Predation Cost of Conspicuous Male Coloration in Collared Lizards (*Crotaphytus collaris*): An Experimental Test Using Clay-Covered Model Lizards

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Abstract

Animal color patterns are a compromise between sexual selection pressures that increase advantages accrued from conspicuousness, and natural selection pressures that decrease those advantages through reduced survivorship. Predation pressure, as a mode of natural selection, often is invoked as a counter-selective force to sexual selection, yet few studies have demonstrated empirically that more conspicuous individuals experience higher rates of predation. We quantified predator attacks on models of collared lizards, *Crotaphytus collaris*, in three well-studied populations (Oklahoma, USA). These populations differ in coloration and in visual backgrounds against which the lizards are viewed by conspecifics and predators. Attack frequencies varied considerably among study sites but at all sites the models exhibiting the strongest color contrast with local rocks were detected and attacked most often. By comparison, inconspicuous models of females were never attacked at any of the sites. These results suggest a survival cost of conspicuous coloration in collared lizards, and reiterate the importance of considering the visual environment as well as differences among populations when examining the influence of predation on the evolution of animal color patterns.

Introduction

Animal coloration represents a local balance between sexual selection through female mate choice and/or male–male competition, and natural selection through predator and/or prey detection, thermoregulation, and other factors (e.g. Endler 1992). Population-level analyses have been useful in elucidating constraints imposed by natural selection on the evolution of sexually selected coloration. For example, Endler's (1978, 1980, 1983, 1987) classic work on the guppy *Poecilia reticulata* revealed a complex interaction of natural and sexual selection on the evolution of color patterns. With increased predation pressure color spots decreased in size and frequency, and the colors exhibited were biased against the spectral sensitivity of the most dangerous predator (e.g., Endler 1991). As one example for lizards,

populations of chuckwallas (*Sauromalus obesus*) that experience higher rates of predation exhibit less conspicuous, sexually selected coloration (Kwiatkowski 2003).

It is widely presumed that males, because of their typically more conspicuous coloration (Andersson 1994; Zuk & Kolluru 1998), will suffer greater predation than females, but support for this notion has been variable. For example, Pocklington & Dill (1995) found that brightly colored male *Poecilia reticulata* suffered less than or equal predation than more drab females. Among lizards, population differences in predation pressure (working counter to sexual selection) have been proposed to explain population level differences in coloration (Baird et al. 1997; Macedonia et al. 2002; Kwiatkowski 2003; Stuart-Fox et al. 2004), but the methods of estimating predation intensity varied greatly among

these studies. Olsson (1993) found that models of male *Lacerta agilis* lizards with green nuptial coloration did not experience greater rates of predation than plastic models of drab females. Martín & López (2001) suggested that *Podarcis muralis* lizards may not have evolved conspicuous breeding coloration because of high levels of predation risk. However, their conclusions were based on the fact that brightly painted lizards exhibited a greater loss of body mass over time than controls, rather than actual predation rates. By comparison, Stuart-Fox et al. (2003) examined predator attacks on painted plaster models of male *Ctenophorus* rock dragons and found that more conspicuous models experienced greater attack frequencies than less conspicuous models. Clearly, more studies that measure relative predation pressure in some manner are needed before generalizations are justified.

We examined the potential cost of conspicuous male coloration in three populations of collared lizards (*Crotaphytus collaris*), in Oklahoma, USA, that differ in coloration. Males of these sexually dichromatic lizards are more conspicuously colored than are females (McCoy et al. 1997; Macedonia et al. 2004), although the relative influence of female choice and male competition on maintaining these sexual color differences remains unclear (Baird et al. 1997). We fashioned clay models to resemble the coloration of males from the three populations, as well as a generalized female, and placed multiple replicates of the four model types in each of the three environments to determine the relative predation risk for each color pattern. We predicted that at each study site more 'male' models would be attacked than 'female' models. We also predicted that the frequency of attacks on a given model type would be consistent with the conspicuousness of that model type at a given study site.

Methods

Study Sites

We studied three populations of collared lizards in Oklahoma that have been the subject of considerable research (Wichita Mountains, WM; Glass Mountains, GM; Sooner Lake, SL). Detailed descriptions of WM and GM can be found in Baird et al. (1997) and Macedonia et al. (2004), and a detailed description of SL is available in Husak & Fox (2003). Briefly, WM lizards inhabit salmon-colored granite rocks that are covered by multi-colored lichens, GM lizards inhabit white to grey gypsum rocks interspersed

with exposed reddish soil, and SL lizards inhabit a man-made dam constructed of grey boulders. Past studies have revealed significant differences among these geographically distinct populations in color conspicuousness (Macedonia et al. 2004), sexual dimorphism (McCoy et al. 1994), sexual dichromatism (McCoy et al. 1997; Macedonia et al. 2004), body size and shape (McCoy et al. 1994), social organization (McCoy et al. 2003), habitat characteristics (Baird et al. 1997), and the frequency of predator sightings (Baird et al. 1997).

