Population differences in the roles of size and coloration in intra- and intersexual selection in the collared lizard, *Crotaphytus collaris*: influence of habitat and social organization

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Previous studies have shown that in three Oklahoma populations of collared lizards, Wichita Mountains (WM), Glass Mountains (GM), and Arcadia Lake (AL), sexual dimorphism in body size varies as WM>AL>GM, whereas dorsal color dimorphism varies as GM>WM>AL. Social organization at these sites also differs such that the environmental potential for sexual selection varies as AL>WM>GM. We conducted female choice and male competition laboratory trials to assess whether advantages to large or bright males correlate best with the interpopulation pattern of sexual dimorphism or with that of the environmental potential for sexual selection. Between-population trials involved bright-colored WM males and dull-colored AL males that were matched for size. AL females preferred bright WM males, but WM females did not. WM males had higher agonistic scores in intrasexual contests when aggression was low, but AL males consistently had higher scores when aggression escalated. Within-population trials involved males that were disparate in color but size matched and disparate in size but color matched. Size was important in male contests in all populations. Color brightness was a factor in male trials only at AL. Also, only AL females preferred brighter males, and larger males were not preferred in any population. The importance of intra- and intersexual selection in these populations cannot be inferred from the observed pattern of size and color dimorphism. Rather, interpopulation differences in the environmental potential for females to assess and choose from among multiple males, and for males to interact, are most consistent with the observed outcomes. *Key words:* collared lizards, *Crotaphytus collaris*, female choice, male aggression, sexual dimorphism, sexual selection. *[Behav Ecol 8:506-517 (1997)]*

Several hypotheses have been advanced to explain the evolution of morphological differences between the sexes, including parasite-mediated mechanisms, differential niche utilization, intersexual food competition, and intra- and intersexual selection (Andersson, 1994; Hedrick and Temeles, 1989; Wade, 1987). Numerous studies provide strong empirical support in several vertebrate taxa for a role of both intrasexual male competition (e.g., Clutton-Brock and Harvey, 1977; Howard, 1978; Stamps, 1983; Warner and Hoffman, 1980) and female mate preferences (e.g., Basolo, 1990; Cooper and Vitt, 1993; Johnson et al., 1993; Sullivan, 1983) in the evolution of sexually selected traits. While providing important tests of theory, many of these studies examined only one of the mechanisms of sexual selection. The few studies that evaluated both mechanisms in the same species usually showed that intra- and intersexual selection act on male traits congruently (Ligon et al., 1990; Luyten and Liley, 1991; Mathis, 1991; Moore, 1990; Warner and Schultz, 1992; Zuk et al., 1990b), but the two may act antagonistically (Boake, 1989).

Many studies of sexual selection are limited because they examine traits in males from only a single population. Such studies ignore growing evidence that the potential strength of sexual selection varies greatly across populations because social organization often shows intraspecific variation (e.g., Davies, 1992; Lott, 1991). Different populations experience varying ecological conditions that almost certainly influence the degree and type of sexual selection that occurs locally (Wade, 1995). For example, strong predation pressure may select against exaggerated male traits in some habitats if these traits increase conspicuousness, and female preferences for male traits may vary accordingly (Endler, 1983; Luyten and Liley, 1991; Stoner and Breden, 1988). In other cases, male signals may have evolved as a compromise between attractiveness to females and predation risk (Ryan et al., 1982). Even when predation risk is low, sexual selection may be limited if local environmental factors do not favor male-male competition, if females do not have the opportunity to select from more than one available mate (Stamps, 1983), or if environmental conditions render male traits ineffective in certain habitats (Luyten and Liley, 1991). Conversely, ecological conditions that promote asymmetries in male mating success such as clumped females or resources (Emlen and Oring, 1977; Wade, 1995), may strongly favor either intra- or intersexual selection for male traits.

Unraveling mechanisms by which sexual dimorphism has evolved can be further complicated by inter- or intraspecific variation in the selective pressures acting on females as well as males. For example, one or more traits may be selected in males, but because intrasexual selection on females may favor the development of the same traits, these species (or populations) may be less dimorphic (Trail, 1990). Because traits in females may also be under sexual (or natural) selection (Fairbairn, 1990) and the strength of selective forces may vary in different populations, it is essential that dimorphism be measured as the difference between males and females in the expression of the trait (McCoy et al., 1994; in press) and interpreted as the difference of the total of selection acting on both sexes.

Table 1

Summary of interpopulation differences in size and color dimorphism and the environmental potential for sexual selection and predicted outcomes of female mate choice and male-male trials based on interpopulation standard differences among these variables

Variable		Population		
		AL	GM	WM
Expression of color dimorphism		Lowest	Highest	Intermediate
Expression of size dimorphism		Intermediate	Lowest	Highest
Environmental potential		Highest	Lowest	Intermediate
Predictions based on				
Color dimorphism	Mate choice	Weak	Strong	Strong
	Male-male	Weak?	Strong?	Strong?
Size dimorphism	Mate choice	Intermediate	Weak	Strong
	Male-male	Intermediate	Weak	Strong
Environmental potential	Mate choice	Strong	Weak	Weak
	Male-male	Strong	Weak	Intermediate

Relatively few studies have examined experimentally the role of dimorphic male characters in both intrasexual competition and female preference in vertebrates that show pronounced geographic variation in these traits (reviewed in Harvey and Bradbury, 1991). Diurnal lizards are good organisms in which to conduct studies on sexual selection. Males often show pronounced dimorphism in both body size and coloration, and these characters could potentially play a role in competitive contests with other males, as well as in interactions with potential mates. Intrasexual selection has been implicated in the evolution of orange head coloration in male broad-headed skinks, *Eumeces laticeps* (Vitt and Cooper, 1985) and increased head depth in the phrynosomatid *Uta palmeri* (Hews, 1990). Males in many diurnal lizards obtain high mating success by excluding competitors from female home ranges, prompting Stamps (1983) to argue that there is little potential for intersexual selection in these lizards. Indeed, demonstrations of female choice are rare in this taxon (Olsson and Madsen, 1995; Tokarz, 1995). However, female preference for mates based on body coloration has been demonstrated in two diurnal lizards (Cooper and Vitt, 1993; Sigmund, 1983) and in a nocturnal gecko (Ellingson JM, personal communication). To our knowledge, no studies have examined intraspecific geographic variation in the importance of both intra- and intersexual selection in sexually dimorphic lizards.

In this study we used individuals from three populations of collared lizards, *Crotaphytus collaris*, to test alternative predictions about the operation of intra- and intersexual selection generated from interpopulation differences in male size and coloration patterns and variation in the environmental potential for sexual selection. We conducted female preference trials and male-male contests in the laboratory using collared lizards from three populations that show differences in sexual size and color dimorphism and the environmental potential for sexual selection (Baird et al., 1996; McCoy, 1995). We also estimated predation intensity in the field to examine the extent to which counterselection against bright male coloration might operate.

