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L. F. Toledo ^a & C. F. B. Haddad ^a

^a Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Rio Claro, Brazil
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Reproductive biology of *Scinax fuscomarginatus* (Anura, Hylidae) in south-eastern Brazil

L. F. TOLEDO & C. F. B. HADDAD

Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Rio Claro, Brazil

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Abstract

The present study describes the reproductive biology of *Scinax fuscomarginatus* in a remnant of Cerrado in south-eastern Brazil. Observations were made between September 2002 and March 2004 at Estação Ecológica de Itirapina, State of São Paulo, south-eastern Brazil. Breeding activities occurred in lentic and temporary bodies of water during the rainy season. *Scinax fuscomarginatus* exhibited a prolonged breeding pattern and a lek mating system. Males were smaller than females and defended individual calling areas through acoustic and physical interactions. Resident males consistently won encounters, but did not differ in size or mass from intruder males. Satellite behaviour was observed, but no female or amplexed pair interception was registered. *Scinax fuscomarginatus* exhibited low operational sex ratios and the general reproductive mode in which eggs are laid in the water and tadpoles are aquatic. Amplexus was axillary and the eggs were deposited at the bottom of temporary ponds. Details on oocytes, egg masses, and eggs are included.

Keywords: *Anura*, aggressive behaviour, Cerrado, chorus organization, hylid treefrog, reproduction, temporary pond

Introduction

Studies of anurans in the Neotropical natural environment have focused mainly on the reproductive biology of the species, such as temporal and spatial distribution, and sometimes, examine the possible influence of abiotic factors on the reproductive activity of males (e.g. Aichinger 1987; Martins 1988, 1993; Haddad and Cardoso 1992; Pombal 1997; Bernarde and Machado 2001; Freitas et al. 2002; Wogel et al. 2002; Guimarães and Bastos 2003). Some detailed studies investigated factors that might be involved in sexual selection, verifying quantitative reproductive aspects and size–fecundity relationships (e.g. Prado et al. 2000; Bastos and Haddad 2001).

Studies of territoriality, including agonistic interactions for limited resources such as calling sites, egg-laying sites, and/or females, have also been important in understanding natural history and variation among anurans (Wells 1977a, 1978; Cardoso and Haddad 1984; Bastos and Haddad 1995, 2002; Martins et al. 1998). Indeed, female mate choice

Correspondence: L. F. Toledo, Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Caixa Postal 199, CEP 13506-970 Rio Claro, Brazil. Email: toledof2@yahoo.com

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may be influenced by the result of the aggressive interactions among males (Arak 1983; Olson et al. 1986; Wagner and Sullivan 1992; Brenowitz and Rose 1999). Therefore, sexual selection may be a causal factor in the size sexual dimorphism found in the majority of the anuran species (Shine 1979).

Most species in the genus *Scinax* Wagler, 1830 exhibit sexual dimorphism in size, with females generally being larger than males (Lutz 1973; Heyer et al. 1990). The genus is also characterized by having diverse reproductive modes: foam nests (*S. rizibilis* (Bokermann, 1964): Haddad et al. 1990); eggs deposited in lotic water bodies (e.g. *S. albicans* (Bokermann, 1967) and *S. trapicheiroi* (Lutz, 1954): Carvalho e Silva and Carvalho e Silva 1994); and, in the majority of the species, the general reproductive mode (Haddad and Prado 2005): eggs are deposited in lentic aquatic environments where the tadpoles develop (Lutz 1973; Haddad et al. 1990; Bourne 1992; Bevier 1997; Toledo et al. 2003). With regard to the reproductive strategy (*sensu* Wells 1977a), some *Scinax* species exhibit the explosive reproductive pattern (e.g. *S. fuscovarius* (Lutz, 1925): Bertoluci 1998; Toledo et al. 2003; *S. ruber* (Laurenti, 1768): Bourne 1992; Bevier 1997; *Scinax similis* (Cochran, 1952): Toledo et al. 2003) and some species exhibit the prolonged reproductive pattern (e.g. *S. albicans*: Carvalho e Silva and Carvalho e Silva 1994; *S. boulengeri* (Cope, 1887): Bevier 1997; *S. rizibilis*: Bastos and Haddad 1999; *S. centralis* Pombal and Bastos, 1996 and *S. fuscomarginatus* (Lutz, 1925): Bernarde and Kokubum 1999; Bastos et al. 2003; Toledo and Haddad 2005).

Males of *S. fuscomarginatus* aggregate around permanent or temporary ponds for reproduction, and use the surrounding vegetation as calling sites (references in Toledo and Haddad 2005). Four different vocalizations were described (Toledo and Haddad 2005) and its reproductive effort relationships were briefly discussed before (Prado and Haddad 2003). *Scinax fuscomarginatus* lays its eggs directly in lentic water bodies (Bastos et al. 2003) and its larval development has already been described (as *Hyla parkeri* in Vizotto 1967; and as *Olohygon fuscomarginata* in Altig and Johnston 1986).

