

ONTOGENETIC AND SEASONAL CHANGES IN COLORATION OF THE  
BLUNT-NOSED LEOPARD LIZARD (*GAMBELIA SILA*)

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**ABSTRACT**—Among crotophytids, the blunt-nosed leopard lizard (*Gambelia sila*) is one of only 2 species known in which adults do not have permanent dichromatic patterns, but both males and females display bright breeding colors. Males in most populations develop a salmon color over most of their head and body, whereas females develop rusty red blotches laterally along the head and trunk. Also unusual is the yellow color exhibited by juveniles. Between 1992 and 1994, we captured adult and juvenile *G. sila* on the Elkhorn Plain, San Luis Obispo County, California, and scored individuals for their coloration. Juvenile *G. sila* developed a yellow color on the undersides of their hind limbs and tail that was apparent when they were about 55 mm snout-vent length (SVL) and was prominent until about 85 to 90 mm SVL. Both males and females developed breeding colors between 85 and 95 mm SVL. Breeding colors of adults developed soon after they emerged each year in April or early May, and most adults retained breeding colors until they ended activity in July or August, although coloration fluctuated within a season for some individuals. Individual differences in the amount of coloration occurred with some large adults never developing fully bright breeding colors. Females produced multiple clutches in each year, and their breeding colors were not immediately apparent with their first clutch and sometimes faded, but did not disappear, between clutches.

**RESUMEN**—Dentro de Crotophytidae, la lagartija *Gambelia sila* es una de las únicas dos especies conocidas en la que los adultos no tienen diseños dicromáticos permanentes, pero tanto los machos como las hembras muestran colores de apareamiento brillantes. Los machos en la mayoría de las poblaciones desarrollan un color salmón sobre la mayor parte de la cabeza y el cuerpo, mientras que las hembras desarrollan manchas rojizas lateralmente por la cabeza y tronco. También inusual es la coloración amarilla exhibida por los juveniles. Entre 1992 y 1994, capturamos adultos y juveniles de *G. sila* en Elkhorn Plain, condado de San Luis Obispo, California, y clasificamos individuos por su coloración. Los juveniles de *G. sila* desarrollan una coloración amarilla abajo de las extremidades posteriores y la cola que fue aparente cuando estaban acerca de 55 mm longitud hocico-cloaca (SVL) y fue prominente hasta acerca de 85–90 mm SVL. Tanto machos como hembras desarrollaron la coloración de apareamiento entre 85–95 mm SVL. La coloración de apareamiento de los adultos se desarrolló poco después de que emergieron cada año en abril o principios de mayo y en la mayoría de los adultos mantuvieron los colores de apareamiento hasta que terminaran la actividad en julio o en agosto, aunque la coloración fluctuó en una temporada para algunos individuos. Las diferencias individuales en la cantidad de la coloración ocurrieron con algunos adultos grandes que nunca desarrollaron completamente colores de apareamiento brillantes. Las hembras produjeron múltiples puestas cada año y sus colores de apareamiento no fueron inmediatamente aparentes con su primera puesta, y algunas veces se destiñeron, pero no desaparecieron, entre puestas.

Many vertebrates display coloration or color patterns that might serve a physiological function and can also influence predator avoidance and social behavior (Cooper and Greenburg, 1992; Stuart-Fox and Ord, 2004). Among the squamates, a number of lizard species are particularly colorful or display striking patterns,

at least during breeding or when young (Montanucci, 1965; Ferguson, 1976; Cooper and Greenburg, 1992; McGuire, 1996). Numerous hypotheses have been proposed to explain the onset of breeding coloration and the behaviors often associated with colors in these lizards. Breeding coloration in male lizards might

function in sexual recognition or it might enhance selection of males by females (Cooper and Greenburg, 1992). In female lizards, breeding coloration might signal males that the female is non-receptive, might be involved in female-female aggression, or might stimulate courtship (Cooper, 1988; Cooper and Greenburg, 1992; Sloan and Baird, 1999; Hager, 2001; Baird, 2004).

