Spatial and temporal distribution of breeding anurans in streams in southeastern Brazil

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Abstract
Anuran communities were studied at eight permanent forest streams located in a preserved site in southeastern Brazil, from August 2003 to October 2004. Nineteen species were recorded in six families: Bufonidae (two), Centrolenidae (one), Cycloramphidae (one), Hylidae (12), Hylodidae (two), and Leiuperidae (one). Twelve species exhibited calling activities during the study period and 10 of these were assumed to be reproductively active. The number of species present in streams was negatively related to stream volume. The composition of anuran assemblages was related to stream volume and structural complexity of the streamside habitat. Levels of dissimilarity between anuran communities from different streams were not related to the geographical distance separating these streams. Rainfall and mean monthly temperatures were not related to anuran species diversity per month, which may be due to forested sites providing appropriate conditions for reproduction for many species year-round and favouring anuran species with long breeding periods. The results obtained indicate that streams of varied sizes, as well as streamside habitats, should be preserved in order to maintain anuran diversity.

Keywords: Anura, southeastern Brazil, species diversity, spatial and temporal distribution, stream size, streamside habitat

Introduction
In breeding anuran assemblages, differential resource use by species has been interpreted as a mechanism to avoid competition (e.g. Crump 1982; Cardoso et al. 1989) or a result of different specific needs (Eterovick & Sazima 2000; Ernst & Rodel 2006). Shared resources may include calling sites, oviposition sites, acoustic space, annual and daily calling periods (Hödl 1977; Cardoso & Haddad 1992; Pombal 1997). Different reproductive modes may occur among sympatric anuran species (Duellman 1989) and aid in resource partitioning (Crump 1982), so that the availability of suitable breeding sites can be the most important
factor determining species distribution (Zimmerman & Bierregaard 1986; Ernst & Rodel 2006). Thus, environmental heterogeneity may be important in determining the number of anuran species that can use a given habitat (Cardoso et al. 1989), so that higher species richness could be expected in an area with more microhabitats and ecological niches (MacArthur 1968).

Nevertheless, habitat features alone are not enough to predict the occurrence of anuran species in most instances. Gascon (1991) found anuran species to respond to abiotic features of several types of breeding habitats, though habitat features were not useful in predicting the composition of local communities in central Amazon. In West Africa, Ernst and Rödel (2005) found a significant relationship between species composition and habitat features in forest sites disturbed by logging, whereas in primary forest sites species composition could not be predicted in the same way. It is important to stress that distance between sites can also influence species composition (Azevedo-Ramos & Galatti 2002; Ernst & Rödel 2005) and should be taken into account when studying species distribution on a broad scale.

In anuran assemblages, the temporal distribution of species may also influence patterns of resource partitioning and species richness (Cardoso & Haddad 1992; Duellman & Trueb 1994). Anuran communities occurring at sites with low annual humidity variations include several species that reproduce continuously or sporadically throughout the year (Crump 1974; Duellman 1978; Wiest 1982). At seasonal neotropical sites, the occurrence of two well-defined seasons, dry and wet, is expected to promote some variation in the temporal distribution of anuran species.

To improve the knowledge of neotropical stream anuran community organization, this study was conducted at the Reserva Particular do Patrimônio Natural (RPPN) Santuário do Caraça, Southeastern Brazil, aiming to (1) test whether features of the streamside habitat (habitat complexity) and stream size (volume) can account for differences in species composition/richness in breeding anuran assemblages, (2) test whether similarities of breeding anuran assemblages from different streams relate to distance between streams, (3) test whether abiotic factors such as rainfall and temperature influence the temporal distribution of species’ activities and contribute to temporal variations in community diversity. Stream size may not affect anuran distribution directly, but it may be a useful parameter to indicate anuran species richness if species select their breeding sites based on features that depend on stream size (see Parris & McCarthy 1999; Eterovick 2003).

The stream tadpole assemblages occurring at the RPPN Santuário do Caraça have been previously studied to assess the role of tadpole microhabitat preferences, tadpole predators and stream features in shaping species composition and richness (Eterovick & Barata 2006). Tadpole assembly depends on the distribution of reproductive effort by adult anurans (Alford 1999). After reproduction takes place, larvae of several species may experience biotic interactions within a water body, which may or may not affect the composition of tadpole assemblages (Dayton & Fitzgerald 2001). For instance, Hero et al. (1998) found tadpole predators to be the main determinants of anuran community richness and species composition at a site in the Amazon. By comparing the distribution of breeding anurans (studied here) and tadpoles (studied by Eterovick & Barata 2006), this study also aimed at assessing the role of adults in shaping tadpole assemblages. Otherwise, differential reproductive success or tadpole survivorship due to biotic interactions or physical factors could lead tadpole and adult frog assemblages to vary in a different way.
Materials and methods

Study site

The RPPN Santuário do Caraça (20°05′S, 43°29′W) is located in the municipality of Catas Altas, Minas Gerais state, southeastern Brazil. The reserve encompasses 10,187.89 ha in the southern portion of the Espinhaço mountain range, between 850 and 2070 m elevation (Figure 1A). The region is formed by the orographic systems of Minas Gerais and Bahia states (Derby 1966), representing a contact zone between the Cerrado and Atlantic Forest biomes in its southern portion and a transition zone between both biomes in its northern portion (Giulietti & Pirani 1988; Giulietti et al. 1997). The region has two seasons, a dry one from April to September and a wet one, from October to March (Figure 2).

