Wagner Rodrigues da Silva

HISTÓRIA NATURAL DA RÃ-PIMENTA SUL-AMERICANA, *LEPTODACTYLUS LABYRINTHICUS* (SPIX, 1824) (ANURA: LEPTODACTYLIDAE)

Dissertação apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação de Recursos Naturais.

Orientador

Dr. Ariovaldo A. Giaretta

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APROVADA em 21 de FEVEREIRO de 2005

Kátia Gouveia Facure
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Agradeço especialmente à minha família (meu pai Valdeídes, minha mãe Arlene e minha irmã Elisa) e à minha namorada (Maylla) por me ajudarem na conquista deste título. Agradeço aos meus colegas do Laboratório pela ajuda; às Dras. Kátia G. Facure, Ariana M. S. Siqueira e Cecília Lomônaco de Paula por participarem da banca examinadora; à diretoria do Clube Caça e Pesca por permitir o desenvolvimento dos trabalhos de campo em suas dependências e a CAPES pela bolsa. Agradeço ao meu orientador Dr. Ariovaldo A. Giaretta pelo seu empenho, respeito, dedicação e paciência, o que possibilitou meu progresso profissional e pessoal conseguido nesses anos em que trabalhamos juntos. Hoje, compreendo que a linha de pesquisa de meu orientador é a mais importante, útil e inteligente que um biólogo pode desenvolver na atualidade. Obrigado Ari por você me ensinar uma das coisas mais importante que um biólogo pode fazer.

Muito obrigado a todos!

RESUMO

Silva, W.R. 2005. História natural da rã-pimenta sul-americana, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura: Leptodactylidae). Dissertação de Mestrado em Ecologia e Conservação de Recursos Naturais. UFU. Uberlândia-MG. 19 pp.

No grupo *Leptodactylus pentadactylus*, algumas espécies possuem girinos que se desenvolvem inicialmente no ninho de espuma e completam o desenvolvimento na água, e outras possuem girinos que completam a metamorfose no ninho. Neste estudo, apresentamos detalhes da ecologia reprodutiva de *L. labyrinthicus* em área de Cerrado no sudeste do Brasil. A proporção de girinos e ovos tróficos foi determinada, bem como o crescimento dos girinos no ninho. O conteúdo estomacal de girinos encontrados sob desovas de outros anuros foi analisado. Machos adultos não diferem de fêmeas quanto ao tamanho corporal, mas possuem braços hipertrofiados e espinhos no prepólex e no peito. A reprodução se iniciava com as primeiras chuvas de Agosto/Setembro e se estendia até meados de Janeiro. A atividade de vocalização dos machos e desova ocorriam em corpos de água temporários e permanentes. Os ninhos de espuma foram construídos em bacias escavadas nas margens dos corpos de água. Os machos determinavam o local de construção da bacia; após o amplexo, a fêmea completava a escavação. O amplexo era axilar. Os ovos são cinza claro tendo 2,3 mm de diâmetro. O número médio de ovos de desovas individuais foi de 2101. O número de girinos em ninhos individuais estava entre 0,05% e 11,40% em relação ao total de ovos postos. Os girinos adentravam a água quando chuvas fortes inundavam a bacia e no ninho incorporavam até 12 vezes o peso de um ovo individual. Os girinos ficavam até 25 dias dentro da espuma e, quando na água, predavam ovos coespecíficos e de outras espécies de anuros. Machos se engajavam em interações agressivas tentando se abraçar numa posição ventre-ventre; braços hipertrofiados e espinhos representam armas. Todas as espécies do grupo *L. pentadactylus* devem construir o ninho de espuma dentro de bacias escavadas. As bacias devem proteger ovos e embriões de girinos canibais e devem ter um efeito antidessecação. Ovos de outras espécies de anuros representam um importante item alimentar para os girinos depois do abandono do ninho.

Palavras-chave: *Leptodactylus labyrinthicus*, reprodução, ecologia, ovos tróficos, predação de ovos de anuros, canibalismo, Sudeste do Brasil.

ABSTRACT

Silva, W.R. 2005. On the natural history of the South American pepper frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura: Leptodactylidae). MSc. Thesis. UFU. Uberlândia-MG. 19 pp.

Silva, W.R., Giaretta, A.A. and Facure, K.G. 2005. On the natural history of the South American pepper frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura: Leptodactylidae), *Journal of Natural History* (England), 39 (7): 555-566.

Some species of *Leptodactylus* of the *L. pentadactylus* group lay their eggs outside water but the tadpoles need to reach water to complete the larval phase or complete development in terrestrial nests. Here we present details of the reproduction of *L. labyrinthicus* in SE Brazil. The proportion of tadpoles and trophic eggs in aged egg clutches was determined, as well as the growth of the tadpoles while in the nest. The gut contents of tadpoles that were in egg clutches of frogs were analyzed. Adult males did not differ from females in size and had hypertrophied forearms and an enlarged spine on the thumb. Reproduction was initiated with the first rains of August/September and extended to mid-January. Calling and spawning occurred at permanent or temporary water bodies. The foam nests were built in excavated basins outside of, but close to the water. The male determined the place of the basin construction; after amplexus, the female completed the excavation. The amplexus was axillary. One female spent the day after spawning in the foam. The eggs were pale grey, the yolk averaging 2.3 mm in diameter. The mean number of eggs was 2101 per egg clutch. The number of tadpoles in individual nests varied between 0.05% and 11.40% in relation to the total laid eggs. The tadpoles entered water when rains flooded the basin. The tadpoles incorporated until 12 times the weight of an individual egg while in the nest; no nesting tadpole was beyond stage 25. The longest time we followed tadpoles in a nest was 25 days. Tadpoles were found preying upon eggs of three other frog species and upon conspecific eggs. Males fought by grasping each other in a belly-to-belly position; the powerful arms and the thumb spines represent weapons. All the species of the *L. pentadactylus* group may build their foam nests within excavated basins. The basins may protect the eggs and embryos from cannibalistic tadpoles and may have an anti-desiccation effect. Anuran eggs represent an important food item for tadpoles after they leave the nest.

