Factors influencing spatial and temporal structure of frog assemblages at ponds in southeastern Brazil

KATIA KOPP & PAULA C. ETEROVICK

Programa de Pós Graduação em Zoologia de Vertebrados, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil

(Accepted 16 September 2006)

Abstract
Anuran assemblages were studied regarding species composition, microhabitat partitioning, temporal distribution, and spatial distribution in three natural ponds. Twenty-two species belonging to four families (Bufonidae, Hylidae, Leptodactylidae, and Microhylidae) were recorded, 11 of these also in the larval stage. Month of occurrence, height above ground, and type of substrate were the most important variables discriminating among adult anuran microhabitats, whereas position in the water column, water depth, and presence of aquatic vegetation were the most important ones to discriminate among tadpole microhabitats. The total number of species and the number of species with calling males recorded were positively correlated with mean monthly rainfall and temperature. Tadpole species richness was not related to the number of types or abundance of potential tadpole predators in ponds. In the studied anuran assemblages, environmental and stochastic factors are more likely to produce the observed patterns of species distribution than biotic interactions.

Keywords: Anura, climatic factors, community structure, microhabitat use, tadpole predators, tadpoles

Introduction
A central goal of ecology is the identification of the roles that abiotic and biotic factors play in determining the distribution and abundance of species (Norton 1991). The main mechanisms responsible for resource partitioning and community structure are individual physiological tolerances and biotic interactions. Whereas the former determines a species’ use of resources independent of other species present, at least in ecological time (Toft 1985), the latter concerns primarily competition and predation.

Many factors have been suggested to influence patterns of species distribution and assemblage composition at specific sites, such as competition (Morin 1983), predation (Gascon 1991; Eterovick and Sazima 2000), morphological and behavioural attributes (Crump 1974; Toft 1985), rainfall (Aichinger 1987; Arzabe 1999; Toledo et al. 2003)
hydrological cycles (Wild 1996; Arzabe et al. 1998; Snodgrass et al. 2000; Beja and Alcazar 2003), ecological and historical factors (Angermeier and Schlosser 1989; Eterovick and Fernandes 2001), stochastic processes (Bonner et al. 1997), habitat duration (Gascon 1992; Eterovick and Fernandes 2002), and interactions between biological and environmental factors (Wilbur 1987). However, resource partitioning in anurans results from many different causes, each one acting at a different intensity (Toft 1985).

Anuran reproductive activities are largely influenced by rainfall and temperature in the tropics (Crump 1974; Aichinger 1987). In climates that are not markedly seasonal, anurans tend to reproduce year-round, whereas in seasonal climates reproductive activities are usually concentrated in wet and hot seasons (Duellman and Trueb 1994). According to Heyer et al. (1975) and Skelly (1997), abiotic factors (e.g. water body duration) are more important than biotic factors (e.g. competition, predation) for species’ reproductive success in temporary water bodies, but predation is not independent of hydroperiod. Studies on spatial and temporal distribution of anuran species usually show segregation in use of calling sites and reproductive period (Cardoso et al. 1989; Cardoso and Vielliard 1990; Pombal 1997). The set of microhabitats used by different species or even different size classes of a species constitutes a compromise between the physiological needs of the animal and its biotic interactions within the ecosystem (Zweimüller 1995).

The main resources partitioned by tadpoles are often considered to be space and time (Toft 1985; Inger et al. 1986), but even so the importance of food resources cannot be neglected (Heyer 1976; Schiesari 2004). Differences in morphological, physiological, and behavioural characteristics of species are among the major factors influencing the distribution of tadpoles in ponds (Inger et al. 1986; Barreto and Moreira 1996). Reproductive behaviour of adult anurans (e.g. Inger et al. 1986; Gascon 1995; Eterovick and Barros 2003), abiotic factors (e.g. weather patterns, rainfall distribution; Aichinger 1987; Rossa-Feres and Jim 1996), competition and predation (e.g. Morin 1983; Azevedo-Ramos and Magnusson 1999; Azevedo-Ramos et al. 1999) may also play important roles.

Some work has been conducted in the neotropics (e.g. Gascon 1991; Rossa-Feres and Jim 1996; Wild 1996; Eterovick and Barros 2003), but much remains to be done to understand neotropical tadpole communities (Gascon 1991). Opinions on the main factors responsible for resource partitioning in tadpoles are still controversial. According to Toft (1985), resource partitioning in anuran larvae may involve complex interactions between physical and biological factors.

Studies on anuran ecology and natural history in Brazil are scarce in relation to the amphibian richness in the country (776 species, SBH 2005, Sociedade Brasileira de Herpetologia, http://www.sbherpetologia.org.br, consulted on 6 September 2006), and are needed for conservation purposes (Eterovick et al. 2005). Since anuran community structure is influenced by several biotic and abiotic factors important for its maintenance, knowledge of such factors is essential to understand how species co-exist and how human influence may disturb assemblages. We studied three anuran assemblages occurring in natural ponds in southeastern Brazil to determine species composition, microhabitat partitioning, temporal and spatial distribution of reproductive activities and tadpoles, and the influence of some biotic and abiotic factors on the observed patterns. These aims were accomplished by (1) surveying the anuran species using the ponds during larval and adult stages; (2) investigating whether different species, in both the adult and tadpole stages, use microhabitats differentially or show spatial and temporal overlap; (3) relating anuran temporal distribution to temperature and rainfall; and (4) recording the potential tadpole predators in these ponds and relating their presence to tadpole species richness.
Materials and methods

Study site

Work was carried out in three ponds in the Reserva Particular do Patrimônio Natural (RPPN) Santuário do Caraça, municipality of Catas Altas, Minas Gerais state, southeastern Brazil. Pond 1 (20°06′33.0″S, 43°29′85.5″W, 1290 m a.s.l.) is an elliptical temporary pond with approximately 85 m² surface area and 70 cm maximum depth during the rainy season. Its edges are covered by shrubs, grasses, ferns, evergreen daisies (*Paepalanthus*), and a forest border in the northern edge. The bottom is sandy and almost completely covered by submerged aquatic vegetation. Pond 2 (20°06′18.3″S, 43°29′19.8″W, 1266 m a.s.l.) is a temporary pond formed by the union of smaller ponds that connect in the rainy season forming a large pond with approximately 2705 m² surface area and 1.73 m maximum depth. Its edges are covered by shrubs, grasses, and *Paepalanthus*. The bottom is a mosaic of silty and rocky substrates either covered by aquatic vegetation or not, aquatic vegetation being more widespread in shallower areas. Pond 3 (20°06′31.9″S, 43°29′24.7″W, 1248 m a.s.l.) is a permanent pond with 503 m² surface area and 1.33 m maximum depth. The edges are covered by shrubs, grasses, *Paepalanthus*, and a forest reaches the western edge. The bottom is silty and almost completely covered by submerged aquatic vegetation, vegetation reaching the water surface at some points. The distance between Ponds 1 and 2 is 1178.3 m; between Ponds 1 and 3 is 1060.3 m, and between Ponds 2 and 3 is 261.7 m.