Sampling procedures

Eight permanent forest streams with varied widths and water volumes (Figure 1B) were sampled monthly for anurans within a 150 m section marked along their courses, from August 2003 to October 2004. These were the same streams studied by Eterovick and Barata (2006). Three to four days were spent monthly in the field in order to inspect each stream twice (once during the day and once at night). Weather conditions were comparable during these 3–4 day periods, though there might have been subtle changes in temperature, humidity or wind, which were not accounted for. The streams studied were selected based on the fact that they are not directly connected to each other, so that the only way migration can occur among them is by movements of adult anurans. Distances between stream pairs vary from 434 to 8141 m. Stream pairs were separated by varied matrix habitats, including other streams (Figure 1B), though any measurement of isolation level would be flawed without knowledge of the suitability of each given habitat in the matrix for frog migration, which is not available. A broad range of stream sizes was included in the study, based on the set of streams available at the study site (see Table I for volumes of 150 m-sampled stream sections). Streams 1, 2, 4, and 5 (Figure 1B) had dried in some sections by the end of the dry season, but were never completely dry. The studied streams are mostly covered by forest canopy, with open sections scattered throughout their course, at points where trees are missing (see Table I for relative cover of vegetation strata along each stream). The underground is usually shaded, the soil may be exposed at some points, or covered with leaf litter or mosses and herbaceous vegetation. In all streams, the bottoms are a mosaic of rocks or sand covered by aquatic vegetation or not. There are sections with current as well as small backwaters throughout the sampled 150 m sections. Stream 5 was an exception for having a large backwater that functioned as a permanent pond to some anuran species that usually breed in lentic water bodies. Microhabitat diversity within these streams has already been related to species composition of tadpole assemblages, but did not relate to tadpole species richness (Eterovick & Barata 2006). The streams shelter no predatory fish. Invertebrate predators, such as Odonata and water bugs, are present and influence both tadpole species composition and richness (Eterovick & Barata 2006).

Each stream was visited during the day (diurnal frogs and tadpoles) and at night (nocturnal species; from sunset to about 11:00 pm) every month and carefully searched for anuran individuals to be recorded in the marked sections. Each sampling at each particular stream took from about one hour to almost two hours and was conducted by two persons. Sampling time differences could be caused either by locomotion difficulty at narrower streams with dense vegetation or by the extra time spent locating and recording frogs where
Figure 1. Location of (A) the RPPN Santuário do Caraça, Minas Gerais state, southeastern Brazil, and (B) the eight streams sampled within the reserve.
they were more abundant. Males were located primarily by their mating calls, but the streamside habitat was inspected up to about 5 m from stream margins in search for silent males or females. Detectability, although possibly different among species, was considered to be comparable among streams, considering the sampling methods employed. Gravid females, amplexed pairs, egg clutches, tadpoles, and post-metamorphic froglets were considered as indicative of the species reproducing or being reproductively active at a given stream, since male calling periods may be longer than the actual specific breeding period (Wiest 1982; Donnely & Guyer 1994), and the occurrence of calling activities itself does not necessarily mean that the species reproduced or will actually reproduce (Cardoso & Haddad 1992).

Some individuals of species that could not be identified in the field were collected for later identification. Collected specimens were deposited in the herpetological collection of the Museu de Ciências Naturais of the Pontifícia Universidade Católica de Minas Gerais (MCN-AM).

Table I. Anuran species richness and quantitative features of vegetation in the streamside habitat at sampled sections of eight forest streams (S1–S8) at the RPPN Santuário do Caraça, southeastern Brazil. H=herbaceous vegetation, Sh=shrubby vegetation, A=arboreal vegetation. Structural complexity (S) refers to the diversity of potential calling sites (for details, see text).

| Streams | S1 | S2 | S3 | S4 | S5 | S6 | S7 | S8 |
|---------|----|----|----|----|----|----|----|----|
| Species richness | 8  | 8  | 5  | 8  | 9  | 1  | 5  | 3  |
| Estimated volume of sampled section (m³) | 47.08 | 17.27 | 118.44 | 19.37 | 72.18 | 235.63 | 104.02 | 283.66 |
| Streamside vegetation cover (%) | H  | 100 | 98.7 | 98.7 | 94.7 | 99.3 | 100 | 100 | 100 |
| | Sh | 90.7 | 92.0 | 88.7 | 94.7 | 98.0 | 100 | 100 | 100 |
| | A  | 64.0 | 66.7 | 81.3 | 91.3 | 76.7 | 98.7 | 92.0 | 92.7 |
| Structural complexity (S) | 7.71 | 7.66 | 8.46 | 6.54 | 6.30 | 7.58 | 6.43 | 7.00 |

