HERPETOZOA 16 (3/4): 115 - 126
Wien, 30. Jänner 2004

Reproductive ecology of *Leptodactylus furnarius* SAZIMA & BOKERMANN, 1978, a frog that lays eggs in underground chambers

(Anura: Leptodactylidae)

Zur Fortpflanzungsökologie von *Leptodactylus furnarius* SAZIMA & BOKERMANN, 1978 einem Frosch, der seine Eier in unterirdische Kammern ablegt
(Anura: Leptodactylidae)

ARIOVALDO A. GIARETTA & MARCELO N. DE C. KOKUBUM

KURZFASSUNG

Die Autoren berichten über die Fortpflanzungsökologie von *Leptodactylus furnarius* SAZIMA & BOKERMANN, 1978 in Minas Gerais, Brasilien. Daten zur Populationsstruktur wurden mittels Fallenfängen erhoben, in denen die Weibchen zahlenmäßig über die Männchen dominierten. In der Trockenzeit wurden weniger Tiere gefangen als in der Regenzeit. Die tatsächliche Gelegegröße wurde anhand der Anzahl von Ovarialeiern abgeschätzt, die zwischen 27 und 119 je Weibchen schwankte; der Dotter-Durchmesser betrug etwa 3 mm. Die Ruf- und Eiablageplätze lagen nahe seichter, langsam fließender Gewässer. Die Rufaktivität war während der Regenzeit kontinuierlich, in der Trockenzeit sporadisch. Die Fortpflanzung erfolgte auch in der Trockenzeit, wie Larvenfunde zu dieser Zeit belegen. Weiters wurde die Balz im Freiland beobachtet. Zur Paarung und Eiablage (die beide nicht beobachtet wurden) führte das Männchen das Weibchen in eine zuvor gegrabene Kammer. Die Kammern waren annähernd rund und direkt oder durch einen kurzen Tunnel zugänglich. Die Larven sind durch ihre Fähigkeit bemerkenswert, selbständig Schaum zu generieren. Im Laborversuch hatten abgespülte Kaulquappen nach 50 Stunden neuen Schaum gebildet. Die Schlange *Liophis meridionalis* ernährte sich von Kaulquappen, die sich innerhalb der Brutkammer befanden.

Wie bei anderen Arten aus der *L. fuscus* – Gruppe legt *L. furnarius* unterirdische Eiablage-Kammern an und scheint die Fähigkeit der Larven, Schaum zu erzeugen, dazu zu dienen, Schaum und damit Feuchtigkeit längere Zeit hindurch aufrechtzuerhalten. Die Fähigkeit zur Schaumbildung dürfte eine Synapomorphie der Arten der *L. fuscus* - Gruppe sein.

ABSTRACT

This report details the reproductive ecology of *Leptodactylus furnarius* SAZIMA & BOKERMANN, 1978, as observed in Minas Gerais, Brazil. The population structure was assessed by trapping individuals, in which females predominated numerically over males. More individuals were captured in the rainy season than the dry. Counting ovarian eggs provided estimations of clutch size ranging from 27 to 119 per female; the yolk of the eggs measured about 3 mm in diameter. Calling/egg laying sites were close to shallow, slow flowing water. Calling activity was constant during the rainy season but varied in the dry season. Reproduction also occurred in the dry season which was corroborated by the appearance of tadpoles at that time. Courtship was observed in the field. The male led the female to a previously excavated chamber for mating and oviposition (unobserved). Access to these nearly round chambers was direct or through a short tunnel. Tadpoles were characterized by their ability of generating foam by themselves. In the laboratory, rinsed tadpoles had produced foam after 50 hours. The snake, *Liophis meridionalis*, preyed upon tadpoles within the chamber.

The reproductive pattern of *L. furnarius* is similar to that of the known species of the *L. fuscus* group, with regard to its habits of building underground chambers to lay eggs. In *L. furnarius*, as in other species of the *L. fuscus* group, the foam-generating behavior of the tadpoles may serve for keeping the foam, and thus moisture, for an extended period. Foaming behavior of the tadpoles may represent a synapomorphy of the species of the *L. fuscus* group.

KEY WORDS

Amphibia: Anura: Leptodactylidae: Leptodactylinae; *Leptodactylus fuscus* group, *Leptodactylus furnarius*, reproduction, ecology, behavior, tadpoles, south-eastern Brazil

INTRODUCTION

Several lineages of frogs are convergent in their habits of laying eggs in a foam nest, which is produced by the parents during oviposition (LAMOTTE & LESCURE 1977; HÖDL 1986; DUELLMAN & TRUEB 1986). Among the Neotropical Leptodactylinae, foam nesting behavior is found in most of the genera and species (HEYER 1969; LYNCH

1971) and seems to be related to egg/tadpole protection against desiccation (HEYER 1969; DUELLMAN & TRUEB 1986) and predators (DOWNIE 1990; MENIN & GIARETTA 2003). As presently defined, the *Leptodactylus fuscus* (SCHNEIDER, 1799) group (sensu HEYER 1978) contains species that build underground chambers in the vicinity of water bodies. The females lay their eggs into foam nests inside these chambers (DENT 1956; PHILIBOSIAN et al. 1974; MARTINS 1988; CALDWELL & LOPEZ 1989; ARZABE & ALMEIDA 1996). The tadpoles hatch inside the chamber but need to arrive at a water body in order to complete their development (SOLANO 1987; DOWNIE 1994). Early tadpoles of two species - *L. fuscus* and *L. mystaceus* (SPIX, 1824) - are known to generate foam by themselves (DOWNIE 1984; DOWNIE 1989; CALDWELL & LOPEZ 1989), a behavior that could be important for restoring foam produced by the parents in the chamber or if the water body the larvae entered dried out (DOWNIE 1984, 1990).

Currently, little is known about the ecology and breeding behavior of most of the 22 species of the *L. fuscus* group. *Leptodactylus furnarius* SAZIMA & BOKERMANN, 1978 is a medium sized species of this group and has not been studied in terms of its ecology and behavior. In this paper, we describe aspects of the reproductive ecology of the species such as habitat and seasonality and behavior such as courtship. We also tested the ability of the tadpoles to generate foam.