In most crotaphytids (and most Iguania), males and females are dichromatic in permanent dorsal patterns, and females display red-orange dorsal banding or spotting when gravid (McGuire, 1996). Among this group, however, only the blunt-nosed leopard lizard (*Gambeliasila*) and the reticulate collared lizard (*Crotaphytus reticulatus*) do not have permanent dichromatic patterns in adults, yet both males and females display breeding colors (McGuire, 1996). In *G. sila*, males in many populations develop a salmon coloring over most of their head and body, whereas females develop rusty red blotches laterally along the head and trunk, which can extend to under the thighs and tail when in breeding coloration (Montanucci, 1965, 1970; Stebbins, 2003). In the congeneric *G. wislizenii*, females develop an orange-red color during the breeding season, but males do not develop any breeding coloration (McGuire, 1996; Stebbins, 2003). Besides the breeding coloration exhibited by adult *G. sila*, young of both sexes develop much yellow under the tail and the undersides of the back legs (Montanucci, 1965), which, among crotaphytids, has additionally only been found in *Crotaphytus antiquus* (McGuire, 1996). In several lizard species, coloration of juvenile males has been proposed as a form of female mimicry to lessen aggression by adult males (Fitch, 1967; Cooper and Ferguson, 1972; Montanucci, 1978; Carpenter, 1995).

We studied the ontogenetic and breeding color patterns of *G. sila* on the Elkhorn Plain, San Luis Obispo County, California. Between 1992 and 1994, we captured and permanently marked adult and juvenile *G. sila*. We scored lizards in the spring and summer for the amount of breeding coloration they exhibited, or for juveniles, how much yellow showed. Quantifying changes in color patterns for this unique species is a prerequisite for future studies to test hypotheses concerning the selective advantages of juvenile and adult coloration.

**METHODS**—The study was conducted on the Elkhorn Plain, San Luis Obispo County, California, which is foothill habitat in the southwestern end of the range of *G. sila* (see Germano and Williams, 2005, for a description of the site). Leopard lizards were censused on two 8.1-ha plots, located about 1.6 km from each other along the dirt road that runs the length of the Elkhorn Plain. From 1989 to 1994, we censused lizards each month of the active season for the lizard when daytime temperatures became high enough for lizards to become active (Germano and Williams, 2005). We used a pole and noose to capture lizards. Once a lizard was captured, we noted its location, determined its sex, and applied a numeral to its dorsal surface with a non-toxic felt-tipped pen. Each captured lizard was placed in a cloth bag and held until after the census, when we took body measurements, including snout-vent length (SVL) and total length (TL), and weighed each lizard to the nearest gram. Finally, we injected a Passive Integrated Transponder (PIT) subdermally or inter-abdominally into each blunt-nosed leopard lizard (Germano and Williams, 1993). After all lizards were processed for a day, each lizard was brought back to its original point of capture and released.

From 1992 to 1994, we subjectively scored lizards for the amount of yellow they had on their legs and tail, and the amount of breeding color they exhibited. We used ANOVA to test for differences in yellow coloration, using sex and size as main effects, and pair-wise interactions of these factors. We determined the best model of main effects and pair-wise interactions by eliminating factors with high *P* values (thus increasing degrees of freedom) until we were left with factors with the lowest *P* values possible for the data set. We compared the amount of yellow males and females exhibited (none, some yellow, yellow) within each sex by grouping lizards into 6 SVL categories: <55 mm, 55 to 64 mm, 65 to 74 mm, 75 to 84 mm, 85 to 94 mm, and 95 to 104 mm. Few individuals of either sex exhibited any yellow past 104 mm SVL. We also used ANOVA to compare differences in breeding coloration (none, light, full or bright) within each sex by size using 6 SVL categories: 85 to 89 mm, 90 to 94 mm, 95 to 99 mm, 100 to 104 mm, 105 to 109 mm, and  $\geq 110$  mm. Although there were multiple captures for many individuals, we used only one capture for scoring yellow and one capture for scoring breeding coloration. To determine if there were differences in breeding coloration of the population within a season, monthly differences in breeding coloration of males and females (none, light, full or bright) within each sex were compared with ANOVA using the categories 15 April to 14 May, 15 May to 14 June, and 15 June to July, which roughly correspond to the beginning, middle, and end of the adult active season (Germano and Williams, 2005). Finally, we tested the difference in breeding coloration (none, light, full, bright) of females with eggs and those without using Chi-square ( $\alpha = 0.05$ ).

