

Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil

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Abstract. Annual patterns of breeding activity, reproductive modes, and habitat use are described for a frog community in a seasonal environment, in the southern Pantanal, Mato Grosso do Sul, Brazil. Data were collected monthly between January 1995 and December 1998. A total of 24 species from four families; Bufonidae (3 species), Hylidae (10 species), Leptodactylidae (9 species), and Microhylidae (2 species) were registered. Three reproductive activity patterns are recognized among these species: continuous, explosive, and prolonged; 50% of the species were explosive breeders. Seasonal pattern of reproduction was verified for three analyzed years (1995-1997); most species reproduced during the rainy season (Nov-Jan). The reproduction was aseasonal in 1998; unexpected rains in the dry season lead to an unusual breeding activity. Five reproductive modes were noted — 62.5% of the species have the generalized aquatic mode, and 33.3% deposit eggs embedded in foam nests. Many species used the same sites for reproduction, although temporal partitioning and calling site segregation was observed. The occurrence of many species that exhibit explosive breeding early in the rainy season is common in seasonal and open environments with variable and unpredictable rainfall, as is the case in the Pantanal.

Introduction

Environmental conditions affect organisms' life history traits and play an important role in structuring and regulating ecological communities (e.g., Toft, 1985; Menge and Olson, 1990; Walther et al., 2002). Anurans are especially dependent on water and/or atmospheric humidity for reproduction, mainly because they are vulnerable to desiccation, at least in one phase of their lives (e.g., egg, tadpole, or post metamorphic). Regarding breeding seasonality, anurans are known to exhibit two basic patterns: (1) tropical species capable of breeding throughout the year; rainfall is the major extrinsic factor controlling reproduction; and (2) temperate species with seasonal breeding activity that is dependent on a combination of temper-

ature and rainfall (Duellman and Trueb, 1986; Bertoluci and Rodrigues, 2002).

Temporal and/or spatial partitioning of resources constitute mechanisms by which syntopic taxa may avoid competition (Schoener, 1974). Anurans may differ in habitat use for breeding, calling site, annual reproductive period, daily period of calling activity, and acoustic features of advertisement call, which are also interpreted as important isolating mechanisms (e.g., Wells, 1977; Haddad et al., 1990). Furthermore, frogs exhibit a great diversity of reproductive modes, mainly in the Neotropics (Duellman and Trueb, 1986). Comprehension of such diversity is crucial to understand anuran community organization, as is information on temporal and spatial distribution (Duellman, 1989; Hödl, 1990; Magnusson and Hero, 1991). In spite of this, descriptive data on reproductive patterns and habitat use in anurans are available for only a few tropical assemblages (Donnelly and Guyer, 1994). Most studies on breeding activity patterns and habitat use of Neotropical anuran communities have been carried out in the Amazon basin (e.g., Crump, 1974; Aichinger, 1987; Neckel-Oliveira et al., 2000) and in the Atlantic rainforest, southeastern Brazil (e.g., Haddad and Sazima, 1992; Bertoluci, 1998;

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Bertoluci and Rodrigues, 2002). Studies on the phenology and habitat use of anuran communities in open seasonal environments in Brazil are scarce (e.g., Arzabe, 1999; Eterovick and Sazima, 2000).

The Pantanal constitutes the world's largest flood plain (Alho et al., 1988). The climate is markedly seasonal, with a wet period and a defined dry season. Floods are common in the region, but the exact period and intensity of floods may vary from year to year. These features make the Pantanal a favourable environment to study reproductive strategies, especially of anurans, which are extremely sensitive to environmental variations. The anuran fauna of the Pantanal is poorly known, both regarding its taxonomic composition and biology (e.g., Lutz, 1946, 1972; Bosch et al., 1996; Prado and Uetanabaro, 2000; Prado et al., 2000; Strüssmann et al., 2000; Prado et al., 2002). Furthermore, studies on anuran community phenology are lacking for this region.

Herein, we present data on the reproduction of an anuran community in a seasonal environment in the southern Pantanal, southwestern Brazil. We have tested the influence of the climatic conditions on the breeding activity of the species using data collected during four consecutive years. Furthermore, habitat use and reproductive modes are described for the assemblage.

