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REVIEW PAPER

# Diversity of reproductive modes in anurans communities in the Caatinga (dryland) of northeastern Brazil

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**Abstract** Anuran reproductive activities in xeric environments are strongly influenced by local rainfall and temperatures. Anuran species that inhabit the Caatinga biome in northeastern Brazil demonstrate numerous behavioral and reproductive strategies that avoid or minimize the negative effects of elevated temperatures and scarce water resources on egg development. Among the various anuran species found in the Caatinga region, members of the family Leptodactylidae demonstrate the greatest number of reproductive modes adapted to a terrestrial life style while most of the Hylidae species are more susceptible to variations in water availability. Laying eggs in foam nests is a common strategy among species that inhabit environments with open vegetation forms and water resources that are restricted to only short periods during the year. Data concerning anuran communities in the localities examined here indicated a greater diversity of reproductive modes in ponds with more diverse vegetation structures and longer periods of water availability indicating that the deeper the temporary ponds (permitting a longer hydroperiod) the more diverse will be the aquatic and bordering vegetation, and the richer will be the diversity of anuran species observed and the number of reproductive modes encountered there.

**Keywords** Anuran communities · Reproductive modes · Caatinga (dryland) · Northeastern Brazil

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## Introduction

Anuran reproductive activity in the Neotropical region is strongly influenced by the availability of water and of amenable temperatures. The species there demonstrate behavioral strategies that avoid (or at least minimize) the adverse effects of drought and high temperatures, and their reproductive periods coincide with the rainy season (Bertoluci and Rodrigues 2002).

Amphibian reproductive modes are classified as a combination of traits that includes oviposition sites, ovum and clutch characteristics, the rates and duration of development, stages and size of hatchling, and types of parental care (*sensu* Salthe and Duellman 1973), and a large number of studies in the last few decades have focused on reproductive modes adopted by neotropical anuran species (Crump 1974; Downie 1984; Duellman 1985; Haddad and Hödl 1997; Prado et al. 2002; Giarreta and Facure 2004; Haddad and Prado 2005).

Anurans demonstrate a wide diversity of reproductive modes, with the most generalized ones involving external fertilization and the production of eggs that develop into aquatic larvae (Duellman and Trueb 1994). Recent studies have indicated that these amphibians demonstrate a total of 39 different reproduction modes (Haddad and Prado 2005), with the more specialized species depositing eggs outside the water but generating aquatic tadpoles, or having terrestrial deposited eggs undergoing direct development, or demonstrating ovoviviparity and viviparity (Duellman and Trueb 1994; Stebbins and Cohen 1995; Pough et al. 2004). Many species demonstrate parental care by actively protecting or transporting the eggs or tadpoles (Prado et al. 2000; Haddad and Sawaya 2000).

Species that inhabit environments with open vegetation forms and water resources that are restricted to only short periods during the year generally demonstrate generalized reproductive modes more resistant to the desiccation and insolation imposed by the surrounding environment (Haddad and Hödl 1997; Haddad and Sawaya 2000; Haddad and Prado 2005), and their reproductive success is facilitated by the use of temporary ponds with sufficient volumes of water (Martins 1988) and a greater structural diversity of the surrounding vegetation (Crump 1974; LaClaire 1995; Eterovick and Fernandes 2001).

The reproductive modes of anuran amphibian communities in the Amazonian Forest and Atlantic Forest biomes of Brazil have been fairly intensively studied (see Crump 1974; Duellman 1978; Aichinger 1987; Hero 1990; Hödl 1990; Duellman 1995; Arzabe et al. 1998; Bertoluci and Rodrigues 2002; Pombal and Haddad 2005; Haddad and Prado 2005). On the other hand, investigations of the diversity of reproductive modes of anuran assemblages from the Caatinga region are much scarcer and geographically limited (see Cascon 1987; Arzabe 1999; Viera et al. 2007a). In light of this lacuna, the present work collected available information on the diversity of reproductive modes of anurans that inhabit areas characteristic of the Caatinga biome in northeastern Brazil based on information obtained in four localities within this biome, together with other previously published surveys. Additionally, we present here a discussion concerning the selective pressures that act on the reproductive modes of anurans in the Caatinga and examine how environmental structure influences their diversity in these temporary ponds.

## Materials and methods

The Caatinga biome is composed of a mosaic of different vegetation types, climates and landscapes that are most adequately defined as the “Brazilian Caatinga” (see Sampaio

1995). The Brazilian Caatinga occupy an area of approximately 734,478 km², with average rainfall levels that vary between 200 and 700 mm and average annual temperatures between 25 and 27°C (Ab'Sáber 1977).

Specimens were collected and observations of anuran reproductive modes were performed between 2002 and 2007 in areas of Caatinga vegetation in Paraíba State, northeastern Brazil. Field work was undertaken in areas located within the municipalities of São João do Cariri, Boa Vista, and São José dos Cordeiros as well as in a complementary site in the municipality of São Mamede, Paraíba. The study areas in São João do Cariri were located in the São João do Cariri Experimental Station—EESJC (07°25′ S and 36°30′ W) and Fazenda Olho D'água (07°22′ S and 36°31′ W); field work within the municipality of Boa Vista was focused on a temporary lake known as "Lagoa do Serrote" (07°18′ S and 36°20′ W); work within the municipality of São José dos Cordeiros studies was developed in the Reserva Particular do Patrimônio Nacional Fazenda Almas (7°28′15″ S and 36°52′51″ W); and in the municipality of São Mamede research was carried out in Fazenda Carnaubinha (6°55′37″ S and 37°05′45″ W).

