

# Use of food and spatial resources by two frogs of the genus *Dendropsophus* (Anura: Hylidae) from La Selva, Costa Rica

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## Abstract

**Use of food and spatial resources by two frogs of the genus *Dendropsophus* (Anura: Hylidae) from La Selva, Costa Rica.** Differences in the use of resources by similar species have been related to a reduction in the interspecific competition that allows coexistence. Also, other factors, such as high availability of resources in the environment, vegetation structure, environmental heterogeneity, reproductive modes, and predation, can influence the use of resources and favor coexistence. We studied the use of space and food resources by males of two species of hylid frogs, *Dendropsophus ebraccatus* and *D. phlebodes*, in two swamps in the Neotropical lowland forest at La Selva Biological Station, Costa Rica. We determined space and food use by characterizing calling sites and the diet of the frogs by stomach flushing. Males call from different substrates, and use different sizes of leaves and perch heights. Both species seem to be feeding generalists. Their diets are similar and indicate a moderate trophic niche overlap based on the type of prey consumed. Many males of both species had empty stomachs, suggesting that food resources are not an important factor affecting the coexistence of these species. Our study also indicates a lack of competitive interactions for space and food resources, and suggests that the abundant and structurally diverse vegetation provides many different vocalization sites for the male frogs and fosters coexistence of these species during the breeding season at La Selva.

**Keywords:** calling site, coexistence, *Dendropsophus ebraccatus*, *Dendropsophus phlebodes*, diet, niche overlap.

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## Resumo

**Uso de recursos alimentares e espaciais por dois anuros do gênero *Dendropsophus* (Anura: Hylidae) de La Selva, Costa Rica.** Diferenças na utilização de recursos por espécies semelhantes têm sido relacionadas com redução na competição interespecífica, que permite a coexistência. Além disso, outros fatores, como a alta disponibilidade de recursos no ambiente, a estrutura da vegetação, a heterogeneidade ambiental, os modos reprodutivos e a predação, podem influenciar o uso de recursos e favorecer a coexistência. Estudamos a utilização de recursos espaciais e alimentares por machos de duas espécies de hílídeos, *Dendropsophus ebraccatus* e *D. phlebodes*, em dois charcos da floresta tropical da Estação Biológica de La Selva, Costa Rica. Determinamos o uso do espaço e do alimento por meio da caracterização dos sítios de vocalização e da dieta (por lavagem estomacal) desses anuros. Os machos vocalizam a partir de diferentes substratos e usam folhas de tamanhos diferentes e poleiros de diferentes alturas. Ambas as espécies parecem apresentar uma dieta generalista. Suas dietas são semelhantes e indicam uma sobreposição moderada de nicho trófico no que se refere ao tipo de presa consumida. Em ambas as espécies, muitos machos apresentaram o estômago vazio, sugerindo que os recursos alimentares não são um fator importante que afeta a coexistência dessas espécies. Nosso estudo também indicou ausência de interações competitivas relacionadas ao uso de recursos espaciais e alimentares e sugere que a vegetação abundante e estruturalmente diversificada fornece aos machos uma grande diversidade de sítios de vocalização, promovendo a coexistência dessas espécies durante a estação reprodutiva em La Selva.

**Palavras-chave:** coexistência, *Dendropsophus ebraccatus*, *Dendropsophus phlebodes*, dieta, sítio de vocalização, sobreposição de nicho.

## Introduction

The coexistence of ecologically similar species has been one of the most difficult topics to understand in ecology and has been widely studied in amphibians and reptiles (Toft 1985, Gordon 2000). Biologists have reasoned that there must be at least minimal differences in resource use by similar, co-occurring species to reduce interspecific competition and facilitate coexistence (Pianka 1974, Gordon 2000, Griffin and Silliman 2011).

The ecological niche concept has been associated with interspecific competition and patterns of resource use among species (Pianka 1981). Niche partitioning may diminish the resource overlap of coexisting organisms, thereby reducing potential competition between species that might result in the extinction of one or more of them (Polechová and Storch 2008, Blanco 2009). However, Pianka (1974) mentioned that a high niche overlap is not necessarily indicative of competition, because if resources are not limited, two or more organisms can share them.

