

ANURAN TEMPORAL OCCUPANCY IN A TEMPORARY POND FROM THE ATLANTIC RAIN FOREST, SOUTH-EASTERN BRAZIL

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Temporal distribution, reproductive mode and pattern, and calling activity were recorded for an anuran community during 13 months in a temporary pond in south-eastern Brazil. Nineteen species from four families (Bufonidae, Hylidae, Leptodactylidae and Microhylidae) were recorded at the pond. Hylidae was represented by the most species, followed by the family Leptodactylidae. The reproductive diversity of the community was represented by five reproductive modes, and three reproductive patterns (prolonged, explosive and opportunistic breeders). Reproductive temporal analysis showed an anuran succession along different conditions of the pond (dry, flooded, and drying pond), probably related to specific reproductive mode and physiological tolerance to temperature and precipitation. Leptodactylid frogs were the first breeders, reproducing before the pond filled up, followed by species that lay eggs in the vegetation above water, and lastly the largest aggregation of Hylidae took place. *Stereocyclops incrassatus* (Microhylidae) was the unique explosive breeder in the community, congregating in the pond just after the first heavy rain at the beginning of the rainy season. Multiple regression analysis showed that air temperature, pond depth, and weather condition were the best predictors to explain the calling activity in anuran species. Hylid and leptodactylid frogs responded in a different way to environmental factors: in general, positive associations for hylid frogs, and negative associations for leptodactylid frogs. There were also species-specific differences in chorus attendance related to environmental factors within each family.

Key words: Anura, breeding patterns, community, reproductive pattern, succession

INTRODUCTION

Studies on anuran communities in the Atlantic Rain Forest have increased in the last 15 years (e.g. Cardoso *et al.*, 1989; Haddad & Sazima, 1992; Rossa-Feres & Jim, 1994, 1996; Bertoluci, 1998; Eterovick & Sazima, 2000; Bertoluci & Rodrigues, 2002). However, the number of studies conducted on temporary ponds is still far below the number of studies on permanent ponds. The former have focused on reproductive aspects related to the hydroperiod of the pond, such as tadpole phenotypic plasticity (e.g. Tejedo & Reques, 1994; Blaustein *et al.*, 1999) and anuran succession (e.g. Dixon & Heyer, 1968; Heyer, 1973; Wiest, 1982). However, we know of no reports about anuran succession in temporary ponds of the Atlantic Rain Forest.

The term anuran succession used here and in community studies on temporary ponds refers to changes in species composition related to temporal resource, such as species arrival, chorus attendance and/or tadpoles phenology. This may correspond to a certain degree of temporal partitioning, so that the arrival of a new species does not necessarily result in the disappearance of another (Dixon & Heyer, 1968; Heyer, 1973; Wiest, 1982). Beyond information on species diversity, these works may provide possible association among species composition and local features, including environmental and biotic factors (Dixon & Heyer, 1968; Wiest, 1982;

Gottsberger & Gruber, 2004). In turn, this may reveal community structure, which can be regulated through predictable interactions of rain, hydroperiod, predation, and competition (Semlitsch *et al.*, 1996).

Among the environmental factors affecting timing of reproduction and the length of the breeding season in tropical anurans, rainfall appears to be the most important abiotic factor (Inger, 1969; Crump, 1974; Aichinger, 1987; Wright, 1991; Donnelly & Guyer, 1994; Bevier, 1997; Gottsberger & Gruber, 2004), followed by air temperature (Bertoluci, 1998; Bertoluci & Rodrigues, 2001). Although anuran calling and breeding activities in seasonal tropical sites are intense during the rainy season, differences in the arrival of the species and reproductive phenology are associated with their reproductive mode (Gottsberger & Gruber, 2004).

In general, little effort has been directed at determining how environmental and/or biotic conditions act on community structure in temporary ponds (e.g. Dixon & Heyer, 1968; Heyer, 1973; Wiest, 1982; Gottsberger & Gruber, 2004). Herein, we describe the anuran temporal occupancy in a temporary pond, examining the possible influence of environmental factors on the breeding activity and number of individuals and species participating in chorus activity. Three major questions are addressed: (1) Does temporal occupancy show anuran succession? (2) Are calling activities of the species affected by the environmental factors air temperature, light level, pond depth, and weather condition? (3) If so, are there common pat-

terns of responses to the environmental factors within each family and between families?

