual dimorphism between these populations may be due to differences in selection.

Keywords: Crotaphytus collaris; Sauria; Crotaphytidae; growth, allometry, age distribution; sexual dimorphism; proximate mechanisms

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Numerous species of animals, both vertebrates and invertebrates, display striking differences in morphology between males and females. The sexes of many species differ in size, or color, or have different body shapes. The usual evolutionary conclusion is that the selective pressures acting upon males and females differ. Ever since Darwin (1871) discussed sexual dimorphism and introduced his hypothesis of sexual selection, numerous researchers have examined this question and many have advanced alternative hypotheses of explanation (Hedrick and Temeles, 1989; Maynard Smith, 1987). Primary focus has been on differences in selective pressures acting on the two sexes. However, the proximate mechanisms producing sexual dimorphism often have been overlooked. Sexual dimorphism may indeed be the result of sexual differences in selection, but may also be a more pedestrian result of local environmental conditions that favor the growth or survival of one sex over the other (Shine, 1990).

Careful elucidation of the proximate mechanisms involved is essential to any study of the evolutionary mechanisms producing sexual dimorphism. Although some proximate mechanisms are subject to selection, others are not. Sexual dimorphism may be a result of sexual differences in juvenile growth rates, age at maturity, growth after maturity, or, in many species, size at which growth slows or stops (Shine, 1990; Stamps, 1993), all of which may be determined by genetic differences subject to selection. However, some proximate mechanisms, such as growth rate, are not solely the result of genetics but are influenced by environmental factors such as temperature and food availability (Dunham, 1978; Sinervo and Adolph, 1989; Smith and Ballinger, 1994). Local environmental conditions and differences in energy budgets are known to produce sexual differences in growth rate (Woolbright, 1989).

Other proximate mechanisms may result in sexual dimorphism within a population in the absence of sexual differences in selection directly on a trait such as body size.

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Differences in mortality rates between the sexes and among populations have been shown to affect the degree of sexual size dimorphism (Andrews and Stamps, 1994; Gibbons and Lovitch, 1990; Stamps et al., 1994). Such differences in mortality could result in sexual size dimorphism where no selection for different sizes of males and females exists.

The collared lizard (Crotaphytus collaris) is a species that displays striking sexual dimorphism (Fitch, 1956; McCoy et al., 1994). Males in this species are larger and more brightly colored than females. Additionally there are sexual differences in body shape as well as size (McCoy et al., 1994). Not only does this species display sexual dimorphism, but the degree of sexual dimorphism, both in body size and in other morphological characters, varies significantly among populations from different geographic locations (McCoy et al., 1994).

The documentation of intraspecific variation is an important step in understanding the evolution of sexual dimorphism in a species, but the report of this phenomenon in C. collaris by McCoy et al. (1994) was based on a static sample and could not address many of the questions regarding the proximate causes of sexual dimorphism. Specifically, are there sexual differences in growth rates, size at sexual maturity, maximum adult size, age distributions, or allometric growth in other morphological characters? And since sexual dimorphism varies significantly among populations we must ask if any of these proximate mechanisms vary among populations. This study further examines two of the three populations reported on by McCoy et al. (1994) and addresses questions regarding the proximate mechanisms resulting in sexual dimorphism in these lizards.

Differences in growth are often cited as determinants of sexual dimorphism. Differences in both growth rate and maximum size may influence sexual dimorphism in a population. Although growth in reptiles continues after sexual maturity, most species grow very slowly as they approach some asymptotic size (Andrews, 1982). Growth in many reptile

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species is well modelled by some variation of the general equation introduced by Richards in 1956 (Andrews, 1982). Growth in several species of lizards is well described by the logistic-by-weight model (Andrews, 1982; Dunham, 1978; Schoener and Schoener, 1978; Stamps et al., 1994). This model provides a means of comparing growth rates, maximum size attained (asymptotic size), and size at which growth rate decreases. I used the logistic-by-weight growth model, fitted to data from two populations of collared lizards, to determine the effects of differences in growth on the observed pattern of sexual dimorphism.

The use of nonlinear models to describe growth within a population affords an opportunity to examine other hypotheses regarding the proximate cause of sexual dimorphism. Often a major question regarding sexual dimorphism is whether or not sexual differences in mortality may be responsible for the observed pattern. If there are sexual differences in mortality, and thus age distributions, the population studied may show sexual dimorphism, but in the complete absence of any sexual difference in selection directly on the character. Stamps et al. (1994) advanced an extension of the use of nonlinear growth models that allows the examination of hypotheses regarding age distributions. Stamps et al. (1994) demonstrated that once a nonlinear model is fitted to describe the growth of a population, the same model can be used in reverse to predict the age distribution of that population. If mortality is the same for both sexes, then similar age distributions would be expected.

There is ample evidence to suspect that mortality rates in C. collaris may differ for males and females. The strong aggressive response of adult male collared lizards to consexual intruders upon a territory (Fitch, 1956; Fox and Baird, 1992; McCoy, unpublished data; Yedlin and Ferguson, 1973) suggests that juvenile males may be restricted to less suitable habitats where they suffer increased mortality. Additionally, patrolling and display behaviors associated with the strong territoriality, along with brighter coloration (McCoy,

unpublished data), may result in greater exposure to predators for males than for females. These factors may result in higher mortality, especially among small males, which could produce sexual size dimorphism in a population. In this study I determine the extent to which sexual size dimorphism among collared lizards is a result of differential mortality.

Because C. collaris displays sexual dimorphism in other morphological characters, as well as body size, it is also necessary to examine the proximate determinants of sexual differences in these characters. If a species displays sexual dimorphism in a given morphological character, the question remains whether there is a sexual difference in that character at all body sizes or if the allometric growth of that character varies between the sexes. Analysis of allometry in sexual dimorphism requires measures of sexual dimorphism independent of body size. Residuals for males calculated from regression of various morphological characters against snout-vent length (SVL) for females provide just such measures (McCoy et al., 1994) and are used here to study differences between males and females in the allometric growth of multiple characters. Also, I examined differences in the allometry of sexual dimorphism between these populations.

The analysis of quantitative characters such as growth is intrinsically mathematical; however, it is important to remember that the hypotheses being tested are basically biological. What we wish to determine are the mechanisms which produce a biological phenomenon. In this paper I address the following questions: What are the differences in growth rates? Do the sexes grow to different sizes? Is the development of other morphological characters different? Finally, do these proximate mechanisms vary among populations?

Methods and Materials

Study Sites and General Methods

For this study, study sites were established in the Glass Mountains in northwestern Oklahoma (Major County) and on the Wichita Mountains National Wildlife Refuge in southwestern Oklahoma (Comanche County). The Glass Mountains site (GM) encompassed about 10 ha while the Wichita Mountains site (WM) was slightly smaller (about 6 ha). Collection of data in the field was conducted from mid-May to mid-August 1992 and 1993, which includes most of the annual activity period for adult collared lizards in this area. All of the lizards on both study sites were captured and marked with unique permanent toe clips and with acrylic paint markings on the dorsum. During the field season, lizards were recaptured as needed in order to replace their paint markings. Six morphological measurements were taken at each capture: 1) head width, 2) head length, 3) front leg length, 4) hind leg length, 5) tail length, and 6) snout-vent length (SVL). Tail length was not measured for those individuals showing evidence of tail loss. Measurements were taken to the nearest 0.1 mm with vernier calipers except SVL and tail length, which were measured to the nearest 0.5 mm with a ruler. Statistical analyses were conducted using the SYSTAT program (Wilkinson 1990). Several of the analyses in this study involved multiple related tests on a single sample and in such cases a sequential Bonferroni adjustment was used to support overall α levels (Rice, 1989). Because preliminary analyses revealed some significant differences between years at both sites, all analyses were conducted for each year separately.

Growth and Sexual Dimorphism in Body Size

To analyze differences in growth rates I used the logistic-by-weight growth model, which has been shown to provide a good fit for several species of lizards (Andrews, 1982;

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Dunham, 1978; Schoener and Schoener, 1978). Although mass was recorded at each capture,

I used SVL as a measurement of body size because it is less sensitive to variation in

temporary condition (i.e. hydration, stomach contents). For each lizard that had been

captured at least twice I calculated the interval between captures (in days) and SVL at the

beginning and end of that interval. These data were fitted to the logistic-by-weight model

using the interval formula provided by Schoener and Schoener (1978):

$$W_2 = aW_1 \,/\, [W_1 + (a-W_1)e^{-rD}]$$

where $\underline{a}$ = the asymptotic weight, $\underline{r}$ = the characteristic growth rate, $\underline{D}$ = time interval in

days, and $\underline{W}_1$ and $\underline{W}_2$ = weights at the beginning and end of the interval. However, rather

than simply assume a cubic relationship between length and mass, I converted all SVL

measurements to mass using the equation:

$$MASS = (c*SVL)^b$$

where $\underline{c}$ and $\underline{b}$ are constants (Niklas, 1994; Sexton et al., 1992; Stamps et al., 1994). These

constants were derived for males and females separately, for each year, for each site. The

logistic-by-weight model contains two parameters that describe the characteristic growth rate

($\underline{r}$), and the asymptotic maximum mass ($\underline{a}$) of the individuals being analyzed. The parameters

for this model were compared between sexes and between sites for both years by looking for

non-overlapping confidence intervals. Because two correlated parameters were fitted for this

model, I used support plane, or simultaneous, confidence intervals (Johnson and Wichern,

1992; Schoener and Schoener, 1978). Some lizards were measured more than twice during

one season and changes in SVL for these individuals over two or more intervals were

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included in the data used to fit the growth model. However, for calculation of confidence intervals, sample sizes were based on the actual number of individual lizards used, not the number of measurements taken.

Once the logistic-by-weight model was fitted for each group of lizards, I used these models to compare the age distributions of males and females at each site (Stamps et al., 1994). For these analyses, only one measurement for each lizard is required and I used the measurement taken nearest to 19 June. Actual dates of measurement ranged from 30 May to 9 July. The equation for the logistic-by-weight model was used to predict the age distributions of females in each group. The characteristic growth rates used in these analyses were obtained from the fitted growth models for each group. For the asymptotic size, however, I used the size of the largest individual in each sample (Stamps and Andrews, 1992). This procedure was used because individual variations in growth rates often produced a population estimate of asymptotic size slightly smaller than the largest individual. Since age could not be predicted using the logistic-by-weight model for an individual larger than the asymptotic size, I used the largest individual of a given sample as my estimate of asymptotic size. The use of nonlinear growth models to predict age also requires an estimate of size at hatching. For these analyses, I used the hatchling SVL of 40 mm reported by Fitch (1956). This size also agrees closely with other reports of hatchling SVL in C. collaris (Sexton et al., 1992). These age distributions of females were then used as null models for the age distributions of males. Using the fitted logistic-by-weight models for males, the size distributions of males were predicted from the null age distributions and compared to the observed size distributions. Size distributions were constructed by dividing the total range in SVL for a sample into 10 equal classes and counting the number of individuals within each size class. The predicted and actual size distributions of males were compared using two-

tailed Kolmogorov-Smirnov tests.

Sexual size dimorphism was also calculated from the actual and predicted size distributions of males as the ratio of average SVL for all males larger than the minimum size at sexual maturity divided by the average SVL for all females larger than the minimum size at sexual maturity. Minimum size at sexual maturity was determined for females at the minimum size at which enlarged ovarian follicles were detected by palpation and for males as the minimum size at which active femoral pores were observed. For both males and females from both populations, the minimum size at sexual maturity was 75 mm SVL. This size agrees closely with other reports for this species (Ballinger and Hipp, 1985; Fitch, 1956; Parker, 1973; Sexton et al., 1992; Trauth, 1978; Trauth, 1979). However, such ratio measures are biased estimators (Atchley et al., 1976; Packard and Boardman, 1988; review in Ranta et al., 1994) and were not used in any statistical comparisons. Rather, these ratio estimates of sexual size dimorphism are reported only for comparison.

The use of growth data collected only during the active season minimizes a confound due to seasonal differences in growth rates (Andrews, 1982; Dunham, 1978). Lizards living in highly seasonal environments such as in Oklahoma can hardly be expected to maintain constant growth trajectories over the entire year. Thus, fitting growth curves to actual ages of lizards introduces a confound in that during much of the year growth is not actually proportional to age since the lizards are inactive. Although there is probably some variation in growth rates from the beginning to the end of the activity season due to food availability and temperature regime, this variation is much smaller in magnitude than the total annual variation. However, when growth curves fitted in this manner are used in the type of growth-based comparisons of age distributions suggested by Stamps et al. (1994), the ages predicted do not actually represent the true ages of the lizards. Rather, these ages represent the number

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of days required to reach a given size if growth is always at the rate seen during the active season. Although this means that true ages cannot be predicted from growth models derived in this manner, this effect should be the same for both males and females and should have no bearing on comparisons between the sexes.

Allometry in Sexually Dimorphic Characters

Because collared lizards from these two sites show sexual dimorphism in characters other than body size, and these populations are significantly different in degree of dimorphism in several of these characters (McCoy et al., 1994), I wished to examine the development of sexual dimorphism in these characters and to compare patterns of development between these sites. Again, due to significant differences between years at both sites, all analyses were conducted separately for the two years. For lizards that were captured more than once during a season, one set of measurements was selected at random. Thus each individual lizard is used only once per year in these analyses.

The allometry of sexually dimorphic characters was first tested by calculating linear regressions of each character against SVL for females from each site. All the characters examined show a good linear relationship with SVL (all P's < 0.05). Such analyses are often conducted on log transformed measurements. However for my data, log transformation did not markedly improve the fit of the linear regressions. Untransformed data were used to simplify explanation of the results. Residuals were calculated for each male from these regressions for females. These residuals represent the difference in that character from the expected measurement of a female of the same size and thus are measures of sexual dimorphism in that character. First, I checked to see if these populations of lizards displayed sexual dimorphism in these characters. Sexual dimorphism is indicated if the mean of the

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residuals for males is greater than zero. This hypothesis was tested for each character using one-sample t-tests. More interesting questions regarding sexual dimorphism in these characters relate to the pattern of their development. For example, is the allometry of these characters different for males and females? Do these characters develop at different rates? How do the populations differ in development?

Sexual difference in allometric growth for various characters was evaluated by calculating regressions of residuals for males (residuals generated for males against the females' regressions; see above) against SVL of males. A positive slope for such a regression indicates that as males become larger the degree of sexual dimorphism in that character increases. Because I expect that sexual dimorphism will not decrease with size, I tested for significance of the slopes of these regressions using one-tailed t-tests. I then tested for differences between the sites by comparing the slopes of these regressions.

Results

Growth and Sexual Dimorphism in Body Size

Although there was some variation in growth rates and asymptotic sizes among these groups of lizards, none of these differences was statistically significant (Table 1). However, comparison of confidence intervals is a highly conservative approach for testing for differences between parameters, an approach made even more conservative in this study by using simultaneous confidence intervals. Additionally, although the logistic-by-weight model generally described the growth of these lizards very well, the fit of the model was substantially better for males than for females (corrected r^2's for males 0.879 - 0.942; for females 0.372 - 0.894). The decreased fit of the model for females is probably a result of energetic requirements for oogenesis, which may affect the rate of growth. In several cases

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the confidence interval predicted for males does not include the estimate of that parameter for females, although the very large confidence intervals for females result in overlap. (Note that the confidence intervals for asymptotic size reported in Table 1 are not symmetrical since they were estimated for mass and then converted to SVL using a nonlinear conversion.)

There are some general patterns that may be extracted from examination of the parameters for the logistic-by-weight growth models. In general, females displayed higher characteristic growth rates than males, especially in the WM population. Male lizards also displayed substantially larger asymptotic size than females from the same population, except during 1992 at GM. Male lizards in the WM population displayed asymptotic sizes substantially larger than any other group.

The use of null growth-based models shows that in general sexual size dimorphism in these populations is not the result of sexual differences in mortality or longevity. The size distributions of males actually observed were very similar to the size distributions that are predicted if males and females have the same age distribution (Figs. 1 and 2). Only at the GM site in 1993 were male lizards significantly larger than would be predicted from the age distribution of females (Table 2). Comparison of the actual and predicted size distributions of males at this site in 1993 shows that this difference was due both to a paucity of males in the smaller size classes and an excess of larger males. At the GM site in 1992, and at the WM site in both years, the actual and predicted size distributions of males were quite similar. These results indicate similar age distributions for males and females. My results also indicate that these age distributions are sensitive to differences in conditions between years. Although actual sexual size dimorphism was similar in both years at the GM site, the predicted sexual size dimorphism was much lower for 1993 (Table 2). Actual and predicted sexual size dimorphism were very similar for both years at WM, although both measures

were somewhat lower in 1993.

Allometry in Sexually Dimorphic Characters

The two populations of collared lizards displayed significant sexual dimorphism in head width, head length, front and hind limb length, and tail length (Table 3). For all five morphological characters examined, the means of residuals for males from regressions calculated for females were significantly greater than zero. This indicates that at any given body size (SVL), male lizards tended to have longer and wider heads, longer limbs, and longer tails. Using the residuals for males (as calculated above) as measures of sexual dimorphism, I regressed these residuals against SVL of the males in order to appraise the ontogeny of this dimorphism. Several characters showed significant linear trends (Table 4). Head length showed the most consistent trend with body size; regressions of sexual dimorphism in head length were significant for both populations in both years. Hind limb length also showed a fairly consistent pattern, with significant regressions against SVL at GM in 1992 and at WM in both years. The male WM lizards in 1992 showed increasing sexual dimorphism in all characters with increasing body size.

To examine population differences in allometry, I compared the slopes of these regressions between populations. Due to the differences in absolute body size between the populations, these comparisons were conducted using standardized residuals. In no character was there a significant difference between the populations in the development of sexual dimorphism. Thus, although there are differences between sites and between years in which characters display sexual differences in allometry, the allometric growth of a given character is fairly consistent across populations.

