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The Ontogeny of a Variable Social Badge: Throat Color Development in Tree Lizards (*Urosaurus ornatus*)

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ABSTRACT.—Two populations of tree lizards (*Urosaurus ornatus*) that differ in morphological and social traits, were used in a comparative study examining the ontogenetic development of throat coloration. Adult males from the Aguirre Spring population exhibited monomorphic throat coloration while Doña Ana males were polymorphic. In a separate study, Aguirre Spring males were found to be in certain respects more aggressive than Doña Ana males. Juvenile males and females from both populations first exhibit orange throat color. Adult Doña Ana females always retain the orange throat coloration but Aguirre Spring females may either retain orange or develop yellow throats. In males from both populations throat badge ontogeny involves a series of throat color changes while ventral belly coloration initially appears as its final hue. This suggests that ontogenetic color change and polymorphic adult coloration serve social functions. Orange throat coloration seen in females and young males may serve to inhibit aggression from adult males. Most dominant Aguirre Spring males have throat colors that are seen late in the developmental sequence suggesting that mature colors (i.e., blue and blue-green) are more socially dominant and are favored by sexual selection.

Animal coloration serves many important roles (Endler, 1978, 1990). While temperature maintenance and camouflage have long been recognized as important functions of color in ectotherms such as lizards, recent studies have emphasized the role of color in social behavior (review in Cooper and Greenberg, 1992). Ventral and ventrolateral coloration in lizards have been the focus of many studies concerning intraspecific communication (Carpenter, 1992; reviewed by Cooper and Greenberg, 1992). In some phrynosomatid lizards adult male color pattern varies discontinuously (Cooper and Guillette, 1991). Recent studies have revealed the roles these polymorphic color patches play as visual social signals in adults (Hover, 1982, 1985; Thompson and Moore, 1987, 1989, 1991a, b; Rand, 1988, 1990, 1991; Moore and Thompson, 1990; Carpenter, 1992). This paper describes and compares the ontogenetic development of one such signal, the throat color badge of tree lizards (*Urosaurus ornatus*).

Studies of ontogenetic change in lizard coloration are few. Many skinks that have cryptically colored tails as adults have brightly colored tails as juveniles. These are thought to function aposematically (Cooper and Greenberg, 1992). Rand and Andrews (1975) described the development of color pattern from neonate to adult in *Anolis cuveiri*, including a description of dewlap (throat) color develop-

ment. Studies of *Tropidurus* have indicated ontogenetic color change (Dixon and Wright, 1976; Werner, 1978). Male red-lipped lizards (*Sceloporus undulatus erythrocheilus*) developed either orange or yellow chin color as juveniles, and, once established, these morphs were fixed (Rand, 1990, 1991). Gates (1963) observed that green and yellow throat coloration was replaced by orange as male *Urosaurus graciosus* matured. Until recently there was little documentation of maturational color change in tree lizards. Hover (1982) observed that young tree lizards in a New Mexico population always had orange throats. Thompson (1991) reported that hatchlings from an Arizona population initially developed either orange or yellow throat coloration. Several studies have concluded that tree lizard throat coloration is stable once established at a few months of age (Hover, 1982; Moore and Thompson, 1990; Thompson, 1991; Thompson and Moore, 1991a, b). My observations of *U. ornatus* reared in captivity and in natural populations in the field indicated that throat color (1) was not fixed at onset, and (2) changed in males as they matured. Tree lizards reared in captivity from two southern New Mexico (Doña Ana County) populations were the subjects of this descriptive study of throat color development. Tree lizards in both populations emerge in April and are active until October. The first population was from Aguirre Spring Recreation Area (AS) in the Organ Mountains and the second was from Mount Summerford in the Doña Ana Mountains (DA). Conditions were slightly more mesic and lizard density was higher at the AS than the DA site,

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and lizards from these populations differed in several regards. The aggressive response of dorsal darkening (Zucker, 1989) was more pronounced in the AS population (Carpenter, 1992), and AS males developed a deeper blue ventral coloration (pers. obs.; Zucker, pers. comm.). Adult AS males observed in the field usually had deep turquoise-blue throats (pers. obs.; Zucker, pers. comm.) and are monomorphic for this trait. Adult DA males on the other hand, exhibited a throat color polymorphism. The most common male morphs in the DA population were (1) an entirely orange throat, (2) a green-centered, orange-rimmed throat, or (3) an entirely green throat. Yellow throats occurred in a small proportion of males (Hover, 1982, 1985; pers. obs.; Zucker, pers. comm.). Females from DA had orange throats when mature, whereas AS female throats may be orange or yellow (Zucker and Boecklen, 1990). This study describes the general sequences seen in tree lizard throat color ontogeny in a monomorphic and a polymorphic population. Based on these observations I then hypothesize upon the social function of ontogenetic color change and relate developmental sequence to relative dominance status of adult morphs.