Figure 2. Mean monthly rainfall (bars), mean air temperature (solid line) and mean water temperature (dotted line) at the RPPN Santuário do Caraça, southeastern Brazil, from August 2003 to October 2004.
Stream characterization

Two different approaches were employed to characterize the complexity/heterogeneity of the streamside habitat of sampled stream sections. Such habitats were intensely used by anurans during breeding activities. The first approach focused on vertical stratification of the streamside vegetation. The presence or absence of vegetation strata (grasses, shrubs, and trees) in the riparian vegetation were recorded at 75 points, every 2 m along the marked stream sections. Measurements were made in both the dry (August 2003) and the wet (January 2004) seasons to account for possible variations in the marginal vegetation along the study period. Vegetation strata were considered as present or absent when the point to be recorded had a given stratum represented (at one or both margins) or not. Thus, a total of 150 (75 x 2) punctual records of strata presence/absence at stream margins was obtained. In case species prefer more shaded microhabitats or prefer to call from some specific height range, these data would likely help explain their presence along the stream sections.

The second approach focused on micro-spatial heterogeneity, in an attempt to estimate the diversity of potential microhabitats/calling sites available for frogs at the streamside habitat. The measurements of microhabitat availability were made following a protocol developed to study microhabitat selection by adult frogs (Afonso & Eterovick, in press). Five photographs of the streamside habitat were taken for each stream, regularly spaced within the marked 150 m sampling sections, with alternating right and left margins. Photograph width was standardized to 3 m and framed so that the water contacted the stream margin at the central lowest point of the picture. A uniform 15 x 21 line grid was superimposed on each picture and microhabitats occurring at line intersections at three height classes (0–70 cm, 70–140 cm, and >140 cm), each one corresponding to five horizontal grid lines, were recorded. Microhabitats were classified into 18 types resulting from the observed 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. There were no leaf litter microhabitats above 140 cm or water microhabitats above 70 cm. Diversity of microhabitats in each stream was estimated based on the numbers of records of each microhabitat type using Simpson’s diversity index (Pianka 1973):

\[ S = 1 / \sum P_i^2 \]

where \( P_i \) represents the proportion of microhabitat ‘i’ in a stream based on total number of microhabitats recorded in the stream. The results obtained were considered as an estimate of habitat structural complexity \( (S) \).

Reach volume was estimated by multiplying the length of the sampled section (150 m) by mean stream width and depth, measured in January 2004 (rainy season). Mean stream width was estimated based on 10 measurements (taken every 15 m in the sampled section) and mean stream depth, based on 75 measurements (taken every 2 m in the sampled section, at alternating distances from the right margin: 1/6, 1/3, 1/2, 2/3, and 5/6 stream width at the measured point). The shortest distances between stream pairs were obtained based on their coordinates, taken in the field, using Geographic Information Systems.

Weather features and temporal variation in anuran communities

Air and water temperatures were measured each month in the field, at sampling sites, during sampling periods in all days of field work. Temperatures may vary within broader...
ranges throughout the day, nevertheless, the temperatures in which data were obtained (that is, when and where anurans were active) would be likely more representative of anuran activity than temperatures obtained in a meteorological station, since streams may have a distinct microclimate. Monthly rainfall data were obtained from a meteorological station located at the RPPN Santuário do Caraça, which is representative of all studied streams. The association of air and water temperature and rainfall (Figure 2) with anuran species diversity throughout the year was tested for. Shannon’s diversity index was used to estimate monthly species diversity ($H$) (Pielou 1975):

$$H = - \sum p_i \log_n p_i$$

where $p_i$ represents the proportion of individuals of species ‘i’ recorded per month, in relation to total number of individuals recorded in the month considered.

For this analysis, species diversity was used instead of richness, because this measurement would take into account the important difference between a species being represented by a few early or late individuals calling and a massive chorus at the peak of the breeding season.

**Statistical analyses**

Linear regression was used to relate the number of anuran species present as adults in each stream to stream volume, to test if species richness varies along the stream size gradient. Linear regression was also used to relate habitat structural complexity ($S$) to anuran species richness. Spearman correlations were used to relate the number of species with calling males in each stream with stream volume and $S$, because data were not normal in this case.

Canonical Correspondence Analysis (CCA; Ter Braak 1986) was used to test for the effects of percentage cover of the three vegetation strata, habitat structural complexity ($S$), and stream size on anuran species composition. A matrix was built crossing streams with these variables, and another matrix was built crossing streams with number of adult individuals recorded for each frog species. Individuals were considered as adults when engaged in reproductive activities or when they fell within the size range of reproductive adults observed. Streams and species scores were standardized by centering and normalizing, and scaling optimized species (McCune & Mefford 1999). Stream scores were given by linear combinations of features (LC scores; sensu Palmer 1993). Statistical significance of eigenvalues and species-environment correlations was evaluated by Monte Carlo tests (1000 randomized runs).

