

Response of conspecifics to reproductive color of female striped plateau lizards, *Sceloporus virgatus*

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Several hypotheses have been posed to explain the evolution and current function of bright reproductive color found among females in over 30 species of iguanian lizards. I use the orange reproductive color of female striped plateau lizards (*Sceloporus virgatus*) to address two of the lesser examined hypotheses: the female signal and sex recognition hypotheses. The female signal hypothesis suggests that female reproductive color functions as a communication signal to conspecific females and predicts that females with more developed color will dominate over females with less developed color. I addressed this hypothesis by examining competition for basking sites and food resources among groups of females painted to express dark orange, pale orange, or no orange reproductive color. I found no consistent pattern to suggest that color affects these interactions: dark orange females had a slight and non-significant advantage in obtaining preferred basking sites, pale orange females were significantly more likely to obtain the first available prey item, yet there was no effect of female color on total number of prey eaten or on feeding sequence. The sex recognition hypothesis suggests that female color functions to improve gender identification. Resident males interacted with male intruders painted to express either male-typical color or female reproductive color in a sequential stimulus design. Intruder color had no significant effect on behavior of the resident. I suggest that other cues, including chemosensory signals, are more important than female reproductive color in close-range sex recognition among *S. virgatus*.

Introduction

Typically, bright sexually dimorphic reproductive color is expressed by males and evolves via sexual selection (Darwin 1871, Andersson 1994). Bright reproductive color among females is less common and has received far less attention in the literature, but may be more common among vertebrates than expected (e.g., Amundsen 2000). Female ornamental color can evolve via genetic correlation to male sexually selected

traits (Lande 1980) or via direct natural or sexual selection on the female. Instances of female-specific color, where females express ornamental color that is not expressed by conspecific males, eliminate the possibility of genetic correlation to males and allow scientists to focus on functional hypotheses for trait evolution.

Female-specific reproductive color is expressed in more than 30 species of lizard, and several non-mutually exclusive hypotheses have been proposed to explain the current func-

tion of this trait (reviewed by Cooper & Greenberg 1992). Of these, the hypotheses that have received the most recent attention suggest that the color functions as a mating signal (e.g., Watkins 1997, Cuadrado 2000, Weiss 2002). One hypothesis suggests that the color functions to stimulate courtship from males during the female receptive period; another suggests that the color functions to reject male courtship when the female is no longer receptive. It is possible for the color to function in both of these contexts if it changes dynamically during the reproductive season and if male response varies with the stage of color development (e.g., Hager 2001).

In previous work, I tested whether the reproductive color of female striped plateau lizards (*Sceloporus virgatus*) functions in either or both of these contexts (Weiss 2002). Female *S. virgatus* develop orange throat color during vitellogenesis that peaks around ovulation and fades during a month-long period of gravidity. This female-specific orange color develops around small, sexually monomorphic, blue throat patches. During the pre-mating season, males associate more closely with dark-orange females and tend to perform more social behavior in the presence of dark-orange females, relative to pale- or no-orange females. During the post-mating season, male affiliation is unaffected by female color, and the trend for social behavior is similar to that found in the pre-mating season – males express a greater degree of social behavior in the presence of dark-orange females than with pale- and no-orange females. Thus, female *S. virgatus* color appears to function as a courtship stimulation signal, and has no apparent function as a courtship rejection signal.

However, courtship stimulation may not be the only selective advantage to color expression that maintains the trait in extant *S. virgatus* populations. Herein, I test two additional, non-mutually exclusive hypotheses for the function of female reproductive color: the female signal hypothesis and sex recognition hypothesis. These hypotheses have limited support in the literature (reviewed by Cooper & Greenberg 1992), but are useful to study as they may elucidate important, albeit secondary effects of female reproductive color.

