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Description of a New Reproductive Mode in *Leptodactylus* (Anura, Leptodactylidae), with a Review of the Reproductive Specialization toward Terrestriality in the Genus

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The genus *Leptodactylus* provides an example among anurans in which there is an evident tendency toward terrestrial reproduction. Herein we describe a new reproductive mode for the frog *Leptodactylus podicipinus*, a member of the "*melanonotus*" group. This new reproductive mode represents one of the intermediate steps from the most aquatic to the most terrestrial modes reported in the genus. Three reproductive modes were previously recognized for the genus *Leptodactylus*. However, based on our data, and on several studies on *Leptodactylus* species that have been published since the last reviews, we propose a new classification, with the addition of two modes for the genus.

THE concept of reproductive mode in amphibians was defined by Salthe (1969) and Salthe and Duellman (1973) as being a combination of traits that includes oviposition site, ovum and clutch characteristics, rate and duration of development, stage and size of hatchling, and type of parental care, if any. For anurans, Duellman (1985) and Duellman and Trueb (1986) recognized 29 modes of reproduction, although in recent studies on ecology and natural history new reproductive modes have been described (e.g., Haddad and Hödl, 1997; Haddad and Pombal Jr., 1998; Haddad and Sawaya, 2000). Amphibians exhibit a great diversity of reproductive modes, especially in the New World tropics, including a clear trend toward terrestriality (Duellman, 1985), that is, reproduction becoming gradually independent of water bodies.

Members of the family Leptodactylidae exhibit several reproductive modes ranging from aquatic to terrestrial breeding, with many intermediate forms depositing eggs embedded in foam nests (Heyer, 1969). Species of *Leptodactylus* and of the related genus *Adenomera* are an example in which a tendency toward terrestriality is evident (Heyer, 1969; Duellman, 1985). Heyer (1969) proposed that *Leptodactylus* species belonging to the "*ocellatus*" and "*melanonotus*" groups have the most primitive reproductive modes. Species of both groups deposit eggs in foam nests on top of the water and tadpoles are exotrophic, feeding and developing in water. According to Heyer's (1969) review, species in the "*pentadactylus*" group show the first step to a more terrestrial life (Heyer, 1969), with foam nests deposited in depressions or burrows at the edges or close to water and producing exotrophic tadpoles. More specialized modes are demonstrated by species of the "*fuscus*" and "*marmoratus*" groups. Heyer (1974) placed the "*marmoratus*" species group in the genus *Adenomera*. Species in the "*fuscus*" group have foam nests that are placed on land in subterranean chambers constructed by males; exotrophic larvae in advanced stages are released through floods or rain into lentic or lotic water bodies. Frogs in the genus *Adenomera* also deposit foam nests in subterranean chambers, and in most species, tadpoles develop inside these chambers and are endotrophic, that is, entire developmental energy is obtained from vitellogenic yolk (Heyer, 1969). More recently, De la Riva (1995) described another reproductive mode for the genus *Adenomera*, which corresponds to the same reproductive mode of the *L. fuscus* group.

In the present paper, we report a new reproductive mode in a leptodactylid frog, *Leptodactylus podicipinus*, a member of the "*melanonotus*" group, in the Pantanal, southwestern Brazil. Based in this new reproductive mode, and on data published after Heyer's (1969) review, we update the reproductive modes exhibited by the species of *Leptodactylus* and propose a new classification of modes for the genus.

MATERIALS AND METHODS

The study was conducted in the southern Pantanal, municipality of Corumbá, State of Mato Grosso do Sul, southwestern Brazil (19°34′S, 57°00′W). The Pantanal is a floodplain, with an area of approximately 140,000 km^2 and an elevation between 75 and 200 m above sea level, delimited mostly by the Paraguay river in the west and Brazilian uplands in the east (see Por, 1995). The region is characterized by a seasonal climate ("Aw" type in Köppen's classification), with a rainy summer from October to April and

a dry winter from May to September. Annual floods occur in the Pantanal, and at the study site, along the Miranda river, floodings are common from January to April. The "cerrado" (savanna-like vegetation) predominates in the area, with patches of semideciduous forests, gallery forests, and grassland fields.

