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Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

Reproductive patterns of *Trachycephalus venulosus* (Laurenti, 1768) and *Scinax fuscovarius* (Lutz, 1925) from the Cerrado, Central Brazil

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Published online: 21 Feb 2007.

To cite this article: Domingos J. Rodrigues, Masao Uetanabaro & Frederico S. Lopes (2005) Reproductive patterns of *Trachycephalus venulosus* (Laurenti, 1768) and *Scinax fuscovarius* (Lutz, 1925) from the Cerrado, Central Brazil, *Journal of Natural History*, 39:35, 3217-3226, DOI: [10.1080/00222930500312244](https://doi.org/10.1080/00222930500312244)

To link to this article: <http://dx.doi.org/10.1080/00222930500312244>

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Reproductive patterns of *Trachycephalus venulosus* (Laurenti, 1768) and *Scinax fuscovarius* (Lutz, 1925) from the Cerrado, Central Brazil

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(Accepted 18 August 2005)

Abstract

Animal mating systems are moulded by ecological factors, mainly the temporal patterns of reproduction. We report the reproductive period, use of microhabitats, clutch and egg sizes, reproductive efforts, occurrence of sexual size dimorphism, and the relation between body size and fecundity in the gravid females of *Trachycephalus venulosus* and *Scinax fuscovarius* at Serra da Bodoquena, Central Brazil. The reproduction of both species was correlated with the rainy season. Females of *T. venulosus* produced more eggs and their eggs were larger than those of *S. fuscovarius*. The females of both species were larger and heavier than males. The reproductive effort was measured as the ratio of gonad mass in relation to body mass. Females of both species presented similar reproductive efforts, but males of *S. fuscovarius* invested more in gonads compared to males of *T. venulosus*. *Trachycephalus venulosus* presented significant correlation between snout–vent length versus number of mature eggs and body mass versus number of mature eggs and ovarian mass. *Scinax fuscovarius* showed significant correlation between body mass versus ovarian mass. *Trachycephalus venulosus* is an explosive breeder, whereas *S. fuscovarius* has prolonged reproduction. These species are able to adapt to several types of habitat, due to behavioural and physiological plasticity.

Keywords: Cerrado, Hylidae, reproductive patterns, sexual dimorphism

Introduction

Animal mating systems are moulded by ecological factors, mainly the temporal patterns of reproduction (Wells 1979). In temperate regions, the reproductive activity of amphibians depends on both temperature and rainfall, usually being cyclical (Rome et al. 1992). However, in tropical regions, anurans are capable of reproducing throughout the year or

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Published 28 October 2005.

ISSN 0022-2933 print/ISSN 1464-5262 online © 2005 Taylor & Francis

DOI: 10.1080/00222930500312244

only in the rainy season, rainfall being the factor that determines seasonality (Aichinger 1987; Duellman and Trueb 1994). Wells (1977) recognized two temporal patterns in anuran reproduction: explosive and prolonged. The explosive pattern is characterized mainly by occurring in short periods (hours or days), low selectivity of males (active search for females), chorus formations, and with synchronous female arrival. In the prolonged pattern, the reproductive period is longer (sometimes for several months), females arrive asynchronously, and males are more selective and territorial. However, intermediate patterns may occur, combining characteristics of prolonged and explosive breeding (Wells 1977; Bastos and Haddad 1999; Prado et al. 2005).

Reproductive strategies evolve to produce the optimum number of offspring under certain environmental conditions (Duellman and Trueb 1994; Stebbins and Cohen 1995). In this way, different strategies or reproductive patterns can minimize the cost and/or risks associated with reproduction (Harvey and Pagel 1993). The cost of reproduction is important to understand life history patterns (Pough et al. 1998) and sexual selection (Trivers 1972). In oviparous species, the energy content of the eggs is considered to be an estimation of the energy spent in reproduction (Tinkle et al. 1970), but energy can be spent in other manners, such as nest construction, vocalization, mating, and egg deposition (Ryan et al. 1983). The estimation of reproductive effort measures the energy expenditure in reproduction (Stearns 1992). A way to assess the reproductive effort in anurans is to measure the size, mass, or volume of gonads, or clutches relative to body size, mass, or volume (e.g. Crump 1974; Stearns 1992; Prado et al. 2000). In general, clutch volume is correlated with female size, because of the limited availability of space in the abdominal cavity of the female (Kaplan and Salthe 1979; Shine 1992; Prado et al. 2000).