Several assistants helped collect coloration data, although the senior author did the majority of scoring. In most cases where there were multiple captures, scoring of yellow coloration was the same among researchers. However, there was more difference among researchers scoring full and bright breeding

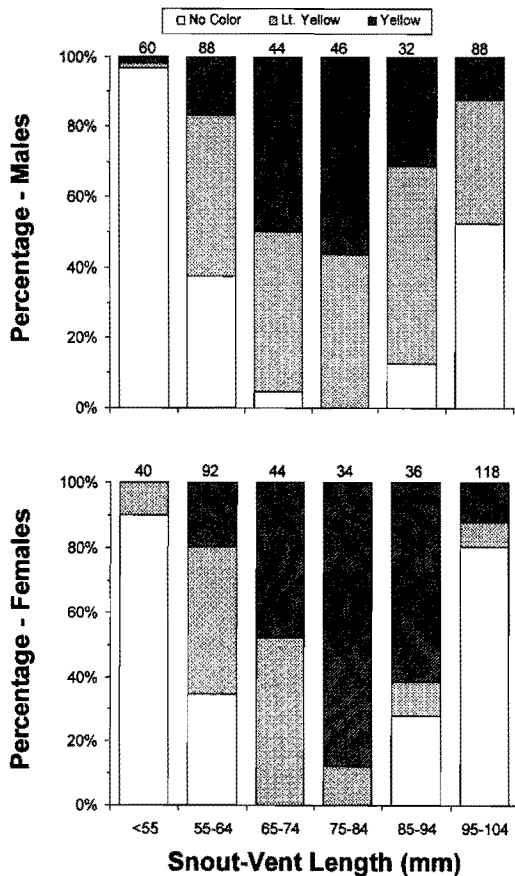


FIG. 1.—Percentage of male (top) and female (bottom) *Gambelia sila* on the Elkhorn Plain, California, displaying yellow color (no color, light yellow, yellow) at various size categories from 1992 to 1994. Numbers at the top of each bar are sample sizes.

colors of adults. Because of this, full and bright coloration was combined in analyses.

**RESULTS**—Hatchling and juvenile *G. sila* had varying amounts of yellow under their hind limbs and tail (Fig. 1). Less than 6% of male and <12% of female lizards <55 mm SVL showed any yellow. By 55 to 64 mm SVL, 66.7% of females and 68.5% of males displayed some amount of yellow, and virtually all lizards 65 to 84 mm SVL displayed yellow coloring (Fig. 1). The percentage of lizards with yellow coloring diminished for lizards >85 mm SVL as they attained breeding coloration, and <6% of male and female lizards  $\geq 105$  mm SVL had yellow coloring (Fig. 1). Significant differences in yellow coloration of juveniles were detected for size, color, and the interaction of size and color, but

TABLE 1.—Results of the best model of ANOVA testing of color, sex, and size (or month) of yellow and breeding colors of blunt-nosed leopard lizards (*Gambelia sila*) from the Elkhorn Plain, San Luis Obispo County, California.

	F value	P
<b>Yellow color</b>		
Size	$F_{5,18} = 4.94$	0.005
Color	$F_{2,18} = 3.27$	0.062
Size*Color	$F_{10,18} = 7.14$	<0.001
<b>Breeding colors (by size)</b>		
Color	$F_{2,15} = 6.84$	0.008
Sex*Color	$F_{2,15} = 6.62$	0.009
Size*Color	$F_{10,15} = 2.04$	0.103
<b>Breeding colors (by month)</b>		
Month	$F_{2,17} = 2.62$	0.121
Color	$F_{2,17} = 2.37$	0.143
Sex*Color	$F_{2,17} = 2.62$	0.122

no differences were detected based on sex (Table 1).

