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DIET OF *DENDROPSOPHUS MICROCEPHALUS* AND *SCARTHYLA VIGILANS* (ANURA: HYLIDAE) AT A LOCALITY IN NORTH-WESTERN VENEZUELA WITH NOTES ON MICROHABITAT OCCUPATION

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ABSTRACT

The coexistence of species with similar ecological requirements (food, space, time) has typically drawn attention of researchers because competition for resources is expected to be high. The diet and microhabitat occupation of two morphologically and ecologically similar species of Hylidae (Anura), Dendropsophus microcephalus *and* Scarthyla vigilans, *were analyzed at a locality in north-western Venezuela, with the aim of addressing the potential for space and food competition between them. Diet was estimated through the analysis of stomach contents and microhabitat occupation was estimated through recordings of perch type, height and horizontal distance to water. Thirty-six prey categories (32 families, 4 orders) of arthropods were identified: 30 categories in* D. microcephalus *and 21 categories in* S. vigilans. *The most important prey (RII) in* D. microcephalus *were Agelenidae (11.1%), Tachinidae (9.32%) and Lepidoptera-larvae (7.96%). Gryllidae (14.13%), Cicadidae (9.1%), Cicadellidae (8.3%) and Delphacidae (8.02%) were the most important in* S. vigilans. *Diet overlap was relatively low (0.32). Both species have relatively generalist diets. Both species occupied the same type of perches (leaves and stems of Dicotyledons and Monocotyledons) and heights (average:* S. vigilans, *24 ± 16.2 cm;* D. microcephalus, *22.7 ± 9.5 cm). The potential for space competition is high if perches are limited and food competition is expected to be low.*

Key-Words: Diet; Generalist; Niche overlap; Resource partitioning; Microhabitat; Morphometry.

INTRODUCTION

Morphological and ecological similarity between species is believed to hinder their coexistence because competition for resources is likely. It is thought that at least one ecological difference in resource use between them (*i.e.,* food, time or space partitioning) is necessary to allow coexistence (Pianka, 1994; Gor-

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don, 2000; Vignoli & Luiselli, 2011). The relative importance of food, time and space use in structuring animal communities varies from one another and between habitats. Several authors have suggested that the space dimension is often more important than the food dimension, and that the latter is often more important than the temporal dimension (Schoener, 1974; Giller, 1984); however, this ordering is by no means universal. For instance, food is the main dimension in structuring several anuran communities (Toft, 1980a,b; Lima, 1998), while microhabitat is in others (*e.g.,* Crump, 1974; Toft, 1985; Cardoso *et al.,* 1989).

Amphibians, and specially anurans, are remarkably abundant in tropical ecosystems and have been considered extremely important in food webs and energy flow (Stebbins & Cohen, 1995). Nonetheless, there are relatively few studies of feeding preferences and behavior in this group (Toft, 1980a,b; Duellman, 1993; Piñero & Durant, 1993; Lima & Magnusson, 1998; Caldwell & Vitt, 1999; Parmelee, 1999), and most of them have focused on a limited number of taxa. With regards to habitat occupation, available literature indicates that in general, there are substantial differences in microhabitat and activity periods both within and among species (Schoener, 1974; Drewry & Rand, 1983; Toft, 1985; Muñoz-Guerrero *et al.,* 2007; Tárano, 2010). Several studies with hylids have demonstrated that microhabitat segregation is associated to body size (Bevier, 1997), which in turn has a strong impact on the diet and prey-capture behavioral strategies (Toft, 1980a, 1981).

In anurans, diet composition is usually related to body size, sex, and habitat and microhabitat preferences (Toft, 1980a,b; Christian, 1982; Woolbright & Stewart, 1987; Piñero & Durant, 1993; Bevier, 1997; Hirai & Matsui, 2000). The diet typically changes with age (*e.g.,* Labanick, 1976; Christian, 1982; Strussmann *et al.,* 1984; Woolbright & Stewart, 1987; Donnelly, 1991; Wiggins, 1992), season (da Rosa *et al.,* 2002) and the size and behavior of preys (Freed, 1980; Lima, 1998; Parmelee, 1999). Since anurans swallow whole prey, mouth width poses an upper limit to the maximum size or volume of prey. Therefore, as an individual grows, the maximum size of its preys may increase concomitantly (Lima & Moreira, 1993; Parmelee, 1999). In general, anurans that consume relatively small and slow-moving prey have narrow mandibles and symmetric feeding cycles (*i.e.,* the time devoted in capturing is similar to that devoted in retrieving to the mouth). On the other hand, anurans feeding on relatively large slow-moving prey have wide mandibles and asymmetric feeding cycles (Emerson, 1985).

Most anurans analyzed so far feed upon invertebrates as adults while a few also prey upon small vertebrates (Duellman & Trueb, 1994). A great majority of the anurans analyzed have been labeled as food-generalists based on estimations of diet richness and equitability, despite the fact that prey availability has not been estimated in most studies (but see Toft, 1980b, 1981; Christian, 1982; Hirai & Matsui, 2000). With regards to prey specificity, anurans can be arranged in a continuum ranging from ant specialists through non-ant specialists to generalists (Toft, 1981).

