
SEASONAL PATTERNS OF ABUNDANCE AND RECRUITMENT IN AN AMPHIBIAN ASSEMBLAGE FROM THE PARANÁ RIVER FLOODPLAIN

Javier A. López, Pablo A. Scarabotti and Romina Ghirardi

SUMMARY

The seasonality of amphibian activity is a long studied and recognized feature but generally includes only the analysis of adult calling males. In this study, seasonal variation in abundance of a whole assemblage (adults and juveniles), coexistence patterns and phenology were analyzed in a community of 16 amphibian species inhabiting lowland river floodplain ponds. Species activity period was wider than reproductive phase and assemblage activity concentrated in the warm season. The seasonal patterns of abundance and population size structure varied among species but nestedness structure and positive co-occurrence was found for adults and juveniles assemblages. Most adult hylids are characterized by prolonged activity periods while bufonids, cycloramphids, leiuperids, leptodactylids and microhylids varied from prolonged to explosive. Recruitment of juveniles was intensive or explosive in nine out of ten evaluat-

ed species, generating a seasonal reduction in population size structure. The gathered recruitment indicates that warm season is particularly favorable for ingress of juveniles to populations. River hydrometric level was the best predictor of anuran activity, although seasonality (temperature and photoperiod), humidity and rainfall also were informative. The slight differences in activity patterns with respect to other studies could be attributed to variations in local factors and differences in habitat seasonality. Since the studied amphibians utilize the same habitat, activity and recruitment differences among species should be the consequence of combined effects of evolutionary fixed life history traits and present ecological interactions. Thus, there is a mixture of profound and proximate factors ruling species activity and seasonal changes in assemblage structure.

Introduction

Recognition of patterns in species assemblages and the factors behind those patterns counts among the oldest pursuits in ecology. In this sense, the study of temporal variation of species in biological communities yields primary information needed to understand the patterns of coexistence and interaction in a taxocenosis (Sandvik *et al.*, 2002). Most works analyzing amphibian assemblages have focused on adult reproductive period or calling activity patterns (Hödl, 1977; Prado *et al.*, 2005; Canavero *et al.*, 2008), but the period of adult activity usually exceeds the reproductive season

(Vaira, 2002). Besides, if juvenile recruitment is seasonally biased, it should impact on population size composition and, thus, the assemblage structure must be closely related to and influenced by the period of incorporation and growth of new cohorts (Watling and Donnelly, 2002). Moreover, as amphibians are crucial components of trophic networks of wetlands (Stebbins and Cohen, 1995), seasonal changes in assemblage composition and size structure should have ecological consequences on wetlands communities.

Several neotropical assemblages have been tested for species nestedness and co-occurrence patterns, and many of

them have been found to respond to one or both of this community structures (Canavero *et al.*, 2009). Nevertheless, nestedness and co-occurrence measures have been analyzed in assemblages of calling males, where temporal segregation could emerge as a way for avoiding breeding competition. And male calling activity may be a biased index of breeding or female and juvenile activity. Thus, coexistence patterns and seasonal dynamics of whole assemblages remains poorly known in the Neotropics.

Global warming is affecting the seasonal timing of animals and plants, and there is evidence of its effect on several species of amphibian (Blaustein *et al.*, 2001; Tryjanowski *et al.*, 2003). Climate changes could imply diverse consequences on amphibian prey-predatory roll and community structure (Blaustein *et al.*, 2001; López, 2009). Notwithstanding, discussion continues on the main environmental factors regulating amphibian activity (Both *et al.*, 2008; Canavero, *et al.*, 2008; Canavero and Arim, 2009). Additionally, most attention has been paid to the adult reproductive phenology (Hödl, 1977; Bertoluci, 1998; Saenz *et al.*, 2006), and little is known about the recruitment pattern and seasonality of many species. Therefore, increasing information of assemblage associations with cli-

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PATRONES ESTACIONALES DE ABUNDANCIA Y RECLUTAMIENTO EN UN ENSAMBLE DE ANFIBIOS DE LA LLANURA ALUVIAL DEL RÍO PARANÁ

