BIOTROPICA 33(1): 131–141 2001

Antipredator Defenses Influence the Distribution of Amphibian Prey Species in the Central Amazon Rain Forest[1]

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ABSTRACT

The high diversity of amphibians in the central Amazon Rain Forest allowed us to examine the influence of tadpole antipredator defenses on assemblage structure and composition within bodies of water (α diversity) and among aquatic sites (β diversity) at a local scale. During a three-year study of tadpole assemblage composition, we found that the anuran community used a variety of bodies of water for reproduction; these ranged from streams and streamside ponds to isolated forest ponds. The distribution of several tadpole species was negatively related to fish density, while other species coexisted with high densities of fish. Tadpole size did not ensure survival against fish, and few tadpoles avoided fish by hiding in the leaf litter. Controlled predation experiments using a single tadpole species in a no-choice situation were conducted over 24- to 48-hour periods. Nearly all species of tadpoles that occurred in habitats with high fish densities were unpalatable to fish (except *Centrolenella oyampiensis*), indicating that unpalatability is a major adaptation allowing tadpoles and fish to coexist in this system. Unpalatability (to fish), however, was not an effective antipredator defense against odonate larvae, the other major tadpole predator in this system. The combination of predation pressure and the antipredator traits exhibited by individual species largely determined the composition of tadpole assemblages in individual bodies of water (α diversity). The heterogeneous distribution of predators among bodies water and the diversity of antipredator defenses exhibited by larval amphibians facilitated high diversity in this community (β diversity).

RESUMO

A elevada diversidade de anfíbios na floresta Amazônica central nos permitiu examinar a influência das defesas antipredadores de girinos na estrutura e na composição das comunidades nos corpos d'água (diversidade alfa) e entre corpos d'água (diversidade beta) em uma escala local. Durante um estudo de três anos da composição da comunidade de girinos nós encontramos que a comunidade de anuros usa uma variedade de corpos d'água para a reprodução; estes variaram de córregos e de poças ao lado de córregos a poças isoladas na floresta. A distribuição de várias espécies de girinos estava negativamente relacionada à densidade de peixes enquanto outras espécies coexistiram com elevadas densidades de peixes. O tamanho do girino não assegurou a sobrevivência no encontro com peixes, e poucos girinos evitaram os peixes abrigando-se na camada de folhiço. Experiências controladas de predação utilizando uma única espécie de girino em uma situação sem-escolha foram conduzidas durante períodos de 24–48 horas. Quase todas as espécies de girinos que ocorreram em habitats com elevadas densidades de peixes eram impalatáveis para peixes (exceto *Centrolenella oyampiensis*), indicando que a impalatabilidade é a principal adaptação permitindo a coexixtência de girinos e peixes neste sistema. Entretanto, a impalatabilidade (aos peixes) não foi uma defesa antipredador eficaz contra larvas de odonata, o outro principal predador de girinos neste sistema. A combinação da pressão de predação e das características antipredador exibidos por cada espécie individualmente determinou em grande parte a composição da comunidade de girinos em corpos d'água individuais (diversidade alfa). A distribuição heterogênea dos predadores entre corpos d'água e a diversidade de defesas contra predadores exibidas por larvas de anfíbios facilitou a elevada diversidade nesta comunidade (diversidade beta).

Key words: *assemblage; community; diversity; palatability; predation; survival; tadpoles.*

[1] Received 2 February 1999; revision accepted 10 February 2000.

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Fish play a key role in structuring freshwater assemblages because of their direct role as predators (Calef 1973; Macan 1974; Wilbur 1972, 1984; Zaret 1980; Smith 1983; Woodward 1983; Bradford 1989; Werner & McPeek 1994; Hecnar & M'Closkey 1997; Hero *et al.* 1998). Indirectly, predators can influence other community processes (*e.g.,* competition among prey species) by altering prey behavior and microhabitat use (Morin 1981, 1983, 1986; Sih *et al.* 1985, 1988; Wilbur & Fauth 1990). Furthermore, the presence of aquatic predators and/or competitors can discourage potential prey species (amphibians and insects) from ovipositing in some freshwater systems (Banks & Beebee 1987, Resetarits & Wilbur 1989, McPeek 1990, Magnusson & Hero 1991, Petranka & Fakhoury 1991, Hopey & Petranka 1994, Petranka *et al.* 1994, Holomuzki 1995).

Heyer *et al.* (1975) have suggested that predation by aquatic predators (primarily fish) was the most important biotic factor influencing the temporal and spatial composition of tadpole assemblages. These authors postulated that tadpole size, use of microhabitat refugia, and unpalatability were possible mechanisms allowing tadpoles to survive with fish. Their model has not been tested in a community context.