The Neotropical region contains more than 50% of the known anuran species of the world (Duellman 1999) which exhibit a great diversity of reproductive modes that, probably, are correlated with habitat variety (Haddad and Prado 2005). Information about life histories of Neotropical frogs is insufficient and there are few detailed studies about reproduction (e.g. Cardoso et al. 1989; Krügel and Richter 1995; Rodrigues et al. 2003, in press). More specific studies, mainly those focusing on reproductive effort, are rare (e.g. Prado et al. 2000). In Brazil, there have been several studies on the reproduction of anurans (e.g. Pradeiro and Robinson 1990; Prado et al. 2000). However, the majority of studies were made in the south-eastern region (e.g. Bastos and Haddad 1996; Pombal and Bastos 1996) and in the Central Amazonian rainforest (e.g. Juncá 1998; Neckel-Oliveira 2004). Studies on the anurofauna of the Cerrado (Brazilian savanna) are recent (Colli et al. 2002) and, despite the high human impact on the environment (deforestation and soybean plantation) in the Cerrado (Beebe 1996), the biology of anurans remains poorly known (Pombal and Bastos 1996; Rodrigues et al. 2003). The Serra da Bodoquena is a preserved area of Cerrado classified by Colli et al. (2002) as a priority area concerning the biodiversity of herpetofauna.

The present study focused on some aspects of the reproduction of *T. venulosus* and *S. fuscovarius* in a temporary pond (artificial cattle drinking pond) and flooded area, at Serra da Bodoquena (Cerrado), State of Mato Grosso do Sul, Brazil. The aims of this investigation were: (1) to identify the reproductive period and pattern of both species; (2) to determine the use of microhabitats; (3) to determine the clutch and egg sizes; (4) to estimate the reproductive effort; (5) to assess the existence of sexual dimorphism in size and body mass; (6) to evaluate the relationship between body size and mass, and the number of mature ovarian eggs and ovarian mass in gravid females; and (7) to evaluate the relationship between the snout-vent length (SVL) and body mass of males and females in reproductive effort.

Study area and methods

The study was carried out at Serra da Bodoquena, Canaã Farm (20°40'30.4"S, 56°45'20.2"W) and Canaã Settlement (20°41'32.3"S, 56°44'34.3"W), municipality of Bodoquena, Mato Grosso do Sul State, Central Brazil. Mean annual temperature is 21 °C, and mean annual precipitation is approximately 1500 mm (Alvarenga et al. 1982; Figure 1). The rainy period occurs from October to April, with a dry season extending from May to September (Rodrigues et al. 2003).

The Serra da Bodoquena is located in the south-central portion of the State, on the border of the Pantanal (floodplain) of Nabileque (Boggiani and Clemente 1999). The vegetation of the plateau varies according to the relief and soil type, having the physiognomy of semi-deciduous forest and grass fields (see Furtado et al. 1982; Rodrigues et al. 2003).

Breeding populations were surveyed in two temporary water bodies: a pond of approximately 100 m², depth ranging from 20 to 40 cm, and vegetation composed of Gramineae and Asteraceae shrubs, and a flooded field with an area of approximately 500 m², depth ranging from 15 to 80 cm, and vegetation composed of Gramineae. Accumulation of water in the flooded field occurs due to soil type and a small depression in the land. The two study sites were approximately 4 km apart.

