

Community Composition and Breeding Success of Amazonian Frogs in Continuous Forest and Matrix Habitat Aquatic Sites

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The main consequences of habitat fragmentation include the obvious loss of native habitat (Dodd 1990; Laurance and Bierregaard 1997a) and edge effects (Andrén and Angelstam 1988; Kapos 1989; Bierregaard et al. 1992; Gascon and Lovejoy 1998; but see Santos and Tellería 1992, Gascon 1993). The amphibian fauna of the BDFFP is well known, having been studied almost since the project's inception (Zimmerman and Rodrigues 1990; Gascon 1991; Tocher 1996), and constitutes a good base for determining how some of these species respond to changes in their habitat.

Much of the BDFFP study area, 80 km north of Manaus, was composed of continuous rainforest until the mid- to late 1970s, when government incentives for cattle ranching resulted in large tracts of forest being cleared for pasture. The net result has been the loss of forested habitat and the appearance in its place of pasture and second-growth forests, which form the "matrix" habitat surrounding the BDFFP forest fragments, in a region where there had been none, at least in recent history (Chapters 1 and 4). Over the years a series of farmlands has appeared along the main highway north of Manaus, linking the matrix habitat of the BDFFP to those much older, degraded tracts

of land around the city to the south. These patches of matrix habitat can impede movement or dispersal of species from continuous forest (Lovejoy, Bierregaard, et al. 1986; Bierregaard et al. 1992), or can serve as corridors for open-area habitat species to move into areas not yet occupied.

Although the landscape has been drastically altered from continuous forest to pasture, many aquatic habitats remain in the man-altered landscape. In this sense it may also be possible for certain continuous-forest species that depend on aquatic habitats for reproduction to use this "new" habitat successfully if they are not physiologically or ecologically restricted to continuous-forest habitat. The degree to which populations of certain species can establish themselves in matrix habitat will influence the dynamics of populations in forest remnants within the same matrix habitat.

Existing studies in the Manaus area have mainly dealt with organisms that rely on the terrestrial component of the forest for all aspects of their life history (summarized in Bierregaard et al. 1992, and more recently in chapters in Laurance and Bierregaard 1997a and Gascon and Lovejoy 1998). Virtually no data exist on how amphibians respond to changes in their habitat (but see Gascon

1993; Tocher, Gascon, and Zimmerman 1997). Many amphibian species rely heavily on aquatic habitats for reproduction (Zimmerman and Bierregaard 1986), and some species will use available sites independent of their location in continuous-forest or matrix habitat (Gascon 1993). To understand how landscape changes in the Manaus area affect the distribution of amphibian species we surveyed different matrix habitat types and continuous-forest areas to determine amphibian species composition. We tested the ability of pool breeders to permeate the matrix habitat by comparing species composition at pools in three matrix types to continuous forest. Also, we used *Phyllomedusa tarsius* as a focal species to look at population size, movement patterns, and recapture rates in both matrix and continuous forest. Finally, we measured larval survival in matrix and continuous-forest pools to give a further indication of habitat quality.

Methods

COMMUNITY COMPOSITION IN DIFFERENT HABITAT TYPES

Study site and habitat types. The BDFFP complex is situated on three ranches: Porto Alegre, Dimona, and Esteio (see Chapter 4 for a description of the primary forest and the BDFFP). Four habitat types were surveyed—continuous forest and three different types of open-area habitat (nonprimary forest) that represent a gradient of human disturbance (areas that were cleared of the original continuous forest, used for pasture at varying intensities and durations, and are covered today by different vegetation types). The three open-area habitats were maintained pasture, second-growth forest that had been both cut and burned, and second-growth forest that had been cut but not burned (see Chapters 24 and 25).

Transects (trails surveyed by the techniques outlined below) within each open-area habitat covered on average 150 ha. Transects in continuous forest covered approximately 3,000 ha and were studied in 1983–89 (Gascon 1990; Zimmerman 1991). Additional transects in continuous forest (c. 500 ha) were performed by the senior author during 1992–94.

Maintained pasture occurred primarily on the Esteio ranch with one additional transect on Porto Alegre (see fig. 4.1 and table 4.3). Maintained pasture consisted of extensive clear-cut areas, usually grazed by cattle and Asian water buffalo, that had been subjected to repeated cutting and burning over a ten- to fifteen-year period. Both Esteio and Porto Alegre pasture were dominated by introduced grass species (Gramineae). The Esteio site had numerous pools (larger than 20 × 20 m) that were occasionally disturbed by buffalo. The Porto Alegre transect had no pools in its vicinity.

