

Resource use and coexistence of two syntopic hylid frogs (Anura, Hylidae)

Marcelo Menin^{1,3}, Denise de C. Rossa-Feres² & Ariovaldo A. Giaretta¹

¹ Instituto de Biologia, Universidade Federal de Uberlândia. 38400-902 Uberlândia, Minas Gerais, Brasil.

² Departamento de Zoologia e Botânica, Universidade Estadual Paulista. Rua Cristóvão Colombo 2265, 15054-000 São José do Rio Preto, São Paulo, Brasil.

³ Present address: Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia. Avenida André Araújo 2936, 69011-970 Manaus, Amazonas, Brasil. E-mail: menin@inpa.gov.br

ABSTRACT. The objectives of this study were to measure and compare niche breadth and overlap of males of *Hyla nana* Boulenger, 1889 and *Hyla sanborni* Schmidt, 1944 in three neighboring ponds. The measured niche dimensions were seasonal occurrence, call site, and diet. The reproductive season of *H. sanborni* was longer in permanent ponds, whereas *H. nana* had a longer reproductive season in the temporary pond. Call site characteristics were similar for both species, however *H. sanborni* called from higher perches than *H. nana*. Diptera (Nematocera) were the most consumed item by both species in the three ponds but, in general, *H. nana* ingested larger prey than *H. sanborni*. For both species, the consumption of prey types was correlated with the availability in the environment. The multidimensional overlap between *H. nana* and *H. sanborni* was higher in the permanent ponds than the temporary pond, in which *H. sanborni* was rare. These species differed in abundance among ponds, consumed prey of different sizes, and probably fed in different time periods. Moreover, the data obtained suggest that structural differences in the ponds may modify the dynamics of resource partitioning between the two species. Beside the great overlap found in the major niche dimensions analyzed the detected differences may be great enough to allow their coexistence.

KEY WORDS. *Hyla*, multidimensional overlap, niche breadth, niche overlap, resource partitioning.

RESUMO. **Uso de recursos e coexistência de duas espécies sintópicas de hílideos (Anura, Hylidae).** Os objetivos deste trabalho foram medir e comparar a amplitude e a sobreposição de nicho de *Hyla nana* e *Hyla sanborni* em três poças vizinhas. As dimensões de nicho medidas foram a ocorrência sazonal, o sítio de vocalização e a dieta, além da sobreposição multidimensional. Machos de *H. nana* são maiores que os de *H. sanborni*. A ocorrência sazonal de *H. sanborni* foi maior nos corpos d'água permanentes, enquanto *H. nana* apresentou maior período de ocorrência no corpo d'água temporário. O sítio de vocalização foi similar para ambas as espécies; no entanto, *H. sanborni* ocupou poleiros mais altos do que *H. nana*. Diptera (Nematocera) foi o item mais consumido por ambas as espécies nos três corpos d'água, mas, em geral, *H. nana* consumiu presas maiores que *H. sanborni*. O consumo de presas foi relacionado à sua disponibilidade no ambiente para ambas as espécies. A sobreposição multidimensional entre *H. nana* e *H. sanborni* foi mais alta nos corpos d'água permanentes do que no corpo d'água temporário, onde *H. sanborni* foi rara. Estas espécies ocorreram em abundâncias diferentes nos três corpos d'água, consumiram presas de tamanhos diferentes e provavelmente possuem diferença no período de alimentação. Além disso, os dados obtidos sugerem que diferenças estruturais nos corpos d'água podem modificar a dinâmica de partilha de recursos entre estas espécies. Apesar da grande sobreposição encontrada nos sítios de vocalização e categoria de presas ingeridas, diferenças detectadas em outras dimensões (ocorrência sazonal e volume de presas consumidas) podem ser suficientes para permitir a coexistência destas espécies.

PALAVRAS CHAVE. Amplitude de nicho, *Hyla*, partilha de recursos, sobreposição de nicho, sobreposição multidimensional.

The coexistence of similar species in ecological communities is one of the most perplexing problems in ecology (GORDON 2000). The degree of overlap in resource use amongst co-occurring species is variable (BOWKER & BOWKER 1979, ETGES 1987,

HEYER *et al.* 1990). In such a context, the 'position' of an organism within a community may be defined in terms of its patterns use of resources and its interaction with other organisms which use the same resources (PUTMAN 1994). This abstraction

of the position that an organism has within the community and its relationships with other organisms is expressed in the ecological niche concept (PUTMAN 1994). Major dimensions of niche are time, space and food (PIANKA 1994). The importance of these dimensions is variable, but generally the habitat dimension is often more important than the food-type dimension, which is often more important than the temporal dimension (SCHOENER 1974, GILLER 1984). Ecological differences in each of these three dimensions may reduce competition and facilitate the coexistence of a variety of species (PIANKA 1975).

Differential use of space and time or food was described in several anuran communities and, in most of them, food (LIMA & MAGNUSSON 1998) or microhabitat was the dimension that promoted the major segregation among species (CRUMP 1974, CARDOSO *et al.* 1989, ROSSA-FERES & JIM 1994). In closely related species of anurans, several mechanisms that promote coexistence were found: temporal segregation (BOWKER & BOWKER 1979, MAC NALLY 1985, DONNELLY & GUYER 1994), habitat segregation (DIAZ & VALENCIA 1985, LIZANA *et al.* 1990) and call site segregation (OLDHAM & GERHARDT 1975, CARDOSO & VIELLIARD 1990).