The smallest *G. sila* to display breeding coloration were lizards in the 85 to 89 mm SVL class; 2 males (6.6% of total) and 5 females (16.2%) had such coloration (Fig. 2). The smallest male was 88 mm SVL and had light breeding coloration, whereas the other male was 89 mm SVL and was in full breeding coloration. The smallest female in breeding coloration was 87 mm SVL, and it was in bright colors, as was one other female in this size class. Breeding coloration was evident for 67.5% of males and 59.6% of females 90 to 94 mm SVL, and the proportion of lizards displaying breeding coloration increased steadily across size classes: from 88 to 98% of males and from 91 to 100% of females  $\geq 95$  mm SVL (Fig. 2). Only 4 males  $\geq 105$  mm SVL had no breeding coloration and all were found in July, past peak breeding times. Both sex and size entered the best model explaining the differences in the proportion of breeding coloration as interactive factors with color (Table 1), but neither was significant as a main effect. Not all males developed bright or even full breeding colors during a season, and coloration in most males varied within a season. Of 16 males with  $\geq 3$  captures (mean = 4.2 captures, range = 3 to 6) in a season, 2 males showed only light breeding coloration, 2 fluctuated from full to light back to full coloration, and

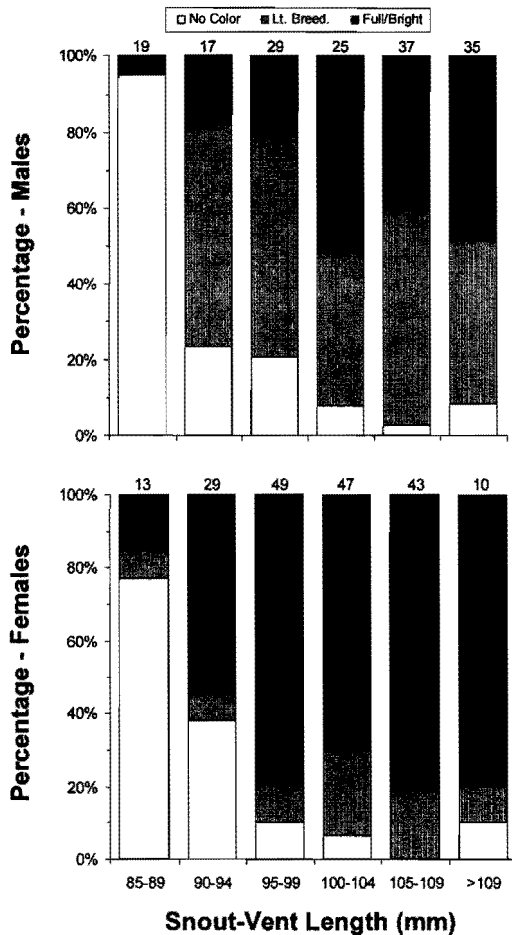


FIG. 2—Percentage of male (top) and female (bottom) *Gambelia sila* on the Elkhorn Plain, California, displaying breeding colors (no color, light, full or bright) at various size categories from 1992 to 1994. Numbers at the top of each bar are sample sizes.

the remainder changed from light or no coloration to full or bright and sometimes back to none or light by the end of the active season. Unlike males, all 20 females for which we had multiple captures (mean = 4.6 captures, range = 3 to 7) attained full or bright breeding coloration at some time during the season, although all varied in coloration over the course of the active season.

Adult male lizards displayed some breeding coloration as early as the beginning of April. On 11 and 13 April 1994, 2 adult males were in light breeding coloration, 3 had full or bright breeding colors, and only one had no color. From 15 April to 14 May, breeding coloration