Key words: *Leptodactylus labyrinthicus*, reproduction, ecology, trophic eggs, anuran egg predation, cannibalism, Southeastern Brazil.

Introdução geral

As 12 espécies formalmente reconhecidas do grupo *Leptodactylus pentadactylus* estão distribuídas na América do Sul e Central (Heyer, 1969, 1979, 1995; Frost, 2002). Informações sobre a ecologia reprodutiva dessas espécies são escassas e dispersas na literatura. *Leptodactylus knudseni* Heyer, 1972 constrói o ninho de espuma em bacias às margens de corpos d'água, porém os girinos completam a metamorfose no ambiente aquático (Hödl, 1990; Hero e Galatti, 1990; Gascon, 1991). Os girinos de *L. fallax* Müller, 1926 (Lescure e Letellier, 1983), *L. stenodema* Jiménez de la Espada, 1875 (Hero, 1990) e algumas populações de *L. pentadactylus* (Laurenti, 1768) (Muedeking e Heyer, 1976) completam a fase larval dentro do ninho de espuma. Os girinos de *L. pentadactylus* (Muedeking e Heyer, 1976), *L. knudseni* (Hero e Galatti, 1990) e *L. rhodomystax* Boulenger, 1884 (Magnusson e Hero, 1991) são conhecidos por serem predadores vorazes de ovos de anuros, mesmo coespecíficos.

Leptodactylus labyrinthicus (rã-pimenta) é amplamente distribuída na América do Sul (Heyer, 1979; Frost, 2002). Esta espécie ocorre em áreas abertas, deposita seus ovos em ninhos de espuma às margens de corpos d'água e possui girinos aquáticos (Cei, 1980; Eterovick e Sazima, 2000; Prado *et al.*, 2002). O girino é conhecido (Heyer, 1979; Cei, 1980; Eterovick e Sazima, 2000), bem como seu comportamento de predar ovos e girinos de outros anuros (Cardoso e Sazima, 1977). O canto de anúncio foi descrito por Haddad *et al.* (1988) e Márquez *et al.* (1995) para populações do Sudeste do Brasil e Bolívia, respectivamente. No presente estudo, apresentamos mais detalhes da ecologia reprodutiva de *L. labyrinthicus*, tais como: estação e local de reprodução; amplexo; comportamento de desova; tamanho ao atingir a fase adulta; dimorfismos sexuais; ovos tróficos e interações agonísticas entre machos.

Introduction

The 12 formally recognized species of the *Leptodactylus pentadactylus* group are distributed in South and Central America (Heyer, 1969, 1979, 1995; Frost, 2002). Information on their reproductive biology and ecology is scarce and dispersed in the literature. *Leptodactylus knudseni* Heyer, 1972 lays its eggs in foam nests outside water, but the tadpoles need to reach water to complete the larval phase (Hödl, 1990; Hero and Galatti, 1990; Gascon, 1991). The tadpoles of *L. fallax* Müller, 1926 (Lescure and Letellier, 1983), *L. stenodema* Jiménez de la Espada, 1875 (Hero, 1990) and of some populations of *L. pentadactylus* (Laurenti, 1768) (Muedeking and Heyer, 1976) complete the larval phase in terrestrial nests. The tadpoles of *L. pentadactylus* (Muedeking and Heyer, 1976), *L. knudseni* (Hero and Galatti, 1990), and *L. rhodomystax* Boulenger, 1884 (Magnusson and Hero, 1991) are known to be voracious predators of anuran eggs, even of conspecifics.

Leptodactylus labyrinthicus (in Brazil called *rã-pimenta*) is widely distributed in South America (Heyer, 1979; Frost, 2002). It is a species that occurs in open areas, lays its eggs in foam nests at pond margins and has aquatic tadpoles (Cei, 1980; Eterovick and Sazima, 2000; Prado *et al.*, 2002). The tadpole has been described (Heyer, 1979; Cei, 1980; Eterovick and Sazima, 2000), as well as its habit of feeding on eggs and tadpoles of other frogs (Cardoso and Sazima, 1977). The advertisement call was described by Haddad *et al.* (1988) and Márquez *et al.* (1995) from populations of southeastern Brazil and Bolivia, respectively. In the present study, further details of the reproductive biology and ecology of *L. labyrinthicus* are presented, such as season and site of reproduction, pairing, egg-laying behavior, size at adulthood, dimorphism in secondary sexual characters, trophic eggs, and male-male aggressive behavior.

Methods

This present study was carried out in the municipality of Uberlândia (18°55'S; 48°17'W; approx. 750 m altitude), State of Minas Gerais, and SE Brazil. The local climate is wet/hot from October to March, and dry/mild from April to September; the annual mean precipitation is around 1,500 mm, varying from 750 to 2,000 mm (Rosa *et al.*, 1991); frosts are sometimes possible during the dry season. The original vegetation was Cerrado (Brazilian Savanna) (Araújo *et al.*, 1997), which can still be found in many countryside places.

Adult sizes and dimorphisms in secondary sexual characters were based on specimens from Uberlândia and nearby municipalities. The minimum size at adulthood was based on the

smallest male caught while calling and on the smallest female bearing oviducal eggs. Differences in mean size (Snout-Vent Length, SVL) between adult males and females were evaluated through Analysis of Variance (ANOVA); sexual differences in the rate of growth of forearms were evaluated through Analysis of Covariance (ANCOVA) (Zar, 1999), using SVL as covariate.

Most of the field observations were made in Uberlândia, mainly at the reservation of the Clube Caça e Pesca (CP) and in the outskirts of the city. Regular observations in the field were made weekly between September and January (2001-03). Data collected irregularly since 1998 were also presented, and include some behavioral information obtained during the dry season. Regular field observations were carried out from the beginning of the calling period (1-2 h before sundown) until midnight. Behavior (such as egg laying, basin digging, and male fights) was followed focally (Martin and Bateson, 1986), from 1-2 m distance. Most behavioral information was gathered in a plot (300 m^2) established around a breeding site in a garden at CP (figure 5 above); this plot was about 150 m from the next nearest breeding site. All the foam nests and the calling sites in the 2002/3 reproductive season occurring in the plot were mapped. The calling sites (points A, E, and I in figure 5) were generally located at the broken ends of buried pipes. The point "E" was a cement box (300 x 300 mm side, 200 mm depth) with a pipe (120 mm diameter; > 1 m length) permanently filled with water; any individual using this site needed to leave the pipe to breath and could be monitored.