Hyla nana Boulenger, 1889 and *Hyla sanborni* Schmidt, 1944 are two small, closely related hylid frogs (snout-vent length 20 mm) included in the *Hyla microcephala* group and are very similar in morphology (LANGONE & BASSO 1987). They reproduce in temporary (ROSSA-FERES & JIM 2001) and permanent (this study) ponds in open areas. In a temporary pond in the northwest of the state of São Paulo in southeastern Brazil, these species occur syntopically during the reproductive season (ROSSA-FERES & JIM 2001).

In order to understand the factors allowing the coexistence between these species, we determined the breadth and overlap of three major niche dimensions: space, time and diet for the two species.

MATERIAL AND METHODS

Study area

The study was carried out in three ponds on the Santo Antonio farm, district of Nova Itapirema, municipality of Nova Aliança (21°11'S, 49°42'W), São Paulo State, Brazil: 1) PP: a permanent pond with Pontederiaceae, surface area of 50 x 30 m, depth 0.60 m, margins covered mainly with grasses (Poaceae and Cyperaceae) and Melastomataceae, Pontederiaceae and Typhaceae occurred in the water; 2) PG: a temporary pond surrounded by grasses (mean duration of hydroperiod seven months), surface area of 54 x 22 m, depth 0.70 m, with aquatic vegetation composed by Poaceae, Cyperaceae and some Pontederiaceae; 3) PT: a permanent pond with Typhaceae, Poaceae and Cyperaceae, surface area of 20 x 10 m, depth 0.70 m. The distance between PP and PG was 50 m, 100 m between PG and PT, and 120 m between PP and PT. The local climate is tropical seasonal (Cwa-Aw of Köppen), with a clearly defined rainy period (generally from October to March, but the rainfall may begin at any time between August and October) and

dry season (April to September). Average temperatures are 22°C in the rainy season and 18°C in the dry season. The area receives 85% of the total annual rainfall during the rainy season (ARID & BARÇA 1973).

The ponds were visited one day per month, from 6:00 to 11:00 p.m., during the rainy seasons of 1997/1998, 1999/2000 and 2000/2001, and weekly from July 1998 to June 1999. A total of 250 hours of fieldwork was performed during 50 visits to the ponds. The seasonal occurrence and call site of *Hyla nana* and *Hyla sanborni* were determined by the occurrence of calling males during each week period in 1998 and 1999. For the analysis of stomach contents, 135 males of *Hyla nana* (37, 62 and 36 individuals from PP, PG and PT, respectively) and 119 males of *Hyla sanborni* (50, 22 and 47 individuals) were collected.

The morphology of both species was characterized according to DUELLMAN (1970) and HEYER *et al.* (1990) using snout-vent length (SVL), mouth width, interorbital distance, eye diameter, tibia length, thigh length, tarsus length, foot length and hand length. SVL was measured with calipers (0.1 mm) and the other dimensions were measured with a grid calibrated for the objective (nearest 0.01 mm) of a stereomicroscope (10 x). The SVL were compared by analysis of variance (ANOVA) (ZAR 1999).

Since the tadpoles, clutches or amplexant individuals were not searched, the presence of calling males indicate breeding activity. To determinate the total number of calling males for each visit, the ponds were searched along their perimeters, two hours after the beginning of the vocalizations and all males found visually or acoustically were counted; three or four of these were collected to analysis of stomach contents in each visit.

The call site was characterized by the following variables: type of substrate (Poaceae, Cyperaceae, Pontederiaceae, Typhaceae or Melastomataceae), position of individuals in relation to water surface (parallel, perpendicular up or down and diagonal), perch height on vegetation in relation to water surface and distance from the edge, towards the inner or outside of the pond. The perch height and distance from the edge were compared by Mann-Whitney U tests. Kruskal-Wallis tests (H) were used for comparisons among ponds. When the null hypothesis was rejected, a nonparametric multiple comparison test was applied to determine which of the samples had significant differences occurred (ZAR 1999).

Prey availability (arthropods) was quantified to compare with prey consumption through monthly samples performed along one edge of each pond. Arthropods were collected with a 30 cm diameter net, by sweeping in vegetation along 10 m (on the bank and over water) to right and left from each one of three points, which were separated from one another by 5 m. The arthropods were preserved in 70% alcohol.

In order to determine the diet of *H. nana* and *H. sanborni*, the calling males were caught, anesthetized and killed in 20% alcohol and fixed in 10% formalin. In the laboratory, the frogs were dissected and the stomach contents identified to order or

family as indicated above. The length and width of each prey item were measured with calipers of 0.1 mm precision. When only fragments were found, they were compared with the specimens collected on the edge of the ponds for identification and inference of size. The volume of each prey was estimated using the spheroid volume formula (COLLI *et al.* 1992): $V = (\pi \cdot \text{length} \cdot \text{width}^2)/6$.

The size (volume) of the prey consumed by *H. nana* and *H. sanborni* was compared by the t test (ZAR 1999). The relation between the number of prey consumed and its availability in each pond was analyzed by the Spearman Correlation test (r_s) (ZAR 1999). In order to determine differences in the frequency of prey types consumed by both species, the Chi-square test was used separately for each pond (ZAR 1999).

The temporal, spatial and trophic niche breadths were estimated for each species using the Shannon-Wiener index (H' , base 10, decits/individual) (KREBS 1999) and the values were compared by the t test (ZAR 1999). The niche overlap along each dimension was measured by the Morisita-Horn index (C_H) (KREBS 1999). The multidimensional overlap was obtained by the arithmetic mean in each niche dimension, because the resource dimensions are interrelated (PUTMAN 1994).