Initial field excursions were undertaken between June and December 2002 to select and inspect observation areas and to determine the best sampling periods. Regular collections were made between January 2003 and February 2007. Capture as well as observations of specimens and their reproductive modes were realized during the day light period from 8:00 to 12:00 and at night between 17:30 and 01:00.

The nocturnal field work and observation of anurans consisted of walking searches around the margins of the ponds. Reference collections of anuran adults and tadpoles were deposited in the Coleção Herpetológica of the Departamento de Sistemática e Ecologia of the Universidade Federal da Paraíba.

Temporary ponds were characterized in terms of the environmental heterogeneity (vegetation structure), their taxonomic composition (species richness), vegetation height (arboreal, shrub or herbaceous), and plant localization in relation to the water (floating plants or plants growing along the pond margins). Hydroperiods were characterized by monthly measurements of pond depth and size (largest width and largest length).

The Spearman correlation coefficient was used to determine if there were significant relationships between the number of reproductive modes, the hydroperiod, and the vegetation structure of the ponds at significance levels of $P < 0.05$ (Zar 1999). Calculations were performed using the Statsoft software.

The classification criteria proposed by Haddad and Prado (2005) were used to characterize the reproductive modes observed in the anuran communities examined. Complementary information concerning reproductive modes previously reported for anuran species occurring in the Caatinga region were based on information contained within studies undertaken by Heyer (1973, 1974), Crump (1974), Aichinger (1987), Cascon (1987), Hödl (1990), Hero (1990), Cardoso and Arzabe (1993), Duellman and Trueb (1994), Rossa-Feres and Jim (1994), Perotti (1994), Zimmerman and Simberloff (1996), Arzabe et al. (1998), Arzabe (1999), Eterovick and Sazima (2000), Prado et al. (2002), Rodrigues (2003), Toledo et al. (2003), Carneiro et al. (2004), Ávila and Ferreira (2004), Gibson and Buley (2004), Prado et al. (2005), Pombal and Haddad (2005), Haddad and Prado (2005), Rossa-Feres and Nomura (2006), Arzabe and Prado (2006) and Viera et al. (2007a, b). The numbers of anuran genera and species found in the Caatinga biome are based on field data, the Coleção Herpetológica of the Departamento de Sistemática e Ecologia/UFPB, on the works of Rodrigues (2003), Frost (2007), and the AmphibiaWeb (2008).

## Results

Nine different reproductive modes were noted among the anuran species occurring in the areas of Caatinga vegetation examined (excluding humid forest enclaves known locally as "brejos de altitude") according to information collected in the study areas and from data available in the literature. Twenty-four species (54.5%) deposited their eggs and tadpoles in lentic water (Mode 1); 8 species (18.2%) deposited their eggs in foam nests floating on the water (Mode 11); 4 species (9.1%) deposited their eggs in foam nest with eggs and early larval stages in subterranean constructed, subsequent to flooting, tadpoles in ponds (Mode 30); 2 species (4.5%) deposited their eggs in foam nests floating on water accumulated in constructed basins (Mode 13) and egg deposition on vegetation (Mode 24); while one species each (2.3%) demonstrated modes 17, 32, 4 and 15. The reproductive modes reported for the various Caatinga anuran species are listed in Table 1.

The family Leptodactylidae demonstrated the greatest diversity of reproductive modes (50%), followed by the family Hylidae with 37.5% of the total number of registered modes (Table 2). The family Leiuperidae demonstrated reproductive modes that are considered "primary", as well as more specialized modes (Table 2). Within this family, species of the genus *Pseudopaludicola* demonstrate Mode 1 (considered the most basal) while species of the genera *Pleurodema* and *Physalaemus* demonstrate Mode 11 (considered the most specialized). *Physalaemus cicada* was observed depositing eggs in foam nests floating on the water surface (n = 30 observations) as well as directly on humid soil near the margins of temporary ponds (n = 8 observations) (Fig. 1). In terms of the Hylidae, species of the genera *Corythomantis*, *Dendropsophus*, *Hypsiboas* (except *Hypsiboas crepitans*, which shows Mode 4 according to Arzabe 1999), *Pseudis*, *Scinax*, *Trachycephalus*, and *Xenohyla* all demonstrated Mode 1, while the species of the genus *Phyllomedusa* demonstrated Mode 24 (Table 1).

The data obtained for the anuran communities examined here indicated greater diversity of reproductive modes in ponds with greater plant structural diversity and a longer hydroperiod, as was reported by Arzabe (1999). The Spearman correlation analyses demonstrated a significant correlation between the number of reproductive modes and the hydroperiod ($r_s = 0.94$; $P = 0.002$; $n = 12$) and the vegetation structure around and within the ponds ($r_s = 0.83$; $P = 0.009$; $n = 8$). This indicates that the longer the hydroperiod of the temporary pond the more diversified will be the structure and species composition of the vegetation both within and around that pond, and the larger will be the diversity of anuran reproductive modes encountered in those environments in areas of Caatinga vegetation.

## Discussion

The anuran fauna examined in the present study of the Caatinga region demonstrated reproductive modes adapted to the unpredictable rainfall patterns of the region and to the hydrological cycles of the temporary ponds found there, including those species that deposit their eggs directly in the water and that are capable of reproducing in times of low rainfall.