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Discussion

Although sexual dimorphism in C. collaris is influenced by environmental factors, these factors cannot explain all the sexual differences observed or the differences in sexual dimorphism between populations. Several proximate mechanisms contribute to the observed morphological differences between males and females in this species. There are sexual differences in growth rates, maximum (asymptotic) sizes, allometry, and in some cases, age distributions. Although most of these traits are subject to environmental influence, results of this study argue against explanations based on environmental factors alone.

Sexual differences in growth rates and asymptotic sizes, estimated from the logistic-by-weight growth model, strongly suggest a genetic component to sexual size dimorphism in this species. Although this analysis failed to reveal any statistically significant differences in these parameters, I found several consistent patterns of variation which suggest real differences in these lizards. Growth rates, which may be strongly influenced by environmental factors (Dunham, 1978; Grant and Dunham, 1990; Sinervo and Adolph, 1989), vary among sites and years but are generally higher for females than for males. In both years, despite substantial annual variation, the ratio of asymptotic size of males to the asymptotic size for females is much greater in the WM population. This observation is consistent with the description of greater sexual size dimorphism in the WM lizards in 1991 (McCoy et al., 1994). Although realized growth rate may be a result of environmental conditions, asymptotic size is almost certainly a function of both environmental and genetic factors. The relative consistency of these patterns suggests that despite variation due to immediate environmental conditions, certain aspects of growth in C. collaris remain fixed between the sexes and between these two populations.

The comparison of age distributions for males and females answers one of the most

serious arguments against differences in selection as an explanation for differences in sexual dimorphism. Theoretically, it is possible that sexual differences in mortality, which produce differences in age distributions, could result in sexual dimorphism in a population. Such an effect could result in sexual dimorphism where no selective pressures for size differences between males and females existed. There were no sexual differences in age distribution in the WM population, nor in the GM population in 1992. That such a difference existed in the GM population in 1993 suggests that age distributions in these lizards are subject to annual variations in environmental conditions. However, sexual dimorphism occurs in these populations even when age distributions of males and females are not different.

Comparisons of sexual difference in the allometry of various characters also argues against explanations based entirely on environmental factors. Certainly if growth is subject to variation due to environmental differences, such as food availability (Dunham, 1978; Smith and Ballinger, 1994), it is not unreasonable to expect that differences in allocation to various characters would likewise produce differences in allometry. Differences between years, especially the observation that the WM population displayed significant sexual differences in allometry for all characters examined in 1992, appear to demonstrate that such differences in allocation exist. However, some morphological characters displayed consistent patterns across sites and years. At both sites and in both years, despite variation in other characters, these lizards showed a consistent pattern of sexual differences in the allometry of head length. Hind limb length also showed a fairly consistent pattern, failing to reach statistical significance only at the GM site in 1993. Despite environmental variations, there appear to be genetic differences underlying the observed pattern.

Sexual dimorphism, and geographic variation in sexual dimorphism, in C. collaris is the result of a combination of genetic and environmental factors. Certain aspects of sexual

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dimorphism in this species, such as differences in growth rates and asymptotic sizes, probably have a genetic basis but are additionally influenced by environmental conditions. This conclusion is further supported by the demonstration that sexual dimorphism in these populations is minimally attributable to differences in age distributions. Whereas differences between years in the pattern of allometric development of sexually dimorphic characters suggests a role for environmental factors, consistency in the pattern of allometry in head length suggests that some characters are also under genetic influence. Since a genetic basis is implied and the pattern of sexual dimorphism cannot be explained by proximate environmental factors alone, my study calls for further work to elucidate the selective mechanisms resulting in sexual dimorphism in this species.

Clearly, any study purporting to examine the selective mechanisms producing sexual dimorphism should first examine the proximate causes of the observed phenomenon. Sexual dimorphism can certainly be the result of sexual differences in selection. However, sexual dimorphism may also result from environmental factors that are not subject to selection. Most proximate mechanisms producing sexual dimorphism are influenced by environmental factors but also include a genetic component, as appears to be true in C. collaris. This study underscores not only the importance of examining proximate mechanisms in studies of sexual dimorphism, but also the contention that Oklahoma collared lizards provide an opportunity to examine mechanisms causing the evolution of sexual dimorphism.

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Table 1. Parameters for logistic-by-weight growth model ($\underline{r}$ = characteristic growth rate, $\underline{a}$ = asymptotic length in mm) for collared lizards (Crotaphytus collaris) from Oklahoma. Entries indicate estimates for each parameter and 95% simultaneous confidence intervals in parentheses.

Sex	Parameter	Glass Mountains		Wichita Mountains	
		Year		Year	
		1992	1993	1992	1993
Male	$\underline{n}$	12	13	10	18
Male	$\underline{r}$	0.0186	0.0154	0.0180	0.0194
		(0.0056-0.0315)	(0.0005-0.0303)	(0.0074-0.0285)	(0.0137-0.0252)
Male	$\underline{a}$	95.1	101.3	106.1	109.2
		(88.2-101.2)	(96.1-106.1)	(95.9-114.8)	(104.0-113.9)
Female	$\underline{n}$	7	11	10	19
Female	$\underline{r}$	0.0173	0.0226	0.0270	0.0210
		(0.0-0.0475)	(0.0092-0.0360)	(0.0060-0.0480)	(0.0-0.0430)
Female	$\underline{a}$	100.2	94.4	89.8	97.4
		(0.0-141.67)	(89.0-99.4)	(81.4-97.3)	(80.2-109.8)

Table 2. Actual and predicted sexual size dimorphism (SSD) ratios for collared lizards from the Glass Mountains (GM) and the Wichita Mountains (WM) in 1992 and 1993, and results of Kolmogorov-Smirnov tests to compare actual and predicted size distributions for males. Sexual size dimorphism ratios are calculated as the average SVL of all sexually mature male lizards divided by the average SVL of all sexually mature female lizards.

Site	Year	No. Males	No. Females	Predicted SSD	Actual SSD	D Value[1]
GM	1992	19	14	1.01	1.06	0.33
GM	1993	19	18	0.93	1.07	0.73**
WM	1992	18	20	1.07	1.09	0.48
WM	1993	27	25	1.04	1.04	0.13

[1] Kolmogorov-Smirnov two sample tests: ** $P < 0.01$, two-tailed.

Table 3. Means ± 1 standard deviation of residuals for male $\underline{C}$. collaris from regressions of morphological characters against SVL calculated for females from the same population in the same year. All measurements are in mm.

	Glass Mountains		Wichita Mountains	
	1992	1993	1992	1993
Sample size ($\underline{n}$)	18	19	18	27
Head width	2.44 ± 1.24 *	1.99 ± 1.35 *	1.84 ± 2.16 *	1.21 ± 1.68 *
Head length	1.97 ± 1.31 *	1.79 ± 0.93 *	1.15 ± 1.55 *	0.94 ± 1.13 *
Front limb length	2.54 ± 1.85 *	1.42 ± 1.51 *	2.84 ± 3.43 *	1.63 ± 2.19 *
Hind limb length	4.16 ± 2.84 *	3.58 ± 3.09 *	5.18 ± 4.70 *	3.19 ± 4.29 *
Tail length[1]	13.16 ± 4.26 *	6.30 ± 4.02 *	10.20 ± 16.61 *	7.92 ± 8.63 *
	($\underline{n}$ = 16)	($\underline{n}$ = 16)	($\underline{n}$ = 14)	($\underline{n}$ = 26)

[1] Sample size for tail length is smaller than for other characters since individuals showing evidence of tail loss were not used for analysis of this character.

* Mean significantly different from 0 at $\underline{P}$ < 0.05 following sequential Bonferroni adjustment for multiple related tests. Single sample $\underline{t}$-tests, two-sided.

Table 4. Slopes of regressions of sexual dimorphism in various characters (using the residuals described in Table 3 as measures of sexual dimorphism) against SVL for male C. collaris from two Oklahoma populations.

	Glass Mountains		Wichita Mountains	
	1992	1993	1992	1993
Sample size (n)	18	19	18	27
Head width	0.046	0.052	0.107 *	0.034
Head length	0.094 *	0.040 *	0.073 *	0.039 *
Front limb length	0.090	-0.011	0.174 *	0.047
Hind limb length	0.213 *	0.036	0.117 *	0.206 *
Tail length[1]	0.207	0.060	0.797 *	0.206
	(n = 16)	(n = 16)	(n = 14)	(n = 26)

[1] Sample size for tail length is smaller than for other characters since individuals showing evidence of tail loss were not used for analysis of this character.

* Significant positive slope at $P < 0.05$ following sequential Bonferroni adjustment for multiple related tests. Single sample t-tests, one-sided.

Figure Legends

Figure 1. Actual and predicted size distributions of male collared lizards (Crotaphytus

collaris) from the Glass Mountains in Oklahoma during 1992 and 1993. Predicted size

distributions are generated from age distributions of females estimated from growth-based

models.

Figure 2. Actual and predicted size distributions of male collared lizards (Crotaphytus

collaris) from the Wichita Mountains in Oklahoma during 1992 and 1993. Predicted size

distributions are generated from age distributions of females estimated from growth-based

models.
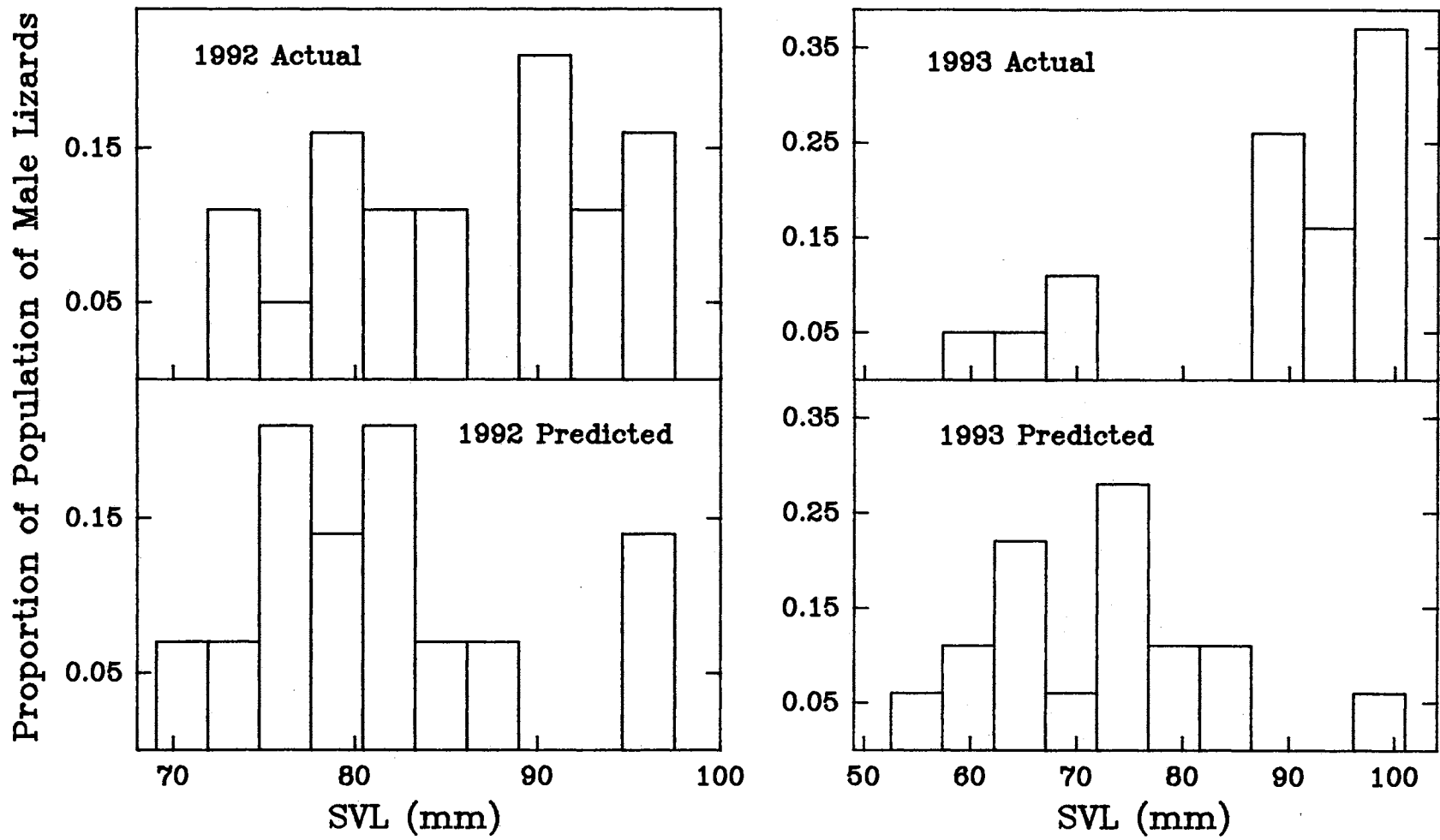
Figure 1
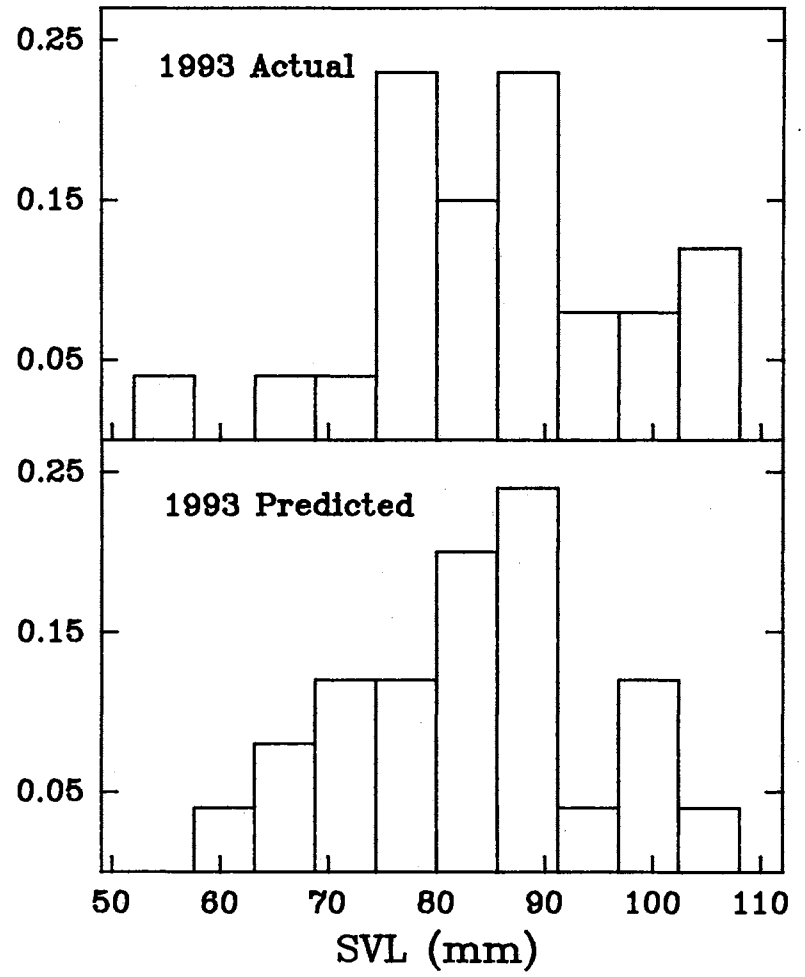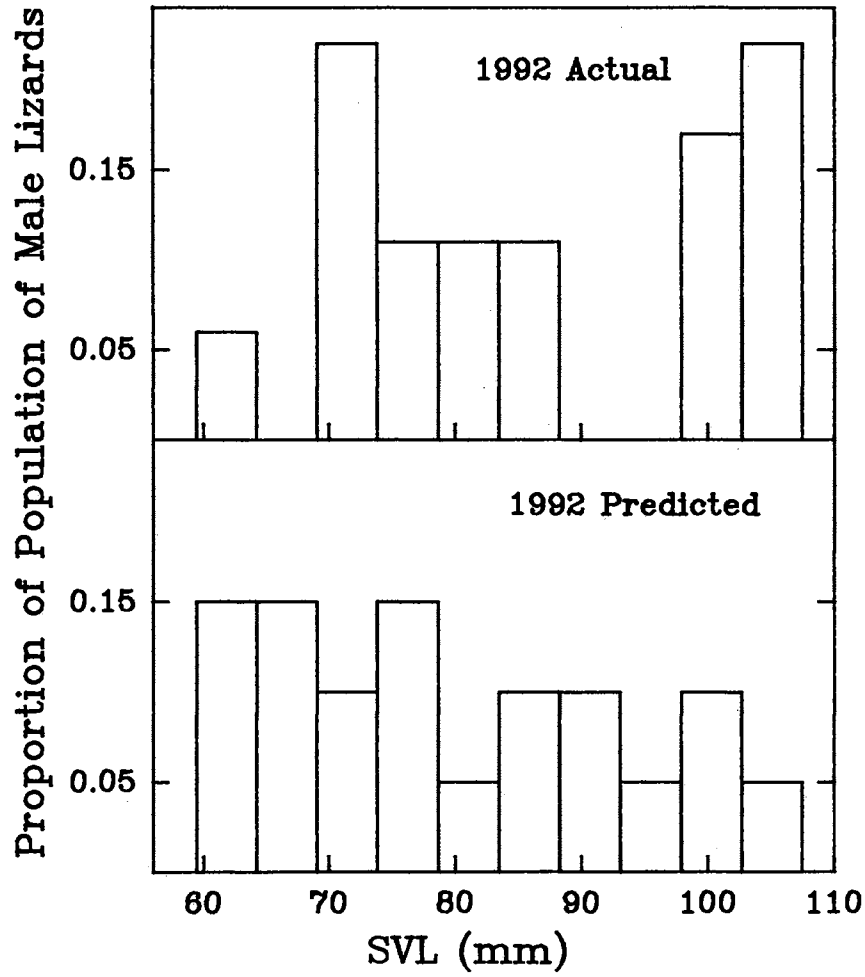
Figure 2

VARIATION IN SOCIAL BEHAVIOR IN TWO POPULATIONS OF THE COLLARED LIZARD, <u>CROTAPHYTUS</u> <u>COLLARIS</u> (SAURIA: CROTAPHYTIDAE).