In the present study we aimed to describe the diet and microhabitat occupation of two hylid frogs of similar morphology which occur syntopically over a wide range in northern Venezuela, *Scarthyla vigilans* and *Dendropsophus microcephalus. Scarthyla vigilans* is an arboreal anuran traditionally thought to be restricted to the Maracaibo Lake basin in northwestern Venezuela (Barrio-Amorós, 1998). It is currently known for inhabiting the northern Caribbean lowlands, the Magdalena River basin in Colombia and the llanos of Colombia and Venezuela (Barrio-Amorós *et al.,* 2006; Lotzkat, 2007; Rojas-Runjaic *et al.,* 2008). The species is currently expanding into the Orinoco River Delta (Rojas-Runjaic *et al.,* 2008) and Trinidad and Tobago (Smith, J.M. *et al.,* 2011). *Dendropsophus microcephalus* has been regarded as widely distributed in Venezuelan lowlands (Barrio-Amorós, 2009). Therefore, both species coexist in vast areas of their distribution providing opportunity to assess the potential for food and space segregation. Previous studies in Colombia have documented similar microhabitat preferences (Lomolino *et al.,* 2006, Muñoz-Guerrero *et al.,* 2007; Armesto *et al.,* 2009), overlapping diets (Muñoz-Guerrero *et al.,* 2007) and partially disjoint activity patterns throughout the rainy season (Muñoz-Guerrero *et al.,* 2007). Nonetheless, so far there is scarce information on the habits of both species. With this study we aimed to add to the comprehension of the coexistence of *D. microcephalus* and *S. vigilans* and to address potential regional differences.

METHODS

Study Site and Subjects

We performed the study at Hacienda La Guáquira (10°20'4"N, 68°39'17"W), in the mountain complex Macizo de Nirgua, at the western-most edge of the Coastal Mountain Chain (Cordillera de la Costa) in northern Venezuela. The ranch spans through lowlands (100 masl) and hills (1,400 masl) and vegetation varies from mist-forest in the highlands to semi deciduous tropical humid forests at the lowlands of Cerro Zapatero (Runemark *et al.,* 2005; Lotzkat, 2007). Large areas of the lowlands have been turned into rice and corn fields and cattle ranching. We collected the individuals in two lagoons arbitrarily labeled Lagoon A (10°17'49"N, 68°40'08"W; 3,392 m^2) and B (10°17'46"N, 68°40'11"W; 12,155 m^2 approx.) in the surroundings of crop and pasture fields.

Dendropsophus microcephalus (Cope, 1886) (Hylidae: Hylinae) is a medium-sized (SVL males: 18-25 mm; SVL females: 24-31 mm) nocturnal-arboreal frog (Duellman, 1970; Savage, 2002). The night color of the dorsum is light yellow with various brown or tan markings; the daylight color is tan-yellow, or light brown with darker brown or red markings (Duellman, 1970). The species ranges from Mexico to Peru, and in Venezuela it has an ample distribution in the lowlands north of the Orinoco River (Barrio-Amorós, 1998). It occupies open lowlands from natural savannas to pasture lands holding ephemeral or long lasting ponds (Barrio-Amorós, 1998). During the reproductive season, males vocalize from emergent vegetation in shallow water (Tárano, 2010). The species has been labeled as least concern (Bolaños *et al.,* 2008) in view of its wide distribution, tolerance of a broad range of habitats, presumed large population, and because it is not facing any known threats.

Scarthyla vigilans (Solano, 1971) (Hylidae: Hylinae) is a medium-sized nocturnal-arboreal frog (average SVL males: 15.6 mm; SVL females 19.5 mm). The dorsum is lime-green with poorly differentiated longitudinal stripes and transparent patches in vent (Barrio-Amorós *et al.,* 2006). The species' range is restricted to northern South America, specifically to Venezuela, northern Colombia (including the Magdalena River basin) (Armesto *et al.,* 2009) and Trinidad and Tobago (Smith, J.M. *et al.,* 2011). It occupies lowlands below 100 masl. Male activity at the study site peaks in October (Lotzkat, 2007); calling activity peaks at night and it can also occur during the day (Lotzkat, 2007). The species has been also labeled as least concern (La Marca *et al.,* 2004) because it is a very adaptable species, which is not facing any known threats.

Diet composition

We used visual and auditory surveys to find the individuals during nightly walks from 2000 to 0000 hrs from July to September 2012. We captured the individuals by hand and immediately fixed each specimen in formalin 4% to stop digestion (Toft, 1980a; Caldwell, 1996); we further preserved it in ethanol 70% until processed. In the lab, we measured the snout-to-vent length (SVL) and mouth width (from corner to corner, mouth closed) with a dial caliper (Kannon) to the nearest 0.1 mm, before dissecting the stomach. Each stomach was preserved in ethanol 70% until further examination. We determined age class and sex by inspection on the gonads; individuals with developed gonads were considered adults, otherwise they were classified as juveniles.

We observed the stomach contents under a stereoscopic microscope (AmScope, Model SE306R-PZ-E) at 20x, 40x and 80x. We identified prey items to the taxonomic level of order, class and family (which we called "prey categories") through the taxonomic key developed by Smith, R. & Silva (1970). Then, we measured the maximum length and width of all items on each prey category with a "hair count" stereoscopic microscope to the nearest 0.01 mm. With these measures we calculated the volume of each prey item by using the equation of a prolate spheroid

$$Vi = \frac{4}{3}\pi\left(\frac{l}{2}\right)\left(\frac{w}{2}\right)^2,$$

where *l* represents the maximum length of the item and *w* its maximum width (Vitt, 1991). Prey volume is a gross estimator of the energetic contribution of an item (Caldwell, 1996). Broken or partially digested items were not measured.