Materials and methods

Study site

The Pantanal is a sedimentary floodplain located in the southwestern Brazil, with an area of approximately 140,000 km² (16-22°S; 55-58°W), and elevation between 75 and 200 m a.s.l. The topography is flat, formed mostly by hydromorphic soils, causing drainage problems, which partially explain the tendency for periodic and prolonged floods (Por, 1995). The low water flow, frequently obstructed by transported alluvial sediments, causes the formation of peculiar water bodies, locally named "baías" (lakes or ponds), "vazantes" (natural water drainage channels during floods), and "corixos" (small permanent water courses with defined channels) (Willink et al., 2000). The climate is seasonal ("Aw" type in Köppen's classification), with wet summers from October to April and dry winters from May to September. Rainfall is concentrated between November and January (fig. 1), with a mean annual rainfall of 1,215 mm at the

study site, along the Miranda river, between 1995 and 1998. For the same period, mean annual temperature was 25.1°C; this varied from 15.8°C (June 1996) to 29.5°C (January 1998). Floods are common in the region from January to April.

Because of its great size and diversified regional topographic, climatic, and floristic traits, the Pantanal is commonly divided into many subregions. We use the division proposed by Adámoli (1982), with 10 subregions. The study was conducted in the subregions Miranda and Abobral, municipality of Corumbá, MS (57°00'W, 19°34'S), which are characterized by open formations included in the Cerrado domain (savanna-like vegetation), with fields and patches of semideciduous forest. Other vegetation types include riparian forests and monospecific stands, such as the "paratadal" (composed by trees 'paratado', *Tabebuia aurea*), and the "carandazal" (composed by palm trees 'carandá', *Copernicia australis*).

Field work and statistical analyses

Data were collected monthly from January 1995 to December 1998 (except during four months: December 1997, February, April, and June 1998), with a minimum of four consecutive days per month in the field. The reproductive period of each species was determined based on calling males observed or heard during diurnal and nocturnal surveys, and/or presence of gravid females, amplexant pairs, and/or tadpoles. Whenever necessary, tadpoles were collected and reared to metamorphosis in the laboratory for identification. Reproductive activity patterns exhibited by the species were classified as: (1) continuous — species with individuals reproducing throughout the year (*sensu* Crump, 1974); (2) prolonged — species reproducing for more than three consecutive months, exhibiting asynchronic arrival of females at the breeding sites, and with males defending territories (*sensu* Wells, 1977); and (3) explosive — species with breeding activity lasting one or a few days, with synchronic arrival of males and females, and males employing alternative tactics, as active search for females (Wells, 1977). Sites used for breeding were classified as: rain puddles, flooded areas, permanent and temporary ponds. Reproductive modes were classified according to Duellman and Trueb (1986) and Prado et al. (2002).

Occurrence of seasonal reproductive pattern in a given year was verified through a circular statistical analysis performed for the years 1995 to 1998 (Zar, 1999). Months were converted to angles (e.g., 0° = January to 330° = December, intervals of 30°), and the number of species breeding in each month were converted to frequencies of each angle observed. The following parameters were estimated for each study year: (1) the mean angle (μ), which corresponds to the mean date of the year around which most species were breeding; (2) the circular standard deviation (SD); and (3) the vector r , a measure of concentration of data around the circle or year. Circular data analyses were performed using the ORIANA software (Kovach, 1994).

The significance of the mean angle (μ), or the occurrence of seasonality, was tested using the nonparametric Rayleigh test (τ). We tested the hypothesis that breeding species

