

TEMPORARY POND AVAILABILITY AND TADPOLE SPECIES COMPOSITION IN CENTRAL AMAZONIA

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ABSTRACT: Habitat availability for larval development is one of the main factors affecting the distribution of anuran species. However, little is known about the spatial distribution of these habitats, and estimates of the number of available ponds for a given reserve size are not available in Amazonia. Temporary water bodies were surveyed in a 30-m strip around a 144-km system of trails in a terra firme tropical forest, and tadpoles were collected to evaluate differences in species composition between isolated and streamside ponds. More than 90% of the ponds were <150 m from a stream, and the tadpole species composition differed between isolated and streamside ponds. Isolated ponds were less common, but were, on average, more stable in time than streamside ponds. Despite the limited distribution of isolated forest ponds, species of frogs dependent on them were found throughout the reserve. The presence of both types of ponds is important for the maintenance of the local pond-breeding anuran community. This study shows that isolated and streamside forest ponds maintain a distinct assemblage of frogs, and isolated ponds are much less common, but are, on average, more predictable in time than streamside ponds.

Key words: Conservation; Frogs; Reserve design; Riparian zone; Spatial scales; Temporary waters

CONSERVATION planning is often based on habitat-suitability analyses (Acevedo et al., 2007; Carroll et al., 2003). However, it is often difficult to show strong habitat partitioning in the tropical forest, the number of distinct habitats apparently being too small to explain the larger number of coexisting species, at least for plants (Wright, 2002). This can be an important consideration in reserve design, because the commonly used species–area relationship may be largely due to the larger number of distinct habitats in larger reserves, rather than an effect of area per se (Manne et al., 2007; Tole, 2006).

Anurans are considered excellent bioindicators of environmental changes, due to their dependence on special microhabitats and microclimatic conditions (Bertoluci et al., 2007; Weyrauch and Gubb, 2004). Zimmerman and Bierregaard (1986) suggested that anurans are not good indicators of forest fragmentation because their strong habitat specialization for reproduction leads to large variation in species composition, due to the vagaries of reproduction habitats that occur in

a given fragment. However, these authors studied forest fragments that were far smaller than most Amazonian reserves, and their conclusions may not be relevant for larger reserves, or for landscapes with a larger number of forest fragments.

Terrestrially breeding frogs in Central Amazonia are not habitat specialists, and most species occur throughout the full extent of most of the environmental gradients likely to affect anurans (Menin et al., 2007). However, species with aquatic larvae appear to partition habitat much more strongly, apparently due to different susceptibility to predators in water bodies (Gascon, 1992*a*, 1995; Hero et al., 1998, 2001; Magnusson and Hero, 1991; Rodrigues et al., 2008).

Studies of habitat use by tadpoles have been based on comparisons of a relatively small number of water bodies selected subjectively to represent obvious environmental gradients, especially those associated with distance from streams (Gascon, 1991, 1992*a,b*; Hero et al., 1998, 2001). Hero et al. (1998, 2001) encountered few isolated (>150 m from a stream) forest ponds, and most of those were artificial pools associated with an access road. In contrast, Gascon (1991, 1992*a,b*, 1995) found more isolated forest ponds than streamside ponds. Although those studies were extremely useful to describe potential mechanisms

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resulting in habitat partitioning, they are of limited utility for decisions about reserve design because they lack information on how ponds are distributed across the landscape, and the number of available ponds for a given reserve size cannot be estimated.

The major limitation of early studies was access to the forest. Most trails were placed for ease of walking or covered only a limited area. In this study, we took advantage of a regular network of trails, 144 km in extent, which covers 64 km² of Reserva Florestal Adolpho Ducke (RFAD), a 10,000-ha reserve on the outskirts of Manaus, Brazil. The trail system samples the entire interior of RFAD, leaving a 1-km buffer strip between the trail grid and the boundary of the reserve (Costa et al., 2005; Magnusson et al., 2005). Although streamside ponds are common in the RFAD (Pazin et al., 2006), preliminary studies (Hero et al., 1998, 2001) indicated a very low density of natural isolated pools, which might not be sufficient to maintain species dependent on that breeding habitat.

