Microhabitat choice and differential use by anurans in forest streams in southeastern Brazil

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Abstract
The use of space by anuran amphibians during reproductive activities was studied at eight forest streams in the Reserva Particular do Patrimônio Natural Santuário do Caraça, southeastern Brazil. Identified microhabitats were classified into 18 types based on substrate and height above ground/water. A total of 440 individual anurans of 19 species was recorded in these microhabitat types. Electivity indices were calculated for the three most abundant species and indicated that specimens actively selected microhabitats. Species with broad niches (generalists) did not occur in more streams than species with narrow niches (specialists), and streams with higher species richness did not contain more specialists. Species showed high levels of overlap in microhabitat use, which were not related to the number of co-occurring species. The distribution patterns observed in the studied anuran assemblages likely reflect specific reproductive preferences and colonization abilities rather than the result of competitive pressures.

Keywords: Anura, Neotropics, breeding microhabitats, spatial distribution

Introduction
Animal taxa are known to select microhabitats in which they are likely to have a better performance in food acquisition (e.g. Urbanič et al. 2005), activity (e.g. Bremset 2000), predator avoidance (e.g. Kopp et al. 2006), refugia use (e.g. Hastie et al. 2000), or breeding (e.g. Kotiahno et al. 2000; Gillespie et al. 2004). The choice of specific microhabitats is related to morphological, physiological and behavioural adaptations of species (e.g. Crump 1971; Pough et al. 1977; Cardoso et al. 1989), and species with broad niches are expected to be more widespread because they may tolerate a greater variety of habitat conditions (Gaston et al. 1997; Pyron 1999). Heterogeneous habitats also favour an increase in species richness, since a higher combination of microhabitat types and ecological niches is available (MacArthur 1968).
Observed patterns of differential use of available resources can be also associated with species co-existence in an assemblage (e.g. Rossa-Feres & Jim 1994; Pombal 1997), where differences in resource use may reduce competition and make the co-existence of a higher number of species possible (MacArthur 1972). The strength of competition between species may be related to the level of overlap in use of a critical resource (MacArthur & Levins 1967; Lehtinen 2005), and species may diverge to avoid competition, reducing overlap in resource use (Schoener 1982). Nevertheless, phylogenetically closely related species tend to be associated with the same or similar ecological niches (e.g. Poe 2005), and in such instances historical factors are more important than recent ecological ones in determining species distribution (e.g. Inger 1969).

To evaluate the available hypotheses outlined above, we examined habitat use in anuran assemblages. Frog species co-exist at water bodies used as reproductive sites, where the spatial niche can be characterized and quantified to study the spatial organization of their assemblages (Eterovick & Barros 2003; Gillespie et al. 2004). During breeding activities, males search for suitable calling sites (Resetarits & Wilbur 1991), and males and females can select sites appropriate for oviposition and development (Donnelly 1989; Gillespie et al. 2004). Differences in reproductive modes result in different microhabitat needs (Duellman 1989). The higher the diversity of reproductive modes in an assemblage, the higher the number of species expected to be able to co-exist, which may result from resource partitioning (Crump 1982). We considered the diversity of microhabitats used by adult anurans during the breeding season as a measurement of their spatial niche breadth (sensu Pianka 1973), and we tested whether (1) anurans select their microhabitats, (2) species differ in microhabitat use, (3) species with broad niches (generalists) occur in a higher number of streams than specialists, (4) species occurring in rich assemblages have narrow niches and (5) co-occurring species have low niche overlaps. We also propose a new method to quantify anuran microhabitat availability and study microhabitat choice quantitatively. Our method allowed systematic sampling and thorough quantification of microhabitats in a large extent of the streamside habitat (5% of the extent searched for frogs, considering both stream margins). With this method, it is feasible to accomplish a broader sample of available microhabitats than with random punctual sampling.

Materials and methods

Study site

The Reserva Particular do Patrimônio Natural (RPPN) Santuário do Caraça is located at Catas Altas municipality (20°05'S; 43°29'W), Minas Gerais, southeastern Brazil. The reserve encompasses 10 188 ha in the southern portion of the Espinhaço mountain range, from 850 to 2070 m above sea level, in a contact zone between the Cerrado and Atlantic Forest biomes (Giulietti & Pirani 1988; Giulietti et al. 1997). The region has a dry season extending from April to September and a wet season, from October to March.