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RESUMEN

La actividad estacional de los anfibios es un hecho reconocido pero generalmente analizado mediante el canto de los machos. En este estudio se analiza la variación estacional en abundancia, patrones de coexistencia y fenología de un ensamble (adultos y juveniles) de 16 especies de anuros del valle de inundación de un río de llanura. El periodo de actividad fue más amplio que la fase reproductiva y se concentró en la estación cálida. Los patrones estacionales de abundancia y la estructura de tamaño de las poblaciones variaron entre especies, pero se observó una estructura anidada y co-ocurrencias positivas para los ensambles. La mayoría de los hílidos adultos tuvieron actividad prolongada, mientras que en bufónidos, ciclorrámfidos, leiupéridos, leptodactílicos y microhílidos varió entre prolongada y explosiva. El reclutamiento de juveniles resultó explosivo o intensivo en nueve de diez especies evaluadas y generó una reducción estacional en la estructura

de tallas. La concentración del reclutamiento durante la estación cálida indicaría una época especialmente favorable para el ingreso de las nuevas cohortes al ensamble. El nivel hidrométrico del río fue el mejor predictor de actividad de los anuros, aunque la estacionalidad (temperaturas y fotoperíodo), humedad y precipitaciones también fueron informativas. Pequeñas diferencias en patrones de actividad respecto a otros estudios pueden atribuirse a variaciones en factores locales y diferencias en la estacionalidad del hábitat. Las diferencias interespecíficas en actividad y reclutamiento serían consecuencia de la interacción entre características de historia de vida fijadas a través de la evolución e interacciones ecológicas actuales. Existe una conjunción de factores históricos y próximos gobernando la actividad de las especies y los cambios estacionales en la estructura del ensamble.

PADRÕES ESTACIONAIS DE ABUNDÂNCIA E RECRUTAMENTO EM UMA MONTAGEM DE ANFÍBIOS DA PLANÍCIE ALUVIAL DO RÍO PARANÁ

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RESUMO

A atividade estacional dos anfíbios é um fato reconhecido, geralmente analisado mediante o canto dos machos. Neste estudo se analisa a variação estacional em abundância, padrões de coexistência e fenologia de uma montagem (adultos e juvenis) de 16 espécies de anuros do vale de inundação de um rio de planície. O período de atividade foi mais amplo do que a fase reprodutiva e se concentrou na estação cálida. Os padrões estacionais de abundância e a estrutura de tamanho das populações variaram entre espécies, mas foi observada uma estrutura aninhada e concorrências positivas para as montagens. A maioria dos hylídeos adultos teve atividade prolongada, enquanto que em bufonídeos, ciclorrámfidos, leiuperídeos, leptodactílicos e microhylídeos a atividade variou entre prolongada e explosiva. O recrutamento de juvenis resultou explosivo ou intensivo em nove de dez espécies avaliadas

e gerou uma redução estacional na estrutura de tamanhos. A concentração do recrutamento durante a estação cálida indicaria uma época especialmente favorável para o ingresso das novas coortes na montagem. O nível hidrométrico do rio foi o melhor mecanismo de predição da atividade dos anuros, ainda que a estacionalidade (temperaturas e foto-período), umidade e precipitações também foram informativas. Pequenas diferenças em padrões de atividade em relação a outros estudos podem atribuir-se a variações em fatores locais e diferenças na estacionalidade do hábitat. As diferenças interespecíficas em atividade e recrutamento seriam consequência da interação entre características de história de vida e interações ecológicas atuais. Existe uma conjunção de fatores históricos e próximos governando a atividade das espécies e as mudanças estacionais na estrutura da montagem.

matic variables and testing of novel environmental factors with biological meaning is crucial to understanding the patterns of species responses to climate change and the assessment of possible implications on amphibian biodiversity conservation.

The neotropical region has the greatest amphibian diversity on the world (IUCN, 2010), and the Paraná River wetlands constitute an important system where different tropical biogeographical lineages reach their highest latitude (Arzamendia and Giraud, 2009). The variation of abiotic and biotic variables

with latitude have been postulated as the mechanism underlying latitudinal changes in diversity, species coexistence patterns and community seasonality (Canavero *et al.*, 2009). In South America, many of the studies analyzing amphibian phenology and assemblage structure and dynamics have been carried on tropical regions (Canavero *et al.*, 2009) and still much is to know about this feature in temperate areas.

Many anurans reach their southern distribution around the last portion of Middle Paraná River section (IUCN, 2010), and the importance of its flood-

plain and its gallery forests for the maintenance of a diverse amphibian fauna has been emphasized (Peltzer and Lajmanovich, 2007). The aim of this work was to analyze and characterize the seasonal patterns of species abundance in an anuran assemblage of the Middle Paraná River and their relationship with classically used climatic variables and flood pulse, an environmental factor particularly important in large floodplain rivers (Junk *et al.*, 1989). Additionally, the temporal distribution of juvenile recruitment and its effect on population size structure of each species was characterized.