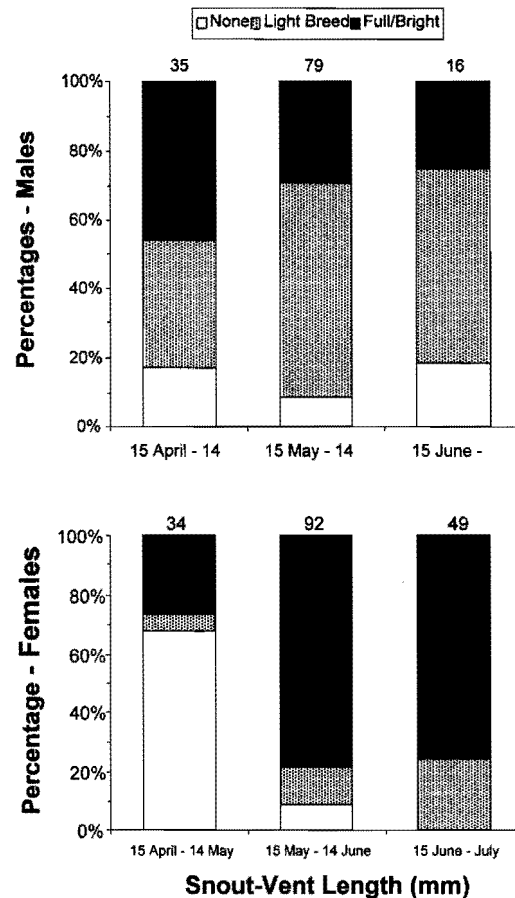


FIG. 3—Percentage of male (top) and female (bottom) *Gambelia sila* on the Elkhorn Plain, California, displaying breeding colors (no color, light, full or bright) by month intervals for 1992 to 1994. Numbers at the top of each bar are sample sizes.

was evident on 83% of adult males, and it stayed around this level through the end of July (Fig. 3). Although most adult leopard lizards were not seen past the end of July (Germano and Williams, 2005), 2 males scored for color were found in mid August: one in light breeding coloration and one in full color. The majority of females displayed no breeding coloration early in the active season, but from mid May to the end of July, virtually all females showed some breeding colors (Fig. 3). Despite these differences, the best model of ANOVA for breeding coloration by sex, month, and color showed no significant differences among factors (Table 1).

Females displayed breeding colors whether they were gravid or not (Fig. 4), but more

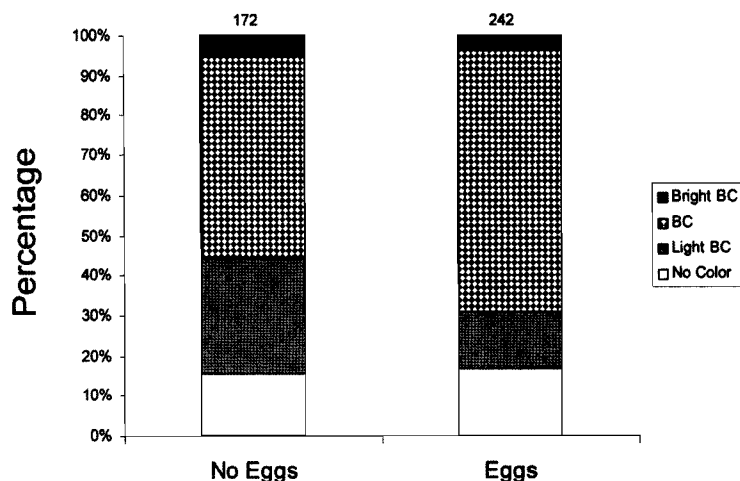


FIG. 4.—Percentage of gravid and non-gravid female *Gambelia sila* on the Elkhorn Plain, California, displaying breeding coloration (BC) from 1992 to 1994. Numbers at the top of each bar are sample sizes.

females with eggs showed full breeding coloration ( $\chi^2_{0.05,3} = 14.76$ ,  $P = 0.002$ ). On a population basis, 50.6% of females without eggs and 65.3% of females carrying eggs exhibited full breeding coloration. Conversely, there was no difference in percentage of females showing some intensity level of breeding coloration (light, full, bright), with about 84% of females without eggs and about 83% of females with eggs displaying breeding coloration of some type (Fig. 4). When tracking individuals, 7 females early in the season had oviductal eggs but had not yet developed breeding coloration. Of 20 females captured multiple times within a season, 3 were found to have full or bright breeding colors, then in light breeding colors (with eggs), and then back in full or bright breeding colors.

