Reproductive activity patterns of anurans in two different altitudinal sites within the Brazilian Caatinga

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ABSTRACT. Six different categories of breeding sites were investigated from August 1989 to July 1990 at São José do Bonfim (240 m above sea level) and Maturéia (770 m above sea level), two sites localized in the Brazilian Caatinga (State of Paraíba). A severe drought affected these areas during the study. Even so, calling males, nests and/or tadpoles of 20 species from 5 families were found. Leptodactylidae was the most numerous family, with nine species distributed among five genera. In Maturéia, due to the low evapo-transpiration rates, less variation of water levels was observed. Males of hylids and leptodactylids began their calling activities together, whereas at São José do Bonfim leptodactylids began their calling activities first. Thus, at Maturéia high concentrations of individuals and large choruses were found at the beginning of the rainy season, whereas in São José do Bonfim high concentrations were found later. Although up to eleven synchronously calling species were recorded in São José do Bonfim and up to ten synchronously calling species in Maturéia, egg masses and tadpoles of few species were found at both study sites, suggesting that some species may vocalize but do not reproduce in adverse periods.
KEY WORDS. Anurans, Caatinga, activity patterns, unpredictable environment

One of the most striking features of anurans is the presence of an integument which is quite permeable to water and cannot limit evaporative water loss. Their eggs are also highly susceptible to desiccation and are usually deposited in pools of water to ensure embryonic and subsequent larval development. The principal problems of anurans living in arid areas arise from high environmental temperatures and rapid evaporative water loss, often accompanied by a limited water supply (BENTLEY 1966).

The Caatinga of northeastern Brazil (defined and mapped by AB'SABER 1977) consists of heterogeneous arid and semi-arid formations surrounded by more mesic phytogeographic formations. The vegetation is xerophytic, summer-deciduous, morphologically and physiologically drought-adapted. Inside of this morpho-climatic domain, occur mesic forest enclaves, denominated "brejos". This term is applied to those hills that are exposed at right angles to humid winds and are forest-covered because their elevation causes the air to cool, with condensation of humidity and consequent precipitation. The lower temperatures are also due to altitude (ANDRADE-LIMA 1982). Apparently each "brejo" has its own characteristic fauna, including a number of endemic species (see references in HOOGMOED *et al.* 1994).

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VANZOLINI *et al.* (1980) found a rich Caatinga reptile fauna inhabiting the arid and semi-arid formations but did not record species with remarkable adaptations of xeric conditions. Similarly, MARES *et al.* (1985) observed that the Caatinga mammal fauna lacks the expected physiological and morphological adaptations to xeric environment and suggested that the high degree of climatic unpredictability, characteristic of the Caatinga, may preclude the development of a unique fauna adapted to arid conditions. These authors also suggested that the present inhabitants of the region avoid the environmental effects of aridity and climatic unpredictability during harsh periods by utilizing the numerous mesic enclaves scattered throughout the Northeast.

In relation to the anuran fauna, HEYER (1988) demonstrated that the Caatinga was one of the most poorly sampled Brazilian Morphoclimatic Domains and apparently this condition remains. Consequently, the degree to which frogs respond in a distributional sense to differences found within this morphoclimatic domain also remain unknown. Therefore, two anuran assemblages of different altitudinal zones in Brazilian Caatinga were investigated during one year, in order to compare their composition and activity patterns.

Study areas

São José do Bonfim (37°19'W, 7°11'S) is located at 240 m above sea level and Maturéia (37°21'W, 7°17'S) is located at 770 m above sea level, both in the State of Paraíba, Northeastern Brazil. Despite the difference in altitude, mean total annual rainfall (between 1911-1980) at these sites is very similar: 800 mm for São José do Bonfim and 730 mm for Maturéia (VENNETIER 1980). In the drought year of 1990, total annual rainfall accumulation was 340 mm for São José do Bonfim and 270 mm for Maturéia.

On the other hand, significant differences in relation to air temperatures, air relative humidity and evapo-transpiration rates occur between these two sites (Tab. I). At São José do Bonfim, the evapo-transpiration rates are high. Water bodies receive no input from springs or streams and water levels are strongly influenced by precipitation and evaporation. These aquatic sites are not available until the onset of heavy rains. At Maturéia the evapo-transpiration rates are low. The water bodies are more stable and several are available before the heavy rains.