Data were collected during about 4 days each month from October 2000 to September 2001 in each water body. The reproductive period was determined based on direct observation of males vocalizing, amplexant pairs or presence of tadpoles. Oviposition sites were characterized by recording the presence or absence of vegetation. One collaborator remained in the area and recorded the anuran species present and precipitation during our absence.

Individuals collected were transported in plastic bags and killed by freezing. The SVL of adults was measured to the nearest 0.1 mm with a vernier calliper. The total body mass

Figure 1. Number of individuals present in monthly samples (black bar is total of individuals of *Trachycephalus venulosus* and stippled bar is total of *Scinax fuscovarius*) and rainfall per month at the study site (black circle is total rainfall during the study and black triangle is rainfall during 4 days of study per month).

(BM) and gonad mass (GM) of males and females were determined to the nearest 0.001 g with a digital balance. Mean number of eggs per clutch was estimated based on the number of eggs deposited by couples in amplexus in the vegetation or water surface. The diameter of the eggs was measured with an ocular micrometer to the nearest 0.1 mm. To assess the fecundity in gravid females, the largest and most pigmented eggs were counted and considered to be mature (Crump 1974), with a size of 1.1 mm for *T. venulosus* and 1.0 mm for *S. fuscovarius*. The gonads were removed through a ventro-lateral incision. Voucher specimens were deposited in the Zoological Collection of the Federal University of Mato Grosso do Sul (*T. venulosus* ZUFMS—519–521; *S. fuscovarius* ZUFMS—540–542).

To evaluate the correlations between female fecundity and body size, linear regression analyses were performed between the following variables: (1) SVL versus number of mature ovarian eggs (NME); (2) BM versus NME; (3) SVL versus ovary mass (OM); (4) BM versus OM. Student's *t*-test was used to compare male and female SVL, reproductive effort (RE), and BM. RE was estimated as the percentage of GM relative to BM. To evaluate the influence of size and BM of females and males on the RE, linear regressions were performed between RE versus SVL and RE versus BM.

Results

The reproductive period of *T. venulosus* lasted 4 months (October to January) whereas that of *S. fuscovarius* lasted 7 months (November to May). Both species reproduced either in the pond or in the flooded field. The reproductive activity of *T. venulosus* was related to the period of high rainfall (daily values >50 mm) (Figure 1), while the reproductive activity of *S. fuscovarius* occurred in periods of high (>50 mm) and medium (between 20 and 50 mm) rainfall. After sunset, males of *T. venulosus* were frequently observed in small shrubs around the flooded field and near to the edge of the pond, vocalizing on the ground. All the reproductive activity observed at the pond and flooded field occurred up to 2 days after heavy rainfall. Males formed choruses to attract females to the flooded field and pond. They swam across all perimeters of the pond and flooded field, performing active searches for females on the water surface. When in amplexus, they were in the central part of the pond and flooded field, depositing eggs as a monolayer on the water surface.

After sunset, males of *S. fuscovarius* called from the canopy of the vegetation at the edge of the pond, and at the flooded field they vocalized among the shrubs near the flooded area. Although we observed more than 200 individuals swimming and calling in the flooded field, only about 50 males of *S. fuscovarius* were successful in achieving amplexus in the morning of the day following high rainfall. The pairs in amplexus deposited eggs on the aquatic vegetation. On four occasions we observed the presence of a second male grasping the couple in amplexus. They remained attached to the couple until the end of oviposition. During the day, the individuals of *S. fuscovarius* were found in the deepest part of the pond and flooded field. We observed several bird predators [*Tigrisoma lineatum* (Boddaert, 1783), *Syrigma sibilatrix* (Temminck, 1824), *Pitangus sulphuratus* (Linnaeus 1766), *Guirra guira* (Gmelin, 1788), and *Crotophaga ani* Linnaeus, 1758] at the edge of the pond and flooded field preying on *S. fuscovarius* and *Scinax* sp. (gr. *ruber*; another species found at the study sites). The reproduction of both species (*S. fuscovarius* and *T. venulosus*) occurred in the pond and flooded field.