**DISCUSSION**—*Gambelia sila* is relatively unique among the crotaphytids in that sexes are not distinguishable by permanent dichromatic coloration and patterning, but both males and females develop breeding coloration, and these colors and patterns differ markedly between them. Also, unlike virtually all other crotaphytids, juvenile *G. sila* obtain a yellow coloring under their hind limbs and tails. We have shown that this yellow coloring was virtually absent in hatchling *G. sila* (<55 mm SVL), but was present in almost all individuals between 65 and 94 mm SVL. Some lizards began to develop breeding coloration as small as 87 mm SVL, and virtually

all *G. sila* >95 mm SVL showed breeding coloration, even if it was only a light shade. Some adult males never developed a full or bright salmon coloring over their bodies at any time of the season, whereas all adult females became fully or brightly colored during the season. For some females, though, the color might fade between clutches of eggs, and females can have no color at the beginning of the season, even with eggs in their oviducts.

The ontogeny of yellow coloration in young *G. sila* might indicate that some type of signal is being sent to adult leopard lizards, although no testing has been done. Possibly the purpose of yellow coloration is to signal to adults that carriers are too small to breed, and, therefore, do not pose a competitive threat. However, adults and small juveniles that have much yellow typically do not occur above ground at the same time (Montanucci, 1965; Germano and Williams, 2005). In most years, young *G. sila* hatch when adults are going underground for the year, and even moderate growth of juveniles means that young will be in the 80 to 90 mm SVL range by the following spring, when both juveniles and adults re-emerge (Tollestrup, 1982; Germano and Williams, 2005). Juvenile males and females can breed by 90 mm SVL (Montanucci, 1970; Tollestrup, 1982; Germano and Williams, 2005), and most still retain yellow coloration. In contrast, hatchlings are the size group most likely to encounter adults before adults retreat underground, and hatchlings do not have yellow

coloration. If adults are still active when young hatch, adults will eat hatchlings (Montanucci, 1965; Germano and Williams, 1994). Therefore, it does not seem likely that yellow on juveniles is a social signal. Recently, a test of presumed adult female mimicry by juvenile male *Crotaphytus collaris* in Oklahoma showed no reduction in aggression by adult males towards juvenile males displaying adult female coloration (Husak et al., 2004).

Conversely, the bright yellow coloration of juveniles could serve as a means of predator avoidance (Cooper and Greenberg, 1992). Juveniles of a variety of lizards have brightly colored tails and highly contrasting body colors that fade to dull, cryptic colors as they grow larger (Cooper and Greenberg, 1992; Stebbins, 2003). These species also have autotomous tails (Zug et al., 2001), and leaving behind a brightly colored, wriggling tail might allow a juvenile time to escape from a predator. Tails of *G. sila* are autotomous, but the yellow coloration of juveniles is restricted to the undersides of the tail and rear legs. Because of its location, the yellow coloration is probably not visible unless intentionally flashed by the lizard. When viewed from above, juveniles are cryptically colored, which generally confers a significant advantage against predation (Macedonia et al., 2002; Stuart-Fox et al., 2004). Intentionally raising the tail and rear portions of the body might be a defensive mechanism for young *G. sila* if they are detected. Young of both *Coelonyx variegatus* and *Eumeces fasciatus* have been shown to raise their tails off the ground to distract snake predators away from striking their more vulnerable bodies (Congdon et al., 1974; Cooper and Vitt, 1985).

Breeding coloration in many male lizards seems to be related to sex recognition, and females might prefer brightly colored males (Cooper and Greenberg, 1992; Baird et al., 1997). Males with bright breeding coloration could also benefit by reducing aggression from competing males. Male *G. sila* are territorial and aggressively defend activity areas against intrusion from other males (Montanucci, 1965; Tollestrup, 1982, 1983). A coloration by dominant males that advertises aggression might save the dominant male energy and the risk of injury. Based on obtaining a size necessary for defending territories, Tollestrup (1982) suggested that most male *G. sila* could not successfully breed until they were 20 to 21 months old (start of

their second full season). However, males develop breeding colors and are sexually mature at just under 90 mm SVL (Montanucci, 1970; Tollestrup, 1982), a size reached within 9 months in many males (Germano and Williams, 2005) and, thus, could fertilize females if not chased off by larger males or actively rejected by females. Interestingly, although small adult males start developing breeding coloration, some do not immediately lose their yellow coloration. Of those males that were in breeding coloration, we found that 82.1% (23 of 28) of males 85 to 94 mm SVL and 51.3% (40 of 78) of males 95 to 104 mm SVL also had yellow coloration. Further observations or experimentation will be necessary to determine the roles of both yellow and breeding coloration in males.