São José do Bonfim is covered by caatinga vegetation (open canopy) and Maturéia by secondary disturbed vegetation (open canopy), both sites under anthropic effects. At São José do Bonfim, rocks were scattered over almost the entire study site. Trees such as *Mimosa hostilis* Benth. (Leguminosae) and *Parkinsonia aculeata* L. (Leguminosae), and palms such as *Copernicia cerifera* (Arr. Cam.) Mart. (Palmae), as well as annual shrubs and grasses, characterize the vegetation. Aquatic plants occur within 80% of the inner zone of the larger temporary pond and along the margins of the reservoir. Both sites, especially the former, were surrounded by trees and shrubs and were partially shaded. Medium sized temporary ponds, without aquatic plants, as well as small temporary ponds, generally were exposed to sunlight. Fishes were found only in the reservoir. During the dry season, the reservoir decreased to 1/3 of its water capacity whereas other aquatic habitats dried out (Tab. II).

Table I. Environmental characteristics of the study sites. Minimum and maximum air temperatures (°C) and maximum air relative humidity (without rain) were measured at 1900 h in the field. Precipitation = mean total annual rainfall.

Characteristics	Study sites	
	Maturéia	São José do Bonfim
Altitud (m)	770	240
Temperature (°C)	15.5 - 22.0	21.0 - 28.0
Precipitation (mm)	730	800
Permanent ponds (n)	3	1
Temporary ponds (n)	2	3
Air relative humidity (%)	88	65
Evapo-transpiration rates	Low	High
Species (n)	12	16
Reproductive modes (n)	6	5

Table II. Characteristics of the aquatic sites. Aquatic plants: Alismataceae (S.J. Bonfim); Umbelliferae (Maturéia). Grasses: Gramineae and Cyperaceae; water: water supply during the dry season.

Aquatic sites	São José do Bonfim				Maturéia			
	Maximum length (m)	Maximum depth (m)	Vegetation	Water/ fishes	Maximum length (m)	Maximum depth (m)	Vegetation	Water/ fishes
Reservoir	150.0	3.00	Aquatic plants trees, shrubs	+ / +	100.0	3.0	Tall grasses shrubs	– / +
Large tem. pond	20.0	1.00	Aquatic plants trees, shrubs	– / –				
Medium temp. ponds	5.0	1.00	–	– / –	10.0	0.5	–	– / –
Small temp. ponds	0.1	0.05	–	– / –				
Swamp					300.0	0.5	Tall grasses Ludwgia sp. Typha sp.	– / +
Water-hole					1.5	0.6	Aquatic plants short grasses	– / –

At Maturéia, during normal periods of rainfall, one half of the swamp remains with shallow water all the time (flooded zone) whereas the other half (wet zone), fills up only during the rainy season. The reservoir and the water-hole (a shallow well) are relatively permanent aquatic sites, except when severe droughts occur. During the study period these aquatic habitats dried out, the flooded zone of the swamp first (April), the water-hole and the reservoir subsequently (May and June).

Tall grasses, *Ludwigia* sp. (Onagraceae) and *Typha* sp. (Typhaceae) characterize the swamp vegetation. In the flooded zone some large ponds occurred, in which fishes (*Astyanax* sp., Characidae; *Geophagus* sp., Cichlidae, and *Poecilia* sp., Poecilidae) were found. Short grasses and aquatic plants occurred in the margins of the water-hole and medium sized temporary ponds formed in the wet zone of the swamp during the rainy season. Other medium sized temporary ponds, without aquatic plants or vegetation cover, were formed near the reservoir (Tab. II). The reservoir is surrounded by a narrow low vegetation zone (especially grasses and shrubs), followed by both abandoned and active agricultural areas. A narrow and relatively dense vegetation zone between the reservoir and the swamp was covered by leaf litter. On May 22, due to the lack of water at the reservoir, the swamp was disturbed by agricultural activities.