As most of the eggs in an egg clutch did not develop into tadpoles, the occurrence of trophic eggs was suspected. The proportions of tadpoles and trophic eggs in older (tadpoles > 10 mm) egg clutches were determined. The growth of the tadpoles while in the foam nest (n = 2) was quantified by comparing the weights of preserved (formal in 5%) samples of five eggs and five tadpoles (> 10 days; ca. 28.5 mm); the samples were dried (60 °C) to constant weight (0.01g).

The gut contents of tadpoles that were collected close to egg clutches of other frog species or that had invaded fresh conspecific foam nests (< 5 days) were analyzed. References to tadpole stages follow Gosner (1960). The time it took for the tadpoles to reach metamorphosis, and their size at that time, was determined by raising five of them in an aquarium (4 l); to these tadpoles were given a foam nest of *Physalaemus cuvieri* Fitzinger, 1826 (Anura, Leptodactylinae) as food every third day. The number of *Beckeriella niger* (Williston, 1897) maggots (Diptera, Ephydridae) infesting older (2-3 days) *L. labyrinthicus* nests was determined. Voucher specimens are deposited at the Coleção de Anuros do Museu

de Biodiversidade do Cerrado (AAG-UFU): *L. labyrinthicus* (AAG-UFU 2287 and 2364); *Beckeriella niger* (AAG-UFU 2462).

Results

In the studied population, the size (SVL) of adult males (mean = 136.5 mm; SD = 17.2; n = 16; range 99.9 - 158.5) did not differ significantly (ANOVA $F_{16,12} = 2.40$; $p = 0.13$) from that of adult females (mean = 127.3; SD = 12.7; n = 12; range 100.9 – 148.0). The variation in size of adults was great (ca. 37 %) in both males (figure 1) and females. The males were sexually dimorphic, showing: 1) hypertrophied forearms; 2) two groups of one to three horny spines on each side of the chest; 3) an enlarged spine at the base of the thumb; 4) presence of tiny horny tubercles forming excrescences in the chin and chest. The presence of the secondary characters was not uniform among adult males; the smallest one (136.5 mm SVL) just showed the spine at the base of the thumb. The males showed greater rates of forearm growth than females (figure 2).

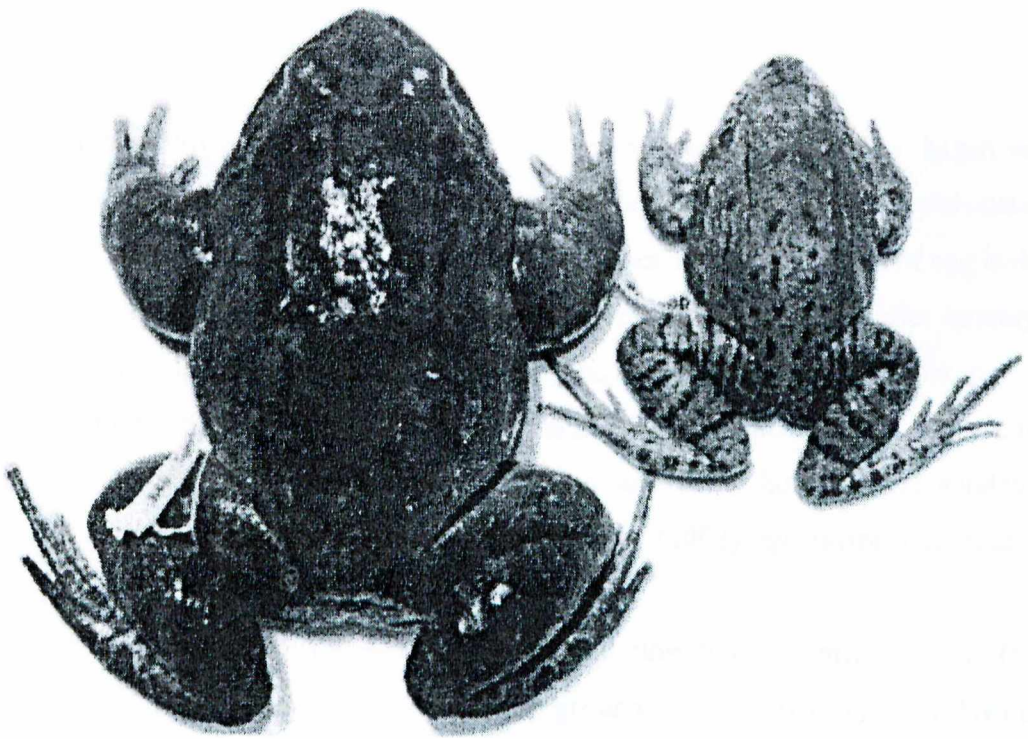

Figure 1. Size at adulthood of *Leptodactylus labyrinthicus*. Largest male, 158.5 mm SVL, smallest 99.9 mm SVL. Specimens from Uberlândia, MG, Brazil.