Data collection

The work was conducted during 3-day monthly field trips from August 2003 to October 2004, when eight permanent forest streams were regularly sampled. Sections of 150 m were marked at each stream (one per stream), and inspected monthly (once during the day and once at night) for adult anurans through visual and auditory searching procedures. The transects were inspected by walking within the streams or at stream banks (to about 3 m
from the stream edges), carefully searching for anurans. For each individual located, we recorded the substrate used, vertical height above ground/water, and the shortest horizontal distance to water. Species were observed mostly during their annual reproductive period (L. G. Afonso and P. C. Eterovick, unpubl. data). When a species was not breeding (no calling males, gravid females or egg clutches recorded) adult individuals were usually not detected along the transects, indicating that they may move to other areas or they are less active/visible. Our data are valid for microhabitat use by adult frogs during reproductive periods.

Specimens not identified in the field were preserved in the manner described by Heyer et al. (1994) for later identification and were deposited in the herpetological collection of the Museu de Ciências Naturais of the Pontifícia Universidade Católica de Minas Gerais (MCN-AM).

Microhabitat selection

Microhabitat availability was quantified in the following way. As the great majority of frogs observed used the perching substrates present at stream banks at varied heights, and rarely the water, we based our analyses on streamside habitats. Five photographs of the streamside habitat were taken for each stream, within the marked 150 m sampling sections. These were taken at 15, 45, 75, 105, and 135 m from the beginning of the section (we avoided photographing at 0 or 150 m due to possible alterations of the vegetation caused by our trails at entry and exit of the streams). The bank (right or left) to be photographed was randomly assigned at the first point, and then alternated at each following point. To make photograph size uniform, a metric tape was stretched at the photographed point and the width of each photograph was adjusted to 3 m. Photographs were framed so that the edge (where water contacted the stream bank) was at their central lowest point. Thus, the water just showed in the photograph where stream edges were irregular, forming backwaters towards the adjacent land. The few frogs observed to call or perch in the water were in such microhabitats (at shallow water close to the edge, with no current) and the frogs did not use the sections with more regular margins, which had either slow or fast water flow. Thus, we considered the photograph framing employed to be adequate for quantification of microhabitats available for the anuran assemblage in the water and at the streamside habitat. We were conservative in interpreting the results for species that had individuals recorded using the water. All photographs were taken with a Nikon FE2 camera, with Nikkor lenses 35–135 mm set at 35 mm, by the same person, from a constant distance, without flash, perpendicular to the centre of the area to be photographed, in a single field trip by the end of the rainy season, in March 2004. We did not observe noticeable changes in the marginal vegetation of sampled streams during the study, so we assumed that the pictures would be representative of the availability of microhabitat types throughout the year. Marginal vegetation and river banks were also relatively uniform along the transects, so we believe that our sample provided a good estimation of microhabitat availability.

A uniform $15 \times 21$ line grid was superimposed on each digitalized photograph (for an example, see Figure 1) and microhabitats occurring at line intersections were recorded at three height classes (0–70 cm, >70–140 cm, >140 cm), each one corresponding to five horizontal grid lines. Height from the ground or above water (measured to characterize microhabitats used by frogs) were assigned to the same height classes and compared to availability data obtained from the photographs (Figure 1). Some bias may be included in these analyses due to the sloping of the stream banks, which could confound information on height above ground and distance from water. Nevertheless, we neglect this possible
bias, because the stream banks were never really steep within the distance range that could be seen in the photographs. In addition, microhabitats closer to the stream might be more visible in the photographs than those farther away; however, they were not projecting towards the water in a way they would look larger than they really were.