MATERIALS AND METHODS

Leptodactylus furnarius was studied in the municipality of Uberlândia (18°55'S; 48°17'W), State of Minas Gerais, Brazil. The original vegetation was Cerrado (ARAÚJO et al. 1997), which can still be found in some areas around the city. The regional climate has two well-defined seasons, a rainy/hot summer and a dry/mild winter (April-August) (fig. 1, data from 1983 - 2002), with occasional frosts. The annual mean precipitation is around 1,550 mm, ranging from 750 to 2,000 mm. Some places used as reproductive sites retain water in the dry season.

The analysis of quantitative population parameters, such as age structure, was based on pitfall-trapped individuals, collected by the senior author (AAG). Voucher specimens are deposited at the Museu de Biodiversidade do Cerrado, Universidade Federal de Uberlândia (MBC-UFU); selected vouchers are in the collection of frogs, AAG-UFU 2155, 2161, 2167, and 2197. Traps were set at the Clube de Caça e Pesca Itororó de Uberlândia (CP) and Estação Ecológica do Panga (EEP). Each pitfall array consisted of three buckets (about 20 liters; 35 cm mouth diameter) in a line, two meters from one another, linked by a fine-meshed nylon net (8 m long x 60 cm deep, 10 cm buried into the ground). Specimens were recovered from the buckets once or twice a week.

At the CP, the traps were set continuously from October 1999 to December 2000; data from the EEP traps were collected from September 2000 to October 2001. At the CP, four arrays of traps were set up; data of a fifth array, set in March 2000 were also included. At EEP, five arrays of traps were set. At both localities, the traps were set up in open areas, generally with vegetation less than one meter tall, and beside water bodies such as rivulets (veredas), ponds, and lakes. Distances between arrays were 100 to 3,000 m.

Behavioral observations were carried out at the CP and in an urban area. The annual pattern of calling was determined weekly during the rainy season of 2001 (September – March) bi-weekly during the drier months of 2001 (April – August) and weekly between May and mid July 2003. The daily pattern of the calling activity was determined occasionally during continuous 24 hours observation periods. In two dry seasons (2001 and 2003) tadpoles were searched for with a sieve in water bodies around which the males called; when they were found, a sample was collected for staging and size measurements. To describe the age structure of the population, the individuals were classified as adult males, adult females and juveniles. The snout-vent length (SVL) of the smallest calling male was used to set the

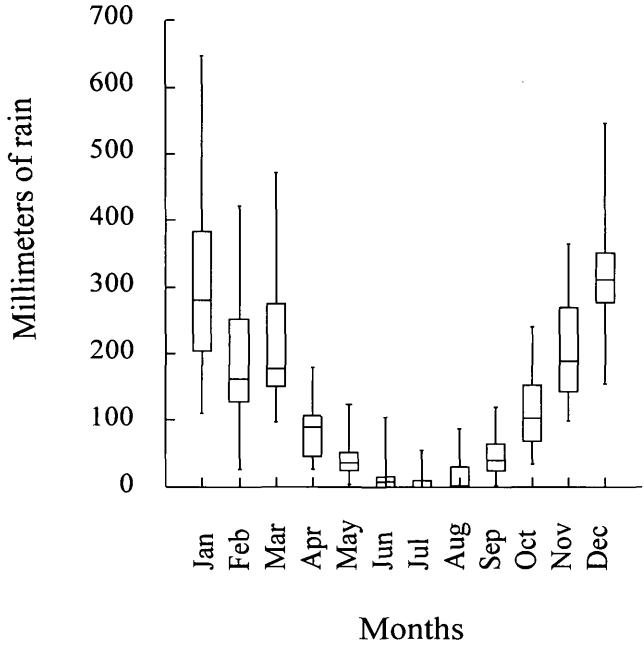

Fig. 1: Monthly rainfall (mm) in Uberlândia (Minas Gerais, Brazil). Data (n = 19 years from 1983 to 2002) from the Estação Meteorológica da Universidade Federal de Uberlândia, MG, Brazil.
Plots indicate minimum, maximum, median and quartiles.

Abb. 1: Niederschlagswerte (mm) (n = 19 Jahre von 1983 bis 2002) der Monate Jänner bis Dezember in Uberlândia (Minas Gerais, Brasilien). Daten der meteorologischen Station der Bundesuniversität Uberlândia, Minas Gerais, Brasilien. Die Plots zeigen Minimum-, Maximum-, Median- und Quartilswerte.

lower size limit to the adult male category; for the females, it was the SVL of the smallest individual bearing mature eggs. Adults and large juveniles (> 30 mm SVL; n = 20) were dissected for sex determination; sex ratios were determined for adults and large juveniles. To test if the egg number from ovaries was representative of the actual number of eggs laid, the number of mature ovarian eggs (≥ 2 mm in diameter) of the females collected in November (2000) was compared with that determined from egg clutches collected in the field in the same month. Courting pairs were searched for (Scanning Sampling) and the most relevant events were noted (Continuous Recording) (MARTIN & BATESON 1986). The developmental time of the tadpoles while in the foam was determined by observing an egg clutch of known age. For identification, eggs and tadpoles were kept in the lab until metamorphosis. A snake, found inside a chamber containing foam and tadpoles, was analyzed for stomach contents.

For descriptions and comparisons gypsum moulds of the chambers of *L. furnarius* and of the syntopic *Leptodactylus fuscus* (SCHNEIDER, 1799) were made.

In the lab we tested the ability of *L. furnarius* tadpoles to generate foam. Tadpoles from three different egg clutches were used. The tadpoles were all the same size (about 15.5 mm total length) and at GOSNER (1960) stage 25. One experimental group contained 23 tadpoles and the other two contained 44 tadpoles each. For this experiment, the tadpoles were removed from the original foam by carefully rinsing them in dechlorinated tap water. The experiment was conducted in a plastic tray containing wet earth, however, without free water where the tadpoles could swim. Each tadpole group was

Table 1: The numbers of adult males, females and the reproductive condition of the females among the individuals of *Leptodactylus furnarius* trapped in two localities in Uberlândia (Minas Gerais, Brazil) from October 1999 to October 2001. Those months with no capture were omitted.