Predictions based on population differences in male size and coloration

Three Oklahoma populations of collared lizards show distinct interpopulation differences in two dimorphic characters that

are under sexual selection in other lizards: body size and body coloration. These populations are the Glass Mountains (GM) in northwestern Oklahoma (Major County), the Wichita Mountains (WM) in southwestern Oklahoma (Comanche County), and Arcadia Lake (AL) in central Oklahoma (Oklahoma County), USA. These populations exhibit sexual dimorphism in body size, but not equally so (McCoy et al., 1994). Males are larger than females at all localities, but the degree of sexual dimorphism in snout-vent length (SVL) varies among populations as follows: WM > AL > GM. Spectrophotometric measurements and subjective rankings of gular, dorsolateral, and ventrolateral coloration also revealed statistically significant differences in the degree of color difference (dimorphism) between males and females from each of the three sites (GM>WM>AL) (McCoy et al., in press).

Numerous studies reveal preferences by female vertebrates for bright, conspicuous male coloration (e.g., Bakker and Mundwiler, 1994; Cooper and Vitt, 1993; Johnson et al., 1993), although color sometimes plays a role in male contests (Zucker, 1994). Large size is often advantageous in male contests (e.g., Clutton-Brock et al., 1992; Howard, 1978; Warner and Schultz, 1992). Therefore, it is reasonable to hypothesize for collared lizards that bright coloration is primarily under intersexual selection, whereas male size is primarily under intrasexual selection. If this hypothesis is correct, then based on the dimorphism pattern alone, intrasexual selection might be strongest in the WM lizards because this population exhibits the largest size dimorphism (Table 1). Strong intersexual selection for color might also be expected in both GM and WM lizards because sexual color difference is pronounced in both populations. Intrasexual selection is expected to be least intense among GM lizards, where size dimorphism is least developed. Finally, strong intersexual selection is not expected among AL lizards because strong dichromatism is absent. Size dimorphism at AL is intermediate, so intrasexual selection for large size might be expected.

Predictions based on population differences in social organization

The three populations also differ in the geometry and distribution of suitable habitat and in social organization. These differences likely influence the potential for male characters to function as effective signals of their ability to defend resources (resource holding power; Maynard-Smith and Parker,

1976), and in females to evaluate several males when selecting mates, such that the environmental potential for sexual selection varies AL > WM > GM. The AL population occupies continuous, extremely homogeneous expanses of granite boulders imported to construct the flood-control spillway for the Arcadia Lake dam (constructed in 1986) and continuous expanses of natural sandstone within 4 km. We used lizards from both the imported rock and surrounding natural rock areas in our trials. Comparisons made in the field using Munsell color charts (see Methods) revealed no differences in coloration hue, value, or chroma readings between lizards occupying imported boulders at the AL dam and those on nearby natural sandstone habitats. Even though they are the most drab of the three populations, AL lizards are visually conspicuous owing to the uninterrupted, homogeneous terrain. In addition, the density of lizards within both artificial and natural habitat patches at AL is higher than at the other two sites. Adult male territories abut one another closely and overlap the home ranges of as many as seven females. Home ranges of 42% of females mapped in 1991 and 1992 were overlapped by two or even three territorial adult males and as many as four nonterritorial, but sexually mature yearling males ($\bar{x}$ overlapping males/female = 3.22, SE = 0.16; Baird et al., 1996). Females occupy highly overlapping home ranges, and intrasexual aggression among females at the AL site is 2.7 and 4.8 times lower than at the GM and WM sites, respectively (Baird et al., 1996; McCoy, 1995). Because the rocky substratum is continuous and male territories are close to one another, females have the potential to readily assess more than one male.

In contrast to AL, the habitat at WM is much more discontinuous, consisting of outcroppings of granite boulders interrupted by grassy expanses. Males display from prominent elevated perches atop these boulders, which may promote distant transmission of visual signals such as bright coloration. Because WM females occupy home ranges within patches of rock that are widely separated from one another, they are overlapped by fewer males than are AL females ($\bar{x}$ number of overlapping males/female = 2.3, SE = 0.8; McCoy, 1995). In addition, intrasexual female aggression at WM ($\bar{x}$ aggressive acts/h = 7.5, SE = 2.7) is the highest of the three sites. Consequently, the potential appears limited for females to move throughout the habitat to assess and choose a mate from among multiple males.

At GM, collared lizards are restricted to narrow, linear outcroppings of gypsum rock that ring the tops of steep buttes. Females in the GM population are the least dense of our three sites and are overlapped by the fewest males per female ($\bar{x}$ = 1.3, SE = 0.3). Rates of intrasexual aggression in GM females ($\bar{x}$ aggressive acts/h = 4.2, SE = 1.5) are lower than those at WM, but are still nearly three times higher than at AL. The elongate geometry of the rock substrate, coupled with low female densities and high intrasexual female aggression, appears not to facilitate polygyny or female assessment of more than one mate.

A different set of predictions about the roles of inter- and intrasexual selection on male traits can be generated on the basis of variation in the environmental potential for female assessment of more than one male and the potential for intrasexual contests (Table 1). Strong intersexual selection is expected at the AL site because high densities of lizards and the continuous habitat would favor female assessment of multiple males. Discrimination among males may be especially probable because both sexes frequent the linear interface between the rock habitat and the surrounding prairie vegetation, perhaps because there is a steady flow of insect prey (see Polis and Hurd, 1995). Intrasexual selection on body size also should be strong because neighboring male territories are

contiguous and defense of boundaries involves a higher rate of patrol and display behavior than in the other two habitats (Baird et al., 1996; McCoy, 1995). In the WM population, the potential for female assessment of male coloration appears lower than at AL because females are overlapped by fewer males, female–female aggression is higher, and rock patches defended by males are separated by grassy expanses over which females rarely traverse. On the other hand, bright male coloration coupled with large size might function effectively in the intrasexual advertisement of territory ownership to competitor males over the long spaces between rocky outcrops. The environmental potential for both intra- and intersexual selection is expected to be lowest in the GM population. The geometry of the habitat and female aggression probably preclude opportunities for females to assess multiple males. The potential for male–male confrontations is low because males are sparsely distributed along linear habitat patches.

METHODS

Study subjects

Lizards used in laboratory trials were captured by noosing from the three study populations. Although male coloration changes ontogenetically during the first year, coloration is maximally developed by the beginning of the second year when males have attained adult body size (Baird et al., 1996; McCoy et al., in press) and does not change henceforth. We selected only large adult males that interact with females frequently in the field (Baird et al., 1996; McCoy, 1995; Rostker, 1983). Because adult male body size varies geographically (McCoy et al., 1994), the size ranges of males used in our trials also varied (GM = 89–102 mm SVL; WM and AL = 98–112 mm). Trials were conducted from 16 May to 1 July, which is the reproductive season of *C. collaris* in Oklahoma. Female reproductive condition was determined by palpation. We used only females with oviducal eggs (size range = 85–107 mm SVL). Lizards were transported to laboratories in Edmond and Stillwater, Oklahoma, for experiments. When experiments were finished, subjects were returned to their precise collection sites and released unharmed.

Between-population experiments

In 1992, we conducted female preference tests and male–male contests with lizards from WM and AL using a between-population design. Twenty-four adult males were used to establish size-matched pairs with one lizard from AL and one from WM (mean difference in SVL among pairs = 3.3 mm). Of the three study populations, difference in color brightness is most pronounced between males from AL and WM, but average male size in these populations is similar. Therefore, experiments giving females a choice between AL and WM males offered the best potential to test the extent to which female *C. collaris* use color as a basis for mate preference and the extent to which males use it in intrasexual contests.