Prey antipredator defenses influence species distributions. Kats *et al.* (1988) demonstrated that some temperate zone tadpoles, which were found in habitats with fish, were either unpalatable to fish or demonstrated behavioral avoidance of fish. Werner and McPeek (1994) found that two species of tadpole responded differently to a gradient of pond types ranging from permanent ponds with and without fish to temporary ponds without fish. In that study, *Rana catesbeiana* had traits that allowed it to survive with fish, while *R. clamitans* survived better in ponds that had high densities of odonate larvae and salamanders, but no fish. Similarly, Holomuzki (1995) found that *Rana palustris* and *Bufo americanus* use several antipredator defenses that facilitate their local coexistence with predatory fish. The influence of tadpole antipredator defenses on assemblage structure and composition within bodies of water (α diversity) and among bodies of water (β diversity) at a local scale has not been investigated. The high diversity of amphibians in the central Amazon Rain Forest provides the opportunity to test these hypotheses.

Hero *et al.* (1998) found fish density to be correlated with species composition and species richness in assemblages of tadpoles in a central Amazonian Rain Forest. Based on experimental manipulations, Gascon (1992) suggested that predators could modify the composition of tadpole assemblages through differential predation. Aquatic egg predators can also influence the structure of tadpole assemblages in this system (Magnusson & Hero 1991) because their presence can influence the species that oviposit in a given body of water.

We investigated how defenses against fish predators influence tadpole community composition in a central Amazonian Rain Forest. The role of unpalatability as a "fixed avoidance trait" (Sih *et al.* 1985) and the complex interactions between key predators (fish) and tadpole antipredator defenses (size, behavior and palatability) were examined. The influence of these interactions on the structure of tadpole assemblages and community diversity was also considered.

STUDY SITE

The study was carried out at Reserva Florestal Adolfo Ducke (RFAD), a 10,000-ha ecological reserve *ca* 25 km northeast of Manaus, Amazonas, Brazil (3°08′S, 60°01′W; 30–90 m elev.) between August 1984 and November 1987. The vegetation consists of terra firme rain forest, a well drained forest not subject to seasonal inundation. The climate is dominated by distinct wet and dry seasons, most of the rain falling between December and May; the mean annual rainfall for the RFAD between 1965 and 1980 was 2362 mm (Marques-Filho *et al.* 1981).

In central Amazonia, 54 species of frogs have been found in association with rain forest, and 42 of these were recorded in the RFAD during this study (Hero 1990). The frog species have a variety of reproductive modes, of which 32 species are known to have a free-swimming aquatic tadpole stage (Hero 1990). Anuran reproduction was studied intensively at 12 sites: eight streamside ponds (sites A-H), two isolated forest ponds (sites I and J), and two 50-m sections of stream (K and L). For further details of the RFAD study site and anuran community, see Hero (1990), Magnusson and Hero (1991), and Hero *et al.* (1998).

FIELD METHODS

Twelve bodies of water were surveyed at approximately weekly intervals between 12 August 1984 and 5 November 1987. Sampling intensity of each water body ranged from 45 to 128 surveys during the three-year period (bodies of water A–G, 121–128 visits, Aug. 1984–Nov. 1987; bodies of water

H and I, 47 and 45 visits, June 1986–Nov. 1987; water body J, 55 visits, Feb. 1996–Nov. 1987; bodies of water K and L, 48 and 51 visits, Apr. 1986–Nov. 1987). We were interested primarily in testing the associations among species of tadpoles and potential tadpole predators. The presence or absence of fish, odonate naiads, dytiscids, and all other potential tadpole and/or anuran egg predators was determined by visual census during diurnal and nocturnal visits, and by five standardized scoops with a dip net in all microhabitats. During nocturnal visits, visual surveys of the density and abundance of predators were recorded in each pond by mapping the number, estimated size, species, and position of potential egg and/or tadpole predators. The sum of the visually estimated lengths (cm) of all fish observed on each nocturnal visit was used as an index of fish biomass (predation risk), and this index was calculated for each water body.

Water body characteristics.—The proportion of tadpole species in the leaf litter was determined as the number of species encountered that primarily utilize the leaf litter microhabitat (Hero 1990) divided by the total number of species. Maximum tadpole sizes (total length) utilized are described in Hero (1990). The maximum tadpole size in each water body (Table 1) is the size of the largest species of tadpole found to occur in that water body (Hero 1990, Hero *et al.* 1998). The proportion of connections to a stream was calculated as the number of diurnal visits (1–2 weeks apart throughout the study period) that the pool was connected to a stream divided by the total number of visits. Percent dry days is the proportion of visits in which the pond was dry.

Palatability experiments.—The palatability of anuran tadpoles to the most common potential predators in the area was investigated in controlled experiments. Experiments were conducted under no-choice conditions (i.e., between individual predator and prey species) as this resembles the way predators encounter prey in this system (J.-M. Hero, pers. obs.) and because conducting all combinations of choice experiments would have increased the number of experiments necessary by a factor of 242. Azevedo-Ramos and Magnusson (1999) showed that choice experiments give similar results to individual tests in another community of Amazonian tadpoles.