Based on the results of ecological studies of Neotropical anuran assemblages, there are important differences in the use of microhabitat, food, and time of activity among sympatric species (Toft 1985, Donnelly and Guyer 1994, Lima and Magnusson 1998, Rossa-Feres and Jim 2001). The differences can be categorized in three niche dimensions: spatial, trophic, and temporal (Schoener 1974). The spatial niche is considered more important than the other dimensions in amphibians (Toft 1985, Lizana *et al.* 1990). Specific mechanisms of microhabitat use, such as the differential use of calling sites, may facilitate optimal exploitation of available resources, allowing coexistence of species (Muñoz-Guerrero *et al.* 2007, Vasconcelos and Rossa-Feres 2008, Blanco 2009). With respect to trophic niche dimension, differences in foraging patterns, feeding strategies, and mating activity might result in dissimilar patterns of food resource use among species (Toft 1985, Duré and Kehr 2004, Solé and Pelz 2007). Although the trophic niche is thought to be a less important factor in the maintenance of

coexistence, it is relevant to an understanding of interspecific interactions (Duré and Kehr 2001). Moreover, a high availability of environmental resources, along with factors such as vegetation structure, environmental heterogeneity, reproductive modes, and predation influence the use of resources and affect coexistence of species (Donnelly and Guyer 1994, Gordon 2000, Menin *et al.* 2005, Vasconcelos and Rossa-Feres 2008). Toft (1985) reported that the ways in which species use and share the resources are important factors for structuring anuran assemblages.

*Dendropsophus ebraccatus* and *D. phlebodes* are two small nocturnal tree frog species (Hylidae) that call and breed syntopically in temporal and permanent swamps at several localities in Costa Rica and Panama during the wet season (Backwell and Jennions 1993, Savage 2002). The males usually call from emergent vegetation, bushes, or trees overhanging the ponds. The diet of neither species is well studied, but both are thought to eat arthropods (Guyer and Donnelly 2005). Studies of resource partitioning between these species are limited to acoustic interactions (Schwartz and Wells 1983) and habitat use (Donnelly and Guyer 1994). Because *D. ebraccatus* and *D. phlebodes* are morphologically and ecologically similar and sympatric, it is of great interest to explore their use and partitioning the available spatial and food resources. Thus we examined how males of these two tree frog species used space and food resources during the breeding season to test the hypothesis that the use of space and food resources will differ between males of both species, thereby reducing interspecific competition and allowing them to coexist.

## Materials and Methods

### Study Site

The 1536-ha La Selva Biological Station is located in Sarapiquí, Heredia Province, Costa Rica (10°26' N, 83°59' W) at the base of the

Central Volcanic Mountain Range and ranges in elevation from 35–137 m (McDade and Hartshorn 1994). The average annual rainfall at La Selva is 3962 mm, with a short dry season from January to April. The mean monthly temperature is 25.8°C (Sanford *et al.* 1994).

We selected two swamps at which both *Dendropsophus ebraccatus* and *D. phlebodes* occurred—the Research Swamp (10°25'73" N, 84°00'83" W) and a swamp along the entrance road to La Selva (10°25'09" N, 84°00'33" W). The Research Swamp is located in an old-growth forest that is dominated by the canopy tree *Pentaclethra macroloba* (Mimosaceae); the middle of the swamp contains aquatic vegetation such as *Paspalum fasciculatum* (Poaceae), whereas *Panicum pilosum* (Poaceae) and *Calyptrocarya glomerulata* (Cyperaceae) are found around the shallow edges. The second swamp is located in a shaded pasture surrounded by secondary forest; *Paspalum fasciculatum* and *Panicum* spp. occurring in the water.

### Sampling

Our field study was conducted at night (from 18:00–23:00 h) for 32 days in the swamps during the rainy season (June and July 2010). We used visual and auditory cues to search for frogs and captured them by hand (Crump and Scott 1994). We measured the snout-vent length (SVL) of all the captured frogs with calipers.