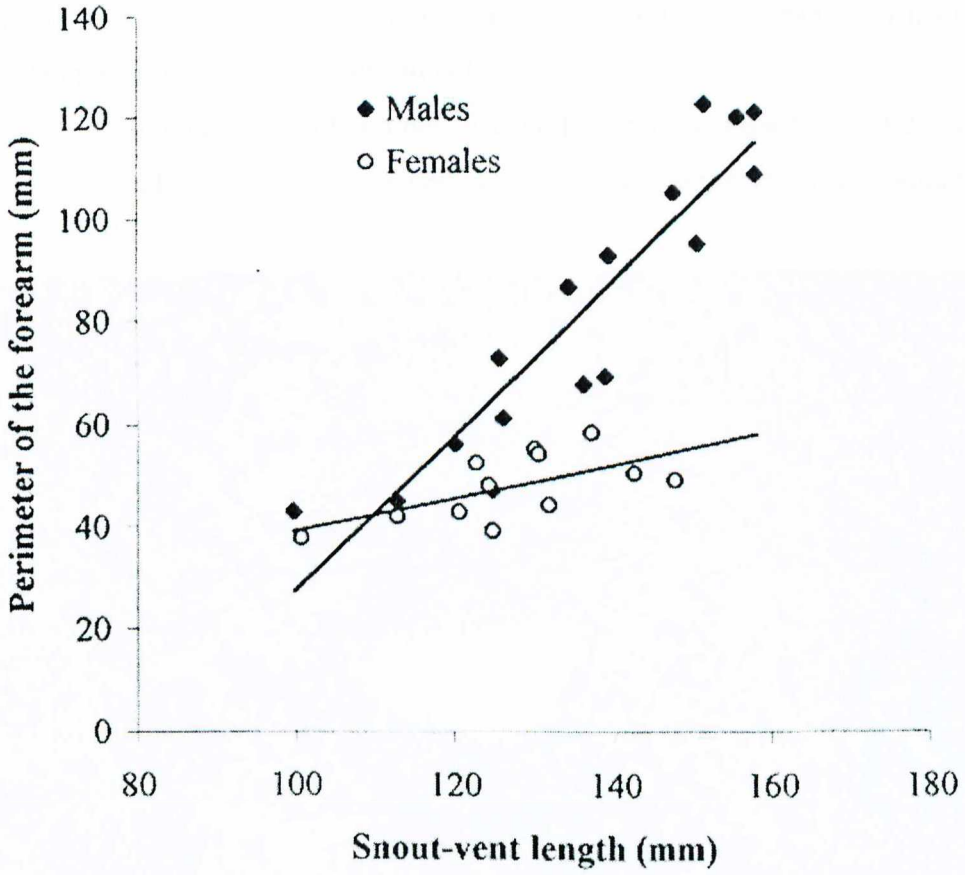

Figure 2. Differential growth of forearms in males and females of *Leptodactylus labyrinthicus*. ANCOVA $F_{16,12} = 20.7$; $p < 0.001$. Specimens from Uberlândia, MG, Brazil.

The reproductive season, as indicated by the presence of egg clutches, began with the first rains of September (2001) or of August (2002); the latest egg laying events occurred in mid-January (2002-3). The calling season (2002-3) was coincident with that of egg laying. In 2003 the rains continued until April, but no reproductive activity was noted after January.

Calling and spawning occurred at the margins of permanent (n = 6 sites; n = 27 egg clutches) or temporary (n = 6 sites; n = 10 egg clutches) water bodies, even in areas in the city outskirts (n = 2 sites; n = 7 egg clutches). Calling started 1-2 hours before sundown (ca. 18:30h) and extended beyond midnight. In September (2002) egg laying occurred during nights as cold as 13 °C.

The foam nests (n = 37) were built outside, but close to (< 15 cm) the water (figure 3 above), in basins that the frogs excavated in the ground (figure 3 below). The basins were excavated among sparse tuffs of low grasses (< 40 cm tall) (n = 20) or were directly exposed

to sunlight (n = 3). Basins constructed on sandy/muddy soil (n = 5) had low rims (ca. 5 mm high), while those built among grasses did not.

In one exceptional case, a foam nest was built under a compact pile of dry grass (140 cm diameter; 25 cm height) over the dry bed of a pond; this foam nest was not within a basin.

