Effects of Forest Disturbance on Breeding Habitat Availability for Two Species of Anurans in the Amazon

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Deforestation may cause substantial changes in community structure along freshwater habitat gradients. This study evaluated how biotic and abiotic factors affect the distribution and reproductive success of two frog species in Central Amazon. Ponds in continuous and disturbed forest were surveyed to determine the distribution of their associated aquatic predators and the production of newly metamorphosed frogs. The effect of each predator assemblage on tadpole survival was tested using mesocosms. Newly metamorphosed *Osteocephalus taurinus* occurred in short hydroperiod ponds in disturbed forest, where they had lower encounter frequencies with aquatic insects and no fish were detected. In contrast, newly metamorphosed *Phyllomedusa tarsius* were associated with longer hydroperiod ponds in continuous forest where fish and aquatic insects were prevalent. In the experimental study, *O. taurinus* tadpoles had lower survival rates than *P. tarsius* tadpoles, suggesting that *O. taurinus* is more vulnerable to fish and insect predators. These results are consistent with the pattern of metamorphic success along the hydroperiod gradient in the study area. If intact continuous forest continues to be harvested, species that require ponds with longer hydroperiods for successful metamorphosis would be prone to population declines.

FOREST removal around basins of ephemeral water bodies can affect light levels and primary productivity, which can affect community structure across freshwater habitat gradients (Werner and McPeek, 1994; Wellborn et al., 1996; Halverson et al., 2003). Increase in direct sunlight on the surface of water bodies may cause greater daily variation in water temperature and raise evaporation rates, which in turn could decrease hydroperiod. If length of time available for larval development of tadpoles decrease, richness of anuran species reproducing in the pond would also decrease (Snodgrass et al., 2000; Paton and Crouch, 2002). Then, habitat availability for potential aquatic invertebrates and fish predators, thus lowering predation risks (Semlitsch and Reyer, 1992).

In Central Amazon, experimental and field studies are limited to pond-breeding anuran species in undisturbed forests (Gascon, 1991, 1992a; Magnusson and Hero, 1991; Hero et al., 2001). Tropical anuran species breed along a pond gradient from temporary to permanent. Some tadpole species occur in temporary ponds where invertebrate predators prevail, while others occur in permanent ponds with both invertebrate and fish predators (Gascon, 1991; Hero et al., 1998). Experimental studies suggest that such differences in habitat use reflect interspecific differences in prey susceptibility to predators (Gascon, 1995; Azevedo-Ramos and Magnusson, 1999; Hero et al., 2001). Nevertheless, no study has evaluated the effects of deforestation on breeding habitat availability

for anurans and assessed the mechanisms that lead to such changes.

In this study, I used field surveys conducted over almost three years to evaluate how forest removal affects the distribution and reproductive success of two of the most common frog species, *Phyllomedusa tarsius* and *Osteocephalus taurinus*, in Central Amazon. I also experimentally assessed the effect of aquatic invertebrate and fish predator assemblages on the survival of *O. taurinus* and *P. tarsius* tadpoles. These results help to understand how landscape changes may affect pond suitability to anuran species in Central Amazon.

MATERIALS AND METHODS

Study site and focal species.—This study was carried out in the Esteio Ranch, a subunit of the Biological Dynamics of Forest Fragments Project (BDFFP) study area. Esteio is located 80 km north of Manaus, Amazonas State, Brazil. This ranch has two main habitats: disturbed and continuous terra-firme forests (Bierregaard and Gascon, 2001). The climate is characterized by distinct dry and rainy seasons. The dry season normally lasts from May to November, while the rainy season occurs from December to April. Annual precipitation varies between 190–230 cm, with a yearly average temperature of 26 C (maximum 35–39 C, minimum 19–21 C; Bierregaard et al., 2001).

The disturbed forest area was covered by primary forest until the mid- to late-1970s, when

government incentives for cattle ranching resulted in large tracts of forest being cleared for pasture (Bierregaard and Gascon, 2001). The study area includes a mosaic of abandoned pasture and secondary forest, which was intensively used by cattle; thus, regeneration is slow and mostly dominated by species of *Cecropia* or *Vismia* (Williamson et al., 1998). Within the disturbed forest study-area boundaries there are 29 ponds ranging from 6–6200 m² in area and 0.3–2.0 m in depth (Neckel-Oliveira and Gascon, 2006). All ponds located in pasture or secondary forest received direct sunlight on the surface, and the surrounding habitat was dominated by grasses (*Pannisetum* sp.).