After we captured each male, we characterized the calling site by determining: (1) type of substrate (leaf or branch); (2) shape of leaf (long or oval); (3) texture of leaf (soft or hard); (4) size of leaf (<50 cm<sup>2</sup> = small, 50–90 cm<sup>2</sup> = medium, >90 cm<sup>2</sup> = large); (5) height above water surface or ground; (6) depth of water depth under call site if applicable; and (7) shortest distance from calling site to swamp (>150 m from water = 1, <150 m from water = 2, 0–150 m within swamp over water = 3, 150–300 m within swamp over = 4, >300 m within swamp over water = 5). We identified the species of plants used as calling sites.

We transferred the frogs to the nearby laboratory within a maximum of 2 hr after capture and flushed their stomachs as described by Solé *et al.* (2005) and Solé and Rödder (2009). The stomach contents of each individual were placed in a small vial with 70% ethanol and analyzed the next day. The prey obtained from stomach flushing were identified to the lowest possible taxonomic level.

For each species of frog, we determined the number of prey, and the relative abundance and the frequency of occurrence of prey items consumed. Prey volume was calculated by photographing the prey items and digitally measuring the length and width of each item with the Image Tool 3.0 and applying the formula for ellipsoid bodies (Colli and Zamboni 1999).

$$V = \frac{4\pi}{3} \frac{L}{2} \left( \frac{W}{2} \right)^2$$

where  $V$  = volume,  $L$  = length, and  $W$  = width of the prey item. We did not attempt to measure prey that were overly digested, but they were identified if possible.

### Statistical Analysis

We used chi-square tests to test for differences in the type of substrate, shape, texture, and size of the leaves used by the species and the distances of the calling sites from the swamp. The perch heights and the water depths were compared by a non-parametric Mann-Whitney U-test. When a chi-square test was performed, the original counts were analyzed, but percentages are presented in the figures. We measured the degree of overlap with the type of calling site (i.e., branch and plant species) used by the males with the niche overlap index (Krebs 1999) to determine the spatial niche.

$$O_{jk} = \frac{\sum_{i=1}^n P_{ij} P_{ik}}{\sqrt{\sum_{i=1}^n P_{ij}^2 \sum_{i=1}^n P_{ik}^2}}$$

where  $O_{jk}$  is the Pianka measure of niche overlap and  $P_{ij}$  and  $P_{ik}$  represent the proportions of the  $i^{\text{th}}$  resource used by the  $j^{\text{th}}$  and  $k^{\text{th}}$  species. The values obtained for this index vary from 0–1; 0 indicates no overlap and 1 signifies complete overlap.

We used the Shannon-Weaver diversity index (Krebs 1999) to obtain the trophic niche breadth (i.e., type of prey) of each species

$$H' = -\sum_{i=1} p_i \log_e p_i$$

where  $H'$  is the Shannon-Weaver diversity index and  $p_i$  is the relative abundance of each prey category and the range is 1– $n$ . We conducted a t-test to compare the trophic niche breadth between the species. We calculated the index of relative importance (IRI) to reduce bias towards the most common species in the animal's diet (Pianka 1973 cited by Solé and Rödder 2009),

$$IRI_t = (PO_t)(PI_t + PV_t)$$

where  $PO_t$  is the percentage of occurrence ( $100 \times$  number of stomachs containing  $t$  item/total number of stomachs),  $PI_t$  is the percentage of individuals ( $100 \times$  total number of individuals of  $t$  in all stomachs/total number of individuals of all taxa in all stomachs) and  $PV_t$  is the percentage of volume ( $100 \times$  total volume of individuals of  $t$  in all stomachs/total volume of all taxa in all stomachs).