MATERIALS AND METHODS

STUDY SITE

The study site was a temporary pond with surface area of approximately 170 m², located in an open area at the forest edge at Palmital (22°50'48" S; 42°27'16" W), Municipality of Saquarema, State of Rio de Janeiro, south-eastern Brazil, inside the Atlantic Rain Forest domains (*sensu* Ab'Saber, 1977). Observations were made on 84 nights from July 1999 to July 2000, consisting of 411 hours of fieldwork which was conducted monthly when the pond was dry (from July to November 1999, and from March to July 2000), and fortnightly when the pond filled up (from December 1999 to February 2000). Each visit lasted a mean of five consecutive nights. In general, fieldwork started before sunset and finished around midnight, except for nights when community calling activity was recorded, when fieldwork lasted the whole night.

SURVEY OF REPRODUCTIVE ACTIVITIES

To evaluate the species reproductive period on a seasonal scale, we defined the potential reproductive period as the period when males were involved in pre-reproductive activity (calling), and defined reproductive period as the period when direct signs of reproduction (pairs in amplexus, ovulated females, clutches or tadpoles at early stages) were observed.

Reproductive temporal pattern of breeding species was defined according to the time spent in reproductive activities (permanency of chorus) in the pond: prolonged breeders (species with a continuous potential reproductive period during the rainy season, dry season or both; chorus activity continuous, with or without rain), opportunistic breeders (species with a short potential reproductive period related to a specific environmental factor, especially, rain; chorus activity in drizzling or heavy rainy nights), and explosive breeders (species with a unique potential reproductive period; chorus activity from one to seven days). Classification of species according to its reproductive mode follows Haddad & Prado (2005).

Community calling activity was measured by the number of calling species quantified during the whole night and the number of calling individuals at the time of peak activity. We counted the number of males acoustically active for each species, during the whole night, in each hour, and determined the activity peak (the time when the largest number of males present at the pond was calling).

RECORDING OF ABIOTIC FACTORS

Air temperature at 1.50 m height above ground (measured with a mercury thermometer to 0.5° C precision), pond depth (in cm) at the deepest point, and

weather conditions during the night (no rain, drizzling rain, or heavy rain) were recorded during fieldwork. The categorical values for each weather condition were 1, 2 and 3, respectively. Light level (categorical measure based upon the lunar calendar – Yearly Publication of the National Observatory 1999, and 2000), and monthly rainfall (in mm; recorded at Estação Rio Mole, located approximately 10 km from the study area) were also obtained for the study period. The categorical values for light level varied from 1 (new moon) to 6 (full moon).

DATA ANALYSIS

We examined possible associations between environmental factors and community calling activity in two ways: (1) a graphical analysis of overlapping figures of monthly rainfall, mean values of air temperature and maximum pond depth (from consecutive nights), and number of calling males per month in the families Hylidae and Leptodactylidae, and (2) statistical analysis – stepwise multiple regression analyses (Zar, 1984) – to determine the relationship between environmental factors and the abundance of calling species and calling males in the whole community, in both families (Hylidae and Leptodactylidae), and between environmental factors and the abundance of calling males in each species. Only species that formed choruses (arbitrarily defined as three or more individuals calling) were analyzed in these statistical tests.

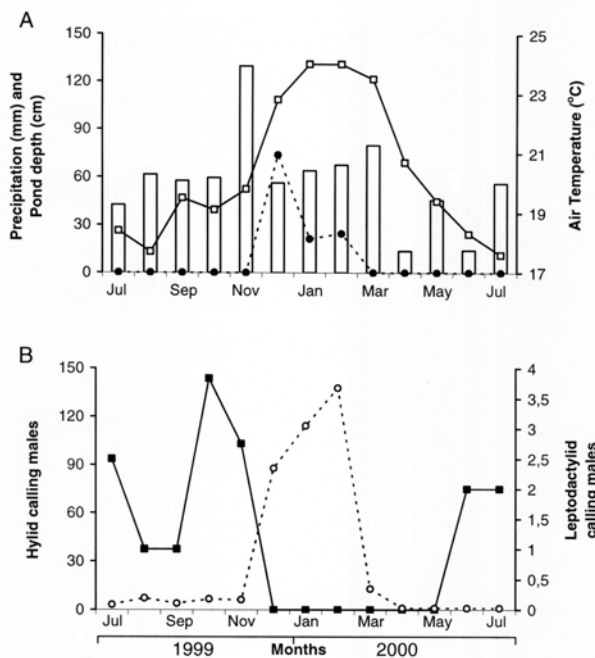


FIG. 1. A, mean air temperature (open squares), mean pond depth (filled circles) and monthly precipitation (bars) at the study site from July 1999 to July 2000. B, mean number of calling males in the families Hylidae (open circles) and Leptodactylidae (filled squares) at the study site from July 1999 to July 2000.