The families Hylidae and Leptodactylidae demonstrate a larger diversity of reproductive modes in relation to the other anuran families. This pattern was observed by Haddad and Sawaya (2000) and Haddad and Prado (2005), and is in agreement with observations made in the Neotropical region (*sensu* Duellman 1978). Additionally, some reproductive modes apparently evolved convergently within the families Hylidae and Leiuperidae (Haddad et al. 1990), as reproduction Mode 1 is very common among the Hylidae and is considered

**Table 1** Diversity of the reproductive modes registered for anurans inhabiting the Caatinga biome of northeastern Brazil

| Reproductive modes | References |
|---|---|
| Mode 1—Deposition of eggs and exotrophic tadpoles in lentic water (24 spp.): *Ceratophrys joazeirensis* (Mercadal, 1986)[b], *Rhinella granulosa* (Spix, 1824)[a], *R. jimi* (Stevaux, 2002)[a], *Corythomantis greeningi* (Boulenger, 1896)[a], *Dermatonotus muelleri* (Boettger, 1885)[a], *Elachistocleis piauiensis* (Caramaschi & Jim, 1983)[b], *Hypsiboas raniceps* (Cope, 1862)[a], *Dendropsophus nanus* (Boulenger, 1889), *D. minutus* (Peters, 1872), *D. branneri* (Cochran, 1948), *D. soaresi* (Caramaschi & Jim, 1983), *Odontophrynus carvalhoi* (Savage & Cei, 1965)[b], *Proceratophrys cristiceps* (Muller, 1884 “1883”)[a], *Pseudis bolbodactyla* (A. Lutz, 1925)[b], *Pseudopaludicola falcipes* (Hensel, 1867), *P. mystacalis* (Cope, 1887), *Scinax auratus* (Wied-Neuwied, 1821), *S. eurydice* (Bokermann, 1968), *S. pachycrus* (Miranda-Ribeiro, 1937), *S. ruber* (Laurenti, 1768), *S. x-signatus* (Spix, 1824)[a], *Trachycephalus atlas* (Bokermann, 1966)[a], *T. venulosus* (Laurenti, 1768), *Xenohyla eugenioi* (Caramaschi, 1998) | Crump (1974), Aichinger (1987), Cascon (1987), Hödl (1990), Hero (1990), Duellman and Trueb (1994), Perotti (1994), Zimmerman and Simberloff (1996), Arzabe et al. (1998), Arzabe (1999), Toledo et al. (2003), Carneiro et al. (2004), Ávila and Ferreira (2004), Prado et al. (2005), Pombal and Haddad (2005, Haddad and Prado (2005), Rossa-Feres and Nomura (2006), Viera et al. (2007a). |
| Mode 4—Eggs and early larval stages in natural or artificial basins, subsequent to flooding, exotrophic tadpoles in ponds or streams (1 sp.): *Hypsiboas crepitans* (Wied-Neuwied, 1824) | Arzabe (1999). |
| Mode 11—Foam nests floating on the water in ponds; exotrophic tadpoles (8 spp.): *Leptodactylus macrosternum* (Miranda-Ribeiro, 1926)[a], *L. ocellatus* (Linnaeus, 1758)[a], *Pleurodema diplolister* (Peters, 1870)[a], *Physalaemus albifrons* (Spix, 1824), *P. centralis* (Bokermann, 1962), *P. cicada* (Bokkerman, 1966)[a], *P. cuvieri* (Fitzinger, 1826), *P. kroyeri* (Reinhardt & Lütken, 1862)[a] | Cascon (1987), Hödl (1990), Hero (1990), Cardoso and Arzabe (1993), Arzabe (1999), Prado et al. (2002), Toledo et al. (2003), Pombal and Haddad (2005), Haddad and Prado (2005), Rossa-Feres and Nomura (2006), Viera et al. (2007a). |
| Mode 13—Foam nests floating on water accumulated in constructed basins, exotrophic tadpoles in ponds (2 spp.): *Leptodactylus vastus* (Lutz, 1930), *L. podicipinus* (Cope, 1862) | Hödl (1990), Arzabe (1999), Prado et al. (2002), Ávila and Ferreira (2004), Haddad and Prado (2005), Viera et al. (2007b). |
| Mode 15—Eggs embedded in dorsum of aquatic female and hatch into exotrophic tadpoles (1 sp.): *Pipa carvalhoi* (Miranda-Ribeiro, 1937)[a] | Arzabe (1999), Haddad and Prado (2005), Viera et al. (2007a). |
| Mode 17—Eggs and early tadpoles in excavated nest, subsequent to flooding, exotrophic tadpoles in ponds or streams (1 sp.): *Leptodactylus syphax* (Bokermann, 1969) | Eterovick and Sazima (2000). |
| Mode 24—Egg deposition on vegetation and hatching into exotrophic tadpoles that drop in lentic water (2 spp.): *Phyllomedusa nordestina* (Caramaschi, 2006)[a], *P. bahiana* (Lutz, 1925)[b] | Arzabe (1999), Duellman and Trueb (1994), Haddad and Prado (2005). |
| Mode 30—Foam nests with eggs and early larval stages in subterranean constructed, subsequent to flooting, exotrophic tadpoles in ponds (4 spp.): *Leptodactylus caatingae* (Heyer & Junca, 2003)[a], *L. fuscus* (Schneider, 1799)[a], *L. mystacinus* (Burmeister, 1861), *L. troglodytes* (A. Lutz, 1926)[a] | Hödl (1990), Perotti (1994), Arzabe et al. (1998), Arzabe (1999), Prado et al. (2002), Toledo et al. (2003), Ávila and Ferreira (2004), Haddad and Prado (2005), Arzabe and Prado (2006), Viera et al. (2007a). |
| Mode 32—Foam nests in subterranean constructed chambers, endotrophic tadpoles complete development in the nest (1 sp.): *Leptodactylus* cf. *marmoratus* (Steindachner, 1887) | Heyer (1973, 1974), Gibson and Buley (2004), Haddad and Prado (2005). |

[a] Species whose reproductive modes were observed in the study areas; [b] species for which no detailed information concerning their reproductive biology is available (although their reproductive modes are indicated by genera according to Duellman and Trueb (1994))

