Structure of wetland-breeding anuran assemblages from the southern section of the Paraná river, Argentina

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Knowledge of anuran reproduction is necessary to understand the organization of their communities and is a first step in developing management strategies in order to conserve amphibian diversity. We studied the reproduction of anuran species in a wetland reserve – Pre-Delta National Park (PDNP) – on the southern section of the Paraná river in the mid-east of Argentina, examining its structure at temporal and spatial levels. We also analysed the influence of environmental factors on breeding activities at habitat and landscape levels. Six waterbodies in the PDNP were monitored from September 2005 to March 2006. Five habitat variables (maximum pond width and length, maximum depth, shore vegetation and presence of predators) and three landscape variables (monthly air temperature, river level and rainfall) were recorded every month and analysed through multivariate analysis. Principal coordinate analysis (PCoA) indicated the existence of four breeding periods. The most frequent breeding call location was the edge of a pond (56.8%), over floating and marsh plants. The presence of tadpole predators and pond width were the main habitat variables that influenced breeding activities. In addition, the number of species with calling males per month was positively correlated with the level of the river which supplies water to ponds. Breeding anuran species co-occurred less often than expected by chance, and exhibited breeding segregation at temporal and spatial scales. The diverse evidence regarding temporal and spatial breeding activities demonstrates the importance of segregation for anuran reproduction in the area studied. We suggest that the nature of breeding interactions can be affected by habitat preference and reproductive strategy, as well as by abiotic (e.g. pond width), biotic (e.g. predators) and landscape (e.g. hydrological variation) variables.

Key words: amphibians, co-occurrence, habitat use, Pre-Delta National Park, reproduction

INTRODUCTION

Comparative studies of ecological interactions between species provide a variety of evidence regarding the importance of ecology in community structure (Schoener, 1974). Temporal and spatial partitioning of reproductive resources may be important mechanisms by which syntopic taxa may avoid competition (Schoener, 1974; Toft, 1985). In this context, anuran species may differ not only in habitat used for reproduction, but also in calling sites, annual reproductive periods, daily period of calling activities, reproductive modes and the acoustic traits of advertisement calls (e.g. Donnelly & Guyer, 1994; Prado et al., 2005). Moreover, mode and time of reproduction in amphibians depend on morphological and physiological responses to environmental features (e.g. biotic and abiotic factors), on the basis of endogenous and exogenous mechanisms (Brizzi & Corti, 2006; Hartel, 2008). Hence, the documentation of reproductive variability is necessary for understanding anuran community organization (Hödl, 1990).

Wetlands are important components of watersheds, have many functions for the environment and supply important resources (Mitsch & Gosselink, 2000), such as transfer and storage of water, flood control, biochemical transformation and decomposition of organic materials, filtering and cleansing water, erosion control, food production (e.g. shrimp, ducks, fish), habitats for living plants and animals (including many rare or endangered species), timber production and recreation areas (Richardson, 1994; US EPA, 2002a). Amphibians are natural wetland species (US EPA, 2002b). They are valuable indicators of habitat condition in wetlands, where they are widespread and play a key role in structuring biological assemblages and moderating fluxes of energy and nutrients (Beja & Alcazar, 2003; Rittenhouse & Semlitsch, 2007), because they are intermediate in food webs: they consume a variety of arthropods and in turn are consumed by predators (US EPA, 2002b).

In Argentina, most studies of anuran reproductive ecology have been done in the semiarid chaco (e.g. Perotti, 1997), in northwest subtropical mountain forests (e.g. Vaira, 2005) and in central areas (e.g. Reading & Jofré, 2003). Anuran reproductive ecology in the wetlands of Argentina has received little attention, and work has mainly focused on the floodplain of the middle section of the Paraná river (e.g. Marangoni & Kehr, 2000; Peltzer & Lajmanovich, 2004; 2007). Wetlands have not always been valued for their many benefits, and more than half of the original wetlands have been lost in the last hundred years in Argentina (Petean & Cappato, 2005). At present, wetlands are still being converted to uplands for
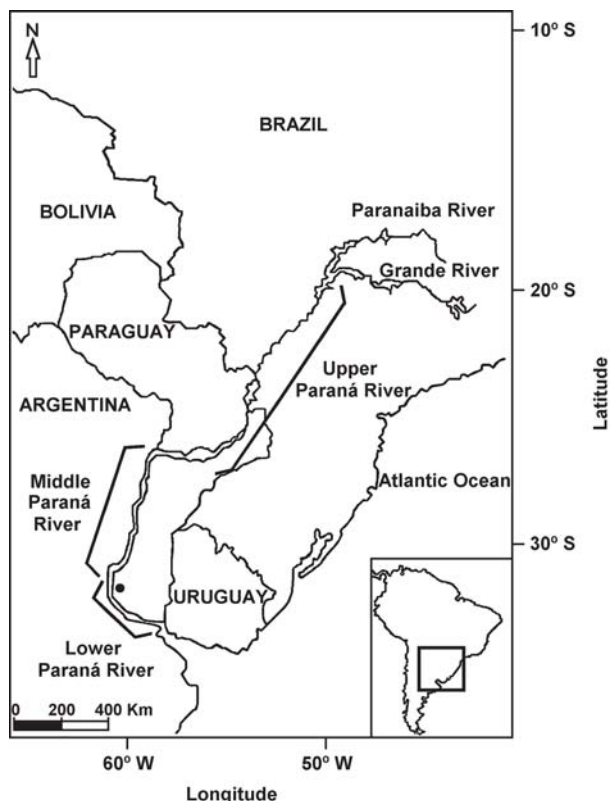
Fig. 1. Location of the Paraná river system, from its birth at the confluence of the Grande and Paranaíba rivers (Brazil) up to its mouth (Argentina), showing its three sections. The black dot indicates Pre-Delta National Park.

human activities (US EPA, 2002a). In this sense, knowledge of anuran reproduction is an important first step in developing good management practices for the conservation of amphibian diversity in wetlands (Paton & Crouch, 2002).