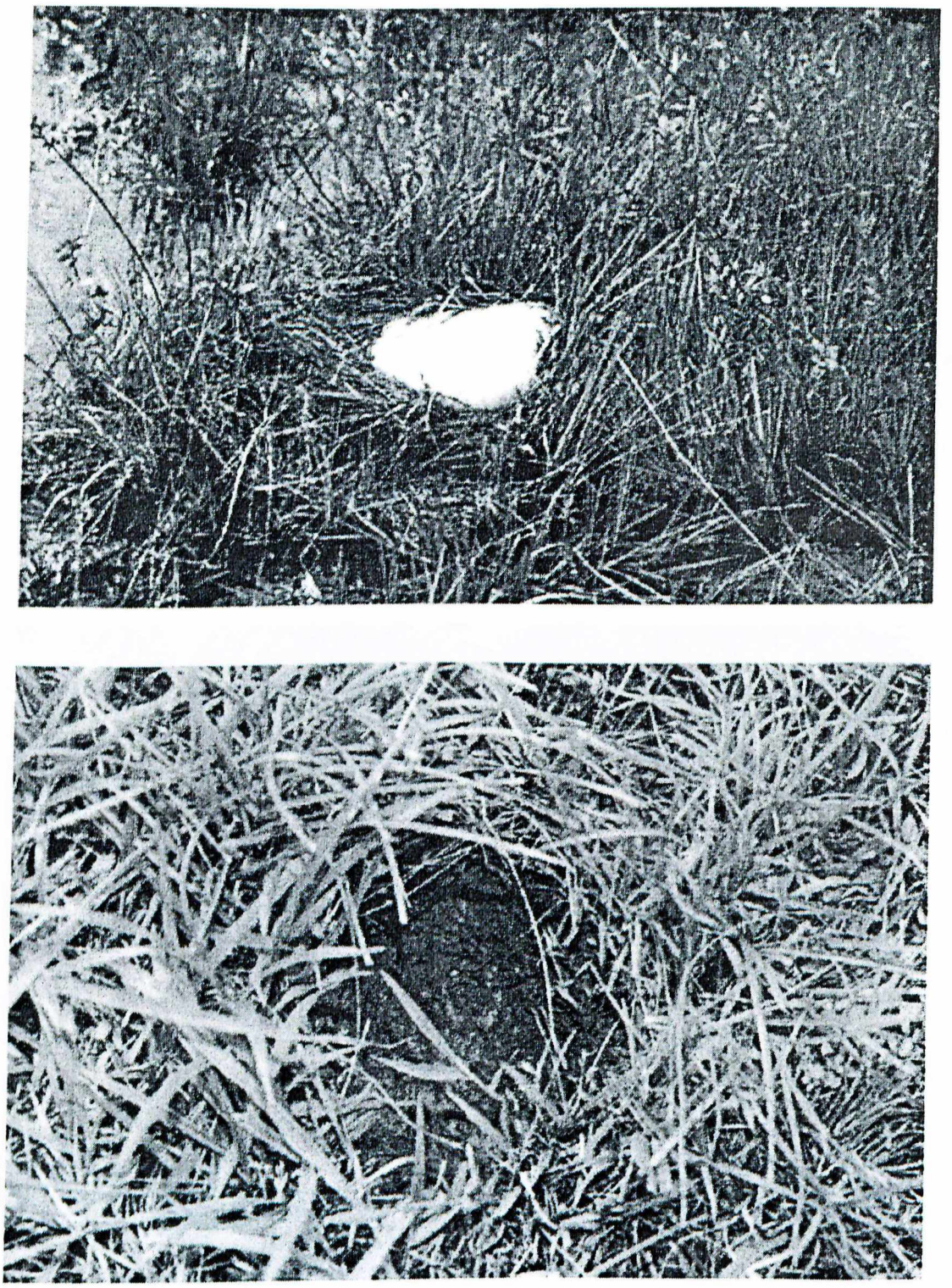

Figure 3. A foam nest (above) and an empty basin (below) of *Leptodactylus labyrinthicus*. Note that the foam nest is not in contact with the main water body. Observations made at Uberlândia, MG, Brazil.

Four partial basin excavation events were observed in the field. A summary of the most important steps is as follows. In the presence of a receptive female, the male indicated the place of basin construction by excavating superficial soil with his hind limbs. After amplexus, the female completed the excavation by pushing away mud with her snout and hands. During excavation, the female constantly turned around, alternating periods of work and rest. The excavation took up to three hours. The male sometimes called from inside an old basin, toward which the female was attracted; after entering the basin the female was amplexed and started reforming the basin.

Amplexus was axillary (n = 3) (figure 4). During foam nest beating, the pair turned around constantly, alternating periods of egg-releasing/foam-beating and rest. At the moment of egg release, the female bent her body by raising her cloacae and the male beat the foam with his legs. The foam-beating movements of males mainly involved the shank, tarsus and foot; in a complete cycle, both legs moved synchronously to the same side (see Heyer and Rand 1977 for a comparison with *L. pentadactylus*). Amplexus and egg laying lasted from eight to 11.5 hours (n = 3). One couple was observed in amplexus at 7:20h (already light); later, at 17:30h, the female was by herself under the foam.

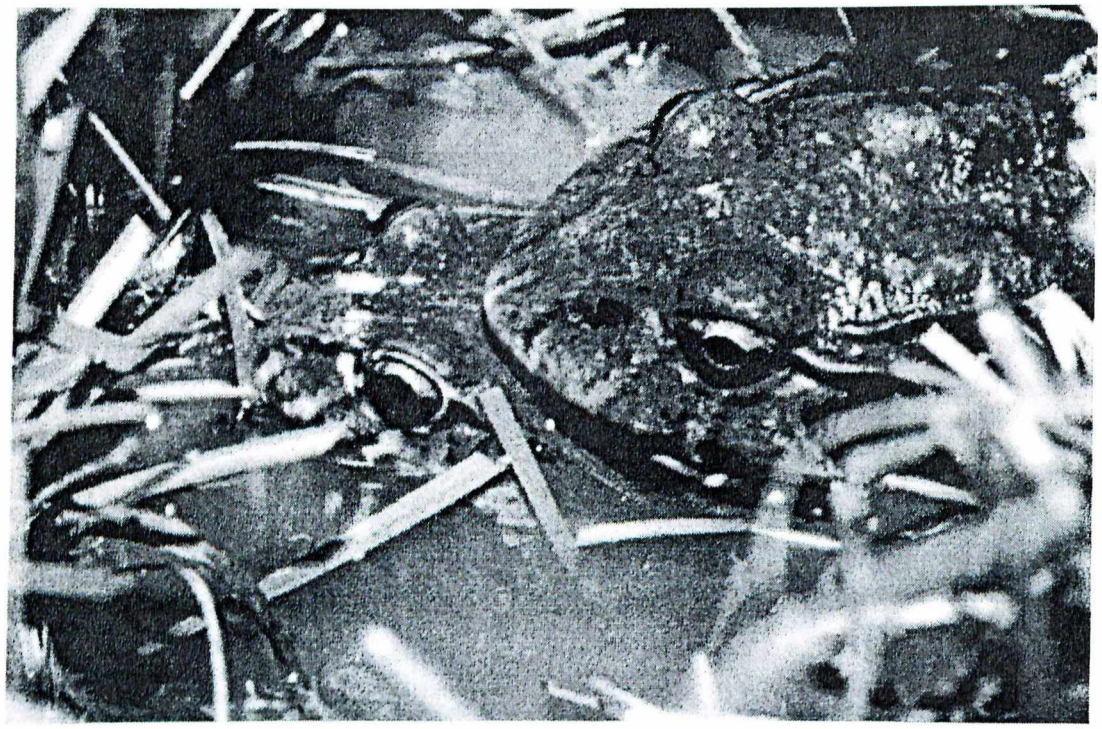

Figure 4. A pair of *Leptodactylus labyrinthicus* in axillary amplexus within a basin, moments before initiating foam beating. Specimens from Uberlândia, MG, Brazil.

Within the plot, the points A, E, and I (figure 5) were the most frequently (90 nights) used calling sites; these sites were close (ca. 30 cm) to shelters into which the males spent the day or fled to when disturbed. Site E was occupied during the whole of 2002-3 reproductive seasons, and was the closest to the point where most of the egg clutches were laid (figure 5). Site E was occupied by at least one individual during all the dry season of 2002; sites A and E were also used in the dry season of 2003.

In the 2002-3 reproductive season, 14 egg clutches were laid inside the plot (figure 5, below). All the 14 foam nests were laid in six basins, so there were eight cases of basin re-utilization.

Adult males were seen entering old (> 1 day) foam nests (n = 3) during the night, where they remained hidden under the foam for periods of more than one hour.