Displaying bright breeding coloration might carry increased risk of predation (Stuart-Fox et al., 2003). Territorial male *G. sila* are often found standing erect and vigilant out in the open on the low rises of kangaroo rat (*Dipodomys*) mounds (Montanucci, 1965; Germano and Williams, 2005). This makes them particularly vulnerable to avian predators. Twice we found brightly colored males captured by raptors (Germano and Carter, 1995; Germano and Brown, 2003). In an experiment of predation risk of Australian *Ctenophorus* lizards, models of brightly colored male lizards were attacked significantly more often by predators than dull-colored models (Stuart-Fox et al., 2003). Certainly there must be a sexually selected advantage to males being brightly colored to offset the naturally selected disadvantages.

Theories for the role of female breeding coloration include sex recognition, maturity advertisement, sexual receptivity or lack thereof, and a social signal to other females (reviewed in Cooper and Greenberg, 1992). Tests of competing theories of female breeding coloration have yielded varied results depending on the lizard species studied. In *Holbrookia propinqua*, brightly colored females aggressively rejected males, and plain colored females were not aggressive to males but tried to avoid them (Cooper, 1988). Also, females of either color pattern did not react to lizards with bright female coloration (Cooper, 1988). In female *H. maculata*, low-intensity breeding coloration seemed to stimulate courtship by males, but bright coloration later in the season, when females were carrying eggs, seemed to signal aggressive rejection of

males (Hager, 2001). Unlike the response in *Holbrookia*, female *C. collaris* that were brightly colored did not behave aggressively towards males and were courted longer and more vigorously than were plain females, even in females that were carrying eggs (Baird, 2004). Sloan and Baird (1999) found no support for bright female breeding coloration functioning among female *C. collaris* as a signal used in nest defense, although they argued that it could be used as a means of re-establishing ownership of home ranges from competing females after egg laying. No behavioral work has been done on the role of breeding coloration in *G. sila*, but a study done by Moore (1983) experimentally tested the role of female coloration in *G. wislizenii*. Although the number of individuals used was low and the number of trials limited, Moore (1983) found that females in breeding colors were aggressive to males and plainly colored females, but were tolerant of other brightly colored females. Plainly colored females also were tolerant of brightly colored females and allowed courtship by males, but were intolerant of other plainly colored females. Finally, males readily courted plainly colored females as well as other males, and sometimes tried to force copulation of females in breeding coloration. It is not clear, though, how bright breeding coloration benefited females with that coloration.

The role of female breeding coloration in *G. sila* is not known, although all adult females develop full or bright breeding coloration. Some adult females actively reject male courtship (Montanucci, 1965; Tollestrup, 1983), but no one has systematically assessed active rejection and female breeding coloration. We witnessed 6 instances of males copulating with females, and in each case, the females were gravid and all but one female were in breeding coloration. It is possible that female breeding coloration in *G. sila* stimulates copulation in males.

We have presented the ontogenetic and seasonal change in patterns of color of juvenile and adult *G. sila* for a population in which both sexes display well developed breeding coloration. Although we did not study the behavioral repertoire associated with color changes, aggressive behaviors in this species are well known (Montanucci, 1965; Tollestrup, 1983). What remains is testing the various hypotheses proposed for the role of juvenile and breeding colors in *G. sila*. Also, quantification of coloration

would be enhanced by using either Munsell color chips or a spectrophotometer to avoid possible bias of subjective scoring (Carpenter, 1995; Macedonia et al., 2003; Stuart-Fox et al., 2004). Because of the unusual combination of male, female, and juvenile color changes in *G. sila*, this species would be valuable for experimental study.

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