MATERIALS AND METHODS

Data on development of throat coloration were collected from lizards reared in captivity. During the summers of 1988 and 1989 females laid eggs and hatchlings emerged in semi-natural outdoor enclosures on the New Mexico State University campus, where the lizards were reared in groups. Hatchlings were toe-clipped for permanent individual identification. The diet included the "native" fauna in the outdoor enclosures (grasshoppers, spiders, ants, and other arthropods), supplemented with crickets, mealworms, fruit flies, and occasional net sweepings, ensuring that all individuals had access to food regardless of social status.

Periodically, lizards were captured and snout-vent length (SVL), weight, and throat coloration measurements were taken. I took measurements of lizards' throat colors by comparison to a standardized color wheel (Zucker, 1988). I used the Munsell system, which consists of a continuum of hues that are assigned numerical values. The hues of lizards' throats used in this study ranged from reddish-oranges through

yellows and greens to blue colors. When the color of the throat center and the throat rim differed, the hue of each was recorded. Color assessment was made immediately upon recapture while active, since throat coloration in these populations fades rapidly upon capture (Zucker, 1988) and as lizards cool (Thompson and Moore, 1991a). To describe general sequences of throat color development the following throat color categories were generated from the Munsell hue values (in brackets): (1) orange-throated (OR) [10–20], (2) yellow-throated (YL) [22.5–27.5], (3) green-throated (GR) [30–42.5], (4) orange-green-throated (an orange rim with a green center = OG), (5) blue-green-throated (BG) [45–50], and (6) blue-throated (BL) [52.5–60]. Throat color measurements were made periodically and intervals between measurements ranged from a few days (during the activity season) to several months (when lizards were hibernating).

RESULTS

Throat color badges appeared in all male and female tree lizards soon after hatching. Males from both AS and DA populations went through a developmental series of throat color changes prior to reaching adult coloration. Throat color onset usually occurred at a small size in both male and female AS and DA lizards (Table 1), most of which exhibited some color by the time they had grown only a few millimeters from a hatching size of about 20 mm SVL. Males from both populations began to develop blue ventral belly coloration at 31–32 mm SVL, but the initial throat color in both populations for both sexes was always a pale orange. Fig. 1 shows the relationship of size to the presence of throat color for lizards from the Aguirre Spring (Fig. 1a) and Doña Ana (Fig. 1b) populations. Most lizards (>50%) had some throat coloration by the time they reached 25–26 mm SVL, and almost all (>85%) showed some color by 30 mm SVL. Every lizard surviving to 40 mm SVL had developed throat coloration. A comparison of 95% confidence intervals for SVL size classes indicated no significant difference in animal sizes at throat color onset either between populations or sexes. Throat color onset is associated with size. Most hatchlings (82%) had some throat color within 15 d of hatching, and lizards that exhibited delayed color onset tended to be small for their age. For example, an AS male that

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PLATE 1. Representative throat morphs in captive reared males from Aguirre Spring (AS) and Doña Ana (DA) populations. A. AS Male 1040 = orange-throated B. AS Male 3214 = orange-green-throated C. AS Male 1025 = green-throated D. AS Male 1031 = green-throated E. AS Male 1233 = blue-green-throated F. AS Male 1145 = blue-throated. G. DA Male 4315 = orange-throated H. DA Male 5025 = orange-green-throated I. DA Male 4000 = green-throated.