Temporary water bodies vary in time as well as space (Rodrigues et al., 2007; Williams, 2006). Rainfall in Central Amazonia is strongly affected by the El Niño Southern Oscillation and unusual heating of the North Atlantic, and many climate-change models predict a reduction in rainfall in the region in the future (Marengo, 2006). Pond formation and maintenance depends on the temporal distribution of rainfall, rather than the yearly averages. The objective of this study was to evaluate the availability of temporary ponds in 3 yr with different rainfall regimes, and the tadpole species composition in these water bodies. The results of this study allow us to show that (1) isolated and streamside forest ponds do maintain a distinct assemblage of frogs, (2) isolated ponds are much less common, but (3) are, on average, more predictable in time than streamside ponds.

MATERIALS AND METHODS

Study Site

We conducted the study at RFAD (02° 55'–03° 01'S, 59° 53'–59° 59'W), adjacent to the city of Manaus, Amazonas State, Brazil. The RFAD covers 10,000 ha of terra firme

(nonflooded) rain forest, a well-drained forest not subject to seasonal inundation (Guillemet, 1987). The forest is characterized by a 30–37-m-high closed canopy, with emergents growing to 40–45 m (Ribeiro et al., 1999). The RFAD is included in the Long-term Ecological Research Program (PELD) and the Program for Research in Biodiversity (PPBio) of the Brazilian Ministry of Science and Technology.

The climate is characterized by a rainy season from December to May and a dry season from June to November; the rainiest months are generally March and April, with >300 mm of rain per month (Marques-Filho et al., 1981). Mean annual temperature is approximately 26 °C (Marques-Filho et al., 1981) and mean annual rainfall was 2362 mm (± 400 mm) between 1985 and 2006. Soils are composed by clay latosols on the ridges, becoming sandier as the inclination increases and altitude decreases (Chauvel et al., 1987) until the mineral fraction in the bottomlands is almost pure sand (Costa et al., 2005). The latosols of the RFAD suffer strong seasonal variations, but with small changes in soil water content, due to limited water availability in the soil. Ponds form in flat areas and their hydroperiod depends on soil type and volume of rainfall in the period. Temporary ponds in valley bottoms near streams (<100 m) may retain water for a few days to >6 mo (Pazin et al., 2006; this study), and they can be subject to irregular inundation by the streams during heavy rains (>50 mm). Isolated ponds (>150 m from stream) are formed in the highest part of RFAD and are affected only by rainfall.

The headwaters of most streams are located within the reserve. A central plateau divides the stream systems into eastern and western drainages. However, five smaller basins are found in the RFAD. Two of these basins are in the western drainage (Acará and Bolívia) and three are in the eastern drainage (Tinga, Uberê, and Ipiranga). Currently, the southern edge of the RFAD is in contact with suburbs, but the eastern edge of the RFAD still has connections to continuous forest.

Fifty anuran species have been recorded from the RFAD (Lima et al., 2006). Eleven species occur mainly near the borders and