Observations on *Leptodactylus podicipinus* were made at ponds and flooded areas near the Base de Estudos do Pantanal/Universidade Federal de Mato Grosso do Sul (57°00′W, 19°34′S). Data reported here were collected between January 1998 and March 1999, and from January to April 2001. Diameter and depth of the depressions where males called were measured with a measuring tape to the nearest 0.1 cm. Calling males were captured and toe clipped according to Waichman (1992) between 23 March and 08 April 2001. Snout–vent length (SVL) was measured in the field to the nearest 0.1 mm with a caliper. Then, individuals were released at their capture point. Calling sites were also marked. Clutches were collected and immediately preserved in 10% formalin; number of eggs per clutch was determined and egg diameter measured with an ocular micrometer in a Zeiss stereomicroscope (± 0.1 mm). The terminology used to describe larval nourishment follows Thibaudeau and Altig (1999).

Results

Basin description.—Basins of *L. podicipinus* were observed at the edges of permanent ponds and flooded areas, among grass clumps or aquatic plants. Each depression was approximately circular, with a mean diameter of 61.0 mm ± 4.5 SD (range = 50–70, n = 16). Water inside the depressions, which permeated from the adjacent water bodies, averaged 31.0 mm ± 4.5 SD of depth (range = 24–40, n = 16). In general, males called from the interior of the basins with their bodies partially submerged (Fig. 1). Calling males were difficult to see because basins were well covered by the marginal vegetation, fallen leaves or dead vegetation, which functioned as a roof. In 24 basins that we observed, all were covered by vegetation and males called beside the basin in two cases; the remaining 22 males were inside the depressions. Mean distance to the nearest occupied basin was 2.5 m ± 2.1 SD (range = 0.6–8.4, n = 12). As water level decreased, new nests were constructed following the water line at the edges of the water bodies, and the older ones were abandoned.

Behavior of males.—Nine vocalizing males that were inside their basins were marked and measured. Five marked males were recaptured from one to three times on successive nights during a 15-day study period. Mean SVL of recaptured males (33.8 mm ± 0.8 SD, range = 32.7–34.5, n = 5) was larger (t = 4.41, P = 0.001) than those that were not recaptured (31.0 mm ± 1.0 SD, range = 30.0–32.4, n = 4). Two males were recaptured three times at the same sites, al-

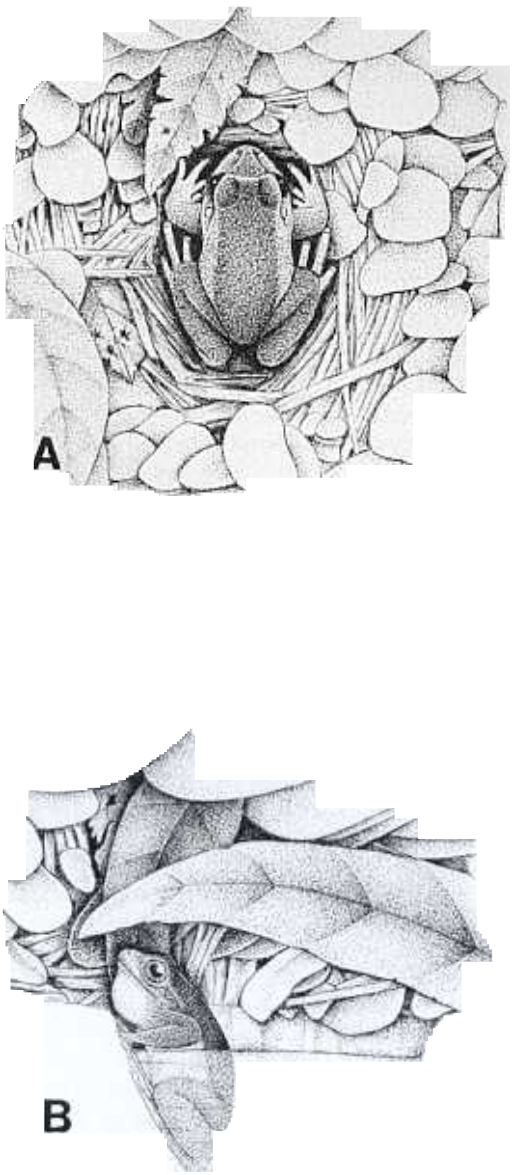

Fig. 1. (A) Dorsal and (B) lateral views of a male of *Leptodactylus podicipinus* calling inside an excavated basin (Corumbá, Mato Grosso do Sul, South Pantanal, Brazil). (B) Note that leaves function as a roof for the basin. Drawn from photographs.