Microhabitats were classified into 18 types resulting from the existing combinations of the three height classes and seven substrate types: green leaves (including ferns, bromeliads, grasses), brown leaves, branches (including roots, fallen branches, lianas), rocks, leaf litter, bare soil (including sand, mud and river banks) and water (Table I). Electivity indices ($D$) give a measurement of preference and were calculated for each microhabitat type, considering availability (estimated from the photographs) and use by individuals of the three most abundant species. We used the method of Jacobs (1974):

$$D = \frac{R_k - P_k}{[(R_k + P_k) - (2R_kP_k)]}$$

where $R_k$ = proportion of microhabitat type ‘k’ among all records of microhabitats used by a species and $P_k$ = proportion of microhabitat ‘k’ in the streams where the species occurred. $D$ varies from +1 (complete selection or preference of microhabitat ‘k’), through 0 (microhabitat ‘k’ is used in the same proportion found in the streams) to −1 (microhabitat ‘k’ is present in the streams but not used by the species). $D$ values were calculated only for species with more than 100 observations. The proportion of microhabitat types available for a given species was estimated using grouped data from the streams where it occurred.

Although the photographs reduce streamside habitat to two dimensions, missing information on distance to water, we expect that suitable microhabitats for the studied frog assemblages were well represented in them (mean horizontal distance to water varied from 0 to 54 cm in microhabitats used by the species analysed). In order to aid to species

Figure 1. Photograph taken at the first point (15 m) of stream 3, with the 15 × 21 line grid superimposed to quantify available microhabitats in three height classes at RPPN Santuário do Caraça, southeastern Brazil. Each height class encompasses five horizontal grid lines. The arrows point to the metric tape.
| Microhabitats                  | All species | Crossodactylus bokermannii | Bokermannohyla nanuzae | Scinax luizotavioi |
|-------------------------------|-------------|---------------------------|------------------------|-------------------|
|                              | Available   | Used                      | Available              | Used              | Available   | Used              | Available | Used              | Available | Used              |
| Green leaves, 0–70 cm         | 1675        | 80                        | 683                    | 7                 | −0.478      | 863              | 12        | −0.134            | 1152      | 49                | 0.568     |
| Green leaves, >70–140 cm      | 2102        | 14                        | 828                    | 0                 | −1.000      | 1144             | 5         | −0.652            | 1457      | 6                 | −0.651    |
| Green leaves, >140 cm         | 1985        | 12                        | 942                    | 0                 | −1.000      | 1098             | 6         | −0.576            | 1273      | 0                 | −1.000    |
| Brown leaves, 0–70 cm         | 332         | 7                         | 162                    | 1                 | −0.630      | 251              | 4         | −0.050            | 219       | 2                 | −0.293    |
| Brown leaves, >70–140 cm      | 459         | 3                         | 213                    | 0                 | −1.000      | 268              | 1         | −0.661            | 274       | 2                 | −0.394    |
| Brown leaves, >140 cm         | 332         | 1                         | 107                    | 0                 | −1.000      | 186              | 0         | −1.000            | 171       | 1                 | −0.484    |
| Branches, 0–70 cm             | 1081        | 109                       | 306                    | 18                | 0.420       | 538              | 23        | 0.479             | 612       | 51                | 0.776     |
| Branches, >70–140 cm          | 1325        | 26                        | 424                    | 0                 | −1.000      | 549              | 10        | 0.020             | 713       | 5                 | −0.427    |
| Branches, >140 cm             | 1710        | 28                        | 560                    | 0                 | −1.000      | 666              | 13        | 0.059             | 1026      | 4                 | −0.652    |
| Rocks, 0–70 cm                | 274         | 36                        | 181                    | 4                 | −0.090      | 177              | 24        | 0.814             | 184       | 1                 | −0.512    |
| Rocks, >70–140 cm             | 48          | 4                         | 45                     | 0                 | −1.000      | 21               | 3         | 0.788             | 33        | 0                 | −1.000    |
| Rocks, >140 cm                | 4           | 2                         | 4                      | 0                 | −1.000      | 4                | 0         | −1.000            | 0         | 0                 | −         |
| Leaf litter, 0–70 cm          | 82          | 28                        | 1                      | 22                | 0.998       | 82               | 0         | −1.000            | 82        | 1                 | −0.153    |
| Leaf litter, >70–140 cm       | 23          | 0                         | 8                      | 0                 | −1.000      | 15               | 0         | −1.000            | 23        | 0                 | −1.000    |
| Bare soil, 0–70 cm            | 383         | 81                        | 173                    | 70                | 0.943       | 47               | 2         | 0.422             | 163       | 0                 | −0.464    |
| Bare soil, >70–140 cm         | 151         | 0                         | 41                     | 0                 | −1.000      | 0                | 0         | −                | 67        | 0                 | −1.000    |
| Bare soil, >140 cm            | 35          | 1                         | 0                      | 0                 | −1.000      | 0                | 0         | −                | 0         | 1                 | −         |
| Water, 0–70 cm                | 57          | 8                         | 4                      | 1                 | 0.800       | 8                | 1         | 0.746             | 12        | 0                 | −1.000    |
| **Total**                     | **12058**   | **440**                   | **4682**               | **123**           |            | **5917**         | **104**   | **7461**          | **123**   |                  |            |
comparison regarding their spatial location, we compared measurements of distance to water and height above ground made for all species to test whether they differed significantly in these parameters, using Kruskal–Wallis analysis, because data distribution was not normal.