To improve understanding and provide baseline data on neotropical wetland anuran reproductive structure at temporal and spatial scales, this study was conducted on a wetland on the southern section of Paraná river. We examined anuran reproduction in terms of breeding period, habitat use and reproductive modes. We also analysed the influence of environmental factors at habitat and landscape levels on anuran breeding activities.

MATERIALS AND METHODS

Study area

Field work was carried out at Pre-Delta National Park (PDNP), a 2458 ha wetland reserve located in Diamante Department, in mid-southern Entre Ríos Province, Argentina (32º03'43"S; 60º38'39"W). The area is part of the Paraná river floodplain close to the birth point of the Paraná delta, in the southern section of this river, and includes a continental area with river ravines and islands (Aceñolaza et al., 2004). The islands are delimited by different tributary orders, streams and rivulets with high ridges. From these high ridges towards the interior of the islands there is a topographic gradient that ends in la-

goons, located in the lowest parts of the islands. The intermediate zones are flat and exposed to periodic floods (Malvárez et al., 1992). It is important to note that the Paraná river begins at the confluence of the Grande and Paranaíba rivers, and its main tributaries are the Paranápanema, Iguazú and Paraguay rivers in Brazil (Fig. 1). This river has three important sections (Camilloni & Barros, 2003); upstream from the confluence with the Paraguay in Corrientes Province, the river is known as Upper Paraná, and from this province down to 32° S is designated the Middle Paraná. Downstream, the last section is named the Lower Paraná river, our study area.

The study area has a temperate climate, with a mean annual temperature of 18.5 ºC and a mean annual precipitation of 995 mm, distributed mostly (80%) from October to April (INTA, 2003). The hydrological pattern responds to the annual pulsatile flood regimen (Junk et al., 1989). The period of low water is in August–September and the greatest river discharge (flood pulse) frequently occurs at the end of summer (Rojas & Saluso, 1987).

Aquatic sites and environmental variables

To determine breeding activity of anuran species in the PDNP, six aquatic habitats with different physionomies and hydroperiod (permanent and temporary ponds) were randomly selected from an aerial photograph (Table 1). Permanent ponds held water for the duration of the study, while temporary ponds dried every year in winter and refilled with rainfall in summer (Peltzer & Lajmanovich, 2004). These habitats were located in continental and island areas of this wetland reserve. Periodical floods supply water to island ponds, but only important floods (> 4.5 m depth) reach the continental area.

Each month we recorded five habitat variables in each pond: width (m), length (m), maximum depth (m, with stick), shore aquatic vegetation and presence of potential tadpole predators, such as fish (Semlitsch & Gibbons, 1988; Hero et al., 1998; Baber & Babbit, 2004), snails (*Pomacea canaliculata*: Peltzer & Lajmanovich, 2003) and aquatic insects (dragonfly nymphs: Skelly & Werner, 1990; McCollum & Leimberger, 1997; Jara & Perotti, 2006; and water bugs *Belostoma*: Relyea, 2001; Swart & Taylor, 2004; Kopp et al., 2006). Potential predators were recorded simultaneously with net sweep sampling for anuran tadpoles (see below). Shore aquatic vegetation was gauged on a qualitative scale ranging from 1 to 5 (Conesa Fernández-Vitora, 1997) where 1 was mono-specific vegetation and 5 was the most diverse vegetation. We also considered three variables at landscape level: mean monthly air temperature (obtained from the nearest meteorological station at the Instituto Nacional de Tecnología Agropecuaria – INTA, Paraná City, 25 km from the study area), mean monthly river level and monthly rainfall (obtained from Prefectura Naval Argentina Sede Diamante, located 3 km from the study sites).

Field surveys

Field work was carried out during spring and summer, from September 2005 to March 2006. The breeding activity at both temporal and spatial levels of each wetland anuran species was determined based on various sources

Table 1. Description of six aquatic sites in Pre-Delta National Park, Entre Ríos Province (Argentina), sampled between September 2005 and March 2006. SD = standard deviation.

Site	Location	Geographical position	Hydroperiod	Length (m) (mean±SD)	Width (m) (mean±SD)	Max. depth (m) (mean±SD)
Pond 1	Continent	32º07´17.6´´S–60º38´02.2´´W	Permanent	115.5±12.9	90.5±16.9	0.55±0.05
Pond 2	Continent	32º07´11.7´´S-60º38´05.0´´W	Temporary	4.8±7.8	2.3±4.4	0.07±0.12
Pond 3	Continent	32º07´17.2´´S-60º37´58.3´´W	Permanent	424.0±18.2	159.0±15.6	0.70±0.09
Pond 4	Island	32º07´37.3´´S-60º38´08.1´´W	Temporary	18.0±11.5	12.3±8.2	0.10±0.08
Pond 5	Island	32º07´38.7´´S-60º38´12.0´´W	Temporary	291.7±70.5	101.7±50.4	0.65±0.19
Pond 6	Island	32º07´27.7´´S-60º38´09.8´´W	Temporary	219.2±109.7	33.7±26.4	0.28±0.12

of evidence: calling males, presence of amplectant pairs, clutches and/or tadpoles (Bertoluci & Rodrigues, 2002; Prado et al., 2005). In order to record calling activity of anurans and presence of amplectant pairs, we conducted four night searches per month at each pond between 2000 and 0500, spending at least 90 minutes at each site. Two observers recorded data using a randomized walk design following Heyer et al. (1994). For calling males, we also recorded type of substrate (e.g. open water, grass, shrub, marsh plants), height in the vegetation (with stick, cm) and their locations in the pond (centre, edge, land periphery, flooded land periphery). We considered "edge" as the aquatic–terrestrial transition zone (ATTZ) (Wantzen et al., 2008).