Herein, we studied the reproductive biology of *S. fuscomarginatus* and report on: (1) the spatial and temporal organization of the individuals at the breeding site; (2) behaviours important for reproduction, such as pair formation, aggressive interactions among males, and male satellite behaviour; (3) quantitative aspects of reproduction, such as female fecundity, reproductive effort of females, and sexual dimorphism; and (4) egg-mass characteristics.

Material and methods

Study site

The present study was carried out at the Estação Ecológica de Itirapina (EEI), located in the municipalities of Itirapina and Brotas, central State of São Paulo, south-eastern Brazil. The EEI has approximately 2300 ha of natural vegetation, including at least five distinct Cerrado physiognomies (Martins 2001). Lentic and temporary ponds are often formed on the physiognomies of “campo sujo” and “campo limpo” during the warm and rainy season of the year (between November and March).

Data collection

Observations were made monthly, lasting from 4 to 10 consecutive days, and were conducted between September 2002 and March 2004. Observations began about 1 h

before sunset and finished when the calling activity decreased considerably (when only one or two males remained calling), or ceased. During the observations, headlamps were used, and the focal animal was only dimly illuminated. Sampling methods included *ad libitum*, focal-animal, all occurrences of some behaviours, and sequences (Altmann 1974; Lehner 1996).

For individual recognition, the animals were toe-clipped following Waichman (1992), and released exactly at the same place from where they were captured. Individuals were weighed to the nearest 0.05 g and the snout–vent length (SVL) was measured with callipers to the nearest 0.05 mm; for females these measurements are taken after oviposition. Air temperature, observation time, distance to the nearest conspecific individual, distance from water and height from the ground of the male's calling site, sex, and presence or absence of ova in the females were also recorded.

The operational sex ratio was determined according to Emlen and Oring (1977): $OSR = \text{ratio of fertilizable females to sexually active males on the studied night}$. Eggs were obtained from clutches deposited by pairs, placed in plastic bags and preserved in 5% formalin 48–72 h after spawning. The eggs were counted, measured, and classified according to Gosner's table (Gosner 1960).

Analysis

The homogeneity of variances and normality of the data set were verified. For comparisons between body mass and SVL of winner versus loser males involved in agonistic interactions, or between calling/dominant versus silent/satellite males, we used a paired *t* test. The comparison between body mass and SVL of males and females was made with a Mann–Whitney *U* test. In all cases, significant values were considered when $P < 0.05$ (Zar 1999). Descriptive statistics are given as mean $\pm$ SD.

Results

The reproductive period of *Scinax fuscomarginatus* at EEI, based on the calling activity of males, lasted approximately 3.5 months in each rainy season, from the middle of December 2002 to the end of March 2003, and from the beginning of December 2003 to the middle of March 2004, the same time the temporary lentic ponds were filled.

Only males were observed at the reproductive aggregations in the beginning of the reproductive season. Females were found about 20 days after the beginning of the calling activity. Females were larger (23.17 ± 0.30 mm; $N=5$) than males (22.21 ± 0.77 mm; $N=52$) ($U=251.2$; $P=0.03$), but not significantly heavier (females body mass = 0.58 ± 0.06 g; $N=5$; males body mass = 0.56 ± 0.07 g; $N=51$) ($U=170.5$; $P=0.43$). The first aquatic larvae were found ca 30 days after the beginning of the calling season in the same ponds where the observations were conducted. Metamorphic individuals were found 40 and 50 days after the beginning of the calling season, perched on branches of vegetation above the water or swimming in the ponds.

Male *S. fuscomarginatus* used the vegetation bordering temporary ponds as calling sites. Despite the apparently erratic distribution of the calling sites around the temporary ponds, 52% of the calling males ($N_{\text{total}}=56$) were found separated by 100–300 cm from each other. When distances were equal to or less than 30 cm, male–male interactions were observed (Figure 1), suggesting that calling territories of *S. fuscomarginatus* were about 60 cm in diameter. Inside the acoustic space of a resident male two sorts of interactions were

Figure 1. Distance between *Scinax fuscomarginatus* nearest males at Estação Ecológica de Itirapina during the calling activity. White bars represent distances where satellite males or agonistic interactions were observed; grey bars represent the distances when solitary males were observed calling without occurrence of agonistic interactions ($N_{\text{total}}=56$).

observed when intruder males approached. First, while the dominant male was calling, one or two other males assumed a submission posture, remaining silently as satellite males. Alternatively, the resident male aggressively defended its calling site, and if the intruder persisted, physical combat resulted (Figure 2).