*Niche breadth and niche overlap*

Niche breadth was estimated for each anuran species using PIE Hurlbert’s diversity index, which is unbiased by sample size (Gotelli & Entsminger 2001):

$$\text{PIE} = \left( \frac{N}{N-1} \right) \left( 1 - \sum P_i^2 \right)$$

where $P_i$ represents the proportional use of microhabitat ‘i’ by a species based on total number of its microhabitat use records ($N$). Rarefaction curves were made for the species with more than 100 observations to test for the effects of sample size on the value of PIE. Estimations of mean diversity indexes had variances no greater than 0.05 after rarefaction for a sample size equal to five. Variances were below 0.02 with a sample size equal to 10.

Diversity measurements were then made using two different approaches. First, the diversity of microhabitats used by each species was estimated using data from all streams where it occurred ($A'$) and the diversity of available microhabitats was estimated for the set of streams used by the species considered ($S'$). Second, the diversity of microhabitats used by each species was estimated separately for each stream where it occurred ($A$), and the diversity of available microhabitats was estimated for each stream ($S$). $A'$ was estimated for species with more than nine records ($n=7$ species) and $A$ for species with more than seven records ($n=6$ species) in a given stream to obtain unbiased estimates of PIE values.

A conservative estimate of niche breadth was given by $A'/S'$ (microhabitat use corrected for microhabitat availability), since species occurring in streams with greater microhabitat diversity would seem to have greater microhabitat use diversity if they were randomly distributed in the habitat. We assumed that higher $A'/S'$ values would indicate species with greater plasticity in microhabitat use, suggesting a generalist behaviour, and we tested whether such species would occur in a greater number of streams using linear regressions (SYSTAT 1998). We considered the number of streams where a species was recorded as the dependent variable and the species niche breadth as the independent variable.

We hypothesized that if the community is structured by competition, the number of species occupying a stream will influence the niche breadth of the species present, as assumed by Pianka (1973). We then related mean niche breadth of species occurring in each stream (mean of $A/S$ values for species present, as the dependent variable) to stream species richness (as the independent variable) using linear regressions.

We also tested whether niche overlap between anuran species regarding microhabitat use was less than expected by chance in streams with several species, that might be the case for communities structured by competition, according to Pianka (1973). We used the software EcoSim (Gotelli & Entsminger 2001), employing Pianka’s (1973) overlap index ($O_{jk}$), with the randomization algorithm RA3 (niche utilization values reshuffled within each row of the matrix, that is, niche breadth retained for each species) to estimate niche overlap between species pairs. This analysis was only conducted for species pairs occurring in the same stream, using data from months when both species were present. We then related the values obtained to the numbers of species co-occurring at the time intervals considered, using linear regression. We tested for departures from normality in the data with skewness and kurtosis tests (SYSTAT 1998) before all statistical tests.
Results