The three populations share many of the same potential predators, but some subtle differences exist (J. Husak and J. Macedonia, pers. obs.). At GM, potential avian predators include Red-tailed Hawks (*Buteo jamaicensis*), Swainson's Hawks (*Buteo swainsoni*) Northern Harriers (*Circus cyaneus*), Roadrunners (*Geococcyx californianus*), Mississippi Kites (*Ictinia mississippiensis*), American Kestrels (*Falco sparverius*), Loggerhead Shrikes (*Lanius ludovicianus*), American Crows (*Corvus brachyrhynchos*), Cooper's Hawks (*Accipiter cooperii*) and Sharp-shinned Hawks (*Accipiter striatus*). Potential snake predators at GM include western diamondback rattlesnakes (*Crotalus atrox*), pine snakes (*Pituophis catenifer*), black ratsnakes (*Elaphe obsoleta*) and coachwhips (*Masticophis flagellum*). SL possesses the same suite of potential avian and snake predators except there are no rattlesnakes, and because the rocks of the dam that the lizards inhabit are near water, water snakes (*Nerodia* spp.) are a potential predator. Likewise, WM has the same suite of potential predators as GM, but prairie rattlesnakes (*Crotalus viridis*) are also present. Eastern yellowbelly racers (*Coluber constrictor*) may be present at all three sites (Conant & Collins 1998), but they have not been seen in areas where lizards occur. Among the potential snake predators it is important to note that whereas all of the species other than coachwhips are sit-and-wait foragers, coachwhips are diurnal, active foragers that rely heavily on vision to hunt their prey (Secor & Nagy 1994).

Models

Construction of models

We constructed collared lizard models by modifying commercially available lizard toys ('Common Agamid,' Wild Republic). In nature, males may suffer greater predation than females because of greater rates of movement in addition to more conspicuous coloration. Using physical models to assess predation risk associated with different degrees of conspicuous coloration allows all variables other than color

manipulations to be held constant (e.g. Brodie 1993; Olsson 1993; Castilla et al. 1999; Stuart-Fox et al. 2003). If the models are constructed of an appropriate material (Brodie 1993; Olsson 1993) the imprints left by different types of predators can be identified at least to large taxonomic groups (e.g. snakes, birds and mammals). The toy lizards [snout-vent length (SVL) = 135 mm] were slightly larger than large *C. collaris* males (SVL = 110–120 mm). Twenty models were constructed for each of the three male color patterns and for the drab female for a total of 80 models. We covered each toy lizard with a thin (approxi. 2 mm) layer of non-toxic, odorless, Sculpey III modeling clay, and then painted the clay based on photographs of adults in each population. We attempted to match (by eye) the coloration of each model type as closely as possible to the sex/population it represented. All 'female' models were painted one shade of brown similar to the dorsum background of females in all three populations. The crowns of 'male' models were painted brown similar to 'female' model coloration, dewlaps were painted yellow and bodies were painted a shade of green or bluish-green that simulated dorsum coloration of live males from the population a model was meant to represent. For simplicity, we will refer to dorsum background coloration simply as 'body' coloration. The models were sufficiently realistic that, in the field, males displayed at and occasionally bit them.

We were unable to obtain spectrophotometric readings of the models until immediately prior to placing them in the field; thus, analytical results of model contrast with visual backgrounds at each study site were not available until the study was completed. Despite some disadvantages of this *a posteriori* approach, it allowed us to quantify imprints from predator attacks on the models in a 'blind' fashion without knowledge of model conspicuousness at each study site.