We determined the number of items per prey category (*Ni*), the proportion of non-empty stomachs which contained a given category (*Fi*) and the volume of each category per stomach (*Ni x Vi*). With these values we estimated the diet richness (number of prey categories), diet diversity through the Shannon-Wiener index

$$H' = -\sum p_i \ln p_i,$$

where p_i corresponds to the proportion of prey *i* in number, equitability through the Alatalo index (Alatalo, 1981)

$$F = \frac{(N_2 - 1)}{(N_1 - 1)},$$

where

$$N_1 = e^{H'}$$

and

$$N_2 = \frac{1}{\lambda}$$

with

$$\lambda = \sum p_i^2,$$

the absolute importance index

$$I = \frac{\%F + \%N + \%V}{3},$$

where

$$\%N = \left(\frac{Ni}{Nt}\right)x100;\ \%F = \left(\frac{Si}{St}\right)x100;\ \%V = \left(\frac{Vi}{Vt}\right)x100$$

(S means stomach), the niche breath per species through the standardized Levins' index (Levins, 1968)

$$\hat{B} = \frac{1}{\sum_i (p_{ji})^2},$$

with the standardization proposed by Hurlbert (1978)

$$\hat{B}_a = \frac{\hat{B} - 1}{n - 1},$$

where n is the number of possible states of the resource, and the diet overlap between *S. vigilans* and *D. microcephalus* through the Pianka's index (Krebs, 1999)

$$O_{xy} = \frac{\sum p_{x,i}\ p_{y,i}}{\sqrt{\sum p_{x,i}^2 \sum p_{y,i}^2}},$$

where Px,i and Py,i are the frequencies of the *i-esim* category in species x and y, respectively. All these indexes with the exception of H' vary between 0 and 1.

Microhabitat occupation

We performed visual and acoustic surveys in both lagoons by slowly walking amidst vegetation, around and within the lagoons at night. For each individual found, we recorded the horizontal distance to the water (in case of being located in the lagoon margins), substrate type (emergent vegetation, floating vegetation, soil), plant type (Monocotyledoneae, Dicotyledoneae), perch type (leaf, stem, stone), and perch height above water or soil. Form these measures we estimated vertical and horizontal segregation between species and segregation by perch type.

Statistical Analysis

We determined the association between SVL and mouth width within species through the Spearman rank correlation coefficient. Then, we determined the association between mouth width and prey length or volume (log transformed) within species (Spearman rank correlation coefficient). We also compared prey size and stomach volume between species through the Mann-Whitney U test (Zar, 1999).

We performed a Principal Components Analysis (PCA) to explore diet segregation between species. In addition, we compared the Shannon-Wienner index between species through the Hutchenson t (Hutchenson, 1970) as:

$$t = \frac{H'_1 - H'_2}{S_{(H'_1 - H'_2)}},$$

where

$$S_{(H'_1 - H'_2)} = \sqrt{S^2_{H'_1} + S^2_{H'_2}},$$

and S is the variance of H for each species, estimated as

$$S^2_{H'} = \frac{\sum f_i \ln f_i^2 - \left(\sum f_i \ln f_i\right)^2 / 2}{\sum f_i^2},$$

where fi corresponds to Ni. The degrees of freedom of t were estimated through

$$= \frac{\left(S^2_{H'_1} + S^2_{H'_2}\right)^2}{\frac{\left(S^2_{H'_1}\right)^2}{n_1} + \frac{\left(S^2_{H'_2}\right)^2}{n_2}}.$$

To determine microhabitat preferences we used the χ^2 test (Zar, 1999) and the standardized residuals analysis in case we found significant associations (*i.e.,* species x distance to water, species x perch type or species x perch height). We used PAST 2.17 (Hammer *et al.,* 2001) and Statistica 6.0 to perform the statistical analyses

RESULTS

Morphometry and Diet Composition

We collected 209 individuals, 99 individuals of *D. microcephalus* (88 males, 6 females, 5 juveniles) and 110 individuals of *S. vigilans* (68 males, 38 females, 4 juveniles.). In both species, females were larger than males (SVL: *D. microcephalus,* males:

TABLE 1: Composition of the diet of *Dendropsophus microcephalus* (N = 50) and *Scarthyla vigilans* (N = 31). %N = Ni/Nt; %F = Si/St. %V = Vi/Vt; (%) RII = (I_i / ΣI) 100; I = (%N+%F+%V)/3. RII > 9% are show in **bold**.