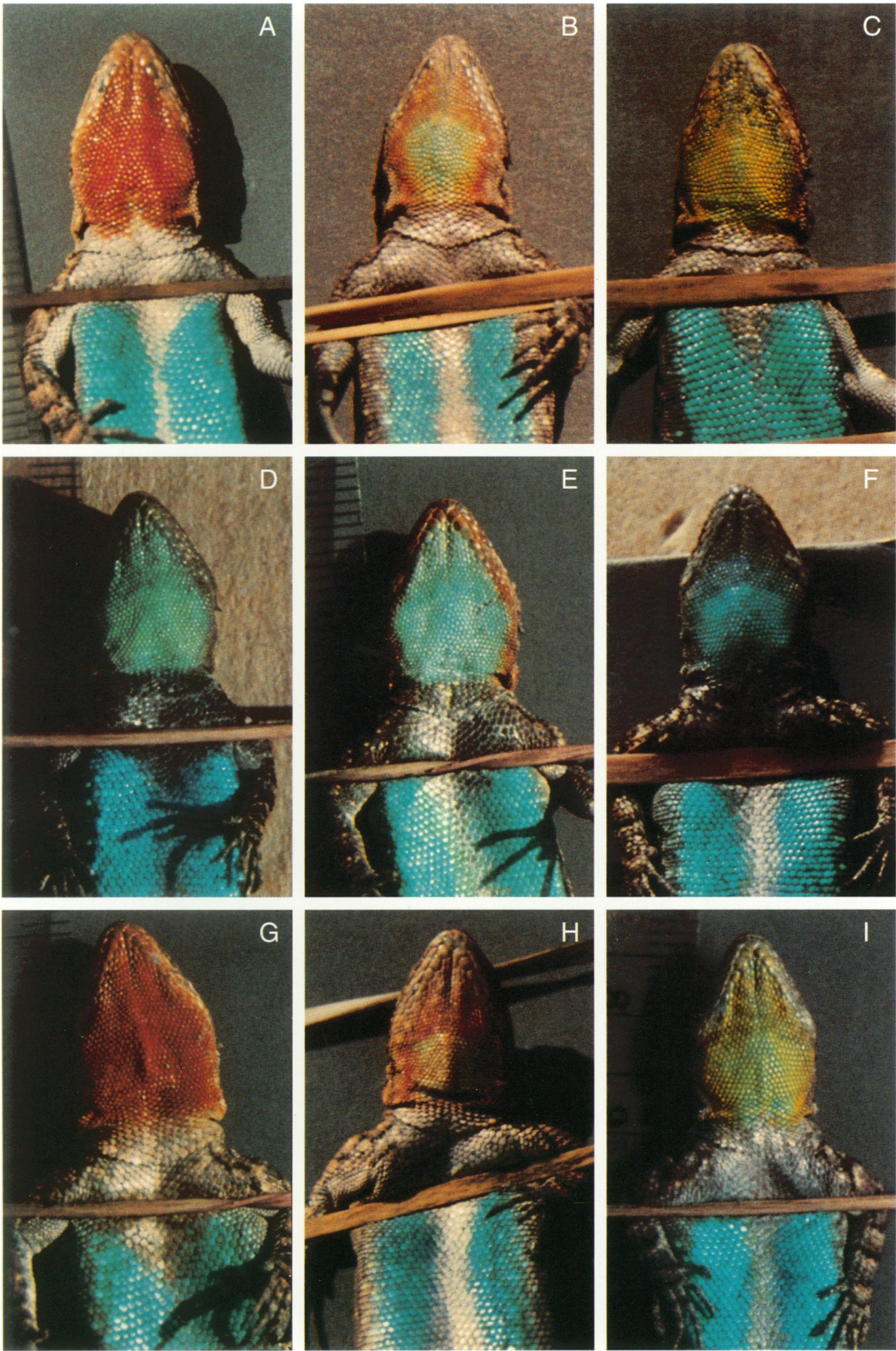


TABLE 1. Average ($\bar{x} \pm \text{SE}$) age and snout-vent length (SVL) at which throat coloration was first observed in male and female tree lizards from Aguirre Spring (AS) and Doña Ana (DA) populations. Only lizards for which hatching date was known were used to generate these numbers.