Dissimilarities were estimated between stream anuran communities (based on number of individuals of each species) using Bray-Curtis dissimilarity measures and a Mantel test was used to compare dissimilarities in anuran community composition and distance between streams (Quinn & Keough 2002). The value of $P$ was calculated through Monte Carlo permutation tests (1000 randomized runs; McCune & Mefford 1999). Closer streams were expected to be more similar regarding species composition. Multiple linear regressions (BioEstat 2003) were used to evaluate the relationships among mean air and water temperatures, monthly rainfall and species diversity per month, as well as diversity of species with calling males per month. Rainy months were expected to relate to greater species diversity, since many anuran species from seasonal sites breed during the rainy season (Duellman & Trueb 1994).
Results

During the study period, 440 adult individuals of 19 anuran species in the families Bufonidae (two), Centrolenidae (one), Cycloramphidae (one), Hylidae (12), Hylodidae (two) and Leiuperidae (one) were recorded at the RPPN Santuário do Caraça (Table II). Based only on records of gravid females, amplexed pairs, egg clutches, tadpoles, or post-metamorphic froglets, reproductive activities were detected for 10 species: Chaunus pombali, Bokermannohyla sp. (gr. circumdata), B. martinsi, B. nanuzae, Hypsiboas faber, Scinax machadoi, Scinax sp. (gr. ruber), S. luizotavioi, Crossodactylus bokermanni and Hylodes uai (Table II).

Species distribution was not uniform among streams. Stream 5 (see Figure 1B) had the greatest species richness (n=9) whereas only Hylodes uai was found in Stream 6 (Table I). From the 19 anuran species recorded during our study, 12 were observed or heard calling (Table II). Bokermannohyla nanuzae, Dendropsophus minutus, Scinax luizotavioi and Crossodactylus bokermanni called year-round. Other species were opportunistic, being active in periods with suitable climatic conditions throughout the year. Chaunus pombali, Bokermannohyla martinsi, Hypsiboas faber, and H. polyaenius chose the hottest and wettest period; Hylodes uai was active by the end of the rainy season and the onset of the dry season, and Proceratophrys boiei called with the first rains of the year (Table II). Phyllomedusa burmeisteri and Hyalinobatrachium cf. eurygnathum were very rare at the studied sites, so that a calling period could not be characterized for these species based on the few individuals found in streams. Species present in two or more streams usually showed the same temporal distribution, so data from all streams were combined to characterize their activity periods.

Anuran species richness was negatively related to stream volume ($r^2=0.760$, $F=23.166$, $P<0.004$, Figure 3A), as was number of species with calling males ($r_s=-0.781$, $P=0.022$, Figure 3B). Structural complexity of streamside habitats ($S$) was not related to species richness ($r^2=0.261$, $P=0.195$) or number of species with calling males ($r_s=-0.122$, $P=0.774$).

Stream volume was also important in determining species composition in anuran communities. In the CCA, it was associated with the first axis, as well as structural complexity of the streamside habitat ($S$) (Table III). The first axis explained 27.3% of the observed variance and was the only one that showed a significant association between species distribution and habitat features (Table III). Stream volume was not correlated to $S$ (weighted correlation=0.381). Distances between stream pairs did not relate to dissimilarities in anuran community composition ($r=0.132$, $Z=164782.0$, $P=0.245$).

Species diversity was not related to monthly rainfall or mean air and water temperatures ($r^2=0.077$, $F_{3,11}=1.389$, $P=0.298$). Diversity of species with calling males was not related to these parameters either ($r^2=0.186$, $F_{3,11}=2.068$, $P=0.162$).

Discussion

In the studied streams, a negative relationship was found between estimated volume of the sampled reach and anuran species richness. Reflecting this pattern, the number of species in the larval stage in the same set of streams tended to decrease with the increase in stream volume, though the relationship was not significant (Eterovick & Barata 2006). Anuran breeding success and tadpole survivorship may act as secondary factors affecting tadpole community composition, after selection of breeding sites by adults.
Table II. Activities and life stages recorded for the anuran species at the RPPN Santuário do Caraça, southeastern Brazil, from August 2003 to October 2004. (*) Silent individuals; (♂) calling males; (♀) gravid females; (❤) amplexed pairs; (*) egg clutch; (T) tadpoles, and (fr) post metamorphic froglet. N= number of adult frogs visually recorded (some males were recorded just by their mating call but could not be located). Data from all streams combined is presented.