MATERIAL AND METHODS

Field work was carried out from August 1989 to July 1990. Data were collected during one-day consecutive visits at each site, at intervals of ten days between visits, more frequently during the wet season (from December 1989 to May 1990). Observations were made between 16:00 and 24:00 h. Rainfall data were collected daily approximately 20 km from São José do Bonfim and 10 km from Maturéia and were given by Empresa de Assistência Técnica e Extensão Rural (Emater, Paraíba). The number of anuran species was determined for each aquatic site. Calling males were counted along the margins of the ponds, aurally and/or visually. Four frequencies of calling males per species were used: a) up to 5; b) 5 to 10; c) 10 to 50; d) 50 or more synchronously calling males at each breeding site (based on AICHINGER 1987). Tadpoles were collected by sweep netting in all types of microhabitats (center, vegetated areas, substratum, and border) of the breeding sites (except reservoirs, that were sampled only along the margins) using fine-mesh plastic strainers. For species whose tadpoles were not easily identified, specimens were maintained in aquarium with water (temperature approximately constant = 26°C) and substratum from the study site until metamorphosis. Developmental stages were recognized according to GOSNER (1960). Egg masses were counted and oviposition sites were characterized. Reproductive behavior such as amplexus, construction of nestings, and male-male interactions were observed and recorded on a tape-recorder and data were transcribed later. Reproductive modes were based on DUELLMAN & TRUEB (1986) and distribution data on FROST (1985). Adult voucher specimens were deposited in the Museu de História Natural Capão da Imbuia, Curitiba, Paraná (MHNCI 2800 to MHNCI 2834) and in the Museu de História Natural da Universidade Estadual de Campinas (UNICAMP), Campinas, São Paulo (ZUEC 9178 to ZUEC 9210).

RESULTS

Species occurrence

Twenty nocturnal species of eleven genera belonging to five families (Bufonidae, Hylidae, Leptodactylidae, Microhylidae, and Pipidae) showed reproductive activity (calling males, nests and/or tadpoles) during the investigation. Sixteen species (1 bufonid, 6 hylids, 8 leptodactylids, and 1 microhylid) were found in São José do Bonfim and twelve (1 bufonid, 4 hylids, 6 leptodactylids, and 1 pipid) in Maturéia (Tab. III).

Eight species occurred at both study sites: *Hyla crepitans* Wied-Neuwied, 1824 (Hylidae), *Hyla raniceps* (Cope, 1862) (Hylidae), *Phyllomedusa hypocondrialis* (Daudin, 1802) (Hylidae), *Leptodactylus fuscus* (Schneider, 1799) (Leptodactylidae), *Leptodactylus labyrinthicus* (Spix, 1824) (Leptodactylidae), *L. troglodytes* Lutz, 1926 (Leptodactylidae), *Physalaemus cuvieri* Fitzinger, 1826 (Leptodactylidae), and *Pseudopaludicola* sp. (Leptodactylidae).

The species display at least five different reproductive modes. Eleven species (55 %) deposited eggs in water (Mode 1 and likely Mode 3) and seven species (35 %) deposited eggs in foam nests (Modes 8 and 21). Only one species (5 %) had eggs imbedded in dorsum of aquatic female (Mode 10) and another one (5 %) had arboreal eggs (Mode 18) (Tab. III).

Table III. Calling patterns, reproductive modes, monthly rainfall (mm), and number of species calling monthly at São José do Bonfim and Maturéia, from August 1989 to July 1990. Reproductive modes according to DUELLMAN & TRUEB (1986). (+) Months when tadpoles were found; (–) habitat disturbed by agricultural activities.