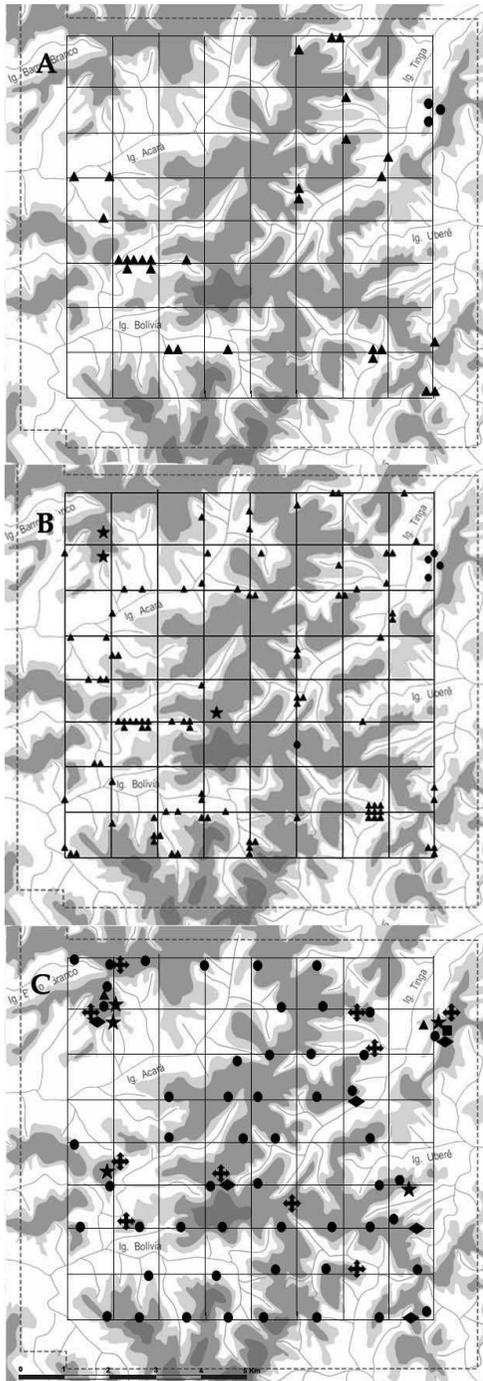


FIG. 1.—Topographical and hydrographic map of the Reserva Florestal Adolpho Ducke (RFAD) with the position of the system of trails. Shading indicates gradients in altitude from the lowest areas (lightest color, >40 m elevation) to the dark areas (darkest shading, >120 m elevation). The limit of the reserve is shown by the dotted

open areas. Of the 39 species that occur deep inside the forest, only 22 species have larval development exclusively in ponds; 4 species develop in streams, 1 in phytotelmata (mainly bromeliads), 1 in tree holes, and 10 species develop independent of water bodies. *Leptodactylus lineatus* vocalizes inside ant nests, but the site of tadpole development is unknown (Lima et al., 2006).

Sampling Design

In RFAD, a system of 18 8-km trails forms a grid covering 64 km² (Fig. 1). We considered isolated ponds to be those >150 m from the stream, and streamside ponds to be those that were <100 m from the stream. These categories were possible because the temporary ponds form in valley bottoms near streams and no ponds were found between 100 m and 150 m from the stream due to presence of slope (base of plateau). We measured the distance from the stream with a 100-m measuring tape. We sampled a 30-m-wide strip (15 m on each side) along the trails, which resulted in a total area of 432 ha.

Tadpole community sampling.—Data on pond availability area were collected from March to May (wet season) in 2003, 2004, and 2005. We collected tadpoles in the streamside ponds between November and May, and in isolated ponds from January to May (period of the formation of these ponds), by sweeping a dip-net through the whole pond area (Gascon, 1991; Shaffer et al., 1994), including the leaf-litter and the bottom substratum, until no specimens were found in a 5–10 min interval. We collected, identified (following Hero, 1990), and returned the tadpoles to the pond. Those unable to be identified in the field were returned to the laboratory for further inspection.

←

line. In parts (A) (2003) and (B) (2005), circles represent isolated ponds, and triangles represent streamside ponds located within 15 m of the trail system. Stars represent isolated ponds found outside the standardized survey. Part (C) shows the distribution of postmetamorphic anurans that reproduce in isolated ponds in the RFAD located during the study. Star = *Phyllomedusa tarsius*; cross = *P. tomopterna*; circle = *Leptodactylus knudseni*; diamond = *L. mystaceus*; square = *Chiasmocleis shudikarensis*; and triangle = *Ceratophrys cornuta*.

Postmetamorphic frogs registered in the trail system throughout the study (wet season) allowed us to map the distribution of frogs that are dependent on isolated ponds. These data were complemented with data on post-metamorphic frogs in 72 plots uniformly distributed across the grid of trails that were collected by M. Menin and that are available in the PPBio data bank (www.ppbio.inpa.gov.br/eng/inventarios/ducke/anuro).