Materials and Methods

Study area and sampling methods

Sampling was carried out on a floodplain island of Middle Paraná River, near Santa Fe City (Sirgadero Island, comprising 2300ha at 31°40'S, 60°40'W; Santa Fe Province, Argentina). Climate is damp and mesothermal. The warmer months are September to February, with a mean annual temperature of 18 ±1°C. Average annual precipitations are slightly below 1000mm and rainfall concentrates in the summer. Amphibians were sampled

monthly between August 2004 and September 2005 on six ponds. On each pond, batteries of five pit fall traps were placed 2m from the water edge, and remained active for ten days per month. To sample aquatic and arboreal species 2h visual encounter transects were conducted, once a month on each site. Visual transects began at the crepuscule and zigzag-crossed through all pond surfaces and 3m around the water edge. Specimens were deposited in the collection of the National Institute of Limnology.

Data analysis

In order to classify specimens as adults and juveniles, gonad maturity, external secondary sexual characteristics and snout-vent length were analyzed and contrasted to size data in the literature (Gallardo, 1987; Peltzer and Lajmanovich, 2007).

Adult and juvenile temporal distribution

Adults or juveniles of a given species were considered as 'active' if one or more specimens were captured in a sample. Richness and abundance comparisons among months were made using paired *t* tests or Wilcoxon matched-pairs signed-ranks tests, depending on data normality. To evaluate juvenile recruitment effects on seasonal variation of the population size structure, population mean and variance SVL differences were assessed between months with elevated recruitment ($\geq 10\%$ of total juveniles captured) and months with none or low recruitment ($< 10\%$ of total juveniles) using Mann-Whitney tests and Fisher tests, respectively.

Adult and juvenile activity patterns were characterized in a three-level scale as prolonged, intensive or explosive, as follows: prolonged when it took three or more months to accumulate 50% of annual captures; intensive when 50-67% of total captures were accumulated in two months; and explosive when more than 67% of the captures were registered in a two month period. This classification fol-

lows the logic of previous scales used to characterize reproductive patterns (Prado *et al.*, 2005) but was adapted to describe anuran activity as defined above.

Species temporal co-occurrence, nestedness patterns and phenology

Adult and juvenile temporal abundance data were tested for temporal random co-occurrence of species using the C-score metric (Stone and Roberts, 1990). To assign a probability value to C-scores 5000 Monte Carlo randomizations were performed using ECOSIM 7.72 software (algorithm SIM4-fixed-proportional model; one-tailed test $\alpha < 0.05$; Gotelli and Entsminger, 2010). The larger the C-score index value, the less paired species co-occurrence (more species pairs are segregated in their occurrence), whereas low values indicate higher co-occurrence.

To explore temporal aggregation patterns of juveniles and adults a nestedness analysis was carried out using the *Nestedness* software (Ulrich, 2006). Species assemblages are nested if the species present in a species-poor month are a proper subset of those present in a species-rich month (Patterson and Atmar, 1986). Perfect nestedness occurs when all species-poor months are proper subsets of the assemblages found in species-rich months (Almeida-Neto *et al.*, 2007). Random sampling was used according to the observed frequencies of occurrence (*o*), which is identical to the Random 1 model of Patterson and Atmar (1986), and 100 iterations were performed. A standardized effect size (SES; Ulrich and Gotelli, 2007) was calculated to quantify the direction and degree of deviation from the null model. SES is a Z-transformed score, $Z = (x - \mu) / \sigma$; where *x*: observed index value, μ : arithmetic mean, and σ : the standard deviation of the 100 index values from the simulated matrices. SES values < -2 or > 2 indicate statistical significance ($\alpha = 0.05$, two-tailed test). Two nestedness indices are informed: the classi-

cally used temperature (T, Atmar and Patterson, 1993) and the recently proposed NODF (nestedness based on overlap and decreasing fill; Almeida-Neto *et al.*, 2008). T is a measure of the symmetry in the distribution of unexpected absences and presences, respectively, on both sides (months) of the perfect nestedness boundary line. When $T = 0$, there is no symmetry (maximum nestedness), while $T = 100$ means the highest symmetry of unexpected absences and presences at both sides of the boundary line (Almeida-Neto *et al.*, 2007). The newer metric NODF is based on two matrix properties, decreasing fill and paired overlap, and enables to differentiate between a part of the overall nestedness introduced by species differences (NODF_{spp}) corresponding to species occupancy and site (months) differences (NODF_m) in species composition (Almeida-Neto *et al.*, 2008).