Each month we also carried out at least two searches looking for tadpoles, always in daylight. The dipnet sweep method (US EPA, 2002b) was used to take samples in a randomized walk design following Heyer et al. (1994) that implied a sequential series of compass directions. We walked in each selected direction and stopped 1–10 times (depending on pond length) to carry out net sweeping, always covering at least 60% of the pond area. The tadpoles that could not be identified in the field were reared to metamorphosis in the laboratory for identification. A maximum of 10 tadpoles were euthanased and fixed according to ASIH, HL and SSAR guidelines (ASIH et al., 2001), and the rest were released at the same site where they were collected. Voucher specimens were deposited in the herpetological collection of Centro de Investigación Científica y Transferencia de Tecnología a la Producción (CICYTTP–CONICET), Diamante, Entre Ríos Province, Argentina.

Data analysis

Reproductive modes were classified according to Lavilla (2004) for Argentinian anurans; we also considered the classification of Duellman & Trueb (1986) and the update by Haddad & Prado (2005).

Breeding temporal analysis. A principal coordinate analysis (PCoA) was done to evaluate the temporal breeding activity of wetland anurans. The original matrix considered all evidences of reproduction (vocalizations, amplectant pairs, spawing and presence of tadpoles) across the time period studied (in months). Then, we built a distance matrix using the Jaccard similarity index (Magurran, 1988). This index was calculated between each pair of species according to the following formula:

$$C_J = j/(a + b - j)$$

where j is the breeding evidence found in both species, a the breeding evidence for species A and b the breeding evidence for species B. This index ranges between 0 and 1, 0 being non-similarity between species and 1 complete similarity. The associated distance index is $1-C_J$. The PCoA was done with the distance matrix using Euclidean distances and was performed with InfoStat demo/Professional (Infostat, 2006).

Breeding spatial analysis. The microhabitat breadth (Bj) for calling activities was calculated following Levins' (1968) criteria (modified by Heyer, 1976), using the formula:

$$Bj = \Sigma Pij^2$$

where Bj is the amplitude of the microhabitat (for types of substrate used by call) of species j and Pij the proportion of species j which occurs in microhabitat i (i = open water, floating plants, grass, burrows, marsh plants, shrubs, trees, etc). The calculation of Pij was based on observations of calling individuals of each species, by calculating the proportion of cases registered in each microhabitat used by the species with respect to all of the observations ($Pij = nij/Nj$). The lower the value, the higher the niche breadth. In addition, the frequency distribution of anuran vocalization sites was calculated according to Rossa-Feres & Jim (2001), who considered the location of each species in the pond, type of substrate and vegetation height.

Environmental relationships. We used principal components analyses (PCA) to summarize the main habitat variables and determine which variables contributed most to anuran breeding activity. The data matrix had five variables, the values of which were standardized before the test was run: width, length and maximum depth of the ponds (monthly averages), shore aquatic vegetation and tadpole predator richness. Only principal components that produced eigenvalues greater than 1.0 were analysed and correlations with an absolute value greater than 0.5 were considered significant (Hair et al., 1979). Variables derived from PCA were used as predictor (independent) variables of the number of anurans breeding within a pond (dependent variable). To test the association among landscape variables and number of species with calling males per month, we performed a forward stepwise multiple regression following Gottsberger &

Table 2. Summary of wetland anuran breeding characteristics according to spatial distribution and reproductive modes at the PDNP, Entre Ríos, Argentina. Permanent ponds: 1 and 3; temporary ponds: 2, 4, 5 and 6. Location in the pond: (C) centre of pond, (E) edge of pond, (L) land periphery, (F) flooded land periphery. Reproductive modes of Argentinian anurans followed Lavilla's (2004) criterion, and generalized reproductive modes were according to Duellman & Trueb's (1986) criterion, and the update made by Haddad & Prado (2005). Lavilla's (2004) criterion: Mode 2: eggs are individually laid, adhered to submerged vegetation. Mode 3: eggs are scatter-deposited in a continuous layer on water surface. Mode 6: eggs are deposited in spherical gelatinous clusters attached to submerged plants or objects. Mode 7: eggs are deposited in a jelly-like strand at the bottom of the water body. Mode 8: eggs are deposited in a floating foam nest. Mode 13: eggs are deposited in terrestrial foam nests, in depressions, cracks or structures specially built in the mud, and generally in flooded areas or near water.

| Anuran species | Habitat for reproduction | | Reproductive modes | |
	Pond	Location in the pond	Lavilla (2004)	Duellman & Trueb (1986)/ Haddad & Prado (2005)
Bufonidae				
Rhinella fernandezae	1, 2, 3, 4, 5, 6	C, E	7	1/1
Rhinella schneideri	1, 2	E, F	7	1/1
Hylidae				
Dendropsophus nanus	1, 2, 3, 4, 5, 6	C, E, L, F	6	1/1
Dendropsophus sanborni	1, 2, 3, 4, 5, 6	C, E, L, F	6	1/1
Hypsiboas pulchellus	1, 2, 3, 6	C, E	6	1/1
Hypsiboas punctatus	1, 3, 5	C, E, F	6	1/1
Hypsiboas raniceps	3, 4, 5, 6	E, L	6	1/1
Pseudis limellum	1	C, E	2	1/1
Scinax acuminatus	2, 3	E, L, F	6	1/1
Scinax berthae	2, 3, 6	C, E, F	6	1/1
Scinax nasicus	1, 2, 3	L, F	6	1/1
Scinax squalirostris	1, 2, 3, 4, 5, 6	C, E, L, F	6	1/1
Trachycephalus venulosus	4, 5	E, L	3	1/1
Leptodacylidae				
Leptodactylus gracilis	1, 2, 3, 5, 6	L, F	13	21/30
Leptodactylus latinasus	1, 3	E, L	13	21/30
Leptodactylus mystacinus	1, 3, 4, 5, 6	L	13	21/30
Leptodactylus ocellatus	3, 6	C	8	8/11
Leiuperidae				
Physalaemus albonotatus	1, 3	F	8	8/11
Pseudopaludicola falcipes	1	F	6	1/1
Microhylidae				
Elachistocleis bicolor	1	F	3	1/1

Gruber's (2004) criterion. The PCA and step-wise multiple regression were performed with STATISTICA, version 6.0 (Statsoft, 2001).