Order	Family	*D. microcephalus*				*S. vigilans*			
		%N	%F	%V	RII (%)	%N	%F	%V	RII (%)
Araneae	Agelenidae	9.21	14.00	14.25	**11.08**	2.17	3.23	0.08	1.67
	Amaurobiidae	1.32	2.00	0.03	0.99				
	Araneidae	2.63	4.00	7.93	4.31				
	Ctenidae	1.32	2.00	0.39	1.10	2.17	3.23	1.26	2.03
	Linyphiidae	1.32	2.00	0.23	1.05				
	Lycosidae	1.32	2.00	0.34	1.08	6.52	6.45	4.58	5.33
	Oecobiidae	2.63	4.00	0.60	2.14				
	Salticidae	1.32	2.00	0.42	1.11	2.17	3.23	1.16	1.99
	Tetragnathidae	5.26	6.00	1.25	3.70				
Coleoptera	Larvae	3.95	6.00	12.39	6.61				
	Staphylinidae					2.17	3.23	0.20	1.70
	Chrysomelidae	5.26	8.00	7.24	6.06	2.17	3.23	0.70	1.85
	Carabidae	1.32	2.00	2.56	1.74				
Dyctioptera	Blattidae	3.95	6.00	10.68	6.10				
Diptera	Calliphoridae				0.00	4.35	6.45	0.42	3.41
	Chiromonidae	2.63	4.00	0.84	2.21				
	Culicidae	1.32	2.00	0.31	1.07				
	Sepsidae	2.63	4.00	0.36	2.07				
	Tachinidae	13.16	10.00	8.36	**9.32**	10.87	9.68	3.09	7.19
	Tipulidae	1.32	2.00	0.07	1.00				0.00
Hemiptera	Nymph					2.17	3.23	0.09	1.67
	Lygaeidae					4.35	6.45	1.95	3.88
Homoptera	Cicadellidae	9.21	12.00	4.97	7.75	8.70	12.90	5.68	8.29
	Cicadidae	1.32	2.00	1.62	1.46	10.87	12.90	6.12	**9.09**
	Delphacidae	2.63	4.00	3.74	3.07	6.52	9.68	10.19	8.02
	Derbidae	3.95	6.00	1.92	3.51				
	Membracidae					2.17	3.23	2.10	2.28
Hymenoptera	Pteromalidae	1.32	2.00	0.33	1.08				
	Formicidae	5.26	8.00	0.93	4.20	4.35	6.45	1.19	3.64
Lepidoptera	Tenthredinidae	1.32	2.00	0.57	1.15				
	Noctuidae	1.32	2.00	0.56	1.15	2.17	3.23	6.18	3.52
	Larvae	6.58	10.00	10.33	7.96	6.52	9.68	6.15	6.79
Orthoptera	Acrididae	1.32	2.00	1.54	1.44	2.17	3.23	16.55	6.67
	Gryllidae	2.63	4.00	3.00	2.85	13.04	12.90	20.54	**14.13**
	Tettigonidae	1.32	2.00	2.23	1.64	2.17	3.23	1.69	2.15
Isopoda	Larvae					2.17	3.23	10.07	4.70
	Nt	76				46			

19.47 ± 1.05 mm; females: 20.53 ± 2.94 mm; *S. vigilans,* males: 15.98 ± 1.06 mm, females: 19.69 ± 2.48 mm). Juveniles' SVL varied from 7 to 9.99 mm in *D. microcephalus* and from 9 to 14.99 mm in *S. vigilans.* Mouth width was on average 6.51 ± 0.89 mm (min-max: 2.54-8.52) in *D. microcephalus* and 5.46 ± 0.75 mm (min-max: 3.12-7.32) in *S. vigilans.* The differences in SVL between species were not significant (Mann-Whitney U: Z = 1.56, p = 0.25) but those in mouth width were (Mann-Whitney U: Z = 4.52; $p < 0.0001$). There was weak correlation between SVL and mouth width in both species (Spearman: *D. microcephalus,* $r_s = 0.52$ $p < 0.0001$; *S. vigilans,* $r_s = 0.74$, $p < 0.00001$). There was no relationship between mouth width and prey length (Spearman: $r_s = -0.182$, $p > 0.05$) or prey volume ($r_s = -0.075$, $p > 0.05$) in *D. microcephalus.* In *S. vigilans* there was no relationship between mouth width and prey length ($r_s = 0.241$, $p > 0.05$) but there was weak correlation with prey volume ($r_s = 0.41$, $p = 0.02$).

We found identifiable contents in 81 out of the 209 stomachs dissected (39%), 50 from *D. microcephalus* (48 males, 1, female, 1 juvenile) and 31 from *S. vigilans* (12 males, 18 females, 1 juvenile); 14 stomachs of *D. microcephalus* and 23 of *S. vigilans* were empty and the remaining 91 stomachs had extremely digested contents which did not allow identification (*D. microcephalus* = 35; *S. vigilans* = 56); one stomach of *D. microcephalus* contained no more than seeds. We found 1.61 ± 0.88 prey items per stomach in *D. microcephalus* corresponding to a total volume of 7.71 ± 13.48 mm³ (min-max: 0.14-62.38 mm³). In *S. vigilans* we found, on average, 1.48 ± 0.996 prey items per stomach, corresponding to a total volume of 18.03 ± 27.97 mm³ (min-max: 0.44-128.70 mm³). We did not find significant differences in prey size (Mann-Whitney U: Z = -0.680, p = 0.5) or volume (Z = -1.705, p = 0.1) between species.