We conducted palatability experiments in the field to minimize differences in temperature and water quality and to reduce transportation effects

TABLE 1. *Summarized data on tadpoles, potential predators, and physical characteristics of each water body over three years. Water body details and variables are described in the methods section (nr = not recorded; na = not applicable). See Hero* et al. *(1998) for details of species encountered in each water body.*

Variable	Water body												
	A	B	C	D	E	F	G	H	I	J	K	L
No. of tadpole species	3	3	4	4	5	4	8	7	3	8	1	3
Tadpole spp. in litter (%)	33	33	50	50	80	75	37.5	28.6	33	37.5	100	33
Max. tadpole size (mm)	55.6	57.0	57.0	57.0	49.5	49.5	57.0	57.0	35.0	69.0	25.3	36.3
Mean fish biomass index	41.6	131	40.7	62.5	9.0	9.7	15.0	25.7	0	0	150	150
Total no. of fish species	6	7	7	8	6	4	7	8	0	0	>8	>8
Visits with naiads (%)	2	2	8	8	5	9	8	5	11	80	nr	nr
Mean no. of dytiscids per visit	0.90	0	0.59	0	6.9	5.3	5.0	1.97	10.2	9	nr	nr
Connections to the stream (%)	4	100	42	68	2	1	1	6	0	0	na	na
Dry days (%)	0	0	0	0	22	23	21	21	40	0	na	na

on predators and prey. Experiments were conducted in colored plastic containers (red, cream, blue, and yellow) and covered by green mesh to stop predators and prey from escaping. Container size varied with the size of the predator tested (see below). Replicates were distributed evenly among colors and were placed in a systematized block (for species of tadpole) design during each experimental period. Although these were not natural background colors, a variety of background colors ensured that differently colored prey did not have a cryptic advantage over other prey.

Individual predators were placed in a container and left without food for 12 hours. Ten tadpoles were then introduced, and the numbers surviving after 24 and 48 hours were recorded. In all experiments, predator and prey sizes were measured using calipers, and tadpoles were preserved. Each predator was used only once. Dead uneaten tadpoles were removed and replaced at 8 to 12 hour intervals (dead uneaten tadpoles were found only in experiments with unpalatable species). To reduce any effects of prey size and to minimize satiation of the predator, the smallest available size of free-swimming tadpoles of each species (all $<$ 30 mm total length, stage 25; Gosner 1960) was used. While palatability generally decreases with tadpole development (Lawler & Hero 1997), the smallest stages are the most vulnerable to fish predators (Brodie & Formanowicz 1987). The mean percentage of tadpoles eaten per individual predator was used as an index of palatability for each species of tadpoles (for each predator species).

The fish *Pyrrhulina* sp. (50–107 mm total length) was used for bioassays of palatability. This species was chosen for palatability experiments because it was common, occurred in both streams and ponds (Hero 1991), and readily ate some species of tadpoles in preliminary experiments. Fish were collected by dipnetting the streams at night and were transported in plastic bags to the campsite where they were immediately placed in the experimental water containers. Experimental containers were 35- $\times$ 25-cm rectangular plastic basins with *ca* 10 cm of water. Nineteen species of tadpole were tested, with *Pyrrhulina* sp. as the predator (277 individual trials; Fig. 2). Experiments were conducted between January 1985 and November 1987, and the number of species and predators used on any one date depended on the availability of predators and prey. At least three trials (per species) were conducted during a single period.

Dragonfly naiads (25–44 mm total length) were caught by dipnetting a series of ponds along an access road within the RFAD. Freshly collected dragonfly naiads (*Gynacantha membranalis*) were placed singly in 22-cm-diameter plastic bowls with *ca* 6 cm of water. Tadpole survival was recorded at 24 hours and the experiment was terminated. Ten species of tadpole were tested in 93 trials (Fig. 2). Preliminary experiments with dytiscid beetles indicated that they did not eat tadpoles and were excluded from further experimentation.

Four tadpole species encountered in bodies of water near the monitored ponds and stream sites were included to improve the power of the analyses, as they were commonly encountered in the area and found in habitats that either had no fish or large numbers of fish. The species and habitats (Hero 1990) were *Bufo granulosus* (stream habitats), *Ololygon rubra, Leptodactylus* cf. *fuscus* (isolated forest ponds adjacent to pond J), and *Osteocephalus* sp. (arboreal bromeliads).

Statistical analyses.—Relationships among predator abundance and water body characteristics were examined with Spearman's rank correlation coefficient (nonparametric test because ordinal data did not satisfy the normality assumption; Zar 1984). In the correlation matrix, probabilities for the paired comparisons were not corrected for the number of comparisons because each examined an independent hypothesis. Relationships among predators, number of species of tadpole, and tadpole palatability were examined with linear regression (parametric test for ordinal data that satisfy the normality assumption, Zar 1984) with the SYSTAT statistical program (Wilkinson 1986). Results for regression analyses are presented as the adjusted squared multiple R (adj. R^2) defined by Wilkinson (1986, p. MGLH-4). As the pond and stream sites contained independent tadpole assemblages (Hero *et al.* 1998), analyses were determined for the pond sites A–I and then repeated to include the stream sites K and L.