Temporal and spatial species co-occurrence analysis. Anuran breeding assemblages at both temporal and spatial scales were tested for random co-occurrence of species using the *C*-score metric (Stone & Roberts, 1990). The *C*-score calculates the average number of checkerboard units for each single species-pair, based on the formula $(ri–S)(rj–S)$, where ri and rj are the number of occurrences for species i and j, and S is the number of co-occurrences. To assign a probability value to an observed *C*-score, we performed a Monte Carlo ''null model'' simulation to randomize each presence–absence (1–0) matrix in the data set. We tested the null hypothesis that co-occurrence patterns could not be distinguished from those that might occur by random processes. The data con-

sisted of breeding activity for each anuran species, measured over seven months from six ponds.

a) Temporal co-occurrence: for this analysis, each row of the data matrix represented a breeding anuran species (based on calling male, spawning, tadpoles, amplectant pairs) and each column represented a month of the study period.

b) Spatial co-occurrence: for this matrix, each row represented breeding anuran species based on calling males, and each column represented a different breeding pond. All values (row: breeding–species; column: sites or months) of each original matrix were randomized 1000 times. A sequential swap permutation algorithm was used in all analyses and the sum of lines and column was fixed (algorithm ECOSIM SIM9-fixed-fixed models; Gotelli, 2000). This model has better statistical properties than equiprobable models (Ulrich & Gotelli, 2007). The statistical significance ($\alpha < 0.05$) of the observed matrices was
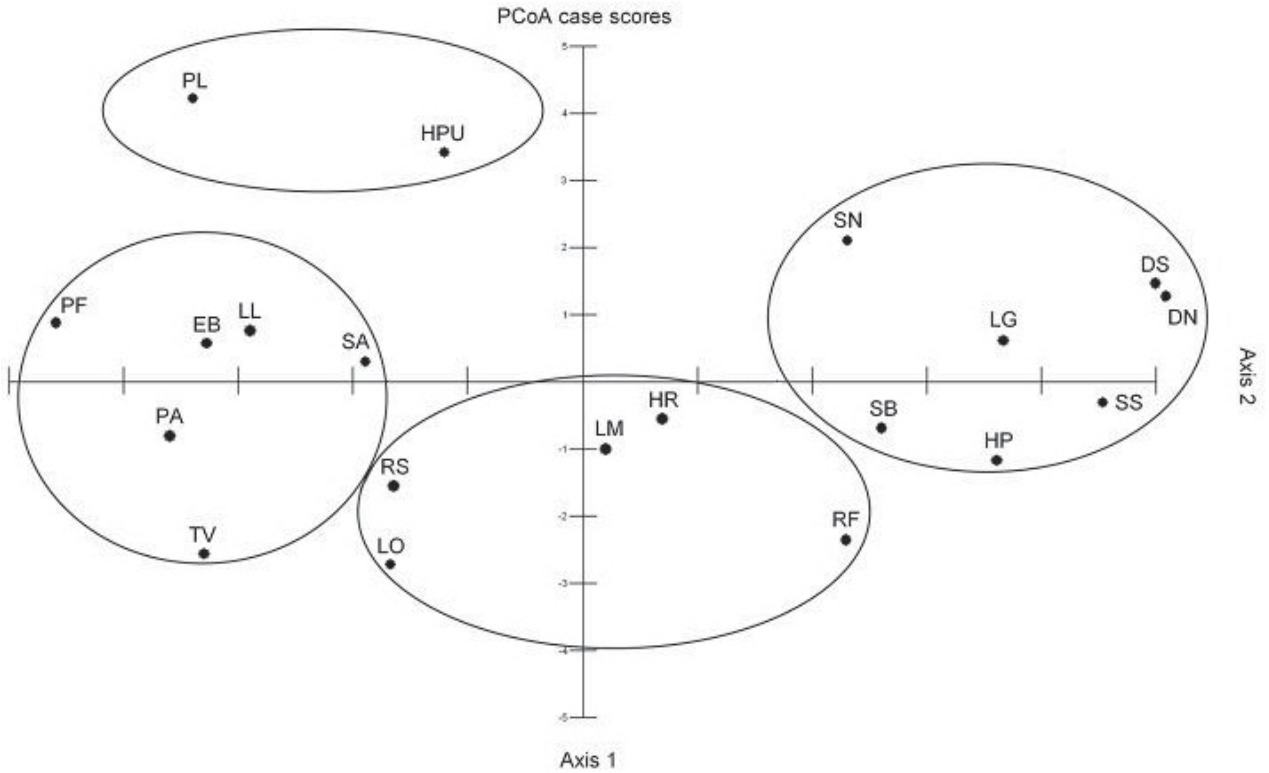
Fig. 2. Ordination by PCoA of the temporal distribution of the 20 species recorded in Pre-Delta National Park with evidence of reproduction between September 2005 and March 2006. RF, *R. fernandezae*; RS, *R. schneideri*; DN, *D. nanus*; DS, *D. sanborni*; HP, *H. pulchellus*; HPU, *H. punctatus*; HR, *H. raniceps*; PL, *P. limellum*; SA, *S. acuminatus*; SB, *S. berthae*; SN, *S. nasicus*; SS, *S. squalirostris*; TV, *T. venulosus*; LG, *L. gracilis*; LL, *L. latinasus*; LM, *L. mystacinus*; LO, *L. ocellatus*; PA, *P. albonotatus*; PF, *P. falcipes*; EB, *E. bicolor*.