We placed the models in typical basking locations at the study sites to mimic the visibility of the actual lizards. Models were secured with monofilament line to prevent removal by predators, and were placed approxi. 15–20 m apart in the sequence: female, GM, SL, WM. The placement of models in this alternating sequence continued until all 80 models were placed at the site. The spacing distance represents the approximate average spacing for lizards at each site. As the area covered by all 80 models was large and in a random location, it is likely that the models were susceptible to attack by multiple predators. At each study site, the models were in place for four 'good weather' days (i.e. sunny, not cold and rainy)

suitable for lizard and predator activity across a range of 5–7 d. This short duration allowed us to complete the entire experiment without the potential confound of seasonal variation in predator abundance among sites. To quantify differential predation attempts by a given predator class, we analyzed bite marks on the models. Models were checked twice daily (early morning and late afternoon) for predation attempts, and imprints were categorized as 'snake', 'bird', 'conspecific', or 'other' (e.g. rodents). The layer of clay on the models allowed accurate identification of predator class based on bite and beak imprints. For example, snakes left elongate, round-tipped dental imprints with parallel tooth rows (similar to an elongate parabola) and a double row of dorsal teeth (maxillary and pterygoid teeth). In contrast, bite marks from conspecifics had pointed tips with angled, posteriorly diverging tooth rows (similar to an unclosed, rounded triangle) and the absence of a double row of dorsal dentition (see also Lappin & Husak 2005). Bite marks were so well preserved that the imprint of each individual tooth usually was visible and distinct. To confirm coachwhips as the primary snake predators, we presented a lizard model to a coachwhip in the laboratory. Bite marks were consistent with those seen on models. Beak impressions were readily distinguished from dental imprints. We classified the attack as 'bird' when there were obvious beak or talon marks, or when a model had been moved off of its perch during the day and there was evidence of an avian (but not snake or mammalian) attack on the model. We also noted the location on the model where the attack occurred (head, neck, body, limbs, or tail). Models damaged from attack were photographed and immediately repaired by adding clay and paint.

Analysis of attack data

For each site, we tested for an association between model type and attack by a predator. Because of small cell counts of attacks in some of the 4×2 contingency tables within sites, we analyzed the data using exact inference with permutation tests (Agresti 2002). First the chi-square value was found for the observed data of a given contingency table. Then 'raw' data were created from the contingency table by assigning each observation a row and column number pair. For example, if the cell at the first row and column position in the contingency table had a value of 12, then there would be 12 observations with the row number and column number pair '(1, 1)'. Under the independence assumption, the observed row numbers and column numbers should

be equally likely to occur with each other. Hence, we permuted the column numbers and recombined them with the row numbers. This then created a new contingency table from which a chi-square* value was calculated (The asterisks denote different chi-square values, i.e., those calculated with the described permutations). We used 1000 permutations, such that the probability of no association could be calculated as the number of chi-square* values greater than or equal to the original chi-square value divided by 1000. This procedure was carried out for each study site.

We used two different analyses to test for differences in predation pressure among sites. Firstly, to coarsely examine differences in predation pressure among sites, we collapsed the data within sites by summing all attacks on all models at a given site. We then used a permutation test (as described above) to test for an association between site and being attacked. To examine population differences in predation pressure at a finer scale, we also created a $3 \times 2 \times 4$ contingency table to test for conditional association (Agresti 2002) between site and being attacked *given* the model type. In this case, we rearranged the data to produce a contingency table with four layers, each representing the number of attacks (and non-attacks) at each site for a different model type. For example, one layer comprised the number of attacks at each site on only WM models. We were then able to use a Cochran–Mantel–Haenszel test (Agresti 2002) to determine whether or not there was an association between site and being attacked given the type of model.

Measurement of Color

Model coloration

We took spectrophotometric measurements of the painted models to compare their resemblance to the actual collared lizards in the three populations. Spectral recordings of the dorsum background of models and real lizards, and of local rocks (as well as lichens growing on them at WM) were obtained using a reflectance probe (Ocean Optics R200-7, Ocean Optics, Dunedin, FL, USA) connected to a xenon light source (Ocean Optics PX-2), an Ocean Optics USB2000 portable spectrometer, and a notebook computer running OOIBASE 32 software (Ocean Optics, Dunedin, FL, USA). To calculate percent reflectance, a diffuse white standard (Optolon 2, ANCAL, Inc., Henderson, NV, USA) was scanned prior to gathering spectral data from each object sampled.