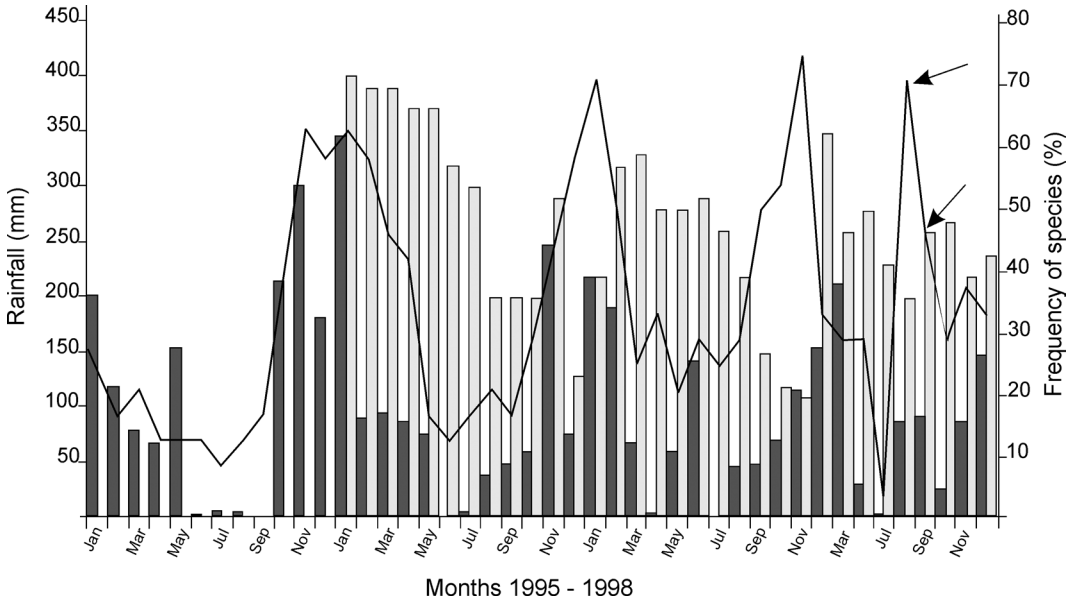


Figure 1. Percentage of anuran species breeding per month (line), monthly rainfall (vertical black bars), and maximum river level in cm (vertical grey bars) registered at the study site in the southern Pantanal, Brazil, from 1995 to 1998 (data on river level was registered from 1996 to 1998). Note the high proportion of species breeding during the dry season in 1998 (Aug-Sep; arrows). Months not sampled are Dec 1997, Feb, Apr, and Jun 1998.

are not uniformly distributed around the year and there is a significant mean angle or mean direction, consequently there is seasonality. The vector r , which may vary from 0 (when data is uniformly distributed) to 1 (when all data are concentrated at the same direction), was used as a measure of the “degree” of seasonality (see Morellato et al., 2000). When the mean angle (a) was significant, i.e., when the annual breeding pattern was seasonal, we performed two-sample Watson-Williams test (F) to verify if each year exhibited the same seasonal pattern, or mean angle (a) (Zar, 1999).

Climatic data were obtained from a meteorological station of the Universidade Federal de Mato Grosso do Sul, located at the study site, at the research station Base de Estudos do Pantanal, and from INPE — Instituto Nacional de Pesquisas Espaciais, in Brazil. As the study site is under the influence of the Miranda river, data on maximum water level of the river measured at the study site was obtained from the Departamento de Hidráulica e Transportes/CCET — Universidade Federal de Mato Grosso do Sul, and was available for the years 1996-1998. Number of species breeding per month was correlated with monthly maximum river level, mean monthly temperature, monthly total rainfall, and monthly relative atmospheric humidity. Relative atmospheric humidity was directly measured using a Vaisala electronic sensor, model HMP5C. As most variables were not normally distributed (Shapiro-Wilk W test), such correlation was determined using the Kendall’s coefficient (Zar, 1999).

Results

Annual breeding activity patterns

A total of 24 anuran species were found at the study site; these are in 13 genera distributed among four families (table 1): Bufonidae (1 genus; 3 species), Hylidae (6 genera; 10 species), Leptodactylidae (4 genera; 9 species), and Microhylidae (2 genera; 2 species). Three species, *Hyla nana*, *Leptodactylus podicipinus*, and *Lysapsus limellus*, reproduced throughout the year and were classified as continuous breeders (table 1). Nine species exhibited prolonged breeding pattern, reproducing for at least three consecutive months, and 50% of the species were explosive breeders, reproducing for short periods, more than once during each year, mainly in the rainy season (table 1). Among the prolonged breeders, the majority also reproduced in the rainy and warm season (October to March; fig. 1), but two hylids, *Hyla punctata* and *Scinax fuscomarginatus*, began reproduction late in the rainy season, after the flood occurred, entering the dry

Table 1. Anuran species registered for the southern Pantanal, Brazil, their reproductive modes, reproductive patterns (E = explosive; C = continuous; P = prolonged), and reproductive period based on calling males and/or presence of gravid females and clutches (black bars), or only on gravid females (grey bars). Reproductive period refers to all reproductive episode registered for each species from January 1995 to December 1998.