| Species                          | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | N  |
|---------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----|
| **Bufonidae**                   |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Chaunus pombali (Baldissera, Caramaschi & Haddad, 2004) | T   | ♂T | ♀T | ♀T | ♀T | ♀T | ♀T | ♀T | ♀T | ♀T | ♀T | ♀T | ♀T | ♀T | ♀T | 5  |
| C. rubescens (Lutz, 1925)       |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Cycloramphidae                  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Hyla rubescens (Lutz, 1925)     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Cycloramphidae                  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Proceratophrys boiei (Wied-Neuwied, 1824) | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 3  |
| **Hylidae**                     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Bokermannohyla sp. (gr. circumdata) |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| B. martinsi (Bokermann, 1964)   | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 9  |
| B. nanuzae (Bokermann & Sazima, 1973) | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 19 |
| Dendropsophus minutus (Peters, 1872) | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 104|
| Hypsiboas albopunctatus (Spix, 1824) | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 13 |
| H. faber (Wied-Neuwied, 1821)   |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| H. polytaenius (Cope, 1868)    | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 7  |
| Phylomedusa burmeisteri Boulenger, 1882 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Scinax luizotavioi (Caramaschi & Kistumacher, 1989) | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 123|
| S. machadoi (Bokermann & Sazima, 1973) | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 5  |
| Scinax aff. perereca            |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Scinax sp. (gr. ruber)          |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| **Hylodidae**                   |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Crossodactylus bokermanni Caramaschi & Sazima, 1985 | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 123|
| *Hylodes uai Nascimento, Pombal & Haddad, 2001* | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | ♀♂ | 8  |
| **Leiuperidae**                 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
| Physallaemus aff. olfersii      |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |
Species seemed to choose the most suitable breeding habitats along a stream size gradient, nevertheless, most species preferred the smallest streams. The same pattern was recorded by Eterovick (2003) in streams at Serra do Cipó, a montane meadow site close to the RPPN Santuário do Caraça, in the southern portion of the Espinhaço mountain range. Both works point to the hypothesis that, although stream size influences anuran species distribution in southeastern Brazil, the relationship between stream size and species richness is not positive as in other sites (e.g. Australia; Parris & McCarthy 1999) and for other species groups (e.g. fishes; Angermeier & Schlosser 1989). Tadpole predators may also respond to water body size gradients, at least when these represent permanency.

Figure 3. Relationship between estimated volume of stream sampled sections (m$^3$) and (A) anuran species richness and (B) number of anuran species with calling males at the RPPN Santuário do Caraça, southeastern Brazil. Numbers in the graphs correspond to streams 1–8.
gradients (Heyer et al. 1975; Skelly 1997) and may influence tadpole distribution (Hero et al. 1998). Predatory fish were not recorded in any of the studied streams, but Eterovick and Barata (2006) found a negative relationship between predatory insects (Belostomatidae and Odonata) and tadpole species richness. Nevertheless, predator abundance was not necessarily higher in larger or more permanent streams at the RPPN Santuário do Caraça (for data on predator abundance and richness in the streams, see Eterovick & Barata 2006).

Zimmerman and Simberloff (1996) stressed that the evolution of neotropical anurans favoured species that breed in lentic water bodies, contrary to the pattern observed in southeastern Asia, because ancestral lineages that evolved in these two continents had adaptations to lentic and lotic aquatic habitats, respectively. Small streams, such as the ones in the lower portion of the size range studied here and by Eterovick (2003), are washed by strong currents just during the rainfall peaks, whereas the largest streams included in such studies have stronger currents and fewer shallow microhabitats (P. C. Eterovick and L. G. Afonso, pers. obs.). Living downstream, in larger sections with larger water volume, would likely imply a greater demand on tadpoles for adaptations to swim against the current, attach themselves to substrates and search for shelters. Tadpoles may also have advantages in shallow microhabitats if these attain high temperatures to increase metabolism and speed development. Ultsch et al. (1999) stated that temperature is one of the main factors influencing microhabitat selection by tadpoles. A detailed study of temperature variation in tadpole microhabitats at the studied streams would be necessary to test this hypothesis. The potential advantages encountered by tadpoles in small streams may have selectively favoured breeding frogs with generalized larvae that chose to breed in such habitats.

Both stream size and streamside habitat complexity \((S)\) influenced anuran species composition. The differential use of streams by anuran species reflects the selection of breeding habitats known to occur in this group (Collins & Wilbur 1979; Gascon 1991). Density of vegetation cover at pond margins constitutes an important factor influencing choice of reproductive sites by anurans (Werner & Glennemeier 1999). In the present study, the variables related to streamside vegetation accounted for a small proportion of the variance in species distribution, so that there may be other factors determining the composition of local anuran assemblages. Stream 5, for instance, has a large backwater that functioned as a permanent pond and sheltered species able to occupy both forest streams and open lentic habitats, such as *Dendropsophus minutus*, *Hypsiboas polytaeniatus* and

| Variable | Axis 1 | Axis 2 | Axis 3 |
|----------|--------|--------|--------|
| Stream section estimated volume | 0.662 | −0.618 | 0.417 |
| Habitat structural complexity \((S)\) | 0.601 | −0.040 | −0.167 |
| Marginal cover of herbaceous vegetation | 0.401 | −0.219 | 0.620 |
| Marginal cover of shrub vegetation | −0.340 | −0.264 | 0.273 |
| Marginal cover of arboreal vegetation | 0.222 | −0.197 | −0.344 |
| Eigenvalue \(\eta\) | 0.889 (0.024) | 0.741 (0.018) | 0.444 (0.004) |
| Cumulative % of variance explained | 27.3 | 50.1 | 63.7 |
| \(P\) (species–environment correlation) | 0.017 | 0.394 | 0.089 |
**Phyllomedusa burmeisteri** (see Cardoso et al. 1989), leading to the high species richness in this stream. It is important to notice that even if this stream is excluded from our analyses, the relationship between species richness and stream size does not change ($r^2=0.857$, $F=29.92$, $P=0.003$), and the relationship between number of species with calling males and stream size does not change either ($r^2=0.566$, $F=6.51$, $P=0.05$; a linear regression was conducted since data were normal after deleting Stream 5).

