On the natural history of the South American pepper frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura: Leptodactylidae)

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Abstract

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; other species complete development in terrestrial nests. Here we present details of the reproduction of *L. labyrinthicus* in south-eastern 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 analysed. 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 grew to 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. Even though males can reach maturity in the season following birth, small size would prevent them from establishing their own territory. 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. In order to produce trophic eggs, the female may delay laying additional unfertilized eggs until after the male has abandoned the foam nest. Anuran eggs represent an important food item for tadpoles after they leave the nest. 

Keywords: *Leptodactylus labyrinthicus*, reproduction, ecology, trophic eggs, anuran egg predation, cannibalism, south-eastern Brazil
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 (Hero and Galatti 1990; Hödl 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) (Muecking and Heyer 1976) complete the larval phase in terrestrial nests. The tadpoles of *L. pentadactylus* (Muecking 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 *rá-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 south-eastern Brazil and Bolivia, respectively. In the present study, further details are presented of the reproductive biology and ecology of *L. labyrinthicus*, such as season and site of reproduction, pairing, egg-laying behaviour, size at adulthood, dimorphism in secondary sexual characters, trophic eggs and male–male aggressive behaviour.

Methods

This present study was carried out in the municipality of Uberlândia (18°55′S, 48°17′W; approximately 750 m altitude), State of Minas Gerais, south-east Brazil. The local climate is wet/hot from October to March and dry/mild from April to September; the annual mean precipitation is around 1500 mm, varying from 750 to 2000 mm (Rosa et al. 1991); frosts are sometimes possible in 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 (2001–2003). Data collected irregularly since 1998 were also presented, and include some behavioural 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. Behaviour (such as egg laying, basin digging and male fights) was followed focally (Martin and Bateson 1986), from 1–2 m distance. Most behavioural information was gathered in a plot (300 m²)
established around a breeding site in a garden at CP (figure 6 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 6) were generally located at the broken ends of buried pipes. The point ‘E’ was a cement box (300 × 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 breathe 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 (formalin 5%) samples of five eggs and five tadpoles (>10 days; ca 28.5 mm); the samples were dried (60°C) to constant weight (0.01 g).

The gut contents of tadpoles that were collected close to egg clutches of other frog species or that had invaded fresh (<5 days) conspecific foam nests were analysed. 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 litres); 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 F16,12=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).

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 h before sundown (ca 18:30 h) 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 tufts of low (<40 cm tall) grasses ($n=20$) 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.

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 3 h. 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 cloaca 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 8–11.5 h ($n=3$). One couple was observed in amplexus at 7:20 h (already light); later, at 17:30 h, the female was by herself under the foam.

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 the 2002–3
reproductive season, 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 1 h.

The basins were always within 15 cm of 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 a 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 analysed 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. Tadpole mortality resulted from pond drying twice. 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

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.
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. When 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 a 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. Once, we found nine tadpoles (>45 mm) in a fresh (<5 days) conspecific foam nest; the largest one (54.6 mm TL) 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 behaviour between males was observed three times. In the longest (30 min) observed sequence (initiated at 20:00 h) two males fought in the water (ca 1 × 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 1–2 s; 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 \((>1 \text{ m})\) and artificial illumination may have caused some inhibition of natural

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.
behaviour. On another 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.

**Discussion**

For both sexes, the minimum size at maturity is smaller than that previously reported (Heyer 1979), on the basis of calling behaviour 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 8 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 2 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 behaviour 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, personal communication) 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 male *L. labyrinthicus* can reach maturity in the season following...
birth, their small size does not enable them to win 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 reutilization 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 to attempt reproduction, even under suboptimal 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 infest 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; Rodriguez and Duellman 1994), grow within the nest expressly 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 with this hypothesis. At present we have no explanation for the behaviour of males entering old foam nests.

Anuran eggs (co- or heterospecific) 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 behaviour 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 to 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 behaviour 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 preparation).

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