The continuous forest has a dense canopy cover of large trees 30–37 m in height, with some emergent trees as tall as 55 m. The understory is dominated by several palm species (Rankin-de-Merona et al., 1992). There are 51 ponds in the continuous forest, ranging from 2–30 m² in area and 0.3–1.0 m in depth (Neckel-Oliveira and Gascon, 2006). The bottom of these ponds contains a thick layer of leaf litter.

In both habitats more than 40 anuran species use these ponds as breeding sites (Tocher, 1998; Tocher et al., 2001). Some species use only the ponds in disturbed areas (e.g., *Bufo granulosus*), some use only those in the continuous forest (e.g., *Ceratophrys cornuta*), and some use both (*Phyllomedusa tomopterna*). To determine the distribution, abundance, and quality of potential breeding habitat for anuran species, I focused research on two common species in the study area: *Phyllomedusa tarsius* and *Osteocephalus taurinus* (Hylidae). Both species reproduce in continuous forest ponds and were also found in nearby disturbed forest ponds. *Phyllomedusa tarsius* lays eggs in arboreal leaf nests above ponds in continuous forest and on grasses in disturbed forest ponds (Neckel-Oliveira, 2004). The eggs hatch in about nine days (Neckel-Oliveira and Wachlevski, 2004), and tadpoles require a minimum of 60 d to complete metamorphosis (pers. obs.). In contrast, *O. taurinus* deposits eggs on the surface of ponds in continuous and disturbed forest. The eggs hatch within 48 h and their tadpoles can complete metamorphosis in 30 d (Gascon, 1989).

Breeding habitat availability.—At the beginning of the rainy season in 1999, I surveyed breeding ponds in disturbed and continuous forests used for reproduction by either species based on the presence of calling males, tadpoles, or occasionally by the presence of egg clutches. I also used spatially explicit survey results from previous studies by Zimmerman (1982), Zimmerman and Rodrigues (1990), Gascon (1991), and Zimmerman and Simberloff (1996) in the same study area. I identified 29 ponds in disturbed forest and 51 ponds in continuous forest.

I characterized each pond with respect to hydroperiod and area. The hydroperiod was determined through monthly visits from March 1999 until July 2001 and was defined as the number of months in which each pond had water. The area of the ponds was estimated during the rainy season (April and May) based on measurements of length and width and assuming that ponds were elliptical in shape. I used Mann-Whitney U-tests to assess whether pond area and hydroperiod differed between areas with continuous and disturbed forest. Also, within each habitat, I tested whether pond area was related to pond hydroperiod using linear regression analysis.

Predation encounters.—Every three months from March 1999 to July 2001, I conducted dip-net surveys of all ponds within a two-week period. Dip-net samples per pond varied according to pond area (between 5 and 20 person minutes, depending on surface area). I used the presence of aquatic invertebrate and fish predators and newly metamorphosed *O. taurinus* and *P. tarsius* to calculate the encounter frequency for each pond. Encounter frequency was calculated as the number of visits during which an anuran species or predator was found in a pond, divided by the total number of visits to that pond (Magnusson and Hero, 1991; Hero et al., 2001). Encounter frequencies apply only to periods when ponds contained water. Since I was particularly interested in estimating the larval success to metamorphosis of both species, I focused on documenting metamorphosing tadpoles with front limbs (development stages > 42; Gosner, 1960). Tadpoles at this stage are no longer feeding in the aquatic habitat and thus are less likely to be preyed upon. Encounter frequency was used to estimate a pond's capacity to maintain local populations of *O. taurinus* and *P. tarsius*. Fishes were identified to genus, and aquatic invertebrate predators were identified to family. I used linear regressions to assess the relationship between encounter frequencies of anuran species with pond hydroperiods, and multiple linear regressions to assess the relationship between encounter frequencies of anuran species with encounter frequencies of each predator type. I used the partial regression coefficients to assess the significance of the relationship. To meet model assumptions, the encounter frequencies of anurans were arcsine square-root transformed to achieve a normal distribution (Zar, 1999).