Morphological and diet comparisons were made through Principal Components Analysis (PCA) (DIGBY & KEMPTON 1987). The morphological data were log-transformed (base 10) prior to analysis (SOKAL & ROHLF 1979). Because the species differed significantly in SVL, this trait was excluded from the PCA. For the diet analysis, the PCA was applied over the proportion of each type of prey. The significance level selected was 5%, but values between 5 and 10% were discussed as suggestive.

Collected arthropods and anurans were deposited at the Scientific Collection of the Department of Zoology and Botany, State University of São Paulo, São José do Rio Preto campus (DZSJRP), and in the Anuran Collection at the Museu de Biodiversidade do Cerrado (AAG-UFU 2253-2270), Uberlândia Federal University (UFU), Minas Gerais State, Brazil.

RESULTS

Morphological traits

The males of *H. nana* (Hn) had a mean SVL of 19.8 mm (± 1.0 ; $n = 10$; range: 17.9 – 21.2 mm) and were larger ($F = 67.6$; $df = 18$; $p < 0.01$) than those of the *H. sanborni* (Hs) (SVL = 16.4 mm ± 0.8 ; $n = 10$; range: 15.3 – 17.7 mm). The PCA showed that size is an important characteristic that contributed to differentiation of species, the first and second principal component accounted for 90.7% and 3.3%, respectively, of the variation among species (Fig. 1).

Seasonal occurrence

Hyla sanborni began its reproductive season in August and its abundance was relatively stable throughout the rainy season in PP and PT in comparison to *H. nana*. However, *H. sanborni* was rare in PG (one individual in August, one in Sep-

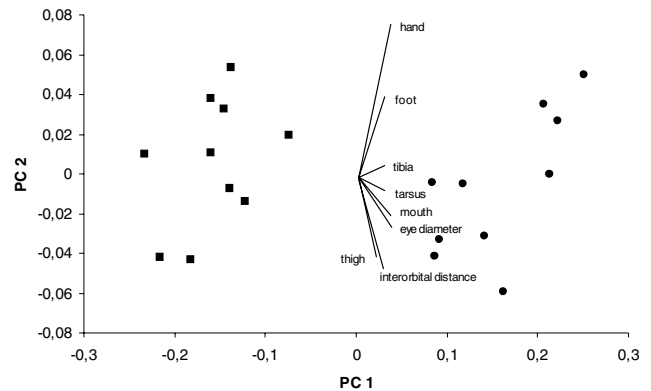


Figure 1. Morphological characterization of the males of *H. nana* (circles) and *H. sanborni* (squares), at the Nova Itapirema, north-western São Paulo, Brazil, based on the first two principal components.

tember and two in January) (Fig. 2). *Hyla nana* began its reproductive season in August in PG and in September at PP and PT, with peaks of abundance in October, November and December (Fig. 2). *Hyla nana* was most abundant in the PG, where it began its reproductive season in August. At PP and PT, *H. sanborni* was more abundant at the beginning of the rainy season, but *H. nana* was more abundant in the middle of season (Fig. 2). The values of the temporal niche breadth were higher in *H. sanborni* than in *H. nana* in PP and PT (Tab. I).

Call site

At PP, the males of *H. nana* and *H. sanborni* called mostly on Pontederiaceae (46 and 38% respectively), in a position parallel to the water surface (42 and 50% respectively). Males of *H. sanborni* called further from the edge of the water than males of *H. nana* (mean Hs = 188.1 cm, mean Hn = 147.1 cm, Mann-Whitney U test = 608.0, $p < 0.05$, Tab. II). Generally, there was no difference in call site niche breadths between these species (Tabs I and II).

Males of *H. sanborni* were rare ($n = 4$) at PG and called on different substrates and on higher perches than *H. nana* (mean Hs = 43.3 cm, mean Hn = 20.1 cm, Mann-Whitney U test = 14.5, $p < 0.01$, Tab. II). The majority of males of *H. nana* called on leaves of Poaceae (55%), in a position parallel to the water surface (65%). There was no difference between these two species regarding niche breadth for type, position on substrate of call sites (Tab. I).

At PT, the males of *H. nana* and *H. sanborni* called mostly on Typhaceae (75 and 93% respectively), perpendicular to the water surface, oriented towards the water (54 and 53% respectively). There were no difference for height of the call site and the distance from the edge of the water (Tab. II). For type of substrate, *H. nana* had a larger niche breadth (Tab. I).

The calling height of *H. nana* differed among ponds ($H = 84.8$, $p < 0.001$); the mean height of the call sites was signifi-