Because the studied streams were all bordered by forest vegetation, variability in cover of vegetation strata would not encompass the whole range of the gradient from completely shaded to completely open sites, although broader streams tend to receive more sunlight than narrow streams. The variability in vegetation strata included in this study was not related to stream occupancy by breeding frogs. However, the cover of arboreal vegetation was related to tadpole community composition at the same set of streams (Eterovick & Barata 2006). Shading may influence water temperature and food availability for tadpoles (Schiesari 2004), and perhaps its effects could not be evaluated by breeding adults, or were not a main determinant factor during choice of breeding sites. Comparisons among streams in open and closed vegetation sites would be interesting to investigate the role of vegetation stratification and shading (canopy cover) in anuran assemblages.

The greater proportion of hylids (63.2% of species and 67.5% of recorded individuals) recorded in the streams may be related to the higher diversity of calling sites available for this group, since the presence of all vegetation strata provides several microhabitats to be explored by these climbing treefrogs. The regional species pool may also play a role in the composition of local assemblages and habitat use. Doan and Arizábal (2002) found anuran species to preferentially use leaf litter microhabitats at several sites in the Peruvian Amazon. At these sites, hylid species accounted for 40.3–51.7% of anuran species recorded, but hylid abundance could be as low as 6.8% of all individual amphibians recorded at a given site. At the spatial scale at which the present study was conducted (stream pairs separated by 434–8141 m), it seems that stream features were more important than distance between stream pairs in determining the composition of anuran assemblages, because dissimilarity between communities was not related to geographical distance. The studied streams may be potentially colonized by the same species pool, each species establishing itself at the streams that are suitable for it. Ernst and Rödel (2005) found a similar distribution pattern among transects for leaf litter anuran communities in a rainforest site disturbed by logging, but not in undisturbed forest, where geographic distance explained a great amount of community composition, and habitat features did not. They related the strong species–habitat relations observed in disturbed forest to the existence of areas that are not suitable for sensitive species, which would only be able to establish in suitable patches. Although the RPPN Santuário do Caraça is a preserved site, streams can vary in quality depending on specific needs of frogs, producing a similar effect.

The annual breeding period and duration of breeding activities of anurans are often related to seasonal climatic variations in temperature and rainfall (Toft and Duellman 1979). Species that occur in permanent shaded water bodies, with high humidity during most of the year, usually show a long reproductive period (Rossa-Feres & Jim 1994). The lack of association between weather variables (rainfall and temperature) and monthly anuran species diversity and between climatic variables and monthly diversity of species with calling males in our study may be due to local habitat conditions at the RPPN Santuário do Caraça. Forest habitats are expected to be more stable and predictable than open habitats (Colwell 1974). The forest vegetation at the streamside habitat may reduce variations in air humidity and temperature at the streams studied, resulting in a lack of
strong correlation between anuran breeding activities and rainfall. Maybe for the same reasons, several anuran species used the studied streams year-round. Tadpoles of *Scinax machadoi* were recorded in all sampling months, indicating continuous reproduction and/or long development. Nevertheless, the number of adult individuals found was relatively low, probably because this was the most difficult species to locate; it has a small size, cryptic coloration, and low, irregular mating call (Bokermann & Sazima 1973). *Crossodactylus bokermanni* also showed reproductive activities year-round, as reported for the same species at the Serra do Cipó (Minas Gerais state, southeastern Brazil) (Eterovick & Sazima 2004) and for *Crossodactylus* sp. at the Parque Estadual Mata dos Godoy (Paraná state, south Brazil; Bernarde & Anjos 1999).

The species showing the greatest plasticity in stream occupancy were those with the highest reproductive activity level (gravid females, egg clutches, tadpoles, and post-metamorphic froglets), such as *Bokermannohyla martinsi, B. nanuzae, Scinax luizotavioi, S. machadoi, Crossodactylus bokermanni,* and *Hylodes uai,* which were observed almost year-round. *Bokermannohyla martinsi* had abundance peaks in the hottest and most humid months, but its tadpoles were recorded in all months, which may be due to continuous reproduction and/or long tadpole development. *Bokermannohyla nanuzae* had a long breeding period with an activity peak during the rainy season, its breeding period being longer than recorded at the Serra do Cipó (Eterovick & Sazima 2004), a more markedly seasonal and open habitat. *Scinax luizotavioi* was recorded in almost all sampling months, with an activity peak during the dry season. Differences in reproductive periods had already been interpreted as a potential mechanism to avoid interspecific competition (Bertoluci & Rodrigues 2002). Nevertheless, climatic factors and physiological adaptations acquired during evolution may play a more important role in determining breeding periods of anurans, and populations of the same species may show variations in breeding pattern at different sites, subject to different climatic conditions, as noticed here for *Bokermannohyla nanuzae.* In addition, 31.6% of the anuran species recorded in forest streams at the RPPN Santuário do Caraça showed evidence of reproduction or reproductive activities year-round, contrasting with only 11.6% (18.5% considering only species that reproduce in streams or associated with them) of the anuran species of the Serra do Cipó, a less stable, open habitat (Eterovick 2003; Eterovick & Sazima 2004).