The female signal hypothesis suggests that female reproductive color is a social signal to

conspecific females, and predicts that females with more developed color will be more likely to “win” female-female interactions. Evidence from other taxa suggests that social interactions among females can influence the evolution of female traits (e.g., West-Eberhard 1983, Trail 1990); however, relative to female reproductive color of iguanian lizards, there is little support for such an effect (reviewed by Cooper & Greenberg 1992). An unpublished study suggests that brightly colored female leopard lizards, *Gambelia wislizeni*, may be more tolerant of bright females than pale females or males (E. M. Moore 1983, unpublished thesis cited in Cooper & Greenberg 1992). In contrast however, studies of keeled earless lizards, *Holbrookia propinqua* suggest that the behavior of females is not affected by the color of introduced females (Cooper 1988). I did not test the female signal hypothesis by staging aggressive interactions between pairs of female *S. virgatus* because females of this species are relatively non-aggressive and have high home range overlap (Vinegar 1975, Smith 1985, Abell 1999, Weiss, personal observations). Instead, I examined how female color influenced basking and feeding behavior among groups of females. The female signal hypothesis will be supported if females with more-developed color attain better basking sites or greater access to food relative to females with less-developed color.

The sex recognition hypothesis suggests that sexually dimorphic traits function to identify gender. Among some sexually dimorphic birds and lizards, male color appears to indicate “maleness” to conspecifics (Cooper & Burns 1987, Cooper & Vitt 1988, Andersson 1994), as evidenced by males attacking females that are painted to express male-typical color. Relative to female-specific color, males are predicted to identify “femaleness” by the expression of female-typical color and therefore are predicted to 1) mistakenly court and 2) respond less aggressively to males painted with female-typical color than to males painted with male-typical color. Females may benefit by increasing male courtship and avoiding aggressive male attacks. To examine this hypothesis, I measured male response to conspecific males that were painted with or without female reproductive color.

Materials and methods

Animal maintenance

I captured striped plateau lizards, *Sceloporus virgatus*, by noose between 15 May and 11 June 1998, within 3.2 km from the Southwestern Research Station (SWRS) of the American Museum of Natural History, in Cochise County, Arizona, USA. I measured individuals for snout-vent length (SVL), body mass, body condition index (body mass/SVL³), and number of ectoparasitic mites. For females, I additionally measured reproductive color intensity by matching throat coloration to glossy color chips (Munsell (Color Company) 1976) under a standard light source (Pelican Super SabreLite). Munsell color chips are defined by three variables: hue, value, and chroma. For analysis, I converted the three variables into a single variable using the formula described by Burley *et al.* (1992). Following conversion, scores for the color chips used ranged from 9 (for Munsell color chip 10R8/6) to 18 (for Munsell color chip 10R4/12), with a higher number indicating a darker and more orange patch. All color chips used were of the hue 10R and thus, varied only value and chroma.

I housed females ($N = 36$) in groups of three size-matched (within 2.5 mm) individuals, forming 12 “triads”, and I housed males ($N = 27$) individually. Each terrarium ($50 \times 25 \times 30$ cm) was visually isolated from all others. The housing facility at SWRS has screen walls on three sides, providing daily light and temperature fluctuations. Shade from the structure’s roof and eaves, however, results in a relatively slow warm-up and a more rapid cool-down of the housing environment than what would be experienced in nature. To provide additional heat and establish a temperature gradient within each terrarium, I suspended a 40 W incandescent bulb, on a 14L:10D light cycle, at one end and placed two logs inside, with one log angled up towards the heat source. This setup, along with a 1–2 cm soil substrate, allowed for species-typical thermoregulatory and burrowing behavior. Soil was collected from areas on SWRS property. Animals were fed crickets (*Acheta* sp.) daily and water was available *ad libitum*.

Effect of female color on female-female interactions

I tested the hypothesis that reproductive color functions in social interactions among females by measuring the effect of color on female basking position and feeding behavior. Each member of a triad was assigned to one of three treatment groups: no-orange, pale-orange, or dark-orange in a semi-random fashion. Treatment groups did not differ in SVL, body mass, body condition index, mite load, or natural coloration (ANOVA: Body condition index: $P = 0.18$; All other variables: $P > 0.60$). For all treatments, I covered the female’s natural throat color with paint that matched the ventral surface of the lizard, and I painted a small dot of blue paint on each side of the throat to match the species-specific sexually monomorphic throat color. All females received these identical paint treatments. For the pale- and dark-orange treatment groups, I additionally painted a ring of orange paint around the blue dot. To the human eye, all three treatments closely mimicked natural coloration of lizards observed in the wild. By spectrometry, neither the natural orange pigmentation nor the orange paints reflect in the UV wavelengths (320–400 nm), and all have a typical “orange” color spectrum (S. Weiss, K. Foerster & K. Dheley unpubl. data).