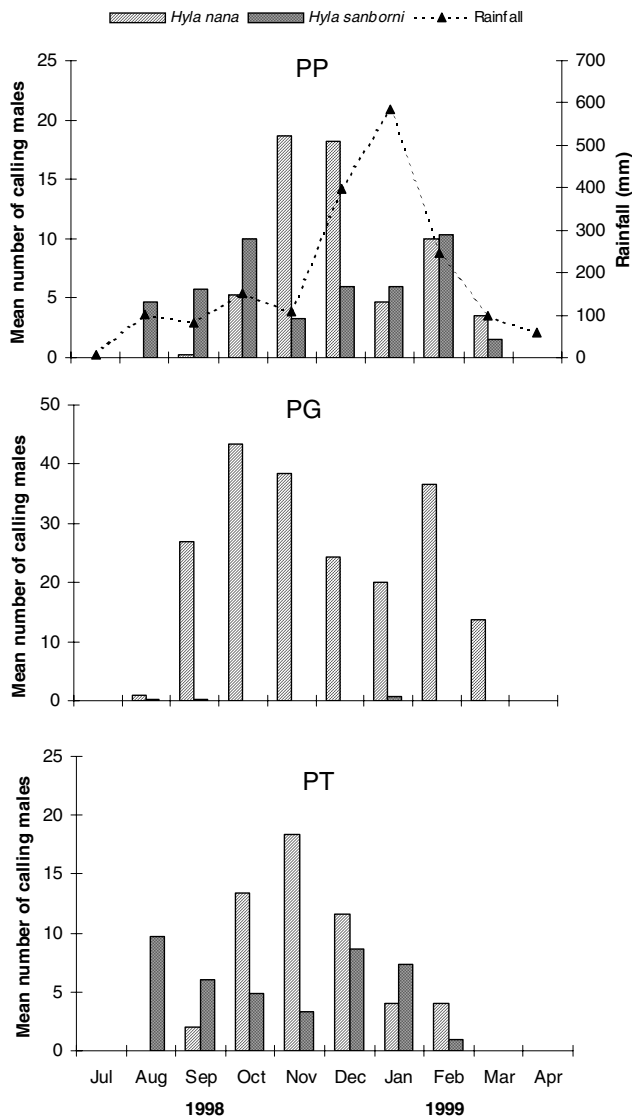


Figure 2. Monthly abundance of calling males of *Hyla nana* and *Hyla sanborni* at three ponds (PP, PG and PT), Nova Itapirema, northwestern São Paulo, Brazil, and monthly rainfall in period from July 1998 to April 1999.

cantly lower in PG than PP and PT. There was no difference in the distance from the edge ($H = 1.7$, $p > 0.10$). *Hyla sanborni* had an inverse pattern: the height of the call site tended to differ among ponds ($H = 4.7$, $p < 0.10$), and the distance from edge differed significantly ($H = 6.1$, $p < 0.05$); the distance from the edge was significantly farther in PP than PG and PT.

Diet

One hundred and two taxa (orders and families) of arthropods were identified at the three ponds. Forty of them were consumed by *H. nana* and *H. sanborni*.

Hyla sanborni had a larger number of empty stomachs (72, 48 and 66%) than *H. nana* (40, 48 and 36%) at PP, PG, and PT, respectively.

At the order level, both species consumed mostly Diptera, although *H. nana* had consumed a larger amount of this item than *H. sanborni* at PT and the inverse had occurred at PP (Tab. III).

Hyla nana consumed arthropods that were frequent and also those that were ephemeral, such as winged Isoptera. *Hyla sanborni* had a less diversified diet, consuming prey that was more abundant in the ponds studied (Tabs IV, V and VI). *Hyla nana* ingested prey with larger volumes than *H. sanborni* ($t = 2.00$; $df = 243$; $p < 0.05$). Nematocera was the most frequently consumed prey type of both species at the three ponds.

The dimensions of trophic niche of *H. nana* and *H. sanborni* were similar at PP (Tab. I). *Hyla nana* consumed mostly Nematocera, Araneae and Formicidae, but the most important item by volume was Blattariae. The most important item by volume was Cicadellidae for *H. sanborni* (Tab. IV). The consumption of prey and its availability were positively correlated for *H. nana* ($r_s = 0.84$, $n = 14$, $p < 0.01$) and for *H. sanborni* ($r_s = 0.90$, $n = 12$, $p < 0.01$).

At PG, *H. nana* had a larger niche breadth for prey types and volume (Tab. I). Both species consumed mostly Nematocera and Cicadellidae, but the most important items by volume were Isoptera and Cicadellidae for *H. nana* and Alleculidae for *H. sanborni* (Tab. V). The consumption of prey and its availability were positively correlated for *H. nana* ($r_s = 0.58$; $n = 22$, $p < 0.01$) and for *H. sanborni* ($r_s = 0.79$, $n = 8$; $p < 0.05$) at this site.

At PT, *H. nana* had a larger niche breadth for number of prey by category and volume of prey (Tab. I). *Hyla nana* consumed mostly Nematocera and Formicidae, but the most important items by volume were unidentified Diptera and Coleoptera. *Hyla sanborni* consumed mostly Nematocera. This item was the most important in volume (Tab. VI). The consumption of prey and its availability were not correlated for *H. nana* ($r_s = 0.19$, $n = 20$, $p > 0.10$), and for *H. sanborni* ($r_s = 0.52$, $n = 9$, $p < 0.10$).

The PCA demonstrated differences in diet related to species and environments. The first and second main components accounted for 34.7% and 27.5% of the variation, respectively. The most important variables in the first principal component were Drosophilidae, Tipulidae, Curculionidae, Cecidomyiidae, Trichoptera, Psocoptera, Tettigoniidae and unidentified Diptera, Hymenoptera and Coleoptera, on the positive side (which contains *H. nana* at PG and PT) and Chloropidae and Cicadellidae on the negative side (that contains *H. nana* at PP and *H. sanborni* of the three ponds) (Tab. VII and Fig. 3). In the second principal component, the most important variables were Chloropidae, Others Nematocera and Collembola on the positive side, which contains *H. sanborni* from the three ponds and *H. nana* from PP and PT (Tab. VII and Fig. 3). The diet of *H. nana* differed among the ponds, as shown by the greater point dispersion of *H. nana* in the food space (Fig. 3).

