

Nuptial coloration in female *Liolaemus quilmes* (Iguania: Liolaemidae): relation to reproductive state

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Abstract: Females of many lizard species exhibit nuptial coloration during the reproductive season. Researchers agree that the coloration reflects the reproductive state of the female but it is not always clear if variations in its expression indicate the female is receptive, gravid or postoviposition. We investigated in female *Liolaemus quilmes*, a lizard from northwestern Argentina, the relationship between nuptial coloration, appearing on both sides of the neck, and reproductive state. Forty-three females of different colorations, going from no nuptial coloration, to light yellow, to an intense orange, were collected during various months of their active season. Results show that females were light-yellow during early vitellogenesis, at the beginning of the reproductive season of the austral spring, reaching an intense orange coloration during the final stages of vitellogenesis and early pregnancy, at the beginning of the summer. The orange color remained when females were gravid, gradually fading after oviposition. Mating in the field occurred when females were light-colored, still in early vitellogenesis, showing behavioral receptivity to males but not physiological readiness. Male courtship may help trigger a female's reproductive physiology and/or females may be capable of storing sperms until vitellogenesis is complete, as has been reported in other lizard species.

Key words: female reproduction, *Liolaemus quilmes*, lizard, nuptial coloration.

Resumen: Coloración nupcial en hembras de *Liolaemus quilmes* (Iguania: Liolaemidae): relación con su estado reproductivo. – En muchas especies de lagartijas las hembras presentan una coloración llamada nupcial durante la etapa reproductiva. Existe acuerdo en que dicha coloración refleja el estado reproductivo de la hembra pero no siempre está claro si indica una hembra receptiva, grávida o postoviposición. Se investigó en hembras de *Liolaemus quilmes*, un lagarto del noroeste argentino, la relación entre la coloración nupcial, que aparece a ambos lados del cuello, y su estado reproductivo. Se colectaron 43 hembras de distintas coloraciones durante los meses de su período activo, que iban desde sin color nupcial, pasando por un amarillo claro, hasta llegar a un naranja intenso. Los resultados muestran que al comienzo de la temporada reproductiva en la primavera austral, las hembras presentan una coloración amarillo claro, estando en ese momento en vitelogénesis temprana, alcanzando una coloración naranja intensa durante las etapas finales de la vitelogénesis y gravididad temprana, al comienzo del verano. El color naranja se retiene cuando las hembras están grávidas, para desaparecer gradualmente después de la oviposición. Los apareamientos observados en el campo ocurren cuando las hembras presentan coloración clara, todavía en vitelogénesis temprana, mostrando receptividad comportamental hacia los machos pero no receptividad fisiológica. El cortejo de los machos podría ayudar a activar la fisiología reproductiva de la hembra y/o la hembra podría ser capaz de almacenar esperma hasta que la vitelogénesis se complete, como se ha descrito en otras especies de lagartos.

Palabras clave: Coloración nupcial, lagarto, *Liolaemus quilmes*, reproducción en hembras.

INTRODUCTION

Females in more than thirty lizard species exhibit colors known as nuptial coloration during the reproductive season (COOPER & GREENBERG, 1992). Because nuptial coloration may incur a cost, the female becoming more conspicuous to predators, it may provide some adaptive advantage to them (COOPER & GREENBERG, 1992; BAIRD, 2004). Different hypotheses have been proposed for the adaptive function of nuptial coloration in female lizards. Some studies propose the receptivity hypothesis, whereby female nuptial coloration indicates their receptiveness to approaching males (e.g., Crotaphytidae: *Crotaphytus wislizenii*, MONTANUCCI, 1965; *C. collaris*, BAIRD, 2004; Chamaeleonidae: *Chamaeleo chamaeleon*, CUADRADO, 1998, 2000; Agamidae: *Ctenophorus ornatus*, LEBAS & MARSHALL, 2000). Other studies suggest the rejection hypothesis (e.g., Phrynosomatidae: *Sceloporus virgatus*, VINEGAR, 1972; Agamidae: *Ctenophorus maculosus*, OLSSON, 1995, OLSSON & MADSEN, 1998), stating that color could be a reliable signal that a female is gravid, thus avoiding the cost of being courted and non successful matings (COOPER & GREENBERG, 1992). Another hypothesis that has been advanced is the conditional signal hypothesis (HAGER, 2001). In this case, light coloration at the beginning of the reproductive season indicates receptivity whereas an increase in coloration together with an increase in female aggression, would indicate a pregnant female (HAGER, 2001).