calculated as the frequency of simulated matrices that had indices that were identical to or more extreme than the index of the observed matrix (one-tailed test) (Gotelli & McCabe, 2002). If the *C*-score index is unusually large in contrast with a null distribution, there is less pairwise species co-occurrence than expected by chance (segregation). If this index is unusually small, there is more species co-occurrence than expected (aggregation). Null model analyses were conducted with ECOSIM 7.0 simulation software (Gotelli & Entsminger, 2001).

RESULTS

Evidence of reproduction by 20 anuran species was found at the study sites (Table 2). There was a maximum breeding activity of 16 species in November and a minimum of seven species in February and March.

Breeding temporal activity

According to the PCoA analysis, we observed four breeding periods (Fig. 2): 1) species with breeding activity during all sample periods, both in spring and summer (*Dendropsophus nanus*, *D. sanborni*, *Hypsiboas pulchellus*, *Scinax berthae*, *S. nasicus*, *S. squalirostris* and *Leptodactylus gracilis*); 2) species that reproduce in spring and early in the summer, from September to Decem-

ber or even January (*Rhinella fernandezae*, *R. schneideri*, *H. raniceps*, *L. mystacinus* and *L. ocellatus*); 3) species with individuals that reproduce in the late spring and in the summer, from December to March (*H. punctatus* and *Pseudis limellum*); 4) species with short breeding activities, during one month or two separated months (*S. acuminatus*, *Trachycephalus venulosus*, *L. latinasus*, *Physalaemus albonotatus*, *Pseudopaludicola falcipes*, *Elachistocleis bicolor*).

Breeding spatial use

Six reproductive modes were observed (Table 2), Mode 6 being the most prevalent (50%) and Mode 2 (5%) the least common in the wetland anuran species analysed.

The most frequent anuran location in the ponds was the edge of the pond (56.8%). Males used several substrates when calling (Table 3), the two most frequent being branches of floating and marsh plants over water. Another important substrate was grasses over water (35%). Thus, *R. fernandezae*, *R. schneideri*, *H. punctatus*, *H. raniceps*, *S. acuminatus*, *S. berthae*, *S. nasicus*, *T. venulosus*, *L. gracilis*, *L. latinasus*, *L. mystacinus*, *L. ocellatus*, *P. albonotatus*, *P. falcipes* and *E. bicolor* showed higher values of niche breadth (*Bj* > 0.5) for calling site, and thus lower amplitude of niche. The remaining

Table 3. Frequency distribution of anuran vocalization sites from the ponds studied in PNPD, Entre Ríos, Argentina. RF, *R. fernandezae*; RS, *R. schneideri*; DN, *D. nanus*; DS, *D. sanborni*; HP, *H. pulchellus*; HPU, *H. punctatus*; HR, *H. raniceps*; PL, *P. limellum*; SA, *S. acuminatus*; SB, *S. berthae*; SN, *S. nasicus*; SS, *S. squalirostris*; TV, *T. venulosus*; LG, *L. gracilis*; LL, *L. latinasus*; LM, *L. mystacinus*; LO, *L. ocellatus*; PA, *P. albonotatus*; PF, *P. falcipes*; EB, *E. bicolor*. Italic numbers indicate the sample size for each species.

Calling sites	RF	RS	DN	DS	HP	HPU	HR	PL	SA	SB	SN	SS	TV	LG	LL	LM	LO	PA	PF	EB
Location in the pond	*14*	*16*	*44*	*122*	*14*	*10*	*2*	*11*	*85*	*6*	*3*	*77*	*6*	*11*	*14*	*2*	*1*	*2*	*1*	*1*
Centre of pond	50.0	0.0	20.5	24.6	7.1	20.0	0.0	54.6	0.0	33.3	0.0	13.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Edge of pond	50.0	50.0	38.6	58.2	78.6	70.0	50.0	45.5	88.2	16.7	0.0	45.5	33.4	0.0	71.4	0.0	100.0	0.0	0.0	0.0
Land periphery	0.0	0.0	13.6	6.6	14.3	0.0	50.0	0.0	7.1	0.0	33.3	28.6	66.6	63.6	28.6	100.0	0.0	0.0	0.0	0.0
Flooded land periphery	0.0	50.0	27.3	10.7	0.0	10.0	0.0	0.0	4.7	50.0	66.7	13.0	0.0	36.4	0.0	0.0	0.0	100.0	100.0	100.0
Type of substrate	*14*	*15*	*38*	*106*	*11*	*5*	*1*	*13*	*85*	*5*	*1*	*74*	*6*	*11*	*14*	*2*	*1*	*2*	*1*	*1*
Floating in open water	100.0	0.0	0.0	0.0	0.0	0.0	0.0	30.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0
Floating plant branches	0.0	0.0	34.2	52.8	63.6	80.0	0.0	53.9	0.0	20.0	0.0	17.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grass over water	0.0	0.0	10.5	3.8	0.0	20.0	0.0	0.0	0.0	0.0	0.0	10.8	0.0	0.0	28.6	0.0	0.0	0.0	100.0	100.0
In burrows	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	71.4	100.0	0.0	0.0	0.0	0.0
Marsh plant branches over water	0.0	0.0	47.4	39.6	36.4	0.0	0.0	15.4	0.0	80.0	100.0	36.5	50.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0
Marsh plant branches over ground	0.0	100.0	7.9	2.8	0.0	0.0	0.0	0.0	52.9	0.0	0.0	28.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Shrub over water	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	47.1	0.0	0.0	6.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tree	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vegetation height (cm)	*14*	*15*	*14*	*57*	*4*	*3*	*1*	*11*	*85*	*6*	*1*	*29*	*6*	*11*	*14*	*2*	*1*	*2*	*1*	*1*
0–10	100.0	100.0	57.1	64.9	75.0	33.3	0.0	100.0	0.0	100.0	100.0	75.9	0.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
11–20	0.0	0.0	28.6	10.5	25.0	0.0	0.0	0.0	0.0	0.0	0.0	6.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21–30	0.0	0.0	7.1	1.8	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
31–40	0.0	0.0	0.0	15.8	0.0	0.0	0.0	0.0	82.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
41–50	0.0	0.0	7.1	7.0	0.0	0.0	0.0	0.0	11.8	0.0	0.0	6.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
51–60	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
61–70	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
71–80	0.0	0.0	0.0	0.0	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
81–90	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
91–100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
>100	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	6.9	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 4. PCA results with the loading of the variables for the first two axes (factors), the eigenvalues and the percentage of total variance. The most important correlations, corresponding to the variables which contributed most to breeding activity, are given in italics.