I allowed females one day to acclimate to the captive environment, and conducted experimental trials over the following four days. These females also were used in a study of male response to female color that is not discussed here (Weiss 2002); for this reason, each female was presented to a male for 20 min per day on three days of this current study.

Basking behavior

At approximately 09:00, I ranked the basking position of each female of a triad relative to the 40 W bulb suspended over the terrarium. The female closest to the heat source was given the rank 1, and the female furthest away was given the rank 3. Ties in rank were allowed and the shared rank was quantified as the average of two ranks.

I averaged the daily rank of each female over the four-day experimental period, and termed this

average “basking status”. Thus, basking status is a continuous variable ranging from 1.0 to 3.0 that meets the assumptions of parametric statistics. I tested whether basking status was related to female color treatment using an analysis of variance (ANOVA) test. I performed Pearson correlations to determine whether basking status was related to female SVL, body mass, condition index, mite load, or natural reproductive color intensity.

Feeding behavior

I conducted feeding trials at approximately 16:00 on each day of the experimental period. I added crickets, one at a time, into the terrarium of a given triad and recorded the sequence in which the females fed. I offered a maximum of 10 crickets to each triad, and I stopped observing feeding behavior after approximately 30 sec had passed without a foraging attempt.

I used an ANOVA to determine whether treatment groups differed in the number of crickets eaten over the four-day experimental period, and used Pearson correlations to determine whether the total number of crickets eaten correlated to female SVL, body mass, condition index, mite load, or natural reproductive color intensity. I tallied the number of times females from each treatment group obtained the first cricket presented during a given feeding trial, combining all observations of all triads, and performed a *G*-test of independence to determine whether the act of eating first was independent of color treatment.

Additionally, I constructed a transition matrix that tallied the number of times a given individual successfully foraged following a successful foraging episode of each member of the triad. The feeding observations of all 12 triads were combined in the construction of this matrix. I calculated transition frequencies and used a *G*-test of independence to determine whether feeding sequence was random with respect to female color treatment.

Effect of female color on sex recognition

To test the hypothesis that female color functions

in sex recognition, I used a sequential trial design to measure the response of focal males ($N = 9$) to two stimulus males: a control and a female-mimic. Control males were painted identically to the no-orange female treatment group detailed above. (Recall that throat color is sexually monomorphic in the absence of the temporarily-expressed, female-specific orange reproductive color.) Female-mimics were painted identically to the dark-orange female treatment group detailed above. Focal males remained unpainted. Focal males were tested once with each stimulus; the two trials were separated by 24 h and the order of stimulus presentation was randomized. The stimulus males and the focal male to which they were introduced were matched for SVL within 1.5 mm (average difference = 0.03 mm) and were matched for body mass within 1.1 g (average difference = 0.14 g; only two cases differed by more than 0.5 g).

Trials were conducted after a 1–4 d acclimation period. To begin a trial, I placed one of the stimulus males (hereafter “intruder”) into the terrarium of the focal male (hereafter “resident”) and recorded the display behavior of each individual for 15 min. I noted the first display behavior performed by each male, and counted the total number of jiggles, headbob bouts, challenge postures and chemosensory behaviors (described below) performed by both the resident and intruder.

Jiggles involve a rapid and shallow nodding of the head (Ruibal 1967), typically performed while walking and only in the context of courtship, and were interpreted as a courtship response. Headbobs involve an up and down movement of the head, typically performed in bouts by an otherwise stationary lizard (Carpenter 1962), are used in both courtship and aggressive contexts (e.g., Martins 1991), and were considered an ambiguous first response. The challenge posture is a lateral compression of the body and extension of the dewlap (Carpenter 1962) that is only performed by males in aggressive interactions with other males, and was interpreted as an aggressive response. Chemosensory behaviors performed by *S. virgatus* include tongue-flicking the surface or a conspecific, nose tapping the surface or a conspecific, wiping the cheek on the substrate, rubbing the vent on the

substrate, digging the nose through the soil, and licking the lips.

Statistics

I examined whether the first display performed by resident males differed as a function of the color treatment of the intruder, and whether the first display performed by the intruder was affected by its own color treatment. I then tested whether resident and intruder males were equally likely to first perform courtship displays, ambiguous displays, or aggressive displays using three separate Fisher exact tests.

Non-parametric statistics were used to examine how intruder color treatment affected the number of displays performed because most display variables were not normally distributed, even following standard transformations. I used Friedman's tests to examine the number of displays performed by resident males towards control and female-mimic intruders. I used Mann-Whitney *U*-test to compare the display behavior of the two types of intruders.