We used a Mann-Whitney U-test to test for differences in the volume of the prey consumed by the species. We also measured the overlap in the trophic niche with the type of prey consumed by males of the two species with the niche overlap index. To determine whether the value of the measured overlap of the spatial and trophic niche differed from the expected based on a random sampling of our species data, we performed a randomization analysis through Monte Carlo randomizations. This analysis creates pseudo-communities and statistically compares the patterns of the randomized communities with the real data. For the simulation, we

randomized our data 1000 times and used the randomization algorithms RA3. This algorithm does a simple reshuffling of each row of the matrix data and retains the niche breadth and the amount of specialization for each species (Gotelli and Entsminger 2001). Species with interspecific competition were assumed when  $p$  [obtained  $\leq$  simulated] = 0.05 or less, whereas presence of species because of unlimited resource, was assumed when  $p$  [obtained  $\geq$  simulated] = 0.05 or less (Gotelli and Graves 1996).

We used the statistical software package "Statistica 8.0" (Statsoft Inc. 2008) for the statistical analysis of the data, the software PAST 2.11 (Hammer *et al.* 2001) for calculation of trophic niche breadth and the t-test, and EcoSim 7.0 (Gotelli and Entsminger 2001) for the niche overlap and its randomization sampling.

## Results

We found a total of 140 male *Dendropsophus phlebodes* and 68 male *D. ebraccatus* in Research Swamp. In the open swamp, we found 40 male *D. phlebodes* and 9 male *D. ebraccatus*. SVLs for *D. ebraccatus* range from 23–26.5 mm (mean  $\pm$  SD:  $25 \pm 0.14$  mm,  $N = 34$ ) and for *D. phlebodes*, 17–25 mm ( $22.17 \pm 0.18$  mm,  $N = 62$ ).

### Comparison of Spatial Niche

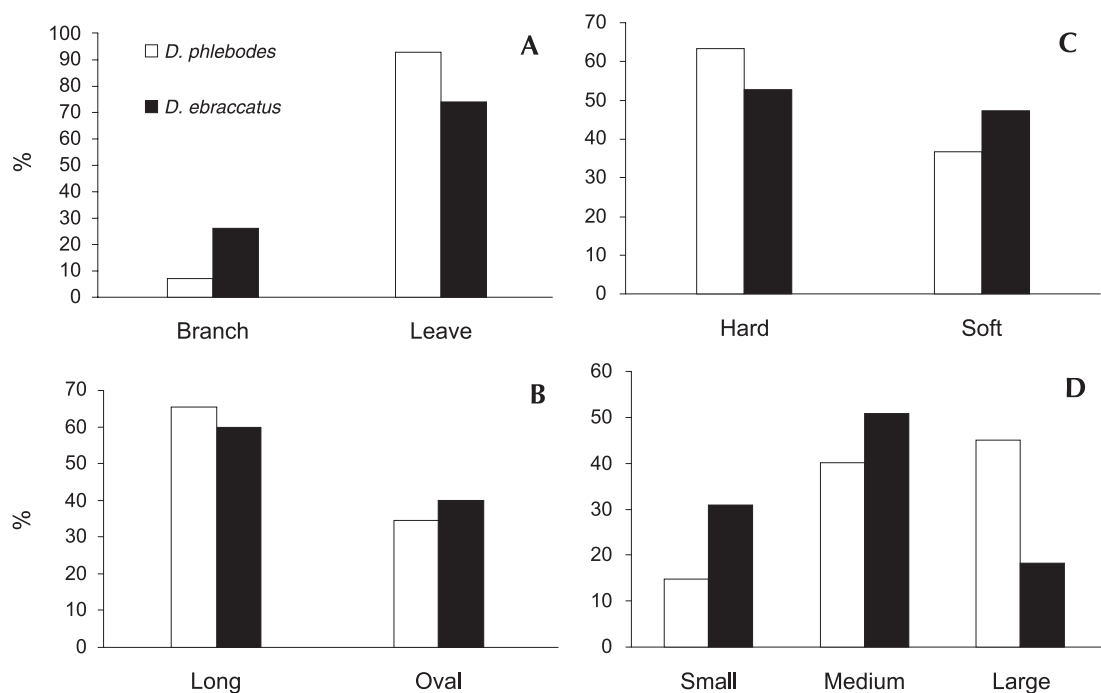
Both species were seen more frequently using leaves as a calling site; however, male *Dendropsophus phlebodes* used leaves (92.85%) more often than *D. ebraccatus* (74.03%), many of which used branches ( $\chi^2 = 14.87$ ,  $p < 0.001$ ,  $df = 1$ , Figure 1A). The frequency with which each species used leaves of different shapes and textures was the same (shape:  $\chi^2 = 0.31$ ,  $p = 0.579$ ,  $df = 1$ , Figure 1B; textures:  $\chi^2 = 1.46$ ,  $p = 0.227$ ,  $df = 1$ , Figure 1C). However, we found that *D. phlebodes* calls more frequently from large leaves (45.97%) than does *D. ebraccatus* (18.18%), which calls from small and medium leaves ( $\chi^2 = 14.04$ ,  $p < 0.001$ ,  $df = 2$ , Figure 1D).