**Table 2** Number of genera, species, and reproductive modes of the different Caatinga anuran families

| Families | No. of genera | No. of species | No. of modes (%) | Reproductive modes |
|---|---|---|---|---|
| Bufonidae | 1 | 2 | 1 (12.5) | Mode 1 |
| Ceratophryidae | 1 | 1 | 1 (12.5) | Mode 1 |
| Cycloramphidae | 2 | 2 | 1 (12.5) | Mode 1 |
| Hylidae | 7 | 18 | 3 (37.5) | Modes 1, 4, 24 |
| Leiuperidae | 3 | 8 | 2 (25) | Modes 1, 11 |
| Leptodactylidae | 1 | 10 | 4 (50) | Modes 11, 13, 30, 32 |
| Microhylidae | 2 | 2 | 1 (12.5) | Mode 1 |
| Pipidae | 1 | 1 | 1 (12.5) | Mode 15 |
| Total | 18 | 44 | | 9 |

The numbers of genera and species are based on field data, material housed at the Coleção Herpetológica of the Departamento de Sistemática e Ecologia/UFPB, and on the works of Rodrigues (2003), Frost (2007), and the AmphibiaWeb (2008)

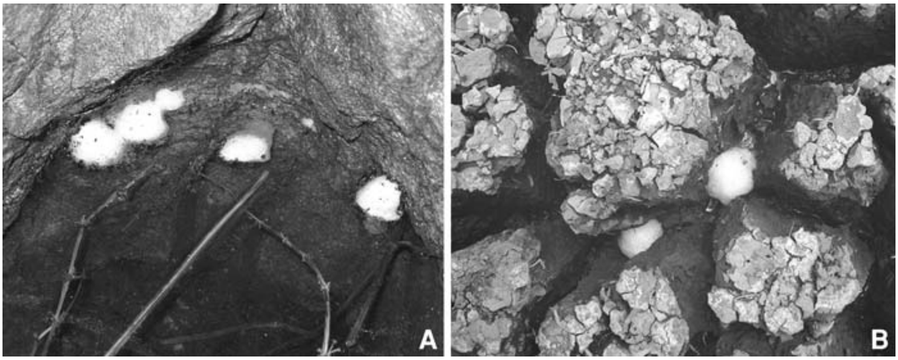

**Fig. 1** (**a**) Foam nest of *Physalaemus cicada* (Leiuperidae) deposited on the water, and (**b**) foam nest on the land near the edge of a temporary pond. Photographs by Washington L. S. Vieira

the most basal and generalized among the amphibians; the other modes (such as deposited eggs in foam nests) represent specializations associated with adaptative radiation into various environments (Duellman and Trueb 1994; Stebbins and Cohen 1995). Among the anuran species of the Caatinga region, the members of the families Leptodactylidae and Leiuperidae demonstrate a larger number of reproductive modes adapted to terrestrial life; a majority of the species of Hylidae as well as species of the families Bufonidae, Microhylidae, Ceratophryidae, and Cycloramphidae are more susceptible to variations in pond water levels and they deposit their eggs in gelatinous masses that are either submerged or floating on the water surface.

Crump (1974) and León (1975) have argued that species demonstrating Mode 1 and that inhabit environments subject to unpredictable rainfall (as was observed for the species of the families Bufonidae, Ceratophryidae, Cycloramphidae, and Microhylidae and some species of Hylidae and Leiuperidae) possess very highly pigmented eggs that presumably absorb more heat, which allows their embryos to develop more rapidly. High concentrations of melanin in these eggs protect them from the deleterious effects of solar radiation (UVB) and the gelatinous mass floating on the water surface allows maximum absorption of oxygen. Additionally, arboreal species belonging to the genus *Phyllomedusa* have eggs that are wrapped in a gelatinous capsule that provides an extra reserve of water for the developing embryos while the leaf blade that covers the egg mass helps protect it from insect attacks or other predators and prevents excessive exposure to sunlight and wind (Crump 1974; Duellman and Trueb 1994; Stebbins and Cohen 1995; De La Riva 1999; Matos et al. 2000).

*Physalaemus cicada* deposited foam nests on humid soil near the margins of temporary ponds and this may represent plasticity in terms of this specie reproductive mode in the Caatinga areas examined, similar to the reports of Haddad and Pombal (1998) for *Physalaemus spiniger*. Their eggs are deposited in foam nests in extremely shallow waters at the edges of the ponds where the low rainfall associated with high solar radiation will sum together and leave the eggs stranded on only humid ground where once there was a temporary pond. According to Wogel et al. (2002) placing foam nests on humid soil can be considered a direct consequence of the instability of the local climate, which can rapidly alter the oviposition sites and transform small pounds into mud.

Overall, the families Leptodactylidae and Leiuperidae show reproductive modes better adapted to dry environments than other anuran families (Heyer 1973; Haddad and Prado 2005). Egg laid in foam nests floating on water surfaces is the most basal characteristic among the members of these families, while deposition in holes or on humid soil represents a more specialized mode (Heyer 1969; Hödl 1990; Prado et al. 2002; Haddad and Prado 2005). The deposition of eggs in foam nests constitutes a common strategy among species that inhabit environments with open vegetation formations and with water availability restricted to short periods during the year (Cardoso and Arzabe 1993). Resistance to desiccation is a preponderant factor in the success of species that live in these xeric environments, particularly if rainfall distribution is erratic during the reproductive season (Heyer 1969; Wilbur 1987; Moreira and Lima 1991). Eggs or larvae that develop within foam nests are more protected from predators and against desiccation (Crump 1974; Muedeking and Heyer 1976; Haddad et al. 1990; Magnusson and Hero 1991; Wogel et al. 2002; Silva et al. 2005) and they are concomitantly exposed to adequate supplies of oxygen and to temperatures that favor the development of the eggs and larvae while still in the isolating environment of that type of nest (Caldwell 1986; Roberts 1989; Petranka et al. 1994; Haddad and Hödl 1997). This reproductive strategy is related to the unpredictability of the rainy season (Haddad and Pombal 1998; Wogel et al. 2002) and to the availability of temporary ponds (Magnusson and Hero 1991), and it represents a behavioral response to the xeric environment conditions that increases the survival rate of both the eggs and the larvae (Heyer 1973).