Experiment 1. Size matched, color different: female choice
For between-population female preference trials, we used rectangular arenas (overall dimensions = 204 cm long × 72 cm wide × 45 cm high) subdivided into three sections by two glass partitions. For each trial, one WM male and one AL male were placed randomly in opposite ends of the choice chamber, and either a WM or an AL female was placed in the center compartment where she could view both males. The chamber was uniformly illuminated and heated to optimal temperatures of 35–40°C by three 100-W incandescent light bulbs and two 120-

Table 2
**Weights of agonistic acts observed during male–male contests used
to calculate three indices of agonistic intensity**

Agonistic act	Total aggression	Total agonism	Graded agonism
Bite	+ 1	+ 1	+ 3
Fight	+ 1	+ 1	+ 3
Superimposition	+ 1	+ 1	+ 3
Supplant	+ 1	+ 1	+ 3
Display	+ 1	+ 1	+ 2
Circle	+ 1	+ 1	+ 2
Pushup	+ 1	+ 1	+ 2
Gape	+ 1	+ 1	+ 2
Approach	+ 1	+ 1	+ 1
Retreat	0	− 1	− 1
Flee	0	− 1	− 1
Crouch	0	− 1	− 1

cm, 40-W fluorescent light bulbs with reflectors. Before trials, we kept lizards in separate cages in the laboratory in a room heated such that optimal body temperatures were maintained. Females were each used only once. Male pairs were used twice, once each with a WM and an AL female in alternating order. The outcome of trials was not related to the order in which females were tested.

At the beginning of each 30-min trial, we placed the female gently on the midline in the center of her compartment. Every 30 s the position of the female was recorded as being to the right or the left of a midline in her section of the arena. As a control for the possibility that females might prefer one side of the arena over the other, we separately placed eight different females in the arena without live males in the end compartments. These females moved about their compartment randomly with no statistically significant preference for one side or the other. For both experimental trials and controls, we computed the percentage of observations that females spent on each side of their chamber as per similar studies (Basolo, 1990; Houde and Torio, 1992) and compared these statistically using a Wilcoxon matched-pairs signed-rank test. Time associated with males is an appropriate measure of female preference in *C. collaris* because throughout the breeding season females approach and physically contact some males but flee from others (Baird et al., 1996). We used one-tailed probabilities ($\alpha = 0.05$) throughout in tests of female preference for bright or large males (run separately) and to test the hypotheses that bright or large males would prevail in intrasexual contests (see later).

Experiment 2. Size matched, color different: male contests
We staged male–male contests using maximally color divergent males from the AL and WM populations (mostly the same pairs used in the previous mate choice trials). We matched 30 males in pairs by size with one lizard from AL (dull) and one from WM (bright). Pairs were introduced into a neutral arena (204 × 72 × 45 cm) and immediately observed for 30 min from a darkened room behind a blind. The chamber was illuminated and heated and males were maintained and allowed to bask as in experiment 1. We tallied agonistic behavior of both animals over 30 min, and males were removed from the arenas at the end of trials. We distinguished the following aggressive behavior patterns: fight, bite, superimposition, supplant, lateral display, circle, gape, pushup, and approach; and the following submissive behavior patterns: retreat, flee, and crouch (Carpenter, 1978; Rostker, 1983; Yedlin and Ferguson, 1973). We computed scores for each male for three indices of agonistic intensity (Table 2).

All three indices were highly intercorrelated (pairwise $r > .90$, $p << .001$), so we used only graded agonism because it best incorporated obvious differences in agonistic intensity.

Results of between-population experiments might be biased because the two males could see one another such that their behavior could have been influenced by the display patterns of opponents or because of inherent population-based differences in behavior (Ruby and Baird, 1994). Despite these possible problems, we think that our between-population experiments are valid because we observed neither a temporal correlation between the display activities of males nor qualitative interpopulation differences in male behavior.

Within-population experiments

In 1993 we conducted male–male contests and female preference tests with lizards from all three populations using a within-population design. We changed the arena design to eliminate any possible transmission of social signals between males. Arenas consisted of two chambers for males (78 cm long × 39 cm wide × 40 cm high) placed side by side but separated by a movable opaque partition, and a chamber for a female (78×39×40 cm) spanned equally the front of each male's chamber, with a pane of glass separating the female's and males' chambers (Figure 1). The female's chamber was fitted with a window covered by a blind with a small viewing port so that the behavior of the female and both males could be observed without disturbing them. A piece of indoor-outdoor carpet in each chamber provided traction for the lizards, and the chambers were washed between trials to remove scent from previous occupants. The chambers were each equally illuminated and heated (33–38°C) by a 100-W incandescent bulb with reflectors. The lights were on a 13 h:11 h light-dark cycle, which is typical of Oklahoma during May–July. Each male's chamber was equipped with a cinderblock shelter, used either for basking or shade. Lizards were fed crickets in the arenas daily, and water was provided by misting.

For-mate choice experiments, males and females were introduced into 11 arenas no later than 1500 h on the setup day. Bright and dull (or large and small) males were placed on right and left sides of arenas alternately. From 1200 h to 1500 h on the following day, we recorded the position of the female at 10-min intervals. Two heats of different females were run for each population ($N = 22$ females for GM and WM, $N = 21$ for AL color trials, $N = 20$ for AL size trials). We calculated the percentage of observations that females positioned themselves on one side or the other and compared preference for bright or large males using a Wilcoxon matched-pairs signed-rank test.

Following female preference trials, we removed the females and between 1000 h and 1600 h of the following day conducted male–male contests using the same males. Males were allowed to interact directly for 30 min, beginning when the partition separating the two males was removed. We recorded the same aggressive behavior patterns as during the between-population tests of males.

Experiment 3. Size matched, color different: female choice
For each population, males were matched for SVL ($\bar{x}$ overall pairwise difference in SVL = 2.72 mm, SE = 0.20, $N = 33$ pairs), and color brightness was varied. Color rankings were made when males had been heated in a 40°C oven to obtain a cloacal temperature ranging from 35 to 38°C, and allowed to bask under incandescent lamps ($T_A = 35$–38°C). Color brightness was assessed on the dorsolateral body surface and the dorsal surface of the limbs where *C. collaris* males reflect in blue-green wavelengths (McCoy et al., in press). Pairings were made by one observer, and then a second observer who
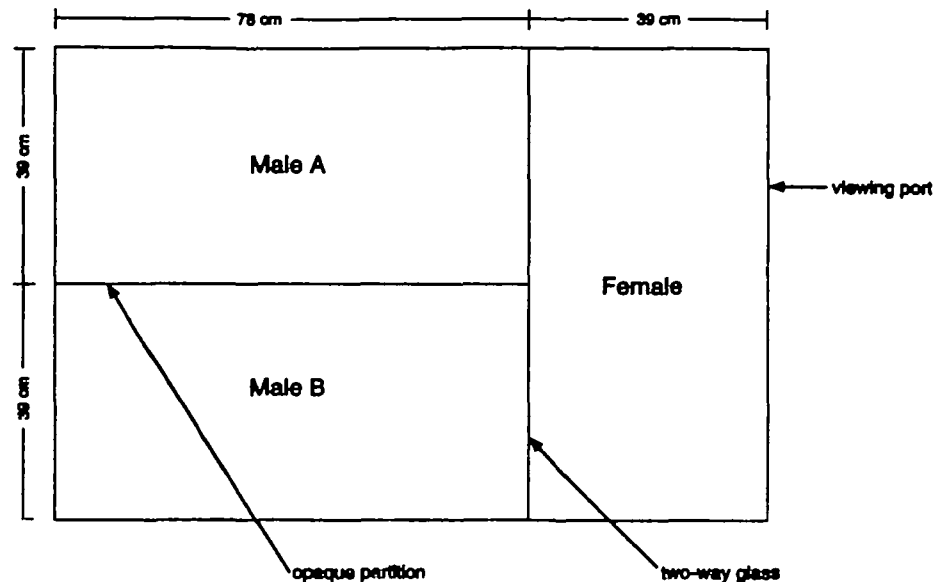
Figure 1
Arena used during within-population female preference trials (experiments 3 and 4) and intrasexual male contests (experiments 5 and 6).