Male *D. phlebodes* call from higher perches than do *D. ebraccatus* (Mann-Whitney U test = 1757.0,  $p = 0.006$ ; *D. phlebodes*:  $79.38 \text{ cm} \pm 34.87$ , *D. ebraccatus*:  $57.51 \pm 30.88$  cm). The depth of the water below the calling perches is the same for males of both species ( $W = 68.0$ ,  $p = 0.398$ ; *D. phlebodes*:  $14.47 \pm 8.80$  cm, *D. ebraccatus*:  $12.82 \pm 8.12$  cm); likewise, the distances between the calling sites and the nearest edge of the swamp are about the same ( $\chi^2 = 3.25$ ,  $p = 0.516$ ,  $df = 4$ ).

At Research Swamp, we observed that male *Dendropsophus phlebodes* called mostly from large leaves of the understory palm *Calypthogyne ghiesbreghtiana* (Arecaceae) (14.52%) and the medium-sized leaves of the herbaceous plant *Heteropterys laurifolia* (Malpighiaceae) (12.10%). Males *D. ebraccatus* called mostly from leaves of *H. laurifolia* (23.84%) and branches (26.87%). In the open swamp, male *D. phlebodes* usually called from large leaves of the herbaceous grass *Paspalum fasciculatum* (81.25%) and *D. ebraccatus* called more frequently from branches (33.33%; Table 1). The spatial niche overlap at the Research Swamp is wide ( $O = 0.81$ ). The randomization analysis generated a significant difference between the obtained and simulated overlaps ( $p$  [obtained  $\leq$  simulated] = 1.000;  $p$  [obtained  $\geq$  simulated] = 0.000). The simulated overlap is lower ( $0.37 \pm 0.02$ ) than the obtained by chance. In the open swamp, we obtained a low overlap ( $O = 0.28$ ). Randomizations with all the data produced no significant difference between the obtained and simulated overlaps ( $p$  [obtained  $\leq$  simulated] = 0.196;  $p$  [obtained  $\geq$  simulated] = 0.804). The simulated overlap ( $0.44 \pm 0.05$ ) is similar to the obtained.

### Comparison of Trophic Niche

We flushed a total of 135 stomachs of *Dendropsophus phlebodes* and only 33.33% had contents. Of these, 30 stomachs contained fragments of animal prey and 17 had unidentifiable digested items. In the 60 stomachs flushed of *D. ebraccatus*, only 33.33% had stomach contents,



**Figure 1.** Characteristics of calling sites used by males of two species at the swamps. (A) type of substrate, (B) shape of leaf, (C) texture of leaf, (D) size of leaf.

of which 16 had prey fragments and 8 had unidentifiable digested items.

The diet of *Dendropsophus phlebodes* consists of 14 types of preys (Table 2), the most common of which are Araneae (20.00%), *Crematogaster* sp. (13.33%) and Diptera larvae (10.00%). We also found that these are the most common items in the diet of *D. phlebodes* (31.58%, 21.05%, and 15.79%, respectively). In terms of volume, the most important were Lepidoptera larvae (mean = 0.61 mm<sup>3</sup>) and *Tetragnatha* sp. (mean = 0.33 mm<sup>3</sup>). The index of relative importance showed that the diet of *D. phlebodes* is primarily dominated by Araneae (IRI = 947.4), *Tetragnatha* sp. (IRI = 355.3), and Diptera larvae (IRI = 342.1).