RESULTS

CLIMATIC ASPECTS

Climate was seasonal, with dry and rainy periods (Fig. 1). From July to November 1999, and from March to July 2000, the pond was dry; in December 1999, it was completely flooded (mean±SD pond depth = 70.4±9.8 cm, $n=11$; and from January to February, pond depth fluctuated according to rain (mean±SD pond depth = 23.0±7.8 cm, $n=11$).

SPECIES COMPOSITION

From 19 calling species belonging to four families (Bufonidae, Hylidae, Leptodactylidae and Microhylidae) recorded at the pond, 15 bred (Table 1). Hylid frogs included the highest number of species, corresponding to 68.4% of the total number, followed by leptodactylids, with 21.0%; the other families constituted together the remaining 10.6%. Reproductive diversity of the breeding community encompassed five

reproductive modes: three for the breeding hylid frogs and two for the leptodactylid frogs (Table 1). The predominant reproductive mode was the most generalist (Mode 1), corresponding to 53.3% of reproductive diversity.

REPRODUCTIVE ACTIVITIES

Temporal occupancy. Potential and realized reproductive period are presented in Table 1. In general, males started to call before females arrived at the pond. Leptodactylid frogs were the pioneers, with potential and realized reproductive periods preceding the hydroperiod of the pond. Realized reproductive period of hylid frogs coincided with the period while the pond was full (although potential reproductive period from *Dendropsophus decipiens*, *Phyllomedusa burmeisteri* and *P. rohdei* began before this). *Chaunus ornatus* and *Leptodactylus spixii* did not form chorus, and for this reason, were not included on analyses.

TABLE 1. Anuran calling species of the temporary pond in Saguarema, south-eastern Brazil, from July 1999 to July 2000. Potential reproductive period (P), realized reproductive period (R), and reproductive mode *sensu* Haddad & Prado (2005): Mode 1 (eggs and exotrophic tadpoles in lentic water), Mode 4 (eggs and early larval stages in natural or constructed basins; subsequent to flooding, exotrophic tadpoles in ponds or streams), Mode 11 (foam nest floating on pond; exotrophic tadpoles in pond), Mode 24 (arboreal eggs hatching into exotrophic tadpoles that drop in lentic water), and Mode 30 (foam nest with eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds).

Species	1999						2000							Reproductive mode
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	
Bufonidae														
<i>Chaunus ornatus</i>								P						1
Hylidae														
<i>Dendropsophus anceps</i>						R								1
<i>D. bipunctatus</i>						R	R	R						1
<i>D. decipiens</i>						R	R	R	R					24
<i>D. elegans</i>						R	R	R						1
<i>D. minutus</i>						R	R	P						1
<i>D. seniculus</i>							R	R						1
<i>Hypsiboas albomarginatus</i>								P						1
<i>H. faber</i>						R	P							4
<i>Phyllomedusa burmeisteri</i>					P	R	R	R						24
<i>P. rohdei</i>	P	P	P	P	P	R	R	R	R	P	P			24
<i>Scinax argyreornatus</i>						P	P	P						1
<i>S. aff. x-signatus</i>						R	R	R						1
<i>Trachycephalus nigromaculatus</i>						R		P						1
Leptodactylidae														
<i>Leptodactylus</i> aff. <i>bokermanni</i>	P	R	P	R										30
<i>L. mystacinus</i>		P	P	R	P									30
<i>L. spixii</i>		P												30
<i>Physalaemus signifer</i>				P	R									11
Microhylidae														
<i>Stereocyclops incrassatus</i>						R								1

TABLE 2. Parameters of the multiple regression explaining the abundance of calling species and calling males in the families Hylidae (H) and Leptodactylidae (L), and in each chorusing species. For each predictor variable the parameters shown are the slope $\pm$ SE, t -test, and significance level. For multiple regression of each chorusing species, F -test, and the resulting P -value is also showed.