Mean number of eggs per clutch was 5635 ± 2219 ($n=23$, range=2834–9794) for *T. venulosus* and 2892 ± 1056 ($n=19$, range=1005–4877) for *S. fuscovarius*. Clutch sizes differed significantly between species ($gl=33$, $t=5.3$, $P<0.001$). Mean diameter of eggs

Table I. Mean±SD of SVL (mm) and mass (g) of males and females of *Trachycephalus Venulosus* and *Scinax fuscovarius*.

		Males			Females			t	P
		n	Mean±SD	Range	n	Mean±SD	Range		
<i>T. venulosus</i>	SVL	34	77.6±6.7	63.1–87.5	22	87.7±5.9	73.0–96.0	5.7	<0.001
	Mass	34	36.3±10.9	19.5–60.8	23	54.9±13.1	33.1–84.7	5.8	<0.001
<i>S. fuscovarius</i>	SVL	45	47.4±1.9	42.2–52.0	23	49.8±2.6	45.0–55.3	4.4	<0.001
	Mass	45	7.6±1.0	5.7–10.2	19	10.2±2.7	5.4–17.6	3.7	0.001

(±SD) was also larger (gl=39, $t=8.9$, $P<0.001$) in *T. venulosus* (1.60 ± 0.20 mm, $n=40$, range=1.20–2.00) compared to *S. fuscovarius* (1.3 ± 0.11 mm, $n=40$, range=1.10–1.50).

Sexual dimorphism both in SVL and BM was verified for *T. venulosus* and *S. fuscovarius*, females being, on average, larger and heavier than males (Table I). The RE of the females of both species was similar. However, males of *S. fuscovarius* had significantly higher RE than *T. venulosus* (Table II).

Females of *T. venulosus* showed a significant and positive relationship between BM versus NME ($n=23$, $r^2=0.40$, $P=0.001$) (Figure 2A); SVL versus NME ($n=22$, $r^2=0.19$, $P=0.04$) (Figure 2B), and BM versus OM ($n=23$, $r^2=0.46$, $P<0.001$) (Figure 2C). The variables SVL versus OM were not significantly correlated in *T. venulosus* ($n=22$, $P=0.07$). Females of *S. fuscovarius* showed a significant and positive relationship between BM and OM ($n=12$, $r^2=0.30$, $P=0.06$) (Figure 2D). The variables SVL versus NME ($n=19$, $P=0.1$), SVL versus OM ($n=13$, $P=0.4$), and BM versus NME ($n=18$, $P=0.6$) were not significantly correlated in *S. fuscovarius*.

Trachycephalus venulosus did not present positive and significant relationships between SVL versus RE for the females ($n=22$, $P=0.35$) or males ($n=34$, $P=0.108$) nor between BM versus RE for the females ($n=13$, $P=0.441$) or males ($n=45$, $P=0.162$). *Scinax fuscovarius* did not present positive and significant relationships between SVL versus RE for the females ($n=13$, $P=0.690$) or males ($n=45$, $P=0.711$) nor between BM versus RE for females ($n=23$, $P=0.870$) or males ($n=34$, $P=0.460$).

Discussion

Trachycephalus venulosus is considered an explosive breeder due to its reproductive characteristics (e.g. chorus formation, male active search for females), according to the classification of Wells (1977). This same explosive pattern was reported by Zimmerman and Hödl (1983). Hoogmoed (1979) and Prado et al. (2005) observed the same reproductive pattern for *T. venulosus* (explosive) in Amazonia and the Pantanal, respectively; Duellman (1978) and Gallardo (1987) also observed chorus formation in

Table II. Mean±SD of gonad mass (GM) and reproductive effort (RE) of males and females of *Trachycephalus Venulosus* and *Scinax fuscovarius* measured as the percentage of mature gonads weight relative to body weight.