| Species | Mode | Pattern | Reproductive period |
|---|----------|---------|--|
| Bufonidae | | | |
| <i>Bufo</i> sp. 1 (gr. <i>granulosus</i>) | 1 | E | Jan, Feb, Nov, Dec |
| <i>Bufo</i> sp. 2 (gr. <i>granulosus</i>) | 1 | E | Jan, Feb, Nov, Dec |
| <i>B. schneideri</i> | 1 | E | Jul, Aug, Sep, Oct |
| Hylidae | | | |
| <i>Hyla nana</i> | 1 | C | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>H. punctata</i> | 1 | P | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>H. raniceps</i> | 1 | P | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>Lysapsus limellus</i> | 1 | C | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>Phrynohyas venulosa</i> | 1 | E | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>Phyllomedusa hypochondrialis</i> | 18 | P | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>Pseudis paradoxa</i> | 1 | P | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>Scinax acuminatus</i> | 1 | E | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>S. fuscomarginatus</i> | 1 | P | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>S. nasicus</i> | 1 | E | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| Leptodactylidae | | | |
| <i>Adenomera</i> cf. <i>diptyx</i> | 21 or 22 | P | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>L. eptodactylus chaquensis</i> | 8 | E | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>L. elenae</i> | 21 | P | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>L. fuscus</i> | 21 | P | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>L. cf. macrosternum</i> | 8 | E | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>L. podicipinus</i> | 3 | C | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>Physalaemus albonotatus</i> | 8 | P | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>P. cf. biligonigerus</i> | 8 | E | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>Pseudopaludicola</i> cf. <i>falcipes</i> | 1 | E | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| Microhylidae | | | |
| <i>Chiasmocleis mehelvi</i> | 1 | E | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |
| <i>Elachistocleis</i> cf. <i>bicolor</i> | 1 | E | Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec |

Reproductive modes: (1) eggs and exotrophic tadpoles in lentic water; (8) foam nest and exotrophic tadpoles in lentic water; (18) eggs on leaves above water; exotrophic tadpoles in lentic water; (21) foam nest in subterranean chamber; exotrophic tadpoles in lentic water; (22) foam nest in subterranean chamber; endotrophic tadpoles inside the chamber (Duellman and Trueb, 1986); (8a) eggs and early larval stages in foam nests in basins constructed by males; exotrophic tadpoles in lentic water (Prado et al., 2002).

months (January to May; table 1). Two explosive breeders, *Bufo schneideri* and *Leptodactylus* cf. *macrosternum*, reproduced sporadically during the dry months (table 1); the latter species is naturally rare at the study site and its reproductive period could be underestimated. Males of *L. cf. macrosternum* were heard calling following unexpected rains or floods.

Reproduction occurred mainly during the rainy season in 1995-1997, with most of the species breeding between November and January (fig. 1). In 1998, after three months with almost no rain, unexpected rains fell in August

and September; this resulted in explosive breeding activity out of the expected pattern for the region (fig. 1). The circular statistical analysis (Rayleigh test of uniformity) revealed that the breeding activity of frogs was significantly seasonal (table 2) for three of the four years tested; the exception was 1998.

Among the years with breeding activity significantly seasonal, the degree of seasonality and mean date of peak of breeding activity were variable. The degree of seasonality (r) varied from 0.92 to 0.57 (table 2). Comparison of the mean angle among the years showed that the

Table 2. Results of circular statistical analysis testing for the occurrence of seasonality on breeding activity of anurans registered in the southern Pantanal, Brazil, in four consecutive years. Mean date (= mean angle) when most species were observed reproducing is shown in parentheses when significant. n = sum of the number of species breeding in each month or sum of observed frequencies of each angle.

| | Years | | | |
|-------------------------------------|---------------------|------------------|---------------------|---------|
| | 1995 | 1996 | 1997 | 1998 |
| Observations (n) | 72 | 101 | 111 | 75 |
| Mean angle (a) | 314.14° (14 Nov) | 4.71° (5 Jan) | 331.04° (30 Nov) | 215.59° |
| Circular standard deviation (SD) | 75.82° | 83.48° | 91.92° | 115.33° |
| Length of mean vector (r) | 0.92 | 0.74 | 0.57 | 0.27 |
| Rayleigh test of uniformity (P) | <0.001 | <0.001 | <0.001 | 0.27 |