Experimental study.—To determine whether habitat use by anurans reflected interspecific differences in susceptibility to predator assemblages, I performed two experiments during the rainy season of 2001 to measure survivorship of each species in the presence of different predator assemblages. I used tadpoles of *O. taurinus* and *P. tarsius* as prey, while the predators were a fish species (*Rivulus* sp.), aquatic bugs (Belostomatidae), and dragonfly larvae (naiads in the families Aeshnidae and Libellulidae). Experiments were conducted in a cleared forest site. Densities of predators and prey were manipulated, while maintaining the proportion of predators and prey, and holding other variables constant.

For the *O. taurinus* experiment, total length (mean ± SD) varied as follows: *Rivulus* sp.: 40.98 ± 5.52 to 42.94 ± 9.29 mm, belostomatids: 65.56 ± 4.87 to 67.96 ± 3.23 mm, libellulids: 17.06 ± 2.56 to 18.18 ± 1.59 mm, and aeshnids: 22.22 ± 6.32 to 24.68 ± 6.09 mm. For the *P. tarsius* experiment, corresponding values were: *Rivulus* sp.: 36.76 ± 6.36 to 38.90 ± 7.63 mm, belostomatids: 56.12 ± 8.11 to 61.38 ± 4.21 mm, libellulids: 10.70 ± 1.41 to 11.62 ± 1.35 mm, and aeshnids: 13.64 ± 3.71 to 15.76 ± 5.76 mm. I used different relative abundances of tadpoles to approximate natural variation in clutch size and observed tadpole densities in the field (Gascon, 1991). *Osteocephalus taurinus* clutch size averaged 2341 eggs (range of 1794–3154; Gascon, 1995). *Phyllomedusa tarsius* clutch size averaged 341 eggs (range of 238–486; Neckel-Oliveira and Wachlevski, 2004).

Five clutches of *O. taurinus* were collected in natural field sites and placed in holding basins until the eggs hatched (= stage 25; Gosner, 1960). Five clutches of *P. tarsius* were suspended over another basin, into which the hatchlings fell. I pooled tadpoles from several clutches of each species to eliminate potentially confounding genetic effects; the appropriate number of tadpoles of each species was taken from this mixed source. Fish and invertebrate predators were captured at ponds throughout the study area, sorted, and measured (total length) before each experiment.

Plastic basins measured 45 cm in diameter and 25 cm in depth, which was similar in size to past mesocosms experiments (Gascon, 1992a, 1992b, 1995). Basins had approximately 32 liters of stream water and 5 cm dry leaf litter to mimic structural complexity. Basins were aged for 3–4 d before introducing the appropriate predator-prey combination. I covered all basins with a fine nylon mesh. At the end of the experiments, I emptied the basins and counted surviving tadpoles and predators of each species.

Each species was tested separately, using the same combination of predator (treatments) and the same control (no predators). Predator combinations were similar to those observed in each habitat type: 1) disturbed forest assemblage: one Aeshnidae + one Libellulidae + one Belostomatidae; 2) continuous forest assemblage: one Aeshnidae + one Libellulidae + one *Rivulus* sp. I placed 200 *O. taurinus* tadpoles plus each predator combination in each treatment, and 200 *O. taurinus* without predators in the control. Similarly, I placed 50 *P. tarsius* plus each predator combination in each treatment, and 50 *P. tarsius* without predators in the control. I replicated each treatment and the control five times, with each experiment trail conducted for 15 d.

I used analysis of variance (ANOVA) to test the effects of the treatments on the percentage of tadpoles that survived. When ANOVA was significant, Tukey's multiple comparisons were used for pairwise comparisons. I conducted separate analyses for *O. taurinus* and *P. tarsius*.