<i>T. venulosus</i>				<i>S. fuscovarius</i>			t	P
	n	GM (g)	RE	n	GM (g)	RE		
Males	33	0.039±0.013	0.11±0.02	44	0.094±0.04	1.21±0.4	15.5	<0.001
Females	23	13.02±5.04	23.6±6.3	13	2.60±0.88	22.6±5.8	0.46	0.650

Figure 2. Females of *Trachycephalus venulosus* (A–C) and *Scinax fuscovarius* (D) collected at Serra da Bodoquena, MS, Brazil, from October 2000 to September 2001. Relations between: (A) BM versus NME ($NME = 106.47BM - 217.34$, $n = 23$, $r^2 = 0.40$, $P = 0.001$); (B) SVL versus NME ($NME = 168.86SVL - 9171.74$, $n = 22$, $r^2 = 0.19$, $P = 0.04$); (C) BM versus OM ($OM = 0.259BM - 1.24$, $n = 23$, $r^2 = 0.46$, $P < 0.001$); (D) BM versus OM ($OM = 0.302BM - 0.8302$, $n = 12$, $r^2 = 0.30$, $P = 0.06$).

Amazonia and Argentina, respectively; Zimmerman and Hödl (1983) also recorded reproductive activity in open areas in Amazonia; and Zweifel (1964) observed in Panamá similar sites for egg deposition as observed in this study. These data suggest that the populations of *T. venulosus* have the same reproductive pattern in different localities.

Haddad and Sazima (1992), at Serra do Japi (São Paulo), Kwet and Di-Bernardo (1999), at Serra Geral do Rio Grande Sul (Pró-Mata-Atlantic Forest), and Norman and Naylor (1994), in the Paraguayan Chaco, observed the same reproductive pattern (prolonged) for *S. fuscovarius*, as observed in the present study, indicating that the populations of this species have the same reproductive pattern. However, *S. fuscovarius* was considered a species with prolonged reproduction due to difficulties in establishing a definite pattern (e.g. duration of the reproductive activity 4 months—continuous reproduction; synchronism of males and females and individuals vocalizing and mating during the day—explosive reproduction). Bastos and Haddad (1999) obtained the same

conclusion when studying the reproduction of *S. rizibilis* (Bokermann, 1964). In the study of Lee and Salzburg (1989), *Bufo valliceps* Wiegmann, 1833 was classified as a species with explosive reproduction, but Wagner and Sullivan (1992) studying this species in south-central Texas observed that the species showed both explosive and prolonged reproduction. Wells (1977) recognized that in conditions of low density, anurans with explosive reproduction can exhibit characteristics typical of species with continuous or prolonged reproduction (e.g. female choice). However, the opposite may be occurring with *S. fuscovarius* in the studied region. Reproduction during the day may expose individuals of *S. fuscovarius* to predation, and a way to avoid the predators could be to adopt an immobile posture and remain in the deepest part of the pond (water colour is similar to individuals' colour). According to Stebbins and Cohen (1995), some amphibians avoid detection by predators through camouflage, being observed close to trunks, stones, and on the water surface, combining the colour of body with the colour of the water.

Females of *T. venulosus* and *S. fuscovarius* were, on average, larger and heavier than males. Similar results have been reported for other hylids (Shine 1979), such as *Hyla faber* Wied-Neuwied, 1821 (Martins 1993) and *Hyla elegans* Wied-Neuwied, 1824 (Bastos and Haddad 1996). Females are larger in 90% of the known species of anurans (Shine 1979) and the causes of that phenomenon are diverse: the most obvious is the capacity of larger females to produce larger clutches and eggs (Crump and Kaplan 1979; Prado et al. 2000; Rodrigues et al. 2003, in press). However, other explanations exist, such as differences in the age of the first reproduction or in the mortality rate caused by higher predation pressure on larger males (Howard 1981); or even restrictions on the growth of males due to energy demand linked to reproductive activity (Woolbright 1989). Therefore, sexual dimorphism in relation to size and body mass between males and females can represent the result of complex interactions (e.g. competition and predation) to which the species is exposed in its environment (Woolbright 1989).