was naive to the first observer's classifications independently ranked the brightness of individuals in each pair. Assignments of bright and dull by the two observers were the same in at least 9 of 11 pairs in each population. In the few cases where the rankings by the two observers did not agree, lizards were re-paired with different individuals to achieve maximum difference in color brightness.

As confirmation of our subjective ability to assess color brightness, we also measured color hue, value, and chroma on the dorsal, dorsolateral, ventrolateral, and gular body regions using Munsell Color Charts for Plant Tissues (MacBeth Division, Kollmorgen Instruments Corporation), which correspond quite closely to the color characteristics of collared lizards. Due to limited variation in all three color parameters at the gular region, these data were discarded. For the other body regions, we 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. We then performed principal components analysis (PCA) on these data, pooling lizards from all three sites, to generate a single set of multivariate axes that characterized color variation over the three populations. Most (75%) of the variation was explained by the first four PCA axes. Factor 1 was primarily a hue attribute (but also with a negative loading for dorsal chroma). Factor 2 was a value attribute, factor 3 was chroma at the dorsal and dorsolateral regions, and factor 4 was chroma at the ventrolateral region.

We then computed pairwise differences of the scores on these first four principal components, bright pairmate minus dull pairmate, and subjected these values to mulitivariate analysis of variance (MANOVA). We rejected the null hypothesis of no color difference between bright and dull lizards of our pairs, considering together the four synthetic variables (Wilks' lambda F-statistic = 3.770; df = 4, 29: $p < .015$). Thus, pairs in experiment 3 were indeed color disparate and size equivalent. Within pairs, these size-matched bright lizards were of bluer hue and higher color value and chroma.

Experiment 4. Size different, color matched: female preference
Using the same subjective ranking procedure as in experiment 3, we matched males for color brightness while varying body size ($\bar{x}$ overall pairwise difference in SVL = 6.94 mm, SE = 0.27, N = 32 pairs). To confirm our subjective pairings of males matched for color brightness, we performed an anal-

ysis parallel to that described above for experiment 3. The lizards used in experiment 4 were mostly the same as those in experiment 3 (only paired differently), but a few new individuals were used to establish better color equivalent, size disparate pairs. Principal components analysis revealed a pattern similar to that of experiment 3. The first four principal components explained 76% of the total variation. However, in this case, MANOVA of the paired differences of the first four principal components indicated that color attributes of pairmates were not significantly different (Wilks' lambda F-statistic = 0.718; df = 4, 28: $p > .5$). Thus, pairs in experiment 4 were size disparate and color equivalent.

Experiment 5. Size matched, color different: male contests
Following experiment 3 and using the same males matched for size and varied for color, we compared graded agonistic scores for bright versus dull males for each population using a Wilcoxon matched-pairs signed-rank test.

Experiment 6. Size different, color matched: male contests
Following experiment 4 and using the same males, we conducted male–male contests using the same protocol as for experiment 5.

Field assessment of predation intensity

We recorded two types of data to assess the relative intensities of predation at our three sites. During May and June of 1992, 1993, and 1994, each day we recorded the number of sightings of terrestrial and avian predators of *C. collaris* to yield a comparative hourly frequency of sightings of potential predators. Predators of *Crotaphytus* observed included snakes (*Masticophis, Nerodia, Pituophis, Crotalus*), birds (*Geococcyx, Buteo, Ictinia, Lanius*), and mammals (*Canis latrans, Procyon*). Multiple recaptures of lizards also allowed us to calculate injury rates. During 1992 and 1993, serious injuries such as tail loss, broken bones, and laceration of skin and muscle were recorded as instances of attacks by predators. Our field observations show that although interspecific aggression sometimes produces bite imprints that match the shape of lizard jaws, male–male contests do not result in these types of serious injuries that we attributed to predation attempts. Injury rates at sites were estimated by dividing the total number of injuries acquired by the number of days of exposure per lizard.

(Size Matched, Color Different)
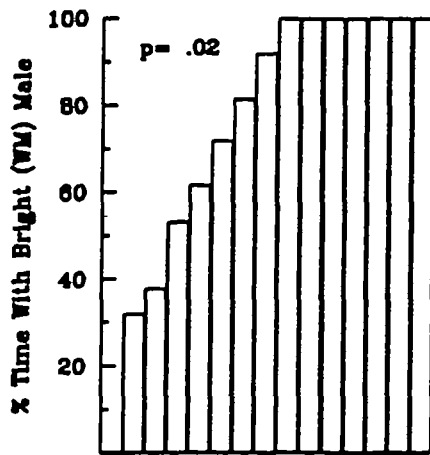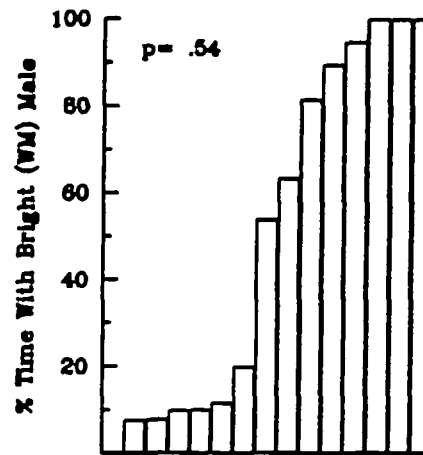
Figure 2
Preferences for bright WM males by AL and WM females. Trials without a bar indicate zero percent time with bright males.

RESULTS

Between-population experiments

Experiment 1

AL females associated with bright WM males more than with dull AL males (Wilcoxon matched-pairs signed-rank test: $Z = 2.40$, 15 pairs, $p = .016$; Figure 2). The WM females did not

Figure 3
Graded agonistic scores for dull AL males graphed versus bright WM pairmates. The diagonal line denotes equal scores for each male of a pair. The dashed horizontal line indicates the graded agonistic score of 36 above which AL males consistently had the higher level of agonism.

associate preferentially with the bright WM males ($Z = 0.26$, 15 pairs, $p = .26$).