Contrast between lizard models and local rocks

To illustrate color differences among model types and rocks on which they were placed, reflectance spectra were reduced to single coordinates and plotted in color space using Endler's (1990) segment classification method. Spectra were partitioned into four, 90 nm-wide color segments corresponding roughly to UV to violet/blue (340–430 nm, 'UV' wavelengths segment), violet/blue to green (430–520, 'blue' or 'B' wavelengths segment), green to orange (520–610 nm, yellow or 'Y' wavelengths segment) and orange to red (610–700 nm, red or 'R' wavelengths segment). The sum of individual wavelength intensities for each color segment (Σ_{UV}, Σ_B, Σ_Y and Σ_R) then was divided by the sum of individual wavelength intensities for the entire spectrum (340–700 nm). These calculations equalize intensity differences among spectra of models, real lizards and rocks and produce a proportional intensity value for each segment ($\Sigma_{UV}/\Sigma_{Total}$, Σ_B/Σ_{Total}, Σ_Y/Σ_{Total} and Σ_R/Σ_{Total}). Subtraction of Σ_B/Σ_{Total} from Σ_R/Σ_{Total} and $\Sigma_{UV}/\Sigma_{Total}$ from Σ_Y/Σ_{Total} produces two values that are plotted as a single color score in color space. The mean body reflectance spectrum for each model type was calculated, reduced to a color score and plotted. Mean color scores for real lizards, and individual color scores for rocks (and lichens at WM), also were calculated and plotted. In color space, the color contrast between two color scores is the Euclidian distance separating them. As each model type was present at each study site, Spearman rank correlation was used to test for an association between the 12 unique model mean-rock mean Euclidian distances and predator attack frequency on each model type at each site. This tests our prediction that attack frequency should be positively correlated with model color conspicuousness.

As intensity differences among spectra of models and rocks are factored out in computing color scores, determining intensity contrast between models and the visual background of rocks requires a different approach. Intensity contrast was calculated as the total reflectance (i.e. sum of individual intensities at each wavelength from 340 to 700 nm) of a given model type's mean spectrum minus the total reflectance of the mean rock spectrum at a given study site, divided by the sum of these two quantities (e.g. Fleishman & Persons 2001). Spearman rank correlation was used to test for a relationship between model-rock intensity contrast and predator attack frequency on each

model type at each study site. Tests of correlation were two-tailed and were conducted with SPSS v. 10 for Macintosh (SPSS Inc., Chicago, IL, USA).

Results

Predator Attacks on Models

At each site, WM models received the most attacks by predators, whereas 'female' models never were attacked at any site (Table 1). The permutation tests for an association between model type and attack by a predator within a particular site revealed significant associations at WM (p = 0.0001) and SL (p = 0.004)

Table 1: Proportion (and number) of each of the four collared lizard model types attacked at each of the three sites studied in Oklahoma, USA. Totals refer to the total number of models attacked at a given site (column totals) and the total number of models of a given type attacked across sites (row totals)

	Population			
Model type	Wichita Mountains	Glass Mountains	Sooner Lake	Total
Wichita Mountains	0.70 (14)	0.20 (4)	0.40 (8)	26
Glass Mountains	0.15 (3)	0.05 (1)	0.10 (2)	6
Sooner Lake	0.05 (1)	0	0.10 (2)	3
Female	0	0	0	0
Total	18	5	12	35

and a marginally significant association at GM (p = 0.056). Most attacks (63.7% of attacks pooled across model types) were made on the neck where conspicuous black bands (i.e. a collar) occur at the junction of the visually contrasting greenish body and yellow dewlap. Fewer attacks were observed on the rest of the body (21.8%), head (7.3%), legs (3.6%) and tail (3.6%). Most attacks were made by snakes at all sites (SL: 100% snakes; WM: 94% snakes, 6% birds; GM: 80% snakes, 20% birds).

The permutation test on the data collapsed across sites revealed a significant association between site and predator attack (p = 0.027). The $3 \times 2 \times 4$ contingency table analysis used to test for a conditional association (Agresti 2002) between site and attack, given model type, also revealed a significant association (Cochran–Mantel–Haenszel $M^2 = 10.867$, df = 2, p = 0.004). These results indicate that the sites differed in potential predation pressure, with GM experiencing the least pressure, SL being intermediate and WM bearing the strongest potential predation pressure.