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Abstract: Social behavior was compared between two populations of collared lizards (<u>Crotaphytus</u> <u>collaris</u>) that display significant differences in sexual dimorphism. Social behavior was examined using focal observations of behavior and an analysis of space use. This study revealed significant differences in space use and in the rates of various categories of behavior between these populations. There was also seasonal variation in the pattern of interpopulation difference in space use. Polygyny and sexual selection were greater in the more dimorphic population. Male-male competition (intrasexual selection) appears to be more important in these populations than mate choice by females (intersexual selection).

Few evolutionary hypotheses have received as much attention or debate as sexual selection to explain sexual dimorphism. Competition among males for access to mates (intrasexual selection) and the choice of potential mates by females (intersexual selection) have been the focus of an enormous amount of research. Despite the large volume of work, the relative importance of sexual selection, and other mechanisms that may result in the evolution of sexual dimorphism, remains controversial (Hedrick and Temeles, 1989). For many sexually dimorphic species, the selective mechanism producing the observed difference in morphology is not clear.

If sexual selection is operating within a population it should be possible to observe its effects not only on morphology, but on behavior as well. Males in populations where sexual selection is strong would be expected to display greater aggression than males not experiencing strong sexual selection. A difference in the degree of polygyny is also generally expected with a difference in sexual selection (Darwin, 1871; Ralls, 1977). Populations experiencing high levels of sexual selection would be expected to display greater polygyny and greater variance in male reproductive success than those subject to low levels (Wade, 1979).

Sexual dimorphism is widespread among lizards (Fitch, 1981; Stamps, 1983). Although several different models have been investigated as explanations of sexual dimorphism in lizards, sexual selection has been the mechanism most often invoked. Several studies have used direct behavioral observations to demonstrate the advantages accrued by larger males either in male-male competition or in mate choice (Anderson and Vitt, 1990; Cooper and Vitt, 1993; Vitt and Cooper, 1985). Other studies have examined the patterns of space use among lizards and inferred sexual selection from the relative sizes of male and female home ranges, and the number of home range overlaps between males and females and

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among males (Stamps, 1983).

To investigate the importance of sexual selection in the evolution of sexual dimorphism, I compared the social behavior of two populations of collared lizards (Crotaphytus collaris). Sexual differences in this species are generally striking (Fitch, 1956); the populations examined in this study show marked sexual dimorphism as well, but differ significantly in the degree of dimorphism (McCoy, 1995; McCoy et al., 1994; McCoy et al., in prep.). If differences in sexual selection explain this effect, it should be possible to demonstrate differences in social behavior between these populations. Social behavior was compared using both direct observations of behavioral interactions and by examination of the pattern of space use by lizards in these populations. These two methods for characterizing social behavior provide an estimate of the importance of sexual selection and some insight into the relative importance of intersexual and intrasexual selection.

Methods and Materials

Study Sites and General Methods

Observations were made on two populations of C. collaris from different areas of Oklahoma. Study sites were established in the Glass Mountains (GM) in northwestern Oklahoma (Major Co.) and in the Wichita Mountains National Wildlife Refuge (WM) in southwestern Oklahoma (Comanche Co.). The GM site encompassed about 10 ha in an area of gypsum outcrops at the top edges of steep buttes. The WM site was somewhat smaller (about 6 ha) but was in an area of extensive granite outcrops. Data for this study were collected between mid-May and mid-August 1992, 1993, and 1994. This period represents the majority of the activity season for adult collared lizards in this area. Both study sites were surveyed and numbered markers were placed every 10-15 meters. Scale maps of the study

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sites were prepared noting the location of each marker. The use of these scale maps allowed precise recording of the locations of lizards.

At both sites, all lizards were captured by noosing and marked for permanent identification using toe-clips and paint markings on the dorsum to allow identification at long range. Several morphological measurements were recorded at each capture. Lizards were recaptured as necessary to renew the acrylic paint markings. After each capture, lizards were released at the precise point of capture as soon as possible (usually within 1 hr) to minimize any influence on social behavior. Data were not collected on any lizard within 1 hr following its release.

Measurement of all lizards within these populations over three years allows me to make fairly accurate predictions of the age of lizards based on body size. Body size was measured using snout-vent length (SVL). These populations display significant differences in overall size as well as sexual size dimorphism (McCoy et al., 1994; McCoy, 1995), thus estimates of size at different ages varies among sites. Collared lizards typically lay eggs mid-to-late summer (June-September) and hatchlings emerge in late summer to early fall (Baird et al., in prep; Fitch, 1956; Sexton et al., 1992; Trauth 1978). All lizards were classified as either yearlings (lizards in their first full season) or adults (lizards at least 1 yr old in May). Ontogenetic changes in growth rates prevent accurate ageing of older lizards. At the GM site males greater than 85.0 mm SVL and females greater than 80.0 mm SVL were classified as adults. At the WM site, where lizards are generally larger, males greater than 90.0 mm SVL and females greater than 85.0 mm SVL were classified as adults. These sizes agree closely with other published reports (Baird et al., in prep.; Sexton et al., 1992). Although many lizards classified as yearlings attain sexual maturity during their first full season, other studies indicate that there are significant differences in social behavior between yearlings and adult

lizards, and yearlings likely mate little or not at all (Baird et al., in prep; Fitch, 1956). Although this study terminated before it was possible to determine the maximum life span of these lizards, several males that were classified as adults at the first capture in 1992 were still present at the end of the 1994 field season, indicating that the maximum life span of lizards on these sites is at least 4 years.

The social behavior of these lizards was analyzed using two distinct methods: space use based on point sightings of known individuals, and focal observations that recorded social interactions. The analysis of space use is based on data collected during 1992 and 1993 only, while focal observations were made in all three years of the study. This allows two distinct comparisons of social behavior between populations. All statistical analyses were conducted using the SYSTAT program (Wilkinson, 1990).

Space Use

Point locations of individuals were collected by walking slowly through the study site and scanning the area using binoculars. All individuals sighted during these censuses were identified using the acrylic paint markings or were captured for marking. Locations were recorded on the scale maps of the study sites. To avoid possible autocorrelation between consecutive sightings (Swihart and Slade, 1985), consecutive sightings for an individual were at least 1 hr apart and usually much more. Point locations recorded on these maps were converted to X-Y coordinates using a digitizing tablet. The coordinates of these sightings were then used to estimate home range size and the number and extent of overlaps between home ranges. Because space use may vary seasonally (Rose, 1982), the field season was divided into two sessions: mid-May to 18 June, and 19 June to mid-August. Space use was analyzed separately for these sessions. In addition to avoiding any confound owing to

temporal shifts in space use, this approach reduces the effect of behavioral differences during different reproductive seasons (Rose, 1982; Yedlin and Ferguson, 1973). Female $\underline{C}$. $\underline{collaris}$ in this area frequently lay two clutches of eggs each year. The division of the field season at 18 June corresponds to the average date of oviposition of the first clutch as determined by palpation of females.

Home range size was estimated using the minimum convex polygon method (MCP). In addition to the size of the home range, I calculated the number of other individuals with overlapping home ranges, both individuals of the same sex (NSS) and individuals of the opposite sex (NOS). Also calculated were the proportions of the home range area that were not overlapped by individuals of the same sex (PSSX) and individuals of the opposite sex (POSX).

Space use was analyzed only for lizards (principal subjects) that had been sighted at least five times within a session (session 1: $\bar{X}$ = 9.9, $\underline{s}$ = 4.7, range = 5 - 23; session 2: $\bar{X}$ = 10.3, $\underline{s}$ = 5.2, range = 5 - 30). Lizards that had been sighted at least three times were used in the calculation of overlaps and proportions of home ranges not overlapped for principal subjects and those sighted less often were included in the number of overlaps for principal subjects but were not used in the calculation of proportions of home ranges not overlapped. Although the use of lizards that had been sighted as few as five times may underestimate home range size (Rose, 1982), there were no significant differences between ages, sexes, or sites in the mean number of sightings per lizard (Mann-Whitney $\underline{U}$-tests, all $\underline{P}$'s > 0.05). Thus, while this approach may not yield accurate estimates of actual home range sizes, there should be no among group bias resulting from underestimation of home range size.

Because the social role of the home range is a complex function of area, the overlaps

with other individuals, and the amount of area exclusively defended (Rose, 1982; Stamps, 1983), I wished to compare space use considering all these variables. Differences between groups were evaluated with pairwise multivariate analyses of variance (MANOVA) using all five of the space use variables described above. For all tests the first and second session were considered separately. I first tested for sexual differences in space use at both sites. Then within each sex, at each site, I tested for differences in space use between adults and yearlings. For the first session at the GM site, age differences could not be tested due to the lack of data for yearlings during this time period. Because adults and yearlings of both sexes at both sites were not different in their space use (all P's > 0.05), I pooled adults and yearlings and compared the use of space for males and females separately between the two populations.

Focal Observations

In addition to inferences about social behavior drawn from analyses of space use, I directly examined social behavior using focal observations of known individuals. Focal observations were conducted by observing a known individual for 20 min and recording all behavior exhibited during that period. Focal observations were conducted only when substrate temperatures were between 35 and 40 C, which is within the range of optimal temperatures for $\underline{C}$. $\underline{collaris}$ (Fitch, 1956). Only one focal observation per day was conducted for any individual. Behavior was analyzed only for those lizards that had been observed for at least three 20-min periods in one year ($\bar{X}$ = 4.3, range = 3 - 9). Small sample sizes prevented division of the active season into two sessions as was done for analyses of space use (see above). During this study, at least 3 focal observations were conducted on a total of 79 lizards (GM: adult males, $\underline{n}$ = 12; yearling males, $\underline{n}$ = 8; adult females, $\underline{n}$ = 8; yearling

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females, n = 8; WM: adult males, n = 11; yearling males, n = 13; adult females, n = 10; yearling females, n = 7).

Social and aggressive behavior recorded during these observations was similar to that previously reported for this species (Carpenter, 1978; Fox and Baird, 1992; Yedlin and Ferguson, 1973). Although all behavior was recorded during focal observations, behavior was grouped into categories for analysis. Behavior such as pushups, head bobs, gular displays, and lateral displays was included in the category of display behavior (DIS). Aggressive behavior (AGG) was defined as all displays listed above plus biting, fighting, approaching, superimposing, or supplanting another individual of the same sex. Courtship behavior (COURT) was directed at individuals of the opposite sex and consisted mainly of the circling behavior described by Yedlin and Ferguson (1973), but also included superimpositions, copulations, and attempted copulations. Interactions with other individuals were classified as contact interactions if the lizards were within 1 m of each other. The total number of other individuals contacted during an interaction, both individuals of the same sex (SSCON) and the opposite sex (OSCON), was scored for each focal observation. Contact with consexuals was so rare (4 occurrences in all focal observations) that it was not possible to statistically analyze differences in this type of behavior. Averages were calculated for the other four variables (DIS, AGG, COURT, and OSCON) as the number of occurrences per focal observation for each individual lizard. Using the average rates of occurrence for these four behavioral variables, I used Mann-Whitney U-tests to compare social behavior between age classes (adults and yearlings) and between sites (pooling age classes when there were no significant differences) for both males and females. In each set of tests a sequential Bonferroni adjustment (Rice, 1989) was applied to support overall α levels when testing four variables on the same samples.

Results

Space Use

There were significant differences in space use between sexes for both sites in both sessions (MANOVA's, all $P << 0.05$), except during session 1 at the GM site ($P > 0.05$) where the sample size of females was very small ($n = 4$). Neither males nor females showed significant differences in the pattern of space use between yearlings and adults (all P's $>> 0.05$). After pooling adults and yearlings, I found significant differences between sites in the pattern of space use for each sex (Table 1). In session 1, males showed significant differences in space use while in session 2, females showed significant differences.

Males had much larger home ranges than females (Tables 2 and 3) and males from the WM population had larger home ranges than males at GM. In session 1, the differences between sites in home range size and the number of overlaps (both with consexuals and heterosexuals) for male lizards were substantial. Males from the GM site had smaller home ranges and overlapped fewer individuals of both sexes. In session 2, males in the GM site used larger home ranges and overlapped more individuals so the pattern of space use among males was more similar between sites. During session 2, the main difference between sites for females appeared to be a greater number of overlaps with consexuals at the WM site. Overall, lizards of both sexes appear fairly territorial, with means of from 61% to 100% of the home ranges not overlapped by consexuals. Although the proportion of the home range not overlapped was similar between the sites, the number of overlaps was generally greater at the WM site.

Focal Observations

The rates of various categories of behavior varied significantly among groups of

lizards, although there were no significant differences in any categories between adult and yearling females at either site (all $\underline{P} > 0.05$). There were significant differences between adult and yearling males at the WM site but not at the GM site (Fig. 1). Consequently, adults and yearlings were pooled for comparisons among sites, except for males at WM. Rates of different categories of behavior of all males from the GM population were compared to those of adult males from WM. Male lizards from the WM population displayed significantly higher rates of courtship behavior and contact with females than did males from the GM site (Fig. 2). Females displayed no significant populational differences in rates of behavior (Fig. 2). In general, male lizards at the WM site tended to show higher rates of displays, aggression, courtship, and opposite sex contact than males from the GM site (Table 4). At the WM site, adult males also showed higher rates of all these categories of behavior than yearlings. Females at both sites showed less variation in the rates of all behavior.

Discussion

Social behavior varies significantly between these two populations of collared lizards. Differences in sexual selection may be, at least in part, responsible for the observed differences in sexual dimorphism. The analysis of social behavior suggests that polygyny is greatest in the WM population, which is also the most dimorphic in body size and several other morphological characters (McCoy et al., 1994). The comparison of space use and the rates of various types of behavior indicate that sexual selection is also strongest in the WM population.

Numerous aspects of social behavior may be inferred from an analysis of space use. The size, use, and function of the home range are closely tied to the mating system and social organization of a population (Hixon, 1987; Stamps, 1977, 1983). In many polygynous mating

systems, males attempt to defend territories that encompass the home ranges of several females (Hixon, 1987; Stamps, 1983). In this situation the size of the home range of females is generally determined by the availability of resources, while the size of males' territories is limited by the energetic expense of defending the territory (Hixon, 1987; Stamps 1983). Females use home ranges that contain sufficient resources, while males maintain the largest possible territory. In some species females may also defend a portion of the home range as a feeding territory (Stamps, 1983). By comparing the sizes of home ranges, the degree of territoriality, and the number of overlaps with other individuals, it is possible to estimate the degree of polygyny and the relative strength of sexual selection.

Collared lizards from these populations (both males and females) displayed significant differences in space use during at least some parts of the active season. Early in the active season males displayed significant inter-populational differences. In the latter part of the season the space use of males was similar in the two populations but the space use of females varied significantly. Although the degree of territoriality, indicated by the proportion of the home range not overlapped by other individuals, was similar between sites for both sexes, the number of individuals overlapped was substantially greater in the WM population. Males in this population had more home range overlaps with individuals of both sexes than males from the GM population. Females from WM had more overlaps with individuals of both sexes than females at GM, but the most striking difference was in the number of female-female overlaps. Male lizards in the WM population had more overlaps with females than males in the GM population, but the number of overlaps with males was similar for females from both sites. This suggests that while polygyny was higher at the WM population, the potential for mate choice was similar.

Comparisons of rates of various categories of behavior obtained from focal

observations of lizards also supported the contention that sexual selection was stronger in the WM population. At the WM site there were significant differences in behavior between adult and yearling males, consistent with expectations for a highly polygynous mating system. Yearling males had much lower rates of display, aggression, courtship, and contact with females. No such ontogenetic difference in behavior existed at the GM site, where polygyny was not as great. Although no interpopulational differences were discovered among females in the rates of various categories of behavior, adult males from the WM population showed significantly higher rates of courtship and contact with females than males from the GM population. Also, the rates of displays and aggressive behavior were slightly higher among adult males from the WM population but the differences are not statistically significant. These differences suggest that polygyny was greater in the WM poplution.

This study also provides some indication of the relative strengths of intrasexual and intersexual selection. The suggested degree of territoriality and the high rates of display and aggressive behavior by adult males from both populations suggest that male-male competition is important in the mating system at both sites. Also, despite indications of a greater degree of polygyny at the WM site, females from both sites have home range overlaps with about the same number of males and display similar rates of courtship behavior and contact with males. This suggests that the potential for mate choice is similar in both populations. Intrasexual selection appears to be more important than intersexual selection in these two populations.

It is extremely interesting that although adult male lizards in both populations maintain home ranges of similar size (in the latter portion of the summer), apparently display similar levels of territoriality, and express roughly similar rates of displays and aggressive behavior, this suite of competitive behavior is more effective in garnering additional mating opportunities for males in the WM population. Males at both sites appear to be acting as

"area maximizers" (Hixon, 1987; Stamps, 1983) and maintain home ranges much larger than those of females. The small size of the home ranges of females shows that sufficient resources are available in a much smaller area than is used by males. These male "super-territories" (Stamps, 1983) are almost certainly an attempt to gain breeding access to as many females as possible. This strategy is apparently less effective at the GM site, perhaps due to lower density of females or to differences in habitat geometry. The rock outcrops inhabited by collared lizards are extensively distributed at WM, but at GM, outcrops are arranged almost linearly along the top edges of steep buttes. Habitat geometry has been shown to be an important factor in determining the cost of territoriality (Stamps et al., 1987). It is possible that the spatial arrangement of habitat in this area limits the number of females whose home ranges can be encompassed by a single male. It is clear that male lizards at the WM site have the potential for greater polygyny and stronger sexual selection. This difference in sexual selection may explain much of the variation in sexual dimorphism between these populations.