Family	Variables	Calling species			Calling males		
		slope $\pm$ SE	t_{35}	P -level	slope $\pm$ SE	t_{35}	P -level
H	Air temperature	0.31 $\pm$ 0.09	3.33	0.002	9.28 $\pm$ 2.63	3.53	0.001
	Light level	0.23 $\pm$ 0.20	1.14	0.26	9.26 $\pm$ 5.73	1.61	0.11
	Pond depth	0.05 $\pm$ 0.01	5.50	<0.0001	0.93 $\pm$ 0.28	3.36	0.002
	Weather condition	1.82 $\pm$ 0.39	4.65	<0.0001	61.61 $\pm$ 10.90	5.65	<0.001
L	Air temperature	-0.05 $\pm$ 0.03	-1.44	0.16	-0.17 $\pm$ 0.14	-1.19	0.24
	Pond depth	-0.005 $\pm$ 0.004	-1.38	0.18	-0.02 $\pm$ 0.01	-1.36	0.20
	Weather condition				0.64 $\pm$ 0.58	1.19	0.24

Species	Variables	Calling males				
		slope $\pm$ SE	t	P -level	F	P -value
<i>Dendropsophus anceps</i>	Light level	0.23 $\pm$ 0.15	1.48	0.14	[3,36]=16.29	<0.0001
	Pond depth	0.04 $\pm$ 0.006	6.95	<0.0001		
	Weather condition	0.58 $\pm$ 0.29	1.95	0.06		
<i>D. bipunctatus</i>	Air temperature	1.86 $\pm$ 0.62	3.00	0.005	[4,35]=16.70	<0.0001
	Light level	5.50 $\pm$ 1.35	4.08	0.0002		
	Pond depth	0.17 $\pm$ 0.06	2.64	0.01		
<i>D. decipiens</i>	Weather condition	14.93 $\pm$ 2.57	5.82	<0.0001	[3,36]=8.32	0.0002
	Air temperature	0.71 $\pm$ 0.46	1.53	0.14		
	Pond depth	0.07 $\pm$ 0.05	1.42	0.16		
<i>D. elegans</i>	Weather condition	7.16 $\pm$ 1.79	4.00	0.0003	[2,37]=42.54	<0.0001
	Air temperature	1.32 $\pm$ 0.59	2.24	0.03		
	Pond depth	0.34 $\pm$ 0.06	5.63	<0.0001		
<i>D. minutus</i>	Light level	-0.60 $\pm$ 0.55	-1.09	0.28	[2,37]=4.75	0.01
	Pond depth	0.06 $\pm$ 0.02	2.72	0.009		
<i>D. seniculus</i>	Air temperature	1.67 $\pm$ 0.52	3.20	0.002	[3,36]=16.31	<0.0001
	Light level	2.46 $\pm$ 1.42	1.74	0.09		
	Weather condition	17.35 $\pm$ 2.69	6.45	<0.0001		
<i>Hypsiboas albomarginatus</i>	Air temperature	0.04 $\pm$ 0.04	1.22	0.23	[3,36]=1.85	0.15
	Light level	0.19 $\pm$ 0.10	1.92	0.06		
	Weather condition	0.31 $\pm$ 0.19	1.63	0.11		
<i>H. faber</i>	Air temperature	0.18 $\pm$ 0.04	4.56	<0.0001	[1,38]=20.84	<0.0001
<i>Leptodactylus</i> aff. <i>bokermanni</i>	Air temperature	-0.33 $\pm$ 0.08	3.33	0.0001	[2,37]=11.84	<0.0001
	Light level	0.39 $\pm$ 0.20	1.14	0.06		
<i>L. mystacinus</i>	Air temperature	-0.21 $\pm$ 0.12	-1.79	0.08	[3,36]=11.42	<0.0001
	Light level	-0.49 $\pm$ 0.23	-2.11	0.04		
	Pond depth	-0.04 $\pm$ 0.01	-3.15	0.003		
<i>Phyllomedusa burmeisteri</i>	Air temperature	0.75 $\pm$ 0.16	4.76	<0.0001	[3,36]=55.00	<0.0001
	Pond depth	0.10 $\pm$ 0.02	6.14	<0.0001		
	Weather condition	2.63 $\pm$ 0.61	4.34	0.0001		
<i>P. rohdei</i>	Air temperature	0.88 $\pm$ 0.25	3.56	0.001	[3,36]=22.95	<0.0001
	Pond depth	0.09 $\pm$ 0.02	3.59	0.0009		
	Weather condition	2.08 $\pm$ 0.95	2.18	0.03		
<i>Physalaemus signifer</i>	Air temperature	-0.15 $\pm$ 0.06	-2.50	0.02	[3,36]=4.99	0.005
	Light level	-0.29 $\pm$ 0.16	-1.76	0.09		
	Weather condition	0.51 $\pm$ 0.31	1.62	0.11		
<i>Scinax argyreornatus</i>	Pond depth	1.04 $\pm$ 0.36	2.91	0.006	[2,37]=6.79	0.003
	Weather condition	0.02 $\pm$ 0.008	2.60	0.01		
<i>S. aff. x-signatus</i>	Air temperature	1.06 $\pm$ 0.49	2.14	0.04	[2,37]=6.79	0.003
	Weather condition	7.51 $\pm$ 2.40	3.12	0.003		
<i>Trachycephalus nigromaculatus</i>	Air temperature	0.76 $\pm$ 0.47	1.60	0.12	[2,37]=6.30	0.004
	Weather condition	7.52 $\pm$ 2.30	3.26	0.002		