	Axis 1	Axis 2
Pond depth	0.269	0.456
Pond width	0.216	*0.568*
Pond length	0.217	0.460
Potential tadpole predators	*-0.777*	-0.500
Vegetation	0.479	0.091
Eigenvalues	41.415	11503
% total variance	95.675	3.473

species showed values of niche breadth lower than $Bj < 0.5$.

We also recorded 15 breeding species in permanent ponds (ponds 1 and 3), whereas temporary ponds (ponds 2, 4, 5 and 6) ranged between seven and 10 species (Table 2). *Pseudis limellum*, *L. latinasus*, *P. albonotatus*, *P. falcipes* and *E. bicolor* only used permanent ponds for their reproduction, while *T. venulosus* only used temporary ponds. The rest of the species used both types of ponds for reproduction (Table 2).

Environmental relationships

The first and second main components of PCA accounted for 95.7% and 3.5% of the variation, respectively (Table 4). The most important variable in the first principal component (I-PC) was the presence of tadpole predators on the negative values. In the second principal component (II-PC), the main variable was pond width on the positive values.

The number of species with calling males per month was positively correlated with mean monthly river level in the second and third models of the forward step-wise multiple regressions. In contrast, no relationship was observed with mean monthly temperature or rainfall (Table 5).

Temporal and spatial co-occurrences

Breeding anuran assemblages had significantly less co-occurrence than expected by chance (large *C*-score) at both temporal and spatial scales (*P* [observed => expected] < 0.05).

DISCUSSION

Models of amphibian community structure in continental aquatic systems indicate that interactions between abiotic constraints (e.g. hydroperiod length, pond size and river level), predation and life history characteristics of individual species may produce predictable patterns of community structure (Wellborn et al., 1996; Wilbur, 1997). In addition, various authors (e.g. Bishop et al., 1999) have pointed out that factors that determine the breeding activities in a pond are strongly influenced not only by the local variables but also by landscape features (Afonso & Eterovick, 2007). Our results indicate that breeding activities and the nature of breeding interactions can be affected by habitat preference and reproductive strategy as well as by abiotic (e.g. pond width), biotic (e.g. predators) and landscape (e.g. hydrological variation) variables.

Breeding temporal activity

Most wetland anuran species in the study area showed breeding activity both in the spring and in the summer seasons, the maximum richness of breeding species being recorded in November. These results are consistent with those found by Lajmanovich (2000). In this sense, *Dendropsophus nanus*, *D. sanborni*, *Hypsiboas pulchellus*, *Scinax berthae*, *S. nasicus*, *S. squalirostris* and *Leptodactylus gracilis* showed breeding activities during all the sample period (breeding period 1). *Hypsiboas pulchellus* and *S. nasicus* were categorized as continuous (species that reproduce for approximately 10 months through the year) and *D.nanus*, *D. sanborni*, *S. berthae*, *S. squalirostris* and *L. gracilis* as prolonged breeders (species that breed for at least 3–4 months in the year) by Peltzer & Lajmanovich (2007), who investigated this over a period of eight years and followed the classification provided by Prado et al. (2005). *Rhinella fernandezae*, *R. schneideri*, *H. punctatus*, *H. raniceps*, *L. mystacinus*, *L. ocellatus* and *Pseudis limellum* showed breeding activities either in spring or summer (breeding periods 2 and 3). *Rhinella fernandezae*, *R. schneideri* and *L. ocellatus* were categorized as explosive breeders (or species reproducing after heavy rains) and the rest as prolonged breeders by Peltzer & Lajmanovich (2007). *Scinax acuminatus*, *Trachycephalus venulosus*, *L. latinasus*, *Physalaemus albonotatus*, *Pseudopaludicola falcipes* and *Elachistocleis bicolor* had short breeding periods (one month or two separated months) during the

Table 5. Forward step-wise multiple regression models relating the number of species breeding per month with the mean monthly river level, monthly rainfall accumulation and mean monthly air temperature at the PDNP, Entre Ríos, Argentina. * indicates statistically significant values.