though they had moved to new basins near the original ones as the water level decreased. Two other males were recaptured; one of them, marked on 29 March 2001, was recaptured six days later calling in a new basin 4.5 m from the original site, and the second male was recaptured six days later approximately 10 m from the original site. One male was recaptured twice inside the same basin. Three other males captured calling inside their depressions were marked at night in March 1999. These males were recaptured resting inside the depressions the next morning.

Clutches and female parental care.—Foam nests of *L. podicipinus* were observed inside basins in January 1998, September 1998, and January 1999. The eggs were pigmented, with a mean diameter of 1.1 mm ± 0.05 SD (range = 1.0–1.2, n = 21 eggs from two clutches), and mean number of eggs per clutch was 2102.5 ± 442.1 SD (range = 1750–2953, n = 6 clutches). The foam nests were covered by dead vegetation and mean water depth inside the basins was 26.3 mm ± 3.2 SD (range = 24–30, n = 3). Oviposition was observed once inside a basin covered by aquatic vegetation in April 2001.

Females of *L. podicipinus* attending tadpoles were observed (n = 14), generally, in the margin of ponds or flooded areas, where water depth was about 5 cm. Females remained close to the tadpole schools. When tadpoles were disturbed, almost all females were aggressive, especially those with hatchlings, jumping and knocking with their heads against observers' hands. They also performed pumping movements (sensu Wells and Bard, 1988), after which they usually dived and emerged at short distances, being followed by the tadpoles. Females were observed attending tadpoles at different developmental stages. For six foam nests examined, we did not observe females attending the eggs, although we suggest that they do because females attended tadpoles.

Discussion

Reproductive mode in Leptodactylus podicipinus.—*Leptodactylus podicipinus* occurs in open formations of Paraguay, Argentina, and Bolivia, and the Amazon basin, central Brazil through the southeast and south of that country (Heyer, 1994). The reproductive biology of this species, like that of many tropical species, is poorly known (Vizotto, 1967; Rossa-Feres and Jim, 1994). Recent studies report the existence of female parental care of eggs and tadpoles (Prado et al., 2000; Martins, 2001), but the exact description of calling and oviposition sites are lacking. An exception is a study conducted by Martins (1996) in which he reported the occurrence of males of *L. podicipinus* calling from basins at the edges of water bodies in the State of São Paulo, Brazil. We observed the same situation for this species in the Pantanal.

We did not observe the construction of the basins, but Martins (1996) observed males constructing basins with their snouts and suggested that males could use either natural or constructed depressions. Female parental care of tadpoles was observed at our study site, but we failed to observe females attending eggs. Nevertheless, Martins (1996, 2001) observed females attending eggs and tadpoles. Based on this information, our observations on the behavior of males, and the uniform dimensions of the depressions we have measured, we consider that *L. podicipinus* exhibits a new reproductive mode, which can be summarized as follows: pigmented eggs and early larval stages in foam nests, which are deposited in water-filled basins constructed by the males adjacent to water; exotrophic tadpoles in ponds; females perform parental care, attending eggs and tadpoles.

Among the reproductive modes exhibited by anurans, the generalized mode of aquatic eggs and tadpoles is considered to be primitive (Duellman, 1985). The evolution of specialized modes, with eggs deposited in protected sites or out of water, have been considered to be adaptations against aquatic predators (Magnusson and Hero, 1991; Haddad and Sawaya, 2000). The reproductive mode of *L. podicipinus* could have evolved in response to predation pressure on eggs, embryos, and even adults (e.g., calling males, amplexed pairs during oviposition, and females attending eggs). Although females of *L. podicipinus* attend nests and tadpoles until metamorphosis (Prado et al., 2000; Martins, 2001; present study), the deposition of foam nests inside vegetation-covered basins may provide additional protection for the eggs and embryos. Adult males were observed inside leaf-covered basins during the day. Visual predators, like wading birds, were observed preying upon other anuran species (*Leptodactylus chaquensis* and *Pseudis paradoxa*) during the day at the study site (CPAP, pers. obs.). It seems that the basins could also function as shelter sites for *L. podicipinus* males, avoiding or diminishing predation risk.