The foam nest deposition in subterranean constructed nest by the males minimizes desiccation of the eggs and tadpoles. Additionally, the foam produced by the movements of the tadpoles helps maintain the nest for a longer period of time and allows the tadpoles to resist desiccation during periods of low rainfall that can often occur even during the rainy season (Downie 1984; Caldwell and Lopez 1989; Prado et al. 2000) supporting the view that species that deposit eggs in foam nests are favored in environments with unpredictable variations in water levels (Haddad and Pombal 1998; Vasconcelos and Rossa-Feres 2005). Various authors (Heyer 1969; Crump 1974; Downie 1984; Roberts 1989; Magnusson and Hero 1991; Haddad and Sawaya 2000; Prado et al. 2002; Silva et al. 2005) have also suggested that the evolution of different semi-terrestrial and terrestrial reproductive modes arose through selective pressure of aquatic predators on the eggs. Depositing eggs in subterranean constructed nest will avoid most terrestrial predators, maintain a high humidity, and minimize water loss. The results of the long-term observations of the present study support the view that environmental factors such as the unpredictability of the rainfall and the lack of permanent bodies of water have acted as selective pressures on reproductive modes in these anurans and that environmental factors have probably had a more significant role in the evolution of the semi-terrestrial and terrestrial modes than aquatic predators.

The nine reproductive modes observed among the Caatinga anurans represent only 23% of the 39 registered reproductive modes encountered among all of the anuran species known throughout the world. These nine modes represent 29% (n = 31) of the total number registered among Neotropical species, 33.3% (n = 27) of those observed among species of the Atlantic Forest, and 40.9% (n = 22) of those reported for species found in the Amazonian Forest (see Duellman 1986, 1999; Hödl 1990; Zimmerman and Simberloff 1996; Haddad and Prado 2005). The greater diversity of reproductive modes registered among anuran species inhabiting the Atlantic and Amazonian Forests reflects the fact that their greater structural diversity of those environments, the greater number of possible ovipositioning sites of these forest areas, their more favorable climatic conditions, and elevated species richness all contribute to a much wider diversity of reproductive modes than is seen among the Caatinga anuran species.

The Caatinga biome has low environmental heterogeneity in comparison to forest areas, for the semi-arid climate, the unpredictable nature of the rainfall, and the short hydroperiods of the temporary ponds limit the variety of humid microhabitats available to species with specialized reproductive modes.

Correlation analysis indicates that greater varieties of reproductive modes are observed in unstable environments within ponds that have long hydroperiods and a greater species and structural richness of the vegetation around them. Plant diversity also diminishes the chances of the complete desiccation of the pond, the loss of the eggs, and predation of the larvae (Caldwell 1986; Roberts 1989; Mitchell 1991; LaClaire 1995). Viera (2006) suggested that in areas of Caatinga vegetation the temporary ponds with a greater plant structural heterogeneity will demonstrate a greater species richness of anurans, and that structurally similar ponds will have very similar anuran compositions.

Ponds with short hydroperiods tend to show larger numbers of species with explosive reproduction patterns. These species form foam nests and they exhibit high mortality rates among the tadpoles, for the permanence time of the ponds regulates the survival of the larvae as well as reflects the fact that the greater rate and their period of metamorphosis (Semlitsch 1987). As a result, selective pressures will direct species to choose ponds with longer hydroperiods and favor adults that can reproduce in these ephemeral environments (Diaz-Paniagua 1990; Zimmerman and Rodrigues 1990; Duellman 1995; Knutson et al. 1999; Ávila and Ferreira 2004; Toledo and Haddad 2005).

The principal factors that have contributed to local declines in amphibian populations include forest fragmentation, deforestation, and the development of agricultural activities in areas subject to flooding (and that would commonly be used as reproductive sites by anurans) (Gibbs 1998; Lehtinen et al. 1999). The Caatinga region (*sensu* Sampaio 1995) has been highly altered by human activities over the decades and, according to Velloso et al. (2002), intensive farming, cattle raising and deforestation have lead to extensive degradation of the regional soils and increased desertification processes in many areas, while Castelletti et al. (2003) observed that even in light of this alarming panorama there are still no firm estimates of the extent of the Caatinga areas altered by human actions.

Within this context, it is clear that anurans are totally dependent on the availability of water for their reproduction, and that their diverse reproduction modes reflect the characteristics of the environments where these animals live and the phylogenetic relationships among the species (Duellman and Trueb 1994). Although there is no definitive information available concerning anuran population declines in the Caatinga region, alteration of this biome caused by anthropogenic actions may be putting various species in risk, principally those that depend on trees as vocalization sites and for ovipositioning. Arzabe et al. (2005) observed, for example, that the lack of any sightings of *Hypsiboas crepitans* (a medium-sized species that is apparently sensitive to anthropogenic disturbances) in recent inventories under taken in Caatinga regions of the states of Ceará, Paraíba and Pernambuco in northeastern Brazil suggests that populations of this species are diminishing due to environmental impacts.

Vegetation removal from lake margins in order to extend agricultural activities within the Caatinga biome exposes the eggs, tadpoles and froglets to prolonged periods of solar radiation by ultraviolet-B (UVB) that can result in their decline. Studies undertaken by Middleton et al. (2000) in various localities in Central and South America have demonstrated a close relationship between high levels of solar radiation and declines in amphibian populations.