Model	R²	df	*F*	*P*	Variable	β	*t*	*P*
1	0.5197	1	5.4099	<0.0676	River level	0.7209	2.3259	0.0676
2	0.7933	2	7.6772	<0.0427	River level	0.8442	3.6149	<0.05*
					Rainfall accumulation	-0.5374	-2.3013	0.0828
3	0.8755	3	7.0344	<0.0717	River level	0.9852	4.2465	<0.05*
					Rainfall accumulation	-0.4921	-2.3240	0.1027
					Temperature	-0.3272	-1.4076	0.2539

period studied (breeding period 4). These five species were categorized as explosive breeders by Peltzer & Lajmanovich (2007), except *L. latinasus* which was categorized as a prolonged breeder. In this sense, *T. venulosus*, *L. latinasus*, *P. albonotatus* and *E. bicolor* were recorded reproducing in November, the month with the greatest rainfalls of the spring season. They could be considered explosive breeders *sensu* Wells (1977), although other behavioural characteristics of explosive species (e.g. active search for females and very dense aggregations) have not been observed. However, simultaneous studies are necessary to determine why anurans present dissimilar breeding activity patterns among different riparian environments or across a river at varying latitudes. For example, *P. albonotatus* is a prolonged breeder in the Pantanal of southwestern Brazil (Prado et al., 2005) and an explosive breeder in environments along the Middle Paraná river (Peltzer & Lajmanovich, 2007).

Dissimilar breeding activity in the three different sections of the Paraná river is predictable if we consider the different level of effects of natural and/or anthropic disturbance among them (e.g. floods, dams, industries, agriculture, forest activities and grazing for livestock, urbanization) (Brown et al., 2006; Healey et al., 1997). All of these factors lead to an increase in spatial heterogeneity in relation to the original landscape of the region, producing a deep change in the structure of the original riparian areas and wetlands of the Paraná river and anuran breeding resources. Another explanation for these intraspecific reproductive variations across the river course may be plastic reproductive strategies (Joly, 2003; Richter-Boix et al., 2006) that allow populations to adjust their breeding period to environmental variables as the latitude varies. A third possibility that could explain reproductive variations is the geographical distribution of the species. Sometimes, populations inhabiting the limit of their geographical distribution could need "optimal conditions" to breed. For example, a population of *Physalaemus cuvieri* from Uruguay seems to behave as "explosive", but its behavioural features are not consistent with such dynamics (Maneyro & Beheregaray, 2007), so explosive breeding may be a response to abiotic conditions less optimal than those in southeastern Brazil, where this species behaves as a "prolonged breeder" (Bertoluci, 1998; Bernarde & Machado, 2000; Both et al., 2008).

Breeding spatial use

The position of an organism within a community may be defined in terms of its pattern of resource utilization and its interaction with other organisms that use the same resources (Pianka, 1982; Menin et al., 2005). In this study, reproductive mode 6 occurred in 50% of the anuran species analysed. This result is similar to the observation of Peltzer & Lajmanovich (2007) in riparian areas of the Middle Paraná river, Argentina, where mode 6 was also the most frequent, with 32% of species exhibiting it. Anuran species used several locations for reproduction in the ponds studied, the most common being the edge of pond. Various substrates for calling activities were also used, the two most frequent being floating plant branches and marsh plant branches over water. In previous work from

southeastern Brazil, anuran species assemblages used different locations and substrates for reproduction, suggesting that spatial segregation allows syntopic anurans to coexist at a breeding pond (e.g. Eterovick & Sazima, 2000; Rossa-Feres & Jim, 2001).

Moreover, in our study we observed a greater number of breeding anuran species in permanent ponds (15 species) than in temporary waterbodies (range 7–10 species) (Table 2). Some authors (e.g. Hartel et al., 2006) have pointed out that this can be explained by the higher diversity of microhabitats (larger structural complexity) provided by permanent ponds. Arzabe et al. (1998) found a greater number of breeding anuran species in permanent ponds, and they suggested that the water supply necessary for reproduction is the major factor involved. Likewise, Weyrauch & Grubb (2004) suggested that if global warming increases the frequency of droughts, ponds with relatively long hydroperiods will be increasingly important to amphibians. Conversely, the unstable hydroperiod of temporary breeding sites is a factor restricting the presence of the species that deposit their eggs individually in the water (Arzabe et al., 1998; Peltzer & Lajmanovich, 2004), such as mode 2. In contrast, mode 6 (the most frequent reproductive mode), together with modes 13, 8 and 7, were recorded in both temporary and permanent ponds. Hödl (1990) proposed that high humidity and temperature are important to permit the evolution of more specialized reproductive modes, such as the deposition of eggs in gelatinous clusters.

Environmental relationships

We found that pond width and presence of tadpole predators were the main habitat variables that explained wetland-breeding anuran activities in our study area. The biggest ponds may retain greater species numbers of reproducing anurans because of their greater structural heterogeneity. Hartel et al. (2008) showed that spatial heterogeneity is important in determining the number of species that can exploit an environment. On the other hand, the use of waterbodies with fewer tadpole predators is probably related to the proposal of Hero et al. (2001) that the combination of suitable adult behaviour that minimizes predation on eggs, such as choice of oviposition site and tadpole antipredator defences, is an important determinant of the distribution of tadpoles among waterbodies.

River level was the main landscape factor controlling anuran reproduction in the assemblages studied. An explanation for this may be that the fluctuation of river level provides different habitats for the reproduction and development of certain anuran species (Lajmanovich, 2000; Tockner et al., 2006; Sanchez et al., 2007). Similarly, the great anuran diversity in the relatively short-lived aquatic habitats of the floodplain may be due to insufficient time to allow competitive exclusion (two species that compete for exactly the same resources cannot stably coexist) (Peltzer & Lajmanovich, 2007). River level not only affects amphibian populations; other vertebrates, invertebrates and vegetation are also strongly conditioned by changes in hydrological level (Neiff, 1999). In this sense, it is important to note that although the concept of hydrological

flood pulse is based on surface floods as the most important driving force (Junk et al., 1989), connectivity in some environments may form earlier from other sources, such as precipitation and infiltration of groundwater (Tockner et al., 2000). Differences in breeding anuran assemblage structure among different phases (disconnected, connected and surface-connected phases; Tockner et al., 2000) should be taken into account in future studies in the river–floodplain system.