Second-growth forest with a history of repeated burn was dominated by *Vismia* spp., which formed a low, open canopy. *Vismia* spp. is a plant genus typically found in cleared and abandoned areas of the Amazon (plate 10; Lovejoy, Bierregaard et al. 1986; Chapter 25). The plants have narrow trunks with thin branches. Few continuous-forest plants grow under the *Vismia* (Williamson, Mesquita et al. 1998). Established 10- to 12-year-old second growth was surveyed for frogs and tadpoles, and additional surveys of breeding pools were made in younger (5- to 6-year-old) second growth on three occasions. All surveys were performed at Dimona and at two Esteio pools. Twelve-year-old cut second growth (without burn) was dominated by *Cecropia* spp., whose seedlings often germinate on decaying trunks (plate 8). Thus mature cecropia plants typically have tangled roots partly above ground leading to a tall trunk. The foliage is concentrated at the

top of the trunk in an umbrella-like fashion. A single leaf and petiole from a cecropia plant can be 1.5 m long. Cecropia formed a deep litter layer with numerous regenerating primary forest plant species in the understory. This second-growth forest is floristically more diverse than *Vismia*-dominated forest (Williamson, Mesquita et al. 1998).

Continuous forest was composed of a high (often taller than 35 m) canopy with many subcanopy layers. The native forest was floristically very diverse (Rankin-de Mérona et al. 1992; Chapters 5 and 6), and the forest floor was covered with regenerating plant species.

The results of seven years of continuous-forest amphibian surveys at the BDFFP were used in this study (Zimmerman 1991; Gascon 1991). The senior author surveyed the same control plot during 1992–94.

FIELD SURVEYS

Because most frog species rely on a particular breeding habitat, no single survey method provided a complete inventory of the species present in each habitat type. Diurnal and nocturnal transect surveys as well as surveys at different types of aquatic habitats were used to inventory species composition in each habitat type.

Diurnal and nocturnal aural and visual surveys. Forest transects by aural and visual surveying have been shown to be the most efficient method of sampling frogs in the BDFFP sites (Zimmerman 1991). Transects were established throughout the areas to be surveyed and were walked repeatedly by the same observer or observers. Frogs were identified by call; species name, time, calling habitat, and number of callers were recorded. Simultaneously, a visual survey was conducted. For each frog encountered, species name, time, habitat, snout-vent length, and sex (where possible) were noted. Zimmerman (1991) used identi-

cal methods. Only presence-or-absence data are presented here.

Aquatic surveys. Within each habitat all available breeding sites were mapped. Tadpoles were surveyed by dip-netting the entire surface area of each pool. For large pools (greater than 20 m²), sufficient sampling effort (usually more than an hour) was exerted to ensure that no species were overlooked. Tadpoles that could not be identified in the field were preserved in 10 percent formalin for lab identification. During these surveys, the presence of juveniles was also noted. Tadpole species, larval stage, and abundance were noted. Habitat variables, including pool type, size, and presence of tadpole predators, were recorded. Pools were numbered for future comparison. Only species presence-or-absence data are presented here for tadpoles.

A common, semipermanent pool type found in continuous forest and all matrix habitats was used here for comparative purposes. This breeding habitat is referred to here as an upland forest pool. Upland forest pools are typically large (more than 20 m diameter), are prone to periodic drying in exposed sites even during the rainy season (i.e., low second-growth forest and pasture land), fill maximally during the rainy season, and often dry up when the rains cease. In sites where cattle have access, the pools appear to have a greater persistence (compared to, for example, continuous-forest upland pools), perhaps because cattle churn up and compact the soil underlying the pools making them more watertight. These pools were visited diurnally for tadpole identifications and nocturnally for breeding adults.

Plastic basins (50 cm diameter × 20 cm deep) are also useful for frog surveys (Gascon 1993) and were used here. Groups of three basins were placed randomly along transects in each habitat type. Each group

was separated by at least 50 m. The basins were buried so their lips were level with the surface of the ground and mimicked peccary wallows, which are important breeding sites for frogs in continuous forest (Zimmerman and Bierregaard 1986) but are usually absent from open-area sites. The basins were used as a survey tool to attract frogs that preferentially breed in wallows and to measure breeding success of cohorts initiated within the basins. For artificial pools in each habitat, only presence-or-absence data of species of tadpoles as determined by dip-netting are presented here.

Survey protocol. For the purpose of this study, sites within the BDFFP landscape were surveyed during two consecutive rainy seasons (November–May 1992–93 and 1993–94), every two weeks during the first rainy season and monthly during the second. We surveyed extensive areas of the above habitats (matrix and continuous forest) for both adult and larval frogs using aforementioned techniques. Equivalent sampling was performed in all habitats (not including the seven-year continuous-forest survey of Zimmerman 1991 and Gascon 1991). Transects surveyed by Zimmerman were repeated as logistics permitted with many transects surveyed on more than twenty occasions (Zimmerman 1991).