We found only nine types of prey in the diet of *Dendropsophus ebraccatus* (Table 2). The most frequently consumed prey is Lepidoptera

(25.00%), which also is the most important in relation to the frequency of occurrence (Table 2). Diptera larvae (mean = 0.45 mm<sup>3</sup>) and Lepidoptera (mean = 0.40 mm<sup>3</sup>) represent the greatest volumes. The index of relative importance (IRI) demonstrates that Lepidoptera, Diptera larvae, and Araneae are the most important prey in the diet of *D. ebraccatus* (1517.1, 977.6, and 567.3, respectively).

The two species differ significantly in the volumes of prey consumed ( $U = 148.0$ ,  $p = 0.001$ ); *Dendropsophus ebraccatus* consumes larger prey ( $0.46 \pm 0.71$  mm<sup>3</sup>) than *D. phlebodes* ( $0.10 \pm 0.12$  mm<sup>3</sup>). The trophic niche breadth of *D. phlebodes* ( $H' = 2.47 \pm 0.14$ ) is similar to that of *D. ebraccatus* ( $H' = 2.17 \pm 0.2$ ) and is not significantly different ( $t$ -test =  $-1.58$ ,  $p = 0.124$ ). The trophic niche overlap is moderate ( $O = 0.42$ ). Randomizations with all data produced no

**Table 1.** Substrate use for calling sites in the two swamps by males of two species at La Selva Biological Station, Costa Rica. Values in columns are percentages of all observations.

Substrate	Research Swamp		Swamp Along Entrance	
	<i>D. phlebodes</i>	<i>D. ebraccatus</i>	<i>D. phlebodes</i>	<i>D. ebraccatus</i>
<i>Aciotis indecora</i>	3.23	—		
<i>Acroceras zizanioides</i>			3.13	22.22
<i>Anemopaegma chrysoleucum</i>	0.81	—		
<i>Anthurium subsignatum</i>	4.84	—		
<i>Calyptrocarya glomerulata</i>	2.42	2.99		
<i>Calyptrogyne ghiesbreghtiana</i>	14.52	7.46		
<i>Clidemia japurensis</i>	4.84	—		
<i>Heteropterys laurifolia</i>	12.10	23.88		
<i>Lindsaea quadrangularis</i>	2.42	—		
<i>Olfersia cervina</i>	3.23	—		
<i>Palicourea crocea</i>	2.42	4.48		
<i>P. guianensis</i>			—	11.11
<i>Panicum pilosum</i>	10.48	16.42		
<i>Panicum</i> sp.			6.25	22.22
<i>Paspalum fasciculatum</i>	4.03	2.99	81.25	11.11
<i>Philodendron alliodorum</i>	3.23	2.99		
<i>Phylodendrum aurantifolium</i>	0.81	—		
<i>Piper xanthostachyum</i>	2.42	—		
<i>Polybotrya osmundacea</i>	2.42	1.49		
<i>Salpichlaena volubilis</i>	—	1.49		
<i>Scleria microcarpa</i>	11.29	8.96	9.38	—
<i>Siparuna thecaphora</i>	0.81	—		
<i>Spathiphyllum friedrichsthali</i>	2.42	—		
<i>Warszewiczia coccinea</i>	1.61	—		
Branch	9.68	26.87	—	33.33

significant difference between the obtained and simulated overlaps based on the prey type ( $p$  [obtained  $\leq$  simulated] = 0.88;  $p$  [obtained  $\geq$  simulated] = 0.11). The observed mean (0.42) was similar to the simulated mean (0.26  $\pm$  0.02).