RESULTS

Tadpole distributions.—Summaries of tadpole and predator surveys and water body characteristics (Magnusson & Hero 1991, Hero *et al.* 1998) are presented in Table 1. Eighteen species of tadpole were encountered in the 12 bodies of water (Magnusson & Hero 1991, Hero *et al.* 1998). The total number of species in each water body ranged from one to eight (Table 1). Some species of tadpole occurred in 7 of the 12 bodies of water surveyed, but several species were found only in a single wa-

TABLE 2. *Spearman's correlation coefficients for relationships among water body characteristics for ponds A–J (N = 10, two tailed, * = P < 0.05, ** = P < 0.01; probabilities were not corrected for the number of tests).*

	Mean fish biomass index	Total no. of fish species	Visits with naiads (%)	Mean no. of dytiscids	Stream connections (%)
Total no. of fish species	0.745*				
Visits with naiads (%)	−0.712*	−0.539			
Mean no. of dytiscids	−0.982**	−0.792**	0.622		
Stream connections (%)	0.924**	0.804**	−0.708*	−0.942**	
Dry days (%)	−0.644*	−0.381	0.321	0.690*	−0.578

ter body. Species assemblages overlapped among pond sites (A–J), but not with the stream sites K and L (Magnusson & Hero 1991). The percentage of species of tadpole in leaf litter (Table 1) varied greatly among bodies of water (28.6–100%). All water bodies, except site K, contained species in both the leaf litter and water column microhabitats.

Water body characteristics.—Fish predators were found in all bodies of water except ponds I and J (Table 1). The water snake *Helicops angulatus* and the turtle *Platemys platycephala* were occasionally encountered in ponds containing fish and were observed eating both tadpoles and fish during nocturnal observations at those sites. Fish biomass index and the total number of fish species in each water body were positively correlated with connectivity to the stream, and the fish biomass index was negatively correlated with pond drying (Table 2).

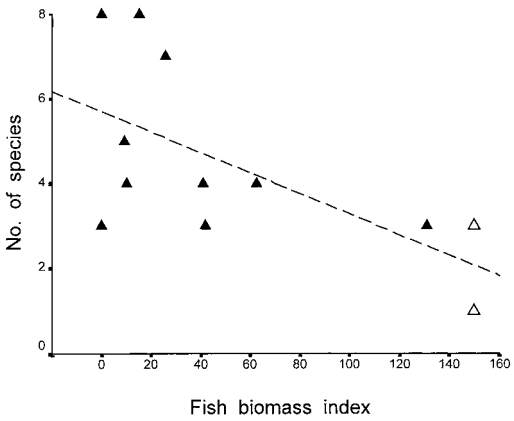

FIGURE 1. Regression of the number of tadpole species against fish biomass index. Closed triangles represent a pond (sites A–J). Open triangles represent the stream sites K and L. The line represents the regression of all bodies of water combined (adj. $R^2 = 0.347$, $P = 0.026$, $N = 12$; $y = 5.69 - 0.024x$).

Odonate naiads and dytiscids were the most common invertebrate predators (Hero *et al.* 1998). Dytiscid beetles and odonate naiads were negatively correlated with fish biomass index and connectivity to the stream (Table 2). Dytiscid beetles were negatively correlated with the total number of fish species and positively correlated with pond drying (Table 2).

Fish predation and the distribution of tadpoles.—Of the 18 species of tadpole found in the water bodies, 14 (77.7%) coexisted with fish. The number of tadpole species in ponds was not significantly related to fish biomass (adj. $R^2 = 0.105$, $P = 0.190$, $N = 10$), although the largest number of species occurred in ponds with low fish biomass. This relationship was significant (adj. $R^2 = 0.347$, $P = 0.026$, $N = 12$) when estimates for the two stream sites were included (Fig. 1). There was no relationship between the number of fish species observed and the number of tadpole species in ponds or all bodies of water combined (adj. $R^2 = 0.122$, $P = 0.893$, $N = 10$; adj. $R^2 = 0.045$, $P = 0.486$, $N = 12$, respectively).

Maximum tadpole sizes (total length) ranged from 14.5 mm for *Chiasmocleis* cf. *ventrimaculata* to 69.0 mm for *Leptodactylus knudseni* (Hero 1990). Within water bodies, the maximum size recorded for the largest species of tadpole that occurred in each water body was not related to the fish biomass index (adj. $R^2 = 0.172$, $P = 0.1$, $N = 12$ water bodies). These results suggest that the size of tadpoles in a particular water body was not influenced by fish predation levels. Furthermore, the maximum size of each species of tadpole was not related to maximum fish biomass index a particular species of tadpole occurred (adj. $R^2 = 0.00$, $P = 0.936$, $N = 12$), suggesting that the size of each tadpole species was not influenced by ambient fish predation levels.