Tab. 1: Die Anzahl von Männchen und Weibchen sowie der Reproduktionsstatus der Weibchen in den Fängen von *Leptodactylus furnarius* an zwei Fundorten in Uberlândia (Minas Gerais, Brasilien) in der Zeit von Oktober 1999 bis Oktober 2001. Monate ohne Fänge nicht angeführt.

Month / year Monat / Jahr	n ♀♀	n ♂♂	Egg-bearing ♀♀ / ♀♀ mit Ovarialeiern	Sex ratio (♀♀ : ♂♂) Geschlechterverhältnis (♀♀ : ♂♂)	Operational sex ratio (Egg-bearing ♀♀ : ♂♂) Operatives Geschlechterverhältnis (♀♀ mit Ovarialeiern : ♂♂)
Oct. 1999	2	1	2	2	2/1
Nov. 1999	9	3	9	3	9/3
Dec. 1999	5	3	5	1.7	5/3
Jan. 2000	19	3	10	6.3	10/3
Feb. 2000	7	5	6	1.5	6/5
Mar. 2000	3	0	0	-	0/0
Apr. 2000	1	0	0	-	0/0
Sep. 2000	1	0	0	-	0/0
Nov. 2000	5	0	4	-	4/0
Dec. 2000	0	3	0	-	0/3
Jan. 2001	1	0	0	-	0/0
Mar. 2001	0	1	0	-	0/1
Total	53	19	36	2.9	36/19

kept in a shallow pit in the earth (about 40 mm diameter and 10 mm deep). The experiment was carried out in the shade, with natural illumination; temperature during the period ranged from 23°C to 27°C. The tadpoles were observed for about 60 hours, at intervals of 3 - 8 hours.

Adult males and females were analyzed for secondary sexual characters and the size of both sexes was compared by analysis of variance (ANOVA). The size of males and females and egg number by month ($n \geq 2$ females) were compared through nonparametric analysis of variance (Kruskal-Wallis) (ZAR 1999); multiple comparison was made as in ZAR (1999). To test if egg number counted from ovaries corresponds to that of effectively laid eggs, both counts were compared using the Mann-Whitney U test (ZAR 1999). The correlations of female SVL vs. ovarian egg number and monthly rainfall vs. mean number of eggs laid were tested using the Spearman test (ZAR 1999). All statistical tests were two-tailed; the level of significance was chosen a priori as 0.05. Some of the quantitative variables are presented in box-plot diagrams, which display the median, 1st and 3rd quartiles and range (WILKINSON 1990).

Calls were recorded with a Nagra™ E tape recorder (tape speed 19 cm/s) and a Sennheiser™ MKH816T microphone. The call was digitized, and the audiospectrogram prepared, with the Spectrogram® software (HORNE 1994). Sample rate was set at 22,050 Hz, with 16 bit resolution. For analysis FFT (Fast Fourier Transformation) at 2,048 data points, frequency resolution at 21.5 Hz, low and high band limit at 1,500 and 7,000 Hz, respectively, were used. AAG-# refers to A. A. GIARETTA record file.

RESULTS

In the studied area, male *Leptodactylus furnarius* called on the ground (n = 30), in or within 10 cm from shallow (1 - 10 cm deep) slow flowing water; in both permanent and temporary water bodies. Natural environments of reproduction were the plains beside rivulets (veredas), where low and sparse vegetation (less than 1.5 m tall) grows; human-disturbed wetlands were also used (2 sites). The chambers (n = 40) were

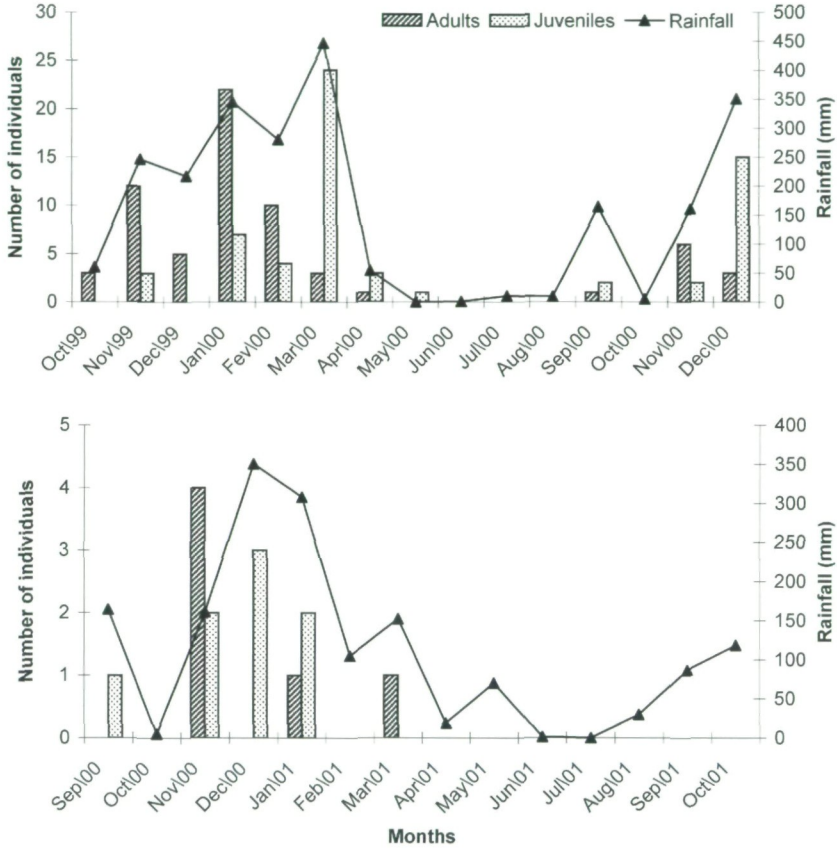

Fig. 2: Seasonal variation in the abundance of adults and juveniles of *Leptodactylus furnarius* trapped in two localities in Uberlândia (Minas Gerais, Brazil) from October 1999 to October 2001. Above, Clube de Caça e Pesca (CP); below, Estação Ecológica do Panga (EEP). The line represents the rainfall (mm) during the study period.