Table I. Niche breadths (H') of *Hyla nana* (Hn) and *Hyla sanborni* (Hs), at three ponds (PP, PG and PT), Nova Itapirema, northwestern São Paulo, Brazil. (NS) difference not significant: $p > 0.05$.

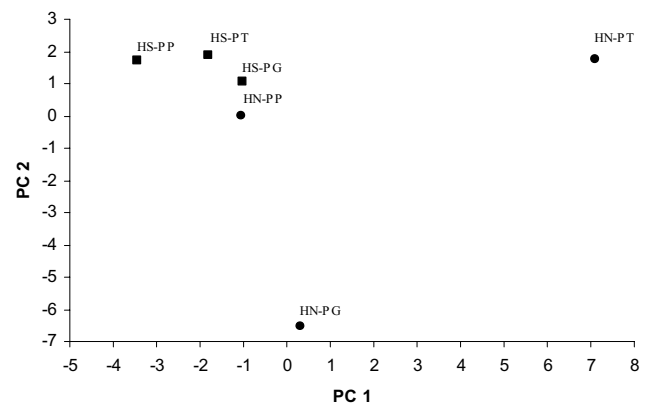
Niche Dimensions	PP					PG					PT				
	Hn	Hs	t	gl	p	Hn	Hs	t	gl	p	Hn	Hs	t	gl	p
Reproductive season	0.69	0.84	-5.50	321	< 0.01	0.81	0.45	4.79	4	< 0.01	0.69	0.78	-3.46	297	< 0.01
Call site															
Perch Height	0.77	0.78	-0.10	81	NS	0.62	0.28	3.97	4	< 0.05	0.88	0.86	0.28	93	NS
Distance from edge	0.77	0.80	-0.49	79	NS	0.87	0.48	27.37	105	< 0.01	0.78	0.65	2.82	82	< 0.01
Type of substrate	0.61	0.57	0.59	79	NS	0.51	0.48	16.69	118	NS	0.37	0.13	2.93	92	< 0.01
Position on substrate	0.54	0.47	1.36	83	NS	0.37	0.28	1.06	4	NS	0.48	0.46	0.37	100	NS
Diet															
Types of prey	1.05	0.94	1.23	49	NS	1.17	0.59	4.93	51	< 0.01	1.01	0.65	3.23	63	< 0.01
Volume of prey	0.70	0.73	-0.46	216	NS	1.06	0.52	8.17	39	< 0.01	1.06	0.77	5.44	83	< 0.01

Table II. Mean perch height (cm \pm 1 SD) and distance from the water's edge of calling males of *Hyla nana* (Hn) and *Hyla sanborni* (Hs), at three ponds (PP, PG e PT), Nova Itapirema, northwestern São Paulo, Brazil. (N) Sample size, (*) significant difference: $p < 0.05$.

	PP		PG		PT	
	Hn	Hs	Hn	Hs	Hn	Hs
Perch height	41.4 \pm 15.3	47.1 \pm 19.6	*20.1 \pm 12.0	*43.3 \pm 5.8	50.6 \pm 23.6	54.2 \pm 19.7
N	39	49	116	3	49	54
Distance from edge	*147.1 \pm 84.1	*188.1 \pm 107.7	151.7 \pm 135.3	163.3 \pm 105.0	159.9 \pm 91.2	150.9 \pm 57.5
N	38	43	105	3	45	50

Table III. Frequency of the most important prey (orders) in diets of *H. nana* and *H. sanborni*, in the three ponds (PP, PG e PT), Nova Itapirema, northwestern São Paulo, Brazil. (*) significant difference.

Pond	Frequency (%)				
	Category of prey	<i>H. nana</i>	<i>H. sanborni</i>	χ^2	p
PP					
	Diptera	45.45	78.57	*3.86	0.05
	Araneae	18.18	14.28	0.09	0.76
	Homoptera	22.72	35.71	0.72	0.40
PG					
	Acari	6.25	9.09	0.10	0.75
	Coleoptera	15.62	9.09	0.29	0.59
	Collembola	12.50	18.18	0.22	0.64
	Diptera	46.87	63.63	0.92	0.34
	Homoptera	28.12	27.27	0.01	0.96
	Hymenoptera	9.37	18.18	0.62	0.43
PT					
	Collembola	13.04	18.75	0.24	0.63
	Diptera	86.95	56.25	*4.67	0.03
	Homoptera	13.04	18.75	0.24	0.63

Figure 3. Characterization of the diet of *H. nana* (HN) and *H. sanborni* (HS), at three ponds (PP, PG and PT), Nova Itapirema, northwestern São Paulo, Brazil, based on the first two principal components.

Niche overlap

The niche overlap between *H. nana* and *H. sanborni* in the call site and types of prey was wide among the three ponds (Tab. VIII). The overlap in prey was low because *H. nana* consumed items with larger volume than *H. sanborni*. At PG, the

Table IV. Prey availability (A), number, volume and frequency in stomachs of prey taxa in the diet of *H. nana* and *H. sanborni* at PP, Nova Itapirema, northwestern São Paulo, Brazil. N = 22 stomachs to *H. nana* and 14 to *H. sanborni*. N = 2212 individual prey in the sample of prey availability.