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Table 1. Results of comparisons of space use between two Oklahoma populations of collared lizards (Crotaphytus collaris) using MANOVA. MANOVA's calculated on home range size, number of overlaps with each sex and proportion of home range exclusively defended against each sex.

Sex	Session	df	Wilks' λ	$\underline{F}$	$\underline{P}$
Male	1	5, 17	0.4769	3.762	0.018
Male	2	5, 34	0.8479	1.220	0.321
Female	1	5, 8	0.6408	0.897	0.526
Female	2	5, 25	0.5840	3.561	0.014

Table 2. Space use characteristics of collared lizards (Crotaphytus collaris) from the Glass Mountains in Oklahoma. (Means ± 1 standard deviation for five space use variables as defined in the text.)

				Space use variable				
Sex	Session	Age	n	MCP	NOS	NSS	POSX	PSSX
Male	1	Yearling	0	-	-	-	-	-
		Adult	8	1034.4 ± 626.1	0.88 ± 0.83	0.75 ± 0.46	0.82 ± 0.29	0.97 ± 0.06
	2	Yearling	7	1352.6 ± 1305.1	1.0 ± 0.58	2.43 ± 0.53	0.94 ± 0.60	0.70 ± 0.26
		Adult	14	2042.8 ± 1313.2	1.50 ± 0.94	2.14 ± 0.95	0.84 ± 0.14	0.65 ± 0.29
Female	1	Yearling	0	-	-	-	-	-
		Adult	4	465.0 ± 520.7	1.25 ± 0.50	0.50 ± 0.58	0.48 ± 0.40	0.97 ± 0.27
	2	Yearling	7	371.0 ± 235.2	2.0 ± 0.58	0.14 ± 0.38	0.10 ± 0.14	0.99 ± 0.02
		Adult	8	377.9 ± 304.9	1.88 ± 0.99	0.25 ± 0.46	0.40 ± 0.39	0.97 ± 0.07

Table 3. Space use characteristics of collared lizards (Crotaphytus collaris) from the Wichita Mountains in Oklahoma. (Means ± 1 standard deviation for five space use variables as defined in the text.)

Sex	Session	Age	n	Space use variable				
				MCP	NOS	NSS	POSX	PSSX
Male	1	Yearling	5	2784.9 ± 2071.0	1.80 ± 1.48	3.40 ± 0.55	0.93 ± 0.11	0.61 ± 0.21
		Adult	10	2386.8 ± 2147.7	1.90 ± 0.99	2.10 ± 1.85	0.91 ± 0.11	0.70 ± 0.34
	2	Yearling	13	2223.2 ± 1548.2	2.31 ± 2.25	3.00 ± 2.04	0.83 ± 0.22	0.62 ± 0.24
		Adult	6	2459.0 ± 2130.9	2.33 ± 1.37	2.50 ± 1.38	0.71 ± 0.24	0.75 ± 0.25
Female	1	Yearling	6	134.8 ± 116.2	1.33 ± 0.82	0.33 ± 0.52	0.37 ± 0.47	0.94 ± 0.11
		Adult	4	408.8 ± 370.1	2.25 ± 1.50	0.00 ± 0.00	0.19 ± 0.24	1.00 ± 0.00
	2	Yearling	11	713.9 ± 763.4	2.18 ± 1.60	1.55 ± 1.29	0.20 ± 0.30	0.64 ± 0.30
		Adult	5	493.0 ± 700.4	1.60 ± 1.14	0.80 ± 1.30	0.63 ± 0.41	0.89 ± 0.20

Table 4. Average rates per 20-min focal observation of categories of behavior (means $\pm$ 1 standard deviation) (categories defined in text) for collared lizards (Crotaphytus collaris) from two Oklahoma populations.

Site	Sex	Age	n	Behavior category			
				DIS	AGG	COURT	OSCON
GM	Male	Yearling	8	3.3 $\pm$ 3.1	3.4 $\pm$ 3.1	0.4 $\pm$ 0.7	0.0 $\pm$ 0.1
		Adult	12	5.4 $\pm$ 4.1	5.5 $\pm$ 4.1	0.4 $\pm$ 0.7	0.0 $\pm$ 0.1
	Female	Yearling	8	4.1 $\pm$ 5.1	4.2 $\pm$ 5.1	2.4 $\pm$ 2.2	0.3 $\pm$ 0.3
		Adult	8	1.4 $\pm$ 1.4	1.4 $\pm$ 1.4	1.5 $\pm$ 1.7	0.3 $\pm$ 0.2
WM	Male	Yearling	13	2.3 $\pm$ 2.8	2.3 $\pm$ 2.9	0.5 $\pm$ 1.0	0.1 $\pm$ 0.1
		Adult	11	6.9 $\pm$ 6.9	7.2 $\pm$ 7.1	2.1 $\pm$ 2.1	0.4 $\pm$ 0.3
	Female	Yearling	7	0.4 $\pm$ 0.4	0.4 $\pm$ 0.4	0.3 $\pm$ 0.9	0.1 $\pm$ 0.2
		Adult	10	2.3 $\pm$ 2.7	2.5 $\pm$ 2.8	1.4 $\pm$ 2.4	0.2 $\pm$ 0.3

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Figure Legends

Figure 1. Comparison of rates of categories of behavior (defined in text) estimated from focal observations between adult and yearling male collared lizards (Crotaphytus collaris) from two Oklahoma populations. Significant differences at an overall $\alpha = 0.05$ using Mann-Whitney U - tests and a sequential Bonferroni adjustment are indicated by *.

Figure 2. Comparison of rates of categories of behavior (defined in text) estimated from focal observations between collared lizards (Crotaphytus collaris) from two Oklahoma populations. Significant differences at an overall $\alpha = 0.05$ using Mann-Whitney U - tests and a sequential Bonferroni adjustment are indicated by *.

Figure 1
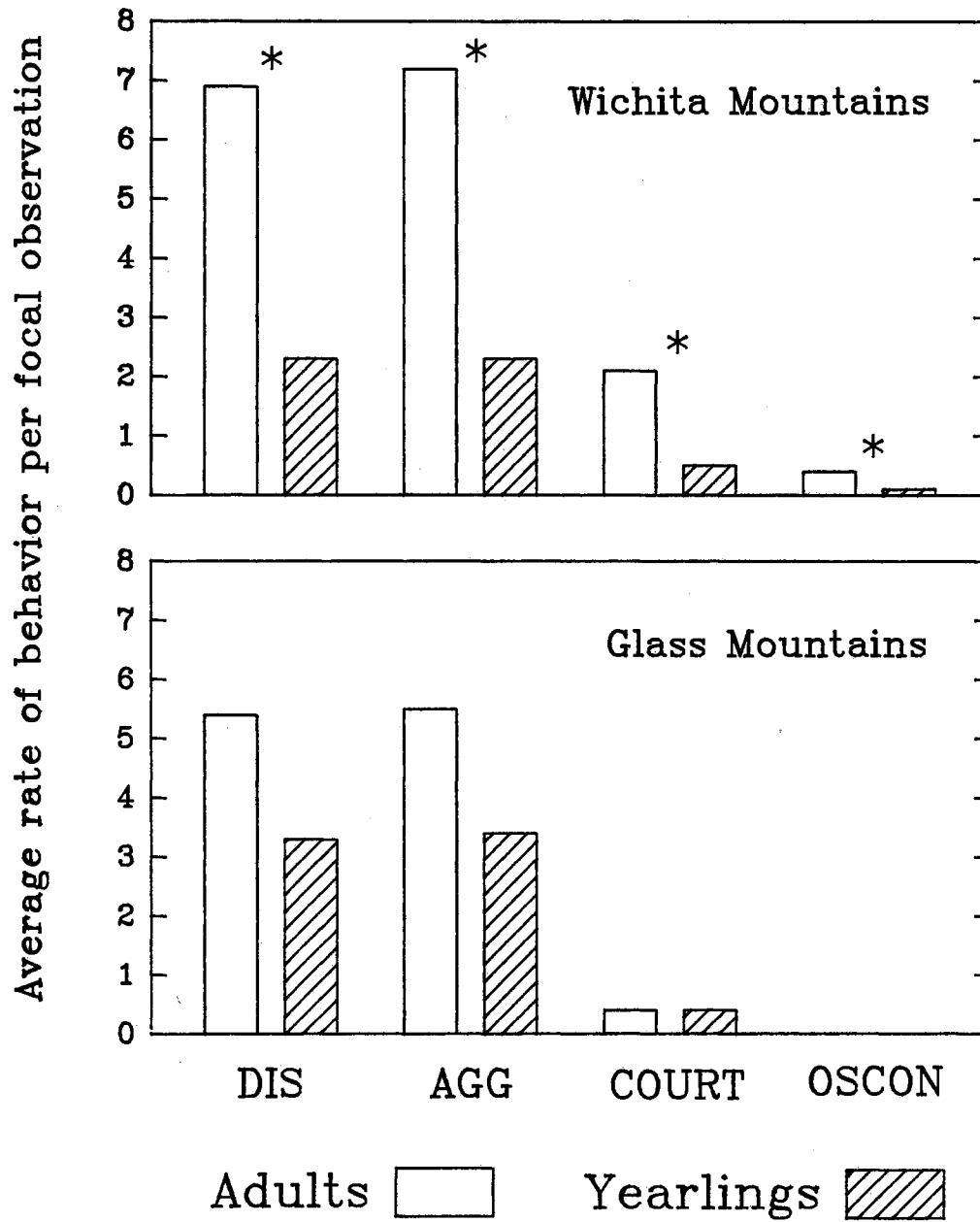
Figure 1
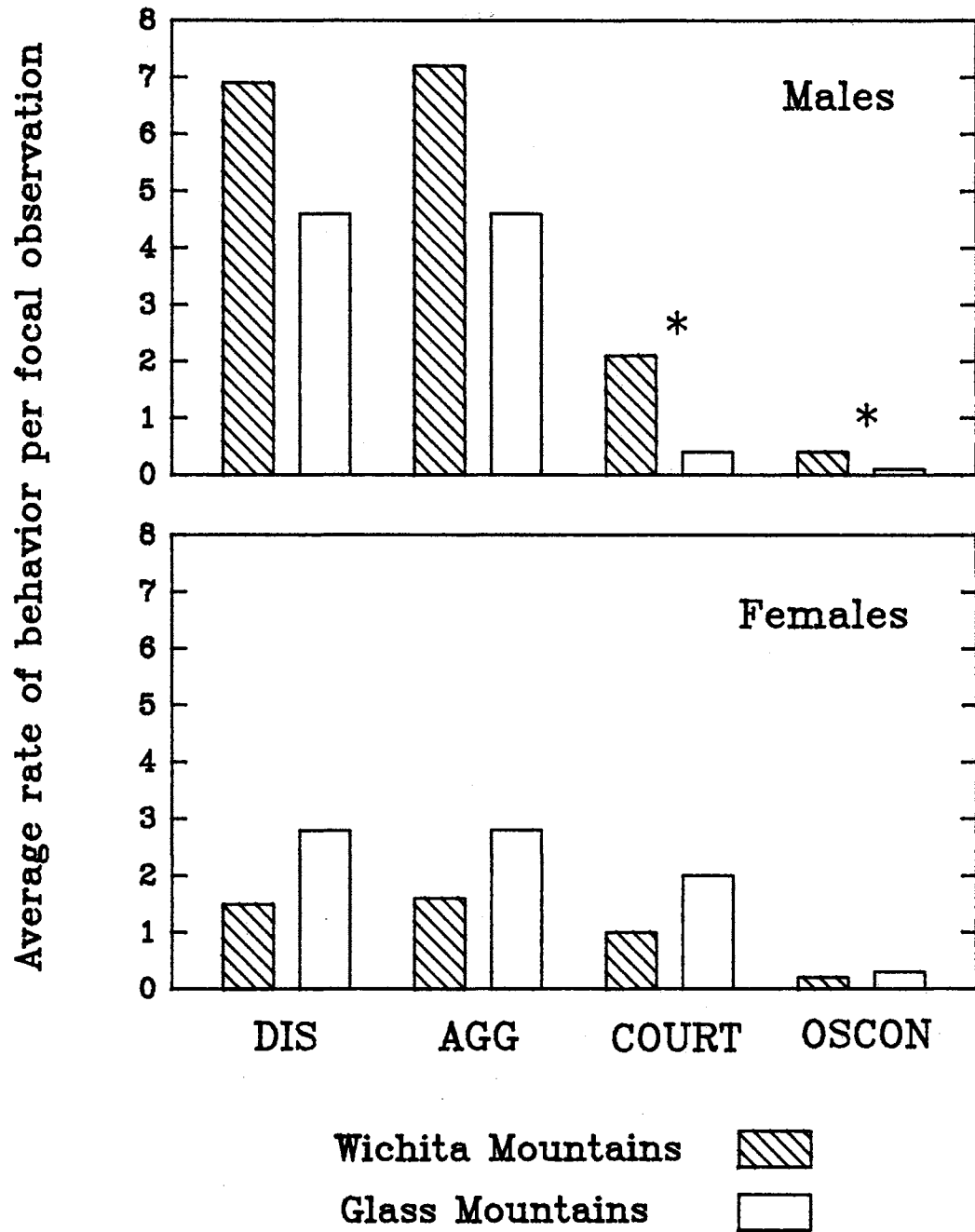
Figure 2

MALE REPRODUCTIVE SUCCESS AND SEXUAL DIMORPHISM IN THE COLLARED LIZARD, CROTAPHYTUS COLLARIS (SAURIA: CROTAPHYTIDAE)

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Abstract: I examined sexual selection in collared lizards (Crotaphytus collaris) from two Oklahoma populations that display significant differences in sexual dimorphism. The mosaic nature of the degree of sexual dimorphism in various characters exhibited by these populations suggests complex differences in the strength of sexual selection on various characters. Correlations and stepwise regressions between male reproductive success and morphological characters show interpopulation differences regarding which characters best explain variance in male reproductive success. Although male reproductive success, and variance in male reproductive success, are greatest in one population, the other population displays stronger sexual selection for male coloration and certain morphological characters.

Key words: Crotaphytus collaris; Sauria; Crotaphytidae; sexual dimorphism; reproductive success; lizard; Oklahoma

Introduction

Natural selection is perhaps the most basic tenet of evolutionary biology. Most biological theory is premised upon the assumption that those individuals whose genotypes define the greatest adaptation to the environment will leave more offspring than individuals not similarly endowed. This differential contribution of offspring to succeeding generations is often effected through improved survivorship or greater competitive abilities. However, in the case of sexual selection, differential fitness is a result of differences in characters that directly influence mating success (Darwin, 1871; Andersson, 1994). Sexual selection acts to promote those characters that confer an advantage either in intrasexual competition for access to mates or in intersexual attractiveness. Sexual differences are inherent in this process, which often leads to morphological differentiation between the sexes (sexual dimorphism).

If natural selection is indeed operating within a population we should be able to detect its effects, and much research effort has been devoted towards this end. The most common approach has been to estimate the mean value (or variance) of some character, or suite of characters, before and after some episode of selection. This technique allows estimation of selection gradients that measure the strength of selection on various characters (Arnold and Wade, 1984a; 1984b; Lande and Arnold, 1983). Using this approach, the effect of natural selection has been demonstrated on morphological characters (Fox, 1975) as well as behavioral traits (Fox, 1978; Fox, 1983).

Implicit in the demonstration of selection by examination of a population before and after some selection event, but within one generation, is the concept that selection involves differential survival. Natural selection, however, is a process not just of differential survival, but also (and ultimately) of differential reproduction. This integrative aspect of selection can be demonstrated by examining changes within a population across generations. For some

organisms with very short generation times (e.g. Drosophila), this has proven to be a highly fruitful approach. For many organisms, however, the logistics of following a population across several generations usually make such an approach untenable.

The demonstration of sexual selection is a bit different. Because sexual selection explicitly involves selection as a result of differential reproductive success, differences in reproductive success alone are often used as demonstration of sexual selection (Andersson, 1994; Wade, 1987). Numerous studies of various taxa, including fish (Endler, 1983; 1988), amphibians (Howard, 1980; 1981; 1988), snakes (Madsen and Shine, 1991), and lizards (Cooper and Vitt, 1988; Hews, 1990; Ruby, 1981; 1984; Vitt and Cooper, 1985), have shown the operation of sexual selection through such means. All of these studies demonstrated clear correlations between reproductive success and certain morphological or behavioral characters of males, indicating the importance of sexual selection in the evolution of sexual dimorphism in these characters.

Though many studies of sexual selection and differential reproductive success have focused on a single character (or suite of characters), the action of sexual selection is by no means confined to a single morphological character. The action of sexual dimorphism also may not be uniform across populations. Some studies (e.g. Endler, 1988) have indicated interpopulational differences in sexual selection but have dealt with fairly simple models wherein male reproductive success was correlated (to a greater or lesser degree) with a single suite of correlated characters.