	Reproductive modes	Months											
		Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
São José do Bonfim													
Leptodactylus fuscus	21					X	X	X	X	X			
Leptodactylus troglodytes	21					X	X	X	X	X			
Physalaemus kroyeri	8					X		X		X	X		
Phyllomedusa hypocondrialis	18							X		X	X		
Physalaemus cicada	8							X		X			
Pleurodema diplolistris	8							X		X			
Pseudopaludicola sp.	1							X		X			
Dermatonotus muelleri	1							X		X			
Hyla crepitans	3 (?)							X					
Hyla soaresi	1							X					
Leptodactylus labyrinthicus	21							X					
Bufo granulosus	1									X			
Scinax x-signata	1									X			
Physalaemus cuvieri	8									X			
Hyla gr. nana	1										X		
Hyla raniceps	1										X		
Rainfall (mm)		0	0	0	0	101	0	96	18	137	73	0	0
Species calling		0	0	0	0	3	2	11	2	11	4	0	0
Maturéia													
Hyla crepitans	3 (?)					X	X	X	X	X	X	–	–
Hyla raniceps	1					X	X	X	X	X	X	–	–
Phyllomedusa hypocondrialis	18					X	X	X	X	X	X	–	–
Leptodactylus fuscus	21					X	X	X	X	X		–	–
Leptodactylus labyrinthicus	21					X	X	X				–	–
Pseudopaludicola sp.	1					X		X	X			–	–
Leptodactylus troglodytes	21					X		X		X		–	–
Physalaemus cuvieri	8					X		X			X	–	–
Bufo marinus	1					X						–	–
Proceratophrys cristiceps	1 (?)							X		X		–	–
Scinax pachychrus	1							X			X	–	–
Pipa carvalhoi	10					+	+	+	+	+	+	–	–
Rainfall (mm)		18	2	4	5	159	7	80	9	54	64	6	22
Species calling		0	0	0	0	9	5	10	5	6	5	0	0

Spatial distribution

At São José do Bonfim the greatest anuran congregation (n=11) occurred in the larger temporary pond. Among these species, 7 were terrestrial and 4 were arboreal. Among the terrestrial species, three reproductive modes were recognized (Modes 1, 8 and 21) whereas among arboreal species, at least two were recognized (Modes 1, 18, and likely also Mode 3) (Tab. IV). Among the species that shared the same reproductive mode 21, *Leptodactylus fuscus* and *L. troglodytes* were the most abundant. The most common calling site of *L. fuscus* was on the wet ground, under broken branches and grasses, whereas most *L. troglodytes* vocalized near or inside rock cavities.

Table IV. Calling species and aquatic sites at São José do Bonfim, from August 1989 to July 1990.

Species	Reproductive modes	Aquatic sites			
		Large temporary pond	Medium sized temporary ponds	Reservoir	Small temporary ponds
Physalaemus kroyeri	8	X	X	X	X
Pleurodema diplolistris	8	X	X		X
Scinax x-signata	1	X	X		
Leptodactylus troglodytes	21	X	X		
Hyla gr. nana	1	X		X	
Dermatonotus muelleri	1	X		X	
Hyla crepitans	3 (?)	X			
Phyllomedusa hypocondrialis	18	X			
Leptodactylus fuscus	21	X			
Leptodactylus labyrinthicus	21	X			
Physalaemus cicada	8	X			
Pseudopaludicola sp.	1		X		
Bufo granulosus	1		X		
Hyla soaresi	1		X		
Hyla raniceps	1			X	
Physalaemus cuvieri	8				X
Number of species		11	7	4	3
Maximum hydro period (day)		23	35	365	7

At Maturéia the greatest anuran congregation (n=6) occurred in the flooded zone of the swamp. Among these species, three were terrestrial and three were arboreal. Among the terrestrial species, three reproductive modes were recognized (Modes 1, 8 and 21), whereas among arboreal species, apparently two occurred (Modes 1 and 3, assuming that *Hyla crepitans* deposited their eggs in natural or constructed basins, similar to other members of the *Hyla boans* group) (Tab. V).

Table V. Calling species and aquatic sites at Maturéia, from August 1989 to July 1990.