The proportion of tadpole species that used

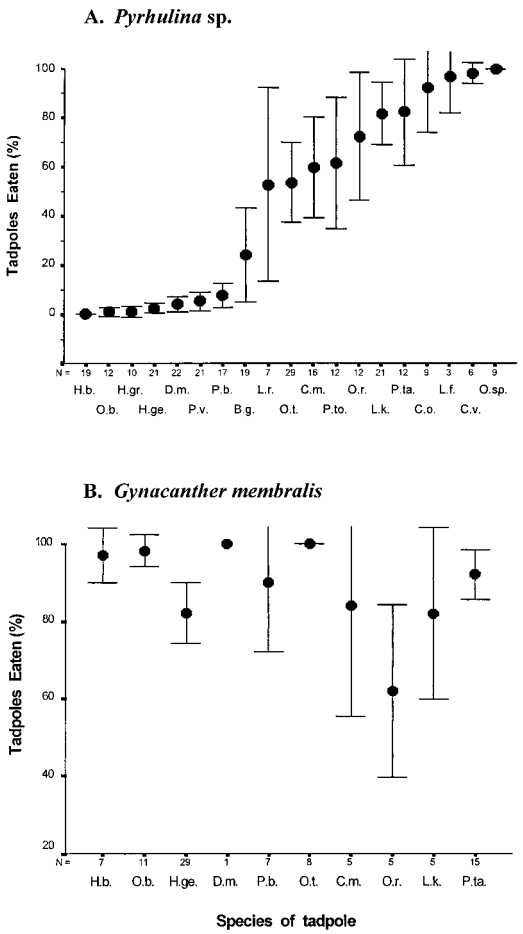

FIGURE 2. Tadpole palatability for the fish *Pyrrhulina* sp., and for the odonate naiad *Gynacantha membranalis.* Points represent the mean number of tadpoles eaten per fish (as a percentage). Bars represent the 95 percent confidence intervals. Species of tadpole: H.b. = *Hyla boans,* O.b. = *Osteocephalus buckleyi,* H.gr. = *Hyla granosa,* H.ge. = *Hyla geographica,* D.m. = *Dendrophryniscus minutus,* P.v. = *Phyllomedusa vaillanti,* P.b. = *Phyllomedusa bicolor,* B.g. = *Bufo granulosus,* L.r. = *Leptodactylus rhodomystax,* O.t. = *Osteocephalus taurinus,* C.m. = *Colostethus marchesianus,* P.to. = *Phyllomedusa tomopterna,* O.r. = *Ololygon rubra,* L.k. = *Leptodactylus knudseni,* P.ta. = *Phyllomedusa tarsius,* C.o. = *Centrolenella oyampiensis,* L.f. = *Leptodactylus* cf *fuscus,* C.v. = *Chiasmocleis* cf. *ventrimaculata,* and O.sp. = *Osteocephalus* species. The number of trials for each species (*N*) are presented on the x-axis.

one of the two broad microhabitats (leaf litter or water column) was independent of fish biomass (adj. R^2 = 0.00; P = 0.632, N = 12), suggesting that hiding in the leaf litter microhabitat was not a major tadpole defense against fish predators in this system. This was not surprising as eight species

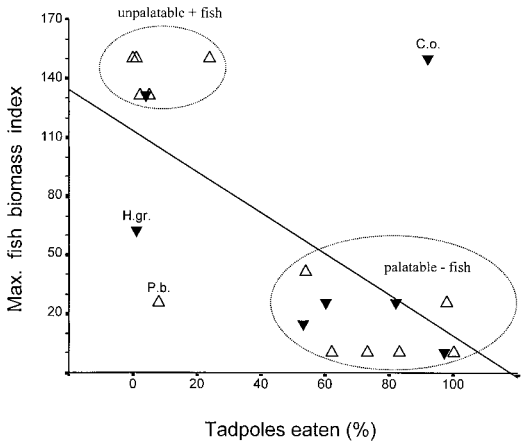

FIGURE 3. Regression of maximum fish biomass index at which a species of tadpole occurs against palatability for the fish *Pyrrhulina* sp. (percent tadpoles eaten); each point represents a different species of tadpole. Open triangles represent species of tadpole that are normally encountered in the open water; closed triangles represent species of tadpole that are normally encountered in the litter. The line represents the regression of all tadpoles combined (N = 19 species; y = 113.49 − 1.048x). Species abbreviations are as for Figure 2.

of tadpole (*B. granulosus, Hyla boans, H. geographica, Phyllomedusa bicolor, P. vaillanti, P. tarsius, P. tomopterna,* and *Osteocephalus taurinus*) often formed conspicuous aggregations that were clearly visible to human observers.