We identified 36 prey categories (32 up to family, 4 up to order) of arthropods of Cheliceriformes, Unirramia and Crustacea (Table 1); 30 categories in *D. microcephalus* and 21 categories in *S. vigilans.* With regards to numeric representation, the diet of *D. mi-*

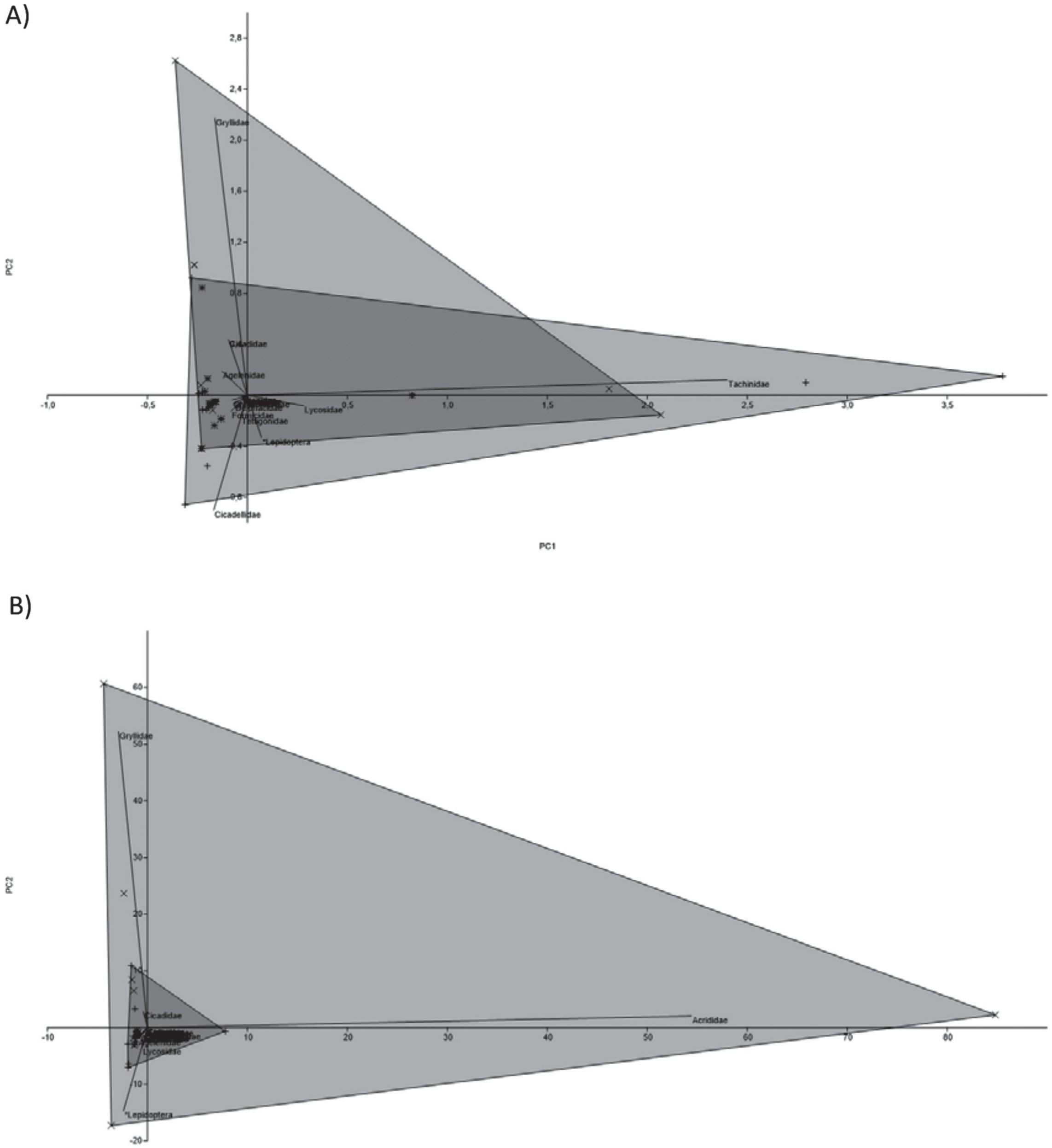

FIGURE 1: Principal components analysis of diet composition of *Dendropsophus microcephalus* and *Scarthyla vigilans.* **(A)** Based on numeric composition (number of items per prey category), **(B)** Based on volumetric composition (volume of each prey category). x: *S. vigilans,* +: *D. microcephalus.*

crocephalus was composed of (in descendent rank; only categories with n > 3 items are listed) Tachinidae, Agelenidae, Cicadellidae, Lepidoptera (larvae and adults), Tetragnathidae, Chrysomelidae, Formicidae, Blattidae and Derbidae; 20 additional categories had less than 3 items as a whole (Table 1). With regards to the frequency of apparition (number of stomachs), the most frequent categories were Agelenidae, Cicadellidae, Tachinidae, Lepidoptera-larvae, Chrysomelidae, Formicidae, Tetragnathidae, Blattidae and Derbidae. As a whole, the most important categories (%RII) were Agelenidae (11.1%), Tachinidae (9.32%) and Lepidoptera-larvae (7.96%).

On the other hand, the diet of *S. vigilans* was composed of (numerical rank, n > 3 items) Gryllidae, Tachinidae, Cicadidae, Cicadellidae, Lycosidae, Delphacidae and Lepidoptera; 14 additional categories had less than 3 items (Table 1). Regarding the frequency of apparition, the most frequent categories were Cicadellidae, Cicadidade, Gryllidae, Tachinidae, Delphacidae and Lepidoptera. As a whole, the most important categories (%RII) were Gryllidae (14.13%), Cicadidae (9.1%), Cicadellidae (8.3%) and Delphacidae (8.02%).