Among leptodactylids, *L. aff. bokermanni* and *L. mystacinus*, two species that build foam nests in burrows and have feeding tadpoles in ponds (after flooding), were the first to colonize the pond when it was completely dry. Potential and realized reproductive periods of *Physalaemus signifer* concentrated on drizzling rainy nights, one to two months before the pond filled completely. After leptodactylids, hylids with arboreal eggs, *D. decipiens*, *P. burmeisteri* and *P. rohdei*, initiated their realized reproductive periods, followed by *Trachycephalus nigromaculatus* and *Stereocyclops incrassatus* (Microhylidae). These last two species exhibited a punctual realized reproductive period, concentrating on the beginning of the rainy season, after heavy rain, although males of *T. nigromaculatus* also formed choruses on one night of heavy rain in February, but did not breed. A large number of clutches and tadpoles in advanced stages of *D. decipiens*, *P. burmeisteri*, *P. rohdei*, and tadpoles of *S. incrassatus* and *T. nigromaculatus* were found soon after the first rains of the period, indicating that the first three species have bred before the pond filled. A large breeding aggregation of hylid species in the pond occurred during the period while the pond was full (from December 1999 to February 2000). Hylid frogs (e.g. *D. decipiens* and *P. rohdei*) that bred late in the season (March 2000) lost their clutches.

Temporal pattern. Leptodactylid frogs were prolonged breeders during the dry season. One exception was *P. signifer*, whose choruses occurred on drizzling rainy nights ($n=4$), when a thin layer of water accumulated in the pond; thus, we considered it an opportunistic breeder. Most hylid frogs were prolonged breeders during the rainy season, but *D. decipiens*, *D. seniculus*, *Scinax* aff. *x-signatus* and *T. nigromaculatus* were considered opportunistic breeders. *Dendropsophus decipiens* bred on drizzling rainy nights, while *D. seniculus*, *S. aff. x-signatus* and *T. nigromaculatus* formed choruses just after heavy rainy nights. Only one species exhibited explosive breeding: *S. incrassatus*, mating only during the first heavy rain at the beginning of the rainy season, when the pond filled up (early December).

Abiotic factor associations. Regarding calling species and calling males of the whole community, three variables (air temperature, pond depth and weather condition) were selected by the forward step-wise model ($F_{3,36}=24.36$; $P<0.001$; $F_{3,36}=15.49$; $P<0.001$, respectively) in the following decreasing order of predictive value: pond depth, weather condition and air temperature for calling species; and air temperature, weather condition and pond depth for calling males. Concerning calling species and calling males of hylid frogs, the four variables (air temperature, light level, pond depth and weather condition) were selected by the model ($F_{4,35}=28.43$; $P<0.001$; $F_{4,35}=20.75$; $P<0.001$, respectively). For calling species of leptodactylid frogs, two variables (air temperature, and pond depth) were selected by the model ($F_{2,37}=5.23$; $P<0.01$), while for

calling males of leptodactylid frogs, the variables selected were pond depth, weather condition, and air temperature ($F_{3,36}=3.51$; $P<0.02$). The predictive values of the selected variables for the regression analyses explaining the abundance of calling species and calling males in both families are in Table 2. Hylid and leptodactylid frogs responded in a different way to environmental factors. Chorus attendance in hylids was positively associated with air temperature and pond depth, while in leptodactylids it was negatively associated with the same factors. Although not all environmental factors were selected by the models – and those that were contributed in different ways – in general whenever associations occurred, they were positive for hylid species, and negative for leptodactylid species (Table 2).