The climate has distinct dry and wet seasons; the rainy season starts in October/November and ends in March. During the study (between September 2003 and December 2004), the accumulated rainfall was 2868.1 mm and the mean temperature was 21.4°C (Figure 1). Monthly rainfall and maximum and minimum temperature data were obtained in the meteorological station of Santuário do Caraça and municipality of João Monlevade (Minas Gerais state), respectively.

Sampling procedures

Pond 1 was sampled from September 2003 to November 2004. Pond 2 was sampled from September 2003 to December 2004. Pond 3 was sampled from January to December 2004. Differences in sampling schedule among ponds were due to logistic difficulties, such as the late discovery and inclusion of Pond 3 in the study and the flooding of the access to Pond 1,
making it inaccessible in December 2004. No other ponds were found in the study site that could be studied concomitantly because of logistical difficulties.

At least two days and two nights were spent monthly in the field. Calling males were located and counted each night, during a period of 1 h per pond. Observations lasted until 3 h after sunset, and ponds were sampled in random order. The following classes for the number of synchronously calling males per species at the three ponds combined were established: (1) 1–2 males, (2) 3–5, (3) 6–10, (4) 11–20, (5) 21–50, and (6) more than 50 males (Aichinger 1987; Bertoluci 1998; Bertoluci and Rodrigues 2002). The presence of amplectant pairs, gravid females, tadpoles, or post-metamorphic froglets was used as evidence of reproduction. Non-calling individuals were also included in the analyses to determine total number of species recorded each month. For each adult individual we recorded species, distance from water, height above ground, kind of substrate, vegetation cover (exposed or covered), and month of record.

We searched for tadpoles visually during the day. In sites where visibility was too poor for visual observation of tadpoles, such as areas with submerged aquatic vegetation, microhabitats were sampled with a small dipnet. With a combination of both these methods, we made an effort to locate and record all tadpoles present in each pond. When tadpole densities were too high, we spent a similar amount of time searching for tadpoles in each microhabitat type not to bias the results on microhabitat use. For each individual found, its species, water depth, type of substrate (rocky, silty, or sandy), aquatic vegetation (presence or absence), and position in the water column (benthic or nektonic) were recorded. Tadpoles that could be easily identified were taken for closer inspection and then returned to the ponds. Tadpoles that could not be easily identified in the field were dipnet collected and fixed to be identified in the laboratory, or collected and reared to metamorphosis. The month when each tadpole was found was also recorded. Specimens collected were deposited in the Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Minas Gerais state, Brazil (MCN-AM).

All microhabitats available in the ponds were checked during the day for potential tadpole predators. The ponds sheltered no fishes. A dipnet was passed each month at several points (at least three) within each pond, depending on pond size and microhabitat heterogeneity within the pond. Each time the dipnet was passed it covered an area of 0.35 m² of the bottom. This method was used to estimate predator abundance in the whole pond, extrapolating results to total pond area. In the case of Pond 2, which was not completely covered by aquatic vegetation, both sites with and without vegetation were sampled and samples were grouped to estimate total predator abundance. Potential tadpole predators collected were fixed in 70% alcohol and identified to family level using literature for invertebrate identification (e.g. Nieser and Melo 1997; Carvalho and Calil 2000).

Data analysis

Variables used to describe adults’ microhabitats were organized in a matrix to conduct discriminant analyses (Klecka 1980). For the discriminant-function analysis of adult-species habitat separation, distance from water and height above ground were included in the analysis as quantitative variables. Vegetation cover was included as binary qualitative data, with their alternative states corresponding to 0 (exposed) or 1 (covered). Types of substrates were numbered from 0 to 4, based on a moisture gradient. Water was given the score 0, Paepalanthus leaf axil was given the score 1, bare soil was given the score 2, herbaceous vegetation was given the score 3, and shrubby vegetation was given the score 4.
Months were numbered from 1 to 12 representing time from the onset of the rainy season (October), so that October corresponds to 1, November to 2, and so on.

For the discriminant-function analysis of tadpole-species habitat separation, water depth was included in the analysis as a quantitative variable, whereas the remaining variables, except for month of occurrence, were included as binary qualitative data, with their alternative states corresponding to 0 or 1. Months were numbered from 1 to 10 representing time from the onset of the rainy season (October). Months that presented the same species set (June, July, and August) were grouped because they would not add any information to the analysis if considered separately. The classification matrices were jackknifed to compensate for usage of the same data set to calculate discriminant functions and classify cases. For each species classified, this analysis eliminates its own data as a form of cross-validation.

To estimate tadpole niche breadth, Simpson’s diversity index was used to calculate diversity in use of microhabitat types by each species. Microhabitat types were classified based on the combination of measured microhabitat features (Table I). Simpson’s diversity index was chosen due to its low sensitivity to sample size, a consequence of the low sensitivity to species richness and high importance attributed to the most common species (Magurran 1988). In this case, though, instead of focusing on species, the index was used to estimate diversity of microhabitat types, so that a higher importance was given to the most used microhabitats and microhabitats used just occasionally were not decisive for the results, reducing the differences in number of microhabitat types used that could be caused by differences in sample sizes among tadpole species. The niche breadth values obtained as described were related (as the independent variable) to number of individuals recorded for each species (as the dependent variable), to test whether species with broader niches are more abundant.