RESULTS

Continuous forest ponds were significantly smaller (median = 6.1 m^2, range = 1.4–29.4 m^2) than disturbed forest ponds (median = 29.7 m^2, range = 0.6–6748.3 m^2; $U = 373.50$, $n = 80$, $P < 0.01$). Nevertheless, the hydroperiod in the continuous forest ponds was longer (median = 25 mo, range = 6–28 mo) than in the disturbed forest ponds (median = 15 mo, range = 5–25 mo; $U = 1124$, $n = 80$, $P < 0.01$). Pond area was positively related with the hydroperiod within both continuous forest ($r^2 = 0.36$, $P = 0.01$) and disturbed forest ($r^2 = 0.53$, $P < 0.01$).

Newly metamorphosed *Osteocephalus taurinus* were encountered in 55% of the 29 ponds in disturbed forest, whereas newly metamorphosed *P. tarsius* were found in the 72% of the 51 ponds in continuous forest (Fig. 1). The occurrence of newly metamorphosed *O. taurinus* was inversely related to pond hydroperiod ($r^2 = -0.64$, $P < 0.01$), whereas the occurrence of newly metamorphosed *P. tarsius* was positively related to pond hydroperiod ($r^2 = 0.25$, $P = 0.02$; Fig. 2).

Predator encounter frequencies were significantly related to *O. taurinus* encounter frequencies in both continuous forest ($R^2 = 0.22$, $F_{4,46} = 3.25$, $P = 0.02$) and disturbed forest ($R^2 = 0.64$, $F_{3,25} = 15.29$, $P < 0.01$), and also for both pooled habitat types ($R^2 = 0.38$, $F_{4,75} = 11.55$, $P < 0.01$). The partial regression coefficients for both habitats indicated a significant negative relationship ($P < 0.05$) between *O. taurinus* and both belostomatids and *Rivulus*; in contrast, the re-
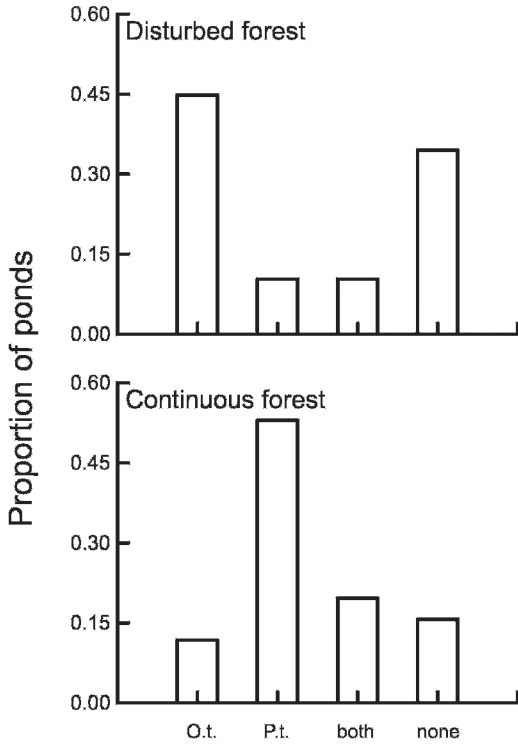
Fig. 1. Proportion of newly metamorphosed occurrences in disturbed and continuous forest ponds; O.t. = *O. taurinus*, P.t. = *P. tarsius*, both = *O. taurinus* and *P. tarsius* together, none = frogs absent.
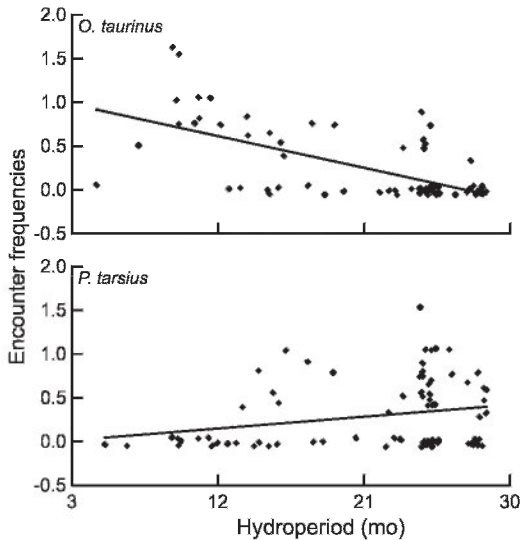