Palatability experiments.—The proportion of tadpoles eaten by fish ranged from <10 to 90 percent eaten (Fig. 2). Tadpoles from three families (Bufonidae, Hylidae and Leptodactylidae) in five genera were unpalatable to *Pyrrhulina* sp. (defined as <30% eaten). Fish seized unpalatable tadpoles but quickly released them, usually unharmed, suggesting that they tasted bad rather than being able to physically avoid fish. Dragonfly naiads ate most of the tadpoles of all species offered except *O. rubra* (Fig. 2).

Palatability and the distribution of tadpoles.—The maximum fish biomass index of sites where a species of tadpole occurred was significantly and negatively correlated with tadpole palatability for *Pyrrhulina* sp. (Fig. 3; adj. R^2 = 0.386, P = 0.003, N = 19 species). This relationship was not significant when considering only those species normally encountered in the leaf litter microhabitat (adj. R^2 = 0.000, P = 0.542, N = 7 species). For those species of tadpole normally occupying the water

column, the relationship was even stronger (adj. $R^2 = 0.643$, $P = 0.001$, $N = 12$). Tadpoles fell into two major groups, species that were unpalatable and coexisted with high fish biomass, and species that were palatable and primarily occurred in bodies of water with low fish biomass indices (Fig. 3). Except for *Centrolenella oyampiensis,* all tadpoles that occurred with high densities of fish were unpalatable to *Pyrrhulina* sp. (upper half of Fig. 3). Most unpalatable species occurred in the open water column, but one unpalatable species was found in the leaf litter; however, two unpalatable species (*Hyla granosa* and *P. bicolor*) were only found in ponds with low fish biomass indices (Fig. 3). There was no obvious relationship between tadpole microhabitat use and palatability for species that occurred in ponds with low fish biomass (lower half of Fig. 3) as five species were normally encountered in the leaf litter and seven species in the open water column.

DISCUSSION

Factors affecting the distribution of tadpoles.—Many species of tadpoles coexisted with fish in the central Amazon, suggesting the weak negative relationship between the number of tadpole species and fish biomass index was not a simple case of fish eliminating species of tadpoles. Fish may eliminate some species of tadpole, while other species are not affected, resulting in shifts in composition of tadpole species (Hecnar & M'Closkey 1997, Hero *et al.* 1998). The weak reduction in species of tadpole may result from alternative explanations such as fish species competitively dominating species of tadpole for food and/or refuges from predators. Alternatively, physical characteristics of the lotic stream such as flood scouring, may also account for the low number of tadpole species observed in that habitat. Unpalatability is an effective defense used by tadpoles to avoid fish predation in this system, but was not effective against odonate predators. This antipredator defense did influence the local distribution of tadpole species in this community. Odonate predators ate tadpoles that were unpalatable to fish, demonstrating that prey defenses that are effective against one predator may not be effective against other predators (Gascon 1992).

It has been suggested that some species of tadpole could avoid gape-limited fish predators when they are large (Pope 1931, Hecnar & M'Closkey 1997). In contrast, Heyer *et al.* (1975) suggested that large size may make tadpoles more susceptible to fish predators. We believe that large tadpole size is not an effective defense against fish for two reasons: (1) tadpole size at hatching for all species is < 25 mm, a size easily eaten by most predatory fish, and (2) there was no significant relationship between tadpole size and fish biomass index. Alternatively, a positive relationship between large tadpole size and their occurrence with fish (Hecnar & M'Closkey 1997) could result indirectly through the relationship between water body permanence (% dry days) and the presence of fish (Table 2). Unpalatable tadpole species in permanent bodies of water with fish can grow to a large size as they are not threatened with desiccation or predation.

Use of microhabitat refugia also has been proposed as an important adaptation of tadpoles to avoid predators (Heyer *et al.* 1975, Sredl & Collins 1992). Kats *et al.* (1988) found that four of five palatable tadpole species demonstrated predator avoidance behavior when exposed to fish chemicals. In the present study, the percentage of tadpole species using the leaf litter microhabitat was not related to fish biomass index, and only *C. oyampiensis* used this defense against fish; this suggests that most species of tadpole in this system do not avoid fish predators by hiding in the leaf litter. Alternatively, microhabitat choice could be a function of many factors such as food choice and/or competition with other species of tadpole for resources (Mitchell 1983, Loschenkohl 1988).