Table I. Use by tadpoles of each microhabitat type recorded at ponds, diversity of microhabitat use, sample sizes and percentage of correct classifications according to the discriminant analysis based on tadpole microhabitat use.

| Microhabitat types\(^a\) | Species\(^b\) | Dm | Ds | Hf | Hp | Sc | Sp | Ss | Po | Eo |
|--------------------------|---------------|----|----|----|----|----|----|----|----|----|
| 0–15 cm (rb) (v)         |               | 1  | 0  | 0  | 0  | 0  | 7  | 2  | 0  | 0  |
| 0–15 cm (rb) (nv)        |               | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 0–15 cm (sb) (v)         |               | 7  | 0  | 1  | 2  | 302| 129| 4  | 7  | 8  |
| 0–15 cm (sb) (nv)        |               | 2  | 0  | 0  | 0  | 4  | 0  | 0  | 4  | 0  |
| >15–30 cm (rb) (v)       |               | 2  | 0  | 0  | 0  | 0  | 5  | 0  | 0  | 0  |
| >15–30 cm (rb) (nv)      |               | 3  | 0  | 0  | 0  | 4  | 0  | 0  | 0  | 0  |
| >15–30 cm (sb) (v)       |               | 91 | 18 | 2  | 2  | 396| 207| 19 | 7  | 0  |
| >15–30 cm (sb) (nv)      |               | 7  | 0  | 0  | 0  | 12 | 3  | 0  | 3  | 0  |
| >30 cm (rb) (v)          |               | 1  | 0  | 0  | 0  | 3  | 0  | 0  | 0  | 0  |
| >30 cm (rb) (nv)         |               | 2  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| >30 cm (sb) (v)          |               | 201| 7  | 0  | 3  | 319| 219| 44 | 5  | 0  |
| >30 cm (sb) (nv)         |               | 1  | 0  | 0  | 0  | 5  | 1  | 0  | 1  | 0  |
| Simpson’s diversity index|               | 0.36|0.60|0.55|0.35|0.32|0.32|0.50|0.20|0.01|
| Sample size              |               | 388| 25 | 3  | 7  | 1045|571 |69 | 27 | 8  |
| % correct                |               | 73 | 0  | 100| 43 | 2  | 28 | 58 | 44 | 100|

\(^a\)(rb), rocky bottom; (sb), sand/silty bottom; (v), vegetation present; (nv), no vegetation. \(^b\)Species: Dm, *Dendropsophus minitus*; Ds, *Dendropsophus seniculus*; Hf, *Hypsiboas faber*; Hp, *Hypsiboas polytaenius*; Sc, *Scinax curicica*; Sp, *S. aff. perereca*; Ss, *S. squalirostris*; Po, *Physalaemus aff. olfersii*; Eo, *Elachistocleis ovalis*.
Similarity among the three studied ponds was estimated using the Sorensen similarity index (Krebs 1999). Correlations between abiotic variables (mean temperature and monthly rainfall), number of species with calling males, and total number of species were tested through Spearman rank correlations (Zar 1996).

Linear regressions (BioEstat Version 3.0; Ayres et al. 2003) were used to relate both number of types of potential tadpole predators and predator abundance (as the independent variable) to tadpole species richness in the ponds (as the dependent variable) each month, using data from the whole study period. We hypothesized that, if anurans are selected to have their larval development during months of lower predation risk, a negative relationship would be expected.

Results

Species occurrence

Twenty-two species belonging to four families (Bufonidae, Hylidae, Leptodactylidae, and Microhylidae) were recorded during the sampling period (Table II). Hylidae had 14 species (63%), followed by Leptodactylidae with five species (23%), and Bufonidae and Microhylidae with two (9%) and one (5%) species, respectively.

Some species were widely distributed, occurring in the three ponds (Dendropsophus minutus, Scinax curicica, S. aff. perereca, S. squalirostris, Physalaemus cuvieri, and P. evangelistai). Bokermannohyla gr. circumdata, Hypsiboas albopunctatus, and Scinax luizotavioli were found only in Pond 1. Hypsiboas polytaenius and Physalaemus aff. olsersii were recorded in Ponds 1 and 3. Chaunus pombali, C. rubescens, and Scinax cf. fuscovarius were found only in Pond 2. Hypsiboas faber and Phyllomedusa burmeisteri were found only in Pond 3. The remaining species (Dendropsophus elegans, D. seniculus, Scinax eurydice, Leptodactylus jolyi, L. ocellatus, and Elachistocleis ovalis) were recorded at Ponds 2 and 3. The similarity indexes were $S_s = 0.462$ between Ponds 1 and 2, $S_s = 0.593$ between Ponds 1 and 3, and $S_s = 0.774$ between Ponds 2 and 3.

Eleven species were recorded as tadpoles in the three ponds. Some species were recorded in only one (Hypsiboas faber, Leptodactylus jolyi, and L. ocellatus), or two months (Dendropsophus seniculus and Elachistocleis ovalis). The maximum species richness was recorded in April 2004 at Pond 1 (six species). Dendropsophus minutus, Scinax curicica, Scinax aff. perereca, and Scinax squalirostris were recorded in the three ponds while other species were recorded in a single pond (Hypsiboas polytaenius in Pond 1; Dendropsophus seniculus, Leptodactylus jolyi, and Leptodactylus ocellatus in Pond 2; Hypsiboas faber in Pond 3). Physalaemus aff. olsersii and Elachistocleis ovalis were recorded in two ponds (Ponds 1 and 3; and Ponds 2 and 3, respectively).

Microhabitat use

Among the variables obtained from microhabitat characterization made for 351 adult anurans (24 Chaunus pombali, five C. rubescens, one Bokermannohyla gr. circumdata, two Dendropsophus elegans, 89 D. minutus, 13 D. seniculus, one Hypsiboas albopunctatus, 12 H. faber, eight H. polytaenius, 42 S. curicica, 11 S. eurydice, one Scinax cf. fuscovarius, 11 S. luizotavioli, 24 Scinax aff. perereca, 34 S. squalirostris, three Phyllomedusa burmeisteri, two Leptodactylus jolyi, two L. ocellatus, 27 Physalaemus cuvieri, four P. evangelistai, 30 Physalaemus aff. olsersii, five Elachistocleis ovalis) those that explained the greatest amount
Table II. Phenology, calling, and breeding patterns of 22 anuran species at the RPPN Santuário do Caraça, southeastern Brazil, from September 2003 to December 2004.