Results

Effect of female color on female-female interactions

Basking behavior

Female color treatment did not significantly affect the basking status of females ($F_{2,33} = 2.24$, $P = 0.12$) although there was a trend for dark orange females to attain better basking

sites than pale and no orange females (Table 1). Individual differences among females in basking status could not be explained by SVL, body mass, condition, mite load, or natural reproductive color intensity, as correlation coefficients between basking status and these variables were weak and statistically insignificant (in all cases, $P > 0.50$, $N = 36$).

Feeding behavior

The total number of crickets eaten by a female during the observation period did not differ with respect to female color treatment ($F_{2,33} = 0.93$, $P > 0.40$; Table 1) or with any other measure of the female (i.e., SVL, body mass, condition, mite load, and natural reproductive color intensity; correlation: for all, $P > 0.05$, $N = 36$). Pale orange females, however, were more likely than either dark orange or no orange females to obtain the first cricket presented on a given day ($\chi^2 = 8.73$, $P < 0.05$, $df = 2$; Table 1). Transition frequencies in feeding sequence were random with respect to female color treatment ($\chi^2 = 4.21$, $P > 0.10$, $df = 4$; Table 2).

Effect of female color on sex recognition

The first display behavior performed by resident males did not appear to differ in response to color treatment of the intruder (Table 3). Similarly, the first display behavior performed by the two types of intruder males (control and female-mimic) towards the resident male did not appear to differ from each other (Table 4). Statistical comparisons of these data (to test for an effect of intruder

Table 1. Effect of female color on basking and feeding behavior. (A) Mean (\pm SE) basking status of females from each of the three treatment groups: no orange (None), pale orange (Pale), and dark orange (Dark). (B) Mean (\pm SE) number of crickets eaten during the four days of the experimental period by females within each treatment group. (C) Percentage of feeding trials in which a female from each treatment group ate the first cricket introduced to their triad. Twelve triads were each fed four times, for a total of 48 feedings. On six occasions (12.5%), no female within a triad fed during the observation period (not included in the Table).

	None	Pale	Dark	Statistic	<i>P</i>
(A) Basking status	2.1 \pm 0.1	2.1 \pm 0.1	1.8 \pm 0.1	$F_{2,33} = 2.24$	0.12
(B) Total eaten	5.5 \pm 0.6	6.2 \pm 1.0	4.6 \pm 0.8	$F_{2,33} = 0.93$	0.40
(C) % ate first	27.1	43.8	16.7	$\chi^2 = 4.21$	0.01

type) were not performed because (1) data were sparse (i.e., most cells had counts fewer than 5), and (2) visual inspection was sufficient to determine no relevant difference between groups.

By combining data from Tables 3 and 4, I could statistically examine the effect of social situation (resident or intruder) on the first display behavior. Relative to residents, intruders were significantly less likely to first perform a courtship display ($P < 0.05$), and were significantly more likely to first perform an aggressive display ($P < 0.01$; Table 5).

The total number of jiggles, headbob bouts, challenge postures, and chemosensory behaviors performed by resident males during the 15 min trial periods was not significantly affected by the color treatment of the intruder males (Fig. 1; jiggles: $T = 2.78$, $P = 0.10$; headbob bouts: $T = 1.78$, $P > 0.10$; challenge postures: $T = 0.11$, $P > 0.70$; chemosensory behavior: $T = 1.00$, $P > 0.30$; $df = 1$ for all). The trend, however, was for resident males to perform more jiggles and headbob bouts towards female-mimic intruders than towards control intruders.

The two types of intruder males did not differ in the number of display or chemosensory behaviors towards focal males (jiggles: $U = 41.0$, $P > 0.90$; headbob bouts: $U = 39.0$, $P > 0.80$; challenge postures: $U = 26.0$, $P = 0.20$; chemosensory behavior: $U = 26.0$, $P > 0.10$; $df = 1$ for all).

Table 2. Matrix of transition frequencies from feeding behavior trials. Data show the frequency in which a given female's foraging event was followed by each of the three members of the triad. For example, data in the first column of the table show that when a female in the no-orange color treatment (None) foraged, she would forage again on the next cricket 40% of the time, the pale orange female (Pale) would forage on the next cricket 34% of the time, and the dark orange female (Dark) would forage on the next cricket 26% of the time. Foraging sequence was independent of color treatment ($P > 0.10$).