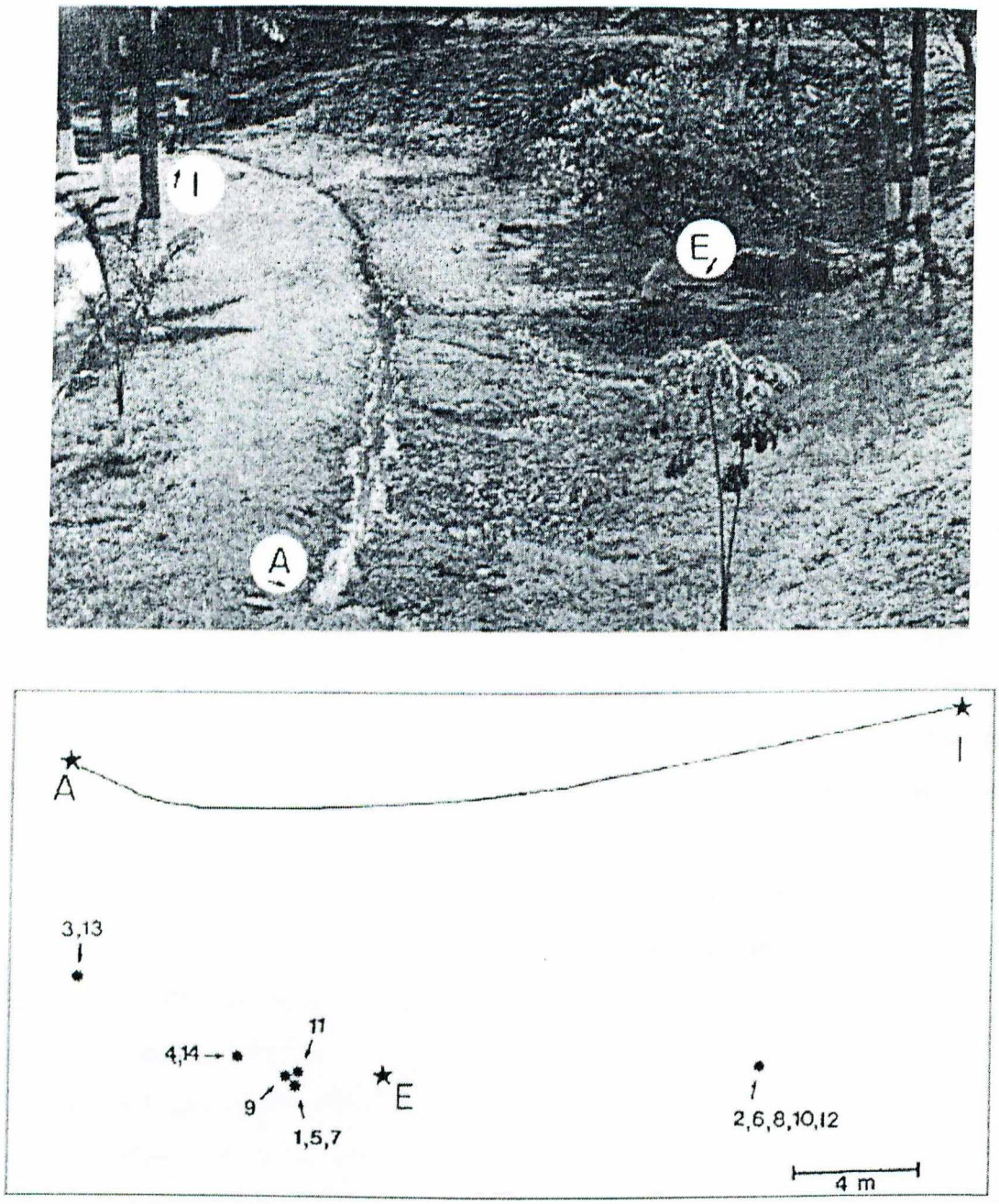

Figure 5. Study plot, representing an area of reproduction of *Leptodactylus labyrinthicus*, in which foam nests and calling sites were mapped in the 2002-3 reproductive season. Above- general aspect of the area. Below- schematic map showing the point of placement of the egg clutches (1-14) and the more frequently used calling sites (A, E, and I). The numbering of the egg clutches follows the chronological order of deposition. Uberlândia, MG, Brazil.

The basins were always within 15 cm from the water (n = 37) (figure 3 below). They were almost circular (n = 12), averaging 239 mm (SD = 54) in their largest diameter (smallest diameter = 155 mm; SD = 24) and 91 mm (SD = 18) deep. Normally, the basins contained

10-30 mm of water in the bottom (n = 20). During prolonged dry periods, the soil in which the basin was built may dry and result in tadpole mortality (n = 2 events).

The eggs were pale grey, the yolk averaging 2.3 mm (SD = 0.16; n = 10 eggs; n = 1 egg clutch) in diameter; the jelly capsules were hard to define, but were around 2.8 mm (SD = 0.24; n = 10). The eggs were embedded in dense white foam. The mean number of eggs was 2101 (SD = 725; n = 7) per egg clutch. The number of tadpoles in individual nests (> 5 days old) varied between one (0.05%) and 377 (11.40%) (n = 7 egg clutches; mean = 6.4%; SD = 3.5) in relation to the total of laid eggs. All seven analyzed foam nests were infested by maggots of *Beckeriella niger*; the number of maggots per foam nest varied between 3 and 210 (mean = 61; SD = 77).

The tadpoles entered water bodies when heavy rains flooded the basins. Twice, tadpole mortality resulted from pond drying. During longer periods (> 7 days) without rains, the foam nests lost volume and acquired a hard crust (n = 6 nests). After light rains, which were insufficient to flood the basin, the foam nests re-acquired a fresh aspect, gained volume and lost the crust (n = 4 nests). Coincident with the renewal of the foam nests, the tadpoles showed great activity on the surface of the foam. While on the surface of the foam, the tadpoles could flee by diving into it when disturbed by an observer (n = 5).

In the field, after entering the water, tadpoles reached 81 mm in total length (TL) (stage 40). In captivity they took 43 days to complete metamorphosis; the newly metamorphosed froglets averaged 21.8 mm (SD = 0.6 mm; n = 3) in length. The maximal observed size the tadpoles reached while in foam nest was 34 mm (TL) (ca. 42% of that at metamorphosis), and at this size they were 12 times the weight of an individual egg (dry mass). No tadpole encountered in a foam nest was beyond stage 25. The longest time we followed tadpoles in a foam nest was 25 days, after that there was heavy rain and the flooding gave them access to a pond.