ETHERIDGE (1993) pointed out the presence of nuptial coloration in several species of the South American genus *Liolaemus*, including *L. quilmes*. In this species, females develop nuptial coloration on the lateral sides of the neck, starting with a light yellow, as they come out of

hibernation at the end of October, becoming more intense as the austral spring advances, changing to orange or even to a reddish coloration by the end of November or early December, after which it gradually fades before females return to hibernation in March or April (HALLOY *et al.*, 2007; SALICA 2008). Here we investigate the relationship between the nuptial coloration of female *L. quilmes* and their reproductive state. Our objectives were to: 1) identify different categories of nuptial coloration in female *L. quilmes*, 2) describe the different reproductive states of female *L. quilmes*, and 3) relate color categories to female reproductive states.

The *Liolaemus* genus (Liolaemidae) corresponds to an iguanian group of lizards from South America (FROST *et al.*, 2001). More than 200 species are presently known (ABDALA *et al.*, 2008). *Liolaemus quilmes* is found in northwestern Argentina between 1600 and 3000 m, in arid to semi arid regions of the phytogeographic province of the Monte (CEI, 1993; ETHERIDGE, 1993) and the Prepuna (HALLOY *et al.*, 1998; for phytogeographic provinces, see CABRERA & WILLINK, 1980). It is a diurnal, insectivorous and oviparous species (HALLOY *et al.*, 2006; RAMIREZ PINILLA, 1992a). Males are slightly larger than females (average snout-vent-length of 66 mm and 61 mm, respectively, ETHERIDGE, 1993; HALLOY, 1996). They also exhibit a more colored pattern than females. Males emerge from hibernation in September, at the beginning of the austral spring, females appearing 4 to 6 weeks later (HALLOY & ROBLES, 2003).

MATERIALS AND METHODS

The study was conducted at a site called "Los Cardones" (26° 40' 1.5" S, 65° 49' 5.1" W, datum: WGS84; 2725 m elevation), Tucumán province, Argentina. We collected monthly

samples of female *L. quilmes* ($n = 43$) between October 2007 and March 2008, corresponding to one austral spring and summer seasons. Female snout-vent lengths and weights were taken upon capture.

Traditionally, two methods have been used to standardize color categories in order to measure and compare individuals or species. These are the Munsell system (e.g., COOPER & CREWS, 1987; HAGER, 2001; WEISS, 2002) and spectrophotometry (e.g., BENNETT *et al.*, 1994; LEBAS & MARSHALL, 2000; WHITING *et al.*, 2006). Although both allow the establishment of color categories, the latter is more objective because it does not rely on human visual perception. Since our study did not require sophisticated measurements but a simple method of categorizing color, we used a method equivalent to the Munsell color system based on computer software that allows categorization of different colors. Digital photos were taken of each live female (see below), after which they were sacrificed to study the reproductive state corresponding to the different color categories.

Color may be characterized by hue (corresponding to what is generally referred to as color, units given in degrees), brightness (or value in the Munsell system, which refers to the relative reflectance of the stimulus, going from pure black 0%, to pure white 100%), and saturation (or chroma in the Munsell system, which corresponds to the intensity of a color, going from 0% for neutral or weak colors to 100% for highly saturated or vivid colors, COOPER & GREENBERG, 1992; HAGER, 2001; MASELLO *et al.*, 2004). Although these parameters are based on human perception, they manifest the physical characteristics of reflected light (ENDLER, 1990). Nevertheless the authors confirmed independently the color categories presented here. The parameters do not measure the

reflection of ultraviolet light (BENNETT *et al.*, 1994), which may be present (e.g., BLEIWEISS, 2004; MOLINA-BORJA *et al.* 2006) but was not considered in this study.