Category of prey	<i>Hyla nana</i>				<i>Hyla sanborni</i>		
	A (%)	Number	Vol.(%)	Freq. (%)	Number	Vol.(%)	Freq.(%)
Acari	3.30	2	0.04	4.54	–	–	–
Araneae	4.11	5	3.46	18.18	2	2.34	14.28
Blattariae	1.04	1	56.27	4.54	–	–	–
Collembola	3.80	–	–	–	2	0.03	14.28
Diptera							
Chloropidae	8.14	3	7.22	13.63	3	15.85	21.42
Ephydriidae	–	–	–	–	1	6.57	7.14
Neriidae	–	–	–	–	1	11.68	7.14
Unidentified Nematocera	25.23	5	1.53	22.72	8	7.30	35.71
Unidentified	0.14	2	3.93	9.09	1	0.22	7.14
Hemiptera							
Pyrrhocoridae	0.05	1	0.56	4.54	–	–	–
Homoptera							
Aphididae	0.10	1	0.56	4.54	1	0.36	7.14
Cicadellidae	21.61	2	4.49	9.09	4	43.54	21.42
Flatidae	0.05	1	2.53	4.54	–	–	–
Unidentified	0.05	1	3.75	4.54	1	11.68	7.14
Hymenoptera							
Formicidae	5.15	5	3.75	18.18	–	–	–
Isoptera	–	1	11.81	4.54	–	–	–
Thysanoptera	–	–	–	–	1	0.08	7.14
Unidentified Insects	–	1	0.04	4.54	1	0.01	7.14
Other	27.23						
Total		31			26		

overlap in reproductive season was low. The multidimensional overlap was larger in the PP and PT, and lower at PG where *H. sanborni* was rare (Tab. VIII).

DISCUSSION

Seasonal occurrence

Hyla nana and *Hyla sanborni* are morphologically very similar species and they occur in sympatry in some sites in Argentina, Paraguay and Brazil (LANGONE & BASSO 1987). They are different in size (this study), and structure of advertisement call (BASSO *et al.* 1985, ROSSA-FERES & JIM 2001, MARTINS & JIM 2003).

In the northwestern region of the state of São Paulo, these two species overlapped in seasonal occurrence at PP and PT, which coincided with the rainy season. The small overlap at PG resulted from the rarity of *H. sanborni* at this site. In tropical regions with seasonal climate, the majority of anuran spe-

cies reproduce during the rainy season (AICHINGER 1987, ROSSA-FERES & JIM 1994, POMBAL JR. 1997). *Hyla sanborni* was more abundant and had a more prolonged reproductive period in permanent ponds, while *H. nana* was more abundant in the temporary pond, as verified by ROSSA-FERES & JIM (2001). At the southeastern region in the state of São Paulo, *H. sanborni* calls from the end of dry season until the end of the wet season (ROSSA-FERES & JIM 1994). The shorter and the annual variability in the reproductive period of *H. sanborni* in the northwestern region is probably a consequence of the pronounced dry season and of the unpredictability of the climate, because the rainfall may begin at any time between August and October depending on the year. Among closely related species of anurans, different patterns of reproductive periods have been found; some species presented broad overlap in temporal niche (OLDHAM & GERHARDT 1975, LIZANA *et al.* 1990, DONNELLY & GUYER 1994) while others were found to have a small overlap (BOWKER & BOWKER 1979, DIAZ & VALENCIA 1985, MAC NALLY 1985).

Table V. Prey availability (A), number, volume and frequency in stomachs of prey taxa in the diet of *H. nana* and *H. sanborni* at PG, Nova Itapirema, northwestern São Paulo, Brazil. N = 32 stomachs to *H. nana* and 11 to *H. sanborni*. N = 1912 individual prey in the sample of prey availability.

Category of prey	A(%)	<i>Hyla nana</i>			<i>Hyla sanborni</i>		
		Number	Vol. (%)	Freq. (%)	Number	Vol. (%)	Freq. (%)
Acari	5.20	2	0.05	6.25	1	0.02	9.09
Araneae	3.40	4	7.40	9.37	–	–	–
Coleoptera							
Alleculidae	–	–	–	–	1	55.05	9.09
Chrysomelidae	0.20	1	0.38	3.12	–	–	–
Cleridae	0.10	2	8.39	6.25	–	–	–
Erotylidae	0.70	1	6.89	3.12	–	–	–
Silphidae	0.10	1	5.74	3.12	–	–	–
Collembola	10.10	4	0.13	12.50	2	0.43	18.18
Diptera							
Drosophilidae	1.10	2	0.70	6.25	–	–	–
Muscidae	0.40	1	3.57	3.12	–	–	–
Tipulidae	0.50	1	0.38	3.12	–	–	–
Unidentified Nematocera	18.00	25	2.08	28.12	17	11.18	63.63
Unidentified	0.30	2	0.27	6.25	–	–	–
Hemiptera							
Lygaeidae	0.20	1	1.43	3.12	–	–	–
Homoptera							
Aphididae	–	2	0.30	6.25	1	1.95	9.09
Cercopidae	–	1	1.14	3.12	–	–	–
Cicadellidae	23.40	7	18.08	15.62	2	25.84	18.18
Delphacidae	0.90	1	0.04	3.12	–	–	–
Hymenoptera							
Formicidae	3.80	3	7.75	9.37	2	5.34	18.18
Isoptera	–	2	18.25	6.25	–	–	–
Odonata	–	1	5.10	3.12	–	–	–
Orthoptera							
Gryllidae	2.50	2	10.62	6.25	–	–	–
Unidentified Insects	0.10	2	1.21	6.25	1	0.14	9.09
Other	29.00						
Total		68			27		