	First female		
	None	Pale	Dark
Second female			
None	0.40	0.39	0.23
Pale	0.34	0.34	0.36
Dark	0.26	0.27	0.41

Discussion

Among *S. virgatus*, female-female interactions and sex recognition may be subtly affected by female reproductive color, however none of these effects appear to be strong enough to fully explain the functional significance of the color. Females do not appear to be the intended receiver of the color signal, and accurate sex recognition at close range is not dependent on female reproductive color. As in any sexually

Table 3. First display behavior of resident males toward intruders. The tally of the number of times in which a given display type was the first response of residents toward control and female-mimic intruders. See text for a description of responses.

First response	by residents toward control	by residents toward female-mimics
courtship	2	3
ambiguous	5	4
aggression	1	2
no display	1	0

Table 4. First display behavior of intruder males toward residents. The tally of the number of times in which a given display type was the first response of intruders toward residents. See text for a description of responses.

First response	by control toward residents	by female-mimics toward residents
courtship	0	0
ambiguous	2	3
aggression	7	5
no display	0	1

Table 5. Comparison of the first response of residents (sum of data in Table 3) and of intruders (sum of data in Table 4). See text for a description of responses.

First response	by residents	by intruders	Statistic
courtship	5	0	$P < 0.05$
ambiguous	9	5	ns
aggression	3	12	$P < 0.01$
no display	1	1	–

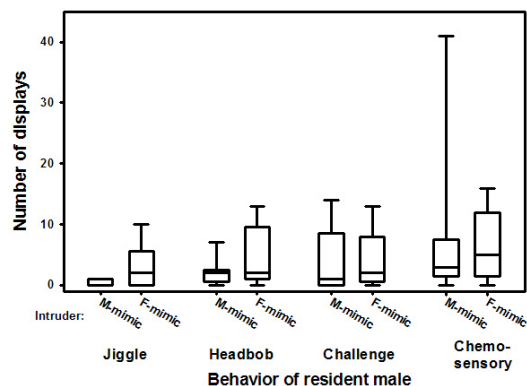


Fig. 1. Effect of intruder color on resident behavior. The number of displays performed by the resident male towards the control (i.e., “male-mimic” (M-mimic)) and female-mimic (F-mimic) intruder males during the 15 min experimental trials. Box plots illustrate 10th, 25th, 50th (median), 75th and 90th percentiles, and show all data points beyond this range. Sample size for each box plot is 9.

dimorphic signal, gender may be an inherent part of the signal’s message, but sex recognition is unlikely to be important for the maintenance of color expression in the extant population. Interpretation of the male-male introduction study generates the hypothesis that chemosensory cues may be important for sex recognition in this species.

Female–female interactions

Because direct female–female aggression is rare among *S. virgatus* (Vinegar 1975, Weiss, personal observation), I did not test the effect of color on female social interactions by staging encounters and measuring display behavior, but rather I examined basking and feeding behavior of female triads in an attempt to elucidate potentially subtle effects of female color. Basking sites and prey availability may be important resources for which females compete. However, basking status was not significantly related to female color treatment or to any other measure of the females, including their natural color intensity. There was a trend, however, for dark orange females to attain better basking positions than pale or no orange females. The ability to acquire good basking sites may influence females’ abil-

ity to obtain preferred body temperatures (e.g., Bakken 1989), which in turn may affect regulatory and reproductive physiology (Huey & Kingsolver 1989).

An advantage to dark orange females was not evident in observations of feeding behavior, where the only non-random pattern with respect to female color revealed a benefit to pale orange females. Pale females successfully foraged on the first cricket introduced into home tanks more often than dark orange and no orange females (Table 1). In an environment with limited food resources, the ability to successfully gain first access to available food items may influence females’ energy reserves (Weiss 2001), which are expected to be important for both future reproduction (Stearns 1992) and overwinter survival (Jones & Ballinger 1987). There was, however, no apparent effect of female color on feeding order or the total number of crickets eaten during feeding trials.

As a whole, then, my observations of basking and feeding behavior failed to reveal any consistent trend in the effect of color on resource competition among female triads. Thus, the results do not provide support for the hypothesis that the female color functions in female–female interactions.