### Conspicuousness and Predator Attack Frequency

Although we were unable to match lizards and models identically for coloration, their mean distances from rocks in color space were quite similar for the GM and SL populations (Fig. 1). WM models fell
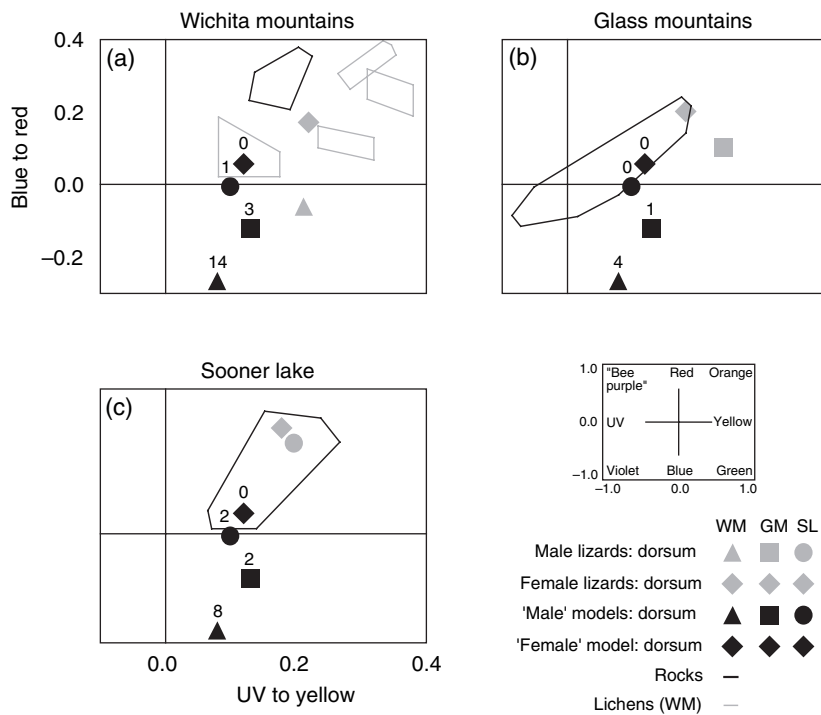
Fig. 1: Reflectance color score means for dorsum background coloration of lizards and models, plotted in the color space of Endler (1990). Spectra were obtained from four randomly sampled models of each type to calculate model color score means. Numbers above symbols for models indicate how many of that model type (of 20) were attacked by predators. Minimum area polygons constructed of thick black lines enclose rock color scores for each population. Lichens were prevalent on rocks only at the WM study site and thus are shown only for that population (polygons of thin gray lines). Only the portion of color space containing color scores is shown, and the inset in the legend depicts the entire color space. Individual objects measured for each population: WM – males: n = 36, females: n = 25, rocks: n = 6, lichens: n = 19; GM – males: n = 18, females: n = 17, rocks: n = 28; SL – males: n = 12, females: n = 17, rocks: n = 29. Model sample sizes in each case: n = 4. Spectral data used to calculate color scores for WM and GM plots from Macedonia et al. 2004

further from rocks in color space than WM lizards, but this difference is not great when considering the small portion of color space occupied (Fig. 1, legend).

Euclidian distance between the mean body color score for model type and the mean rock color score at each study site was significantly correlated with predator attack frequencies across the sites ($r_s = 0.857$, $p < 0.001$, $n = 12$). For example, WM models were most conspicuous in color against rocks at all study sites, and at each study site more WM models were attacked than any other model type (Fig. 1). Similarly, 'female' models were less conspicuous in color than other model types at each site and no 'female' models were attacked at any site.
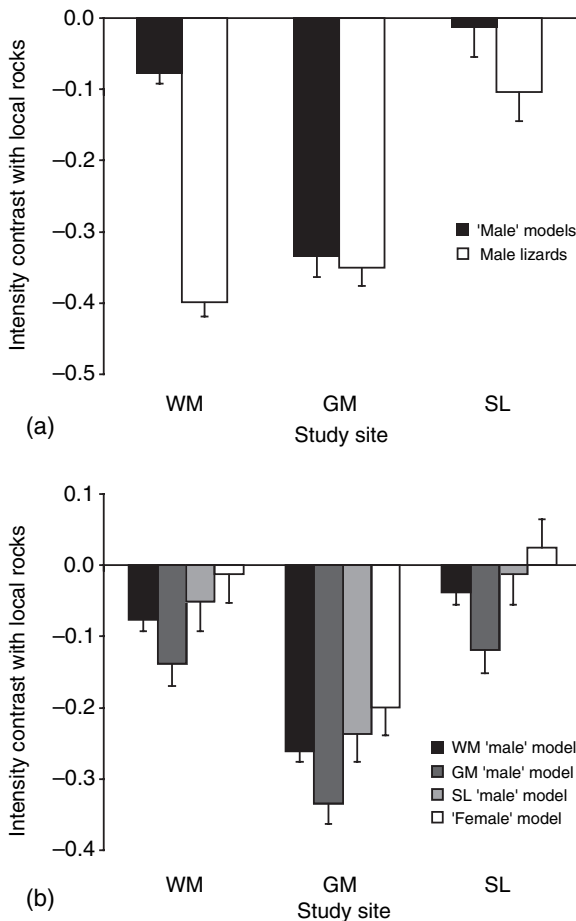
Fig. 2: (a) Intensity contrast ($\bar{x} \pm$ SE) of 'male' models (black bars) and male lizards (white bars) with local rocks at the three study sites. (b) Intensity contrast of all four model types with local rocks at each study site. For both (a) and (b), negative values indicate that the objects (model or lizard reflectance spectra) are darker than the backgrounds (rock mean reflectance spectra); positive values indicate that the objects are lighter than the backgrounds