Call site

Males of *H. nana* and *H. sanborni* called from the same type of substrate, adopting the same position in calling perch in each pond, which resulted in wide overlap in spatial niche. Despite the fact that the perch height did not differ significantly in the PP and PT, the mean perch height of *H. sanborni* at the three ponds was higher than *H. nana*, as verified by ROSSA-FERES & JIM (2001) at PG. At PP, the size and the hydroperiod of the pond seemed to have allowed the exploitation of different substrates by *H. sanborni*, because the aquatic vegetation is

available before the beginning of the rainy season. The later occurrence of *H. sanborni* at PG and its large abundance in permanent ponds, may be related to the physical structure of the vegetation, because this species perches in higher places in vegetation. On other hand, *H. nana* perched in lower sites at PG, because the aquatic vegetation, growing only after the beginning of the rainy season, is composed only by grasses and determines a lower environmental heterogeneity.

MAC NALLY (1985) and DONNELLY & GUYER (1994) verified a wide overlap in call site for closely related species. According

Table VI. Prey availability (A), number, volume and frequency in stomachs of prey taxa in the diet of *H. nana* and *H. sanborni* at PT, Nova Itapirema, northwestern São Paulo, Brazil. N = 23 stomachs to *H. nana* and 16 to *H. sanborni*. N = 1833 individual prey in the sample of prey availability.

Category of prey	A(%)	<i>Hyla nana</i>			<i>Hyla sanborni</i>		
		Number	Vol. (%)	Freq. (%)	Number	Vol. (%)	Freq. (%)
Acari	11.13	3	0.07	13.04	–	–	–
Araneae	6.23	1	7.22	4.35	1	3.98	6.25
Coleoptera							
Curculionidae	–	2	4.28	8.69	–	–	–
Unidentified	–	1	16.27	4.35	–	–	–
Collembola	12.77	3	0.35	13.04	3	0.50	18.75
Diptera							
Cecidomyiidae	1.58	2	0.43	8.69	–	–	–
Chloropidae	2.35	–	–	–	1	11.94	6.25
Drosophilidae	1.96	1	3.70	4.35	–	–	–
Psychodidae	0.38	–	–	–	1	0.05	6.25
Tipulidae	0.11	2	6.23	8.69	–	–	–
Unidentified Nematocera	15.06	23	6.27	52.17	18	29.26	43.75
Unidentified	0.11	4	22.41	13.04	–	–	–
Hemiptera							
Lygaeidae	0.49	1	3.66	4.35	1	3.98	6.25
Homoptera							
Aphididae	0.05	2	1.19	8.69	–	–	–
Cercopidae	0.05	–	–	–	1	11.94	6.25
Cicadellidae	15.00	1	0.72	4.35	2	15.44	12.50
Hymenoptera							
Formicidae	4.14	9	10.74	21.74	–	–	–
Unidentified	–	1	0.18	4.35	–	–	–
Isoptera	–	2	3.61	4.35	–	–	–
Orthoptera							
Tettigoniidae	0.71	1	7.23	4.35	–	–	–
Psocoptera	0.54	1	0.26	4.35	–	–	–
Trichoptera	0.11	1	4.07	4.35	–	–	–
Unidentified Insects	0.05	1	1.08	4.35	3	22.89	12.50
Other	27.18						
Total		62			31		

to HEYER *et al.* (1990), the habitat type seems to be an evolutionarily conservative trait among closely related species. However, the call site partition (BOWKER & BOWKER 1979, ETGES 1987) or microhabitat partition (LOMAN 1978, DIAZ & VALENCIA 1985, HEYER *et al.* 1990, LIZANA *et al.* 1990) seems to be common in anurans. In sympatric species of *Rana*, the structural aspects of vegetation were an important feature of discrimination of microhabitat (MCALPINE & DILWORTH 1989). Besides that, species with wide overlap in call site present small overlap in the structure of call (DUELLMAN & PYLES 1983, ROSSA-FERES & JIM 2001),

which is the most important mechanism of reproductive isolation between co-occurring species (HÖDL 1977, CRUMP 1982).

Diet

The two species were diet generalists, consuming prey types in proportion to their abundance in the environment, including ephemeral resources, such as winged termites, which reinforces the idea that anurans are opportunists (LABANICK 1976). A major difference between the diets of both species was the consumption of Araneae, Formicidae and Cicadellidae in abundance by *H. nana*, while *H. sanborni* ingested only

Table VII. Eigenvalues of prey items for the first two principal components (PC) of *H. nana* and *H. sanborni* in the three ponds (PP, PG and PT), Nova Itapirema, northwestern São Paulo, Brazil.

Category of prey	PC 1	PC 2
Acari	0.234	-0.118
Araneae	0.177	-0.154
Blattariae	-0.038	0.001
Coleoptera		
Alleculidae	-0.037	0.049
Cleridae	0.011	-0.298
Chrysomelidae	0.011	-0.298
Curculionidae	0.256	0.081
Erotylidae	0.011	-0.298
Silphidae	0.011	-0.298
Unidentified Coleoptera	0.256	0.081
Collembola	0.073	0.108
Diptera		
Cecidomyiidae	0.256	0.081
Chloropidae	-0.179	0.136
Drosophilidae	0.263	0.025
Ephydriidae	-0.125	0.080
Muscidae	0.011	-0.298
Nematocera	-0.067	0.142
Neriidae	-0.125	0.080
Psychodidae	0.256	0.081
Tipulidae	0.259	0.064
Unidentified Diptera	0.255	0.081
Hemiptera		
Lygaeidae	0.150	0.048
Pyrrhocoridae	-0.038	0.001
Homoptera		
Aphididae	0.096	0.075
Cercopidae	-0.066	0.060
Cicadellidae	-0.190	0.020
Delphacidae	0.011	-0.298
Flatidae	-0.038	0.001
Unidentified Homoptera	-0.139	0.081
Hymenoptera		
Formicidae	0.238	-0.112
Unidentified Hymenoptera	0.256	0.081
Isoptera	0.035	-0.272
Odonata	0.011	-0.298
Orthoptera		
Gryllidae	0.011	-0.298
Tettigoniidae	0.256	0.081
Psocoptera	-0.066	0.088
Trichoptera	0.256	0.081
Tysanoptera	-0.125	0.080
Unidentified Insecta	-0.055	0.078