Highway construction and the increasing growth of cities and towns within the Brazilian semi-arid region can act in tandem to destroy ovipositioning sites and to provoke the direct mortality of large numbers of anurans. Santos and Tabarelli (2002) observed a close correlation between the effects of roadways and cities and the fragmentation of the Caatinga vegetation causing impacts that could extend for 12–15 km into adjacent areas. It is very common to observe dead anuran specimens on roadways near towns and cities during the rainy season as these animals migrate towards reproductive sites. Trombulak and Frissel (1999) discussed numerous effects of highways on aquatic and terrestrial environments, including alterations of the physical and chemical properties of the water, the reproductive behavior of the animals, and the dispersal of exotic species. All of these factors can act strongly and directly on eggs and tadpoles over essentially the entire range of anuran species native to the Caatinga region.

In view of this general panorama of intense anthropogenic alteration of the Caatinga biome and its possible effects on anuran populations and their ovipositioning sites, there is a great need for programs to monitor, manage and conserve these species and these efforts must be tied to actions that will preserve the natural vegetation cover. However, these programs will only be efficient if the local human populations are invited to participate in their development and execution; any other situation is condemned to failure. Additionally, there is an enormous need for more information concerning the ecology and reproductive biology of many anuran species that justifies the undertaking of more research into the anuran communities found in the Caatinga biome.

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## References

Ab'Sáber NS (1977) Problemática da desertificação e da savanização no Brasil intertropical. Geomorfologia 53:1–19

Aichinger M (1987) Annual activity patterns of anurans in a seasonal neotropical enviroment. Oecologia 71:583–592. doi:10.1007/BF00379302

AmphibiaWeb (2008) Information on amphibian biology and conservation. http://amphibiaweb.org. Cited 04 Feb 2008

Arzabe C (1999) Reproductive activity patterns of anurans in two different altitudinal sites within the Brazilian Caatinga. Rev Bras Zool 16(3):851–864

Arzabe C, Prado CPA (2006) Distinct architectures of subterranean nests in the genus *Leptodactylus* of the *fuscus* group (Anura, Leptodactylidae). Herpetol Rev 37(1):23–26

Arzabe C, Carvalho CX, Costa MAG (1998) Anurans assemblages in Crasto Forest ponds (Sergipe, State, Brazil): comparative, structure and calling activity patterns. J Herpetol 3:111–113

Arzabe C, Skuk G, Santana GG, Delfim FR, Lima YCC, Abrantes SHF (2005) Herpetofauna da area de Curimataú, Paraíba. In: Araújo FS, Rodal MJN, Barbosa MRV (eds) Análise das variações da biodiversidade do bioma Caatinga: Suporte a estratégias regionais de conservação. Ministério do Meio Ambiente, pp 260–273

Ávila RW, Ferreira VL (2004) Riqueza e densidade de vocalização de anuros (Amphibia) em uma área urbana de Corumbá, Mato Grosso do Sul, Brasil. Rev Bras Zool 21(4):887–892. doi:10.1590/S0101-81752004000400024

Bertoluci J, Rodrigues MT (2002) Utilização de habitats reprodutivos e micro-habitats de vocalização em uma taxocenose de anuros (Amphibia) da Mata Atlântica do sudeste do Brasil. Pap Avulsos Zool 42(11):287–297

Caldwell JP (1986) Selection of egg deposition sites: a seasonal shift in the southern leopard frog, *Rana sphenocephala*. Copeia 1:249–255. doi:10.2307/1444923

Caldwell JP, Lopez PT (1989) Foam generating behavior in tadpoles of *Leptodactylus mystaceus*. Copeia 2:498–502. doi:10.2307/1445453

Cardoso AJ, Arzabe C (1993) Corte e desenvolvimento larvário de *Pleurodema diplolistris* (Anura: Leptodactylidae). Rev Bras Biol 53(4):561–570

Carneiro MCL, Magalhães PS, Junca FA (2004) Descrição do girino e vocalização de *Scinax pachychrus* (Miranda-Ribeiro, 1937) (Amphibia, Anura, Hylidae). Arq Mus Nac 62(3):241–246

Cascon P (1987) Observações sobre Diversidade, Ecologia e Reprodução na Anurofauna de uma Área de Caatinga. Dissertation, Universidade Federal da Paraíba

Castelletti CHM, Santos AMM, Tabarelli M, Silva JMC (2003) Quanto ainda resta da Caatinga? Uma estimativa preliminar. In: Leal IR, Tabarelli M, Silva JMC (eds) Ecologia e conservação da Caatinga. Editora da Universitária da UFPE, pp 719–734

Crump ML (1974) Reproductive strategies in a tropical anuran community. Misc Publ Mus Nat Hist Univ Kans 61:1–68

De La Riva I (1999) A new *Phyllomedusa* from southwesttern Amazonia (Amphibia: Anura). Rev Esp Herpetol 13:123–131

Diaz-Paniagua C (1990) Temporary ponds as breeding sites of amphibians at a locality in southwestern Spain. Herpetol J 1:447–453

Downie JR (1984) How *Leptodactylus fuscus* tadpoles make foam, and why. Copeia 3:778–780

Duellman WE (1978) The ecology of an equatorial herpetofauna in Amazonian Ecuador. University of Kansas Museum of Natural History, Kansas

Duellman WE (1985) Reproductive modes in anuran amphibians: phylogenetic significance of adaptive strategies. S Afr J Sci 81:174–178

Duellman WE (1986) Diversidad y evolucion adaptativa de los hilidos neotropicales (Amphibia: Anura: Hylidae). An Mus Hist Nat Valpar 17:143–150