When an intruder male approached, the resident calling male turned towards the intruder and started to emit territorial calls. If the intruder did not assume a submissive posture, with the head and belly touching the substrate, and with the vocal sac deflated,

Figure 2. Summary of the agonistic interactions between adult males of *Scinax fuscomarginatus* at Estação Ecológica de Itirapina, State of São Paulo, south-eastern Brazil.

both males initiated an acoustic exchange. First, the intruder emitted few advertisement calls, but soon began to emit territorial calls. Males called intensively, interrupted by silent periods of up to 30 s until the acoustic exchange restarted when one of the males called again. On one occasion, during the calling context, both resident and intruder performed rapid extension and contraction of arms and legs.

If the intruder did not assume a satellite strategy ($N=7$) or did not move away ($N=3$), the resident male approached the intruder using short-distance hops, and initiated physical combat. During the combat, males gave chest-to-chest hugs, with the heads orientated in the same direction, and both males emitted fighting calls. The fight finished when the loser males (which were also the intruders) moved away. These interactions lasted for 15 and 70 s.

Resident males always won these interactions. These males were not significantly larger ($t=1.23$; $df=5$; $P=0.27$) nor heavier ($t=1.17$; $df=5$; $P=0.30$) than intruders or satellite males (Table I). Females were not observed defending areas or involved in agonistic interactions.

In three observations of satellite males, the dominant males were removed by the observer and after 2–4 min the satellite males began to produce advertisement calls. Satellite males were observed regardless of chorus density and no females were observed near groups of dominant and satellite males.

Throughout the study, nine females were observed, five of which were captured. The average operational sex ratio obtained for nights when females were present was 0.083 ($SD=0.053$; range=0.025–0.143; $N=6$ nights). Two females with ovules at different stages of development were captured near the temporary ponds in January 2003; only females with mature ova were found in the breeding site moving toward calling males. Gravid females ($N=4$) were also observed motionless for up to 4 min in front of calling males, with their heads orientated toward them. After that, females were observed moving toward the nearest male, or in the direction of other males in the vicinity. When a male perceived the presence of a female, he moved toward her, producing courtship calls with short duration and low energy intensity ($N=1$). When the male was less than 10 cm from the female, he jumped on the female's dorsum and entered into axillary amplexus.

During amplexus, the male pressed his ventral region to the dorsal surface of the female. He arrhythmically contracted his arms on the female's flanks at a rate of six to eight per minute. Pair formation occurred, on average, 2 h after sunset (range=1 h 5 min to 2 h 25 min; $N=4$). The female moved down from the vegetation branches to the pond's water level between 2 h 30 min and 4 h after the amplexus (mean=3 h 15 min; $N=4$). At the

Table I. Body mass and snout–vent length (SVL) of *Scinax fuscomarginatus* males (winners or dominants and losers or satellites) of the agonistic encounters observed at the Estação Ecológica de Itirapina, State of São Paulo, Brazil.

	Encounters without combat		Encounters with combat	
	SVL (mm)	Mass (g)	SVL (mm)	Mass (g)
Winners or dominants	22.2 ± 0.74 (21.0–23.0; 5)	0.57 ± 0.06 (0.5–0.65; 5)	21.9	0.6
Losers or satellites	22.4 ± 1.48 (20.0–24.0; 7)	0.55 ± 0.08 (0.45–0.7; 7)	21.8	0.6

Values of SVL and mass are expressed as mean ± SD (range; N). The males were captured, measured, and weighed in only one combat.

pond, the paired female jumped into the water and remained floating on the surface or resting on the emerging branches of the aquatic vegetation for approximately 5 min. Subsequently, the pair dived and remained submerged for up to 20 s before returning to the surface. These dives, during which oviposition occurred, were repeated four to six times, 5 h 30 min after sunset (range=4 h 45 min to 6 h 5 min; $N=4$). The male released the female while still in water, and the individuals rapidly moved to the edge of the ponds, hiding on the nearest vegetation clump ($N=3$).

Gravid females had a mean of 346 ± 33.5 ova in their ovaries (range=316–382; $N=4$), that were 0.82 mm in diameter ($SD=0.07$; range=0.74–0.93 mm; $N=12$). Ovules were black on the animal pole and beige on the vegetative pole. The egg mass was a single circular layer of eggs, whose coloration and diameter were similar to those of the ova. Eggs had two gelatinous capsules (not visible in the ovules). Eggs at stage 13 had a mean diameter of 0.98 ± 0.07 mm (range=0.86–1.08 mm; $N=18$). The inner gelatinous capsule had a mean diameter of $1.17 \text{ mm} \pm 0.04$ (range=1.13–1.19 mm; $N=6$) while the outer capsule had a mean diameter of 2.65 ± 0.34 mm (range=2.22–3.33 mm; $N=8$). When submerged in water, the eggs remained with the animal pole upwards.