To depict the association between environmental variables and species activity, multiple regressions were performed. To avoid multi-collinearity among predictors, seven climatic variables (monthly lowest temperature, LT; monthly highest temperature, HT; monthly mean temperature, MT; monthly accumulated rainfall, AR; number of days with precipitations in the month, DP; mean relative humidity during sampling days, RH; and absolute heliophany, AH) were summarized using principal component analysis (PCA). Then, the three first factors of PCA and river hydrometric level (RL) were used to model monthly species richness and abundances with multiple regressions. Best model selection criterion was adopted on the basis of the adjusted coefficient of determination $AdjR^2 = ((n-1) \times R^2 - p) / (n-p)$, where *n*: number of observations, *p*: number of parameters in the model, and R^2 : determination coefficient. Climate data were obtained from the meteorological station of the Universidad Nacional del Litoral, located less than 7km from any sampled ponds, and river hydrometric level was obtained

from the hydrometer of Santa Fe city Port.

Results

Sixteen anuran species belonging to six families (9 Hylidae, 1 Microhylidae, 2 Leptodactylidae, 1 Leiuperidae, 1 Cycloramphidae, 2 Bufonidae) were registered. Assemblage diversity was 0.853 (Shannon index using *ln*; Shannon and Weaver 1949). The most abundant species were *Dendropsophus nanus*, *Pseudis limellum* and *Elachistocleis bicolor* (26.19, 18.87 and 14.6% of total captures respectively).

Adult activity

In general, species richness remained elevated in all seasons. Assemblage activity was high from late spring to middle autumn (November-April), exhibiting a peak in February and March (Table I). Most of hylids and *Leptodactylus latrans* showed prolonged activity periods, which in turn was explosive in *L. chaquensis*. Species of remaining families had intensive activity (Table I). No adults of the bufonid *Rhinella schneideri* were captured, but field observations revealed that adults were active in spring and summer, with an activity peak in November-January.

Recruitment of juveniles

In leptodactylids and leiuperids, the total number of juveniles exceeded the total number of adults (Table I). The differences between the number of adults and juveniles through the year were significant in species of hylids (Table I). In all species the mean SVL was smaller in months with high juvenile recruitment and was larger in months with none or low recruitment (Table I). Size variance was also greater in months with elevated recruitment for hylids species and *E. bicolor* (Table I).

Juveniles' recruitment was explosive or intensive in eight out nine studied species (in *D. nanus* it was prolonged), and in most cases concentrated in the warm season (Table I). Even so,

TABLE I
ACTIVITY PATTERNS OF SPECIES AND ASSEMBLAGE STRUCTURING

	Difference N°A vs. n°J	Mean SVL: (+)J vs. (-)J	SVL variance: (+)J vs. (-)J	Act. Pat and (N)	summer		autum		winter			spring		
					Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
<i>R. fernandae</i>				I (115) (1)	█			█		█		█	█	█
<i>R. schneideri</i>				(14)	█	█						█	█	█
<i>O. americanus</i>				(3)			█	█				█	█	
<i>D. nanus</i>	t ₁₃ =4.146**	U=74536**	F _{460,643} =1.239**	P (892) P (218)	█	█	█	█	█				█	█
<i>D. sanborni</i>	Wilcoxon**	U=1558.5**	F _{50,137} =5.951**	P (160) E (31)	█	█	█	█	█			█	█	
<i>H. acuminatus</i>				(1)			█	█						
<i>H. pulchellus</i>	t ₁₃ =0.0026**	U=8101**	F _{105,197} =6.924**	P (304) I (22)	█		█	█	█	█	█	█	█	█
<i>H. punctatus</i>	t ₇ =2.877*	U=4458.5**	F _{110,110} =1.591*	I (215) (7)	█	█	█	█	█	█				█
<i>H. raniceps</i>	Wilcoxon*	U=60**	F _{12,27} =4.215**	P (36) (8)	█		█	█	█	█	█	█	█	█
<i>P. limellum</i>	Wilcoxon**	U=55553**	F _{94,402} =1.612**	P (668) E (132)	█	█	█	█				█	█	█
<i>S. nasicus</i>	t ₁₁ =3.641**	U=2293**	F _{65,98} =2.332**	P (142) E (29)	█		█	█	█	█	█	█	█	█
<i>S. squairostris</i>	Wilcoxon**	U=408.5*	F _{12,97} =29.923**	I (122) (4)		█	█	█			█	█	█	█
<i>P. albonotatus</i>	t ₁₀ =1.144	U=19**	F _{71,2} =20.197*	I (30) E (55)	█	█	█			█		█	█	█
<i>L. chaquensis</i>	T ₇ =0.08544	U=164*	F _{48,10} =1.51	E (29) E (31)	█	█	█	█						
<i>L. latrans</i>	t ₁₃ =1.371	U=164**	F _{255,89} =1.028	P (101) I (250)	█	█	█				█	█	█	█
<i>E. bicolor</i>	t ₁₂ =0.7956	U=19064**	F _{499,117} =1.585**	I (368) I (251)	█	█	█	█				█	█	█