Species	Reproductive modes	Aquatic sites				
		Swamp/ flooded zone	Swamp/ wet zone	Water-hole	Reservoir	Medium sized temporary ponds
Hyla crepitans	3 (?)	X		X		
Hyla raniceps	1	X			X	
Scinax pachychrus	1	X				
Leptodactylus labyrinthicus	21	X				
Physalaemus cuvieri	8	X				
Pseudopaludicola sp.	1	X				
Phyllomedusa hypocondrialis	18		X	X		
Leptodactylus fuscus	21		X			
Leptodactylus troglodytes	21		X			
Pipa carvalhoi	10			X		
Bufo marinus	1					X
Number of species		6	3	3	1	1
Maximum hydro period (day)		243	12	304	324	25

At São José do Bonfim *Physalaemus kroyeri* (Reinhardt & Lütken, 1862) (Leptodactylidae) and *Pleurodema diplolistris* (Peters, 1870) (Leptodactylidae) were the most abundant species. The former utilized the greatest number of different breeding sites (n=4), followed by the latter (n=3). *Physalaemus kroyeri* were found especially in small temporary ponds, each individual vocalizing from fixed sites at each breeding site, whereas *Pleurodema diplolistris* were most common in medium sized temporary ponds, several individuals vocalizing while being in motion at the same breeding site (CARDOSO & ARZABE 1993). Only *Hyla raniceps* utilized the reservoir as its only calling site (Tab. IV).

At Maturéia, the most abundant species vocalizing was *Physalaemus cuvieri*, in the flooded zone of the swamp. Few species (*Hyla raniceps*, *Hyla crepitans*, and *Phyllomedusa hypocondrialis*) utilized more than one microhabitat as calling/breeding site. *Pipa carvalhoi* (Miranda-Ribeiro, 1937) (Pipidae) was found only in the "permanent" water-hole. The reservoir was utilized as calling site only by *Hyla raniceps* (Tab. V).

Species phenology

At both sites, the calling activity occurs only from December to May. During this period, three peaks of rainfall occurred. At Maturéia the heavy rains occurred in December and at São José do Bonfim these occurred in April. Two principal peaks of calling activity were recognized at each study site. At Maturéia these coincided with the first two peaks of rainfall (December and February) and at São José do Bonfim these coincided with the last two (February and April) (Fig. 1). Thus, at Maturéia high concentrations of individuals and large choruses were found at the beginning of the rainy season, with males of hylids and leptodactylids beginning their calling activities together. At São José do Bonfim high concentrations were found later and leptodactylids (*Leptodactylus fuscus*, *L. troglodytes* and *Physalaemus kroyeri*) beginning their calling activities first (Tab. III).

The calling activity in São José do Bonfim was more dependent on monthly rainfall (Fig. 1). *Hyla crepitans*, *H. raniceps* and *Phyllomedusa hypocondrialis* vocalized for six consecutive months in Maturéia whereas in São José do Bonfim specimens of these same species vocalized only for short periods. Only *Leptodactylus fuscus* and *L. troglodytes* vocalized uninterruptedly (five consecutive months) in São José do Bonfim, whereas the other species vocalized for short periods, especially restricted to the second and third peaks of rainfall (Tab. III).

Although there were recorded up to eleven synchronously calling species in São José do Bonfim and up to ten synchronously calling species in Maturéia (Tab. III), egg masses and tadpoles of only a few species were found at both study sites. At São José do Bonfim tadpoles of four species (1 hylid, 2 leptodactylids, and 1 microhylid) were found whereas at Maturéia tadpoles of three species (2 hylids and 1 pipid) were found. At São José do Bonfim, among the species present as tadpoles, two species (50 %) deposited eggs in water (Mode 1) and two species (50 %) deposited eggs in foam nests (Mode 8). At Maturéia one species (33.3 %) deposited eggs in water (likely Mode 3), one species (33.3 %) had eggs imbedded in dorsum of aquatic female (Mode 10), and another one (33.3 %) had arboreal eggs (Mode

18) (Tab. VI). No species present as tadpoles at São José do Bonfim were collected at Maturéia, whereas two species present as tadpoles in Maturéia (*Hyla crepitans* and *Phyllomedusa hypocondrialis*) were found at São José do Bonfim. *Pipa carvalhoi* was found only in Maturéia.