Some tadpoles after leaving the nest were found feeding on eggs of three other frog species. Seven tadpoles (mean = 30.2 mm TL; SD = 3.6) collected in a recently filled pond (ca. 10 h) had eaten a mean of 49.4 (SD = 34.9; total = 346; 1.3 mm diameter each egg) eggs of *Hyla minuta* Peters, 1872 (Anura, Hylidae) and a mean of 22.6 (SD = 21.5; total = 158; 1.2 mm diameter each egg) eggs of *Physalaemus* cf. *fuscomaculatus* (Anura, Leptodactylidae); each egg was swallowed entire. All tadpoles collected under foam nests (n = 14) of *Physalaemus cuvieri* had preyed upon eggs. In a fresh (< 5 days) conspecific foam nest, the largest tadpole (54.6 mm TL) of nine had cannibalized 28 eggs, each swallowed entire. Once,

three tadpoles (< 62.0 mm) were found eating a dead juvenile (22.0 mm) of *Hyla albopunctata* Spix, 1824 (Anura, Hylidae).

Aggressive behavior between males was observed three times. In the longest (30 min.) observed sequence (initiated at 20:00h) two males fought in the water (ca. 1 x 1 m pond) (figure 6). The most intense part of the aggressive act occurred when the males violently grasped each other in a belly-to-belly position (n = 5). The grasp lasted about 1-2s; afterwards, each male fled by diving or swimming to the pond margin. When 30-40 cm apart, one or other started emitting advertisement calls; this stimulated the other to re-approach and start a new bout. At the moment of a grasp, a scream was frequently given by the combatants (n = 2). The fight finished when one male left the area. The presence of the observer (> 1 m) and artificial illumination may have caused some inhibition of natural behavior. On an other occasion, a large male approached a smaller one that was calling and jumped at it. The smaller male left the site and the aggressor started calling there. From the 16 adult males in our sample, six (37%) had scars on their shoulders, coincident with the position of the thumb spine of the opponent during grasps.

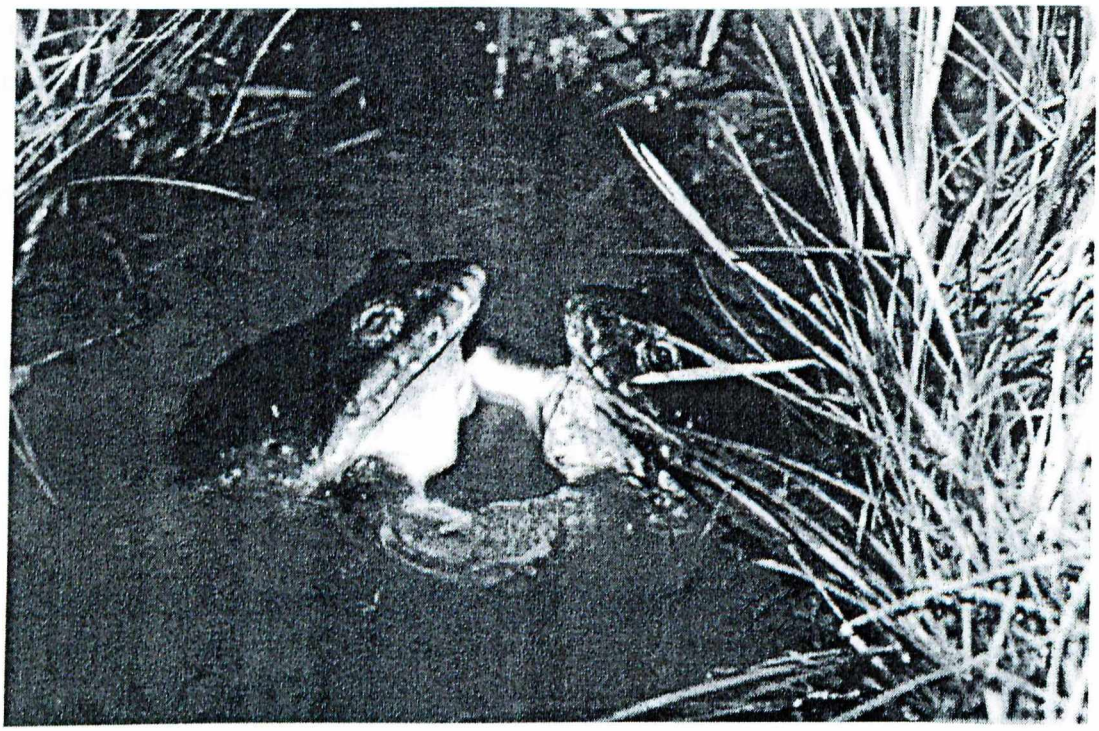

Figure 6. Combat between males of *Leptodactylus labyrinthicus*. These males were in position to grasp each other. Observation in Uberlândia, MG, Brazil.

Discussion

For both sexes, the minimum size at maturity is smaller than that previously reported (Heyer, 1979); on the basis of calling behavior and the presence of mature eggs. Considering the growth curve presented by Agostinho *et al.* (1991), small (ca. 100 mm SVL) adults may be about eight months old; this means that the individuals born in one reproductive season may be able to start reproduction in the next. The estimated time for *L. pentadactylus* to reach maturity in the wild is about two years (Galatti, 1992).

Hypertrophied arms and spines on fingers are found in the *Leptodactylus ocellatus* and *pentadactylus* species group, (*sensu* Heyer, 1969) (Cei, 1980; Heyer *et al.*, 1990; Heyer and Thompson, 2000). Fighting behavior is expected among frog species whose males have weapons such as spines, and which are the same size as, or larger than females (Shine, 1979). Males of *L. ocellatus* (Linnaeus, 1758) (Langone, 1994) and *Leptodactylus sp.* (gr. *pentadactylus*) (Rivero and Esteves, 1969; W. R. Heyer, pers. com.) are known to fight by grasping one another. In *L. labyrinthicus*, the secondary sexual dimorphisms of males, mainly the powerful arms, the thumb and chest spines, represent weapons that may cause injuries to opponents. When in combat position, the thumb spines can produce injuries to the shoulder of the opponent, such as those found in museum specimens. Even though males *L. labyrinthicus* can reach maturity in the season following birth, their small size does not enable them winning combats against larger males and normally this would prevent them from establishing good quality territories.