Abb. 2: Jahreszeitliche Schwankungen in der Häufigkeit der Adulten und Jungtiere von *Leptodactylus furnarius*, die während der Untersuchungszeit (Oktober 1999 bis Oktober 2001) an zwei Orten in Uberlândia (Minas Gerais, Brasilien) in Fallen gefangen wurden. Oben: Clube Caça e Pesca (CP); unten: Ökologische Station Panga (EEP). Die Linie stellt die Niederschlagswerte (mm) während der Untersuchungszeit dar.

constructed in mud-sandy or organic soil, amidst the dead or live roots of herbs (grasses and/or Cyperaceae).

Gravid females (n = 39) were found between September and February; from October on they were collected in the traps (table 1). Egg clutches were found between October and February. Between September and February, males started calling 3 – 4 hours before sunset; during 2 – 3 hot and rainy days at mid reproductive season (December - January) they called throughout the 24 h period. During the dry season, calling activity was sporadic (3 days in June and July 2001) or continuous (until August in 2003) and was restricted to hot (air 30.0 °C, water 27.8 °C) hours of the day (12:30 to 17:00).

More frogs were trapped at the CP than at the EEP (fig. 2). Capture of individuals was low to zero in months during which precipitation was below 100 mm (figs. 1 and 2). Females predominated numerically in the samples, with a high operational sex

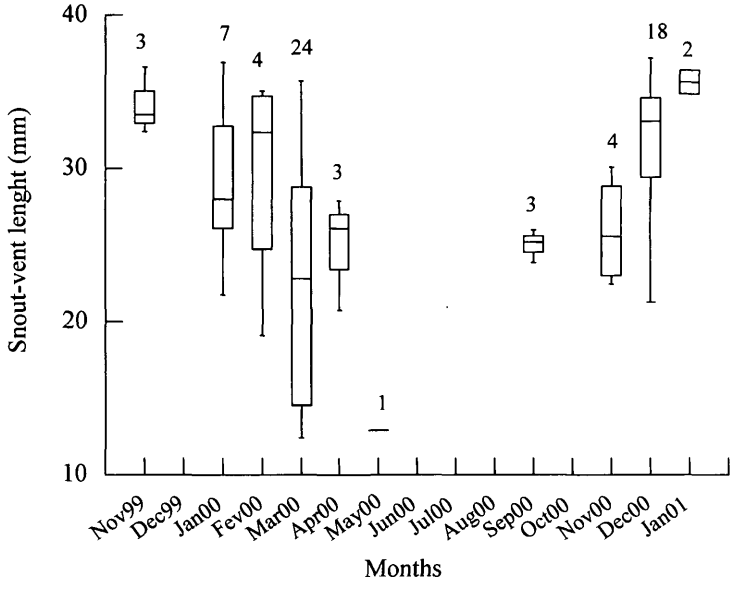

Fig. 3: Seasonal variation in the abundance and size (SVL, in mm) of juvenile *Leptodactylus furnarius* (n = 69) trapped in Uberlândia (Minas Gerais, Brazil) from October 1999 to October 2001. No individual was trapped after January 2001. The number above each plot represent the sample size. Plots indicate minimum, maximum, median and quartiles.

Abb. 3: Jahreszeitliche Schwankungen in der Häufigkeit und Größe (Kopf-Rumpflänge, mm) von Jungtieren von *Leptodactylus furnarius* (n = 69), die während der Untersuchungszeit (Oktober 1999 bis Oktober 2001) in Uberlândia (Minas Gerais, Brasilien) gefangen wurden. Nach Jänner 2001 wurde kein Jungtier mehr gefangen. Zahlen über den Plots bezeichnen Stichprobenumfänge. Die Plots zeigen Minimum-, Maximum-, Median- und Quartilswerte.

ratio (egg-bearing females / males) during most of the rainy season (table 1); 36 out of 53 trapped females (=69%) bore mature eggs. Among the large juveniles (n = 20), the sex ratio was balanced (10/10). Secondary sexual dimorphism was found in SVL ($F_{19, 53}$ = 123.7, $P < 0.001$), the males averaged 38.0 mm SVL (SD = 1.13, n = 19), and the females 42.4 mm SVL (SD = 1.58, n = 52). Size of the males (Kruskal Wallis F = 2.18; df = 3; $P > 0.10$) and females (Kruskal Wallis F = 6.54; df = 6; $P > 0.10$) did not vary significantly by month while among juveniles the variation was considerable (fig. 3). Those juveniles caught at the beginning (November) of the rainy season 1999/2000 were particularly large; smaller juveniles (SVL < 25 mm) appeared from January to May (2000) and September to December (2000) (fig. 3). Juveniles tended to be more abundant between December and March (figs. 2 and 3).

The number of ovarian eggs per female varied from 27 to 119 (n = 36 females), and varied significantly by month (Kruskal Wallis F = 12.40; df = 5; P = 0.03); the values at the end of the rainy season (February 2000) tended to be smaller than those of mid season (December 1999) (fig. 4). The correlation between mean egg number and monthly rainfall was not significant (Spearman r = -0.14; $P > 0.10$; n = 6). Within months correlation between female size and number of ovarian eggs was not significant ($P > 0.10$); considering all the available females, this correlation was positive and close to significant (Spearman r = 0.22; $P < 0.10$; n = 36). The egg clutches collected in November (2000) contained between 31 and 99 eggs (mean = 56; SD = 16.4; n = 16), not

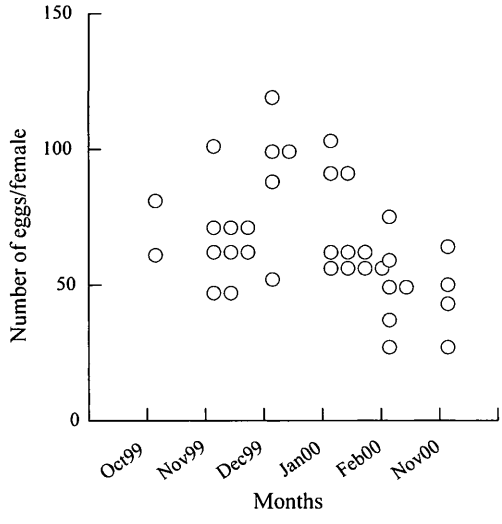

Fig. 4: Number of ovarian eggs in 36 females of *Leptodactylus furnarius*. Specimens trapped in two localities in Uberlândia (Minas Gerais, Brazil) from October 1999 to October 2001. Individuals with a similar number of eggs are displayed side by side.