| Species | Months (September 2003 to December 2004) |
|---------|-----------------------------------------|
|         | S | O | N | D | J | F | M | A | M | J | J | A | S | O | N | D |
| **Bufonidae** |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Chaunus pombali (Baldissera, Caramaschi and Haddad, 2004) |   |   |   |   |   |   |   |  1 | a, f |  1 |  1 |  4 |  1 |  A |   |   |   |
| Chaunus rubescens (Lutz, 1925) |   |   |   |   |   |   |   |   |   |   |   |  1 |  A |   |   |   |   |
| **Hylidae** |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Bokermannohyla gr. circumdata |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Dendropsophus elegans (Wied-Neuwied, 1824) |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Dendropsophus minutus (Peters, 1872) |   | t |  1 |  3 |  6 |  4 | t, m |  3 | t, m | t | t | t, m |  2 | t, m |  3 | t |  6 | t |  6 | t |
| Dendropsophus seniculus (Cope, 1868) |   |   |   |   |   |   |   |   |   |   |   |   |   |  1 | a, f |  1 | t |  3 | t |  4 | t |
| Hypsiboas albopunctatus (Spix, 1824) |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Hypsiboas faber (Wied-Neuwied, 1821) |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Hypsiboas polytaeniatus (Cope, 1870) |   | A |  1 |  2 |  1 |  2 | a, f |  1 | t |  1 | t |  1 | t |  1 | t |  1 | t |  1 |
| Phyllomedusa burmeisteri Boulenger, 1882 |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Scinax curicica Pugliese, Pombal and Sazima, 2004 | t |  1 |  3 |  4 |  5 | t, m |  4 | t, m |  2 | t, m |  2 | t, m | t | t | t | t | t |  4 | t |  5 | t, m |
| Scinax eurydice (Bokermann, 1968) |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Scinax cf. fuscovarius (Lutz, 1925) |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Scinax lutzotavioi (Caramaschi and Kisteumacher, 1989) |  2 |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Scinax aff. pereroca Pombal, Haddad and Kasahara, 1995 | t |  5 |  4 |  2 | t |  3 | t |  1 | t | t | t | t | t | t |  2 | t |  2 | t | a, f |
| Scinax squalirostris (Lutz, 1872) |   | – |  1 |  5 |  6 |  2 | t |  3 | t | t | t | t | t | t | t |  2 | t |  6 | t |  6 |
| **Leptodactylidae** |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Leptodactylus jolyi Sazima and Bokermann, 1978 |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Leptodactylus ocellatus (Linnaeus, 1758) |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Physalaemus cuvieri Fitzinger, 1826 |   | – |  1 |  2 |  5 |   |   |   |   |   |   |   |   |   |   |   |   |   |   |  4 |
| Physalaemus evangelistai Bokermann, 1967 |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Physalaemus aff. efferisi (Lichtenstein and Martens, 1856) | t |   |   |  3 |  6 |  3 | t |  2 | t | t | t | t | t | – |   |   |   |   |   |  5 |  6 | t |
| **Microhylidae** |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Elachistocleis ovalis (Schneider, 1799) |   | – |  1 | t |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Species with calling males |  2 |  5 |  6 | 12 |  6 |  8 |  5 |  4 |  3 |  2 |  2 |  4 |  1 |  6 | 15 |  11 |
| Total number of species |  3 |  5 |  6 | 12 |  8 | 11 |  6 |  6 |  6 |  4 |  3 |  4 |  4 |  7 | 16 |  11 |

Classes of abundance of calling males in the three studied ponds: (1) 1–2; (2) 3–5; (3) 6–10; (4) 11–20; (5) 21–50; (6) more than 50. A, non-calling individuals recorded. Evidence of breeding: t, tadpole; a, amplexant pair; f, gravid female; m, post-metamorphic froglet.
of variation among species were month, height above ground, and kind of substrate, which were associated to first, second, and third functions, respectively. The third derived function was influenced by both height above ground and substrate type. The first function derived by discriminant analysis explained 50% of total dispersion of data, whereas the second function explained an additional 31%. Both functions plus the third function explained 92.9% of total dispersion (Table III; Figure 2).

A total of 2143 tadpoles of nine species was recorded during the study, from September 2003 to November 2004. Two additional species were recorded but not included in the analyses of microhabitat use. Leptodactylus ocellatus was not included in the analyses because tadpoles of this species form aggregations, so that microhabitat choice could not be studied at the individual level as in the remaining species. Leptodactylus jolyi was excluded from the analyses too, because this species was recorded only in December 2004.

The first function derived by discriminant analysis explained 87.1% of total dispersion of tadpole data, while the second function explained an additional 7.3%. The first three functions explained 97.7% of total dispersion. Tadpole position in the water column (benthic or nektonic), water depth, and aquatic vegetation contributed most for first, second, and third functions, respectively (Table IV; Figure 3).

Considering that nine species were included in the analysis, the probability of random assignment of an individual to the right species is close to 11%. Thus, the proportions of correct classifications obtained with a Jackknifed Classification Matrix were high for many species (from 43 to 100% correct classifications), but low for others (Dendropsophus seniculus, Scinax curicica, and Scinax aff. perereca; Table I).

Species niche breadth (diversity in microhabitat use) had no relation to species abundance (total number of individuals recorded) ($R=0.015$, $P=0.901$; Table I).

Climatic factors and species phenology

The number of species per month with calling males was positively correlated with monthly rainfall ($r_s=0.7230$, $P=0.0015$, $n=16$) and temperature in the field ($r_s=0.8667$, $P=0.0000$, $n=16$). The total number of species recorded for the three ponds was also positively correlated with monthly rainfall ($r_s=0.7679$, $P=0.0005$, $n=16$) and temperature in the field ($r_s=0.8215$, $P=0.0001$, $n=16$).

Maximum calling activity was recorded in November 2004, when 16 species called. Minimum calling activity was recorded in September 2004, when only one species called (Table II). Some species called year-round and showed evidence of reproduction at the

### Table III. Canonical discriminant functions of the five variables used for adult anuran species differentiation, eigenvalues, canonical correlations, and cumulative proportion of total dispersion (variables that contributed most for species differentiation in each axis are in bold).

| Variable               | Function 1 | Function 2 | Function 3 |
|------------------------|------------|------------|------------|
| Vegetation cover       | 0.062      | 0.134      | 0.423      |
| Distance from water    | 0.118      | -0.332     | 0.108      |
| Height above ground    | 0.301      | -0.585     | -0.902     |
| Substrate              | 0.208      | -0.384     | 0.749      |
| Month                  | -0.897     | -0.435     | 0.098      |
| Eigenvalues            | 1.502      | 0.935      | 0.355      |
| Canonical correlations | 0.775      | 0.695      | 0.512      |
| Cumulative % of total dispersion | 0.500 | 0.811 | 0.929 |
Figure 2. Distribution of adult individuals of 22 anuran species at Santuário do Caraça, southeastern Brazil, according to variables used to describe microhabitat use and activity periods, in the first three axes of the discriminant function. Centroids for each species are shown on the right.