Difference in N° A vs N° J are results of paired t test or Wilcoxon matched-pairs signed-ranks test (depending on data normality), used to evaluate monthly differences in the number of adults and juveniles through the year. Mean SVL: (+)J vs (-)J: results of Mann-Whitney test used to evaluate population mean SVL differences between months with elevated recruitment of juveniles (>10% of total juveniles captured) and months with none or low proportion of juveniles recruitment (<10% of total juveniles captured). SVL variance: (+)J vs (-)J: results of Fisher test used to evaluate population SVL variance differences between months with elevated recruitment of juveniles and months with none or low proportion of juveniles recruitment. Statistical significance is ** p<0.01, * p<0.05. Adult and juvenile activity pattern was classified as P: prolonged (≥3 months to accumulate 50% of annual captures), I: intensive (50-67% of total captures accumulated in two months), or E: explosive (>67% of captures registered in two months). This classification was not applied in species or age groups where few data was gathered. The number of juveniles and adults is given within parenthesis (N). Black bars indicate months where at least one adult was found active; grey bars indicate months where at least one juvenile was registered. Numbers in bars represent monthly percentage of captures for each age class. Percentages are presented only for months with high recruitment, or accumulating ≥80% of annual captures, to illustrate intensity and seasonality of activity patterns. In species where there were <10 specimens (adults or juveniles) in the analyzed period, or all registers concentrate in one month, no percentage is shown. # indicates the presence of metamorphosing specimens that still have not reabsorbed entirely their tail.

there were differences in the seasonal peak and width of the recruitment period among species, with most of species peaking in late summer, *D. nanus* peaking in autumn and *Hypsi-*

boas pulchellus in early spring (Table I). Only one juvenile of *R. fernandae* was captured, in autumn, but its reproduction was observed to concentrate in spring (September-November).

Temporal co-occurrence and nestedness pattern

Species pairwise co-occurrence was higher than expected by chance for adults (Obs. C-

score index= 1.5; Mean of simulated indices= 3.093, S2= 0.19220, p(obs≤exp)= 0.0004) and for juveniles (Obs. C-score index= 3.099; Mean of simulated indices= 4.876, S2= 0.601,

$p(\text{obs} \leq \text{exp}) = 0.013$). The temporal activity was nested for both adult and juvenile abundances (T and NODF), indicating a seasonal aggregation in activity. Nestedness introduced by species (NODFspp) and by months (NODFm) were similar (Table II).

Environmental variables and assemblage activity

The seven climatic variables were summarized into three components with PCA analysis, which together explained 92.6% of the data variation. Component 1 (PC1S) was correlated to LT (0.96), MT (0.95) and AH (0.92) and synthesized information about seasonality. Component 2 (PC2H) was correlated to DP (0.89) and RH (0.73) and synthesized information about humidity. Component 3 (PC3P) was mainly correlated with precipitations (AR of 0.44). PC1S, PC2H and PC3P were used as composite variables together with RL in the modeling of amphibian activity. Multiple regression models showed that assemblage richness correlated with climatic variables and river hydrometric level (Table III). Flood pulse (RL) also took part in every species activity model and was the only variable selected in five models, while seasonality and humidity variables appear in seven species models, and precipitations in eight (Table III).