Data Analysis

Only the data for 2005 (year of highest pond occurrence) were used for analysis of species composition. Some ponds were larger than 50 m² and due to the large size the species abundance could not be estimated. Therefore, we used only presence–absence data. We measured pond area by counting squares of a nylon grid (12-cm mesh) extended over the pond. In 2005, we found a larger availability of streamside ponds (98) in relation to isolated ponds (5). Due to the small number of isolated ponds found in the RFAD, we included in the analysis three isolated ponds recorded inside the grid, but outside the sampled strip. Both types of ponds occurred in all five of the RFAD catchments.

The dimensionality of tadpole community composition was reduced by multivariate analyses. Tadpole community structure was represented by Principal Coordinates Analysis (PCoA) axes to meet the linearity and orthogonality assumptions of the multivariate analyses (Anderson and Willis, 2003). Ordinations were based on presence–absence (qualitative) data for species in isolated and streamside ponds. We used the data for the eight isolated ponds and all streamside ponds collected in 2005.

The association matrix used in the PCoA was constructed using the Bray–Curtis distance (Belbin, 1992). We used Multivariate Analysis of variance to test for differences in the species composition of tadpoles between the two pond categories, using the scores of the three axes of the ordination that captured most variation in the data. We used the R program (R Development Core Team, 2007) for PCoA analyses and association matrices, and SYSTAT 8.0 (Wilkinson, 1998) for other analyses.

RESULTS

In 2005, rainfall in January was close to average (267 mm), but rainfall totals in February and March were well above average (424 mm and 437 mm, respectively). In 2003, rainfall in January (50 mm) was typical of dry-season months rather than the wet season, and well below the 21-yr average for this month in Reserva Ducke ($\bar{X} = 268 \pm 83$ mm). February (178 mm) and March (213 mm) were also below the 21-yr averages ($\bar{X} = 285 \pm 99$ mm and $\bar{X} = 318 \pm 83$ mm, respectively). In 2004, rainfall in January (180 mm) and February (211 mm) were below average, but rainfall was above average in March (462 mm).

The number of ponds encountered varied strongly between years, with 32 in 2003, 67 in 2004, and 103 in 2005. Most ponds were <100 m from the stream in each year (29, 63, and 98 respectively). No pond was found between 100 m and 150 m from the stream. Isolated ponds (>150 m from a stream) were rare (3, 4, and 5, respectively) in the sample along trails, but were much larger ($\bar{X} = 133 \pm 59.85$ m²) than streamside ponds ($\bar{X} = 1.75 \pm 0.22$ m²). Only three other natural isolated ponds were encountered outside the standardized surveys, and these were also relatively large ($\bar{X} = 82.3 \pm 41.79$ m²).

Streamside ponds were found throughout the reserve, although the distribution was much more limited in 2003 (Fig. 1A) than in 2005 (Fig. 1B). In contrast, the isolated ponds recorded in the surveys were aggregated within a limited part of the reserve, and their distribution did not expand much between 2003 (Fig. 1A) and 2005 (Fig. 1B). The survey covered only 4.3% of the reserve. Based on the number of ponds and the area of the reserve sampled, we estimate that there were 671 streamside ponds in the reserve in 2003 and 2269 in 2005. In contrast, we estimated that there were only about 69 isolated ponds in 2003 and 115 in 2005.

Ordination based on qualitative data captured 59% of the variation in the dissimilarities among ponds in three axes. The tadpole species composition differed significantly (*Pillai Trace* = 0.6122; $F_{3,77} = 40.520$; $P > 0.0001$) between isolated ponds and streamside ponds. The isolated ponds occupied a distinct region of the multivariate space

representing tadpole composition (Fig. 2). The tadpoles of *Leptodactylus knudseni*, *L. mystaceus*, *Chiasmocleis shudikarensis*, *Ceratophrys cornuta*, *Phyllomedusa tomopterna*, and *P. tarsi* were found only in isolated ponds clumped within a limited part of the reserve, but postmetamorphic individuals of these species were found in many localities throughout the reserve (Fig. 1C). *Leptodactylus rhodomystax*, *L. riveroi*, *Dendrophryniscus minutus*, *Dendropsophus* cf. *brevifrons*, *Hypsiboas cinerascens*, *H. geographicus*, *P. vaillanti*, and *Rhinella proboscidea* were only found in streamside ponds. *Osteocephalus taurinus*, *Allobates* sp., *A. femoralis*, *P. bicolor*, and *C. hudsoni* were found in both types of ponds.