year 1996 (05 January) differed significantly from the years 1995 (14 November; $F = 14.22$; $P < 0.001$) and 1997 (30 November; $F = 6.31$; $P = 0.01$) regarding the peak of breeding activity. The years 1995 and 1997 were not significantly different concerning to the mean date when most species were breeding ($F = 1.46$; $P = 0.23$). Number of species reproducing per month in all years combined was positively correlated to local rainfall ($r_s = 0.43$; $P < 0.05$; $n = 44$) and temperature ($r_s = 0.36$; $P < 0.05$; $n = 44$), but was not correlated to relative atmospheric humidity ($r_s = 0.12$; $P > 0.05$; $n = 32$) and river level at the study site ($r_s = -0.09$; $P > 0.05$; $n = 32$); river level was not correlated with local rainfall ($r_s = 0.11$; $P > 0.05$; $n = 32$; fig. 1).

Reproductive modes and habitat use

Among the 24 species, five reproductive modes were observed (table 1). The generalized mode 1 (*sensu* Duellman and Trueb, 1986), where eggs are deposited in lentic water and exotrophic tadpoles (*sensu* Thibaudeau and Altig, 1999) develop in water, was the most common mode, occurring in 15 species (62.5%) in the families Bufonidae, Hylidae, Leptodactylidae, and Microhylidae (table 1). Eggs in foam nests occurred in eight species (33.3%) in the fam-

ily Leptodactylidae, but doubts remained concerning the occurrence of a sixth mode in the leptodactylid *Adenomera* cf. *diptyx*, because we failed to find nests and tadpoles. Mode 18, with eggs deposited on leaves above water and exotrophic tadpoles in lentic water, occurred in only one hylid species (4.2%), *Phyllomedusa hypochondrialis*.

Habitat use was temporally and spatially partitioned by the anuran community at the study site. Three distinct periods could be distinguished based on the breeding activity of the anurans (fig. 2): dry season, rainy season, and flooding season. During the dry season, the three continuous breeders, *Hyla nana*, *Lysapsus limellus*, and *Leptodactylus podicipinus*, were observed reproducing syntopically in permanent ponds, although, calling site segregation occurred (fig. 2A). Males of *H. nana* generally called from grass clumps or emergent aquatic vegetation at the edge, or in the middle, of the water bodies; *L. limellus* called from the emergent aquatic vegetation with leaves on the water surface, and *L. podicipinus* called from the ground at the edge of ponds. Another species that reproduced during the dry season was the explosive breeder *Bufo schneideri*; males called from the margin of large ponds, generally in places lacking aquatic vegetation. Males of *L. cf. macrosternum* were observed calling during the dry season in flooded areas formed by unexpected rains or floods.

In the early rainy season, a maximum of 18 species were heard simultaneously. Many species used the same sites for reproduction (fig. 2B); at least nine species, some of them explosive breeders, were observed reproducing syntopically in recently formed rain puddles. Among these nine species, males differed regarding calling sites (fig. 2B). Other species called from large ponds, as *H. nana*, *Hyla raniceps*, *L. limellus*, and *Pseudis paradoxa*, but they occasionally also occurred in large rain puddles. The leptodactylids *Adenomera* cf. *dyp-tix*, *Leptodactylus elenae*, and *L. fuscus* deposit eggs in foam nests in subterranean chambers