Discussion

Seasonal fluctuation in species activity and community structure is a recognized property of amphibian assemblages (Bertolucci, 1998; Both *et al.*, 2008; Canavero *et al.*, 2009; Sánchez *et al.*, 2009). There are ultimate factors that shape the evolution of this seasonality (e.g., competition, predation, physiological restrictions, seasonality of resources availability) and proximate fac-

TABLE II
NESTEDNESS ANALYSIS RESULTS

	Index	SimIndex	StdDev	Z-score	L95%Conf	U95%Conf
Temp						
Adults	7.11	78.94	8.94	-0.04	63.52	100.00
Juveniles	13.57	20.93	3.17	-2.32	16.30	28.43
NODF						
Adults	87.06	50.00	3.71	9.99	41.31	57.32
Juveniles	72.61	37.96	3.77	9.19	31.34	45.80
NODFspp						
Adults	85.65	53.92	4.54	6.98	42.53	61.31
Juveniles	71.78	57.99	6.77	2.03	45.05	69.98
NODFm						
Adults	88.29	46.59	4.60	9.07	36.99	56.37
Juveniles	73.44	17.92	6.35	8.75	11.43	34.77

T: temperature; Index: matrix nestedness index; NODF, NODFspp and NODFm; SimIndex: null model simulated; StdDev: standard deviation of simulated index; Z-score: standardized effect size as a Z-transformed score; L95%Conf: lower 95% confidence limit; U95%C.I.: upper 95% confidence limit; NODFspp and NODFm: overall nestedness introduced by species differences and by months differences respectively. Matrices fill: AdultsMat.= 0.71, JuvenilesMat.= 0.41.

tors that supply the direct stimuli for the physiological regulation of the biological seasonality (e.g., photoperiod, biological clocks; Canavero and Arim, 2009). In Sirgadero Island assemblage all species presented a seasonal activity, although the length and focal season of activity period varied among species. Three activity patterns were identified: prolonged, intensive and explosive, which were also different between adults and juveniles in most taxa. Adults of the majority of hylid species had a prolonged activity period. The prolonged pattern is consistent

with the extent of the broad reproductive phase of hylids (Prado *et al.*, 2005; Peltzer and Lajmanovich, 2007; Sánchez *et al.*, 2009), but was not restricted to the male calling or mating period. The intensive activity of *H. punctatus*, concentrated in summer during the rainfall season, was an exception to other hylids strategy but focused on its reproductive period (Prado *et al.*, 2005; Peltzer and Lajmanovich, 2007). *Scinax squalirostris*, previously classified as a prolonged breeder (Peltzer and Lajmanovich, 2007), showed an intensive activity in the present

TABLE III
MODELING OF AMPHIBIANS ACTIVITY WITH ENVIRONMENTAL VARIABLES

Multiple regression models	R ²	p
Richness= 10+0.72*PC1S+0.72*PC2H+0.62*PC3P+0.11*RL	0.63	F ₄ =3.9 0.04
<i>L. latrans</i> = -0.93+2.61*RL	0.09	F ₁ =1.17 0.3
<i>L. chaquensis</i> = -9.03+3.55*RL	0.41	F ₁ =8.34 0.01
<i>P. albonotatus</i> = -4.56+0.71*PC1S-0.21*PC2H+0.78*PC3P+2.15*RL	0.66	F ₄ =8.78 0.03
<i>R. fernandezae</i> = 52.37+4.44*PC1S-0.11*PC2H-4.88*PC3P-14.13*RL	0.44	F ₄ =1.78 0.22
<i>E. bicolor</i> = -3.18+8.12*PC1S+7.82*PC2H+26.1*PC3P+9.43*RL	0.6	F ₄ =3.38 <0.06
<i>P. limellum</i> = -41.11+13*PC1S+6.88*PC2H+7.51*PC3P+28.42*RL	0.7	F ₄ =5.24 0.02
<i>H. raniceps</i> = -2.72+1.69*RL	0.2	F ₁ =3.03 0.11
<i>H. pulchellus</i> = 63.2-13.27*RL	0.2	F ₁ =3.01 0.11
<i>H. punctatus</i> = -41.28+14.12*PC3P+18.12*RL	0.42	F ₂ =4.03 <0.05
<i>D. nanus</i> = -109.82+55.52*RL	0.63	F ₁ =20.77 <0.01
<i>D. sanborni</i> = 27.04+2.7*PC1S+1.21*PC2H-2.83*PC3P-5*RL	0.37	F ₄ =1.33 0.33
<i>S. nasicus</i> = 17.04+4.59*PC2H+1.76*PC3P-2.21*RL	0.48	F ₃ =3.02 0.08
<i>S. squalirostris</i> = 26.86+2.22*PC1S-2.07*PC2H-0.59*PC3P-5.81*RL	0.33	F ₄ =1.09 0.42

Multiple regression models of monthly changes in assemblage richness and species abundances using river hydrometric level (RL) and climatic variables resumed with a PCA analysis: PC1S: resumed information about environmental seasonality, PC2H: resumed information about humidity, and PC3P: principally correlated with precipitations.

study, concentrated in the humid months of spring (Sánchez *et al.*, 2007).