Abb. 4: Anzahl von Ovarialeiern bei 36 Weibchen von *Leptodactylus furnarius*. Die Tiere wurden an zwei Fundstellen in Uberlândia (Minas Gerais, Brasilien) zwischen Oktober 1999 und Oktober 2001 in Fallen gefangen.

differing significantly from the counts of ovarian eggs (mean = 46; SD = 15.4; $n = 4$) of the females of the same month (Mann-Whitney U = 22.0; $P > 0.10$) (fig. 4). Eggs were laid inside the chamber, amongst a white foam. The yolk was cream colored and measured about 3 mm in diameter; the gelatinous portion was about 3.8 mm. In the lab, the embryos hatched 78 hours after deposition, approximately at GOSNER (1960) stage 19; at 122 hours they had reached stage 24, with pigmented eyes and back, and about 10.5 mm in total length. In nature, the tadpoles reached a total length of 40 mm prior to metamorphosis; when the tail was resorbed, the juveniles measured about 12 mm in SVL. The tadpoles were found in water bodies around calling sites.

In the dry season of 2001 (July), no tadpole was found in places where males were calling. In May 2003 no tadpole was found either, but at the same place 35 days later, some were found. These tadpoles were between 31 and 40 mm in total length and between stage 25 and 36 ($n = 7$).

In the lab, after 50 hours, all groups of tadpoles (stage 25) tested were inside newly produced foam. The new foam was similar in consistence to the original, so that the tadpoles could swim freely within it.

The advertisement call was composed of a series of regular pulses (fig. 5) emitted at a rate of 315 pulses/minute at 24°C. Each pulse lasted about 70 ms; minimum pulse interval was about 100 ms. The lowest and highest frequencies were at about 2,600 and 3,130 Hz, respectively.

Courting pairs were found three times in the field. The main steps were: the male called near (0.5 – 1.5 m) a previously excavated chamber; when the female approached, the male went ahead in the direction of the chamber; on its way the male called constantly; the female frequently touched the rear of the male with her snout; reaching the chamber, the male entered and was followed by the female; after both male and female had entered the chamber, the male immediately turned and blocked the entrance, keeping its head partially outside. The call emitted during courtship (not recorded) sounded softer than the regular advertisement call. Chamber construction was not observed, neither was amplexus.

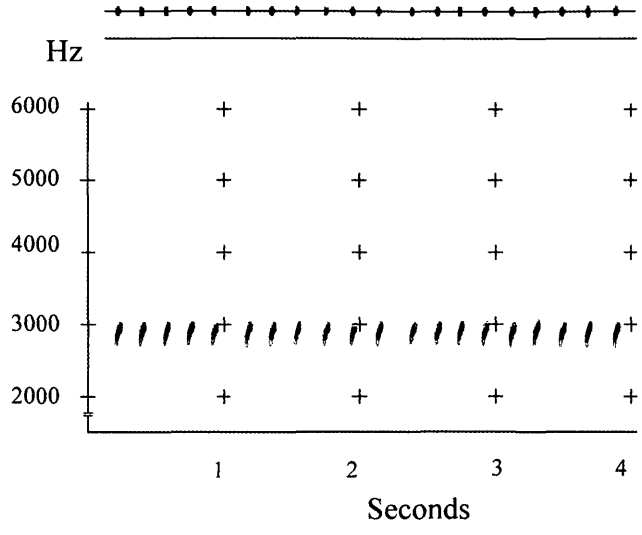

Fig. 5: Oscillogram (above) and audiospectrogram (below) of the advertisement call of *Leptodactylus furnarius*. Uberlândia (Minas Gerais, Brazil; December 3, 1999; air temperature 24 °C; 19:00 h). AAG-021.

Abb. 5: Oszillogramm (oben) und Audiospektrogramm (unten) des Anzeigerufes von *Leptodactylus furnarius*. Uberlândia (Minas Gerais, Brasilien; 03. Dezember 1999; 19.00 Uhr; Lufttemperatur 24 °C). AAG-021.

The subterranean chambers of *L. furnarius* (n = 40) were of simple construction, almost spherical (50 mm diameter) with a direct entrance or with access through a short tunnel (figs. 6a and 6c). The roof of the chamber can be above the ground, nonetheless, it is quite difficult to distinguish from the surrounding soil. The aperture of the chamber can be lateral or close to the top and was never found sealed by mud.

The chambers of *L. fuscus* (n = 20) were of ovoid shape (a regular chicken egg can just be accommodated inside) and had long and well-defined entrance tunnels (figs. 6b and 6d). The main chamber was about 70 mm long, 67 mm wide and 46 mm deep; the entrance tunnel was about 49 mm long. The roof was rarely projected above the ground. The chambers were dug in bare soil or under rocks or pieces of wood and were beside permanent or temporary ponds. The aperture of the chamber was never found sealed by mud.

A juvenile (293 mm total length) snake, *Liophis meridionalis* (SCHENKEL, 1902) (MBC-UFU 1338), was found inside a chamber of *L. furnarius*, in its stomach there were 17 tadpoles (stage 25, total length about 16 mm). An adult (total length = 510 mm) snake *Thamnodynastes strigilis* (THUNBERG, 1787) (not collected) was found preying on an egg-bearing female at a calling site.

DISCUSSION

As indicated by the presence of calling males and the appearance of tadpoles, in the studied region *Leptodactylus furnarius* reproduces all year round. Coherently with a potentially constant recruitment, no pattern regarding the size of juveniles throughout the year was found. In the summer, tadpoles may be transported to the water bodies by rains, but, how they reach the water in the dry season still needs to be determined.