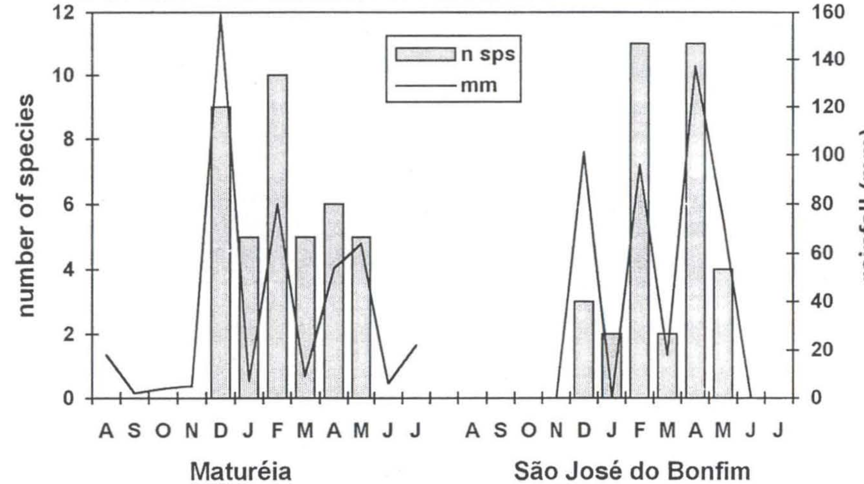

Fig. 1. Monthly maximum number of synchronously calling species at Maturéia and São José do Bonfim, and rainfall accumulation, from August 1989 to July 1990.

Table VI. Tadpoles occurrence and aquatic sites at São José do Bonfim and Maturéia, from August 1989 to July 1990.

Species	Reproductive modes	Aquatic sites				
		Large temporary pond	Medium sized temporary ponds	Small temporary ponds	Water-hole	Swamp/ flooded zone
Physalaemus kroyeri	8	X	X	X		
Pleurodema diplolistris	8	X	X	X		
Scinax x-signata	1	X	X			
Dermatonotus muelleri	1	X				
Hyla crepitans	3 (?)				X	X
Phyllomedusa hypocondrialis	18				X	
Pipa carvalhoi	10				X	
Number of species		4	3	2	3	1
Maximum hydro period (day)		23	35	7	304	243

Leptodactylus fuscus and *L. troglodytes* were abundant and vocalized uninterruptedly in São José do Bonfim, but tadpoles of these two species were never collected. Similarly, at Maturéia *Physalaemus cuvieri* was the species with the highest number of individuals vocalizing (only during the heavy rains), but no foam masses and tadpoles were observed.

At São José do Bonfim, the most abundant egg masses and tadpoles were those of *Physalaemus kroyeri* and *Pleurodema diplolistris*. On December, during the first peak of rainfall, only *P. kroyeri* was calling (Tab. III) but there were no foam nests of this species. On February and on April foam nests of both species (*Physalaemus kroyeri* and *Pleurodema diplolistris*) were found, generally solitary in small temporary ponds, and communal at large aquatic sites. Tadpoles were found in shallow water reading 38°C at 12:00 h. High reproductive failure occurred in both months.

Communal foam nests may be built by pairs either simultaneously or separately. When pairs build a communal foam nest simultaneously, these are generally close to each other. Eleven pairs of *Physalaemus kroyeri* in simultaneous activity, close to each other, were encountered building a single communal foam nest, in which it was impossible to distinguish the foam nest of each pair. On the other hand, sometimes two or three pairs distant from one another were observed aggregating their foam nests adjacent to other fused foam nests, in which it was possible to count the number of foam nests present. Fifteen foam nests of *Pleurodema diplolistris* were found fused into a single communal foam nest.

Tadpoles of *Dermatonotus muelleri* (Boettger, 1885) (Microhylidae) were collected only during February and April, whereas tadpoles of *Scinax x-signata* (Spix, 1824) (Hylidae) were found only in April, during the heavy rains. In Maturéia, tadpoles of *Hyla crepitans* were found from December to March, whereas tadpoles of *Phyllomedusa hypocondrialis* occurred only from May to June. Tadpoles of *Pipa carvalhoi* occurred from December to May.

Eggs and tadpoles of all species (including *Pseudopaludicola* sp., collected near the study site) were observed in laboratory. Complete metamorphosis (with total reabsorption of tail) of all species varied between 25 and 40 days. The duration of the larval development, especially among the leptodactylids, was variable among larvae of one single spawning. Tadpoles of leptodactylids utilize both plant and animal food, and cannibalism was common.