Nuptial coloration of female *L. quilmes* was estimated using a modified version of the RGB method (Red, Green and Blue) of GERALD *et al.* (2001). With this method digital images are processed with Adobe Photoshop and numerical values extracted for three color components. To determine color categories, first digital pictures (Kodak Easyshare CX6230) were taken of the lateral side of the head and neck of each live female. In order to standardize conditions, all photographs were taken with flash in the lab, with a white background and a ruler for scale. The images were calibrated in order to measure an "absolute zero" independent of light exposure (GERALD *et al.*, 2001). The calibrated images were then analysed using Adobe Photoshop CS. In order to improve the detection of color variability and facilitate the selection of pixels, images were amplified 800%. With the tool "color sample" (a variation of the eyedropper tool), three pixels were selected within the color patch. Using the function "Info", the color mode HBS (hue, brightness, saturation, corresponding to hue, value and chroma, respectively, of the Munsell system) in the palette option was selected to measure these variables. Later the average hue, value and chroma were calculated for each individual (MASELLO *et al.*, 2004).

Although changes in coloration were continuous, in order to facilitate organizing and understanding the results, we arbitrarily grouped the lizards into five categories according to their values of hue and chroma. Value (brightness) was not included in the analysis since this parameter did not vary among the females. There is no clear consensus on whether to use, as in this case, a

continuous variable or discrete categories. For example, COTE *et al.* (2008) suggest that the continuous color variation from pale yellow to orange in adult female *Lacerta vivipara* should be maintained, finding no evidence for distinct color morphs, whereas VERCKEN *et al.* (2008) consider that this continuous color variation may be divided into three discrete categories. The color categories we obtained were: no nuptial coloration (NN), light yellow (LY), strong yellow (SY), medium orange (MO), and strong orange (SO). The intensity range increases as the chroma (saturation) index of the color increases. At the same time the hue index diminishes (Table 1, Fig. 1).

The animals were sacrificed using pentothal sodium, after which they were placed in 10% formaldehyde for 24 h, then preserved in 70% alcohol. Females obtained in monthly samples between October and March were dissected to determine their reproductive state. A Nikon SMZ-10 microscope with a micrometric Nikon 15x lens was used. To characterize a reproductive state, we considered the type of oviduct (whether folded or not), presence of yolked follicles, size of the biggest follicle from the two ovaries, eggs in the oviduct and corpora

TABLE 1. Color categories defined by maximum and minimum averages of hue and chroma. LY: light yellow, MO: medium orange, NN: no nuptial coloration, SO: strong orange, SY: strong yellow.

TABLA 1. Categorías de coloración definidas por los valores promedios máximos y mínimos de matiz y croma. LY: amarillo claro, MO: naranja medio, NN: sin color nupcial, SO: naranja fuerte, SY: amarillo fuerte.

| COLOR | HUE | CHROMA |
|-------|----------|--------|
| NN | 25° -40° | 15-24% |
| LY | 35° -50° | 25-34% |
| SY | 35° -50° | 35-55% |
| MO | 15° -34° | 45-64% |
| SO | 15° -34° | 65-85% |