Sex recognition

The sex recognition hypothesis suggests that female reproductive color functions to identify an individual as a female (e.g., Cooper & Greenberg 1992), and predicts that *S. virgatus* males will respond to orange color with increased courtship and decreased aggression. Resident males tended to perform more courtship behaviors towards female-mimic intruders than to control intruders (Fig. 1), but this result fell short of significance. Intruder treatment had no effect on the number of aggressive displays performed.

Evidence from this study, as well as from Weiss (1999), suggests that female color is not essential for rapid or accurate sex recognition in *S. virgatus*. Assume that an “error” in sex recognition is indicated by a male either (1) initially responding to an orange-painted male with courtship or (2) initially responding to a

blue-painted female with aggression. Are males more likely to court orange-painted males than males without orange paint? The first response of resident males was not affected by the color treatment of intruder males (Table 3). Thus, at least in some contexts, errors in sex recognition are not related to dewlap color. Are males more likely to aggressively challenge a female if she does not express orange reproductive color? In previous work, with 54 trials in which painted females were presented to males, males performed challenge postures only three times: twice to a female with no-orange color, and once to a female with dark-orange color (Weiss 1999). Thus, misidentifying a female as a male is rare, and appears to be independent of female color. In total, these data suggest that female throat color does not have a significant effect on rates of error in sex recognition among *S. virgatus*.

Vinegar (1972) conducted a study similar to this current study and found that color treatment of stimulus animals did significantly affect the first response of male *S. virgatus*. She presented free-ranging males with pairs of painted animals (one with and one without orange reproductive color) that were tethered to each end of the cross-member of a T-shaped bar. When the members of the stimulus-pair were male, courtship to a male (i.e., an error in sex recognition) was the first response in eleven of 20 trials; nine times (82%) to orange males and two times (18%) to no-orange males. When the members of the stimulus-pair were female, the focal males' first response was an aggressive display (i.e., an error was made) in eight trials; aggression was more often directed to no-orange females (75%) than to orange females (25%). These increased rates of error towards less appropriately painted animals support the hypothesis that dewlap color may facilitate sex recognition in some contexts, and contrast with the data presented herein.

The conflicting results between Vinegar's study and my own are likely due to differences in methodology. For instance, Vinegar used a simultaneous presentation design while I used a sequential presentation design. In a simultaneous test protocol, the behavior of focal males towards a given stimulus type may be influenced by the presence of the other stimulus, as well as by the ability to directly compare the two stimuli,

and may make differential responses to the two stimuli appear stronger than they actually are (Wagner 1998). On the other hand, it is possible that throat coloration serves as a long-distance sex-recognition signal and that other cues, such as chemosensory signals (Hews & Benard 2001, López *et al.* 2002), take precedence at close proximity. Although Vinegar did not report the distance between the focal male and the tethered intruders, it is likely to have been farther than the limitations of the terraria used in my study. Overall, dewlap color may be sufficient for sex recognition in some contexts, but it certainly is not necessary. Other cues appear to be available for the assessment of gender.

Evidence for sex-identifying chemosensory cues

While color of the intruder male did not significantly affect the likelihood of an error in sex recognition, social situation did have an influence. Intruder males were more likely to challenge and less likely to court (i.e., made fewer errors) relative to the resident male (Table 5). The opposite prediction may have been made *a priori* with respect to aggressive behavior; resident males typically are found to be more aggressive towards intruding males than *vice versa* (Krebs 1982, Baugh & Forester 1994, Mathis *et al.* 1998). I suggest that the ability of intruding males to more accurately assess the sex of resident males may have been related to the presence of sex-identifying chemosensory cues deposited by the residents in their terraria. In contrast, the resident male initially had little, if any, chemosensory information about the intruding male. In the absence of chemosensory cues indicating the intruder's gender, the resident male may have been more motivated to initiate courtship with a potential female than to defend his "territory" from a potential male, especially given that these experiments were conducted in captivity towards the end of the reproductive season when reproductively active males were faced with a shrinking population of receptive females. Striped plateau lizards perform many behaviors that suggest chemosensory cues may indeed play an important role in the communication of this

species (Weiss 1999, Hews & Benard 2001), and recent work in other lizards suggest that chemosensory cues are more important than color signals for close-range sex recognition (López *et al.* 2002). Future research that directly addresses the functional role of chemical communication among *S. virgatus* would be beneficial.

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