DISCUSSION

Species occurrence and relationships with the environment

Seven species (35 %) have distributions restricted to northeastern Brazil: *Hyla soaresi* Caramaschi & Jim, 1983 (Hylidae), *Scinax pachychrus* (Miranda-Ribeiro, 1937) (Hylidae), *Leptodactylus troglodytes*, *Physalaemus cicada* Bokermann, 1966 (Leptodactylidae), *Physalaemus kroyeri*, *Pleurodema diplolistris*, and *Proceratophrys cristiceps* (Müller, 1884) (Leptodactylidae).

Amphibians may have physiological and/or anatomical attributes that allow them to survive in arid and semi-arid areas. Besides, a surprising variety of successful life-history strategies exists (LOW 1976). The simple selection of a microenvironment where conditions are more suitable (such as nearby permanent aquatic sites, like reservoirs) allow the anurans to escape or moderate the effects of the climate (see BENTLEY 1966). Breeding in these permanent waters or opportunistic breeding (generally involving high fecundity and short larval life), highly fossorial life, and cannibalism are considered usual characteristics of these arid-land amphibians (BLAIR 1976; LOW 1976).

Some kinds of reproductive modes, such as production of foam nests, are adaptations for subhumid environments (DUELLMAN 1985). The results obtained by PEROTTI (1994, 1997) in the Chaco Domain, about number of species, reproductive modes, proportion among different families, and among different reproductive modes are similar to those reported in this present study.

Both Caatinga and Chaco Domains are markedly characterized by seasonal rainfall. Here, temporary ponds, whose margins change rapidly when it does not rain daily, are the breeding sites most commonly used. As rainfall tends to be erratic during the breding season, eggs and larval resistance to desiccation may be an important factor in the success of species living in such environments (see HEYER 1969). Eggs and larval resistance to desiccation may justify the frequencies of leptodactylids (specially *Leptodactylus*, *Physalaemus* and *Pleurodema*) and their foam nests (see BLAIR 1976). Nevertheless, observing the short duration of some foam nests, especially those of *Pleurodema diplolistris*, three other possible functions of foam nests may be considered.

First, in species that breed in water with external fertilization, males must release sperm closer to the eggs to obtain higher fertilization because sperm disperses immediately in water. For species that reproduce in unpredictable environments and may not breed for several years, the increase of the fertilization rates may be an important adaptive advantage. In spite of the cloacae being very close to each other and eggs probably being inseminated prior to egg deposition in foam mass, as observed by HÖDL (1992) in *Pleurodema diplolistris*, the foam platform built prior to egg extrusion (HÖDL 1990, 1992) may function as a place where eggs and sperm may be concentrated whereas the movement of the hindlimbs of the male may ensure a close mixture of the eggs with sperm, increasing the fertilization rates. LEON-OCHOA & DONOSO-BARROS (1970) suggested that the high fertilization rates observed in foam nests of *Pleurodema brachyops* may be related to the movement of hindlimbs of the males.

The second function is related to the rapid egg and larval development, characteristic of species occupying temporary ponds. Larvae of *Pleurodema brachyops* and *P. diplolistris* hatch 22 to 26 hours after oviposition and begin to leave the foam (LEON-OCHOA & DONOSO-BARROS 1970; HÖDL 1992; CARDOSO & ARZABE 1993). This short and quick embryonic development occurs in shallow ponds with high temperatures and consequently low dissolved oxygen. DOBKIN & GETTINGER (1985) indicated the importance of studies that clarify gas and water exchange within foam nests. As foam nests are a mixture of protein, air bubbles and water, it is possible that these function as oxygen supply for eggs and very early larval stages of *Pleurodema diplolistris*, once these foam nests dissolve completely within 36 to 45 hours after construction (HÖDL 1992; CARDOSO & ARZABE 1993).

Finally, HÖDL (1990, 1992) observed that the eggs of *Physalaemus ephippifer* and *Pleurodema diplolistris*, once they are out of the foam, are readily eaten by their conspecific larvae, and suggested that foam nests also may reduce conspecific predation.