Duellman WE (1995) Temporal fluctuations in abundances of anuran amphibians in a seasonal Amazonian rainforest. J Herpetol 29(1):13–21. doi:10.2307/1565080

Duellman WE (1999) Distribution patterns of amphibians in South America. In: Duellman WE (ed) Patterns of distribution of amphibians: a global perspective. Johns Hopkins University Press, Baltimore, pp 255–328

Duellman WE, Trueb L (1994) Biology of amphibians. Johns Hopkins University Press, Baltimore

Eterovick PC, Fernandes GW (2001) Why do breeding frogs colonize some puddles more than others? Phyllomedusa 1(1):31–40

Eterovick PC, Sazima I (2000) Description of the tadpole of *Leptodactylus syphax*, with a comparasion of morphological and ecological characters of tadpoles and adults of the species in the *L. pentadactylus* group (Leptodactylidae, Anura). Amphib-reptil 21:341–350. doi:10.1163/156853800507534

Frost DR (2007) Amphibian species of the world. http://research.amnh.org/herpetology/amphibia/index.php. Cited 04 Feb 2008

Giarreta AA, Facure CG (2004) Reproductive ecology and behavior of *Thoropa miliaris* (Spix, 1824) (Anura, Leptodactylidae, Telmatobiine). Biotaneotropica 4(2):1–10

Gibson RC, Buley KR (2004) Maternal care and oblicatory oophagy in *Leptodactylus fallax*: a new reproductive mode in frogs. Copeia 1:128–135. doi:10.1643/CE-02-091R2

Gibbs JP (1998) Distribution of woodland amphibians along a fragmentation gradient. Landsc Ecol 13:163–168

Haddad CFB, Hödl W (1997) New reproductive mode in anurans: bubble nest in *Chiasmocleis leucosticta* (Mycrohylidae). Copeia 3:585–588. doi:10.2307/1447563

Haddad CFB, Pombal JP (1998) Redescription of *Physalaemus spiniger* (Anura: Leptodactylidae) and description of two new reproductive modes. J Herpetol 32(4):557–565. doi:10.2307/1565210

Haddad FB, Sawaya RJ (2000) Reproductive modes of Atlantic Forest Hylid frogs: a general overview and description of a new mode. Biotropica 32(4):862–871. doi:10.1646/0006-3606(2000)032[0862:RMOAFH]2.0.CO;2

Haddad CFB, Prado CPA (2005) Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. Bioscience 55(3):207–217. doi:10.1641/0006-3568(2005)055[0207:RMIFAT]2.0.CO;2

Haddad CFB, Pombal JP, Gordo M (1990) Foam nesting in a hylid frogs (Amphibia, anura). J Herpetol 24(2):225–226. doi:10.2307/1564239

Hero JM (1990) An illustrated key to tadpoles occurring in Central Amazon rainforest, Manaus, Amazonas, Brazil. Amazoniana 11(2):201–262

Heyer WR (1969) The adaptive ecology of the species group of genus *Leptodactylus* (Amphibia, Leptodactylidae). Evolution Int J Org Evolution 23:421–428. doi:10.2307/2406697

Heyer WR (1973) Systematics of the *mamoratus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). Contrib Sci 252(9):1–50

Heyer WR (1974) Relationships of the *marmoratus* species group (Amphibia, Leptodactylidae) within the subfamily Leptodactylinae. Contrib Sci Nat Hist Mus Los Angel Cty 253:1–46

Hödl W (1990) Reproductive diversity in Amazonian lowland frogs. Fortschr Zool 38:41–60

Knutson MG, Sauer JR, Olsen DA, Mossman MJ, Hemesath LM, Lannoo M (1999) Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. Conserv Biol 13(6):1437–1446. doi:10.1046/j.1523-1739.1999.98445.x

LaClaire VL (1995) Vegetation of sekected upland temporary ponds in north and north-central Florida. Mus Nat Hist 38(3):69–96

Lehtinen RM, Galatowitsch SM, Tester JR (1999) Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19(1):1–12

León JR (1975) Desarrollo temprano y notas sobre la historia natural de la larva de *Hyla x-signata* (Amphybia: Hylidae). Caribb J Sci 15(1–2):57–65

Magnusson EE, Hero JM (1991) Predation and evolution of complex oviposition behaviour in Amazon rainforest frogs. Oecologia 86:310–318. doi:10.1007/BF00317595

Martins M (1988) Biologia reprodutiva de *Leptodactylus fuscus* em Boa Vista, Roraima (Amphibia, Anura). Rev Bras Biol 48(4):969–977

Matos RHR, Andrade GV, Hass A (2000) Reproductive biology and territoriality of *Phyllomedusa hypochondrialis* in northeastern Brazil. Herpetol Rev 31(2):84–86

Middleton EM, Herman JR, Celarier EA, Wilkinson JW, Carey C, Rusin RJ (2000) Evaluating ultraviolet radiation exposure with satellite data at sites of amphibian declines in Central and South America. Conserv Biol 15(4):914–929. doi:10.1046/j.1523-1739.2001.015004914.x

Mitchell SL (1991) Intermale spacing and calling site characteristics in a southern Mississippi chorus of *Hyla cinerea.* Copeia 2:521–524. doi:10.2307/1446601

Moreira G, Lima AP (1991) Seasonal patterns of juvenile recruitment and reproduction in four species of leaf litter frogs in Central Amazonia. Herpetologica 47(3):295–300

Muedeking MH, Heyer WR (1976) Descriptions of eggs and reproductive patterns of *Leptodactylus pentadactylus* (Amphibia: Leptodactylidae). Herpetologica 32:137–139

Pough FH, Andrews RM, Cadle JE, Crump ML, Savitzky AH, Wells KD (2004) Herpetology, 3rd edn. Prentice Hall, New Jersey