Like *L. labyrinthicus*, *L. fallax* (Kaiser, 1994; Davis *et al.*, 2000), *L. pentadactylus* (Muedeking and Heyer, 1976; Hödl, 1986; Hero and Galatti, 1990), and *L. knudseni* (Hero and Galatti, 1990; Hödl, 1990; Gascon, 1991) most, if not all species of the *pentadactylus* group may build their foam nests within excavated basins. Rivero and Esteves (1969) also reported that female *Leptodactylus sp.* (gr. *pentadactylus*) excavate the basin. The re-utilization of basins for egg laying by *L. labyrinthicus* may indicate that digging them requires a lot of energy or that suitable places for nest construction are in short supply.

Among frogs, the deposition of eggs in basins outside the water may be primarily related to avoidance of aquatic predators (Martins, 1993; Burger *et al.*, 2002). In *L. labyrinthicus* the basins may protect the eggs/embryos from cannibalistic tadpoles, at least while isolated from the main water body. Among leptodactyline frogs, the foam nests are thought to protect eggs/embryos from predation and/or desiccation. The anti-predatory effects of the foam nests have been demonstrated for *Physalaemus* species, in which the anti-desiccation effect, however, may be of little importance, since they usually complete the foam

phase in 2-3 days (Downie, 1988, 1993; Menin and Giaretta, 2003). For *L. labyrinthicus* however, the anti-desiccation effect of the foam may be more important, since the tadpoles may remain in the foam for up to 25 days before entering the water. The basin may guard against desiccation because the foam is in direct contact with the wet soil and it reduces the contact with the air. The single case we found of the foam nest constructed under debris may represent an alternative way for individuals attempt reproduction, even under sub-optimal water availability.

In our region, the maggots of *Beckeriella niger* infest foam nests of all leptodactyline frogs (Bokermann, 1962; Menin and Giaretta, 2003); the mortality caused to *P. cuvieri* reaches 70%, but the impact caused to *L. labyrinthicus* is unknown. *Beckeriella* spp. also infests foam nests of *L. knudseni* in Amazônia (Gascon, 1991).

The tadpoles of *L. labyrinthicus* (Agostinho, 1994; present study), and probably those of *L. knudseni* (Hero and Galatti, 1990; Rodríguez and Duellman, 1994), grow within the nest expressively by the consumption of trophic eggs, but the greater part of development occurs in water. The tadpoles of certain populations of *L. pentadactylus* (Muedeking and Heyer, 1976; Hero and Galatti, 1990), those of *L. fallax* (Davis *et al.*, 2000) and probably those of *L. stenodema* (Hero, 1990) complete their development within the nest and, also for these species, the consumption of trophic eggs is expected. A way to explain the existence of trophic eggs in *L. labyrinthicus* is that the female may delay laying additional unfertilized eggs until after the male has abandoned the foam nest. Our observation of a female remaining in the foam nest for a full day following egg laying is consistent whit this hypotheses. At present we have no explanation for the behavior of males entering old foam nests.

Anuran eggs (co- or heterospecifc) may still represent an important food item for tadpoles of species such as *L. rhodomystax* (Magnusson and Hero, 1991), *L. knudseni* (Hero and Galatti, 1990), and *L. labyrinthicus* (present study), after they leave the nest. This predatory behavior may represent a strategy to occupy low-productive habitats (Heyer *et al.*, 1975; Petranka and Kennedy, 1999) or to opportunistically use an abundant and nutritive food source.

In the studied region, most of the frog species concentrate their reproductive activities between October and January (Giaretta, unpublished). *Leptodactylus labyrinthicus* starts the reproductive season with the onset of rains (August-September), so that the tadpoles are well developed when the eggs of other frog species become abundant in October and December; the species may also avoid reproducing after mid-February because of the scarcity of egg clutches for the tadpoles to prey upon. The predatory behavior and commonness of tadpoles

of *L. labyrinthicus* may allow future work to establish the role they play in the determination of the richness and abundance of frogs in the communities they live with, as demonstrated for predatory fishes and tadpoles in Amazonian environments (Heyer, *et al.*, 1975; Magnusson and Hero, 1991; Azevedo -Ramos *et al.*, 1999; Hero *et al.*, 2001).

Functionally, the reproductive pattern of the species of the *pentadactylus* group resembles that of *Leptodactylus fuscus*, as the tadpoles of both grow in a terrestrial nest (Martins, 1988) and, after entering the water, prey upon eggs of other frog species (Downie, 1988, Giaretta, in prep.).

Conclusões

Os tamanhos mínimos de *Leptodactylus labyrinthicus* na fase adulta, determinados com base em dados comportamentais, são menores que os descritos com base em espécimes de coleções.

As brigas entre machos de *L. labyrinthicus* reforçam a hipótese de que, entre os anuros, a agressão entre machos deve ser comum em espécies de grande porte, cujos machos apresentam tamanho igual ou superior ao das fêmeas e com ornamentações do tipo espinho.

Igualmente a *L. knudseni, L. labyrinthicus* constrói o ninho de espuma em bacias às margens de corpos d'água.

O efeito de antidessecação da espuma deve ser particularmente importante em *L. labyrinthicus*, pois os girinos podem permanecer até 25 dias no interior do ninho e a bacia reduz a superfície de contado da espuma com o ar.

Na região de estudo, as larvas de *Beckeriella niger* (Diptera) são predadoras de ovos de *L. labyrinthicus*.

Como observado em *L. labyrinthicus*, ovos tróficos e girinos predadores de ovos de anuros devem ser características comuns entre as espécies do grupo *L. pentadactylus*, p. ex. em *L. pentadactylus, L. knudseni* e *L. fallax*.

Em termos funcionais, o padrão reprodutivo de *L. labyrinthicus* é semelhante ao de *Leptodactylus fuscus*, pois os girinos de ambas as espécies possuem desenvolvimento inicial fora d'água e, quando carriados para ela, predam ovos e girinos de outros anuros.

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