Species typical of forest habitats are probably more specialized and have reproductive modes with more restrictive needs (see Duellman & Trueb 1994) being potentially more sensitive to habitat changes. The RPPN Santuário do Caraça is located in the domains of the Espinhaço mountain range, where many Brazilian endemic genera and local endemic species occur (Drummond et al. 2005). The Espinhaço is an important area for amphibian conservation in the state of Minas Gerais and its surroundings are suffering strong human impacts caused by mining activities and tourism, which may alter natural spatial and temporal distributions of anuran communities. The present study shows that stream dwelling anuran species select breeding habitats based on factors related to stream size and structural complexity of the streamside habitat. Thus, human activities that can potentially disturb streams and their margins should be avoided. This is valid for every stream size, since anuran species are not uniformly distributed along the stream size gradient.

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References

Afonso LA, Eterovick PC. 2007. Microhabitat choice and differential use by anurans in forest streams in southeastern Brazil. Journal of Natural History 41:937–948.

Alford RA. 1999. Ecology. Resource use, competition, and predation. In: McDiarmid RW, Altig R, editors. Tadpoles. The Biology of Anuran Larvae. Chicago: The University of Chicago Press. p 240–278.

Angermeier PL, Schlosser JJ. 1989. Species-area relationships for stream fishes. Ecology 70:1450–1462.

Azevedo-Ramos C, Galatti U. 2002. Patterns of amphibian diversity in Brazilian Amazonia: conservation implications. Biological Conservation 103:103–111.

Bernarde PA, Anjos L. 1999. Distribuição espacial e temporal da anurofauna no Parque Estadual Mata dos Godoy, Londrina, Paraná, Brasil (Amphibia: Anura). Comunicações do Museu de Ciência e Tecnologia, PUCRS 12:127–140.

Bertoluci J, Rodrigues MT. 2002. Seasonal patterns of breeding activity of Atlantic Rainforest anurans at Boracéia, Southeastern Brazil. Amphibia-Reptilia 23:161–167.

BioEstat. 2003. Versão 3.0. Manaus: Sociedade Civil Mamirauá/MCT – CNPq.

Bokermann WCA, Sazima I. 1973. Anfíbios da Serra do Cipó, Minas Gerais, Brasil.1: Duas espécies novas de Hyla (Anura, Hylidae). Revista Brasileira de Biologia 33:241–249.

Cardoso AJ, Andrade GV, Haddad CFB. 1989. Distribuição espacial em comunidades de anfíbios (Anura) no sudeste do Brasil. Revista Brasileira de Biologia 49:241–249.

Cardoso AJ, Haddad CFB. 1992. Diversidade e turno de vocalizações de anuros em comunidade neotropical. Acta Zoologica Lilloana 41:93–105.

Collins JP, Wilbur HM. 1979. Breeding habits and habitats of the amphibians of the Edwin S. George Reserve, Michigan, with notes on the local distribution of fishes. Occasional Papers of the Museum of Zoology, University of Michigan 68:1–34.

Colwell RK. 1974. Predictability, constancy and contingency of periodic phenomena. Ecology 55:1148–1153.

Crump ML. 1974. Reproductive strategies in a tropical anuran community. Miscellaneous Publications, Museum of Natural History, University of Kansas 61:1–68.

Crump ML. 1982. Amphibian reproductive ecology on the community level. In: Scott-Jr NJ, editor. Herpetological Communities. Washington, DC: Wildlife Research Report 13. p 21–36.

Dayton GH, Fitzgerald LA. 2001. Competition, predation, and the distribution of four desert anurans. Oecologia 129:430–435.

Derby OA. 1966. The Serra of Espinhaço. Brazilian Journal of Geology 14:374–40.

Doan TM, Arizábal WA. 2002. Microgeographic variation in species composition of the herpetofaunal communities of Tambopata region, Peru. Biotropica 34:101–117.

Donnelly MA, Guyer C. 1994. Patterns of reproduction and habitat use in an assemblage of Neotropical hylid frogs. Oecologia 98:291–302.

Drummond GM, Martins CS, Machado ABM, Sebaio FA, Antonini Y, editors. 2005. Biodiversidade em Minas Gerais: um Atlas para sua Conservação. 2nd ed. Belo Horizonte, Brazil: Fundação Biodiversitas.