Experiment 2

Graded agonistic scores of bright WM males were not statistically greater than those of dull AL males (Wilcoxon matched-pairs signed-rank test: $Z = 1.612$, $N = 18$ pairs, $p = .07$). We examined the distribution of cases in which the AL or WM male had the higher score with respect to the level of graded agonism displayed by the AL male. WM males had higher scores as long as the graded agonism of the AL lizard was low (i.e., did not exceed a score of 36; Figure 3). Beyond this score, AL males consistently had higher scores than their WM opponents (Mann-Whitney U test: $U = 77$, $N_1 = 11$, $N_2 = 7$, $p < .001$). In contrast, the distribution of cases in which AL and WM males had higher scores with respect to the graded agonism of WM lizards was not statistically different ($U = 59.5$, $N_1 = 11$, $N_2 = 7$, $p = .06$).
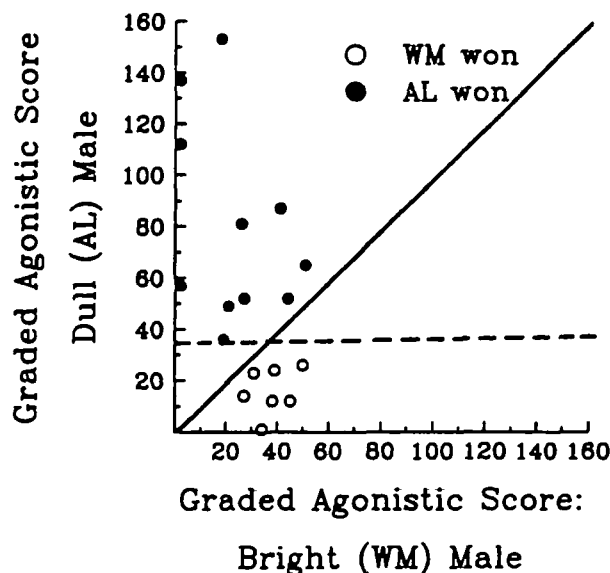
Within-population experiments

Within minutes of being placed in arenas (experiments 3 and 4), females explored their chambers such that they detected both males. During these trials, females spent a large percentage of the time (83% of observations for all populations pooled) positioned at the front glass oriented such that they could see the males.

Experiment 3

Neither WM nor GM females demonstrated a statistically significant preference for bright males when male size was controlled (WM, $p = .36$; GM, $p = .10$; Figure 4). In contrast, AL females associated more frequently ($p = .013$) with brightly colored males than with dull ones (Figure 4).

Experiment 4

Females did not display a significant preference for large over small males that were matched for color in any of the three
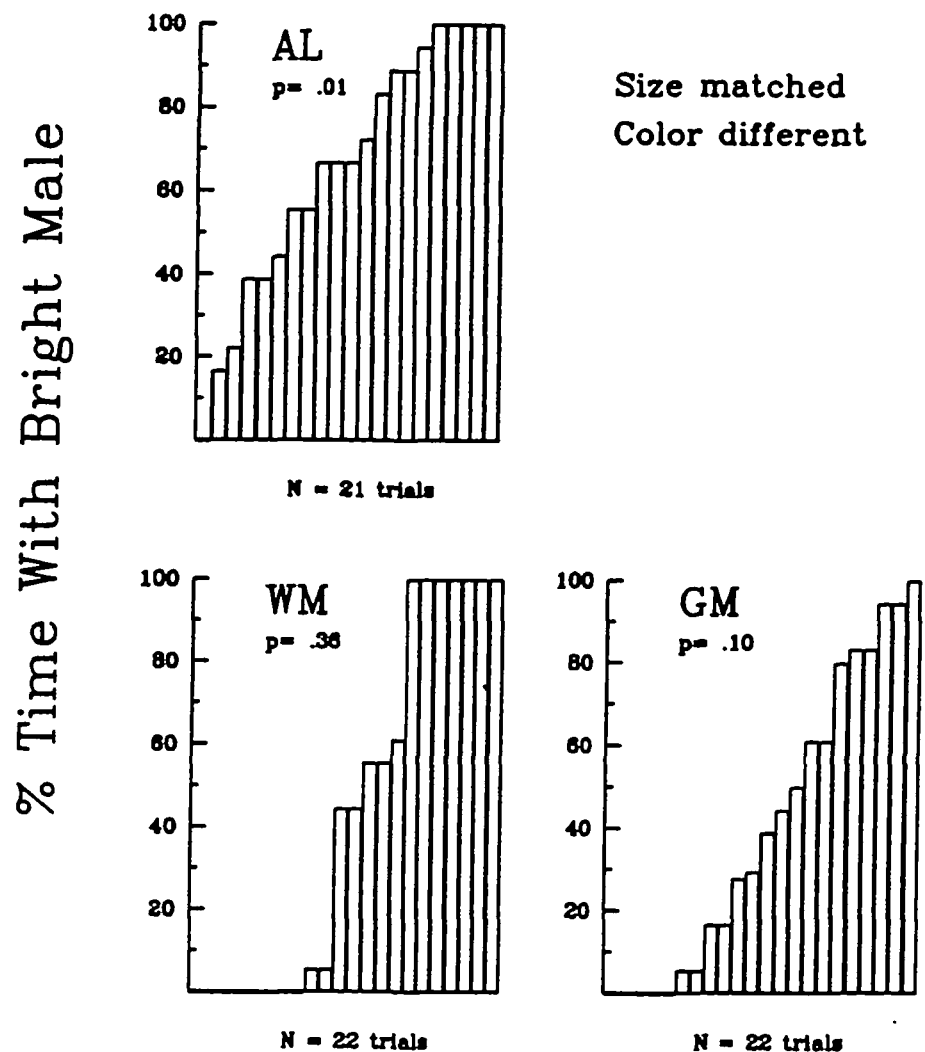
Figure 4
Female preferences for bright males within the three study populations when males were matched for size. Trials without bars indicate zero percent time spent with bright males.

populations (WM, p = .18; GM, p = .37; AL, p = .21; Figure 5).

Experiment 5
Males interacted agonistically in 30 of 32 trials (all populations pooled = 94%) where color was varied and size controlled. The more brightly colored AL males had significantly higher graded agonistic scores than dull males (p = .02), while brightly colored GM and WM males did not (p = .25, p = .09, respectively; Figure 6).

Experiment 6
Males interacted agonistically in 30 of 32 trials (all populations pooled = 94%) where size was varied and color controlled (Figure 7). Larger males had statistically higher graded agonistic scores than smaller males in all three populations (GM, p = .002; WM, p = .016; AL, p = .002).

Predation intensity

Sightings of potential predators suggested that predation intensity was highest at AL, intermediate at GM, and lowest at

WM. Potential predators were sighted at AL 1.2–4.6 times more frequently than at GM and 3.5–16.3 times more frequently than at WM (Table 3). Total injury rates revealed a similar pattern (Table 4), although differences among sites for either males or females were not statistically significant (Kruskal-Wallis ANOVA; males, F = 1.08, p = .34, females, F = 1.76, p = .17). Although males sustained more injuries at all sites, sexual differences were not statistically significant (p > .17). No lizards at GM or WM experienced tail breakage during our study, whereas the mean tailbreak rate for AL males was significantly higher (F = 3.04, p = .05, Kruskal-Wallis ANOVA). Although tailbreak was also recorded in AL females, the rate was not significantly higher than at GM and WM (F = 1.30, p = .27, Kruskal-Wallis ANOVA). At AL, males tended to suffer more tailbreaks than females (Table 4), but this was not statistically significant.