The intent of this study is to examine sexual selection and male reproductive success in a somewhat more complex system. Using behavioral observations I estimated reproductive success for male collared lizards from two geographically separate populations within Oklahoma, and compared the strength of sexual selection on morphology and color. These

populations exhibit significant differences in sexual dimorphism in color, body size, and other morphological characters (McCoy, 1995a, McCoy et al., 1994; McCoy et al., in prep.); but do not represent a simple case of greater sexual dimorphism at one location and less sexual dimorphism at the other. Rather, these populations display a complex mosaic in the degree of sexual dimorphism in various characters. The population of lizards from the Wichita Mountains, in southwestern Oklahoma, displays greater sexual dimorphism in body size and several other characters, while the population from the Glass Mountains, in northwestern Oklahoma, is more dimorphic in color and in head length.

This complex pattern of interpopulational differences in sexual dimorphism presents a unique opportunity to study the action of sexual selection. Several hypotheses to explain these interpopulational differences are also suggested. It is possible that sexual selection is not responsible for the evolution of sexual dimorphism in some of these characters (in one or both populations). Such characters would show no correlation with reproductive success. It is also possible that the strength of sexual selection acting upon a given character varies between populations, and since several characters are involved, the interpopulational differences in strength of selection could vary among characters. Examination of sexual selection in these populations should distinguish which of these hypotheses accounts for the observed interpopulational differences in sexual dimorphism in various characters, thereby advancing our understanding of this evolutionary phenomenon.

Methods and Materials

For this study I observed two populations of C. collaris from different geographic areas of Oklahoma. Two study sites were established, one in the Glass Mountains (GM) in northwestern Oklahoma (Major Co.) and one in the Wichita Mountains National Wildlife

Refuge (WM) in southwestern Oklahoma (Comanche Co.). The GM site encompassed about 10 ha in an area of gypsum outcrops at the top edges of steep buttes. The WM site was somewhat smaller (about 6 ha) but was in an area of extensive granite outcrops. Data were collected between mid-May and mid-August 1993. This period represents the majority of the activity season for adult collared lizards in this area. Both study sites were surveyed and numbered markers were placed every 10-15 meters. Scale maps of the study sites were prepared noting the location of each marker. The use of these scale maps allowed precise recording of the locations of lizards.

At both sites, all lizards were captured by noosing, sexed, and marked for permanent identification using toe-clips and acrylic paint markings on the dorsum to allow identification at long range. Several morphological measurements were recorded at each capture. Lizards were recaptured approximately every two weeks to renew the paint markings and to determine by palpation the reproductive state of females. After each capture, lizards were released at the precise point of capture as soon as possible (usually within 1 hr) to minimize any influence on social behavior. Data were not collected on any lizard within 1 hr of its release even though lizards appeared to resume normal activity immediately after their release.

These populations have been observed for three years as part of a larger study on the ecology of this species and measurements of all individuals over this time span allow me to make fairly accurate prediction of the age of lizards based on snout-vent length (SVL). The populations display significant differences in overall size as well as sexual size dimorphism (McCoy, 1995a; McCoy et al., 1994), thus estimates of size at different ages varies among sites. Collared lizards typically lay eggs mid-to late summer (June-September) and hatchlings emerge in late summer to early fall (Baird et al., in prep; Fitch, 1956; 1967; Sexton et al., 1992; Trauth, 1978). All lizards were classified as either yearlings (lizards in their first full

season) or adults (lizards at least 1 yr old in May). Ontogenetic changes in growth rates prevent accurate ageing of older lizards. At the GM site males greater than 85.0 mm SVL and females greater than 80.0 mm SVL in May were classified as adults. At the WM site, where lizards are generally larger, males greater than 90.0 mm SVL and females greater than 85.0 mm SVL in May were classified as adults. These sizes agree closely with other reports (Baird et al., in prep; Fitch, 1967; Sexton et al., 1992). Although lizards classified as yearlings attain sexual maturity during their first full season, other studies indicate that there are significant differences in social behavior between yearling and adult lizards; if adult males are present, yearling males likely mate little or not at all (Baird et al., in prep; Fitch, 1956, 1967; McCoy, 1995b).

Point locations of individuals were collected by walking slowly through the study site and using binoculars to scan the area. All individuals sighted during these censuses were identified using the paint markings or were captured for marking. Locations were recorded on the scale maps of the study sites. To avoid possible autocorrelation between consecutive sightings (Swihart and Slade, 1985), consecutive sightings for an individual were at least 1 hr apart and usually much more. Point locations recorded on these maps were converted to X-Y coordinates using a digitizing tablet. The coordinates of these sightings were then used to estimates home ranges using the minimum convex polygon method, and the number and extent of home range overlaps between males and females.

Fecundity of each female was estimated from regressions of clutch size vs. SVL. The clutch size-SVL regression for the GM population was estimated from a sample of females collected from an area near the study site. Females examined from the WM population were specimens in the Oklahoma State University Department of Zoology Vertebrate Collection (OSUS) from that locality. All females were collected during May and June and autopsied to

determine the number of yolked follicles or oviductal eggs. If no oviductal eggs were present, follicles greater than 8 mm in diameter were counted. These regressions provide estimates only for the first clutch during the summer. For those females that produced two clutches (see below), the size of the second clutch was estimated at 94% of the clutch predicted from the regressions. This corresponds to the average change in clutch size reported by Trauth (1978) for 12 collared lizards that produced two clutches during one season.

Because the active season of collared lizards comprises two distinct bouts of reproductive activity (Fitch, 1967; Trauth, 1978, 1979), I divided the season into two sessions: mid-May to 18 June, and 19 June to mid-August. In the populations examined, most adult females produce a clutch of eggs early in the summer that are oviposited during mid-June. During the later part of the summer many of the yearling females attain reproductive maturity and produce a clutch of eggs that are oviposited late-June to mid-August. Some of the adult females also produce a second clutch of eggs during the second half of the activity season. Repeated captures of all females and determination of reproductive state by palpation allowed me to distinguish which females produced a clutch of eggs during each session and whether this was the first or second clutch for that female. Thus, female reproductive output was estimated for the first and second sessions separately.

Male reproductive success was also estimated for the first and second sessions separately, and then for those males present during both sessions, for the entire summer. I estimated male reproductive success by assigning the reproductive output of each female to those males whose home ranges overlapped the home range of that female (Ruby, 1984). Home ranges and overlaps were estimated for each session separately. The division of the active season into two sessions not only allows separate estimates of reproductive success

from each of the two bouts of reproductive activity, but avoids any confound owing to temporal shifts in home range (Rose, 1982). Reproductive success was estimated only for males that had been sighted at least five times within a session. In those cases where the home range of a female was overlapped by more than one male, the total area of home range overlap with all males was determined and the reproductive output of that female was divided and assigned to those males in the same proportions as the area of overlap with each male. This approach yields probabilities of male reproductive success rather than specific predictions of exact numbers of offspring, so estimates of reproductive success for both males and females were not rounded off to integer values.

In the GM population there are no significant differences in social behavior between adult and yearling males (McCoy, 1995b), suggesting that reproductively mature yearling males may also have some reproductive success. However, in this population there were no yearling males that had been sighted frequently enough to estimate reproductive success. In the WM population yearling males display significantly lower rates of courtship behavior and contact with females than do adult males (McCoy, 1995b), indicating that yearlings in this population are unlikely to mate with females. But, three of the adult males in this population disappeared within one week of 18 June (possibly victims of predation by a large Masticophus flagellum frequently sighted on the study site). Six males classified as yearlings expanded their home ranges into the area vacated by these adults and displayed increased rates of interaction with the females in this area. These yearlings had attained SVL's of at least 90 mm by this time and were reproductively mature. Reproductive success for these six males was estimated for the second session and for the entire summer (although they had no fitness during the first session). For the three adult males that disappeared, reproductive success was estimated for the first session but not for the entire summer.

These estimates of male reproductive success were then compared to variation in phenotypic characters using Spearman's rank-order correlations and stepwise monotonic regressions based on ranks (Conover 1980) to determine those combinations of characters that best explain the observed variation in reproductive success. Six morphological characters were used in these analyses: SVL, head width, head length, front limb length, hind limb length, and tail length -- all characters in which these populations display significant sexual dimorphism (McCoy, 1995a; McCoy et al., 1994). Because most lizards were measured more than once per season, for each lizard I used that set of measurements taken nearest 18 June. All of these morphological characters are substantially correlated (all characters are significantly correlated in the WM population: Pearson's correlations, all $\underline{P}$'s < 0.05), so to avoid problems resulting from multicollinearity (Neter et al., 1989), I used a principal components analysis (PCA) to reduce the dimensionality of the data set and to produce a set of uncorrelated variables describing morphological variation in these lizards. Principal components analysis was conducted using adult male lizards from both sites and PCA scores were used to test the relationships between morphology and reproductive success. A number of male lizards that were not used in the estimates of the reproductive success were included in the PCA to better describe the variation in morphology.

Variation in color was compared to reproductive success in a similar manner but separately from other phenotypic characters. Color hue, value, and chroma, of each lizard were appraised in the field using Munsell® Color Charts for Plant Tissues (MacBeth Division, Kollmorgen Instruments Corporation) (Zucker, 1988). The body temperatures of all lizards were between 35 and 40 C when color was appraised. Color was quantified at three places on the body: gular, dorsolateral, and ventrolateral. For analysis I converted hue to a continuous variable by ordering the Munsell color categories spectrally along a 100-unit scale.

Munsell value and chroma are already continuous variables. Again, these variables are substantially correlated, so PCA was conducted on the nine color variables to produce a set of uncorrelated variables that explain the color variation among male lizards from these two populations. The scores from this PCA were then used to determine the importance of various aspects of color to male reproductive success. All statistical analyses were conducted using the SYSTAT program (Wilkinson, 1990).

Results

For females from both populations there was a highly significant relationship between clutch size and SVL (Fig. 1). These significant regressions indicate that SVL is a good indicator of fecundity for females from these populations. Male reproductive success, for both sessions and for the entire summer, was greater in the WM population than in the GM population (Table 1). During the second session this difference was statistically significant (Mann-Whitney U - test, $P < 0.05$). Variance in male reproductive success was also higher at the WM site (Table 1), although not statistically significant.

For the PCA calculated for morphological characters, the first three principal components explained 87.3 % of the total variance (Table 2). The first principal component was a general size factor; head length had the largest loading on this component, although SVL, head width, and both limb lengths also had fairly large loadings. The second principal component was mainly a tail length factor with all other characters having small loadings. The third principal component appeared to be a limb length factor. Both limb lengths had larger loadings on this component than any other character.

Spearman's rank-order correlations revealed a strong relationship between the first principal component (general size factor) and reproductive success during the first session at

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the GM site (Table 3). Male reproductive success in the WM population was most strongly

correlated with the second and third principal components (tail and limb length factors,

respectively). There were no significant correlations between reproductive success and

morphology during the first session at WM, during the second session at GM, or at either site

for the entire summer.

Stepwise regressions of morphology on male reproductive success showed that in the

GM population only the first principal component explained a significant proportion of the

variance, and only for the first session (reproductive success = 0.825*PC1 + 0.875, F =

15.32, df = 1 and 7, P = 0.006, percent of variance explained = 68.6 %). During the

second session, and for the entire summer, stepwise regression produced no significant models

for the GM population. In the WM population the second and third principal components

were included in models that explain significant amounts of the variance in male reproductive

success during the second session and for the entire summer (second session: reproductive

success = 0.487*PC2 + 0.665*PC3 - 0.837, F = 10.74, df = 2 and 7, P = 0.007, percent

of variance explained = 75.4 %; entire summer: reproductive success = 0.552*PC2 +

0.524*PC3 - 0.418, F = 6.39, df = 2 and 7, P = 0.026, percentage of variance explained

= 64.6 %). No significant model was found to explain variance in reproductive success

during the first session at the WM site.

Analysis of the principal components of variation in color in male collared lizards

showed that the first five principal components explained 86.0% of the total variance in color

(Table 4). The first principal component, with large loadings for value and chroma in both

the ventral and gular areas reflected the intensity of coloration in these areas. The second

principal component was mainly spectral, with highest loadings for the hue of the ventral and

dorsal areas. Intensity of coloration in the dorsal area was represented by the third principal

component, which had substantial loadings for both dorsal value and dorsal chroma. The variable which loaded most heavily on the fourth principal component was the hue of the gular region. Only dorsal hue had a large loading on the fifth principal component, indicating that this component was mainly reflective of the spectral value in this region of the body.

Examination of correlations between the principal components describing color and male reproductive success revealed no distinct patterns. After sequential Bonferroni adjustments for multiple related tests (Rice, 1989), there were no significant correlations between any of the principal components and reproductive success at either site. However, stepwise regressions showed a marked difference between these populations. At the GM site multiple regression models explained a significant amount of variance in reproductive success (session 1: reproductive success = -0.675*PC5 + 8.375, F = 5.94, df = 1 and 7, P = 0.04, percent of variance explained = 45.9 %; session 2: reproductive success = -0.557*PC1 - 0.811*PC4 - 0.901*PC5 + 16.344, F = 16.03, df = 3 and 5, P = 0.005, percent of variance explained = 90.6 %; entire summer: reproductive success = 0.381*PC3 - 0.071*PC5 + 6.625, F = 14.01, df = 2 and 6, P = 0.005, percent of variance explained = 82.4 %). No multiple regression models explained a significant amount of the variance in male reproductive success at the WM site.

Discussion

Clearly, these populations of collared lizards represent a system in which the action of sexual selection on various characters is highly complex. Also apparent from this study is that examination of a single character, or a single population, may be insufficient for an understanding of the operation of sexual dimorphism. These populations of collared lizards display not only differences in the strength of sexual selection on various characters, but also

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in which characters are sexually selected. The action of sexual selection does not provide a simple explanation for differences in sexual dimorphism.

Differences between populations in male reproductive success suggest that sexual selection is greater in the WM population. Males in this population have higher average reproductive success and greater variance in reproductive success, both suggested as measures of the strength of sexual selection (Andersson, 1994). These observations suggest a more important role for sexual selection in this population, which is consistent with behavioral observations that indicate greater polygyny at WM (McCoy, 1995b). However, a simple assumption of greater sexual selection in the WM population would predict greater sexual dimorphism in this population in all characters. Since this is not the case, I abandon the simple explanation that sexual selection is stronger in the WM population.

Interpopulational differences in sexual dichromatism appear to be explained by differences in sexual selection. Despite other indications of greater sexual selection in the WM population, correlations of male reproductive success with color, and stepwise regressions of reproductive success with color, clearly show that color is more important in determining reproductive success in the GM population. Variation in male coloration explains a significant amount of variation in reproductive success at the GM site, but not at the WM site. This appears to be best explained as a result of the action of sexual selection since the GM population exhibits greater sexual dimorphism in color (McCoy et al., in prep).

Analysis of the relationships between other morphological characters and male reproductive success reveals a far more complex relationship. Not only does the strength of sexual selection vary, but which characters show significant effects of sexual selection varies between sites. In the GM population overall size in various characters, especially head length, has the greatest effect on male reproductive success. This effect is most pronounced

during the early summer and diminishes as the summer progresses. In the WM population, however, other morphological characters, including front limb length, hind limb length, and tail length, have significant effects on male reproductive success. The role of head length in the GM population is especially interesting because this population, although less dimorphic in most characters, displays the greatest dimorphism in head length and also a significant sexual difference in the allometry of this character (McCoy, 1995a; McCoy et al., 1994).

The seasonal differences in sexual selection (in both populations) revealed in this study are also interesting. Crotaphytus collaris is a long-lived species with multiple reproductive bouts per season and the potential to reproduce for many years (Fitch, 1967). Behavioral differences noted at different times during the summer (McCoy, 1995b; Yedlin and Ferguson, 1973) suggest that the roles of various social behaviors may vary temporally. It is possible that certain morphological characters are more important in some aspects of social behavior than in others, and that this accounts for the seasonal variation in sexual selection. Because the relative importance of those aspects of social behavior may vary between sites, these results may also appear as interpopulational differences in sexual selection.

The difference in average male reproductive success also obfuscates interpopulational differences in the strength of sexual selection. Although there are clear differences between populations in which characters are subject to sexual selection, the importance of those characters to lifetime fitness is unclear. Differences in color and in head length clearly explain some of the variance in male reproductive success in the GM population, but other morphological characters explain more variance in the WM population. Since reproductive success (and variance in reproductive success) is greater in the WM population, it is not possible to assign exact importances to various characters. That is, it is not possible to say

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with certainty that an increase in head length for a male at GM results in a greater increase in fitness than an increase in front limb length for a male at WM.

Sexual selection is not a simple phenomenon, and the action of sexual selection should not be examined through simplistic studies. Although sexual selection implies differences in reproductive success, estimation of reproductive success in itself is not a simple matter (Howard, 1979). However, estimates of the probability of male reproductive success should provide at least estimates of the potential for sexual selection (Andersson, 1994). Estimates of male reproductive success and the potential for sexual selection in two populations of collared lizards demonstrate the complexity possible in the action of sexual selection. Although both of these populations display sexual dimorphism in several characters, there are marked interpopulational differences in estimates of the strength of sexual selection. Examination of this system reveals that measuring sexual selection on a single character, or in a single population, is insufficient for complete understanding of this phenomenon. Not only does the strength of sexual selection on various characters differ between populations, but there appear to be seasonal differences in sexual selection. This phenological variation indicates that differences in mating and social systems may significantly impact the action of sexual selection. Although sexual selection may be demonstrated by differences in male reproductive success within a population, this phenomenon is sufficiently complex that a complete understanding of its action cannot be achieved except through more expansive studies.

Cooperative Research Unit at Oklahoma State University.

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Table 1. Estimates of male reproductive success for two Oklahoma populations of collared lizards (Crotaphytus collaris).

	WM			GM		
	n	x̄	s^2	n	x̄	s^2
Session 1	6	9.53	34.95	9	4.98	29.13
Session 2	10	6.56	25.00	9	2.92	11.30
All summer	10	9.47	95.43	9	7.91	45.47

Table 2. Results of principal components analysis on six morphological characters of male collared lizards (Crotaphytus collaris) from two Oklahoma populations (GM: n = 19; WM: n = 27).