Nematocera in abundance. In Argentina, *H. nana* consumed preponderantly Diptera (BASSO 1990), Formicidae and Araneae (PELTZER & LAJMANOVICH 2000), indicating a strong environmental influence in the diet of this species. *Hyla sanborni* consumed preponderantly Diptera and Homoptera in Argentina (BASSO 1990). *Hyla nana* had a larger niche breadth for types and volume of prey in two ponds. The larger volume of the prey consumed by *H. nana* may be a consequence of its larger size, as observed for sympatric species of Urodela of the genus *Bolitoglossa* Duméril, Bribon, and Duméril, 1854 (ANDERSON & MATHIS 1999).

The presence of a high percentage of empty stomachs in *H. sanborni* than *H. nana* may be related to differences in timing of feeding. Males of *H. sanborni* perhaps feed after calling or alternate feeding nights with calling nights, while *H. nana* perhaps feed before the beginning of calling activity. This fact could be corroborated by observations of males that not interrupted your vocal activity to feed insects that locomoted on or around them (D.C. Rossa-Feres, personal observation). The alternating between calling nights and feeding nights has been recorded for *Physalaemus pustulosus* (Cope, 1864) in Panama (RYAN 1985) and for three sympatric species of anurans in the United States (ANDERSON *et al.* 1999).

Niche overlap and coexistence

In general, the multidimensional overlap between *H. nana* and *H. sanborni* was wide, in disagreement with the theory of a limit of similarity between coexisting species (MACARTHUR & LEVINS 1967). According to ABRAMS (1983), the idea of a universal limit is probably system specific, varying between species and environments. The intraspecific variation in resource use at the three water bodies, registered in the present study, reinforces this idea. On other hand, the wide overlap found can be a consequence of taxonomic relationships of these species. Related species share behavioral, physiological and morphological traits, because they are descendants of a common ancestor (ZIMMERMAN & SIMBERLOF 1996).

The empirical approach to the ecological coexistence problem is embodied by resource partitioning studies; both make the assumption that communities are competitively structured (GORDON 2000). But other processes beyond interspecific competition, such as predation, parasitism, environmental variability and heterogeneity, set more important limits to the growth of natural populations (GORDON 2000) and coexistence of species. In addition, variations in the use of time, space and food result from two or more factors, such as competition, predation, morphological and physiological constraints (TOFT 1985) and evolutionary history (BROOKS & McLENNAN 1991) which may operate independently, interactively or both (TOFT 1985). The wide 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 (PIANKA 1974).

Table VIII. Niche overlap (%) between *H. nana* and *H. sanborni* along each niche dimension and the multidimensional overlap, at the three ponds (PP, PG e PT), Nova Itapirema, northwestern São Paulo, Brazil.

	Reproductive season	Call site	Diet		Multidimensional overlap
			Type of prey	Volume of prey	
PP	61.0	93.5	68.9	11.7	58.8
PG	36.4	62.4	87.2	21.7	52.0
PT	57.0	94.4	82.3	16.9	62.6

In this study, the data indicate that environmental structure, such as vegetation structure and hydroperiod directly influence the occurrence and the use of the resources used by these species. For example, the position and type of substrate used as a call site varied among the ponds, depending on the available vegetation. Because of this, the overlap in the use of the resources may be directly related to the degree of environmental heterogeneity.

Despite of the differences found in the trophic niche dimensions, there was wide overlap between *H. nana* and *H. sanborni* in the type of prey consumed. This fact might cause competition, if these resources were limited, or yet, could be a consequence of the level of identification of the prey. However, in natural assemblages of amphibians, food competition appears to be an unusual event, which plays a minor, or insignificant, role in the structure and dynamics of the assemblage, and has never been demonstrated in the field (KUZMIN 1995). Moreover, a wide overlap in diet was found for many sympatric species of anurans and skinks. However in all the following studies, the large food availability (MAC NALLY 1983, TWIGG *et al.* 1996), differences in microhabitat use (DIAZ & VALENCIA 1985, VRCIBRADIC & ROCHA 1996, VITT *et al.* 2000) or the structural differences in habitats (MCALPINE & DILWORTH 1989), permitted the coexistence of the species.

In conclusion, *H. nana* and *H. sanborni* of Nova Itapirema showed different relative abundance in distinct ponds, consumed prey of different size and probably fed at different periods. The data obtained suggest that the environmental structure, such as hydroperiod and vegetation structure, may change the dynamics of resource partition between these coexisting species. The coexistence of these species in the area seems to be conditioned, in some degree, to differences in major niche dimensions (reproductive season and diet), as well as the possibility that resources (arthropods and call sites) are not in short supply.

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