DISCUSSION

Our results are most consistent with the hypothesis that variation in the environmental potential for sexual selection ex-
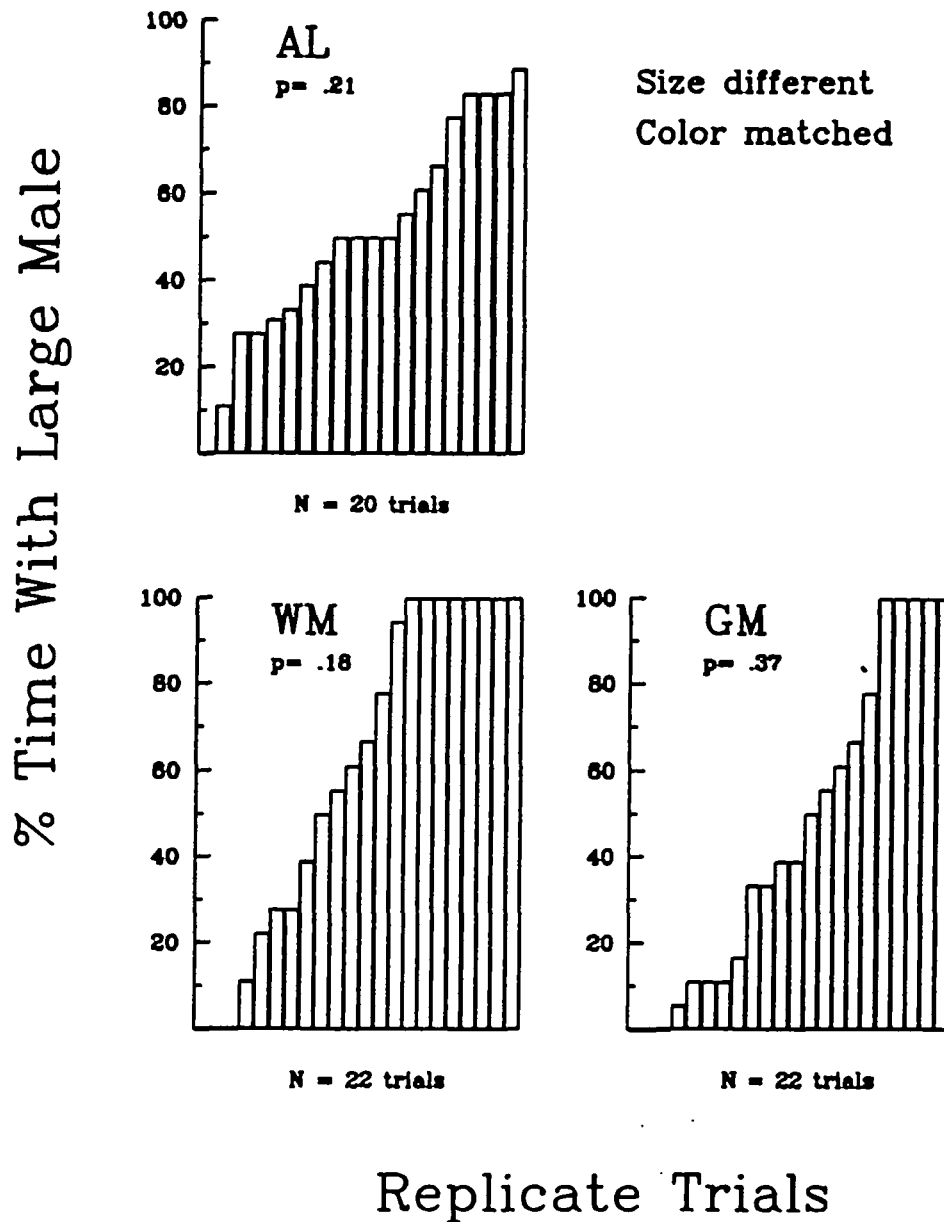
Size different

Color matched

Figure 5
Female preferences for large males within the three study populations when males were matched for color brightness. Trials without bars indicate zero percent time spent with large males.

plains the observed pattern of male character development in these three populations of *C. collaris*. Larger males had higher agonistic scores in all three populations, suggesting that large size is under intrasexual selection, especially in the polygynous AL and WM populations. Size dimorphism is the least developed in the GM lizards (both mature males and females are smaller, McCoy et al., 1994), where polygyny is least developed and the males have the fewest opponents due to the linear distribution of habitat. Large size is an important determinant of male social status in many vertebrates, and it is not surprising that size would be under strong intrasexual selection in collared lizards. Larger males would be better equipped for escalated male contests that can involve attacks and bites (Baird et al., 1996; Fox and Baird, 1992). Even when contests do not escalate to attacks, it would be advantageous for smaller males to acquiesce to minimize the threat of injury.

Contrary to our intitial expectations, color was important in intrasexual contests. Taken together, results of between- and

within-population male contests suggest that bright coloration is under intrasexual selection where the social organization is most polygynous (AL). Furthermore, results suggest that the role of color depends on the difference between contesting males, and the extent to which color is an effective signal of resource holding power (RHP). In trials pitting dull AL males versus bright WM males (experiment 2), the AL males showed much greater variation in agonism. In almost half of the interactions, the graded agonistic score for the AL male was higher than any of the scores recorded for WM males. One interpretation of this outcome is that in the highly polygynous AL population there has been greater selection for the potential to escalate encounters. Although color had a marginally significant ($p = .09$) effect on the outcome of male–male interactions at WM where bright color could readily transmit across the areas separating rocky outcrops defended by males, in contests with AL males the brighter WM males did not escalate agonism to the same level as their AL opponents.
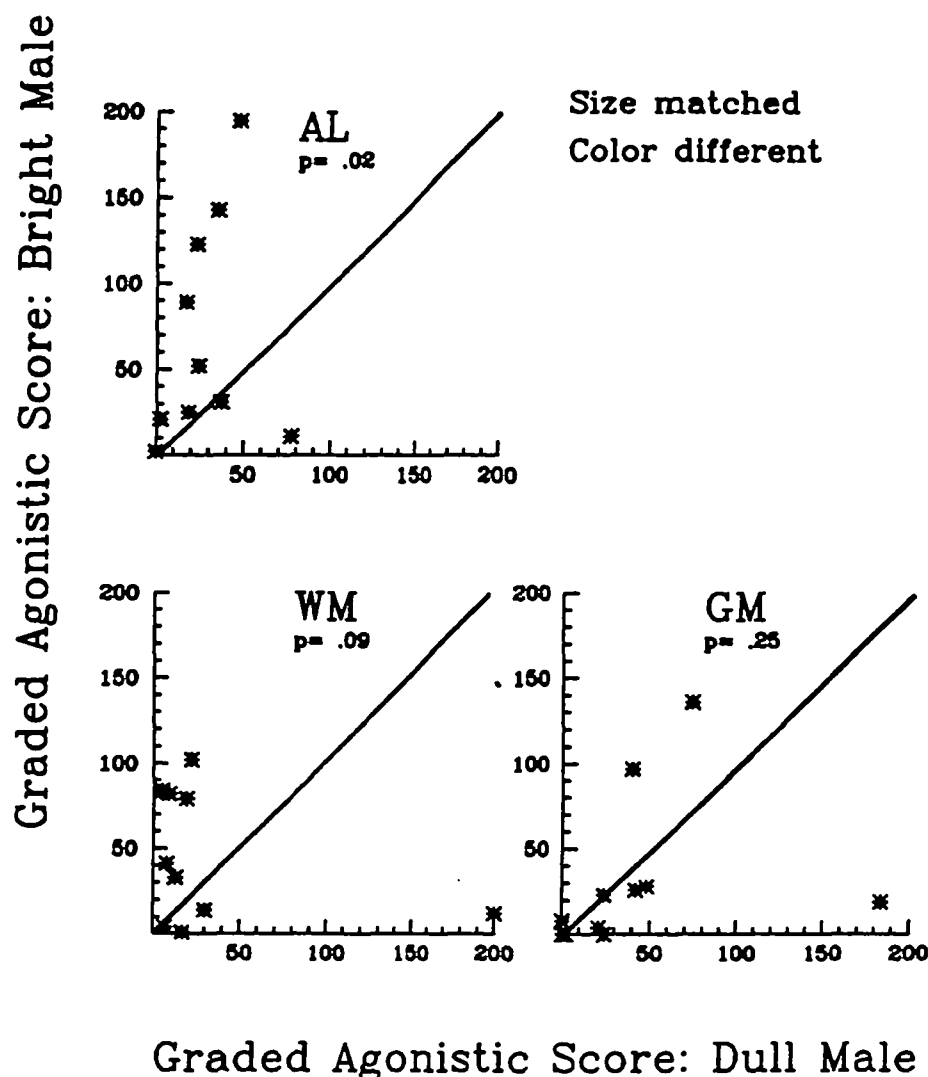
Figure 6
Graded agonistic scores for bright males graphed versus dull pairmates matched for size within the three study populations. The diagonal line denotes equal scores for each male of the pair.