Fig. 2. The effect of hydroperiod on encounter frequency of newly metamorphosed *Osteocephalus taurinus* and *Phyllomedusa tarsius* in 80 ponds in disturbed and continuous forests in Central Amazon. The values on y-axis are the encounter frequency transformed to arcsine square root.

lationship with libellulids was positive (Table 1). Positive relationships indicated that predators and prey co-occurred in the same ponds, while negative relationships indicated differential pond use by predators and prey. There was no relationship between predator encounter frequencies and *P. tarsius* encounter frequencies in either continuous forest ($r^2 = 0.02$, $F_{4,46} = 0.30$, $P = 0.88$), disturbed forest ($r^2 = 0.19$, $F_{3,25} = 2.05$, $P = 0.13$), or both habitats combined ($r^2 = 0.08$, $F_{4,75} = 1.77$, $P = 0.14$; Table 1).

Survival of *O. taurinus* and *P. tarsius* tadpoles differed among experimental treatments ($F_{2,12} = 91.38$, $P < 0.01$; $F_{2,11} = 48.01$, $P < 0.01$, respectively). Both tadpole species were more likely to survive in control than in disturbed forest assemblage treatments (Tukey's test, $P < 0.05$; Fig. 3). Continuous forest assemblage treatments decreased survival rates of *O. taurinus* tadpoles (Tukey's test, $P < 0.05$), but it did not significantly affect the survival of *P. tarsius* tadpoles (Fig. 3).

DISCUSSION

Forest removal and current landscape structure are key determinants of aquatic habitat characteristics in the BDFFP study site (Tocher et al., 2001). In disturbed forest, ponds had short hydroperiods and were dominated by aquatic predatory insects, such as odonate naiads and belostomatids, whereas continuous forest ponds had longer hydroperiods and predator community structure was dominated by predatory insects and a fish species. Regardless of where ponds were located (forest or disturbed areas), the newly metamorphosed *O. taurinus* were associated with short hydroperiod ponds. These ponds had lower encounter frequencies of predatory insects and no *Rivulus* (a fish predator), whereas newly metamorphosed *P. tarsius* were associated with those ponds with longer hydroperiod that had *Rivulus* and aquatic insects. When tadpoles of these species were exposed to two different predator assemblages, *O. taurinus* tadpoles were vulnerable in both assemblages, whereas *P. tarsius* tadpoles were only vulnerable to assemblages dominated by aquatic invertebrates. The different susceptibilities to predators reflects the pattern of metamorphic success along the hydroperiod gradient in the study area (Hero et al., 2001). Similar results were found for *Ambystoma talpoideum* and *A. maculatum* (Caudata; Semlitsch, 1988) and *Rana clamitans* and *R. catesbeiana* (Anura; Werner and McPeek, 1994). For example, tadpoles of *R. catesbeiana* were found in permanent ponds that typically contain fish, whereas *R. clamitans* were distributed along

TABLE 1.   RESUME OF PARTIAL REGRESSION COEFFICIENTS TO ENCOUNTER FREQUENCY OF NEWLY METAMORPHOSED WITH THE ENCOUNTER FREQUENCIES OF PREDATOR TYPES IN 80 PONDS IN THE DISTURBED AND CONTINUOUS FORESTS (OVERALL REGRESSION TO *O. taurinus*: $r^2 = 0.38$, $F_{4,75} = 11.55$, $P < 0.01$, AND *P. tarsius*: $r^2 = 0.08$, $F_{4,75} = 1.77$, $P = 0.14$).

Effect	O. taurinus		P. tarsius	
	Coefficient ± SE	P	Coefficient ± SE	P
Constant	0.10 ± 0.13	0.46	0.21 ± 0.16	0.20
Aeshnid	−0.05 ± 0.13	0.71	0.30 ± 0.16	0.06
Libellulid	0.58 ± 0.15	**0.01**	−0.10 ± 0.18	0.58
Belostomatid	−0.55 ± 0.12	**0.01**	−0.21 ± 0.14	0.14
Rivulus sp.	−0.44 ± 0.13	**0.01**	0.22 ± 0.15	0.15