The diversity of the diet of *D. microcephalus* (H') was 3.18, the equitability (F) was 0.76 and niche breath (B_α) was 0.467. The diversity of the diet of *S. vigilans* was 2.89, the equitability was 0.82, and niche breath was 0.65. Hutchenson's *t* indicated that diet diversity differed significantly between species ($t = 2.16$, $p = 0.03$), being larger in *D. microcephalus* than in *S. vigilans.* Niche overlap (O) between the species was 0.316.

The PCA performed with the numeric composition confirmed moderate diet overlap between the species (Fig. 1A), while that performed with volumetric data indicated slight overlap (Fig. 1B). Nonetheless, the first two components (PC1 and PC2) only explained 50% of the variance, both numerically and volumetrically (Table 2). Numerically, Tachinidae was the most important category in PC1 and Gryllidae and Cicadellidae were in PC2 (Fig. 1A, Table 2). Volumetrically, Acrididae was the most important category in PC1 and Gryllidae and Lepidoptera in PC2 (Fig. 1B, Table 2).

Microhabitat occupation

We recorded habitat occupation from 95 individuals of *D. microcephalus* (31 males, 3 females, 9 juveniles, 52 unknown sex) and 94 individuals of *S. vigilans* (10 males, 7 females, 8 juveniles, 69 unknown sex). All the individuals of both species were perched on emergent vegetation inside the lagoon at the moment of sight (none individual was observed perching on soil, on floating vegetation or at the lagoon margins above dry soil), on leaves and stems of Monocotyledons and Dicotyledons with the same probability ($\chi^2 = 1.021$, $p > 0.05$, d.f. = 3). They perched at an average height of 24 ± 16.2 cm (min-max: 5-54 cm) in *S. vigilans,* and of 22.7 ± 9.5 cm (min-max: 0.5-93 cm) in *D. microcephalus.* Despite the fact that *D. microcephalus* occupied a wider range of heights (Fig. 2), vertical distribution was homogeneous between species (10 height classes, defined every 10 cm from 0 to 100 cm; $\chi^2 = 9.52$, $p > 0.05$, d.f. = 7, Fig. 2). Both species were more common from 21 to 30 cm than at other height intervals; therefore, microhabitat preferences coincide.

TABLE 2: Eigenvalues of prey categories, numerically and volumetrically, for the first two principal components (PC1 and PC2) of *Dendropsophus microcephalus* and *Scarthyla vigilans.* The most important category for each PC is shown in **bold**.

Prey category	Number of items		Volume of items	
	PC1	PC2	PC1	PC2
Agelenidae	-0.052	0.077	-0.018	-0.035
Ctenidae	-0.011	-0.002	-0.001	-0.001
Lycosidae	0.115	-0.033	-0.009	-0.063
Salticidae	-0.011	-0.012	-0.001	-0.001
Chrysomelidae	-0.031	-0.015	-0.008	-0.015
Tachinidae	**0.984**	0.049	-0.010	-0.023
Cicadellidae	-0.069	-0.369	-0.008	-0.020
Cicadidae	-0.038	0.178	-0.007	0.051
Delphacidae	-0.026	-0.026	-0.013	-0.023
Formicidae	-0.033	-0.051	-0.001	-0.003
Noctuidae	-0.009	-0.008	-0.005	-0.008
Lepidoptera-larvae	0.028	-0.136	-0.043	-0.268
Acrididae	-0.009	-0.008	**0.997**	0.037
Gryllidae	-0.066	**0.891**	-0.053	**0.957**
Tettigonidae	-0.013	-0.069	-0.002	-0.004

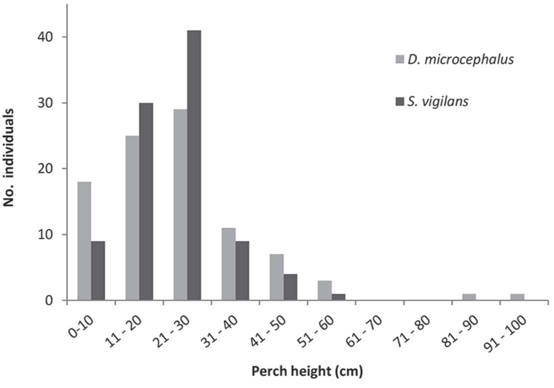

FIGURE 2: Vertical distribution of individuals of *Dendropsophus microcephalus* and *Scarthyla vigilans* on emergent plants.

TABLE 3: Comparison of the diet of of *Dendropsophus microcephalus* and *Scarthyla vigilans* at two localities: La Guáquira (Venezuela, this study) and El Botillero, Colombia (Muñoz-Guerrero *et al.,* 2007) based on RII (%). RII for El Botillero were calculated from data shown in Table 1. pp 420, Muñoz-Guerrero *et al.* (2007). Other includes unidentified items and larvae. "?" indicates incomplete data not allowing calculation. RII > 15% are shown in **bold**.