Perotti MG (1994) Aportes preliminaries sobre la reproducción en una comunidad de anuros chaqueños en Argentina. Cuad Herpetol 8(1):39–50

Petranka JW, Hopey ME, Jennings BT, Baird SD, Boone SJ (1994) Breeding habitat of wood frogs and American toads: the role of interespecific tadpole predation and adult choice. Copeia 3:691–697. doi: 10.2307/1447185

Pombal JP, Haddad CFB (2005) Estratégias e modos reprodutivos de anuros (Amphibia) em uma poça permanente na Serra de Paranapiacaba, sudeste do Brasil. Pap Avulsos Zool 45(15):201–213

Prado CPA, Uetanabaro M, Lopes FS (2000) Reproductive strategies of *Leptodactylus chaquensis* and *L. podicipinus* in the Pantanal, Brazil. J Herpetol 34(1):135–139. doi:10.2307/1565249

Prado CPA, Uetanabaro M, Haddad CFB (2002) Description of a new reproductive mode in *Leptodactylus* (Anura, Leptodactylidae), with a review of the reproductive specialization toward terrestriality in the genus. Copeia 4:1128–1133. doi:10.1643/0045-8511(2002)002[1128:DOANRM]2.0.CO;2

Prado CPA, Uetanabaro M, Haddad CFB (2005) Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. Amphib-reptil 26(2):211–221. doi:10.1163/1568538054253375

Roberts JD (1989) Non-foamy egg masses in *Limnodynastes tasmaniensis* (Anura: Myobatrachidae) from South Australia. Copeia 2:488–492. doi:10.2307/1445450

Rodrigues MT (2003) Herpetofauna da Caatinga. In: Leal I, Tabarelli M, Silva JMC (eds) Ecologia e conservação da Caatinga. Universidade Federal de Pernambuco, pp 181–236

Rossa-Feres DC, Jim J (1994) Distribuição sazonal em comunidades de anfíbios anuros na região de Botucatu, São Paulo. Rev Bras Biol 54(2):323–334

Rossa-Feres DC, Nomura F (2006) Characterization and taxonomic key for tadpoles (Amphibia: Anura) from the northwestern region of São Paulo State, Brazil. BiotaNeotropica 6(1):1–26

Salthe SN, Duellman WE (1973) Quantitative constraints with reproductive mode in anurans. In: Vial JL (ed) Evolutionary biology of the anurans. University of Missouri Press, Columbia, pp 229–249

Sampaio EVSB (1995) Overview of the Brazilian Caatinga. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, New York, pp 35–63

Santos AM, Tabarelli M (2002) Distance from roads and cites as a predictor of habitat loss and fragmentation in the Caatinga vegetation of Brazil. Braz J Biol 64(4):897–905

Semlitsch RD (1987) Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum.* Copeia 1:61–69. doi:10.2307/1446038

Silva WR, Giaretta AA, Facure KG (2005) On the natural history of the South American pepper frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura: Leptodactylidae). J Nat Hist 39(7):555–566. doi:10.1080/00222930410001671273

Stebbins RC, Cohen NW (1995) A natural history of amphibian. Princeton University Press, New Jersey

Toledo LF, Haddad CFB (2005) Acoustic Repertoire and call behavior of *Scinax fuscomarginatus* (Anura, Hyliade). J Herpetol 39(3):455–464. doi:10.1670/139-04A.1

Toledo LF, Zina J, Haddad CFB (2003) Distribuição espacial e temporal de uma comunidade de anfíbios anuros do município de Rio Claro, São Paulo, Brasil. Holos Environ 3(2):136–149

Trombulak SC, Frissel CA (1999) Review of ecological effects of roads on terrestrial and aquatic communities. Conserv Biol 14(1):18–30. doi:10.1046/j.1523-1739.2000.99084.x

Vasconcelos TS, Rossa-Feres DC (2005) Diversidade, distribuição espacial e temporal de anfíbios anuros (Amphibia, anura) na região noroeste do Estado de São Paulo, Brasil. BiotaNeotropica 5(2):1–14

Velloso A, Sampaio EVSB, Paryen FGC (2002) Ecorregiões: propostas para o bioma Caatinga. Instituto de Conservação Ambiental, The Nature Conservancy do Brasil, Associação Plantas do Nordeste

Viera WLS (2006) Anurofauna associada a ambientes aquáticos temporários em uma área de Caatinga (São João do Cariri, Paraíba, Brasil). Dissertation, Universidade Federal da Paraíba

Viera WLS, Arzabe C, Santana GG (2007a) Composição e distribuição espaço-temporal de anuros no Cariri Paraibano, Nordeste do Brasil. Oecol Bras 11(3):383–396

Viera WLS, Santana GG, Vieira KS (2007b) Description of the tadpole of *Leptodactylus vastus* (Anura: Leptodactylidae). Zootaxa 1529:61–68

Wilbur HM (1987) Regulation of structure in complex systems: experimental temporary pond communities. Ecology 68(5):1437–1452. doi:10.2307/1939227

Wogel H, Abrunhosa PA, Pombal JP (2002) Atividade reprodutiva de *Physalaemus signifer* (Anura, Leptodactylidae) em ambiente temporário. Iheringia Ser Zool 92(2):57–70

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, New Jersey

Zimmerman BL, Rodrigues MT (1990) Frogs, snakes, and lizards of the INPA–WWF Reserve near Manaus, Brazil. In: Gentry AH (ed) Four neotropical rainforests. Yale University Press, New Haven, pp 427–454

Zimmerman BL, Simberloff D (1996) An historical interpretation of habitat use by frogs in a central amazonian forest. J Biogeogr 23:27–46. doi:10.1046/j.1365-2699.1996.d01-218.x