the hydroperiod gradient and were most successful in ponds where *R. catesbeiana* were absent. In a laboratory study, *R. catesbeiana* were more vulnerable to odonates than *R. clamitans*; *R. clamitans*, on the other hand, were more vulnerable to fish than *R. catesbeiana* (Werner and McPeek, 1994). Some tadpole species that co-occur with fish normally produce unpalatable
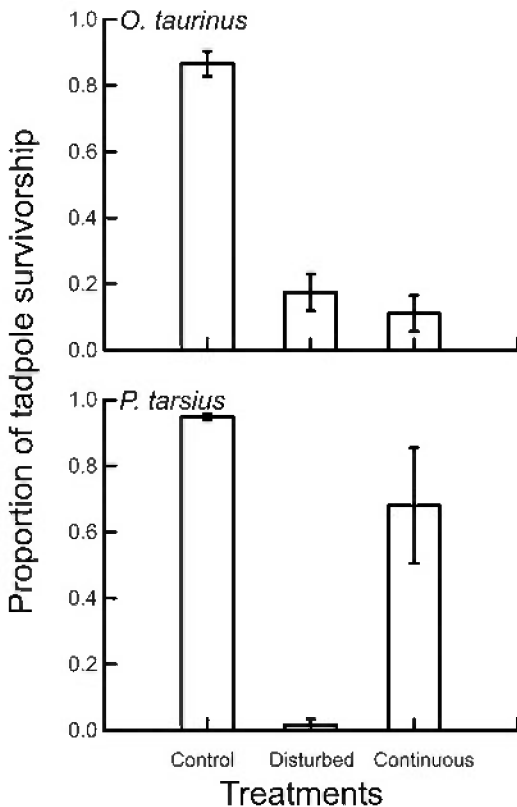

Fig. 3. Survival of *Osteocephalus taurinus* and *Phyllomedusa tarsius* tadpoles in the control (without predators), disturbed (with belostomatids and odonate naiads), and continuous forest (*Rivulus* sp. and odonate naiads) assemblage treatments over 15 d.

substances or accelerate their development when in the presence of predators (Petranka et al., 1987; Kats et al., 1988; Stauffer and Semlitsch, 1993), while those that co-occur with invertebrate predators adopt strategies such as reducing activity or producing large clutches to satiate their predators (Sih et al., 1985; Wilbur, 1987; Van Buskirk, 1988).

Habitat uncertainty and predation are key factors that affect the population biology of tadpoles (Smith, 1983; Werner and Glennemeier, 1999; Halverson et al., 2003). Frog species can be arranged by larval habitat hydroperiod, and different species may adapt their growth patterns to varying levels of uncertainty in pond duration (Heyer et al., 1975). Despite these adaptations when ponds dry prematurely, mortality is often catastrophic (Semlitsch and Reyer, 1992; Griffiths, 1997; Lardner, 1998). If a pond is likely to dry, natural selection will favor those species that develop faster. Anuran species that have longer larval period (e.g., *P. tarsius*) are likely to suffer more from desiccation in disturbed forest ponds than those anuran species that have shorter larval period (e.g., *O. taurinus*), which synchronize their reproduction with the hydroperiod of the ponds. Nevertheless, in areas where a gradient of hydroperiods exists, as in my study area, both species may be able to maintain long-term population viability.

When tropical forests are altered from their natural condition to a mosaic of disturbed forest areas, the dynamics of pond habitats will also change and so will the community of aquatic predators that inhabit them (Zimmerman and Simberloff, 1996). If intact continuous forest disappears, amphibian species may be forced to use breeding habitats in disturbed areas, where they will encounter ponds with different physical attributes (e.g., temperature and hydroperiod) as well as different predator communities. This combination of environmental and biological changes may be too stressful for some frog species such as *Phyllomedusa bicolor, Phrynohyas coriacea, Ceratophrys cornuta, Leptodactylus riveroi,*

Ctenophryne geayi, and *Colostethus marchesianus* (Tocher, 1998), and this may help explain why these species show strong affinities to primary forest. In contrast, amphibian species that exploit disturbed habitats must be able to cope with drastically altered habitats for breeding. In the study area, species like *Hyla minuta, H. brevifrons, H. leucophyllata, Scinax rubra, Bufo granulosus,* and *Leptodactylus mystaceus* have high population abundances, and they may be able to maintain long-term population in the disturbed forest areas.

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