Pop-ulation	Sex	(N)	Age (days)	SVL (mm)
AS	Males	(45)	19.69 \pm 1.99	26.57 \pm 0.41
AS	Females	(57)	24.7 \pm 1.99	26.7 \pm 0.32
DA	Males	(25)	24.28 \pm 2.7	24.86 \pm 1.07
DA	Females	(24)	26.08 \pm 2.65	26.3 \pm 1.21

showed no color at 36 d was only 23 mm (mean SVL for AS males at 34 d = 32 mm; N = 11).

Females from the DA population remained OR but some AS females became YL. Throats of individual males from both AS and DA populations went through a series of color changes as they matured. Developmental sequences varied within each of the populations (Fig. 2). Most AS males (Fig. 2a) became green-throated (GR) at some point during development but two remained OR and two developed only YL. Some males become yellow-throated (YL) prior to GR (16 of 44 = 36%) while others become GR directly from OR (17 of 44 = 39%). Measurements were incomplete for 11 of 44 males that became GR and it is not clear whether or not they were YL prior to GR. Six AS males developed an orange-rimmed, green-centered throat (OG) after being OR, GR and/or YL. Thirteen males developed blue-green throats (BG) and five blue throats (BL). The mature colors of the 42 males reared to 50 mm SVL or greater were as follows: two were OR (4.7%), two were YL (4.7%), 21 were GR (50%), eight were BG (20%), three were BL (7.1%), and six were OG (14.3%). The developmental sequences in DA males (Fig. 2b) were (1) to remain OR, (2) to become YL and then GR, (3) become GR directly from OR, or (4) become OG via OR, YL or GR. Only 24 DA males were reared to 50 mm or greater SVL. Of these 10 were OR (42%), 7 were GR (29%) and 7 were OG (29%). Plate 1 shows the throat coloration and ventral belly coloration in representative AS and DA males.

Data from both field and captive studies (Zucker, pers. comm.; pers. obs.) show a trend for some males to undergo seasonal throat color change. Some males' throat colors also faded when they were dominated in social contests (Carpenter, 1992). It is important to note that these color changes involved fading from the final adult coloration and did not disrupt the sequences seen in the development of the color. In fact, even when the males' throats faded they

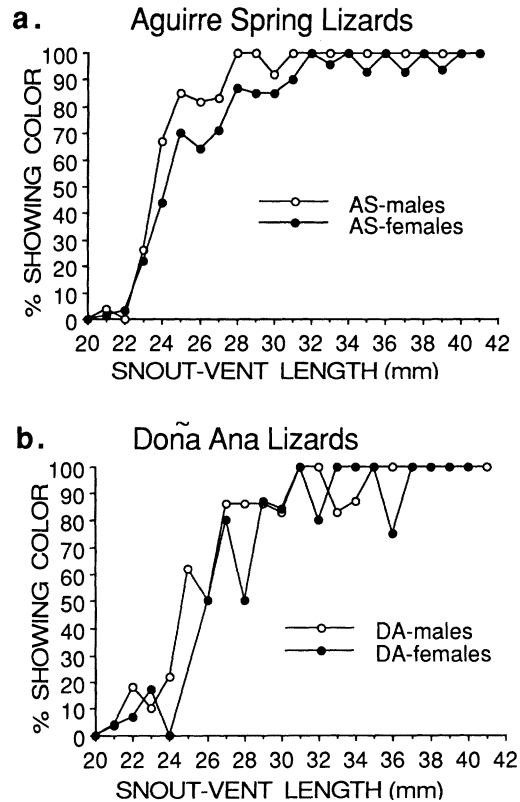


FIG. 1. The relationship of size to throat color onset in males and females from two populations of tree lizards. Percentages of all lizards measured at a particular snout-vent length are represented at one mm intervals.

usually remained in the same throat color category.

DISCUSSION

Ontogenetic Pattern.—The size or age at which color was first seen in males and females from the two populations did not vary significantly between sexes or populations. Because all lizards were not measured at each millimeter interval, some may have acquired coloration at sizes smaller than first recorded. Although values representing average sizes of throat color onset may be overestimates, they clearly indicate that throat color appeared at a small size. In a study of captive-reared *Urosaurus ornatus* from a polymorphic Arizona population, Thompson (1991) reported male throat color onset at an average of 32–34 mm SVL, a larger size than lizards in this study. While my lizards were reared outdoors, Thompson (1991) reared his lizards indoors, which may have affected throat color development. Throat color onset at larger sizes in his study may be due to effects of UV light, photothermal regime, or levels of vita-