Bright color also transmits well in the continuous AL habitat; however, color alone appears not to be a sufficiently strong signal of RHP where territories are densely packed. In trials where color differences were extreme (experiment 2), AL males obviously did not use color brightness as the sole signal of RHP because WM males were brighter in all pairings. However, when male color differences were more subtle (experiment 5), color brightness influenced the outcome of trials involving AL males. The average agonistic score of dull AL males during trials with bright WM males was more than twice that when AL males were contesting one another. Taken together, results support the hypothesis that color brightness functions as a signal of RHP in AL males, particularly when coloration differences are not extreme, but that high levels of agonistic behavior are also important in this population, especially when contesting a male that is much brighter. We suggest that AL males rely on both signals because the intensity of territorial competition is higher in this habitat due to increased densities and higher environmental potential for polygyny. That color did not play a role in the outcome of contests between GM males where the potential for polygyny and male confrontation is low is also consistent with this explanation.

Because female-choice trials preceded male–male contests in our within-population protocol, a possible alternative explana-

tion of the higher agonistic scores of bright AL males is that female preference for these males elevated their androgen levels which in turn increased the probability of aggression by these males. Intersexual contact over periods of several days has produced hormonally based behavioral effects in male birds (Moore, 1983, 1984). Although this is possible, we do not think that increased androgen levels explain our results. Male agonistic scores were not correlated with preference scores of females. Our experimental protocol allowed visual contact between males and females for a maximum of 15 daylight h, and there were no cases in which nonpreferred males lacked visual interaction with females altogether. Also, male–male contests were run at least 17 h after females were removed from arenas. Therefore, the duration of intersexual contact in our trials was much shorter than that in bird studies (Moore, 1983, 1984), and the female stimulus was absent during our male–male contests.

The environmental potential for sexual selection is also the best predictor of the strength of intersexual selection based on male color. At AL where the potential for females to assess and choose from among more than one male is highest, females displayed significant preferences for bright males when color differences were extreme (between-population trials) and subtle (within-population trials). We suggest that, even though
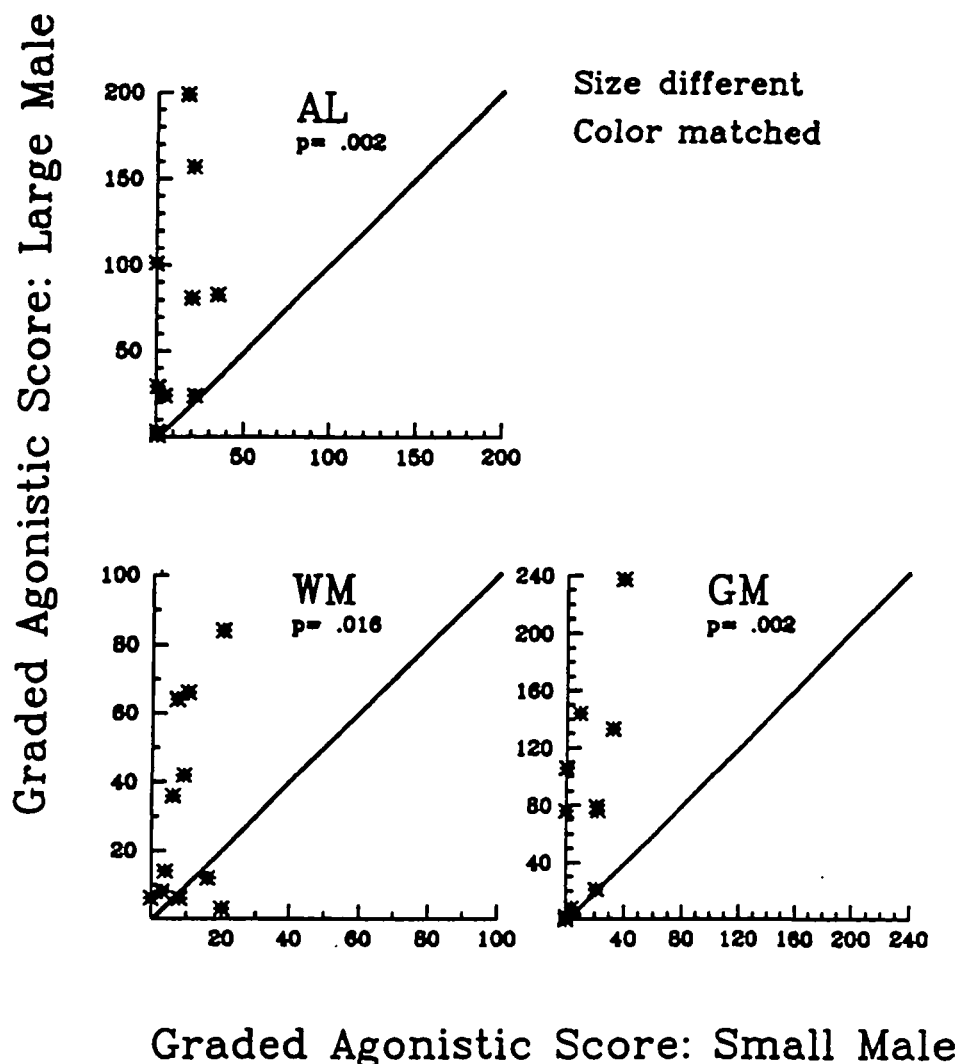
males in this population are the least bright of our populations, the habitat and social system promote female use of color in assessing males. Male territories abut one another closely and the home ranges of many females are overlapped by more than one adult male as well as up to four first-year satelite males (Baird et al., 1996) that have not yet developed their full intensity adult coloration (McCoy et al., in press). Therefore, because AL females are overlapped by several yearlings as well as adult males, they may be more strongly selected to use coloration in their mating choices than are females in the WM and GM populations. In addition, AL females show very low levels of intrasexual aggression, perhaps because perches suitable for