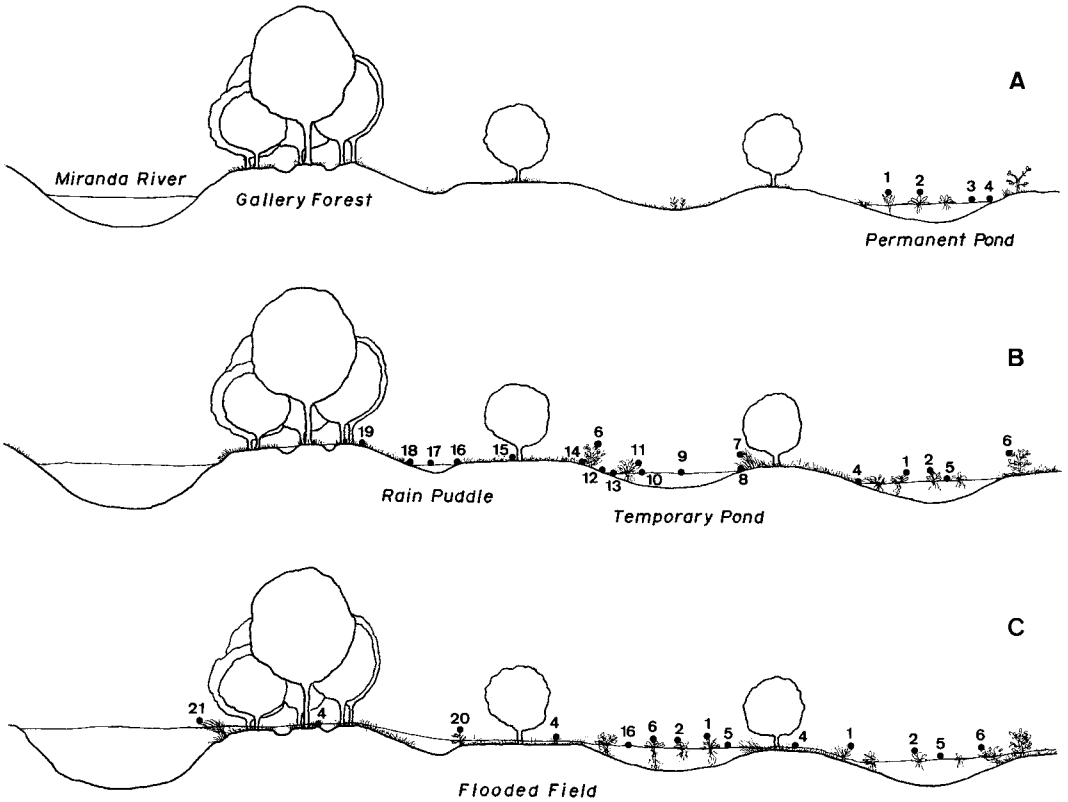


Figure 2. Schematic representation of the spatial and temporal distribution of the anurans registered for the south Pantanal. (A) Dry season; (B) rainy season; (C) flooding season. Species: 1 — *Hyla nana*, 2 — *Lysapsus limellus*, 3 — *Bufo schneideri*, 4 — *Leptodactylus podicipinus*, 5 — *Pseudis paradoxa*, 6 — *H. raniceps*, 7 — *Phyllomedusa hypochondrialis*, 8 — *L. chaquensis*, 9 — *Phrynohyas venulosa*, 10 — *Scinax nasicus*, 11 — *S. acuminatus*, 12 — *Bufo* sp. 1 (gr. *granulosus*), 13 — *Bufo* sp. 2 (gr. *granulosus*), 14 — *L. fuscus*, 15 — *Adenomera* cf. *diptyx*, 16 — *Pseudopaludicola* cf. *falcipes*, 17 — *Physalaemus albonotatus*, 18 — *Elachistocleis* cf. *bicolor*, 19 — *L. elenae*, 20 — *S. fuscomarginatus*, and 21 — *H. punctata*.

out of the water bodies. Males of *A. cf. dyptix* called from the ground, among grass clumps, in the grassland field subjected to periodic floods. Males of *L. elenae* called from the ground, among the forest litter in the gallery forest subjected to floods, and males of *L. fuscus* called from the ground, in open areas at the edge of temporary ponds or depressions also subjected to floods. *Phyllomedusa hypochondrialis* deposited eggs on blades of grass above water, which were wide enough to be wrapped. Males of this species were observed emitting advertisement calls from the grasses in temporary ponds or recently flooded areas with clear water.

Periodic floods were common from January to April, and after the water had invaded the fields, the number of species reproducing decreased from about 18 to eight (fig. 2C). During this period, along with the three continuous breeders, some prolonged breeders, *Hyla raniceps*, *Pseudis paradoxa*, and *Physalaemus albonotatus*, continued breeding in permanent ponds and flooded areas. The hylids, *Hyla punctata* and *Scinax fuscomarginatus* began reproducing after the floods. Males of *H. punctata* called from the emergent aquatic vegetation in the middle of large water bodies, generally associated with the river. Males of *S. fuscomarginatus* called from the emergent grass clumps in flooded fields. Among the continuous breeders,

Hyla nana and *Lysapsus limellus* reproduced in all types of water bodies whereas *Leptodactylus podicipinus* occurred only in permanent ponds and flooded areas.