Studies on other species of the "*melanonotus*" group show no evidence of basin construction by males (e.g., *L. leptodactyloides*: Heyer and Bellin, 1973, reported as *L. wagneri*; either *L. leptodactyloides* or *L. wagneri*: Duellman, 1978; *L. val-*

idus: Downie, 1996). Nevertheless, Downie (1996) pointed out that clutches of *L. validus* in Trinidad were always found at the edges of small ponds, usually well covered by dead vegetation. It is possible that the reproductive mode described here for *L. podicipinus* occurs in other species of the "*melanonotus*" group, but more detailed studies on their reproductive behavior are necessary.

Female parental care of eggs and tadpoles in species of the "*ocellatus*" and "*melanonotus*" groups (e.g., Wells and Bard, 1988; Prado et al., 2000; Martins, 2001) reinforces Heyer's (1969) proposition that members of both groups are the most closely related of the four *Leptodactylus* groups he identified. However, the reproductive mode of *L. podicipinus*, a member of the "*melanonotus*" group, represents a specialization possibly derived from the primitive mode present in species of the "*ocellatus*" group and some species of the "*melanonotus*" group, representing one step toward terrestrial reproduction in the genus.

Reproductive modes in the genus Leptodactylus.—Heyer (1969) proposed four reproductive stages for the species groups of the genus *Leptodactylus*, including the species of *Adenomera*. Several studies on *Leptodactylus* species have been published since, resulting in new information regarding their reproductive biology (e.g., Rodríguez and Duellman, 1994; Davis et al., 2000; Eterovick and Sazima, 2000). An interesting group concerning reproduction within the genus *Leptodactylus* is the "*pentadactylus*" group, which has at least two reproductive modes. The first mode is the deposition of foam nests in water-filled depressions at the edges of water bodies; subsequent to flooding, exotrophic tadpoles develop in water (e.g., *L. knudseni*: Hero and Galatti, 1990; Rodríguez and Duellman, 1994; *L. labyrinthicus*: Agostinho, 1994; CFBH, pers. obs.). Whether these depressions are natural or constructed remains unclear. The ultimate specialization in the "*pentadactylus*" group is the total terrestrial reproductive mode described for *L. fallax* (Davis et al., 2000). In this species foam nests are placed in burrows in the ground, and tadpoles develop inside the nests, but some details on reproduction and larval development need to be clarified. Also in this species it is not clear whether the cavities used are natural or constructed (Davis et al., 2000). Although Lescure and Letellier (1983) reported that tadpoles of *L. fallax* develop to metamorphosis inside the nest by metabolizing vitelline reserves, Davis et al. (2000) described tadpoles without yolk sacs. If tadpoles develop only on their yolk, this reproductive mode could be considered comparable to the mode described for some species of *Adenomera* (Heyer, 1969; De la Riva, 1995).

Fig. 2. Schematic representation of sequential steps of the reproductive modes in the genus *Leptodactylus*, from the most aquatic to the most terrestrial. (1) Eggs in foam nest on top of water; tadpoles in lentic water, (2) eggs in foam nest in depressions close to water; tadpoles in lentic water, (3) eggs in foam nest in water-filled basins excavated by males; tadpoles in lentic water, (4) eggs in foam nest in subterranean chambers constructed by males; tadpoles in lentic water, (5) eggs in foam nest in burrows; larval development in the foam nest inside the burrows. New steps proposed for the genus *Leptodactylus* since Heyer (1969) are (3) and (5).