Unpalatability of tadpoles is an important deterrent to some predatory fish (Liem 1961, Bragg 1965, Voris & Bacon 1966, Walters 1975, Kruse & Francis 1977, Cecil & Just 1979, Kruse & Stone 1984, Kats *et al.* 1988, Werner & McPeek 1994). In this study, fish that had not eaten for at least 60 hours consistently rejected some species of tadpoles. Tadpoles produce toxic compounds (Voris & Bacon 1966, Wassersug 1971) and the mouthing and consequent rejection by the fish suggest that the unpalatability of tadpoles in the Amazon community is also the result of distasteful chemicals. In contrast to the results of Kats *et al.* (1988), only one species of tadpole (*C. oyampiensis*) was highly palatable and occurred in bodies of water with high fish densities. The fossorial behavior of *Centrolenella* tadpoles (Villa & Valerio 1982; J.-M. Hero, pers. obs.) probably allows this species to live in an effectively "fish-free" microhabitat deep in the leaf litter. These results suggest that unpalatability is the primary mechanism that allows tadpoles to coexist with fish in this community.

Unpalatability can affect the outcome of choice

tests with dragonfly naiads (Heusser 1970, Brodie & Formanowicz 1987, Werner & McPeek 1994); however, choice experiments can be confounded by tadpole behavior which strongly influences predation by odonate naiads (Azevedo-Ramos *et al.* 1992, Chovanec 1992). In our no-choice experiments, dragonfly naiads ate most of the tadpoles of all species offered, except *O. rubra* (Fig. 2). *Ololygon rubra* is cryptically colored and makes little movement, and thus did not attract the attention of the naiads. This species, in contrast, was highly palatable to fish. Azevedo-Ramos *et al.* (1992) demonstrated that the reduced consumption of *O. rubra* by odonate naiads is probably due to behavior rather than palatability. Furthermore, naiads readily ate *O. rubra* when the tadpoles were induced to swim in front of them (J.-M. Hero, pers. obs.). The results in this study agree with Heyer and Bellin (1973), Heyer *et al.* (1975), and Heyer and Muedking (1976) in demonstrating that tadpoles that are unpalatable to fish are readily accepted by naiads in a no-choice situation. In a no-choice situation, unpalatability is probably not an effective adaptation to avoid odonate naiad predation. Using species of tadpoles that are palatable as well as species that are unpalatable to fish (results in this study), Azevedo-Ramos *et al.* (1992) demonstrated that tadpole survival in the presence of naiads depended on tadpole movement. These results support the contention that behavioral adaptations are probably more important than unpalatability for tadpoles to avoid predation by odonate naiads (Azevedo-Ramos *et al.* 1992; Chovanec 1992; Skelly 1994, 1996; Werner & McPeek 1994).

Three (Bufonidae, Hylidae, and Leptodactylidae) of the five families of anurans with aquatic tadpoles had some species that were unpalatable to fish, suggesting that unpalatability has evolved independently several times among species of tadpoles in the Amazon. This agrees with the results of Kats *et al.* (1988) who found that the genus *Rana* includes species that are palatable, and others that are unpalatable, to sunfish. Tadpoles of the family Bufonidae are well known for their toxicity to predators (Licht 1968, Lawler & Hero 1997); yet in this study, several species of Hylidae (*H. boans* and *O. buckleyi*) were more unpalatable to the fish tested than were bufonids. Unpalatability of tadpoles may be independent of adult toxicity. Of four species of *Phyllomedusa,* all of which probably have adults that are toxic (W. Hodl, pers. comm.), only two had unpalatable tadpoles.

Palatability and tadpole assemblage structure.—Within freshwater communities, predators influence both tadpole species composition and richness (Morin 1983, Wilbur 1984, Werner & McPeek 1994, Hecnar & M'Closkey 1997, Hero *et al.* 1998). Heyer *et al.* (1975) proposed a model based on the assumption that few species of tadpole can survive with fish. Similar to the temperate community examined by Hecnar and M'Closkey (1997), we found that many species of tadpole live with fish; yet, there is a reduction in species numbers in those bodies of water with high fish biomass.

The strong relationship between palatability and the maximum fish abundance at which a species of tadpole occurred in this study indicates that unpalatability is an important antipredator defense that allows tadpoles to survive with predaceous fish. Prey antipredator defenses are an important determinant of species distributions (α diversity) in this system. Tadpoles use a variety of defenses to coexist with vertebrate (primarily fish) and invertebrate predators (Table 3). Subsequently, only tadpoles with the appropriate defenses are expected to survive in a particular water body with specific types of predators.