Among leptodactylids, the cryptic co-genetics *L. latrans* and *L. chaquensis* differed markedly in the spread of their activity periods. These species have a quite similar diet and the same feeding strategy (López *et al.*, 2005) and, even though they are syntopic in the Middle Paraná River system, *L. chaquensis* is typical of the Chaco region, where climate (temperature and rainfall) have a strong seasonality, whereas *L. latrans* is widely distributed in eastern South America (Cei, 1950; IUCN, 2010). Endogenous factors like differences in seasonality of gametogenesis of these species (Cei, 1950) may be driving the temporal segregation in activity length and season herein described, limiting the chance of any competition between them in their area of sympatry. The remaining species of the assemblage showed intensive activity, focused on their reproductive seasons (Moreira *et al.*, 2007; Peltzer and Lajmanovich, 2007; Both *et al.*, 2008; Sánchez *et al.*, 2009). Canavero *et al.* (2009) suggested that environmental seasonality and biotic features will determine assemblage composition and richness and, thus, the proportion of species with prolonged, intensive and explosive activity should gradually change through environmental/latitudinal gradients (Sánchez *et al.*, 2007; Duré *et al.*, 2008).

Seasonal changes in size structure of anuran populations represent tendencies related with reproductive cycles and juveniles recruitment periods (Watling and Donnelly, 2002). In most species there was a temporal segregation between peaks of abundances of adults and juveniles. Since the anuran diet is known to change throughout post-metamorphic ontogeny (Lajmanovich, 1996;

Hirai, 2002; López *et al.*, 2007), the cyclic variations in size composition of amphibian populations produces seasonal modifications in the structure of wetland trophic webs. Additionally, differences among families in the proportion of juveniles recruited vs adult population size indicate the existence of two strategies within assemblage species; while high rates of recruitment of leptodactylids and leiperids could lead to a fast replacement of adult population, the replacement could take several years among hylids and microhylids. Nevertheless, time to maturity and survival rate of each species will influence replacement periods.

Juveniles recruited in an explosive or intensive manner during the warm season, independently of whether they were explosive, intensive or prolonged in adult activity strategy, indicate that there is an environmental restriction for the metamorphosis period and timing with resources availability. The marked seasonal segregation between the peak of adult activity and recruitment of *H. pulchellus* juveniles is explained by the long larval period of this species (Lajmanovich, 2000). During a systematic annual survey (2004-2005) of an amphibian larval assemblage in Los Sapos island (4km southeast from Sirgadero Island), Scarabotti (2009) found *H. pulchellus* tadpoles in different developmental stages from April to October, connecting adult and juvenile activity peaks described in this study. Overwintering tadpoles of this species make it the earliest juvenile recruiter of the warm season in the assemblage, with a peak in early spring. *Dendropsophus nanus* was the only species recruiting juveniles in low abundance during a long period of time (flat peak in autumn). However, the ecologically similar and cryptic co-generic *D. sanborni* (Gallardo, 1987; Menin *et al.*, 2005) was an explosive recruiter (peak in early summer). The segregation of reproductive and life history traits between these species may contribute to a reduction of competition possibilities

(Menin *et al.*, 2005). The recruitment patterns of *L. latrans* and *L. chaquensis* were more similar than adults' activity pattern, but with slight difference in intensity and beginning date. Besides, *L. latrans* recruitment peak was one month earlier than that reported by Sánchez *et al.* (2007) in Pre-Delta National Park (PDNP, Lower Paraná River). Also, *P. limellum* and *E. bicolor* recruitment patterns clearly differ from those described in PDNP (Sánchez *et al.*, 2007), so local factors could be triggering and timing reproduction and metamorphosis in each population (Lavilla and Rouges, 1992).