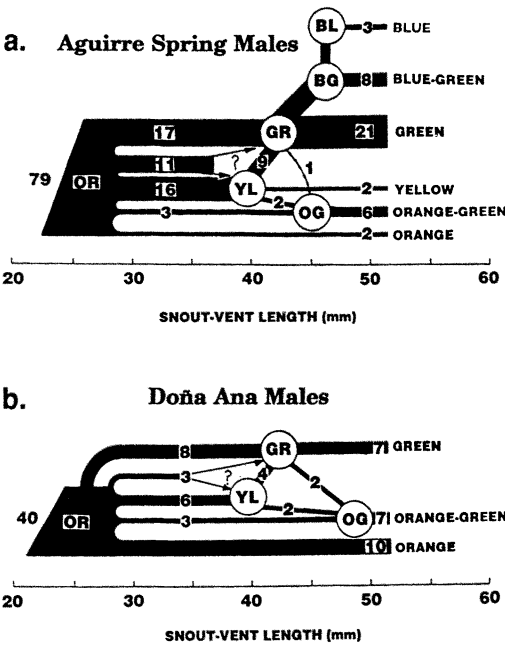


FIG. 2. Sequences of throat color development in tree lizards from two populations. Width of bars proportional to numbers of males changing from one color to another and actual numbers are shown within lines. Horizontal location of throat color represents the average size at which males obtained those colors. Numbers of males surviving to a SVL of greater than 50 mm are shown above the "50." OR = orange-throated, YL = yellow-throated, OG = orange-green throated, BG = blue-green-throated and BL = blue-throated.

mins and other nutrients in the diet. Different results in the two studies may also reflect inherent differences between the populations studied. Thompson (1991) concluded that size was a better predictor of throat color onset than age. My study supports his conclusion; AS and DA lizards not showing color until older ages had smaller SVLs than average.

While orange is always the first color seen in both male and female throats (also observed by Hover, 1982) developmental sequences vary among individuals that ultimately have the same adult morph, but certain throat colors tend to precede others. Most females remained orange, but some AS females shifted to yellow. This shift is likely related to reproductive state and not ontogeny per se (see Zucker and Boecklen, 1990) as in related species (Cooper and Greenberg, 1992). In AS males, BL invariably developed from BG, which in turn always followed GR. A YL phase may or may not precede GR in both AS and DA lizards. Males that are ultimately OG may be YL, GR, or both first. Although almost all adult AS males observed in

the field are BL or BG, in captivity GR, YL, OG, and OR were also observed. DA morphs GR, OG, and OR, were the same as those observed for this population in the field (Hover, 1982, 1985; Zucker, pers. comm.; pers. obs.) minus the rare YL morph.

Some AS and DA males continued to exhibit throat color change until they were almost full size. Moore and Thompson (1990) found that throat color in a polymorphic Arizona population was fixed once established at about 43 mm SVL and at 5 months of age. Based on field observations of the same DA population, Hover (1982) concluded that throat color did not change after lizards were approximately one month old. The current detailed study, however, revealed that males from both the AS and DA populations exhibited color changes at greater than 50 mm SVL and when older than 6 months of age. In particular, males that became BG or BL at AS or OG in both populations, completed color development at larger sizes.

Adaptive Significance of Ontogenetic Color Change.—In both field and captive lizards blue belly coloration initially appears as blue in male tree lizards as small as 31–32 mm (Carpenter, unpubl. data). It is possible that the different throat colors seen during development represent nonfunctional, disorganized stages, and the adaptive value of badges may not be realized until maturity. However, the fact that other colors are not necessarily precursors to blue in this species suggests that ontogenetic throat color change and polymorphic adult pattern may serve social functions. Male *U. ornatus* throat coloration does affect social relationships (Hover, 1982, 1985; Thompson and Moore, 1987, 1989, 1991b; Moore and Thompson, 1990; Thompson, 1991; Carpenter, 1992), so colors seen during developmental sequences may be correlated with changing social roles of lizards as they mature.