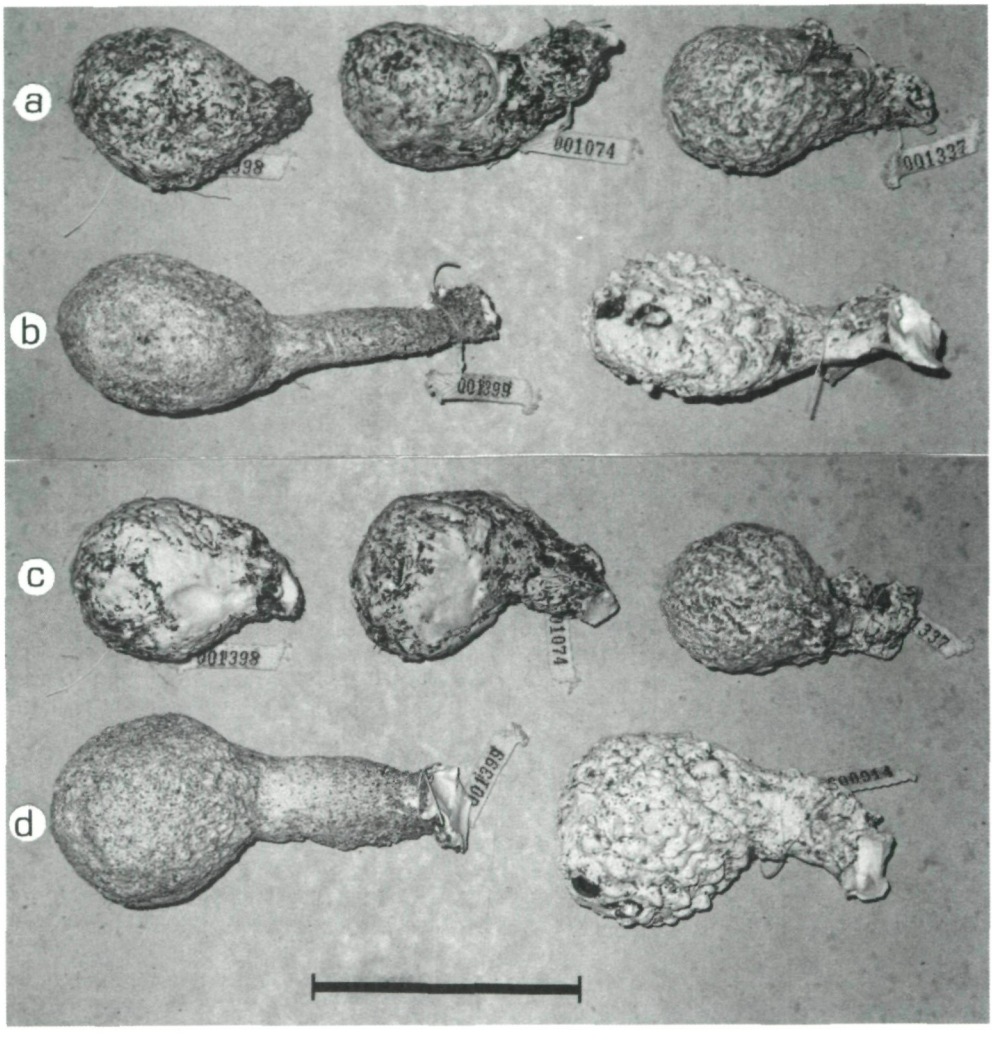

Fig. 6: Gypsum molds of three underground chambers of *Leptodactylus furnarius* (a and c) and two of *Leptodactylus fuscus* (b and d). a and c represent different perspectives of the chambers; b - lateral view; d - view from above. Scale = 80 mm.

Abb. 6: Gipsabgüsse von drei unterirdischen Kammern von *Leptodactylus furnarius* (a, c) und von zwei Kammern von *Leptodactylus fuscus* (b, d). a und c zeigen die Kammern aus unterschiedlichen Blickwinkeln; b - Seitenansicht; d - Ansicht von oben. Maßstab: 80 mm.

The abundance of egg-bearing females in the traps and the longer time of daily calling indicate that most of the reproductive activities of the species occur in the rainy season. As for other frogs (SEEBACKER & ALFORD 1999), the increase in precipitation may allow long range movements by adult *L. furnarius*, but the generation of water bodies and tadpole transportation to water may be of secondary importance to this species, since many of the sites used for reproduction are permanent.

The reproductive pattern of *L. furnarius* is similar to that of the known species of

the *L. fuscus* group, with regard to its habits of building underground chambers to lay eggs (CEI 1949; SOLANO 1987; MARTINS 1988). *Leptodactylus furnarius* is distinguished from *L. fuscus* by having a chamber without a well-defined entrance tunnel, and never building its chamber under pieces of rock or wood (SOLANO 1987; AAG unpublished). Because of its larger size, *L. fuscus* is also able to dig deeper chambers in apparently harder soil. The chamber of *L. bufonius* BOULENGER, 1898 does not have a tunnel either, although it has a well-defined jar-shape (see figs 7 and 8 in CEI 1949 and PISANÓ et al. 1993), is built in bare soil and can be sealed by the female after egg deposition (CEI 1949; CRUMP 1995). As in *L. fuscus* (MARTINS 1988), the male *L. furnarius* blocks the entrance of the chamber with his head after the female enters, possibly waiting for her to ovulate. The time of construction of the chamber appears to be variable among the species of the *L. fuscus* group. *Leptodactylus furnarius* and *L. fuscus* lead the female to a previously excavated chamber, while *L. mystacinus* (BURMEISTER, 1861) excavate the chamber after the arrival of the female (SAZIMA 1975).

In natural populations of dioecious species, the usual sex ratio is one to one (WILLIAMS 1975). The predominance of females here reported for *L. furnarius* is similar to that described for *L. elenae* HEYER, 1978 (MERCOLLI et al. 1995) and, for both, the deviation may represent an artifact of sampling, with behavioral causes. In both species, the females may be more mobile and, thus, more prone to be trapped than the males, which may remain around calling sites. Moreover, female frogs may leave reproductive sites after oviposition because of predators concentrated there (LEMCKERT & SHINE 1993; BERNARDE et al. 2000; this study).