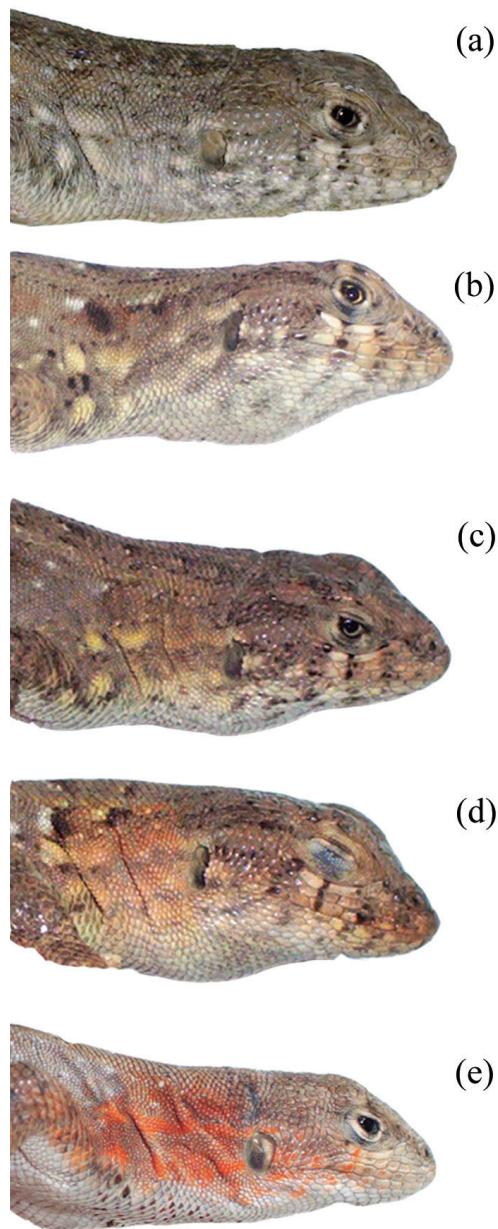


FIGURE 1. Digital photographs of nuptial coloration in female *Liolaemus quilmes*. a) no nuptial coloration (NN), b) light yellow (LY), c) strong yellow (SY), d) medium orange (MO), e) strong orange (SO).

FIGURA 1. Fotografías digitales de la coloración nupcial en hembras *Liolaemus quilmes*. a) sin color nupcial (NN), b) amarillo claro (LY), c) amarillo fuerte (SY), d) naranja medio (MO), e) naranja fuerte (SO).

lutea. We defined five reproductive states (CREWS, 1980): 1) pre-reproductive females: non-yolked ovarian follicles and non-folded, transparent oviduct present; 2) early vitellogenesis: reproductive females with yolked ovarian follicles with a diameter less than 5 mm and folded oviduct; 3) late vitellogenesis: reproductive females with yolked ovarian follicles with a diameter greater than 5 mm and folded oviduct; 4) gravid: females with eggs in the oviduct; 5) postoviposition: non-reproductive females with small non-yolked ovarian follicles, folded oviduct, with or without the presence of corpora lutea.

RESULTS

Forty-three females of *Liolaemus quilmes* were collected, eight of which were still pre-reproductive juvenile females (snout-vent length and weight: 5.4 ± 0.3 cm, 5.2 ± 1.1 g) without nuptial coloration, except for one very light colored female, and 35 adult females (snout-vent length and weight: 5.9 ± 0.3 cm, 6.3 ± 1.4 g) showing various degrees of nuptial coloration. The following analyses include only the adult females.

Nuptial coloration changed throughout the active period of the lizards (Fig. 2). In October, adult females emerged from hibernation with a predominantly light yellow coloration. All five females were in the early vitellogenic stage. In November and December, the light yellow coloration gradually becomes more intense, changing to orange with time. In November, the non-colored female presented early vitellogenesis, three females were in late vitellogenesis (2 SO and 1 MO), the rest being gravid (1 SO, 1 MO, and 3 SY). In December, two of six females were still in late vitellogenesis (1 MO and 1 SY), one was gravid (1 SO) and three had laid their eggs (1 SO and 2 MO). In

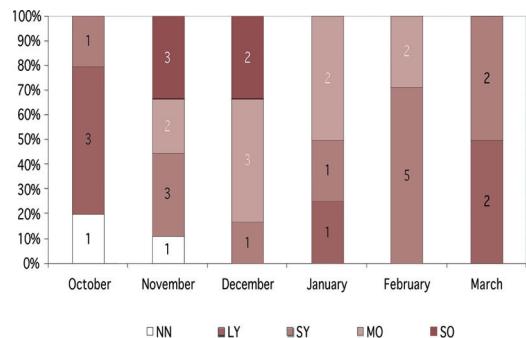


FIGURE 2. Percent of adult females of different color categories by month. Numbers in the bars indicate the size of the sample. NN: no nuptial coloration; LY: light yellow; SY: strong yellow; MO: medium orange; SO: strong orange. Mating was observed end of October and beginning of November.