DISCUSSION

This study shows that isolated ponds and streamside ponds are distinct habitats for tadpoles, and that the amphibian communities found in each type of pond are clearly different. Only a few species use both types of ponds, and some isolated-pond species such as *P. tarsi* and *L. knudseni*, were found once in streamside ponds by Hero (1990) in the RFAD and by Gascon (1991) in the Biological Dynamics of Forest Fragment Project, respectively. In this study and in the study of Lima et al. (2006), these species were found reproducing in isolated ponds only, indicating that the encounter of individuals of these species reproducing in streamside ponds may be casual.

Zimmerman and Bierregaard (1986) suggested that the specific habitat requirements for breeding by anurans make them poor indicators of habitat change because their distributions are naturally patchy. That is not true for terrestrially breeding species (Menin et al., 2007), and this study indicates that there is a large segment of the aquatic breeding species for which this theory applies only at a small scale. For fragments greater than a few km², in most of Central Amazonia, there are probably sufficient streamside ponds to provide habitat for most of the frogs that breed in streamside ponds. Riparian habitats are frequently the most impacted by human activities (Williams, 2006), so this assemblage is

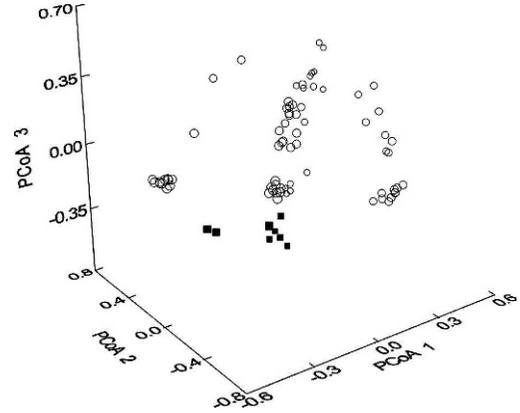


FIG. 2.—Tadpole species composition based on presence-absence data in the Reserva Florestal Adolpho Ducke, summarized by the Principal Coordinate Analysis. The open circle represents streamside ponds and closed squares represent isolated ponds.

probably a useful indicator of riparian habitat degradation.

Breeding habitat for species whose tadpoles are adapted to isolated ponds seems to be relatively rare in the RFAD. However, naturally occurring isolated ponds in the RFAD were relatively larger, making them predictable habitats even in a very dry year and, postmetamorphic individuals of the isolated-pond specialists were found at widespread localities throughout the reserve. Most of these species also colonize artificial pools along roads (Hero et al., 2001) and around the reserve border, as long as forest cover is maintained, so they are frequently the most encountered and most studied species (Lima et al., 2006; Neckel-Oliveira and Gascon, 2006). These are probably poor indicator species because their distributions are naturally patchy, and their densities are likely to increase with human disturbance, such as road construction.

Neckel-Oliveira (2004) showed that some isolated-pond species are good colonizers, some species even crossing open pasture to reach ponds. However, we know little about the relative roles of dispersal and persistence in the maintenance of populations of most Amazonian frogs. This information is going to become more important for conservation as the Amazon forest becomes more fragmented and reserves become smaller.

Both terrestrially breeding frog species (Menin et al., 2007) and species that breed in streamside ponds (in this study) are likely to be useful indicator species of anthropogenic impacts for monitoring most Amazonian protected areas. However, the situations in which species that breed in isolated ponds can be used as indicators of anthropogenic change are much more limited. Therefore, concentrating studies on easily accessible isolated ponds near reserve boundaries is likely to give a biased impression of anthropogenic impacts.

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