Table 3

Rates of sightings of potential predators of *Crotaphytus collaris* (predators/h) at three Oklahoma study sites

| Year | Site | | |
	GM	WM	AL
1992	0.234	0.082	0.284
1993	0.145	0.140	0.663
1994	0.166	0.046	0.752

scanning for prey are abundant (Baird, TA, unpublished data) and the habitat is continuous. Therefore, females may incur little if any cost of intrasexual aggression from moving to consort with and assess different males. In contrast, both WM and GM females probably have less potential for choosing among several males. In both habitats the geometry of rocky patches does not promote overlap and interaction with multiple adult and yearling males. At WM the rock outcroppings defended by males are dispersed, and at GM the long, narrow territories of males do not share long mutual borders. In addition, in both populations intrasexual female aggression is higher than at AL, making it costly for females to move among male territories to assess multiple mates.

Preference by AL females for the much brighter WM males might possibly be explained as choice of males with novel characteristics. However, the fact that AL females also chose brighter males during trials with the less extreme male color differences to which females are routinely exposed does not support this hypothesis. Preference for brighter males by AL females but not by WM and GM females might also indicate that there is a critical threshold for male brightness that determines mate preference in collared lizards. When one male is above the threshold and the other below it, the female is expected to choose the above-threshold male (Zuk et al., 1990a). When

Table 4

Rates of total injuries (injuries/lizard/day) and tailbreaks (breaks/lizard/day) at three Oklahoma study locations

	GM		WM		AL	
	M (N = 24)	F (N = 21)	M (N = 28)	F (N = 28)	M (N = 37)	F (N = 117)
All injuries						
Mean	0.0050	0.0	0.0018	0.0	0.0054	0.0002
SE	0.0128	0.0	0.0068	0.0	0.0128	0.0015
Tailbreaks						
Mean	0.0*	0.0	0.0*	0.0	0.0019*	0.0005
SE	0.0	0.0	0.0	0.0	0.0003	0.0005

* Kruskal-Wallis ANOVA, $F = 3.04$, $p = .05$ for males among all sites.

both males are above the threshold, females may mate with either male randomly or may discriminate based on the degree of character development and choose the male with the more developed trait. Assuming that bright and dull AL males were above and below such a threshold, respectively, and both WM and GM males surpassed it, the outcome of within-population mate-choice trials supports this model. Between-population mate-choice trials do not entirely support the threshold model, however, because both AL and WM females would be expected to prefer WM males when only the AL females showed this preference.

Females did not prefer larger over smaller males in any of the populations, refuting a role of current intersexual selection in the observed variation in the degree of size dimorphism. Experiments on *Anolis carolinensis* also failed to demonstrate female preferences for larger males (Andrews, 1985). Nonetheless, this result is surprising in *C. collaris* because field studies on AL lizards showed that females often fled smaller, first year males, whereas they almost always participated in courtship activities when approached by large adult males (Baird et al., 1996). This apparent discrepancy between field and laboratory results in AL females may be explained by the fact that size differences and/or other age-related phenotypic differences between adult and yearling AL males were greater than those between adult males used in our laboratory trials.

If AL females prefer brightly colored males, why is coloration least developed in this habitat? One possible explanation is that high predation pressure produces strong counterselection against bright male coloration. In guppies, predation risk has a strong influence on male coloration such that the location, size, and display of color spots that attract females have been shaped to minimize conspicuousness to predators (Endler, 1983). Sightings of potential predators on collared lizards were highest in the AL habitat, total injury rates tended to be higher in AL lizards (although not statistically so), and tailbreak rates of AL lizards were higher than in the other two populations. Injury rates in males were somewhat higher than in females at all sites. These results are consistent with the hypothesis that predation pressure is highest at AL, and further suggests that males may incur risk due to their conspicuous coloration and/or displays. Selection against bright male color may be particularly strong on the light-colored imported boulders at AL. However, the fact that male lizards on surrounding natural substrata are the same color indicates that the dull coloration of AL lizards is not merely a consequence of living on these imported rocks. Injury rates were also high in GM lizards, which are the most dimorphic population and also occupy lightly colored gypsum rock, suggesting that counterselection alone probably does not explain the pattern of male color development in these three populations. At WM, bright coloration may actually be cryptic. The spring/summer vegetation at this site in-

cludes several plant species that produce bright flowers and leaves, and bright green, yellow, and red lichens grow on the rocks. Against this bright background, even the brightly colored WM males were often inconspicuous to us, and they may also be inconspicuous to predators. There could be female mate choice of bright males at WM (although our results indicate otherwise), but because there is also selection for bright female coloration either for crypsis or for intrasexual interactions among females, the result is a less dichromatic population (Trail, 1990).

Sexual dimorphism is a complex phenomenon that may be influenced by many different past and present selective mechanisms such as parasite load, reduced intersexual competition, counterselection due to predation, and environmental potential for polygyny (Andersson, 1994; Wade, 1987). Our results indicate that in collared lizards the importance of sexual selection on male size and color cannot be predicted simply by the degree to which these traits are developed (i.e., current selection is not predicted by current expression). We did not investigate all current potential mechanisms that may explain the evolution of sexual dimorphism. However, two of our populations showed no evidence that parasite-mediated sexual selection or competition avoidance have any effect on sexual dimorphism (McCoy, 1995). Our results suggest a strong role of local contemporary environmental potential for female assessment of multiple males in female mating preferences for color, and use of color among males as a cue for intrasexual RHP. Color was involved in male contests and female preferences only at AL, where the potential for inter- and intrasexual interactions was extremely high. To our knowledge, the color-based preference in AL females is only the fourth such report in lizards and the first demonstration of a color advantage in contests between size-matched males. Olsson and Madsen (1995) have proposed that female choice is rare in lizards perhaps because male phenotypic traits are not reliable indicators of heritable fitness qualities (i.e., offspring survivorship or parasite resistance) for choosy females and/or because risks to females (e.g., time waste, energy expenditure, increased predation) associated with mate choice are high. We do not have data to address whether offspring of bright males survive better. However, for AL females the risk of aggressive intrasexual encounters while assessing multiple males appears to be low, while the potential for assessment is very high. Furthermore, selection for female mate choice theoretically can evolve through stochastic emergence of female preference even in the absence of initial fitness advantages (Kirkpatrick, 1982; Lande, 1981). We suggest that females in the AL population are selected to be choosy through sexual selection because the habitat promotes assessment of multiple mates without high temporal and energetic costs and intrasexual female aggression is low, allowing for low-cost movements from one male to another.

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