Table IV. Canonical discriminant functions of the five variables used for tadpole species differentiation, eigenvalues, canonical correlations, and cumulative proportion of total dispersion (variables which contributed most to species differentiation in each axis are shown in bold).

| Variable            | Function 1 | Function 2 | Function 3 |
|---------------------|------------|------------|------------|
| Substrate           | 0.685      | 0.236      | 0.375      |
| Depth               | -0.035     | 0.722      | 0.329      |
| Vegetation          | 0.259      | 0.463      | -0.759     |
| Position            | -1.109     | -0.022     | 0.169      |
| Month               | 0.499      | -0.562     | -0.074     |
| Eigenvalue          | 0.967      | 0.080      | 0.037      |
| Canonical correlation| 0.701      | 0.273      | 0.188      |
| Cumulative % of total dispersion | 0.871 | 0.944      | 0.977      |
onset of the rainy season, from October to November (*Dendropsophus minutus*, *Hypsiboas polytaenius*, *S. curicica*, and *S. squalirostris*); some species were active in summer (wet season), with longer or shorter breeding seasons (*Hypsiboas faber*, *Phyllomedusa burmeisteri*, *Scinax aff. perereca*, *Leptodactylus jolyi*, *Physalaemus cuvieri*, *P. evangelistai*, and *Physalaemus aff. olfersii*); some species could be considered explosive breeders, with intense calling in a short time period (*Dendropsophus seniculus*, *Scinax eurydice*, and *Elachistocleis ovalis*); and other species were active during winter (dry season, *Chaunus pombali* and *Scinax luizotavioi*). *Chaunus rubescens*, *Bokermannohyla gr. circumdata*, *Dendropsophus elegans*, *Hypsiboas albopunctatus*, *Scinax cf. fuscovarius*, and *Leptodactylus ocellatus* were found sporadically (1 or 2 months), preventing a satisfactory characterization of breeding pattern.
Tadpole predators

Aquatic insects considered as potential tadpole predators belonging to 12 families were recorded in the three ponds (Table V). Tadpole species richness was not related to the number of types of potential tadpole predators in ponds ($R=0.250$, $P=0.667$), and no relationship was found between monthly predator abundance and tadpole species richness at any pond (Pond 1: $R=0.265$, $P=0.087$; Pond 2: $R=0.007$, $P=0.813$; Pond 3: $R=0.095$, $P=0.357$).

Besides aquatic invertebrates, other potential tadpole predators were also recorded in the ponds. *Helicops* sp., *Liophis miliaris*, and *Thamnodynastes* sp. (Serpentes, Colubridae) were observed foraging within the ponds. Snakes from these genera are considered to be predators of adult anurans (Marques et al. 2001) and may also prey upon their larvae. *Pitangus sulphuratus* (Linnaeus, 1766) (Aves, Tyrannidae) was observed eating tadpoles on two occasions: in March 2004 at Pond 1 and in April 2004 at Pond 3. On the first occasion, a bird ate 12 tadpoles in a 23-min interval. *Pitangus sulphuratus* is a common bird at the study site and is frequently seen close to ponds (K. Kopp, personal observation).

Discussion

Species occurrence

Most anuran species did not use all the available ponds to breed. The greatest similarity in species composition between Ponds 2 and 3 may be related to a shorter distance between these sites (261.71 m), though the number of ponds studied is not enough to test for the effects of distance, species interactions, pond features, or stochastic processes in anuran community composition variation among ponds.

The largest representation of species of Hylidae (63%) in the ponds may be due to the abundant cover of shrubby vegetation at their margins and surroundings, providing suitable habitat for hylids that showed a great behavioural plasticity and used varied microhabitat types for calling (Figure 2).

Table V. Potential invertebrate tadpole predators found in the three studied ponds at Santuário do Caraça, southeastern Brazil, from September 2003 to November 2004.

| Pond | Coleoptera | Heteroptera | Odonata     | Richness |
|------|------------|-------------|-------------|----------|
| 1    | Hydrophilidae  | Notonectidae | Coenagrionidae | 10       |
|      | Noteridae    | Belostomatidae | Libellulidae |          |
|      | Dysticidae   | Pleidae     | Aeshnidae    |          |
|      | Gyriquinae   |            |             |          |
| 2    | Hydrophilidae  | Notonectidae | Coenagrionidae | 12       |
|      | Noteridae    | Belostomatidae | Libellulidae |          |
|      | Dysticidae   | Pleidae     | Aeshnidae    |          |
|      | Gyriquinae   | Naucoridae  |             |          |
|      |            | Nepidae     |             |          |
| 3    | Hydrophilidae  | Notonectidae | Coenagrionidae | 11       |
|      | Noteridae    | Belostomatidae | Libellulidae |          |
|      | Dysticidae   | Pleidae     | Aeshnidae    |          |
|      |              | Naucoridae  |             |          |
|      |              | Nepidae     |             |          |
The phenology of tadpole species recorded in the studied ponds seems to be determined mainly by seasonality and temporal distribution of reproductive activities by adult anurans, the latter also influencing species distribution among ponds. Some species were more widespread, occurring at the three ponds as tadpoles (Dendropsophus minutus, Scinax aff. perereca, S. curicica, and S. squalirostris), indicating that they may be better colonizers of breeding habitats or their demands for breeding habitat features may be less restrictive. According to Alford (1999), the spatial and temporal distribution of tadpole species may be related to spatial and temporal distribution of reproductive effort by adult anurans, which can be influenced by factors other than the ecological requirements of their larvae. It is also possible that some years prove unsuitable for reproduction by certain species due to a combination of environmental features and these species may remain in the area without reproducing (Eterovick and Fernandes 2002). This may aid the heterogeneous distribution of tadpole species among the three studied ponds with similar microhabitats for tadpoles.

Tadpoles of Dendropsophus seniculus were found in a single pond (Pond 2) for two consecutive years, only in December. Adult individuals of this species were not recorded in the first year, but they may have been overlooked since their reproductive pattern is explosive. The record of Hypsiboas faber tadpoles only in Pond 3 may be also related to the preference for this pond by reproducing adult individuals. Indeed, breeding adults of this treefrog were only recorded in Pond 3.

From the 22 anuran species recorded as adults at the ponds, only 11 were recorded in the larval stage. Since our sampling was intensive and careful, we believe that many species used the ponds (either to call or other activities) but did not succeed in breeding or attempt to breed there (see Table II).