There are few reports of predation upon eggs and tadpoles of species of the *L. fuscus* group while in the chamber; known predators include conspecific adults (SOLANO 1987), insect larvae (MARTINS 1988; DOWNIE et al. 1995), a spider (LANGONE 1994), and snakes (SOLÉ & KWET 2003; present study). In the studied region, maggots of the fly *Beckeriella niger* (Diptera, Ephydridae) infest nests and prey upon eggs/embryos of all leptodactyline frogs that have exposed foam nests; the underground chamber of *L. furnarius* appears to confer protection against *B. niger* maggot predation (MENIN & GIARETTA 2003).

Species of the *L. fuscus* group show a lower egg number when compared to other Leptodactylinae frogs of similar size (CRUMP 1974; AICHINGER 1992). Large eggs represent an increased investment in individual offspring (STEARNS 1999). In *L. furnarius* and probably in other species of the *L. fuscus* group, the large eggs may allow the tadpoles of these frogs to enter the pond at a larger size and have a shorter aquatic larval period. As in other species of the *L. fuscus* group, the free larval period in the water may be shorter than 30 days in *L. furnarius* (SAZIMA 1975; MARTINS 1988; LANGONE 1994).

The quantitative sampling resulted in fewer individuals in the second trapping season (2000). This difference may be due to an area effect, with the EEP (Estação Ecológica do Panga) presenting lower densities of the species or, most probably, because of the lower rainfall during this sampling period.

The call of *L. furnarius* described by SAZIMA & BOKERMANN (1978) is quite similar to that we described here. The high rate of pulse emission they report (420 – 480 pulses/min at 21 °C versus 300 at 24 °C in our sample) may be attributed to individual variation.

In *L. furnarius*, as in other species of the *L. fuscus* group, the foam-generating behavior of the tadpoles may serve for keeping the foam, and thus moisture, for an extended period (DOWNIE 1984). Foaming behavior of the tadpoles may represent a synapomorphy of the species of the *L. fuscus* group. There is some evidence that the *L. fuscus* group is paraphyletic in relation to the genus *Adenomera* (HEYER 1998), a taxon in which the species also lay eggs in underground chambers (DE LA RIVA 1995). At present, we are conducting experiments to look for foaming behavior in *Adenomera* tadpoles. This information could contribute to the understanding of the relationships between *Adenomera* and the *L. fuscus* group.

ACKNOWLEDGEMENTS

We thank our colleagues of the Laboratório de Ecologia e Sistemática de Anuros Neotropicais for help with the fieldwork; the directors of the CP for allowing work on their reservation; J. M. VIELLIARD (UNICAMP, Campinas, BR) for loaning the recording devices; C. WESTERKAMMP (UFU, Uberlândia, BR) for the translations to German. W. R. HEYER (NMNH – Smithsonian Institute, Washington D.C., USA), M. MENIN (UFA-INPA, Manaus, BR) and K. G. FACURE (UNIT, Uberlândia, BR) for suggestions on the manuscript. Fellowships by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo a Pesquisa do Estado de Minas Gerais (FAPEMG) to Marcelo N. de C. KOKUBUM.

REFERENCES

AICHINGER, M. (1992): Fecundity and breeding sites of an anuran community in a seasonal tropical environment.- Studies Neotropical Fauna Environment, Jena / Lisse; 27: 9-18.

ARAÚJO, G. M. & NUNES, J. J. & ROSA, A. G. & RESENDE, E. J. (1997): Estrutura comunitária de vinte áreas de Cerrados residuais no município de Uberlândia, MG.- Daphne, Uberlândia; 7: 7-14.

ARZABE, C. & ALMEIDA, C. C. (1996): Life history notes on *Leptodactylus troglodytes* (Anura, Leptodactylidae) in northeastern Brazil-. Amphibia-Reptilia, Leiden; 18: 211-215.

BERNARDE, P. S. & MOURA-LEITE, J. C. & MACHADO, R. A. & KOKUBUM, M. N. de C. (2000): Diet of the colubrid snake, *Thamnodynastes strigatus* (GÜNTHER, 1858) from Paraná state, Brazil, with field notes on anuran predation.- Rev. Brasileira Biol., Rio de Janeiro; 60: 695-699.

CALDWELL, J. P. & LOPEZ, P. T. (1989): Foam-generating behavior in tadpoles of *Leptodactylus mystaceus*.- Copeia, Lawrence; 1989: 498-502.

CEI, J. M. (1949): Costumbres nupciales y reproduccion de um batracio caracteristico chaqueño (*Leptodactylus bufonius* Boulenger).- Acta Zool. Lilloana, Tucumán; 8: 105-110.

CRUMP, M. L. (1974): Reproductive strategies in a tropical anuran community.- Misc. Publ. Mus. Nat. Hist. Univ., Kansas; 61: 1-68.

CRUMP, M. L. (1995): *Leptodactylus bufonius*. Reproduction.- Herpetol. Rev., Saint Louis; 26: 97-98.

DE LA RIVA, I. (1995): A new reproductive mode for the genus *Adenomera* (Amphibia: Anura: Leptodactylidae): taxonomic implications for certain Bolivian and Paraguayan populations.- Studies Neotropical Fauna Environment, Jena / Lisse; 30: 15-29.

DENT, J. N. (1956): Observation on the life history development of *Leptodactylus albilabris*.- Copeia, Lawrence; 1956: 207-210.

DOWNIE, J. R. (1984): How *Leptodactylus* tadpoles make foam and why.- Copeia, Lawrence; 1984: 778-780.

DOWNIE, J. R. (1989): Observations of the foam-making by *Leptodactylus fuscus* tadpoles.- Herpetol. J., London; 1: 351-355.

DOWNIE, J. R. (1990): Temporal changes in the behavior of foam-making *Leptodactylus fuscus* tadpoles.- Herpetol. J., London; 1: 498-500.

DOWNIE, J. R. (1994): Developmental arrest in *Leptodactylus fuscus* tadpoles (Anura: Leptodactylidae). II: Does a foam-borne factor block development?- Herpetol. J., London; 4: 39-45.