Order	*D. microcephalus*		*S. vigilans*	
	This study	**El Botillero**	**This study**	**El Botillero**
Acari		1.46		
Araneae	**26.56**	**17.74**	11.02	**24.37**
Collembola			10.62	
Coleoptera	14.41	**15.68**	3.56	11.51
Dyctioptera	6.1	**19.80**		
Diptera	**15.68**	**16.55**	10.60	4.21
Hemiptera		?	5.54	4.87
Homoptera	**15.79**		**27.67**	
Hymenoptera	5.28	9.52	3.64	**19.07**
Lepidoptera	10.26		10.31	
Neuroptera	6.31			
Mantodea		?		
Orthoptera	5.93	10.31	**22.95**	**16.68**
Psocoptera		?		
Isopoda			4.7	
Other		2.64		8.66

DISCUSSION

The results of the present study indicate a high probability of competition for calling or prey-ambushing perches (but see below) and a relatively low probability of competition over food between *D. microcephalus* and *S. vigilans* at the study site. Both species use emergent plants and show identical vertical distribution. The species share approximately 42% of the prey categories identified (15 out of 36) but their relative importance varies between them; the most important categories in one species are usually amongst the least important in the other. In *D. microcephalus,* arachnids of Agelenidae and dipterans of Thachinidae are the most important (RII ≈ 10%), while the most important prey in *S. vigilans* are orthopterans of the family Grillydae. Our results contrast with those of Muñoz-Guerrero *et al.* (2007) with regards to microhabitat use and diet composition; we discuss potential factors favoring the differences between studies.

At our study locality, we found total micro spatial overlap between *D. microcephalus* and *S. vigilans;* both species occupy the same type of perch and their vertical distribution coincides. We often found individuals of both species on the same plant separated by as much as 20 cm, as well as on neighboring plants less than one meter apart. In addition, during the study season, the abundance of both species (estimated from acoustic surveys and captures) was similar, despite the fact that *D. microcephalus* has often been regarded as more abundant than *S. vigilans* (S. Boher, *pers. comm.*). While habitat use suggests high potential for space competition between these species, we do not take this for granted because competition depends on resource abundance (Pianka, 1994) and nightly activity rhythms. If suitable perches are abundant and/or their activity patterns are disjointed (within the night and/or along the season), both species might coexist without major interference. We did not estimate perch abundance in relation to population numbers, but qualitatively, at the height of the rainy season, emergent vegetation formed a continuous cover along the lagoon margins; thus calling perches did not seem to be limited. Additionally, during the study period we never observed any type of aggressive interaction (vocal or physical) between *D. microcephalus* and *S. vigilans.* We believe that acoustical cues may help to avoid direct interspecific encounters and maintain interindividual distances much as it has been demonstrated in intraspecific spacing (Whitney & Krebs, 1975; Wilczynski & Brenowitz, 1988). We understand, however, that our characterization of the microhabitat was not detailed enough because we did not identified plants to species level, or estimated the size and shape of the leaves and stems. For instance, Jiménez & Bolaños (2012) found similitude in microhabitat use between *D. ebraccatus* and *D. phlebodes* but they detected microhabitat segregation when they considered other more specific variables such as leaf size and shape (long-thing, short-wide) and plant type (herb, sedge, shrub, vine).

Our results contrast with those of Muñoz-Guerrero *et al.* (2007), who found some evidences of spatial segregation between *D. microcephalus* and *S. vigilans* at a locality in a dry forest in Colombia; while both species preferentially perched from 40-50 cm above shallow water, *D. microcephalus* preferred herbaceous plants whereas *S. vigilans* preferred heliconias (although it also used herbs). We propose that floristic and physiognomic differences between sites (Colombia and Venezuela) may explain these differences. Nevertheless, the striking differences in microhabitat species-segregation between our study and that of Muñoz-Guerrero *et al.* (2007) identify the need of more extensive studies encompassing more habitat and microhabitat types to better understand potential space interactions between *D. microcephalus* and *S. vigilans.*

While the microhabitat-niche dimension of *D. microcephalus* and *S. vigilans* at our study locality coincides, the food dimension differentiates. Both species rely on arthropods, but at the taxonomic level of order, and especially at the level of family, their diets segregate. Agelenidae, Tachinidae and Lepidoptera larvae represent 28.4% of the diet of *D. microcephalus,* but only 15.7% of the diet of *S. vigilans.* On the other hand, Gryllidae, Cicadidae, Cicadellidae and Delphacidae represent 39.5% of the diet of *S. vigilans* (but only 15.1% of the diet of *D. microcephalus*). These seven prey categories are consumed by both species, but there are 21 additional prey categories which are not shared (Table 1). This differentiation is expressed in a relative low index of food-niche overlap (approx. 30%). Reduced niche overlap between syntopic hylids has been documented in several anuran communities (*e.g.,* Toft, 1980a,b; 1985; Van Sluys & Rocha, 1998).