The models contrasted less in intensity with local rocks than the lizards on which model coloration was based, particularly the WM model (Fig. 2a). At all study sites, the GM model exhibited the strongest intensity contrast (Fig. 2b). The 'female' model was weakest in intensity contrast at the WM and GM sites, but not at the SL site (Fig. 2b). Unlike color contrast, intensity contrast between models and rocks at each study site was uncorrelated with predator attack frequency ($r_s = 0.150$, $p = 0.642$, $n = 12$).

Discussion

Results of this study supported our prediction that attack rates on lizard models would be determined by color conspicuousness. Despite being placed in study sites hundreds of kilometers apart, the same pattern of results was found at every site: the greater the color contrast between a lizard model and the rocks on which it was placed, the greater the frequency of attacks from predators. This finding is consistent with the general tenet in behavioral ecology that benefits arising from increased conspicuousness can be offset by increased predation risk. By comparison, we did not detect a significant relationship between intensity contrast and predator attacks, although in theory intensity contrast should be no less important for detection of prey by predators (or predators by prey) than color contrast.

Our results do not make clear whether differences in numbers of models attacked at each site stem from among-site differences in predators or in model conspicuousness, or both. For example, differences in attack frequency among sites could be due to the presence of different predator guilds or to differences in predator abundance (as suggested by Baird et al. 1997). Alternatively, identical predator guilds and abundance of guild members might produce the results we obtained if habitat structure rendered the models more visible to a given predator class at one site than another.

Results of this study also suggest that the balance between sexual selection for conspicuous coloration and natural selection for inconspicuous coloration may differ among these three collared lizard populations. At SL, where the lizards have little opportunity for concealment against a relatively homogenous visual background of grayish rock, adult males are a dull greenish-brown color that overlaps rock coloration and is not dramatically different from female coloration. At GM, where the visual background is more complex and more diverse spectrally, adult males are more colorful than females and do not

overlap in coloration with local rocks (Macedonia et al. 2004). More than double the number of attacks by predators on models at SL than at GM may indicate that natural selection constrains sexual selection for conspicuous male coloration at SL more effectively than at GM.

It has been suggested for the Arcadia Lake (AL) population in Oklahoma, which is very similar in habitat and coloration to SL (Macedonia et al. 2004; J. Husak and J. Macedonia, unpubl. data), that predation pressure greatly constrains how colorful males can be and survive to achieve high lifetime reproductive success (Baird et al. 1997; McCoy et al. 1997). Interestingly, female mate choice experiments have shown that AL females (but not GM females) prefer more colorful than less colorful AL males and prefer the very colorful WM males to their own duller AL males (Baird et al. 1997). Additionally, brighter individuals of size-matched males interacting in staged encounters dominated duller individuals in trials with AL lizards, but not GM (or WM) lizards (Baird et al. 1997). These results are consistent with the prospect that predation pressure has a greater influence on limiting color conspicuousness in AL males than in GM males (Baird et al. 1997). Similarities in habitat and in lizard coloration at AL and SL, together with greater attack frequencies of models at SL than at GM, suggest that predation pressure may be the primary factor responsible for the differential in male color conspicuousness between these two populations.

The balance between natural and sexual selection appears to be fundamentally different in the WM population, however. WM males are much more conspicuous than males in the other populations, and yet predation pressure appears to be stronger at WM than elsewhere. How might this apparent anomaly be reconciled?