Leptodactylus pentadactylus apparently has two reproductive modes: (1) deposition of foam nests in open depressions ("potholes"); subsequent to flooding, exotrophic tadpoles develop in water (Breder, 1946), as in other species of the group mentioned above; (2) a reproductive mode similar to that described for *L. fallax* (Hero and Galatti, 1990; Rodríguez and Duellman, 1994), that is, a foam nest inside burrows in the ground and development of larvae inside the nest. Muedeking and Heyer (1976) observed nests of *L. pentadactylus* in Panama deposited in apparently excavated potholes, and at a distance from water bodies. These authors also registered the coexistence of larvae and eggs in the same nests, and noted that some of the larvae had yolk-colored guts, which was interpreted to indicate ingestion of eggs by the larvae. As suggested by Muedeking and Heyer (1976), possibly the normal pattern for *L. pentadactylus* is the release of tadpoles in water through floods of potholes, as observed by Breder (1946). Nevertheless, in unfavorable conditions of rain, larvae could remain in the nest feeding on eggs up to metamorphosis (Muedeking and Heyer, 1976). The latter situation was observed by Hero and Galatti (1990) in Central Amazonia, although they did not mention how larvae were nourished. It is possible that the alternative modes present in *L. pentadactylus* are partially associated with feeding diversity exhibited by the larvae, which can feed on algae, foam (Vinton, 1951), other tadpoles (Heyer et al., 1975), and eggs (Muedeking and Heyer, 1976). Also, the presence of a foam

TABLE 1. DIVERSITY OF REPRODUCTIVE MODES IN LEPTODACTYLID FROGS OF THE GENUS *Leptodactylus*, FROM THE MOST AQUATIC TO THE MOST TERRESTRIAL. In bold, the new steps proposed since Heyer (1969).

Reproductive mode	Examples
1. Eggs and early larval stages in foam nest on top of the water; exotrophic tadpoles in lentic water.	Species of the *L. ocellatus* (e.g., *L. bolivianus, L. chaquensis, L. ocellatus*) and *L. melanonotus* groups (e.g., *L. leptodactyloides, L. validus*).
2. Eggs and early larval stages in foam nest in water-filled depressions close to water; subsequent to flooding, exotrophic tadpoles in lentic water.	Some species of the *L. pentadactylus* group (e.g., *L. knudseni, L. labyrinthicus, L. pentadactylus*).
3. Eggs and early larval stages in foam nest in water-filled basins constructed by males; exotrophic tadpoles in lentic water.	**One species of the *L. melanonotus* group (*L. podicipinus*).**
4. Eggs and early larval stages in foam nest in subterranean chambers constructed by males; subsequent to flooding, exotrophic tadpoles in lentic or lotic water.	*L. fuscus* group (e.g., *L. cunicularius, L. elenae, L. furnarius, L. fuscus, L. jolyi, L. mystaceus, L. notoaktites*).
5. Eggs in foam nest in burrows, either close or far from water; larval development in the foam nest inside the burrows[a].	**Some species of the *L. pentadactylus* group (e.g., *L. fallax, L. pentadactylus*).**

[a] It remains unclear whether tadpoles of *L. fallax* develop only on their vitelline reserves, or whether they have another nutrition source (see text for references).

nest provides protection from desiccation to tadpoles, as previously mentioned by Heyer (1969). Alternatively, the occurrence of these different reproductive modes could indicate the existence of more than one species (W. R. Heyer, pers. comm.).

Oophagous tadpoles are also known for other species of the "*pentadactylus*" group. Tadpoles of *L. knudseni* feed on conspecific eggs placed later in the same pond (CFBH, pers. obs.). Agostinho (1994) verified that a mean of 90% of eggs present in foam nests of *L. labyrinthicus* were not fertilized and were consumed by the tadpoles, which could survive in the nest for almost 30 days before being carried to water by rain. Female deposition of eggs that are not fertilized, but instead, supply nourishment for tadpoles can occur in other species of the "*pentadactylus*" group and could explain larval nutrition in *L. fallax*.

The reproductive mode of *L. podicipinus* is one of the transitional steps from aquatic to terrestrial breeding within the genus (Fig. 2). In this case, males construct water-filled basins at the edges of ponds, which are covered by leaves or dead vegetation. Exotrophic tadpoles hatch in these nests and develop in water. In Table 1, we summarized the reproductive modes known for the genus *Leptodactylus*. Analysis of all available information reveals that the pathway to terrestrial reproduction in the genus *Leptodactylus* is complex, with many intermediate steps, similar to the one described in our study, remaining to be discovered.

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