Reproductive aggregations of leptodactylid frogs occurred during the dry period (dry pond), and the greatest concentration of calling males was coincident with the period of lowest air temperature (Fig. 1). In contrast, chorus attendance of hylid frogs increased with air temperature. However, the seasonal variation in the number of calling males did not follow the fluctuation of rainfall and pond depth, indicating that other factors may have contributed to the observed result.

DISCUSSION

Microhabitat diversity, niche range and niche overlap between species are non-mutually exclusive categories used to explain species diversity in a community (Inger & Colwell, 1977). Open areas offer a major horizontal distribution of calling sites for species, benefiting ground or litter species, like leptodactylid frogs, while areas with higher vegetation strata offer a vertical distribution of species related to environmental stratification, benefiting arboreal species, like hylid frogs (Cardoso *et al.*, 1989). We did not find this pattern in our study. Our data showed that although the pond was located in an open area, the family Hylidae contributed the largest number of species (68.4% versus 31.6% in the remaining families). According to Murcia (1995), species composition and the relative abundance of species can be positively or negatively affected by edge effects, depending on the taxon. The great species diversity in communities located on or near the forest edge (e.g. Blamires *et al.*, 1997; Pombal, 1997; Arzabe *et al.*, 1998; and the present study site) could be explained by the invasion of matrix-associated species not normally found in primary forest (Tocher *et al.*, 1997).

Temporal occupancy analysis showed that neither species arrival nor chorus attendance on pond were synchronized among the whole community, characterizing an anuran succession along different stages of the pond (dry and flooded). Such succession was related to the reproductive mode of the species, following the next order of appearance: leptodactylids with foam nest (*L. aff. bokermanni*, *L. mystacinus*, and *P. signifer*), hylids with arboreal eggs (*D. decipiens*, *P. burmeisteri*, and *P. rohdei*), the explosive breeder microhylid (*S.*

incrassatus), and hylids with aquatic eggs (*D. anceps*, *D. bipunctatus*, *D. elegans*, *D. minutus*, *D. seniculus*, *Hypsiboas albomarginatus*, *H. faber*, *S. argyreornatus*, *S. aff. x-signatus*, and *T. nigromaculatus*). Differences in reproductive phenology of anuran species have already been attributed to their reproductive modes (Gottsberger & Gruber, 2004), and to specific physiological characters, such as levels of tolerance to temperature and precipitation (Duellman & Trueb, 1986; Wiest, 1982).

Species that bred before the pond fills (leptodactylids with foam nest and hylid with arboreal eggs) obtained a competitive advantage of the type of nest or oviposition site, which ensures protection against desiccation, development and survival of eggs and tadpoles during a dry period (Dixon & Heyer, 1968; Duellman & Trueb, 1986). Similar patterns for foam-nesting species and leaf-breeding species were found, respectively, by Arzabe (1999) during a study conducted at a temporary pond in the Brazilian Caatinga, and by Donnelly & Guyer (1994), studying a hylid community in north-eastern Costa Rica. They observed that *Agalychnis callidryas*, as a species of the sub-family Phyllomedusinae, does not depend directly on water to breed, at least in the initial phase, as the *Phyllomedusa* species studied. Moreover, *P. burmeisteri* and *P. rohdei* liberate a great number of eggless capsules with the eggs, and fold the leaf around the eggs, allowing great moisture retention (Abrunhosa & Wogel, 2004; Wogel et al., 2005). The case of *D. decipiens* is similar: the only requirement for the developmental success is the synchrony between spawning and rain, since this species does not liberate eggless capsules and the clutches remain exposed, although oviposition site can be, generally, sheltered, in other words, protected by surrounded leaves (pers. obs.). The lack of rain in subsequent days from clutch deposition can be lethal to eggs, as a result of dehydration. During a study conducted at a neotropical temporary community in French-Guiana, Gottsberger & Gruber (2004) observed that breeding in *Phyllomedusa* species occurred later in the rainy season than in *Dendropsophus* species, which have arboreal eggs. The rolling of leaves around the eggs in *Phyllomedusa* species may prevent desiccation of the eggs. Sheltered oviposition sites seemed to correspond with early reproduction in *D. decipiens*. With the exception of *D. decipiens*, members of the sub-family Phyllomedusinae initiate reproductive aggregations before species of the sub-family Hyliinae.