	Component Loadings		
	PC1	PC2	PC3
Head length	0.8517	0.3343	0.3048
SVL	0.7822	0.3758	0.3976
Hind limb length	0.6038	0.4435	0.5230
Head width	0.5967	0.4274	0.3624
Front limb length	0.5949	0.3938	0.6508
Tail length	0.3182	0.8943	0.2455
% total variance explained	41.88	26.45	18.99

Table 3. Spearman's rank-order correlations between male reproductive success and scores on principal components of morphology for collared lizards (Crotaphytus collaris) from two Oklahoma populations (sample sizes listed in Table 1).

	WM			GM		
	PC1	PC2	PC3	PC1	PC2	PC3
Session 1	0.314	0.314	0.257	0.829*	-0.193	-0.218
Session 2	0.091	0.564	0.721*	0.034	0.220	-0.017
All summer	0.333	0.612	0.588	0.633	0.100	-0.250

* Indicates a significant correlation at an overall $\alpha = 0.05$ after a sequential Bonferroni adjustment for multiple related tests.

Table 4. Results of principal components analysis on color (Munsell hue, value, and chroma, for three locations on the body) of male collared lizards (_Crotaphytus collaris_) from two Oklahoma populations (GM: n = 16; WM: n = 18).

	Component Loadings				
	PC1	PC2	PC3	PC4	PC5
Ventral value	0.7163	0.2854	0.3748	-0.2810	0.0718
Gular value	0.7045	-0.3150	0.1605	0.3845	0.3588
Ventral chroma	-0.6513	0.2421	0.3606	0.4922	-0.1986
Gular chroma	-0.6480	-0.4339	0.1263	-0.1508	0.2557
Gular hue	-0.5966	0.4814	-0.0492	-0.5699	0.0223
Ventral hue	0.4227	0.6367	0.0157	0.2362	-0.4104
Dorsal hue	0.1251	0.6189	-0.3402	0.0301	0.6518
Dorsal value	0.3136	-0.0619	0.7501	-0.4367	-0.0155
Dorsal chroma	-0.4855	0.3005	0.6047	0.3163	0.3238
% total variance explained	30.42	17.13	15.10	12.93	10.42

Figure Legends

Figure 1. Regressions of clutch size against snout-vent length (SVL) for female collared

lizards (<u>Crotaphytus</u> <u>collaris</u>) from two Oklahoma populations.

Figure 1
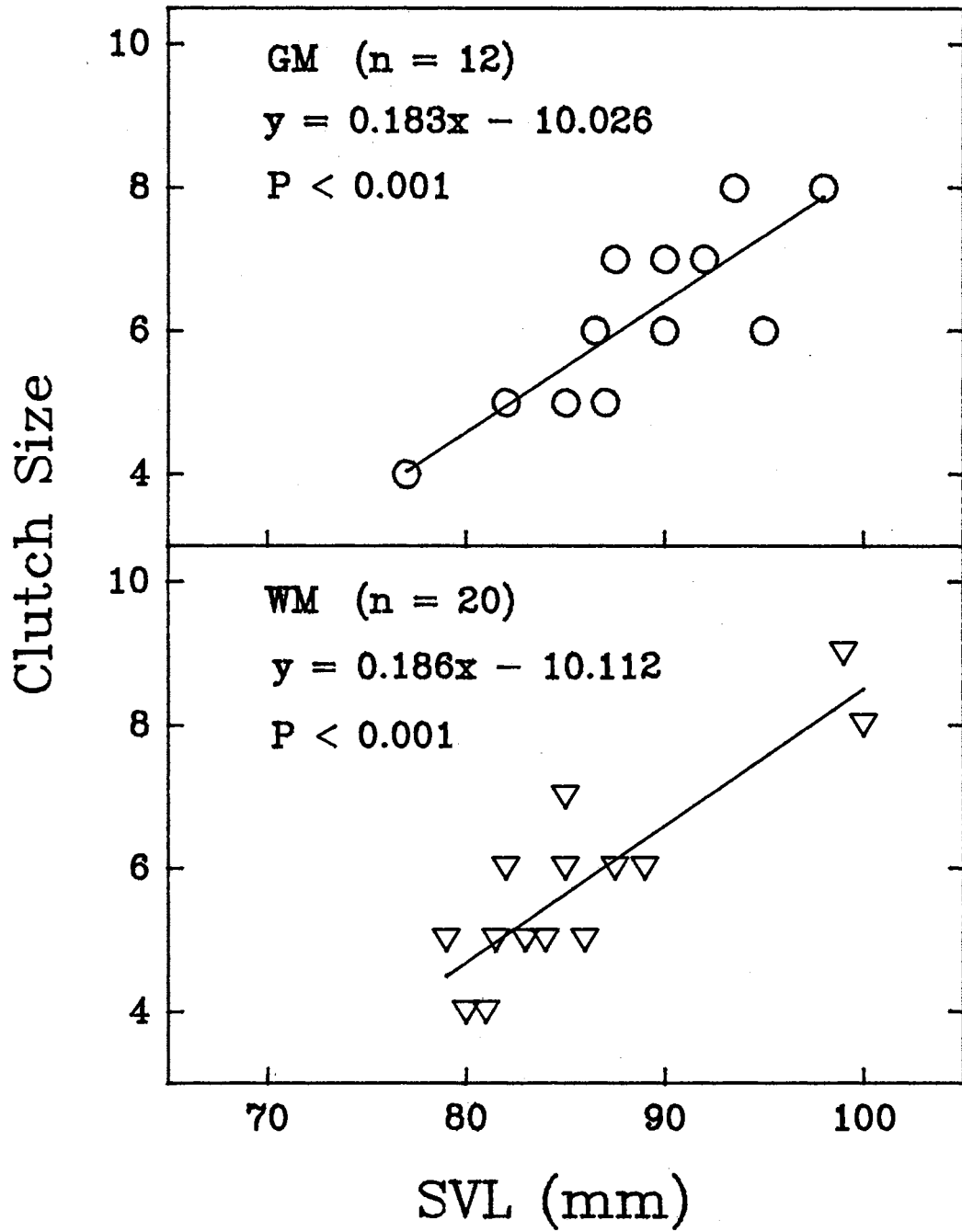
Figure 1

PARASITES, PARASITISM, AND SEXUAL DIMORPHISM IN THE COLLARED LIZARD, <u>CROTAPHYTUS</u> <u>COLLARIS</u> (SAURIA: CROTAPHYTIDAE)

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Abstract: Although numerous empirical tests of parasite-mediated sexual selection (PMSS) exist, interspecific correlational studies and studies within a single population have largely failed to demonstrate conclusively the action of PMSS. In this study the parasite communities of two populations of collared lizards (<u>Crotaphytus</u> <u>collaris</u>) are compared to examine PMSS in this species. This approach allows testing of the interpopulational prediction of greater sexual dimorphism in populations with greater parasite loads, and the intrapopulational prediction that males with higher parasite loads will display reduced showiness (i.e., less exaggeration of sexually dimorphic characters). This study also examines the roles of several parasite taxa. The interpopulational predictions were supported by some parasite taxa, but other taxa showed contradictory patterns of prevalence and average infection rate. Intrapopulational predictions were not supported. Although few previous studies of PMSS within a single population have examined more than one parasite species, contradictory conclusions could result from the study of different parasite taxa.

<u>Key</u> <u>words</u>: <u>Crotaphytus</u> <u>collaris</u>; Sauria; Crotaphytidae; sexual dimorphism; parasitism; lizard; Oklahoma

Introduction

Parasitic organisms have doubtless been known to man for thousands of years. Scientific study of parasites began in earnest about three centuries ago (Chandler, 1955) and enormous research effort has been devoted to the topic of parasites and parasitism. The majority of this research, however, has focused on a relatively narrow aspect of this phenomenon: the effect of parasites on human beings or their domesticated animals (Cheng, 1991). Despite a brief flurry of activity in the early 20th century, the role of parasites in ecological systems has been largely overlooked (Toft, 1991). As if to atone for this history of neglect, ecologists are now rushing to study the effects of parasites on natural populations.

Much of the recent interest in the effect of parasites on the ecology of their hosts has been directed at the impact of parasites on sexual selection in their hosts. This focus was largely prompted by the introduction of a model for the evolution of bright male coloration as a signal to prospective mates of heritable resistance to parasites (Hamilton and Zuk, 1982). Since its introduction, numerous researchers have tested this hypothesis in a variety of host taxa (reviews in Andersson, 1994; Clayton, 1991; Sullivan, 1991). The attention focused on parasite-mediated sexual selection (PMSS) has also led to the presentation of other models which, unlike Hamilton and Zuk's hypothesis, do not require heritable resistance to parasites (Andersson, 1994; Clayton, 1991).

The explosive growth of interest in PMSS is undoubtedly also a reflection of widespread interest in the evolution of sexual dimorphism. Biologists have long been fascinated by sexual differences in morphology, and much effort has been devoted to the explanation of this phenomenon. Individuals (usually males) of numerous taxa display bright coloration or exaggerated morphological characters (ornaments) that cannot be explained by the action of ordinary natural selection (Andersson, 1994). Darwin (1871) proposed sexual

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selection as a model to explain the evolution of such characters. While intrasexual selection, competition among males for access to mates, is widely accepted as a mechanism leading to the evolution of sexual dimorphism; intersexual selection, the choice of mates by females, has been less universally accepted. This reticence probably stems from the difficulty in explaining why, or how, females may increase their fitness by being selective. Parasite-mediated sexual selection is one possible explanation. In PMSS, females gain a fitness advantage by choosing mates that have heritable resistance to parasites, are free from parasites that may be directly transmitted to the female, or are better able to provide parental care for offspring because they are free from parasites (Andersson, 1994; Clayton, 1991, Møller and Saino, 1994). All of these models provide excellent reasons for the evolution of choosiness among females.

Although PMSS provides several heuristically pleasing explanations for intersexual selection, empirical studies of this phenomenon have so far been highly equivocal. Some studies have suggested that PMSS may be operating, while others fail to support the concept. The reason for lack of conclusive support for PMSS lies partly in the methodology used and partly in the organisms themselves. Studies of PMSS have used either interspecific comparisons looking for correlations between parasite load and sexual dimorphism, or examination of a single population looking for correlations between parasite load and display of sexually dimorphic characters among males within a population (Clayton, 1991; Sullivan, 1991). Both approaches are open to criticism.

Methodological failings are probably most serious among the interspecific comparisons. In addition to confound owing to phylogenetic relatedness (Harvey and Purvis, 1991; Pagel and Harvey, 1988), these studies are subject to criticism regarding the measurement of sexual dimorphism (Clayton, 1991; McCoy et al., in prep), and regarding the estimation of parasite load (Clayton, 1991). That several such studies have failed to support

the predictions of PMSS cannot be accepted as evidence that the model does not work.

Various characteristics of parasites and aspects of parasitism further confound studies of PMSS. The operation of PMSS assumes that the parasites are in some way costly to their hosts. The costliness of parasites is not easy to quantify, or even define (Cheng, 1991; Toft, 1991), and has been infrequently addressed in studies of PMSS (Clayton, 1991; Sullivan, 1991). The dispersion of many parasite species also adds to the difficulty in demonstrating PMSS. Most parasites tend to be highly aggregated, with a few individual hosts having very high infection rates and most individuals having very few, or no, parasites. Parasite species that display such patterns of aggregation are unlikely to produce PMSS since there will be little variation in parasite load among most males and thus little for females to base their choice upon (Poulin and Vickery, 1993). The concept of prevalence, often used as a measure of parasite load, presents problems as well. Due to the aggregated nature of most parasites, and the mathematical method for estimating prevalence, this measure is highly dependent on host sample size (Gregory and Blackburn, 1991).

Models for PMSS predict that among populations, those populations with the greatest parasite load should display the greatest sexual dimorphism, and that within a population, those males with the smallest parasite load should display the greatest showiness (exaggeration of sexually dimorphic characters) (Clayton, 1991; Hamilton and Zuk, 1982; Sullivan, 1991). Ideally, studies of PMSS should examine both predictions, and should do so in species that harbor parasites likely to engender PMSS. That is, the parasites should be costly, with high prevalence and high variation in infection rate. To address these issues I have adopted a slightly different approach to the study of PMSS. I have conducted a study which compares parasitemia and sexual dimorphism between two populations of collared lizards (Crotaphytus collaris) from Oklahoma. These populations display significant differences in sexual

dimorphism in color (McCoy et al., in prep), body size, and other morphological characters (McCoy, 1995a; McCoy et al., 1994). I examined lizards from both populations for haemoparasites, ectoparasites, and gastrointestinal helminths. The prevalences and average infection rates of all parasites were compared between populations. I also examined correlations between parasite load and various measures of male showiness within each population. This approach avoids some of the problems of interspecific comparisons while testing more of the prediction of PMSS than studies conducted within a single population.

Methods and Materials

Collared lizards from the Glass Mountains (GM: n = 14 males, n = 18 females) in northwestern Oklahoma (Major Co.) and the Wichita Mountains (WM: n = 15 males, n = 21 females) in southwestern Oklahoma (Comanche Co.) were captured during late July and early August, 1993. All lizards used in this study were classified as adults (lizards that were at least 1 yr old in May) based on comparisons of body size with lizards of known ages from these sites (McCoy, 1995a). Using only adults minimizes possible confound owing to differences in parasite load among lizards of different ages (McAllister and Trauth, 1985). Snout-vent length (SVL), head length, head width, front limb length, and tail length were recorded for all lizards. Color of each lizard was appraised at three areas on the body (gular, dorsolateral, and ventrolateral) using Munsell ® Color Charts for Plant Tissues (MacBeth Division, Kollmorgen Instruments Corporation) (Zucker, 1988). Color in each area was recorded as Munsell hue, value, and chroma. All lizards were examined for ectoparasites using a dissecting microscope and all ectoparasites were identified and counted. Thin-film blood smears were prepared for each lizard to examine for haemoparasites.

A sample of lizards from each site (GM: n = 4 males, n = 12 females; WM: n = 4

males, $\underline{n}$ = 12 females) was euthanized by injection of sodium pentobarbital and fixed in 10% formaldehyde within 24 hrs of capture. All other lizards were released at the point of capture after other data were collected. Those lizards that were euthanized were autopsied to examine for gastrointestinal helminths. The body cavity of each lizard was opened using a mid-ventral incision and the entire gastrointestinal tract was removed. The esophagus, stomach, small intestine, and large intestine were then separated and each was opened and examined for helminths. Helminths were located and counted using a dissecting microscope. Representatives of each type of helminth found were mounted in glycerol wet-mounts and examined under higher magnification (400x) to aid in identification.

Blood smears were fixed in absolute methanol and then stained for 30 min in 3% Giemsa stain. Each smear was examined under 1000x magnification for 10 minutes. All haemoparasites found were counted. These counts were converted to infection rates of parasites per 1000 erythrocytes, using the number of fields examined and the average of 60 erythrocytes per field.

For each type of parasite found at both sites, prevalence and average infection rate were compared between sites. Prevalences were compared using two-sample binomial tests. Average infection rates were compared between populations using Mann-Whitney $\underline{U}$ - tests. Within each population, correlations between infection rate with each type of parasite and various measures of male showiness were calculated. Showiness was estimated by conducting a discriminant function analysis based on morphological characters and using males and females as the groups to be discriminated. This produces a single linear function that describes the sexual differences in several morphological characters. The discriminant function score for each male describes how different that male is from females, or how showy that male is. A discriminant function was calculated using SVL, head width, head length,

front limb length, hind limb length, and tail length. A separate discriminant function was calculated using the Munsell color scores converted to continuous variables. For males from each site, Spearman's rank-order correlations were calculated between each measure of showiness and the infection rate for each type of parasite. Pearson's correlations were also calculated between each measure of morphology or color and the infection rate for each type of parasite. All statistical analyses were conducted using the SYSTAT program (Wilkinson, 1990).

Results

Five types of parasites were found in these populations of lizards. Two ectoparasites were quite common. Most lizards from both populations were infected with larval trombiculid mites (Eutrombicula alfred-dugesi). Larval ixodid ticks (Ixodes scapularis) were also quite common in the WM population. Only one haemoparasite, a haemogregarine, was found and it was present only in the WM population. Two types of nematodes were present in lizards from both populations. A spiruroid nematode was present in the esophagus, stomach, or small intestine of several lizards. An oxyuroid nematode was present, often in very large numbers, in the large intestine of most lizards examined.

Comparison of the prevalences and infection rates of various parasites between populations yields slightly confusing results. The prevalence of both ectoparasites was greater in the WM population (significantly greater for I. scapularis) (Table 1). However the GM population had higher prevalences of both nematodes. Although prevalence of E. alfred-dugesi was slightly higher in the WM population, the average infection rate was greater in the GM population. Average infection rate for I. scapularis was significantly higher in the WM population. Both nematodes showed higher infection rates in the GM population. The rate of

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infection with spiruroid nematodes was significantly higher in the GM population.

Discriminant function analyses of morphology and color produced highly significant functions at both sites (all $\underline{P} \ll 0.0001$). Except for the discriminant function describing color differences between males and females at the WM site, all functions reassigned all lizards to the correct sex. The discriminant function for color at the WM site incorrectly reassigned one male. The loadings on the discriminant functions for morphological characters (Table 2) indicate that head width and length are important in morphological discrimination between the sexes. Limb length also contributes substantially to morphological separation of the sexes, and tail length is important in the WM population. Ventral hue (wavelength) and gular chroma (color saturation) are the characters contributing most strongly to color differences between the sexes (Table 2).