Spatial distribution of anurans

After month of occurrence, height above ground and kind of substrate were the most important variables to discriminate among anuran species. Species with values lower than zero in the second axis tended to use microhabitats closer to the ground. Most species used calling sites at varied heights (see Figure 2). Hylids showed the greatest plasticity in microhabitat use, positioning themselves on the ground (Dendropsophus minutus, D. seniculus, Hypsiboas faber, Scinax curicica, S. eurydice, S. luizotavoi, Scinax aff. perereca, and S. squalirostris) and up to 2 m high (Dendropsophus elegans, Dendropsophus seniculus, Hypsiboas polytaenius, Phyllomedusa burmeisteri, and Scinax squalirostris). Most species also used all kinds of substrates, showing high behavioural plasticity in microhabitat use. On the other hand, leptodactylids, bufonids, and the only recorded microhylid showed little variation in microhabitat use. Behavioural plasticity of hylids may be associated with morphology, since adhesive discs adapt these frogs to climb different types of substrates at varied heights (Cardoso et al. 1989; Pombal 1997).

According to Cardoso et al. (1989), open areas shelter a number of anuran species greater than the number of available microhabitat types, contributing to overlap in microhabitat use. In the studied anuran assemblages, overlap in microhabitat use may be generated by shared preferences. Hylids may be more plastic than leptodactylids regarding microhabitat use during the larval stage due to their phylogenetic history (Eterovick and Fernandes 2001), this may also be true for adult individuals, as noticed here. Alternatively, species may differ in their tolerance and their competitive abilities, so they may become differentially distributed along environmental gradients as determined by their position within a competitive hierarchy (Wisheu 1998). However, it does not seem to
be the case of the anuran assemblage studied here, since species showed great overlap in microhabitat use, contrary to the pattern expected under strong competition pressures (Pianka 1973).

Position in the water column was the most informative variable in discriminating among tadpoles. *Hypsiboas faber*, *H. polytaenius*, *Physalaemus aff. olfersii*, and *Elachistocleis ovalis* were always found on the bottom. The use of bottom microhabitats by *Physalaemus aff. olfersii* is in accordance with the pattern recorded by Eterovick and Fernandes (2001) for leptodactylid tadpoles at Serra do Cipó, southeastern Brazil. *Hypsiboas faber* also used bottom microhabitats in the studied ponds, corroborating the pattern reported for the same species by Rossa-Feres and Jim (1996) at Botucatu, southeastern Brazil. Heyer et al. (1990) observed *Hypsiboas polytaenius* to use the bottom of ponds during a study conducted at Boracéia, SP, and the present work corroborated this pattern.

Rossa-Feres and Jim (1996) observed *Elachistocleis ovalis* at the water surface. This pattern differs from the one recorded in this study for the same species, which could be due to the small sample size (*n* = 8). The other species, *Dendropsophus minutus*, *D. seniculus*, *Scinax curicica*, *Scinax aff. perereca*, and *S. squalirostris*, were found throughout the water column. These genera can be both nektonic and benthic (Altig and Johnston 1989; Altig and McDiarmid 1999).

Water depth was also an important variable for discriminating among tadpole species. *Hypsiboas faber* and *Elachistocleis ovalis* used shallow parts of ponds. The remaining species used both shallow and deep sites. Other studies also reported use of both shallow and deep sites by certain tadpole species (e.g. Rossa-Feres and Jim 1996; Eterovick and Fernandes 2001).

Aquatic vegetation was a less important microhabitat variable for tadpole species differentiation. Five species (*Dendropsophus seniculus*, *Hypsiboas faber*, *H. polytaenius*, *Scinax squalirostris*, and *Elachistocleis ovalis*) always used sites with aquatic vegetation. Although *Hypsiboas faber* and *H. polytaenius* occurred in Ponds 1 and 3 respectively, which were almost completely covered by aquatic vegetation, the other species also occurred in Pond 2, that has a mosaic of bottom surfaces with and without aquatic vegetation. The other four species (*Dendropsophus minutus*, *Scinax curicica*, *Scinax aff. perereca*, and *Physalaemus aff. olfersii*) used both sites with or without aquatic vegetation. Of the 571 individuals of *Scinax aff. perereca* sampled, 567 (99%) used microhabitats with aquatic vegetation. The use of microhabitats with aquatic vegetation was also recorded for the remaining species. *Scinax curicica* used microhabitats with aquatic vegetation in 97% of records; *Dendropsophus minutus*, in 96% of records, and *Physalaemus aff. olfersii* in 70% of records. Use of microhabitats with aquatic vegetation has been proved to reduce mortality of *Dendropsophus minutus* and *Scinax curicica* through decreased predation by water bugs in an experiment conducted in Pond 2 (Kopp et al. 2006).

The selection of microhabitats with aquatic vegetation by tadpoles may confer a selective advantage that keeps tadpole species from partitioning space through differential use of microhabitats with/without vegetation cover, so that aquatic vegetation becomes a factor of low influence on species differentiation. Selection of vegetated microhabitats may influence predator–prey interactions and reduce predation rates on tadpoles (Babbitt and Tanner 1998; Lewis and Eby 2002; Kopp et al. 2006). Besides, microhabitats with vegetation may provide benefits other than protection against predators for tadpoles, such as increased food availability (Brockelman 1969). Predation pressures and food quality gradients can be considered as potential forces shaping pond tadpole communities at Santuário do Caraça, and deserve further studies.
Most tadpole species studied here used varied types of microhabitats, but species abundance was not related to niche breadth regarding microhabitat use. According to Levins (1968), abundant species tend to have broader niches than rarer ones. This author suggests that broad niches could be an adaptation to unstable habitats. Heyer (1974) also found a relationship between niche breadth and species abundance in a study conducted in Thailand. Alternatively, other factors, such as distribution of reproductive effort by adult anurans, may be more important than the ability of tadpoles to use a great range of spatial resources to determine species distribution and abundance.

Heyer (1973, 1974) encountered very little food partitioning in ephemeral ponds in Thailand. According to Heyer (1973), tadpoles are specialized in their ability to feed in different positions in the water column, and this microhabitat partitioning may serve as a secondary way to partition the small particulate food that most tadpoles consume and which is hard to partition directly. Schiesari (2004), though, stressed the importance of food quality, acquisition, and processing for tadpole survivorship, showing that food availability may ultimately affect tadpole species composition at a site due to different food requirements and feeding abilities of species. Future studies should address food use and partitioning by tadpoles at the Santuário do Caraça, since their feeding habits remain unknown.