Discussion

Annual breeding activity patterns

A total of 24 anuran species was recorded in this study for the southern Pantanal. Approximately 113 species of frogs occur in the Cerrado domain (Colli et al., 2002), where the Pantanal is included. This number is considered low regarding its size of ca. 4,655,000 km² and attributed mainly to the low annual rainfall, rather long dry season, and low relief of the region (Duellman, 1999). Rainfall and topography are considered important factors determining diversity and degree of endemism among amphibians in South America (Duellman, 1999). To date, 41 anuran species are known to occur in the Pantanal and surrounding plateau (PCBAP, 1997; Strüssmann et al., 2000), although many regions have not been adequately sampled (Strüssmann et al., 2000). Thus, the low diversity of anurans registered for the study site in comparison to forested and humid areas known to exhibit great anuran diversity through South America was expected (e.g., Crump, 1974; Heyer et al., 1990; Duellman, 1999).

At the study site, most species reproduced during the rainy season, where 50% were explosive breeders, 37.5% were prolonged breeders, and 12.5% exhibited continuous reproduction. This seems to be the common pattern in seasonal environments throughout the Neotropics. In southeastern Brazil, at two seasonal sites in the Atlantic rainforest, only 11-16% of the species exhibited continuous breeding, and 60-70% of the species reproduced exclusively or predominantly during the rainy season (Bertoluci, 1998; Bertoluci and Rodrigues, 2002). At two sites in northeastern Brazil, in the Caatinga domain, with a severe dry season, of the 20 species registered, most reproduced in

the rainy season with none observed reproducing throughout all the year (Arzabe, 1999).

Breeding activity of anurans was seasonal at the study site, with most species reproducing in the rainy season in three of the four studied years. Number of species breeding correlated positively to rainfall and temperature. The breeding activity of anurans that inhabit seasonal environments is generally correlated with periods of rain, mainly in the tropics (e.g., Aichinger, 1987; Donnelly and Guyer, 1994; Bertoluci and Rodrigues, 2002), but also in temperate regions in conjunction with temperature (e.g., Banks and Beebe, 1986; Caldwell, 1987). However, the occurrence and quantity of rains varied among the years 1995-1997 at the study site, and this had a direct effect on the breeding period of the anurans; years differed regarding number of active species and peak of breeding activity. The year 1998 did not exhibit seasonality regarding the breeding activity of anurans and this could be related to the fact that three months in 1998 were not sampled (February, April, and June). However, we strongly suggest that the unexpected explosive breeding activity following rainfall during the dry season in 1998 was responsible for the lack of seasonality. A similar situation was reported for an anuran community in another seasonal region in Venezuela (Hoogmoed and Gorzula, 1979), where anuran reproduction is generally seasonal; reproductive activity of some species occurred in the dry season due to unexpected rains.

Reproductive modes and habitat use

The generalized reproductive mode, where eggs are deposited in lentic water bodies and with aquatic tadpoles, occurred in 62.5% of the species in the present study. This proportion is similar to those in other seasonal environments in South America, such as the Chaco, in Argentina, with 50% of the species exhibiting this mode (Perotti, 1997), and in a savanna area in Venezuela, where 57.7% of the frog species exhibit it (Hoogmoed and Gorzula, 1979). Repro-

ductive modes tend to be more diversified in forest habitats, with the occurrence of many terrestrial modes, mainly because of high temperatures, high rainfall, and high atmospheric moisture, which in combination prevent eggs from desiccation (Hödl, 1990). In seasonal habitats with a pronounced dry season, the generalized mode is most widespread (Duellman and Trueb, 1986). Apart from the markedly seasonal climate, other factors may contribute to the great occurrence of species that exhibit the generalized mode in the Pantanal, as the habitat is homogeneous (absence of small streams and rocky habitats) mainly due to the plain relief which characterizes the region.

The reproductive modes that include eggs in foam nests were the second most frequent among the frogs at the study site, being present in 33.3% of the species. High proportions of species with eggs in foam nests were reported in other seasonal environments: in a study in the Caatinga domain, northeastern Brazil (Arzabe, 1999), 35% of the species exhibited such modes, in the Cerrado domain (Eterovick and Sazima, 2000) approximately 38% of the species were registered laying eggs in foam nests, and in a savanna-like area in Venezuela (Hoogmoed and Gorzula, 1979) 30.8% of the species deposited eggs in foam nests. In more humid and forested habitats these proportions decrease substantially, in part because many other species and consequently reproductive modes occur. Studies conducted at the Atlantic rainforest, southeastern Brazil, report the occurrence of species with foam nests at proportions varying from 8.7 to 19.2% (Haddad and Sazima, 1992; Bertoluci, 1998; Bertoluci and Rodrigues, 2002), and in the Amazon basin the proportions varied from 6.2 to approximately 20% (Crump, 1974; Aichinger, 1987; Hödl, 1990). The foam nest is considered to be an adaptation to seasonal environments, with unpredictable rainfall, as the foam prevents egg desiccation when water bodies dry up (Heyer, 1969). Furthermore, other functions of foam nests have been proposed, such as the maintenance of a