In many phrynosomatid species orange coloration is associated with female sex recognition or courtship rejection (Ferguson, 1966; Carpenter, 1970; Vinegar, 1972; Werner, 1978; Cooper et al., 1983; Cooper, 1984, 1986, 1988; Cooper and Greenberg, 1992). Development of adult pattern in male *Tropidurus delanonis* proceeds in a sequence that involves a change in both hue and general pattern (Werner, 1978). Hatchlings are cryptically colored, but juveniles develop bright orange, female-like, coloration at about 6 wk. Males are attracted to females showing orange coloration and tolerate juveniles showing this color in their territories (Werner, 1978). In the crotophytid *Crotaphytus collaris*, juvenile males develop orange coloration similar to adult females (Fitch, 1967; Rand, 1986). Such orange coloration inhibits male ag-

gression in *Holbrookia* spp. (Clarke, 1965; Cooper, 1984), a phrynosomatid. Zucker and Boecklen (1990) found that yellow-throated AS females tended to turn orange just prior to ovulation. Therefore, orange may be a color that invites courtship and/or inhibits aggression in tree lizards (but see Cooper and Greenberg, 1992 for alternative hypotheses). The initial orange throats of juvenile *U. ornatus* may act as female mimics and, thus serve to protect them from adult male aggression. In both field and captive settings juvenile *U. ornatus* are tolerated and were seldom approached aggressively when in the territories of adult males (pers. obs.).

Colors developed by males later in life are likely associated with dominance and territoriality. In separate studies of different polymorphic populations, other authors have concluded that male *U. ornatus* with blue or green throats dominate orange-throated males (Hover, 1982; Thompson and Moore, 1987, 1989, 1991b; Moore and Thompson, 1990; Thompson, 1991). The social functions inferred by the above studies are supported by data from a study using the monomorphic (AS) population (Carpenter, 1992) in which GR, BG, and BL males were dominant over OR and OG males. In the DA population (the same one that Hover [1982, 1985] studied), however, OR was the most dominant morph. With the exception of my DA population (Carpenter, 1992), results from the above studies suggest more dominant lizards exhibit colors seen later in developmental sequences (blues and greens).

Throat colors seen in the development of males from the monomorphic (AS) population essentially mirror the morphs seen in the polymorphic (DA) population. The more ultimate colors developmentally are GR and OG in the polymorphic DA population and BG and BL in the AS population. The bluer hues (BL and BG) are exhibited only in the AS population, where lizard density is higher, and males behave more aggressively (Carpenter, 1992). Higher population density may lead to more frequent social encounters and favor aggressive males. The morphs BL and BG may be favored as dominant social signals by intrasexual selection, as suggested by other studies (Hover 1982, 1985; Moore and Thompson, 1990; Thompson and Moore, 1987, 1989, 1991b). Conversely, in polymorphic populations, relatively infrequent aggressive social encounters may relax sexual selection.

The dissimilarity of color morph proportions in the captive reared AS lizards used in this study, where relatively few developed BL and BG, and those observed in the field, which are virtually all turquoise blue (BG), suggests an effect of captive rearing on throat color expression. The throat color development of half of

the AS males reared to greater than 50 mm SVL (21 of 42) proceeded to green but not to blue-green or to blue. Only 7% of AS males developed blue throats and only 19% developed blue-green throats. Differences in social environments between captive and wild settings may have produced this discrepancy. For instance, some AS males used in this study were also used in a dominance study (Carpenter, 1992) and were moved to a novel enclosure for each staged dominance contest they were involved in. Thus these males were precluded from establishing and maintaining the same territory over a long period of time. Gates (1963) found that maturation of throat color in a closely related species, *Urosaurus graciosus*, was affected by social interactions. In *U. graciosus* orange replaces yellow and green as lizards mature. Gates (1963) found that orange coloration was realized only by males that held territories. Perhaps the expression of BL and BG in *U. ornatus* males from the AS population is related to long-term territory ownership. This seems likely as BL and BG males observed in the wild at AS are usually territory owners. Another possibility is that BL and BG males, although in the minority, competitively exclude other throat color morphs by maturity and gain access to territories, and turquoise-throated males are exclusively seen at AS as a result of differential survival.