Antipredator defenses are tuned by evolution to allow prey species to survive with specific predators (*e.g.,* fish), but this process may enhance the potential for predation from alternative predators (*e.g.,* aquatic insects). Many unpalatable species of tadpole form conspicuous aggregations and/or are brightly colored, and this may function aposematically to fish that can learn to avoid these species (Waldman & Adler 1979, Kruse & Stone 1984). Bodies of water without fish often contain large numbers of odonate naiads, another efficient tadpole predator (Gascon 1992, Werner & McPeek 1994, Hero *et al.* 1998). Considering that odonate naiads can eliminate tadpoles from some habitats (Smith 1983) and that unpalatability is not an effective deterrent to naiad predators in this system (Fig. 2), we suggest that the distribution of some unpalatable species of tadpole could be restricted to bodies of water with fish, due to predation by odonate naiads. This may be because conspicuousness and aggregating behavior by many unpalatable species would enhance the probability of their being preyed upon by odonate naiads (Pritchard 1965, Caldwell 1982, Skelly & Werner 1990, Azevedo-Ramos *et al.* 1992, Chovanec 1992). Similarly, the distribution of two species of *Rana* across a similar habitat gradient (Werner & McPeek 1994) was attributed to both the direct effects of

TABLE 3. *Antipredator defenses of tadpoles associated with invertebrate and vertebrate predators (Heyer* et al. *1975, Caldwell 1982, Travis* et al. *1985, Kats* et al. *1988, Lawler 1989, Resetarits & Wilbur 1989, Richards & Bull 1990, Wilbur & Fauth 1990, Magnusson & Hero 1991, Azevedo-Ramos* et al. *1992, Chovanec 1992, Hopey & Petranka 1994, Werner & McPeek 1994, Anholt & Werner 1995, this study). The symbols: (+) represents a predicted increase in tadpole survival; (−) represents a predicted decrease in tadpole survival; (±) represents a predicted increase in tadpole survival dependent on predator size; and (0) represents no effect predicted.*

Tadpole antipredator defenses		Against invertebrate predators	Against vertebrate predators
Spatial avoidance	Water body selection	+	+
Temporal avoidance	Phenology	+	+
	Diurnal/nocturnal activity	+	+
Behavioral avoidance	Microhabitat selection	+	+
	Reduced movement	+	0
	Active movement	−	+
	Sprint escape	+	0
Physiological avoidance	Rapid growth	+	±
	Unpalatability/noxiousness	±	+
Morphological avoidance	Large size	+	±
	Aposematic coloration	−	+ (with unpalatability)
	Cryptic/disruptive color pattern	+	+
	Deflective color pattern	+	−

predation and the indirect effects of fish preying on other tadpole predators (insects and salamanders). These two species had differing defenses (unpalatability to fish and behavioral responses that allowed them to coexist with odonate predators).

The use of a particular water body by amphibians for reproduction results from a combination of species-specific characteristics. The adult male will vocalize at a water body to attract female mates; the female (rarely the male) will choose the oviposition site (Resetarits & Wilbur 1989, Petranka *et al.* 1994); embryos must survive to swimming larval stage (Magnusson & Hero 1991); and finally, larvae must have the antipredator defenses that facilitate survival to metamorphosis (frequency of tadpole occurrence was used as an index of success to metamorphosis in this study; Hero *et al.* 1998). Our data suggest that tadpole antipredator defenses are essential for successful reproduction in a particular water body. The combination of suitable adult behavior that minimizes predation on eggs (Magnusson & Hero 1991, Petranka *et al.* 1994) and tadpole defenses (Kats *et al.* 1988, this study), is an important determinant of the distribution of tadpole species among bodies of water in this and other systems.

The distribution of tadpole species results from complex interactions between prey defenses and predator distributions. Predator levels may influence composition of tadpole assemblages within bodies of water (α diversity) as only species of tadpole with the appropriate antipredator defenses persist. Unpalatability is not effective against all predators; thus the heterogeneous distribution of fish and insect predators among bodies of water creates a mosaic of habitats available to anuran larvae, which increases prey species diversity at the community level (β diversity). This predator-induced α and β diversity results in a complex and diverse anuran community.

ACKNOWLEDGMENTS

This research was partially funded by grant no. 301299-86/ZO from the Brazilian Conselho Nacional de Desenvolvimento Cientifico e Tecnologico to W. Magnusson. Logistic support was provided by I.N.P.A. Brasil through Maria de Nazare Goes Ribeiro and Angelo Augusto dos Santos and by Jane Hughes at Griffith University, Australia, and would not have been possible without the warm support provided by the Brazilian people. We also wish to thank the secretarial staff of the Department of Ecology, Hygia Thein, Maria Ribeiro, and Sandra Revoredo. Our drivers, Lourival dos Santos, Agousto Ribeiro, Joao Rodrigues, and Jose Souza, generously drove us to and from the study site, both within and often out of normal work hours. We thank Renato Cintra, Ceinwen Edwards, Ulisses Galatti, Neusa Hamada, Leo Joseph, Albertina Lima, Tania Sanaiotti, Roselis Souza, Jill Windle, and all the people who helped in the fieldwork. Many people assisted by criticizing drafts of this manuscript, in particular C. Abercrombie, A. Arthington, P. Becker, B. Congdon, J. Endler, P. Fairweather, S. Fickling, B. Fors-

berg, D. Jones, B. Pusey, W. J. Resetarits, R. Retallick, F. Robertson, M. Wong, C. Gascon, C. Guyer, and several anonymous reviewers who are thanked for their helpful comments.

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