Correlations between male showiness and parasite load revealed no clear pattern. Negative correlations between male showiness and parasite load, as predicted by PMSS models, were found for morphology at the GM site with E. trombicula, I. scapularis, and spiruroid nematodes (Table 3). For showiness in color, negative correlations were found with spiruroid nematodes at the GM site, and with I. scapularis and both types of nematodes at the WM site. However, the only significant correlation was between infection with oxyuroid nematodes and showiness in morphology at the WM site, and this correlation was positive. There were no significant correlations between any individual male character and parasite load at either site. There were also no multivariate models combining the infection rate for several parasites which explained a significant amount of variance in male showiness at either site.

Discussion

The analysis of parasitism and sexual dimorphism in these populations of collared

lizards does not provide conclusive support for the action of PMSS, but neither does it conclusively discount this hypothesis. The rather ambiguous nature of these results derives mainly from the novel approach of this study. In an interspecific, correlational study of parasite load and sexual dimorphism, the results will certainly be either a significant positive correlation, a significant negative correlation, or no significant correlation. In a study within one population, and considering only one parasite, one could find a significant correlation between parasite load and male showiness (either positive or negative) or no correlation. If many parasites are studied, and male showiness is examined both between and within populations, the number of different possible outcomes increases tremendously. The difficulty is further compounded by the fact that these two populations display a complex mosaic of sexual dimorphism in various characters, rather than a simple pattern of greater sexual dimorphism in one population and reduced sexual dimorphism in the other (McCoy et al., 1994; McCoy et al., in prep).

Interpopulational comparisons of sexual dimorphism and parasite load do not provide unambiguous results. Prevalence of some parasites is greater in the GM population (which is least dimorphic in body size and most morphological characters, but most dimorphic in color and head length), but prevalence of I. scapularis is significantly greater in the WM population. Comparisons of average infection rates are similarly inconclusive. Most parasites show higher infection rates in the GM population, but I. scapularis has a significantly higher infection rate in the WM population. Since interpopulation differences vary among parasite taxa these comparisons provide little conclusive evidence, either positive or negative, for the action of PMSS in collared lizards.

Within populations, correlations between male showiness and parasite load are equally equivocal. The infection rate of some parasites is negatively correlated with male showiness

(as predicted by PMSS models) but is positively correlated for other parasites. The only significant correlation between male showiness and parasite load is a positive correlation between male showiness in morphology and the infection rate by oxyuroid nematodes at the WM site. This effect however, is based on a very small sample and is probably an artifact of positive correlations between SVL and showiness, and SVL and infection with oxyuroid nematodes.

Part of the difficulty in examining PMSS between these populations lies in the complex nature of the interpopulation differences in sexual dimorphism. These populations do not represent a system wherein one population displays greater sexual dimorphism in all characters. Rather, the WM population is more dimorphic in body size and most other morphological characters while the GM population displays greater dimorphism in head length and color. This mosaic of dimorphism in various characters complicates the interpopulation predictions of PMSS. It is not possible to say which population should have the greater parasite load since it is not possible to say which population is the more dimorphic. Not only is the degree of sexual dimorphism complex, but the selective importance of sexually dimorphic characters is not simple. Although the WM population displays greater polygyny (McCoy, 1995b), male reproductive success is more strongly correlated with color in the GM population (McCoy, 1995c).

If these lizards had displayed clear correlations between male showiness and parasite load, the data would have provided strong support for PMSS. However, the sample sizes used in this study (especially of lizards examined for internal parasites) were quite small, and thus do not provide strong evidence against the action of PMSS. Several measures of male showiness are negatively correlated with parasite load, suggesting that the potential for PMSS does exist. Further studies with larger samples will be necessary to conclusively determine

the effect of parasite load on male showiness in these lizards.

Several aspects of this study at least suggest the potential for PMSS in collared lizards. There are significant differences in parasite load between two populations that also display significant differences in sexual dimorphism. Some of the parasites examined also display the type of dispersion pattern that should most likely impact host sexual selection (Poulin and Vickery, 1993). Although the cost of parasitism was not examined in this study, nor previously measured for the parasites studied, Lehman (1993) has suggested that ectoparasites may have greater impacts on host fitness than most endoparasites.

This study clearly demonstrates the importance of examining parasite communities, rather than single parasite species, to determine the action of PMSS (Clayton, 1991; Sullivan, 1991). Various parasite taxa examined in this study provide conflicting results when prevalence and infection rate are compared between populations. Had only one species of parasite been studied the results would depend on which parasite was selected. However, this study also clearly demonstrates the difficulty in studying the action of parasite communities on host sexual selection. With conflicting results provided by various parasite taxa, no clear interpretation can be made. The greatest single contribution of this study is probably the demonstration that PMSS may be a far more complex phenomenon than previously believed.

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Table 1. Prevalence (% infected, number infected / number examined) and mean infection rate (parasites per host except haemogregarines which are reported as parasites / 1000 erythrocytes) of various parasites in collared lizards (Crotaphytus collaris) from two Oklahoma populations.

Parasite	Prevalence		Mean Infection Rate	
	GM	WM	GM	WM
Eutrombicula alfred-dugesi	96.9% (31/32)	100% (36/36)	126.28	109.39
Ixodes scapularis	3.1% (1/32) *	30.6% (11/36)	0.03 *	3.36
Haemogregarine	0.0% (0/32)	11.1% (4/36)	-	0.38
Spiruroid nematode	46.8% (7/16)	25.0% (4/16)	1.75	0.44
Oxyuroid nematode	93.8% (15/16)	75.0% (12/16)	241.48 *	119.81

* Indicates a significant difference ($P < 0.05$) between sites.

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Table 2. Character loadings on discriminant functions separating male and female collared lizards from two Oklahoma populations on the bases of morphological characters and color characters.

Morphology			Color		
Character	GM	WM	Character	GM	WM
SVL	0.315	0.397	Dorsal hue	-0.170	0.160
Head width	0.834	0.678	Dorsal value	-0.047	0.128
Head length	0.561	0.661	Dorsal chroma	0.063	-0.156
Front limb length	0.407	0.572	Ventral hue	-0.535	0.646
Hind limb length	0.463	0.678	Ventral value	-0.117	0.240
Tail length	0.158	0.584	Ventral chroma	0.087	-0.088
			Gular hue	0.059	-0.159
			Gular value	-0.127	0.209
			Gular chroma	0.497	-0.878

Table 3. Spearman's rank-order correlations between male showiness, in color and morphology, and rate of infection by various parasites for male collared lizards from two Oklahoma populations.

Parasite	Morphology		Color	
	GM	WM	GM	WM
	ρ, n, P	ρ, n, P	ρ, n, P	ρ, n, P
Eutrombicula alfred-dugesi	-0.510, 12, 0.09	0.000, 13, 1.00	0.059, 14, 0.84	0.104, 15, 0.71
Ixodes scapularis	-0.480, 12, 0.11	0.191, 13, 0.51	0.241, 14, 0.41	-0.043, 15, 0.88
Haemogregarine	-	0.310, 13, 0.28	-	0.186, 15, 0.51
Spiruroid nematode	-0.529, 4, 0.47	0.730, 4, 0.27	-0.447, 4, 0.55	-0.517, 4, 0.48
Oxyuroid nematode	0.529, 4, 0.47	0.969, 4, 0.03	0.447, 4, 0.55	-0.754, 4, 0.25

EXAMINING MULTIPLE SELECTIVE MECHANISMS FOR THE EVOLUTION OF SEXUAL DIMORPHISM: A CASE STUDY USING THE COLLARED LIZARD, CROTAPHYTUS COLLARIS (SAURIA: CROTAPHYTIDAE).

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Within many animal taxa, individuals of one sex (usually males) display bright colors or greatly exaggerated morphological characters. The evolution of these ornaments often cannot be explained through the action of ordinary natural selection alone because bright coloration might attract predators, and exaggeration of some morphological characters (such as tail length) may result in reduced mobility, or lessened efficiency in capturing prey or avoiding predators (Andersson, 1994). However, the fact that these ornaments exist suggests that they confer one or more advantages. This apparent evolutionary paradox has led to a tremendous amount of research effort devoted to explaining the evolution of sexual dimorphism, and a bewildering array of alternative evolutionary models. With even a brief perusal of the relevant literature, a reader will find a staggering number of evolutionary models proposed to explain sexual dimorphism. Several reviews are available (Andersson, 1994; Hedrick and Temeles, 1989; Maynard Smith, 1987) to serve as guides through this maze of evolutionary models. Fortunately, many of the proposed models are only modifications of a broader theory and most can be placed into one of a few general categories (Hedrick and Temeles, 1989).

Most of the proposed selective mechanisms that may lead to the evolution of sexual dimorphism fall within the heading of sexual selection. Originally proposed by Darwin (1871), sexual selection is the selection for any character conferring a direct advantage in mating success. Sexual selection is generally divided into intrasexual selection, selection for characters that provide an advantage in competition for access to mates (usually among males); or intersexual selection, selection for characters that increase attractiveness to potential mates (Andersson, 1994; Maynard Smith, 1987). The general category of intersexual selection includes such models as the sexy son hypothesis (Weatherhead and Robertson, 1979), the handicap theory (Zahavi, 1975), and parasite-mediated sexual selection (Hamilton and Zuk, 1982). Other models involve minor refinements of these hypotheses (Andersson, 1994; Smith, 1987).

It has also been suggested that sexual dimorphism could evolve as a result of competition between the sexes for a limited resource such as food (Hedrick and Temeles, 1989; Selander, 1966; Slatkin, 1984). According to this model, if morphological differentiation between the sexes allows males and females to exploit different resources, sexual dimorphism will increase overall fitness. Although controversial, theoretical analyses (Slatkin, 1984) and empirical studies (Camilleri and Shine, 1991; Forsman, 1991) have indicated that it is at least possible that competition for resources could lead to the evolution of sexual dimorphism.

The plethora of possible models to explain the evolution of sexual dimorphism has led to an even more impressive number of tests of these models. A number of theoretical and genetic studies (Andersson, 1986; Heywood, 1989; Lande, 1980; Slatkin, 1984) have demonstrated that many of these models can potentially lead to the evolution of sexual dimorphism. Literally hundreds of empirical studies have demonstrated the action of one or

the other of these models in natural populations. In a review of empirical studies of sexual selection prior to 1990, Andersson (1994) cites 232 studies. Despite this wealth of evidence, certain questions regarding the evolution of sexual dimorphism remain unanswered (Andersson, 1994). These questions remain unanswered largely as a result of several characteristics common to most empirical studies of the evolution of sexual dimorphism.

The relative importance of sexual selection and other mechanisms for the evolution of sexual dimorphism, both within and among populations, remains unclear (Andersson, 1994). Although numerous empirical studies have demonstrated the action of one selective model or another, few studies have considered the simultaneous operation of multiple selective mechanisms. Certainly the demonstration of one evolutionary mechanism does not preclude the action of others. Some studies have examined the effects of both intrasexual and intersexual selection (e.g. Hews, 1990; Moore, 1990) but very few have simultaneously tested more specific models such as the competition avoidance hypothesis or parasite-mediated sexual selection.

Also lacking in many studies of sexual dimorphism is an examination of the proximate mechanism that leads to the observed difference between the sexes. Sexual dimorphism may occur through sexual differences in growth rates, differences in size at sexual maturity, differences in the size at which growth slows or stops, or differences in mortality rates (Shine, 1990, Stamps, 1993). Although often overlooked in searches for the ultimate cause of sexual dimorphism, these proximate mechanisms may impinge strongly on the interpretation of empirical data. For example, if there is a demonstrable mating advantage for large males within a population, the interpretation of that mating advantage will be quite different if sexual dimorphism in this population is a result of higher mortality among females, rather than increased growth rates or larger maximum size among males. Analysis of the proximate

mechanisms resulting in sexual dimorphism may provide substantial insight into the operation of various selective mechanisms and may answer many of the remaining questions regarding heritability of sexually dimorphic characters (Andersson, 1994).

Another topic often inadequately addressed is the possibility of constraints on sexual selection, or on sexually selected characters. Although sexual selection may be constrained by many factors (Andersson, 1994; Price et al., 1987), perhaps the most obvious constraint is the possibility of increased predation risk. The exaggerated characters, colors, or behavior resulting from sexual selection may place their owners at increased risk of mortality due to predation (Ryan, 1985). Despite the clear possibility of counter-selective mechanisms, few studies of the evolution of sexual dimorphism address constraints on that dimorphism. Reduced sexual dimorphism within a population, or a species, is often attributed to reduced sexual selection without a comparison of the strength of constraints. Counter-selective mechanisms such as predation could clearly impact the interpretation of empirical data regarding the strength of sexual selection.

All of these effects have been suggested as possible confounds to the study of the evolution of sexual dimorphism, but very little empirical evidence exists to demonstrate their importance. Not only do questions regarding the evolution of sexual dimorphism remain unanswered, but several questions regarding studies of the evolution of sexual dimorphism remain largely unasked. The simultaneous operation of several selective mechanisms may obscure the relative importance of sexual selection in the evolution of a species, but very few studies exist that test for the operation of more than one selective mechanism, and the importance of multiple selective mechanisms remains unclear. Although the genetics underlying sexual selection are not well known (Andersson, 1994), very few studies have examined the heritability of sexually dimorphic characters, or even the proximate mechanisms

that lead to sexual dimorphism. Without understanding which proximate mechanism (growth, size at maturity, growth after maturity, maximum body size) accounts for the observed sexual dimorphism, it will be impossible to determine how selection affects the genotypes of the organisms being studied. The action of constraints on sexual dimorphism and counter-selective mechanisms will have the greatest influence on comparative or correlational studies, but will also impact the results of studies within a population. There are numerous studies, however, that purport to measure the strength of selection on sexually dimorphic characters but do not address the possibility of constraints on that selection.

I conducted an intraspecific study of sexual dimorphism in the collared lizard, Crotaphytus collaris, with the expressed purpose of examining multiple selective mechanisms which could impinge upon the evolution of sexual dimorphism. For this study a variety of data were collected on a population of collared lizards from the Glass Mountains (GM) in northwestern Oklahoma, and a population from the Wichita Mountains (WM) in southwestern Oklahoma (see McCoy, 1995a; McCoy et al. 1994; for descriptions of study sites). Although the same subspecies (C. c. collaris), and separated by only 200 km, these populations display significant differences in sexual dimorphism in color (McCoy et al., in prep), body size, and other morphological characters (McCoy, 1995a; McCoy et al., 1994). The relationship in sexual dimorphism between these populations is not a simple, transitive one, where one population is more dimorphic in all characters, but instead is a complex mosaic of greater or lesser sexual dimorphism in various characters (McCoy et al., 1994, in prep). This mosaic of sexual dimorphism in various characters suggests that not only does the strength of selection vary between populations, but that different selective mechanisms may be operating in them. Initial observations of these populations indicated that differences in proximate mechanisms, sexual selection, parasite-mediated sexual selection, intersexual competition for food, and

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predation could all affect the evolution of sexual dimorphism. In this study I address all of these hypotheses to assess their potential influence on the study of the evolution of sexual dimorphism.

PROXIMATE CAUSES OF SEXUAL DIMORPHISM

Since sexual dimorphism could arise through the action of a number of proximate mechanisms (Shine, 1990; Stamps, 1993), in any comparative study it is important to determine if the proximate mechanisms vary across populations. McCoy (1995a) examined potential proximate causes of sexual dimorphism in the two populations of collared lizards described here. Using the logistic-by-weight growth model (Andrews, 1982; Dunham, 1978; Schoener and Schoener, 1978), growth rates and asymptotic sizes of males and females were compared between populations. The age distributions of males and females were also compared within each population to determine the extent to which sexual differences in mortality affect sexual dimorphism (Andrews and Stamps, 1994; Stamps et al., 1994). Allometry in various sexually dimorphic characters was also examined and compared between populations.

Although there was substantial variation in growth between years at both sites, males generally displayed greater asymptotic sizes. The difference between asymptotic sizes for males and females was consistently greater in the WM population, which displays the greatest sexual dimorphism in body size (McCoy et al., 1994). The asymptotic size for males was also substantially greater in the WM population.

Comparisons of age distributions for males and females revealed that differences in mortality do not account for sexual dimorphism in body size in these populations. For the two years analyzed in this study, there were no significant differences in age distributions

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between males and females at the WM site. In one year at the GM site males and females displayed significantly different age distributions. However, there was appreciable sexual size dimorphism even in those cases where there was no difference in age distribution, indicating that sexual dimorphism in these lizards is not mainly a result of sexual differences in mortality or longevity.

There were also interpopulational differences in the pattern of sexual differences in the allometry of various morphological characters. These populations display significant sexual dimorphism in head width and length, limb length, and tail length (McCoy, 1995a; McCoy et al., 1994). However, in the GM population there were consistent sexual differences in allometry only for head length. At the WM population there were sexual differences in allometry for head length and hind limb length in one year, and in all morphological characters in another. The results for head length at the GM population are particularly interesting, because although this population is less dimorphic in body size and other morphological characters, it is more dimorphic in head length.

This analysis of the proximate mechanisms producing sexual dimorphism in collared lizards indicates that sexual dimorphism in these lizards is a result of multiple mechanisms that are probably genetically controlled. This analysis further indicates that the several different mechanisms produce sexual dimorphism in various characters. Clearly the potential exists for different selective mechanisms to be operating within these populations, and for these different mechanisms to act on different morphological characters.

EXAMINATION OF MULTIPLE SELECTIVE MECHANISMS

Sexual Selection

Comparisons of space use and social behavior between these populations indicate

greater polygyny at the WM site (McCoy, 1995b). Male reproductive success and variance in reproductive success were also greater at WM (McCoy, 1995c). Degree of polygyny and variance in male reproductive success have been suggested as measures of the strength of sexual selection (Andersson, 1994; Wade, 1987). Based on this evidence, sexual selection appears to be stronger in the WM population. Although this is consistent with greater sexual dimorphism in body size and several other characters within this population, it does not explain why the GM population is more dimorphic in head length and in color.