Males of *S. fuscovarius* had larger investment in gonads (RE) than *T. venulosus*. This difference was related to testes size, which is both absolutely and relatively larger in *S. fuscovarius* than in *T. venulosus*. Variations in testes size can be found in numerous species of mammals, birds, and amphibians (Coker et al. 2002). Species involved in intense spermatic competition have larger testes than species that experience low competition intensity (Møller 1991; Møller and Briskie 1995; Dixson 1999). Prado et al. (2000) observed that males of *Leptodactylus chaquensis* Cei, 1950 had larger gonads than *L. podicipinus* (Cope, 1862), and the behavioural differences between both species (time and amount of energy spent in the vocalization) could partially explain this difference. Also, *L. chaquensis* and *L. podicipinus* exhibit polyandry (more than one male trying to fertilize the eggs of a female) (Prado and Haddad 2003), which was observed in *S. fuscovarius* (in the present study) and may be an important factor in determining testes size. According to Jennions and Passmore (1993) and Emerson (1997), in species exhibiting multi-male spawning, males have larger testes than species where this behaviour is absent. Polyandry was also described for hylids (Roberts 1994) and genetic studies demonstrated the occurrence of multiple paternity in *Agalychnis callidryas* (Cope, 1862) (D'Orgeix and Turner 1995).

The fact that females of both species exhibited the same reproductive effort in the present study suggests that they can be responding to similar selective pressures in relation to reproduction which, consequently, would lead to a similar gonad investment. Our results support the conclusion of Crump and Kaplan (1979), that females of any species produce clutches with similar amounts of energy. Perhaps, the lack of difference in the reproductive

investment of the females of both species may be due to the same mode and reproductive period.

Various studies have demonstrated that female size is positively correlated with the number and size of eggs produced (e.g. Pradeiro and Robinson 1990; Prado et al. 2000; Rodrigues et al. 2003). For females of *S. fuscovarius*, 0.54% of the variation in OM was explained by the BM. For females of *T. venulosus*, 0.19% of the variation in NME was explained by the SVL. However, in *T. venulosus*, 0.40 and 0.46% of the variation in NME and OM, respectively, were explained by the BM. Larger body size confers to females reproductive advantages with increase in the egg number or egg size (Crump 1974; Howard 1978, Prado et al. 2000). According to Lang (1995), volume is a more accurate measure to assess the NME than the SVL. In this way, body mass being correlated with the volume can also be considered an accurate measure, emphasizing the differences obtained in the determination coefficient above.

The lack of relationship between SVL and BM versus RE in males and females of both species (*T. venulosus* and *S. fuscovarius*) possibly indicates that small individuals invest the same amount of energy (RE) compared to larger individuals of the same species. However, there was a greater variation in RE in males of *S. fuscovarius* than in *T. venulosus*, causing the differences described above when the species were compared. Possibly, the reproductive pattern of *S. fuscovarius* can explain the difference. Nevertheless, more studies on reproduction in Neotropical anurans are necessary to understand the differences among species, principally for the relation between testis size and SVL and BM for males.

Acknowledgements

The authors thank W. R. Heyer, P. J. Hayward, F. Glaw, M. Menin, and T. Izzo, for their many valuable comments on and criticism of the manuscript. We thank C. P. A. Prado for correction of the language, and P. L. Filho, F. R. D. Fonseca, R. Arruda, T. S. F. Souza, and all the people who helped in the field. We are also grateful to Canaã Farm (Sr. Pita) and Canaã Settlement (Sr. Vândir) for the logistic support, to CNPq for the scholarships to D. J. Rodrigues (proc. 1311741/2000-4), for the financial support to the project “Padrões de biodiversidade da fauna e flora do Pantanal” (proc. 521746/97-3), to Fundação o Boticário de Proteção à Natureza (proc. 046820002) and to IBAMA (collecting permit no. 020/2001; proc. 02014-2486/00-89).

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