So, increase of the fertilization rates, oxygen supply and protection of conspecific predation may be the primary functions of foam nests such as those with short duration, whereas reduction of desiccation would be a secondary function, especially related to longer lasting foam nests. However, experiments are necessary to test these hypotheses.

Spatial distribution

The high number of calling species occupying the large temporary pond in São José do Bonfim and the flooded zone of the swamp in Maturéia was associated with the spatial heterogeneity provided by inner and surrounding vegetation structure through its potential to provide sites which may act as refuges, calling and nesting sites. Different reproductive strategies allowed the species to share these aquatic sites.

In São José do Bonfim, *Physalaemus kroyeri* and *Pleurodema diplolistris* showed high plasticity related to the use of breeding sites. As suggested for plasticity in development (NEWMAN 1989), plasticity in the use of different breeding sites may be adaptive in an unpredictable environment. Species that are able to breed in different aquatic sites may have higher fitness than others restricted to a particular aquatic habitat.

The majority of the species avoided the large permanent aquatic sites (reservoirs), probably due to the presence of established predators, such as fishes, turtles, and aquatic birds. These permanently residing predators, together with those that complete metamorphosis and leave these sites, such as larval insects, probably maintain a more constant and strong predator pressure than those exerted by temporary predators found in aquatic sites with short duration (HEYER *et al.* 1975).

Species phenology

The time for breeding among frogs of arid areas coincides with periods of rain. These frogs spawn when water is available, but if there is little or no rain they may not breed for several years (BENTLEY 1966).

The lack of rain during some days in São José do Bonfim has more impact on the general conditions of the climate and on the water levels than in Maturéia. So, in spite of the erratic rain distribution at both study sites, in São José do Bonfim the calling activity (species number calling monthly) was more dependent on monthly rainfall.

The species that vocalized for long periods in Maturéia (all arboreal species) avoided the periods without rains in São José do Bonfim, interrupting their calling activities. Tadpoles of these species were not found at São José do Bonfim, suggesting that localized populations may vocalize but not reproduce when the climate is adverse.

Species that produced tadpoles during this present study built foam nests (*Physalaemus kroyeri* and *Pleurodema diplolistris*), and had either rapid egg and larval development (*Scinax x-signata* and *Dermatonotus muelleri*), or reproduction only in aquatic sites at high altitudinal zone (*Hyla crepitans*, *Phyllomedusa hypocondrialis* and *Pipa carvalhoi*).

The species that produced tadpoles at São José do Bonfim are well adapted to arid regions and were not found at Maturéia, probably because of the lower temperatures characteristic of this site. *Dermatonotus muelleri* was reported inside the Chaco Domain (CEI 1980) whereas *Scinax x-signata* was reported in other areas with xerophytic vegetation (RADA DE MARTINEZ 1981). Other species of the *Scinax x-signata* group were associated with arid areas by CEI (1980).

The species that produced tadpoles at Maturéia are more dependent on moisture, vegetation (*Phyllomedusa hypocondrialis*) and hydroperiod of the water body (*Pipa carvalhoi*).

The lack of *Leptodactylus fuscus* and *L. troglodytes* tadpoles at São José do Bonfim may suggest that terrestrial foam nests (see ARZABE & ALMEIDA 1997) have less potential advantages for reproduction in arid areas than aquatic foam nests, al least during adverse conditions.

The absence of *Physalaemus cuvieri* tadpoles at Maturéia may be explained by severe drought which affected this area during the study, suggesting that this species is not adapted to these adverse conditions. However, the importance of a site to a local population may not be appreciated without multiyear sampling that includes favorable years of reproduction (DODD 1993).

Communal foam nests of *Pleurodema diplolistris* were more common than those of *Physalaemus kroyeri*, probably because of the differential preferences related to the size of breeding sites. *Physalaemus kroyeri* generally vocalized in small temporary ponds, where only one pair can build a foam nest. In medium sized and large temporary ponds, communal foam nests may be built by several pairs simultaneously. The pairs may be close to each other (see also BARRETO & ANDRADE 1995). This proximity may favor egg fertilization of one female by more than one single male (multiple paternity), increasing genetic variability, as an important adaptive advantage for unpredictable environments.

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