Four amplexed pairs were measured and weighed. Male body mass was 65.17% of the female body mass after egg-laying ($SD=4.25$; range=62.5–71.43%). Male SVL was 95.76% of the female SVL ($SD=2.45$; range=93.3–99.13%). The mass of ova represented 37.13% of the mass of the females after oviposition ($SD=9.72$; range=23.08–45.45%; $N=4$). A mean of 86.22% of the eggs were fertilized ($SD=11.19$; range=75.63–97.94%; $N=3$).

Discussion

Scinax fuscomarginatus at the EEI is a prolonged breeder (*sensu* Wells 1977a): individuals participated in an extended reproductive season that persisted for at least 3 months; males called to attract females; males did not actively search for females; males did not attempt to dislodge paired males; and males defended calling sites using acoustic and physical aggressive interactions.

The reproductive system of *S. fuscomarginatus* is here classified as lek, in concordance with the criteria proposed by Bradbury (1981). Such classification is based on that (1) there was no parental care; (2) males formed exhibition arenas around temporary ponds; (3) females moved around the arena having the opportunity for sexual selection, evaluating acoustic displays produced by males; and (4) the calling site did not grant any resource required by females, besides the male. Besides this, the lek system of reproductive choruses is proposed to occur in species that (1) have prolonged breeding patterns, in which females attend the choruses in an asynchronic manner, while males remain in reproductive activity (calling) during the whole reproductive season of the females; (2) have low operational sex ratios; and (3) males are incapable of controlling essential resources for females (Emlen and Oring 1977). The lek mating system seems to be widespread among hylids, since it has also been described for other species, such as *Hyla elegans* Wied-Neuwied, 1824, *H. minuta* Peters, 1872, *Scinax rizibilis*, and *S. ruber* (Bourne 1992; Haddad and Cardoso 1992; Bastos and Haddad 1996, 1999).

Adult males of *S. fuscomarginatus* defend calling sites during the breeding season. The escalated aggressive behaviour observed (see also Bastos and Haddad 1995, 2002; Martins and Haddad 1998) was sufficient for defending sites from intruding males, in most of cases without leading to physical interactions. The rarity of physical interactions observed in this

study may also be related to the abundant availability of calling sites, and low population density, at the studied ponds.

The lack of differences in body mass and SVL between dominant and satellite, winner and loser males, and the lack of differences in body mass between females and males may be related to the small sample size, and/or to the low precision of the scale used in the field. Males who won the territorial interactions were the resident males, a recurrent situation among hylids, probably because resident males are typically in better physical conditions when compared to the intruders (references in Bastos and Haddad 2001) or satellite males (Robertson 1986; Haddad 1991; Guimarães and Bastos 2003).

Satellite behaviour was rarely observed in this study, and female interception by satellite males was not observed. Therefore, satellite male behaviour in *S. fuscomarginatus* could be related to the dynamics of the chorus (Robertson 1986; Bevier 1997). For example, they could be waiting for the availability of calling sites, abandoned by dominant males (Wells 1977b). Alternatively, satellite males could be waiting for a change in the physical condition of dominant males, as there is considerable energetic costs in calling for consecutive days (Bevier 1997), promoting alternation of dominance at a calling site (Robertson 1986). However, these alternatives do not exclude the possibility of satellite males waiting to intercept females attracted by the dominant males.

Females had greater SVLs than males. This dimorphism could be related to greater fecundity associated with greater SVL (Crump 1974; Shine 1979) or could be related to different growth rates between the sexes (Halliday and Verrell 1988). The hypothesis of different mortality rates among the sexes (Shine 1979; Monnet and Cherry 2002) is unlikely because *S. fuscomarginatus* probably has an annual life cycle, since there were no recaptures from one reproductive season to the other (L. F. Toledo, unpublished data). Therefore, all individuals that attended the chorus should be same age, ca 1 year.

Pair formation behaviour was similar to other hylid species, because males did not wait for a female contact before the amplexus (Morris 1989; Bastos and Haddad 1996; Haddad and Sawaya 2000). This behaviour may be a strategy to avoid interception of the females by satellite or neighbouring males (Arnold 1976; Haddad 1991; Carvalho e Silva and Carvalho e Silva 1994). In many hylids, pairs that form above vegetation remain practically motionless for a few hours until they move down to the water for oviposition (e.g. Carvalho e Silva and Carvalho e Silva 1994; Bastos and Haddad 1996; present study). During this period, the female could be receiving a stimulus for oviposition (see Scarlata and Murphy 2003), such as the arhythmic compression of her flanks by the male (present study). This could also be another strategy to reduce the chances of pair interception and displacement of the amplexed male by waiting for surrounding males to stop calling activity and/or leave the neighbourhoods (Bastos and Haddad 1996; Bertoluci 1998).

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