DOWNIE, J. R. & DISNEY, R. H. L. & COLLINS, L. & HANCOCK, E. G. (1995): A new species of *Megaselia* (Diptera, Phoridae) whose larvae prey upon the eggs of *Leptodactylus fuscus* (Anura, Leptodactylidae).- J.Nat. Hist., London; 29: 993-1003.

DUELLMAN W. E. & TRUEB, L. (1986): Biology of Amphibians. New York (McGraw-Hill Inc.), 670 pp.

GOSNER, K. L. (1960): A simplified table for staging anuran embryos and larvae with notes on identification.- Herpetologica, Lawrence; 16: 183-190.

HEYER, W. R. (1969): The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae).- Evolution, Lawrence; 23: 421-428.

HEYER, W. R. (1978): Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae).- Nat. Hist. Mus. Los Angeles Country Sci. Bull., Los Angeles; 29: 1-85.

HEYER, W. R. (1998): The relationships of *Leptodactylus diedrus* (Anura, Leptodactylidae).- Alytes, Paris; 16: 1-24

HÖDL, W. (1986): Foam nest construction in south American Leptodactylid frogs; pp. 566–570. In: ROÈEK, Z. (Ed.): Studies in Herpetology. Proc. European Herpetol. Meeting (3rd OGM SEH), Prague; 566-570.

HORNE, R. S. (1994): Spectrogram. www.monumental.com/rshorne/gram.html.

LAMOTTE, M. & LESCURE, J. (1977): Tendances adaptives a l'affranchissement du milieu aquatique chez les amphibiens anoures.- Terre Vie, Paris; 2: 225-312.

LANGONE, J. A. (1994): Ranas y sapos del Uruguay. Reconocimento y aspectos biológicos.- Museu Damaso Antonio Larrañaga, Serie de Divulgacion, Montevideo; 5: 1-123.

LEMCKERT, F. L. & SHINE, R. (1993): Costs of reproduction in a population of the frog *Crinia signifera* (Anura: Myobatrachidae) from southeastern Australia.- J. Herpetol., Saint Louis; 27: 420-425.

LYNCH, J. D. (1971): Evolutionary relationships, osteology, and zoogeography of Leptodactyloid frogs.- Univ. Kansas Publ. Mus. Nat. Hist., Lawrence; 53: 1-258.

MARTIN, P. & BATESON, P. (1986): Measuring behavior. An introduction guide. Cambridge (Cambridge University Press), 200 pp.

MARTINS, M. (1988): Biologia reprodutiva de *Leptodactylus fuscus* em Boa Vista, Roraima (Amphibia, Anura).- Rev. Brasileira Biol., Rio de Janeiro; 48: 969-977.

MENIN, M. & GIARETTA, A. A. (2003): Predation on foam nests of leptodactyline frogs (Anura, Leptodactylidae) by larvae of *Beckeriella niger* (Diptera, Ephydridae).- J. Zool., London; 26: 1-5.

MERCOLLI, C. & YANOSKY, A. A. & DIXON, J. R. (1995): The ecology of *Leptodactylus elenae* HEYER, 1978 (Anura: Leptodactylidae) in a protected area in a subtropical Argentina.- Bull. Maryland Herpetol. Soc., Baltimore; 31: 130-141.

PHILIBOSIAN, R. & RUIBAL R. & SHOEMAKER V. H. & MACCLANAHAN, L. L. (1974): Nesting behavior and early larval life of the frog *Leptodactylus bufonius*.- Herpetologica, Lawrence; 30: 381-386.

PISANÓ, A. & RENGEL, D. & LAVILLA, E. D. (1993): Le nid souterrain comme chambre nuptiale pour un amphibien d'Argentine.- Rev. Française Aquariol., Nancy; 19 (1992): 125-126.

RYAN, M. J. (1985): The túngara frog: a study in sexual selection and communication. Chicago (Univ. Chicago Press), 230 pp.

SAZIMA, I. (1975): Hábitos reprodutivos e fase larvária de *Leptodactylus mystacinus* e *L. sybilatrix* (Anura, Leptodactylidae), 71 pp. Unpubl. MS. Dis., Univ. Est. Campinas, São Paulo, Brasil.

SAZIMA, I. & BOKERMANN, W. C. (1978): Cinco novas espécies de *Leptodactylus* do centro e sudeste brasileiro (Amphibia, Anura, Laptodactylidae).- Rev. Brasileira Biol., Rio de Janeiro; 38: 899-912.

SEEBACHER, F. & ALFORD, R. A. (1999): Movement and microhabitat use of a terrestrial amphibian (*Bufo marinus*) on a tropical island: Seasonal variation and environmental correlates.- J.Herpetol., Saint Louis; 33: 208-214.

SOLANO, H. (1987): Algunos aspectos de la biologia reproductiva del sapito silbador *Leptodactylus fuscus* (SCHNEIDER) (Amphibia, Leptodactylidae).- Amphibia-Reptilia, Leiden; 8: 111-128.

SOLÉ, M. & KWET, A. (2003): *Liophys jaegeri* – Diet.- Herpetol. Rev., Hays; 34(1): 69.

STEARNS, S. C. (1999): The evolution of life histories. Oxford (Oxford Univ. Press), 249 pp.

WILKINSON, L. (1990): Systat: the system for statistics. Evanston, IL. (Systat Software Inc.), 677 pp.

WILLIAMS, G. C. (1975): Sex and evolution. Princeton (Princeton Univ. Press), 200 pp.

ZAR, J. (1999): Biostatistical analysis. 4th ed. New Jersey (Prentice Hall Inc.), 718 pp.

DATE OF SUBMISSION: October 16th, 2002

Corresponding editor: Heinz Grillitsch

AUTHORS: Ariovaldo A. GIARETTA, Laboratório de Ecologia e Sistemática de Anuros Neotropicais - Instituto de Biologia - Universidade Federal de Uberlândia - CEP 38400-902 - Uberlândia, Minas Gerais, Brasil; < giaretta@nanet.com.br >. Marcelo N. de C. KOKUBUM, Curso de Pós-graduação em Ecologia e Conservação de Recursos Naturais - Instituto de Biologia - Universidade Federal de Uberlândia - CEP 38400-902- Uberlândia, Minas Gerais, Brasil.