On the other hand, we found that temperature and rainfall did not play an important role in influencing breeding activities. Amphibians are ectothermic, so it would be expected that abiotic factors such as temperature would determine activity level. The literature on this matter is controversial; some authors have found an association between activity patterns and temperature (Bertoluci, 1998; Bertoluci & Rodrigues, 2002) while others have produced contrary results (Pombal, 1997; Bernarde & dos Anjos, 1999). More recently, cyclic variables determining endogen rhythms have been proposed as predictors of activity patterns (Both et al., 2008; Canavero et al., 2008). In this way, the annual pattern of amphibian calling activity could be mainly determined by a response to all of the components of seasonal variation or a variable that synthesizes seasonal trends in the environment (e.g. photoperiod) rather than by a specific response to temperature or rainfall (Canavero et al., 2008).

Temporal and spatial species co-occurrence

According to Donnelly & Guyer (1994), syntopic taxa of anurans would segregate reproductive resources temporally and spatially to avoid competition. Our results show that wetland anurans in the PDNP presented breeding segregation in both temporal and spatial dimensions, resulting from habitat and landscape variables, differences in habitat preference and reproductive strategies. Considering the PCoA analysis and personal observation, temporal partitioning was evident in the four breeding periods recorded. Spatial partitioning was manifested in the variability of habitat used for reproduction, microhabitat breath for calling sites and reproductive modes. For example, *H. raniceps* and *H. punctatus* differed temporally in their reproductive period and also in the spatial subniche use for mating vocalizations (microhabitat breadth). *H. raniceps* reproduced predominantly in spring and was frequently found in riparian trees (such as *Salix humboldtiana* and *Erythrina crista-galli*), while *H. punctatus* centred its reproduction in summer and was usually found in the middle parts of floating plants (*Eichhornia azurea*, *E. crassipes*). Conversely, some species had the same breeding period (such as *H. punctatus* and *P. limellum*, which reproduced in the late spring and in the summer), or shared habitat for reproduction (such as *L. gracilis* and *L. mystacinus*, which used the same locations in the pond and calling sites). In the co-generic pairs, segregation could be explained because mating vocalizations were different among the species. For example, with *L. gracilis* and *L. mystacinus*, the first species has a metallic and spaced call, its dominant frequency being especially accentuated at 1500, 3500 and 5500 cycles per second (c.p.s.), while the dominant frequency of

L. mystacinus varies from 2200 to 2500 c.p.s. (Cei, 1980). In this sense, the species-pair is reproductively isolated due to mating vocalizations, which are considered a pre-mating isolating mechanism (Duellman & Trueb, 1986). Donnelly & Guyer (1994) found a wide overlap in calling sites for closely related species. Niche overlap does not necessarily indicate competition, because if resources are not in short supply, two organisms can share them without detriment to one another (Menin et al., 2005). In addition, in our study, most species with extensive overlap in a calling site showed a smaller overlap in the temporal breeding period; this result is consistent with that found by Prado et al. (2005) in a seasonal environment in Brazil. In this context, Heyer et al. (1990) stated that habitat type seems to be an evolutionarily conservative trait among closely related species.

The *C*-score co-occurrence index presented here reinforced these observations, determining segregation (non-random pattern) in wetland anuran breeding activities at both temporal and spatial scales. Non-random resource distribution can also influence species coexistence by causing species composition to vary non-randomly (Stone & Roberts, 1990). The evidence for breeding segregation between anuran species among different months (temporal scale) and sites (spatial scale) was determined based on null models, but these negative co-occurrence patterns (non-random) are not necessarily a result of competitive exclusion. Similarly, factors other than competitive exclusion can also limit species co-occurrence in the anuran breeding assemblages we studied in the PNDP. River level may be one of the factors that structures breeding anuran assemblages in spatial dimension in the southern region of the Paraná river. This observation is related to Junk et al.'s (1989) postulation that the hydrological cycle as a whole has a fundamental role in shaping the organization of aquatic communities in seasonally isolated floodplain ponds from the Paraná river, explained by the non-competitive exclusion in such environments discussed above. Furthermore, habitat preference (e.g. location on the pond; breeding vocalizations on floating plant branches or in burrows; location in the breeding site either edge or flooded land periphery) and reproductive mode (e.g. eggs attached or not to aquatic plants) are clearly also important parameters that lead to segregation at spatial scales. These observations are similar to those made by Eterovick & Sazima (2000) and Prado et al. (2005). Lastly, according to the results presented here, predation pressure on eggs and tadpoles may be inhibitory factors that limit reproductive activity of many anuran species or prevent the permanence of some species, exercizing negative pressure when ponds retract or begin to desiccate (e.g. competition for space or limiting abiotic conditions) as well as when ponds were flooded by hydrological expansion (connection with the main channel or surface connectivity) (Prado et al., 2005; Peltzer & Lajmnovich, 2007).

Conclusion

In conclusion, the diverse evidence regarding temporal and spatial patterns of anuran assemblages demonstrate

the importance of reproductive segregation in the anuran assemblages studied from the southern section of the Paraná river. The structure and organization of the assemblages are closely associated with reproductive strategies (e.g. modes), parameters that operate independently of interspecic interactions (physiological constraints), habitat variables (e.g. habitat preference, pond width, predators) and landscape variables (e.g. hydrological variation). Further studies are necessary to evaluate possible plasticity in reproductive strategies and ecological responses to different environmental and landscapes variables through long periods, different hydrological phases and water quality (e.g. eutrophication, pollution).

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