thermally advantageous environment for larval development, as the white foam reflects heat (Gorzula, 1977; Dobkin and Gettinger, 1985; Downie, 1988), which is also important in open and warm habitats as the study site in the Pantanal.

Many species used the same sites for reproduction at the study area in the southern Pantanal, although, year-round temporal partitioning could be observed. Interspecific competition for reproductive resources (e.g., calling sites, oviposition sites) was suggested to be important in organizing tropical frog assemblages (Crump, 1971). However, many studies have been suggesting that resource partitioning in amphibians may result from three main causes, of which competition is only one; the other two are predation and factors that operate independently of interspecific interactions, as physiological constraints (e.g., Toft, 1985; Duellman, 1989; Donnelly and Guyer, 1994). Duellman (1989) pointed out that in seasonal habitats, abiotic factors, especially seasonal droughts, have detrimental effects on some species populations, mainly anurans. During the dry months, only four species reproduced in permanent ponds at the study site, and this low activity might be attributed to physiological constraints related to lower temperatures and decrease in water availability.

More than two thirds of the species, most of them explosive breeders, reproduced in the early rainy season at the study site. In this period, after the first heavy rains and soil saturation, temporary ponds and rain puddles formed and were rapidly colonized. At least nine species could be observed breeding at the same habitat type, forming huge and noisy choruses. However, males differed in relation to calling site utilization. For frog communities breeding synchronically, differences in the advertisement call characteristics, and partitioning of calling and oviposition sites are assumed to be important reproductive isolation mechanisms, facilitating species recognition and preventing mismatings (Hödl, 1977; Duellman and

Pyles, 1983; Haddad et al., 1990, 1994). Many studies on frog assemblages have demonstrated differential use of calling and oviposition sites (Crump, 1974; Hödl, 1977; Eterovick and Sazima, 2000), as observed for the anuran assemblage in the Pantanal (this study).

In the flooding season, almost all water bodies become connected at the study site and form a large shallow lake. The number of species of frogs breeding in the flooding season decreased from 18 to about eight. In this period, fish and insect larvae colonize the flooded fields. During this great extent of water, predation pressure on eggs and tadpoles may be inhibitor factors that restrict reproductive activity of many species. Predation on anuran eggs and larvae, the latter mainly by water bugs (Belostomatidae, Hemiptera) and dragonfly nymphs (Odonata), was frequently observed at the aquatic sites during the study. The utilization of recently formed and ephemeral water bodies in the early rainy season, mainly by explosive breeders in seasonal environments, is generally correlated with avoidance of aquatic predators (Crump, 1974; Heyer, 1976; Eterovick and Sazima, 2000). Frog species that breed early in the rainy period in seasonal environments, generally, reproduce in rain puddles, deposit many small eggs, exhibit multiple clutches, and rapid larval development, which allow the larvae to exploit food sources before insect and fish colonization, while at the same time avoiding predators (Barreto and Moreira, 1996; Eterovick and Sazima, 2000). These features make the early breeders extremely successful in seasonal and unpredictable habitats, a trait which seems to be confirmed by the great occurrence of early breeders and explosive species at the study site in the southern Pantanal.

Acknowledgements. The authors thank D.C. Rossa-Feres, M. Denoël, R.P. Bastos, and the reviewers for critically reading the manuscript and for the valuable comments, J.R. Somera for the drawing, and L.P.C. Morellato for the help with the statistical analyses and suggestions on the text. We also thank T.S. Azevedo for the help with the figures, Base de Estudos do Pantanal — Universidade Federal de Mato Grosso do Sul for the logistical support, CNPq

(proc. 521746/97-3/NV, 351228/97-7, 140397/2000-0), and FAPESP (proc. 01/13341-3) for financial support.

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Received: December 21, 2003. Accepted: March 27, 2004.