There appear to be seasonal and social effects on throat coloration. Fully mature AS males in the field that do not exhibit BL or BG are most often observed either very early (i.e., March–April) or very late (i.e., September–November) in the activity season (pers. obs.). Recapture data indicate that males' blue throats tend to fade to blue-green and green late in the season (pers. obs.). This trend was observed in captivity also, and some males' throats faded when they lost dominance contests (Carpenter, 1992). These changes were post-maturity, however, and did not affect the developmental sequence described in this paper. Thompson (1991) concluded that throat color development in male *U. ornatus* is hormonally mediated, as castrated males do not achieve colors other than orange (Thompson, 1991). Color changes associated with season and social setting, in BL and BG AS males for instance, may be related to seasonal and dominance effects on hormonal levels.

In a four-year field study of DA lizards, Hover (1982, 1985) found ratios of male throat-color morphs similar to the ratios of captive reared lizards in this study: 43.3% OR versus 42% in this study, 53.3% green which is equivalent to my GR plus OG = 59% and 3.4% YL (versus 0% in this study). In my study the similarity of throat color morph ratios between captive-reared and wild DA lizards suggests that the

environmental effects of captive rearing do not affect expression of throat color in this population. Conversely a discrepancy between morph ratios of captive reared and wild AS males suggests that captive rearing does affect throat color development in that population. However, comparisons between populations should be made cautiously. Obvious differences exist between monomorphic and polymorphic populations and different polymorphic populations have various sets and proportions of morphs represented (Thompson, 1991). In a comparative study of female throat coloration and reproductive state, Zucker and Boecklen (1990) concluded that female throat color may be under differing social pressures and may serve different social functions between AS and DA lizards. The discrepancy between the results of the present study and others with regard to throat color development (Thompson, 1991) and dominance (Hover, 1982, 1985; Thompson and Moore, 1987, 1989, 1991b; Moore and Thompson, 1990; Thompson, 1991) strongly suggests that selection on male throat color and subsequent evolutionary scenarios may also vary among populations. Such variation precludes firm deduction about the general social functions of particular morphs both within and among populations.

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Temporal Fluctuations in Abundances of Anuran Amphibians in a Seasonal Amazonian Rainforest

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ABSTRACT.—Anuran amphibians were sampled over a period of 6 yr at a site in seasonal lowland tropical rainforest in southern Amazonian Peru. Three sampling periods were at the beginning of the rainy seasons in 1986, 1989, and 1991; two were in the middle of the rainy seasons of 1986 and 1990, and one was in the dry season of 1989. Temperature and rainfall were recorded throughout all sampling periods. Sampling was done along a system of trails and in four series of quadrats. A total of 5236 individuals of 61 species of anurans was recorded during the sampling period. Analysis of the data on the 20 most abundant species reveals that anuran activity is closely correlated with the occurrence of peaks of heavy rainfall and not total rainfall during a sampling period. There is no compelling evidence for declines in anuran populations at this site.

RESUMEN.—Se muestrearon los anfibios anuros en un sitio en el bosque lluvioso tropical estacional de tierras bajas en el sur del Perú amazónico a lo largo de un periodo de 6 años. Tres periodos de muestreo fueron en los comienzos de las estaciones de lluvia en 1986, 1989, y 1991; dos a mediados de las estaciones de lluvia en 1986 y 1990, y uno en la estación seca en 1989. Se registraron la temperatura y cantidad de lluvia a lo largo de todos los periodos de muestreo. El muestreo se realizó a lo largo de un sistema de trochas y en cuatro series de cuadrantes. Se registró un total de 5236 individuos de 61 especies de anuros durante el periodo de muestreado. El análisis de los datos de las 20 especies más abundantes revela que la actividad de los anuros está estrechamente correlacionada con la ocurrencia de máximos de lluvia torrencial y no con la cantidad de lluvia durante un periodo de muestreo. No existe evidencia convincente de descensos en las poblaciones de anuros en este sitio.

The lowland tropical rainforest in the vast Amazon Basin is home to more than 217 species of frogs, of which nearly 60% are endemic to the region (Frost, 1985; Duellman, 1993). Intensive studies have focused on the anuran faunas

at selected sites—Belém, Brazil (Crump, 1971), Manaus, Brazil (Zimmerman and Rodrigues, 1990), Santa Cecilia, Ecuador (Duellman, 1978), Panguana, Peru (Schlüter, 1984), and Cocha Cashu, Peru (Rodríguez, 1992). With the exception