A series of environmental determinants such as temperature, rainfall, humidity, among others have been classically called to explain amphibian seasonal reproductive activity (Bertoluci, 1998; Saenz *et al.*, 2006; Peltzer and Lajmanovich, 2007; Sánchez *et al.*, 2007; Both *et al.*, 2008; Canavero *et al.*, 2008). In tropical regions, rainfall seems to be the main factor controlling anuran reproductive patterns, because frogs are vulnerable to desiccation and extremely dependent on water availability (Moreira *et al.*, 2007) while temperature becomes a major determinant in temperate climates (Saenz *et al.*, 2006). Nevertheless, Canavero and Arim (2009) recently highlighted that the poor performance of precipitation and/or temperature against photoperiod as determinants of amphibian activity, and the wide use of this last environmental cue in very different organisms, suggest photoperiod to be the most plausible variable leading to seasonal variation in amphibian activity. Seasonality (represented by temperature and photoperiod), humidity and rainfall were significant predictors of seasonal changes in Sirgadero Island assemblage richness and of several individual species activity.

Flood pulse (hydrometric level) was an important predictor of changes in assemblage richness and constituted the model of activity of every species, being the only predictor variable for some of them.

Flood pulses represent one of the most important phenomena ruling cyclical dynamics in the Paraná River system (Neiff, 1990) and other large rivers with alluvial valleys (Junk *et al.*, 1989). For amphibians, variations in hydrological level provide habitat diversity for reproduction and development of diverse species (Lajmanovich, 2000; Moreira *et al.*, 2007) and floods were recognized as a main factor controlling amphibian richness on river-associated assemblages (Real *et al.*, 1993; Peltzer and Lajmanovich, 2007; Sánchez *et al.*, 2007; Scarabotti, 2009). For anuran assemblages of large floodplain rivers, flood pulse may act as an important proximate factor regulating assemblage dynamics, due to its shaping effect on ultimate factors such as reproductive habitat seasonality, quality and diversity, predation and food resources availability (Eterovick and Sazima, 2000; Lajmanovich, 2000; Poulin *et al.*, 2001; Peltzer and Lajmanovich, 2007; López, 2009; Scarabotti, 2009). Nevertheless, climate change and human activities (dams, roads embankments, wetland drainages, etc.) are increasingly affecting the Paraná River flood dynamics (Trenberth and Hoar, 1997; Camilloni and Barros, 2003; Prieto, 2007), potentially impacting on amphibian assemblages (Peltzer *et al.*, 2003).

Anuran species of Sirgadero Island assemblage showed high temporal nestedness, a fact probably related to the environmental seasonality (Canavero *et al.*, 2009). A positive co-occurrence pattern suggests a lack of segregation of species pairs, both at adult activity level and juvenile recruitment pattern. Studies based on male calling activity frequently show negative co-occurrence patterns (Bertoluci, 1998; Prado *et al.*, 2005) that could be interpreted as temporal segregation on breeding activity (Moreira *et al.*, 2007; Canavero *et al.*, 2009), even though species reproductive segregation does not necessarily imply seasonal segregation on other activities, like adults foraging and juvenile recruitment. Since the present

survey design is not limited to calling activity, we could identify the real coexistence pattern of species, regardless of whether amphibian were reproducing, foraging, migrating, etc.

Taking into account the extensive distribution range of all the species analyzed, future studies should investigate the degree of plasticity of seasonal activity patterns (not restricting themselves to adult calling season) and size structure dynamics of the species herein described, and how these features determine the characteristics of assemblages.

Conclusions

Since amphibians of Sirgadero Island utilize the same environment, where resources such as food, breeding sites and refuge are abundant, differences among species in width and intensity of adult activity periods and juvenile recruitment patterns should be the consequence of combined effects of evolutionary fixed life history traits (profound factors) and present day ecological interactions, such as competition, predation, climate, floods periodicity and intensity (proximate factors). Hence, the characteristics of assemblages such as richness, structure and dynamic (nestedness, species co-occurrence) are the result of a number of variables, among which some may be affected by climate changes or human activities.

On the one hand, local habitat variables and landscape factors probably are responsible for differences in the activity patterns of the populations analyzed and of these species in other environments (Lavilla and Rouges, 1992; Afonso and Eterovick, 2007; Canavero *et al.*, 2009). On the other hand, abrupt rise of juveniles richness and abundance during the summer strongly coordinates breeding activity periods (Sánchez *et al.*, 2009), suggesting that reproduction and recruitment are adjusted to match with favorable environmental conditions and resource availability during the warm and rainy season. Finally, there is evidence that

flood pulses play an important role among the determinants of amphibian activity on the studied floodplains.

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