A total of 440 individuals of 19 anuran species was recorded during the study in the families Bufonidae (Chaunus pombali, C. rubescens), Centrolenidae (Hyalinobatrachium cf. eurygnathum), Cycloramphidae (Proceratophrys boiei), Hylidae (Bokermannohyla martinsi, B. nanuzae, Bokermannohyla sp. (gr. circumdata), Dendropsophus minutus, Hypsiboas albopunctatus, H. faber, H. polyaenius, Phyllomedusa burmeisteri, Scinax luizotavioi, S. machadoi, S. aff. perereca, Scinax sp. (gr. ruber)), Hylodidae (Crossodactylus bokermanni, Hylodes uai) and Leiuperidae (Physalaemus aff. olfersii). Microhabitats used by each species differed significantly in height ($U=140.28, P<0.001$) and distance to water ($U=30.61, P<0.001$; Table II).

Species with broad niches (generalists), that is, those with higher $A'/S'$ values, did not occupy more streams than species with narrow niches ($R^2=0.348, P=0.164$; Table III). The number of species occupying a stream did not influence the niche breadth of the species present ($A/S$) ($R^2=0.632, P=0.108$; Table IV). Species pairs occurring at the same stream sections and at the same time had niche overlaps higher than expected by chance, except for Bokermannohyla nanuzae and Hypsiboas polyaenius at one stream (Table V). Values of spatial niche overlap were not related to total number of species present at the time interval they were using the streams ($R^2=0.527, P=0.102$; Table V).

Crossodactylus bokermanni preferentially used leaf-litter and bare soil at heights of 0–70 cm (Table I). Water also had a high electivity value, while branches at heights of 0–70 cm had a low positive value. Most of the remaining microhabitats were never used by this species. Bokermannohyla nanuzae utilized mainly rocks at heights of 0–70 cm, followed by rocks at

| Species                  | Distance from water | Height above ground/water | n  |
|--------------------------|---------------------|---------------------------|----|
| Crossodactylus bokermanni| $3.3 \pm 7.0$ (0–50)| $3.1 \pm 10.3$ (0–60)    | 123|
| Hylodes uai              | $0.0 \pm 0.0$ (0–0) | $32.9 \pm 19.5$ (0–50)   | 8  |
| Bokermannohyla martinsi  | $54.5 \pm 54.8$ (0–150)| $50.5 \pm 64.9$ (0–200) | 19 |
| Bokermannohyla nanuzae   | $20.1 \pm 47.1$ (0–250)| $74.3 \pm 63.9$ (0–250) | 104|
| Dendropsophus minutus    | $0.0 \pm 0.0$ (0–0) | $15.0 \pm 8.0$ (5–30)    | 13 |
| Scinax luizotavioi       | $5.3 \pm 16.1$ (0–100)| $34.9 \pm 38.8$ (0–170) | 123|

Table II. Quantitative features of microhabitats used by the most common anuran species at RPPN Santuário do Caraça, southeastern Brazil. Measurements are given in cm as mean ± SD (range).

Table III. Number of streams occupied and diversity of microhabitats used by seven anuran species and diversity of available microhabitats in the set of streams used by them in RPPN Santuário do Caraça, southeastern Brazil. *=species that occurred year-round. The remaining species occurred during the rainy season (October to February).

| Species (n)                  | Number of streams occupied | Diversity in microhabitat use ($A'$) | Diversity of available microhabitats ($S'$) | $A'/S'$ |
|------------------------------|-----------------------------|-------------------------------------|--------------------------------------------|---------|
| Crossodactylus bokermanni (123)* | 3                           | 0.623                               | 0.874                                      | 0.712   |
| Bokermannohyla sp. (gr. circumdata) (9) | 3                           | 0.861                               | 0.867                                      | 0.993   |
| Bokermannohyla martinsi (19)    | 4                           | 0.830                               | 0.866                                      | 0.958   |
| Bokermannohyla nanuzae (104)*   | 4                           | 0.859                               | 0.872                                      | 0.985   |
| Dendropsophus minutus (13)*     | 1                           | 0.667                               | 0.821                                      | 0.812   |
| Hypsiboas polyaenius (12)      | 1                           | 0.818                               | 0.821                                      | 0.996   |
| Scinax luizotavioi (123)*       | 5                           | 0.669                               | 0.870                                      | 0.769   |
Table IV. Diversity of microhabitats used by six anuran species, diversity of microhabitats available in local streams and estimated niche breadth for species in particular streams (A/S) at RPPN Santuário do Caraça, southeastern Brazil. Used streams included in this table are only the ones with seven or more records of the species considered.