## Discussion

The similarities of the calling sites of *Dendropsophus phlebodes* and *D. ebraccatus* may be related to their taxonomic relationship

and similar body sizes, as has been shown in related species by Rossa-Feres and Jim (2001) and suggested by Menin *et al.* (2005). However, despite the similarities, there are significant differences in the substrate and leaf sizes used by these species. Although we found male *D. phlebodes* calling from a variety of substrates, the frogs call mostly from leaves of grasses, sedges, and broad leaves from vegetation at the edge of the ponds, as mentioned by Duellman (1970). In contrast, male *D. ebraccatus* usually call from leaves of vines, and emergent herbs

**Table 2.** Type of prey in diets of *Dendropsophus phlebodes* and *D. ebraccatus* at La Selva Biological Station, Costa Rica. N = number of prey; %N = percentage proportion of the prey; F = frequency of occurrence; %F = percentage of the frequency of prey taxa in stomachs; V = mean volume of the prey (mm<sup>3</sup>); IRI = Index of Relative Importance.

Prey taxa	<i>Dendropsophus phlebodes</i>						<i>Dendropsophus ebraccatus</i>					
	N	%N	F	%F	V	IRI	N	%N	F	%F	V	IRI
<b>Insecta:</b>												
Coleoptera	2	6.67	2	10.53	0.01	78.9	—	—	—	—	—	—
Crysmelidae	—	—	—	—	—	—	—	—	—	—	—	—
Diptera	—	—	—	—	—	—	—	—	—	—	—	—
Culicidae	—	—	—	—	—	—	2	12.50	2	16.67	0.1	295.1
Lonchidae	1	3.33	1	5.26	0.21	63.6	—	—	—	—	—	—
Diptera (larvae)	3	10.00	3	15.79	0.09	342.1	2	12.50	2	16.67	0.45	989.6
Blattodea	2	6.67	2	10.53	—	—	1	6.25	1	8.33	—	—
Lepidoptera	—	—	—	—	—	—	4	25.00	4	33.33	0.4	1527.8
Lepidoptera (larvae)	2	6.67	2	10.53	0.61	337.7	—	—	—	—	—	—
Hymenoptera	—	—	—	—	—	—	—	—	—	—	—	—
Formicidae	—	—	—	—	—	—	1	6.25	1	8.33	—	—
Myrmicinae	—	—	—	—	—	—	—	—	—	—	—	—
Crematogaster sp.	4	13.33	4	21.05	0	280.7	—	—	—	—	—	—
Not-Formicidae	1	3.33	1	5.26	0	17.5	—	—	—	—	—	—
Homoptera	1	3.33	1	5.26	0.2	61.4	1	6.25	1	8.33	—	—
Cicadellidae	1	3.33	1	5.26	0.03	24.1	—	—	—	—	—	—
Dermaptera	1	3.33	1	5.26	0	17.5	—	—	—	—	—	—
Mantidae	—	—	—	—	—	—	1	6.25	1	8.33	0	52.1
Hemiptera	—	—	—	—	—	—	1	6.25	1	8.33	—	—
Miridae	—	—	—	—	—	—	—	—	—	—	—	—
Bryocorinae	2	6.67	1	5.26	0.01	39.5	—	—	—	—	—	—
<b>Arachnida:</b>												
Araneae	6	20.00	6	31.58	0.04	947.4	2	12.50	2	16.67	0.21	572.9
Tetragnathidae	—	—	—	—	—	—	—	—	—	—	—	—
Tetragnatha sp.	2	6.67	2	10.53	0.33	355.3	1	6.25	1	8.33	0.1	95.5

and bushes in the swamps; this is consistent with the observations of Savage (2002) and Miyamoto and Cane (1980). We also found individuals calling from branches (contra Miyamoto and Cane 1980). Furthermore, in Research Swamp, we found a significantly high spatial niche overlap between males of both species ( $O = 0.81$ ), indicating an abundance of reproductive resources that are shared and a lack of competition between the two species (Gotelli and Graves 1996). Also, in the Open Swamp, we found a low and insignificant spatial niche overlap ( $O = 0.28$ ), which demonstrates a differentiation on spatial resource use. We suggest that the observed spatial niche overlaps and the exploitation of different type of substrates and leaf sizes by calling males is influenced by the availability of a structural diversity of vegetation in the swamps during the study. Menin *et al.* (2005) found that vegetation structure influences the resource use of two closely related, sympatric hylid frogs. Consequently, the degree of environmental heterogeneity may be directly related to effectiveness of the support for the coexistence of similar species (Wang *et al.* 2002).