With regards to diet composition, our results partially differ from those of Muñoz-Guerrero *et al.* (2007): they found 15 orders as a whole, 11 orders in *D. microcephalus* and 7 in *S. vigilans* while we found only 10 orders as a whole, 8 orders in *D. microcephalus* and 9 in *S. vigilans.* In addition, the orders Acari, Collembola, Mantodea, Neuroptera and Psocoptera were not found in our study populations, while the relative important order Homoptera in our study was not quantified in theirs. Muñoz-Guerrero *et al.* (2007) did not calculate the %RII of each prey category but from their published data we estimated that Dyctioptera, Araneae, Diptera and Coleoptera (all with similar importance, altogether 70% of the diet) were the most important prey in *D. microcephalus* (Table 3), while Araneae, Hymenoptera and Orthoptera were the most important in *S. vigilans* (Table 3). We found similitude between studies in the composition of the diet of *D. microcephalus* (Araneae, Coleptera and Diptera represent 56% of the diet in our study), with the remarkable difference that Araneae was the most important prey in ours (instead of Dyctioptera) and that Homoptera, the second category in our study, was absent in the Colombian study. The largest differences in diet between studies correspond to *S. vigilans,* in which Homoptera and Orthoptera represent 50% of the diet at our study locality but only 16% in the Colombian site, where, on the other hand, Araneae and Hymenoptera altogether represent 43% of the diet (but only 15% in our study). In addition, Muñoz-Guerrero *et al.* (2007) estimated a much higher niche overlap (O = 0.82) than we did (0.411, when calculated at the taxonomic level of order). It is very interesting that in our study, niche overlap calculated from family-level prey categories was even lower than that from order-level categories, as we expected. This result raises a caution on conclusions about potential food competition between species based on coarsely identified prey categories. From our results, based on family-level analysis, the probability of competition for food is relatively low between *D. microcephalus* and *S. vigilans,* and we expect that a finer-scale identification of preys (to genus or species) could reveal wider diet segregation. The differences in diet composition between studies surely relate to variation in prey diversity and availability between localities, and support our conclusion that both species are food generalists (see below) that opportunistically capture prey as they pass by their ambushing perch; this foraging strategy does not imply that frogs do not select perch sites with high probability of prey capture, on the contrary. It is very interesting that Araneae and Diptera are also amongst the most important prey in the diets of *D. ebraccatus* and *D. phlebodes* (Jiménez & Bolaños, 2012), *D. sanborni* and *D. nanus* (Macale *et al.*, 2008) suggesting that these prey are the most or among the most abundant in wet habitats (Candia, 1997; Aiken & Coyle, 2000).

Diet diversity, equitability and niche breath indexes of both species roughly correspond to those expected for species toward the generalist end of the diet-specialization continuum. Despite the fact that most studies on anuran diet have not estimated prey availability, most authors agree that most anurans are generalist consumers based on the assumption that their diets represent prey availability (Duellman & Trueb, 1994; Menéndez-Guerrero, 2001). Nonetheless, in a multispecies study with hylids, Parmelee (1999) found that some species have wide diets while others seem to be specialized in “large” preys. Further study is necessary to address feeding preferences variation in this abundant and diverse group.

In our study, a number of stomachs was empty (approx. 17%); this proportion is below the interval documented for other hylids (36-78%, Parmelee, 1999; Menin *et al.,* 2005; Jiménez & Bolaños, 2012). Information on time budgets in anurans is lacking, but high proportions of empty stomachs have been regarded to specific feeding schedules (Parmelee, 1999). For instance, males may feed before beginning their calling activity each night, or later at night, after calling, or alternate feeding nights with calling nights (*e.g.,* Ryan, 1985; Anderson *et al.,* 1999). In addition, it has been documented that males do not feed while calling (Woolbright & Stewart, 1987; Solé & Pelz, 2007). The high proportion of empty stomachs together with that of stomachs with digested contents suggest that *D. microcephalus* and *S. vigilans* alternate feeding nights and calling nights or feed quite early before beginning to call.

Surprisingly we did not find difference in prey size and volume between species, despite the fact that mouth width was significantly different between species (*D. microcephalus* > *S. vigilans*). Two results may explain this finding: the weak correlation found in both species between mouth width and prey size and the generalist diet. We propose that diet specialization is more likely to allow for a relationship between predator and prey morphometry in anurans (Lynch & Duellman, 1997). For a relationship between anuran morphometry and prey size in other hylid assemblages see for instance: Toft (1980a, 1981), Duré & Kehr (2001) and Jiménez & Bolaños (2012).

In conclusion, at the locality of this study, *D. microcephalus* and *S. vigilans* occupy the same microhabitats and the potential for space competition would be high if perch sites were limited; nonetheless, segregation of their diets would reduce competition and favor their coexistence. The composition of their diets is biased toward the generalist end of the continuum of prey specialization in anurans (ant-specialist, non-ant specialist and generalist).

RESUMEN

La coexistencia de especies con requerimientos ecológicos similares (alimento, espacio, tiempo) típicamente ha atraído a los investigadores porque se espera que la competencia por recursos sea alta. La dieta y la ocupación de microhábitat de dos especies morfológica y ecológicamente similares de Hylidae (Anura) se analizaron en una localidad al noroeste de Venezuela, con el objetivo de evaluar el potencial para competencia entre ellas. La dieta se estimó a través del análisis de los contenidos estomacales y la ocupación del microhábitat por medio de registros del tipo y altura de la percha y la distancia horizontal al agua. Se identificaron 36 categorías de presa (32 familias, 4 órdenes); 30 en D. microcephalus *y 21 en* S. vigilans. *Las presas más importantes (RII) en* D. microcephalus *fueron Agelenidae (11,1%), Tachinidae (9,32%) y Lepidoptera-larva (7,96%). Gryllidae (14,13%), Cicadidae (9,1%), Cicadellidae (8,3%) and Delphacidae (8,02%) fueron las más importantes en* S. vigilans. *Ambas especies tienen dietas relativamente generalistas. La superposición de las dietas fue relativamente baja (0,32). Ambas especies ocuparon el mismo tipo de perchas (hojas y tallos de dicotiledóneas y monocotiledóneas) a las mismas alturas. El potencial para la competencia por espacio es alto si las perchas fuesen escasas, pero se espera que la competencia por el alimento sea baja.*

Palabras-Clave: Dieta; Generalista; Superposición de nicho; Partición de recursos; Microhábitat; Morfometría.

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