Table V. Niche overlap ($O_{jk}$) between anuran species pairs recorded at the same habitat and during the same time intervals at RPPN Santuário do Caraça, southeastern Brazil.

Discussion

All species analysed at RPPN Santuário do Caraça showed preferences in microhabitat use, indicating that they actively select their breeding microhabitats, as also noted by Gillespie.
et al. (2004) for three out of four species breeding in a stream in Sulawesi, Indonesia. In the present study, whereas *Scinax luizotavioi* selected microhabitats in the vegetation, *Bokermannohyla nanuzae* selected microhabitats of several types, as shown by its larger niche breadth (Tables III and IV). The presence of adhesive discs on hylid fingertips give species the ability to explore the vegetation vertically (Cardoso et al. 1989). These treefrogs can also use rocks and leaf litter as substrates as other frogs do. This may contribute to large spatial niche breadths in species of Hylidae. Indeed, the hylodid *Crossodactylus bokermanni* had narrower niches than all hylids studied (Tables III and IV). As the remaining species recorded are nocturnal, the diurnal *C. bokermanni* is not supposed to compete for space with other species during breeding activities, so that the narrow niche recorded for this hylodid frog likely is due to specific behaviour and physiological tolerances instead of competitive interactions with other species. Physiological differences in tolerance to water loss may influence microhabitat choice (Pough et al. 1977). Almost all microhabitats selected by the species analysed were at heights from 0 to 70 cm above ground/water, which may be due to the higher humidity expected to occur close to the ground (Cardoso & Martins 1987; Cardoso & Haddad 1992).

The electivities for water and leaf-litter may have been slightly overestimated for *C. bokermanni*, since we observed a few individuals using an emergent pile of litter in the stream bed, where they used the debris or shallow water. This was the only instance in which frogs used microhabitats that were not included in the photographs, though similar microhabitats were recorded at the stream edges and also used by *C. bokermanni*. Although this is an exception in our study and would not change the general pattern of microhabitat selection observed, it is important to stress that some measurement of microhabitat availability in the stream bed is important for species using such microhabitats frequently. No other anuran species recorded in this study used microhabitats at the stream bed.

According to Pianka (1973), species occurring in habitats with higher species richness can be expected to have narrower niches or tolerate greater niche overlap if the spatial niche dimension is fully occupied. On the other hand, in herpetofaunal assemblages that are not too species rich, species may expand their niches and attain high local densities (Rodda & Dean-Bradley 2002). Considering microhabitats used during reproduction, values of species spatial niche breadths were not related to species richness in streams at RPPN Santuário do Caraça. This may indicate that the available niche space is not completely occupied, and competition is not strong enough to influence community structure making species narrow their niches (Pianka 1973). A similar pattern was recorded for tadpoles at montane meadow streams at Serra do Cipó, southeastern Brazil (Eterovick & Barros 2003). It is important to notice that microhabitats used during reproduction are just part of the whole spatial niche of a species, and even if they do not compete for such microhabitats, they may still compete for sites used at other times, like shelters. Nevertheless, Ernst and Rodel (2006) found species interactions to have no apparent influence in the spatial distribution of leaf-litter anuran communities at a site in West Africa, considering a spatial scale broader than the one studied here.