Firstly, it may be more difficult to be conspicuous against the structurally and spectrally complex visual background at WM compared with a simple one (e.g. SL). For example, it has been suggested that WM males, which are very boldly colored when viewed in the hand, might actually be cryptic within the complexity of their natural visual background (Baird et al. 1997; McCoy et al. 1997). Fieldwork conducted to test this hypothesis (Macedonia et al. 2004) found mixed support for it: spectral reflectance measurements of lizards and background elements revealed that parts of WM male bodies should be inconspicuous when viewed by predators against some background features (e.g. lichens, flowers and some vegetation) but conspicuous when viewed against others (e.g. rocks, other vegetation). The complex visual background

against which WM males are viewed by predators and conspecifics therefore may have favored more conspicuous advertisement coloration (Baird et al. 1997). If true, and considering that WM females have not been shown to prefer more colorful over less colorful males (Baird et al. 1997), sexual selection for increased conspicuousness might be maintained primarily by male-male competition among WM males. Greater male body size, bite force and sexual dimorphism in the WM population, compared with GM and SL, is consistent with this idea (A. K. Lappin and J. Husak, unpubl. data), although Baird et al. (1997) did not find that more colorful WM males dominated duller ones in laboratory encounters.

Secondly, the characteristic tall grass component of the mixed-grass prairie habitat at WM provides unusually good cover for visually hunting snakes. The snake predator responsible for most attacks was probably the coachwhip, *Masticophis flagellum*, which we frequently have observed hunting at WM. This snake is a fleet, actively foraging, diurnal, visual predator (Secor & Nagy 1994) that, like many lizard species (including *Crotaphytus*), possesses four classes of retinal photoreceptors (E. Loew, unpubl. data). As many of the large boulders on which WM males perch protrude well above the grass, coachwhips can effectively stalk the lizards while hidden in the grass but must ascend the boulders to attack them. It therefore seems plausible that predation attempts often may fail when WM males detect and flee the snakes during the final stage of their approach. If so, results of attacks on the models would overestimate the magnitude of natural selection in constraining conspicuous coloration through snake predation at the WM site. Alternatively, sexual selection for increased color conspicuousness, size and aggressiveness in WM males may provide such substantial benefits that it persists in the face of truly intense predation in this population.

Given the observed predator strike frequencies on models at the three study sites, one could predict that WM lizards should be the most wary of predators and GM lizards the least wary. A concurrent study of anti-predator behavior in these populations confirmed this prediction (J. Husak & M. Rouse, unpubl. data). Yet, behavioral compensation for increased conspicuousness to predators cannot be open-ended. Adult males must remain visible on prominent perches to advertize their presence to females, to defend territories against would-be intrusions by other males, and to scan for potential prey.

Visual background complexity, at sites like WM and GM, may offset the cost of increased color conspicuousness by making the visual search task more

time consuming and visual information processing more taxing for predators. Complex visual environments also may provide a greater diversity of refuges from predators. We therefore predict that, where predation pressure is moderate to strong, conspicuous coloration in collared lizards should be fundamentally incompatible with visually simple environments.

In sum, results of prior studies have left a lingering question in understanding the constraints imposed by natural selection on conspicuous color signals favored by sexual selection. Such research has suggested that an important cost of sexually selected color signals is increased conspicuousness to predators (e.g. Ryan et al. 1982; Endler 1983) and to prey (Grether & Grey 1996), and some recent studies have increased the amount of support for this hypothesis (Huhta et al. 2003; Stuart-Fox et al. 2003), but empirical evidence for this proposition remains limited (Andersson 1994; Zuk & Kolluru 1998; Kotiaho 2001). The work reported here has revealed a direct link between color conspicuousness and detection by predators. These results likewise suggest that if the reproductive benefits of such coloration are to be realized in locations where predation pressure is appreciable, a commensurate increase in vigilance against predator threat will be crucial for survival.

Acknowledgements

Literature Cited

Agresti, A. 2002: Categorical Data Analysis. Wiley, Hoboken, NJ.

Andersson, M. 1994: Sexual Selection. Princeton Univ. Press, Princeton, NJ.

Baird, T. A., Fox, S. F. & McCoy, J. K. 1997: Population differences in the roles of size and coloration in intra- and inter-sexual selection in the collared lizard, *Crotaphytus collaris*: influence of habitat and social organization. Behav. Ecol. **8**, 506—517.

Brodie, E. D., III 1993: Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. Evolution **47**, 227—235.

Castilla, A. M., Gosa, A., Galan, P. & Perez M. V. 1999: Green tails in lizards of the genus *Podarcis*: do they influence the intensity of predation? Herpetologica **55**, 530—537.

Conant, R. & Collins, J. T. 1998: A Field Guide to Reptiles and Amphibians: Eastern and Central North America, 3rd edn. Houghton Mifflin, Boston, MA.

Endler, J. A. 1978: A predator's view of animal colour patterns. Evol. Biol. **11**, 319—364.

Endler, J. A. 1980: Natural selection on color patterns in *Poecilia reticulata*. Evolution **34**, 76—91.