**Climatic factors and species phenology**

The reproductive activities of species present at the study site were influenced by temperature and/or rainfall. L. G. Afonso and P. C. Eterovick (unpublished data) studied forest stream anuran communities at the Santuário do Caraça concomitantly with the present study and found no relationship between species richness and temperature and rainfall in streams throughout the study period. Since the studied ponds are temporary and the streams are permanent, the great instability of ponds may make anuran species reproducing there more susceptible to climatic conditions than those using permanent forested streams. Besides, open habitats tend to be less predictable and stable with regard to climatic conditions compared to forests (Inger and Cowell 1977). Month of occurrence was the most informative variable to discriminate among anuran species in the studied ponds. Except for *Chaunus pombali*, which reproduced during the dry season, all the species tended to breed during the rainy season. Some species were able to breed both during rainy and dry months (see Table II; Figure 2).

The pattern described for *Chaunus pombali* corresponds to patterns followed by other *Chaunus* species (e.g. *Chaunus marinus* (Linnaeus, 1758)—Aichinger 1987; *Chaunus rubescens*—Eterovick and Sazima 2004), but differs from the pattern observed by Bertoluci and Rodrigues (2002) for this same species at Boracéia, São Paulo state, where it showed two explosive reproductive peaks (in the onset and in the end of the rainy season). Evans et al. (1996), studying *Chaunus marinus*, found this species to show preference for temporary water bodies and related such preference to the shallow depths and short borders that favour higher water temperatures, suitable to reduce time to metamorphosis. In the present study, *C. pombali* was recorded only in a temporary pond (Pond 2), corroborating the hypothesis proposed by Evans et al. (1996). Indeed, this pond shows shallow depths during the dry season, when *C. pombali* breeds. Mean water temperature was 17.9°C during the reproductive period of this species, a high value for the dry/cold season (see Figure 1). The high temperature associated with shallow depths may have favoured the presence of *C. pombali* at Pond 2.
Preference for dry or wet periods for reproductive activities is related to life cycle, adaptations, and reproductive modes of anuran species (Duellman and Trueb 1994). Differences in the beginning and duration of the breeding period determine a temporal segregation in both adult and larval communities and could also reduce interspecific interactions (Bertoluci and Rodrigues 2002). According to Aichinger (1987), many anuran species from seasonal climates show seasonality in their reproductive patterns, most of them breeding during the hot, rainy season. This pattern was corroborated by several subsequent studies (e.g. Bertoluci 1998; Toledo et al. 2003; this study). In general, the availability of aquatic breeding sites restricts the reproductive activities of anurans to the rainy season (Aichinger 1987), and species reproductive pattern may be related to particular features of their habitat (Toledo et al. 2003) as different cues are used by different species for the onset of reproduction (Gascon 1991).

According to Crump (1974), a high proportion of continuous breeders is more common in communities of non-seasonal environments. In the present study, only four (Dendropsophus minutus, Hypsiboas polytaenius, Scinax curicica, and Scinax aff. perereca) out of 22 anuran species showed reproductive activity year-round.

Tadpole predators

Twelve types of invertebrate potential tadpole predators were recorded in the studied ponds: Odonata naiads (Coenagrionidae, Aeshnidae, Libellulidae), Heteroptera (Notonectidae, Nepidae, Belostomatidae, Pleidae, and Naucoridae), Coleoptera (Hydrophilidae, Noteridae, Dysticidae, and Gyrinidae). These taxa occur in the ponds and can prey upon anuran eggs and larvae (Borror et al. 1992). The lack of relationship between number of predator types and tadpole species indicates that adults may not be assessing tadpole predation risk when choosing reproductive sites, as also reported by Eterovick and Fernandes (2002). Our results corroborate this hypothesis, as a coincidence of larval period of anuran species with periods of lower predator richness and/or abundance was not recorded. This indicates that there may be factors more important than predation risk determining reproductive success and population maintenance in the studied tadpole assemblages.

Concluding remarks

Climatic factors seem to be important in determining the spatial and temporal distribution of reproductive activities of the pond anuran assemblages studied at the RPPN Santuário do Caraça. The communities studied did not show indicatives of competition such as spatial niche differentiation. The patterns of microhabitat use observed may simply reflect specific preferences. Predation pressures may also have some influence on selected patterns of microhabitat use, but they do not seem to determine the spatial and/or temporal distribution of tadpoles and/or adults alone. Empirical studies in ecology are usually accorded great importance, though natural history studies are essential to provide basic knowledge to interpret anuran assemblages and species attributes in different environments.

Acknowledgements

We are grateful to M. Wachlevski and A. D. M. Ferreira for help during field work, L. B. Nascimento and R. P. Bastos for helpful suggestions on the manuscript, the RPPN
Santuário do Caraça staff for permits and logistics, the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis for a permit (128/2004), the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and the Fundo de Incentivo à Pesquisa (FIP) of the Pontificia Universidade Católica de Minas Gerais for financial support.

References

Aichinger M. 1987. Annual activity patterns of anurans in a seasonal neotropical environment. Oecologia 71:583–592.

Alford RA. 1999. Ecology: resource use, competition, and predation. In: McDiarmid RW, Altig R, editors. Tadpoles: the biology of anuran larvae. Chicago: University of Chicago Press. p 240–278.

Altig R, Johnston GF. 1989. Guilds of anuran larvae: relationships among developmental models, morphologies, and habitats. Herpetological Monographs 3:81–109.

Altig R, McDiarmid RW. 1999. Diversity: familial and generic characterizations. In: McDiarmid RW, Altig R, editors. Tadpoles: the biology of anuran larvae. Chicago: University of Chicago Press. p 295–337.

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

Arzabe C. 1999. Reproductive activity patterns of anurans in two different altitudinal sites within the Brazilian Caatinga. Revista Brasileira de Zoologia 16:851–864.

Arzabe C, Carvalho CX, Costa MAG. 1998. Anuran assemblages in Castro Forest ponds (Sergipe State, Brazil): comparative structure and calling activity patterns. Herpetological Journal 8:11–113.

Ayres M, Ayres M Jr, Ayres DL, Santos AS, dos. 2003. BioEstat. Version 3.0. Maraus, Brazil: Sociedade Civil Mamirauá/MCT-CNPq.

Azevedo-Ramos C, Magnusson WE. 1999. Tropical tadpole vulnerability to predation: association between laboratory results and prey distribution in an amazonian savanna. Copeia 1999:58–67.

Azevedo-Ramos C, Magnusson WE, Bayliss P. 1999. Predation as the key structuring tadpole assemblages in a savanna area in Central Amazonia. Copeia 1999:22–33.

Babtitt KJ, Tanner GW. 1998. Effects of cover and predator size on survival and development of Rana utricularia tadpoles. Oecologia 114:258–262.