FIGURA 2. Porcentaje de hembras adultas de distintas categorías de coloración por mes. Los números ubicados en las barras corresponden al tamaño de la muestra. NN: sin color nupcial; LY: amarillo claro; SY: amarillo fuerte; MO: naranja medio; SO: naranja fuerte. Cópulas fueron observadas al final de octubre y principio de noviembre.

January, February and March, yellow pigments gradually replaced the orange coloration. All females were postoviposition. Considering both orange color categories, MO and SO, there were significantly more late-vitellogenic females with these colors than in the gravid or postovipositon stages (Chi-square goodness-of-fit test: $\chi^2 = 16.06$, $df = 2$, $p < 0.01$; SIEGEL & CASTELLAN, 1988). Figure 3 illustrates this gradual change considering average values of chroma (saturation) and hue (color). Color goes from a less saturated yellow in early vitellogenic females, becoming an intense orange in late vitellogenic females, followed by a progressively lighter orange in gravid females, finally turning to yellow, increasingly less saturated, in postoviposition.

DISCUSSION

The nuptial coloration in female *L. quilmes* developed in a similar way as that reported

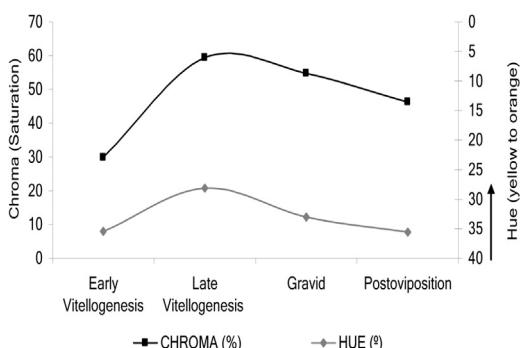


FIGURE 3. Average values of hue (color) and chroma (saturation) for adult females at different reproductive stages.

FIGURA 3. Valores promedio de matiz (color) y croma (saturación) para hembras adultas correspondiente a los diferentes estados reproductivos.

for other lizard species (e.g., *Gambelia wislizeni*, MEDICA *et al.*, 1973; *Crotaphytus collaris*, FERGUSON, 1976; *Holbrookia propinqua*, COOPER *et al.*, 1983). At the time of their emergence from hibernation in October, females presented mostly light yellow nuptial coloration with maximum intensity reached during the final stages of vitellogenesis. Orange colors remained in half of the gravid females, gradually disappearing towards the end of the reproductive season (Figs. 2, 3).

Results show a relationship between female nuptial coloration and reproductive state, light-colored females being in early vitellogenesis and more intensely colored females in late vitellogenesis or in the early stage of pregnancy. Thus mating could be expected to occur when females were more intensely colored indicating physiological receptivity. However, mating was observed in the field at the end of October, beginning of November, when females were light-colored, corresponding to the early vitellogenic stage. Females were therefore behaviourally receptive during early vitellogenesis,

understood as “the behaviour of females that is required for insemination to occur” (WHITTIER & TOKARZ, 1992:24), often thought to be restricted to the final stages of vitellogenesis when follicles have been released into the oviduct and can be fertilized by incoming sperm. Here females were receptive to males even though their reproductive physiology needed further development. Males, on the other hand, reach their peak testicular growth by October (see RAMIREZ PINILLA, 1992a, for a study on males of the same population). This would explain the mating seen in the field at that time, i.e., increase in male reproductive activity, female behavioral receptivity but not female physiological reproductive readiness. It may be that copulation helps to stimulate or trigger the reproductive physiology of the female (e.g. *Anolis carolinensis*, CREWS, 1975). On the other hand, sperm retention has been reported in many reptiles (see review in SEVER & HAMLETT, 2002), including in *L. quilmes* (RAMIREZ PINILLA, 1992b). Therefore, male courtship and mating, combined with female behavioral receptivity during early vitellogenesis and retention of sperm in her oviducts, may allow for fertilization to occur at a later time. Observations reported here point to several new lines of study as well as to the importance of integrating studies on reproductive physiology and behavioural information.

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