A stable hydroperiod at the reproductive site in temporary ponds, especially after the first rains, is one of the factors responsible for the aggregation of species that spawn directly in water (Arzabe et al., 1998). We observed this in the studied community for hylid species. Some of these formed choruses only after heavy rain (*D. seniculus*, *S. aff. x-signatus*, and *T. nigromaculatus*); others, on drizzling rainy nights (*D. decipiens*); and the majority, when the pond resembles a permanent habitat (especially in sequentially rainy nights). Similar patterns

of aggregations related to rain were observed in other communities (Wiest, 1982; Aichinger, 1987; Gascon, 1991; Arzabe et al., 1998; Gottsberger & Gruber, 2004).

Semlitsch et al. (1996) observed that the annual dynamic of a temporary pond varied among years, and just when the pond filled up, many species were at the peak of their reproductive activity. During the 13 months of study, the pond was filled during a short period (about three and a half months) in December, 1999 when the major reproductive aggregation of the community was observed, based upon the number of calling species and calling males, corroborating the results of Semlitsch et al. (1996).

Potential reproductive period was greater than realized reproductive period for most species. In general, males started to call before females arrived at the pond, which could be important in attracting more males to increase chorus intensity, to finally attract females. However, some species (*H. albomarginatus* and *S. argyreornatus*) did not breed in this pond, and this was consistent with the small number of individuals and calling males observed.

Although we have defined reproductive temporal pattern of breeding species, it is important to clarify that these patterns can change from site to site, and among years. So, a species classified as an opportunistic breeder may have a prolonged breeding season at another site or a different year. Selective pressures at each pond can result in different reproductive temporal patterns for the same species (Wells, 1977), just as it does with *P. signifer*. In our study, this species exhibited reproductive activity only over four nights, and it was classified as an opportunistic breeder, but other populations of *P. signifer* have shown a longer period of breeding activity (see Wogel et al., 2002). In general, the specific conditions to initiate realized reproductive period of each species are relatively fixed: determined by reproductive mode or physical factors, but if there are no ideal breeding conditions, some species exhibit plasticity in their reproductive mode, as observed for *Hypsiboas boans* and *H. crepitans* (Caldwell, 1992), *H. rosenbergi* (Höbel, 1999), and *Physalaemus spiniger* (Haddad & Pombal, 1998). Annual patterns of calling and breeding activities of *D. minutus*, *D. seniculus*, *H. faber*, and *L. mystacinus* (see Rossa-Feres & Jim, 1994; Bertoluci, 1998; Bertoluci & Rodrigues, 2002) in other Atlantic Rain Forest sites are similar to those in our study. According to the definitions of reproductive temporal patterns established in our study, all of these species would be classified as prolonged breeders with the exception of *D. seniculus*, whose temporal pattern in that study (after copious spring rains, see Bertoluci, 1998) suggests an opportunistic breeding pattern.

The forward stepwise multiple regressions revealed that air temperature, pond depth, and weather condition were the best predictors of calling activity in anurans. Hylid and leptodactylid frogs responded in a different

way to environmental factors. Chorus attendance in leptodactylid frogs was associated with cooler nights during the dry season, while in hylid frogs it was associated with warmer nights of the rainy season. This contrasting pattern may be due to differences in reproductive mode between hylid and leptodactylid frogs. Studies in the Atlantic Rain Forest in which environmental factors (e.g. air temperature) were correlated with numbers of calling species (Bertoluci, 1998; Bertoluci & Rodrigues, 2002) did not report differences between hylid and leptodactylid frogs.

Associations between environmental factors and calling activities indicated species-specific differences in chorus attendance. All the significant negative associations between environmental factors and calling activities were exhibited by foam-nesting species. On the other hand, hylid species revealed positive associations with environmental variables. Almost all opportunistic species showed positive associations with weather conditions, except for *P. signifer* which showed strong associations with air temperature.

Concluding, anuran succession in a temporary pond depends on the particular ecology of the species involved (Barbault, 1991), specifically on the reproductive mode and reproductive temporal pattern. Temporal partitioning decreases species interactions in an anuran succession pond community (Crump, 1982; Garcia & Narins, 2000; present study), however considering time as the sole reproductive resource responsible for species coexistence is inappropriate, since congeneric species exhibited temporal overlap yet did not hybridize, showing that other factors may contribute to the reproductive isolating mechanisms.

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