Barreto L, Moreira G. 1996. Seasonal variation in age structure and spatial distribution of a savanna larval anuran assemblage in Central Brazil. Journal of Herpetology 30:87–92.

Beja P, Alcazar R. 2003. Conservation of Mediterranean temporary ponds under agricultural intensification: an evaluation using amphibians. Biological Conservation 114:317–326.

Bertoluci J. 1998. Annual patterns of breeding activity in Atlantic rainforest anurans. Journal of Herpetology 32:607–611.

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

Bonner L, Diehl W, Altig R. 1997. Physical, chemical and biological dynamics of five temporary dystrophic forest pools in central Mississippi. Hydrobiologia 353:77–89.

Borrero DJ, Triplehorn CA, Johnson NF. 1992. An introduction to the study of insects. 6th ed. Philadelphia: Harcourt Brace College Publishers.

Brodecker WY. 1969. An analysis of density effects and predation in Bufo americanus tadpoles. Ecology 50:632–644.

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, Viellard J. 1990. Vocalizações de anfíbios anuros de um ambiente aberto, em Cruzeiro do Sul, Estado do Acre. Revista Brasileira de Biologia 50:229–242.

Carvalho AL, Calil ER. 2000. Chaves de identificação para as famílias de odonata (Insecta) ocorrentes no Brasil, adultos e larvas. Papeis Avulsos de Zoologia, São Paulo 41:224–241.

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

Duellman WE, Trueb L. 1994. Biology of amphibians. Baltimore (MD): Johns Hopkins University Press.

Eterovick PC, Barros IS. 2003. Niche occupancy in south-eastern Brazilian tadpole communities in montane-meadow streams. Journal of Tropical Ecology 19:439–448.

Eterovick PC, Carnaval ACOQ, Borges-Nojosa DM, Silvano DL, Segalla MV, Sazima I. 2005. Amphibian declines in Brazil: an overview. Biotropica 37:166–179.
Eterovick PC, Fernandes GW. 2001. Tadpole distribution within montane meadow streams at Serra do Cipó, southeastern Brazil: ecological or phylogenetic constraints? Journal of Tropical Ecology 17:683–693.

Eterovick PC, Fernandes GW. 2002. Why do breeding frogs colonize some puddles more than others? Phyllomedusa 1:31–40.

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. Anfíbios da Serra do Cipó: amphibians from the Serra do Cipó. Belo Horizonte (MG, Brazil): Ed. PUC Minas.

Evans M, Yáber C, Hero JM. 1996. Factors influencing choice of breeding site by Bufo marinus in its natural habitat. Copeia 1996:904–912.

Gascon C. 1991. Population- and community-level analyses of species occurrences of a Central Amazonian rainforest tadpole. Ecology 72:1731–1746.

Gascon C. 1992. Aquatic predators and tadpole prey in Central Amazonia: field data and experimental manipulations. Ecology 73:971–980.

Gascon C. 1995. Tropical larval anuran fitness in the absence of direct effects of predation and competition. Ecology 76:2222–2229.

Heyer WR. 1973. Ecological interactions of frog larvae at a seasonal tropical location in Thailand. Journal of Herpetology 7:337–361.

Heyer WR. 1974. Niche measurements of frog larvae from a seasonal tropical location in Thailand. Ecology 55:651–656.

Heyer WR. 1976. Studies on larval amphibian habitat partitioning. Smithsonian Contributions to Zoology 242:1–27.

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

Heyer WR, Rand AS, Cruz CA da, Peixoto OL, Nelson CE. 1990. Frogs of Boracéia. Arquivos de Zoologia, São Paulo 31:231–410.

Inger RF, Colwell RK. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. Ecological Monographs 47:229–253.

Inger RF, Voris HK, Frogner KJ. 1986. Organization of a community of tadpoles in rain forest streams in Borneo. Journal of Tropical Ecology 2:193–205.

Klecka WR. 1980. Discriminant analysis. Sage University Paper Series on Quantitative Applications in the Social Sciences 07-019:1–71.

Kopp K, Wachlevski M, Eterovick PC. 2006. Environmental complexity reduces tadpole predation by water bugs. Canadian Journal of Zoology 84:136–140.

Krebs CJ. 1999. Ecological methodology. 2nd ed. Menlo Park (CA): Addison-Wesley Educational Publishers.

Levins R. 1968. Evolution in changing environments. Monographs in Population Biology, Princeton 2:1–120.

Lewis DB, Eby LA. 2002. Spatially heterogeneous refugia and predation risk in intertidal salt marshes. Oikos 96:119–129.

Magurran AE. 1988. Ecological diversity and its measurement. Princeton (NJ): Princeton University Press.

Marques OAV, Eterovic A, Sazima I. 2001. Serpentes da Mata Atlântica: Guia Ilustrado para a Serra do Mar. Ribeirão Preto (SP, Brazil): Holos Editora.

Morin PJ. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53:119–138.

Nieser N, Melo AL de. 1997. Os heterópteros aquáticos de Minas Gerais: guia introdutório com chave de identificação para as espécies de Nepomorpha e Gerromorpha. Belo Horizonte (MG, Brazil): Editora UFMG.

Norton SF. 1991. Habitat use and community structure in an assemblage of cottid fishes. Ecology 72:2181–2192.

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

Pombal JP Jr. 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.

Rossa-Feres DC, Jim J. 1996. Distribuição espacial em comunidades de girinos na região de Botucatu, São Paulo. Revista Brasileira de Biologia 56:309–316.

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.

Snodgrass JW, Komoroski MJ, Bryan AL Jr. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. Conservation Biology 14:414–419.

Toft CA. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1–21.
Toledo LF, Zina J, Haddad CFB. 2003. Distribuição espacial e temporal de uma comunidade de anfíbios anuros do Município de Rio Claro, São Paulo, Brasil. Holos Environment 3:136–149.

Wilbur HM. 1987. Regulations of structure in complex systems: experimental temporary pond communities. Ecology 68:1437–1452.

Wild ER. 1996. Natural history and resource use of four Amazonian tadpole assemblages. Publications of the Museum of Natural History, University of Kansas 176:1–59.

Wisheu IC. 1998. How organisms partition habitats: different types of community organization can produce identical patterns. Oikos 83:246–258.

Zar JH. 1996. Biostatistical analysis. Upper Saddle River (NJ): Prentice Hall.

Zweimüller I. 1995. Microhabitat use by two small benthic stream fish in a 2nd order stream. Hydrobiologia 303:125–137.