Sexual selection also predicts that there should be a correlation between male reproductive success and development of the character being selected for (Andersson, 1994). Comparisons between male reproductive success and several morphological characters showed that there are differences between these populations in the importance of several characters (McCoy, 1995c). Head length and color are most important in explaining the variance in mating success among males from the GM population. Limb length and overall body size are strongly related to variance in male reproductive success in the WM population, but color is not. These results are further evidence that selection for exaggeration of sexually dimorphic characters is fundamentally different in these populations.

Parasite-Mediated Sexual Selection

Differences in sexual dimorphism between these populations could be affected by differences in parasite load. Although usually applied to sexual dimorphism in color (sexual dichromatism), parasites could affect sexual selection on other morphological characters as well (Clayton, 1991; Sullivan, 1991). Examination of the parasite loads within these populations of lizards revealed no clear support for the action of parasite-mediated sexual selection (PMSS) (McCoy, 1995d). All models of PMSS predict that among populations

greater sexual dimorphism is expected in populations with the greater parasite load, and within a population the most heavily parasitized males should display the least showiness (exaggeration of sexually dimorphic characters). Results of between-population comparisons were largely inconclusive due to differences between different types of parasites examined. Prevalences and infection rates for some parasites were greater in the GM population, but for other parasites were greater in the WM population. Within population tests revealed no significant correlations between parasite load and male showiness.

Although these comparisons failed to conclusively demonstrate the action of PMSS within these populations, neither did they conclusively discount it. Further examination of the relationship between parasite load and certain characters of male collared lizards reveals the potential for PMSS in these populations. Within populations, male showiness in color is not significantly correlated with infection with any of the parasites identified from these lizards. However, if male showiness in color (measured as scores on a linear function estimated to maximize discrimination between males and females) for adult lizards pooled from both populations is plotted against the number of trombiculid mites per lizard (Eutrombicula alfred-dugesi), the most heavily parasitized lizards display relatively low showiness, and individuals with the greatest showiness have relatively few parasites (Fig. 1). This plot indicates that there is considerable variation in showiness which is not explained by the number of parasites, but that parasite load may impose an upper limit to showiness. Parasitism may also impact host sexual selection through effects on behavioral characteristics (Andersson, 1994; Clayton, 1991). For adult males pooled from both populations there is a significant negative correlation between the number of E. alfred-dugesi per lizard and the rate of display behavior (Fig. 2). These results are still not conclusive evidence of the action of PMSS within these lizards, but strongly suggest that parasites may affect sexual selection in these populations.

Sexual Dimorphism to Reduce Intersexual Competition

Several of the characters (head width and head length) exhibiting sexual dimorphism in collared lizards could directly affect the size of prey that could be eaten. Sexual dimorphism in these trophic characters (Camilleri and Shine, 1991) could be a result of niche differentiation to avoid intersexual competition. Best and Pfaffenberger (1987) examined the diet of collared lizards in New Mexico and concluded that the diets of males and females were sufficiently different to suggest some niche differentiation.

To examine the possibility that competition for food affects sexual dimorphism in these lizards, samples of arthropods were collected at random locations on each study site using a sweep net. Each sample was collected from an area of 2 m x 10 m. At each site three samples were collected each month (May, June, and July) during summer, 1993. Arthropods in these samples were mainly orthopterans, coleopterans, and hymenopterans, but there were small numbers of hemipterans, dipterans, and arachnids. All of these are potential prey for collared lizards (Best and Pfaffenberger, 1987). All arthropods were assigned to size categories based on body length, and Shannon's index of diversity was calculated using these size categories. The total number of arthropods in each sample was also counted. Size diversity and total abundance were compared between sites using analysis of variance.

Size diversity tended to increase during the summer at both sites except for a very small decrease from June to July at the WM site (Table 1). Abundance of arthropods was generally greater at the WM site and increased substantially during the summer (Table 1). Size diversity of arthropods was significantly greater at the GM site (F = 5.899, df = 1, 14, P = 0.029). There were also significantly fewer arthropods collected at the GM site (F = 10.037, df = 1, 14, P = 0.007). Greater size diversity and lower abundance of potential prey has been shown to promote increased sexual dimorphism (Forsman, 1991). This

suggests that the potential for the evolution of sexual dimorphism to avoid competition is greater in the GM population. This result is also consistent with the observed pattern of sexual dimorphism if head length has the greatest effect on the maximum size of prey that can be eaten.

PREDATION AS A COUNTER-SELECTIVE MECHANISM

It is possible that a counter-selective mechanism, such as predation, could account for part of the mosaic nature of differences in sexual dimorphism in various characters displayed by these populations. Sexual selection could be promoting greater sexual dimorphism in multiple characters simultaneously while predation could limit the development of some of them, such as bright coloration, which might increase predation risk. Although predation, and predation risk, are difficult to measure, indirect measures such as sightings of potential predators or injury rates can indicate the relative degree of predation pressure. During 650.6 hours of observation on these populations (GM: 314.5 hrs, WM: 336.1 hrs) over three years, records were kept of all potential predators sighted on the study sites. Predators sighted included birds (red-tailed hawks, loggerhead shrikes, Mississippi kites, and roadrunners), snakes (coachwhips, prairie rattlesnakes, western diamondback rattlesnakes, and bullsnakes), and mammalian predators (coyotes, raccoons). For each year, the number of predators sighted per hour of observation was calculated for each site. Although there is substantial year to year variation, the rate of predator sightings was consistently greater at the GM site (Table 2).

Multiple recaptures of marked individuals in both populations allowed me to estimate injury rates for collared lizards. Injury rates were estimated by dividing the total number of injuries acquired by the number of days of exposure. There were no significant differences

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among years at either site (Mann-Whitney $\underline{U}$ - tests, all $\underline{P} > 0.05$), so lizards were pooled across years. Male lizards at the GM site, but not the WM site, acquired injuries at a significantly higher rate than females (GM: $\underline{P} = 0.02$; WM: $\underline{P} = 0.38$). Although males have slightly higher injury rates at the GM site (Table 3), the differences between sites were not significant for either sex.

The rates of predator sightings indicate that predation pressure is greater at the GM site but the rates of injury only mildly suggest this is so. The interpretation of injury rates as a measure of predation is complicated by the possibility that many injuries are probably sustained during intraspecific agonistic encounters. The potential for confound owing to this type of injury is manifest in the difference in injury rates between males and females. However, the intent of this portion of this study is to examine the possibility that predation constrains the expression of male showiness. Inherent in this hypothesis is that males will be subject to greater predation risk due to morphological (or behavioral) characters that are promoted by sexual selection. Thus males would be expected to have higher injury rates even in the absence of injuries due to intraspecific encounters.

Unfortunately, the comparison of relative predation pressure is not consistent with the observations of sexual dimorphism in these lizards. Apparently, predation pressure is greater in the GM population, but the GM population displays greater sexual dimorphism in color, which is the only character examined that would be expected to markedly increase predation risk. Although this suggests that predation may not be important as a direct constraint on the expression of sexually dimorphic characters, it does not preclude the possibility that predation affects sexual selection through constraint on behavior.

DISCUSSION

It is quite clear that the evolution of sexual dimorphism cannot be understood through studies testing only a single selective mechanism. This possibility has been suggested by several authors (Andersson, 1994; Wade, 1987), but very few studies of the evolution of sexual dimorphism have addressed more than one selective mechanism. Most often the potential for the operation of a single selective mechanism is promoted as evidence of the action of that mechanism. Despite theoretical discussion of confounds owing to the simultaneous operation of several selective mechanisms, empirical evidence demonstrating the potential for confusion has been lacking. That potential for confusion exists, in great measure, within populations of collared lizards from Oklahoma. Perhaps the clearest result of this study is demonstration of the potential for spurious results that could derive from the study of a single morphological character, or a single selective mechanism.

That the study of a single morphological character could lead to incorrect interpretation of the evolution of sexual dimorphism is evident in the mosaic nature of sexual dimorphism displayed by these populations. Had head length been the only character examined, the clear conclusion would have been that sexual selection is not responsible for the evolution of sexual dimorphism in this species. The population displaying the greater sexual dimorphism in head length (GM) also displays less polygyny and less variance in male reproductive success, both measures of the strength of sexual selection. On the other hand, it would also have been possible to conclude that sexual selection does indeed operate within this species, since the population displaying the greater sexual dimorphism in color also has the stronger correlation between male reproductive success and male showiness in color.

Different selective mechanisms also provide different interpretations for the evolution of sexual dimorphism in these lizards. Although sexual selection on most characters appears

to be greatest in the WM population, the potential for the evolution of sexual dimorphism to avoid intersexual competition for food is greatest in the GM population.

Even within a single selective mechanism, the potential for confound owing to the measurement of too few variables is evident. For collared lizards, this is probably most clear in the analysis of the effect of parasites on sexual selection. Many intraspecific studies of PMSS have considered only a single parasite (Clayton, 1991; Sullivan, 1991). The results of such an analysis in collared lizards would depend entirely upon which parasite was studied. If oxyuroid nematodes were the only parasites considered, it would be clear that PMSS is important in the evolution of sexual dimorphism in this species since the population displaying the greater sexual dichromatism also displays the greater prevalence and average infection rate for this parasite (McCoy, 1995d). If ixodid ticks were the only parasite studied, the results would be exactly opposite, since the population displaying greater sexual dimorphism also has a lower prevalence and lower average infection rate for this parasite.

The proximate mechanism producing sexual dimorphism could also significantly impact the interpretation of evolutionary mechanisms. If only a single year were studied it could be concluded that sexual dimorphism in the GM population is a result of sexual differences in mortality (McCoy, 1995a). However, data from more than one year and two populations indicates that sexual dimorphism arises mainly from sexual differences in growth. Further examination also revealed that sexual dimorphism in various characters is affected differently by sexual differences in allometry.

Analysis of sexual dimorphism in Oklahoma collared lizards clearly demonstrates that this phenomenon cannot be fully understood without testing all possible evolutionary hypotheses. Incorrect interpretations are highly likely as a result of incomplete studies. The examination of only a single selective mechanism, or a single sexually dimorphic character,

may yield results that do not correctly explain the evolution of sexual dimorphism. Clearly, the question that must be asked is not "is this mechanism operating within this population?", but "what is the relative strength of this mechanism within this population?" (Wade, 1987).

SUMMARY

Despite a wealth of empirical data regarding the evolution of sexual dimorphism, several questions regarding this phenomenon remain unanswered (Andersson, 1994). The lack of answers for most of these questions can be attributed to certain inadequacies in the majority of empirical studies of the evolution of sexual dimorphism, such as the failure to address multiple selective mechanisms, the failure to describe proximate mechanisms for sexual dimorphism, or the failure to consider counter-selective pressures. Despite theoretical discussion (Andersson, 1994), there exists no empirical data to demonstrate the potential for confound owing to these shortcomings. In this study, intraspecific variation in sexual dimorphism in the collared lizard (<u>Crotaphytus collaris</u>) is examined to determine the extent to which such failings may confuse the interpretation of data regarding the evolution of sexual dimorphism. Clearly demonstrated in this study is the possibility of spurious conclusions arising from the examination of a single selective mechanism, or a single dimorphic character. It is evident that the complete understanding of the evolution of sexual dimorphism will require studies which examine multiple dimorphic characters, and multiple selective mechanisms.

ACKNOWLEDGMENTS

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Table 1. Size diversity and total abundance (mean ± 1 standard deviation) of arthropods from two sites in Oklahoma.

Site	Size diversity[1]			Abundance[2]		
	May	June	July	May	June	July
GM	0.631 ± 0.20	0.960 ± 0.30	1.356 ± 0.39	11.33 ± 7.50	7.33 ± 5.13	7.33 ± 4.93
WM	0.458 ± 0.19	0.798 ± 0.20	0.750 ± 0.27	16.33 ± 10.02	21.00 ± 8.89	33.33 ± 15.57

[1] Shannon-Weiner diversity index based on length categories.

[2] Number of arthropods collected in a 2 x 10 m area.

Table 2. Rates of sightings of potential predators of _Crotaphytus collaris_ (predators per hour) at two Oklahoma locations.

Site	Year		
	1992	1993	1994
GM	0.234	0.145	0.166
WM	0.082	0.140	0.046

Table 3. Injury rates (injuries per day, mean $\pm$ 1 standard deviation) for male and female collared lizards from two Oklahoma populations.

Site	Males	Females
GM	0.030 $\pm$ 0.04 ($\underline{n}$ = 24)	0.009 $\pm$ 0.02 ($\underline{n}$ = 21)
WM	0.020 $\pm$ 0.04 ($\underline{n}$ = 28)	0.009 $\pm$ 0.05 ($\underline{n}$ = 28)

Figure 1. Male showiness in color versus the number of trombiculid mites (Eutrombicula alfred-dugesi) for adult collared lizards (Crotaphytus collaris) from Oklahoma.

Figure 2. The rate of display behavior by adult male collared lizards (Crotaphytus collaris) from Oklahoma versus the number of trombiculid mites (Eutrombicula alfred-dugesi) per lizard.
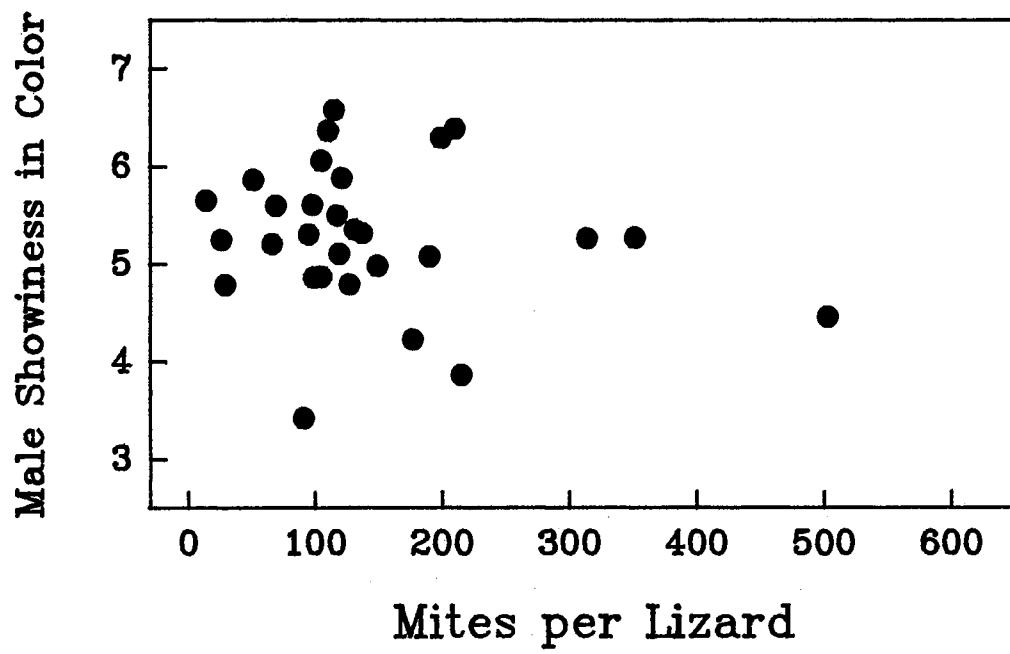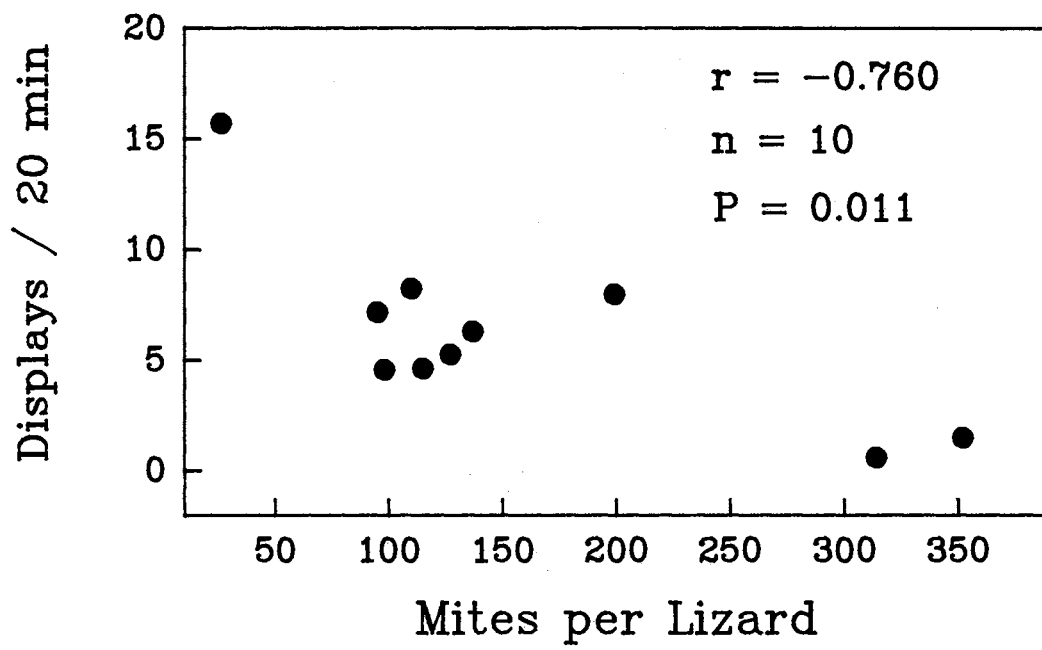
Figure 1

Figure 2

VITA

J. Kelly McCoy

Candidate for the Degree of

Doctor of Philosophy

Thesis: MECHANISMS OF SELECTION FOR THE EVOLUTION OF SEXUAL
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