A species' ability to occupy many different water bodies was not related to the ability to occupy a large microhabitat diversity. *Scinax luizotavioi* and *Dendropsophus minutus* were the species with the highest value of niche overlap ($O_{jk} = 0.945$). Although these species used the same microhabitats, they were distributed throughout Stream 5 in a way that *S. luizotavioi* was more frequent at stream sections with more closed canopy and *Dendropsophus minutus* was more frequent at an open section around a large backwater, indicating that habitat partitioning may occur at intermediate scales, within the studied
transects. *Scinax luizotavioi* was also observed calling in a lake surrounded by herbaceous and shrubby vegetation at the RPPN Santuário do Caraça by Caramaschi and Kisteumacher (1989). The large backwater present in Stream 5 was unique and was likely used by some species, such as *Dendropsophus minutus*, because it resembles ponds which such species use to breed. *Dendropsophus minutus* uses puddles and swamps besides stream backwaters during reproduction (Eterovick & Sazima 2004), and has already been recorded in large numbers in ponds at RPPN Santuário do Caraça (Kopp & Eterovick 2006). In spite of being able to occupy different types of water bodies, both *Scinax luizotavioi* and *Dendropsophus minutus* had low values of niche breadth compared to other co-occurring hylids (Tables III and IV). These species may occupy water bodies opportunistically to breed, but have a restricted spatial distribution within them, reflecting specific preferences. Microhabitat use may be more likely related to specific behaviours and reproductive modes than to any kind of niche separation caused by competition, provided that there is a great availability of the preferred microhabitats in the set of habitats used by the species. In addition, habitat occupancy may be related to differential migration and colonization abilities of species, so that species niches were not related to number of streams occupied.

The high levels of niche overlap between species pairs indicate that selective pressures may not be strong enough to lead to a complete species differentiation in microhabitat use, as also noticed by Eterovick and Barros (2003) for tadpole assemblages at Serra do Cipó, southeastern Brazil. Zimmerman and Simberloff (1996) showed that the habitat types used by anurans for reproductive activities and development are largely influenced by phylogenetic constraints of species colonizing each site, rather than environmental or competitive pressures. These authors suggest that competition might assume a greater importance at a finer spatial scale, but here we show that competition does not seem to have a great influence on breeding microhabitat use by adult anurans at permanent streams. Our results indicate that specific preferences for breeding microhabitats exist in the studied anurans, and are probably more important than competitive pressures in determining the spatial distribution of their assemblages. The availability of leaves and branches at the preferred heights may be high enough to meet the needs of co-occurring species, making competition unlikely.

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**References**

Bremset G. 2000. Seasonal and diel changes in behavior, microhabitat use, and preferences by young pool-dwelling salmon, *Salmo salar*, and brown trout, *Salmo trutta*. Environmental Biology of Fishes 59:163–179.
Poe S. 2005. A study of the utility of convergent characters for phylogeny reconstruction: do ecomorphological characters track evolutionary history in Anolis lizards? Zoology 108:337–343.
Pombal-Jr JP. 1997. Distribuição espacial e temporal de anuros (Amphibia) em uma poça permanente na Serra de Paranapiacaba, sudeste do Brasil. Revista Brasileira de Biologia 57:583–594.
Pough FH, Stewart MM, Thomas RG. 1977. Physiological basis of habitat partitioning in Jamaican Eleutherodactylus. Oecologia 27:285–293.
Pyron M. 1999. Relationships between geographical range size, body size, local abundance, and habitat breadth in North American suckers and sunfishes. Journal of Biogeography 26:549–558.
Resetarits WJ, Wilbur HM. 1991. Calling site choice by Hyla chrysoscelis: effect of predators, competitors, and oviposition sites. Ecology 72:778–786.
Rodda GH, Dean-Bradley K. 2002. Excess density compensation of island herpetofaunal assemblages. Journal of Biogeography 29:623–632.
Rossa-Feres DC, Jim J. 1994. Distribuição sazonal em comunidades de anfíbios anuros na região de Botucatu, São Paulo. Revista Brasileira de Biologia 54:323–334.
Schoener TW. 1982. The controversy over interspecific competition. American Scientist 70:586–595.
SYSTAT for Windows. 1998. Statistics, Version 9 Edition. Evanston, IL: SYSTAT, Inc.
Urbanicˇ G, Toman MJ, Krušnik C. 2005. Microhabitat type selection of caddisfly larvae (Insecta: Trichoptera) in a shallow lowland stream. Hydrobiologia 541:1–12.
Zimmerman BL, Simberloff D. 1996. An historical interpretation of habitat use by frogs in a Central Amazonian Forest. Journal of Biogeography 23:27–46.