Duellman WE. 1978. The biology of an equatorial herpetofauna in Amazon Ecuador. Miscellaneous Publications, Museum of Natural History, University of Kansas 65:1–352.

Duellman WE. 1989. Tropical herpetofaunal communities: patterns of community structure in neotropical rainforests. In: Harmelin-Vivien ML, Bourliere F, editors. Ecological Studies, vol. 69 – Vertebrates in complex tropical systems. New York: Springer-Verlag. p 61–88.

Duellman WE, Trueb L. 1994. Biology of amphibians. New York: McGraw-Hill.

Ernst R, Rödel M-O. 2005. Anthropogenically induced changes of predictability in tropical anuran assemblages. Ecology 86:3111–3118.

Ernst R, Rödel M-O. 2006. Community assembly and structure of tropical leaf-litter anurans. Ecotropica 12:113–129.
Eterovick PC. 2003. Distribution of anuran species among montane streams in south-eastern Brazil. Journal of Tropical Ecology 19:219–228.

Eterovick PC, Barata I. 2006. Distribution of tadpoles within and among Brazilian streams: the influence of predators, habitat size and heterogeneity. Herpetologica 62:367–379.

Eterovick PC, Sazima I. 2000. Structure of an anuran community in a montane meadow in southeastern Brazil: effects of seasonality, habitat, and predation. Amphibia-Reptilia 21:439–461.

Eterovick PC, Sazima I. 2004. Anfibios da Serra do Cipó – Amphibians from the Serra do Cipó, Minas Gerais, Brasil. Belo Horizonte, Brazil: Ed. PUC Minas. 152 p.

Gascon C. 1991. Population and community level analysis of species occurrences of Central Amazonian rainforest tadpoles. Ecology 72:1731–1746.

Giulietti AM, Pirani JR. 1988. Patterns of geographic distribution of some plant species from the Espinhaço Range, Minas Gerais and Bahia. In: Vanzolini PE, Heyer WR, editors. Proceedings of a workshop on Neotropical distribution patterns. Rio de Janeiro, Brazil: Academia Brasileira de Ciências. p 36–69.

Giulietti AM, Pirani JR, Harley RM. 1997. Espinhaço Range region, Eastern Brazil. In: Davis SD, Heywood V H, Herrera-MacBryde O, Villa-Lobos J, Hamilton AC, editors. Centres of plant diversity, a guide and strategy for their conservation, v. 3. Oxford, England: Information Press. p 397–404.

Hero JM, Gascon C, Magnusson WE. 1998. Direct and indirect effects of predation on tadpole community structure in the Amazon rainforest. Australian Journal of Ecology 23:474–482.

Heyer WR, MCDiarmid RW, Weigmann DL. 1975. Tadpoles, predation and pond habitats in the tropics. Biotropica 7:100–111.

Hödl W. 1977. Call differences and calling site segregation in anuran species from central Amazonian floating meadows. Oecologia 28:251–263.

MacArthur RH. 1968. The theory of the niche. In: Leotin RC, editor. Population biology and evolution. New York: Syracuse University Press. p 159–176.

McCune B, Mefford MJ. 1999. Multivariate Analysis of Ecological Data. Version 4.10. MiM Software, Gleneden Beach, Oregon, USA.

Palmer MW. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74:2215–2230.

Parris KM, McCarthy MA. 1999. What influences the structure of frog assemblages at forest streams? Australian Journal of Ecology 24:495–502.

Pianka ER. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74.

Pielou EC. 1975. Ecological diversity. New York: Wiley Interscience Publishers.

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.

Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists. Cambridge: Cambridge University Press.

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.

Schiesari LC. 2004. Performance tradeoffs across resource gradients in anuran larvae [PhD dissertation]. Ann Arbor: University of Michigan.

Skelly DK. 1997. Tadpole communities. American Scientist 85:36–45.

Ter Braak CJF. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

Toft CA, Duellman WE. 1979. Anurans of the lower Rio Lullapichis, Amazonian Peru: a preliminary analysis of community structure. Herpetologica 35:71–77.

Ultsch GR, Bradford DF, Freda J. 1999. Physiology: Coping with the Environment. In: MCDiarmid RW, Altig R, editors. Tadpoles: the biology of anuran larvae. Chicago: The University of Chicago Press. p 189–214.

Werner EE, Glennemeier KS. 1999. Influence of forest canopy cover on the breeding pond distributions of several amphibian species. Copeia 1999:1–12.

Wiest-Jr JA. 1982. Anuran succession at temporary ponds in a post oak-savanna region of Texas. In: Scott-Jr NJ, editor. Herpetological communities. Wildlife Research Report 13, Washington, DC. p 39–47.

Zimmerman BL, Bierregaard RO. 1986. Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from Amazonia. Journal of Biogeography 13:133–143.

Zimmerman BL, Simberloff D. 1996. An historical interpretation of habitat use by frogs in a Central Amazonian Forest. Journal of Biogeography 23:27–46.