Endler, J. A. 1983: Natural and sexual selection on color patterns in poeciliid fishes. Environ. Biol. Fishes **9**, 173—190.

Endler, J. A. 1987: Predation, light intensity, and courtship behaviour in *Poecilia reticulata*. Anim. Behav. **35**, 1376—1385.

Endler, J. A. 1990: On the measurement and classification of colour in studies of animal colour patterns. Biol. J. Linn. Soc. **41**, 315—352.

Endler, J. A. 1991: Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. Vision Res. **31**, 587—608.

Endler, J. A. 1992: Signals, signal conditions, and the direction of evolution. Am. Nat. **139**, S125—S153.

Fleishman, L. K. & Persons, M. 2001: The influence of stimulus and background colour on signal visibility in the lizard *Anolis cristatellus*. J. Exp. Biol. **204**, 1559—1575.

Grether, G. F. & Grey, R. M. 1996: Novel cost of a sexually selected trait in the rubyspot damselfly *Hataerina americana*: conspicuousness to prey. Behav. Ecol. **4**, 465—473.

Huhta, E., Rytkonen, S. & Solonen, T. 2003: Plumage brightness of prey increases predation risk: an among-species comparison. Ecology **84**, 1793—1799.

Husak, J. F. & Fox, S. F. 2003: Adult male collared lizards (*Crotaphytus collaris*) increase aggression toward displaced neighbours. Anim. Behav. **65**, 391—396.

Kotiaho, J. S. 2001: Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. Biol. Rev. **76**, 365—376.

Kwiatkowski, M. A. 2003: Variation in conspicuousness among populations of an iguanid lizard, *Sauromalus obesus* (= *ater*). Copeia **2003**, 481—492.

Lappin, A. K. & Husak, J. F. 2005: Weapon performance, not size, determines mating success and potential

reproductive output in the collared lizard (*Crotaphytus collaris*). Am. Nat. **166**, 426—436.

Macedonia, J. M., Brandt, Y. M. & Clark, D. L. 2002: Sexual dichromatism, adaptive colouration and differential conspicuousness in two populations of the collared lizard, *Crotaphytus collaris*. Biol. J. Linn. Soc. **77**, 67—85.

Macedonia, J. M., Husak, J. F., Brandt, Y. M., Lappin, A. K. & Baird, T. A. 2004: Sexual dichromatism and color conspicuousness in three populations of collared lizards (*Crotaphytus collaris*) from Oklahoma, USA. J. Herpetol. **38**, 343—357.

Martín, J. & López, P. 2001: Risk of predation may explain the absence of nuptial coloration in the wall lizard, *Podarcis muralis*. Evol. Ecol. Res. **3**, 889—898.

McCoy, J. K., Fox, S. F. & Baird, T. A. 1994: Geographic variation in sexual dimorphism of *Crotaphytus collaris*. Southwest Nat. **39**, 328—335.

McCoy, J. K., Harmon, H. J., Baird, T. A. & Fox, S. F. 1997: Geographic variation in sexual dichromatism of *Crotaphytus collaris*. Copeia **1997**, 565—571.

McCoy, J. K., Baird, T. A. & Fox, S. F. 2003: Sexual selection, social behavior, and the environmental potential for polygyny. In: Lizard Social Behavior (Fox, S. F., McCoy, J. K. & Baird, T. A., eds). Johns Hopkins Univ. Press, Baltimore, MD, pp. 149—171.

Olsson, M. 1993: Nuptial coloration and predation risk in model sand lizards, *Lacerta agilis*. Anim. Behav. **46**, 410—412.

Pocklington, R. & Dill, L. M. 1995: Predation on females or males: who pays for bright male traits? Anim. Behav. **49**, 1122—1124.

Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982: Sexual advertisement and bat predation in a Neotropical frog. Am. Nat. **119**, 136—139.

Secor, S. M. & Nagy, K. A. 1994: Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. Ecology **75**, 1600—1614.

Stuart-Fox, D. M., Moussalli, A., Marshall, N. J. & Owens, I. P. F. 2003: Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. Anim. Behav. **66**, 541—550.

Stuart-Fox, D. M., Moussalli, A., Johnston, G. R. & Owens, I. P. F. 2004: Evolution of color variation in dragon lizards: quantitative tests of the role of crypsis and local adaptation. Evolution **58**, 1549—1559.

Zuk, M. & Kolluru, G. R. 1998: Exploitation of sexual signals by predators and parasitoids. Q. Rev. Biol. **73**, 415—438.