Furthermore, the habit of male *Dendropsophus phlebodes* calling from significantly higher perches than *D. ebraccatus* is consistent with the findings of Donnelly and Guyer (1994) for the same species in Research Swamp. Rossa-Feres and Jim (2001) found partitioning in the perch height of two congeneric species of tree frogs (*Dendropsophus sanborni* and *D. nanus*); male *D. sanborni* called from significantly higher perches in herbaceous emergent vegetation than did *D. nanus*. Additionally, Ptasek (1992) found vertical segregation in the height of the call site of two sympatric species of gray tree frogs (*Hyla versicolor* and *H. chrysoscelis*). Muñoz-Guerrero *et al.* (2007) considered perch height to be a segregation factor among species of similar body size; this may imply an important factor in resource partitioning that supports coexistence of male *D. ebraccatus* and *D. phlebodes* during the breeding season at La Selva.

Males of both *Dendropsophus ebraccatus* and *D. phlebodes* ate terrestrial invertebrates in exclusion to aquatic invertebrates. Terrestrial invertebrates usually dominate the diet of hylid frogs (Muñoz-Guerrero *et al.* 2007). We found a wide variety of types of prey consumed by males of both species; thus, we consider them to be generalist predators. The diet of generalist amphibian predators is thought to depend on prey availability in the habitats (Duellman and Trueb 1986). We suggest that the most frequently consumed prey by both frog species (Araneae, *Crematogaster* sp., Diptera larvae, and Lepidoptera) were the most abundant invertebrates in the swamps during the study. Also, we think that vegetation structure in the area studied permitted the presence of all arthropod species found in the frog stomachs. Spiders such as *Tetragnatha* sp. prefer herbaceous habitat vegetation of wet environments (Aiken and Coyle 2000). Additionally, *Crematogaster* sp. tend to be found in trees and bushes, because their nest colonies usually are located in dead branches or trunks and scout ants usually forage searching for resources and recruiting nestmates (Longino 2003). On the other hand, differences found in the prey volume could be explained by the larger body size of *D. ebraccatus*, which allows it to feed on larger prey. The results of other studies of hylid assemblages also report that differences in prey volume are related to the predator's size and mouth width (Duré 1999, Macale *et al.* 2008).


The niche breadths of both species are similar and the niche overlap is moderate ( $O = 0.42$ ) and insignificant, thereby demonstrating similar diets and lack of a negative interaction between the species. This similarity can be related to high availability of prey that satisfies the needs of both species in the habitat; thus, competition between them is infrequent or nonexistent (Muñoz-Guerrero 2007, Kovács *et al.* 2010). Kuzmin (1995) mentioned that competition for food is a rare event in natural amphibian communities.

Furthermore, we must think that the high percentage of empty stomachs and few prey

consumed by *Dendropsophus phlebodes* and *D. ebraccatus* may indicate that males of both species are focused primarily on vocalization, rather than on feeding activities during their breeding period. Solé and Peltz (2007) reported similar results for three hylid species with short reproductive periods. They suggested that males of these species concentrate less on feeding and more on advertisement calls because of competition with conspecifics. Consequently, this may suggest that trophic dimension is not relevant for explaining coexistence in our study.

We conclude from our results that competitive interactions between *Dendropsophus ebraccatus* and *D. phlebodes* for spatial and trophic resources during their reproductive period either was nonexistent or was infrequent during the time spent at our study sites in La Selva. We think that differences in the use of calling sites are related to the high availability of diverse vegetation structure in the habitats, which allows segregation of perch height within the available resources. The similarity of diets may be related to the high prey availability at our study site. However, the high percentage of empty stomachs indicates that males concentrate on calling, rather than on feeding, thereby demonstrating that food resources are less important to the coexistence of these anurans in our study. Last, our findings suggest that differences in the use of space resources in a habitat with a high availability of diverse vegetation structure, is an important factor supporting the coexistence of male *D. ebraccatus* and *D. phlebodes* at La Selva.

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