In this study, species that were recorded in extensive surveys of continuous forest by Zimmerman (1991) are referred to as species of closed forest (table 19.1), whereas species that were added only after surveys in forest fragments, second-growth forest, and pasture are referred to as species of open areas. Within closed forest and open-area habitat categories there was considerable overlap, with some species (e.g., *Hyla minuta*) being more common in pasture than in continuous forest. Such species were still referred to as closed forest species, as they had been initially observed in continuous forest before

the existence of cattle ranches in the area (Zimmerman and Rodrigues 1990).

FOCAL-SPECIES POPULATION

COMPARISONS—*PHYLLOMEDUSA TARSIVS*

Breeding population size and movement. Breeding populations of *P. tarsius* were sampled in twenty-one continuous-forest pools and nine matrix-habitat pools. The type of matrix habitat varied; it included maintained pasture as well as low second growth dominated by *Cecropia* spp. Continuous-forest pools were generally small (less than 20 m²) and shallow and usually dried up in the dry season (Gascon 1991). Matrix habitat sites were much larger (at least 100 m²) and are variable in persistence throughout the year. Vegetation structure surrounding the pools differed substantially between locations. Continuous-forest sites have a dense understory composed of seedlings of many different species with wide leaves (e.g., Melastomataceae). Matrix habitat sites were surrounded in some cases by grasses (i.e., Gramineae) as for those located in pasture, or had low second growth encroaching the water margin.

Sites were visited approximately every two weeks from November 1995 to June 1996, which corresponded to the bulk of the breeding season (Gascon 1991). During each visit, all individuals present (calling males and gravid females) were noted and marked with individually numbered bands. During subsequent visits, the presence of marked individuals was noted, as well as any new individuals present at each site. The bands were affixed to the upper arm region and proved more reliable than toe-clipping. Finally, we measured the perimeter length of each breeding site and used it as our estimate of pool size. Because pools were of different sizes, we tested for differences in chorus size between pool locations using

TABLE 19.1. Frog Species Encountered in Each Habitat Type Within the BDFPP Landscape

	Survey ¹	Habitat type			Continuous forest
		Pasture	Cut and burn	Cut only	
Leptodactylidae					
<i>Adenomera andreae</i>	U	x	x	x	x
<i>Adenomera hylaedactyla</i>	D	x		x*	
<i>Ceratophrys cornuta</i>	U			x	x
<i>Eleutherodactylus fenestratus</i>	U	x	x	x	x
<i>Eleutherodactylus zimmermanae</i>	U		x	x	x
<i>Eleutherodactylus</i> sp. A	D			x*	
<i>Leptodactylus knudseni</i>	U	x	x	x	x
<i>Leptodactylus mystaceus</i>	U	x	x	x	x
<i>Leptodactylus pentadactylus</i>	U		x	x	x
<i>Leptodactylus rhodomystax</i>	U	x	x	x	x
<i>Leptodactylus riveroi</i>	U		x		x
<i>Leptodactylus stenodema</i>	U		x	x	x
<i>Leptodactylus petersii</i>	U	x	x	x	x
<i>Leptodactylus leptodactyloides</i>	D		x		x
<i>Lithodytes lineatus</i>	U	x	x	x	x
Unknown tadpoles sp. A	D			x*	
Hylidae					
<i>Hyla boans</i>	U				x
<i>Hyla brevifrons</i> -like	U		x	x	x
<i>Hyla calcarata</i>	D		x		x
<i>Hyla geographica</i>	U		x	x*	x
<i>Hyla granosa</i>	U	x	x	x	x
<i>Hyla lanciformis</i>	D	x	x	x	
<i>Hyla leucophyllata</i>	U	x	x	x	x
<i>Hyla marmorata</i>	U	x	x	x	x
<i>Hyla microcephala</i> -like	U				x
<i>Hyla minuta</i>	U	x	x	x	x
<i>Hyla nana</i>	D	x			
<i>Hyla parviceps</i>	U		x		x
<i>Osteocephalus buckleyi</i>	U				x*
<i>Osteocephalus leprieurii</i>	D			x*	
<i>Osteocephalus</i> sp. A	U		x	x	x
<i>Osteocephalus taurinus</i>	U	x	x	x	x
<i>Phyllomedusa bicolor</i>	U			x	x
<i>Phyllomedusa tarsius</i>	U	x	x	x	x
<i>Phyllomedusa tomopterna</i>	U		x	x	x
<i>Phyllomedusa vaillanti</i>	U	x*			x
<i>Phrynohyas coriacea</i>	U				x
<i>Phrynohyas resinificatrix</i>	U				x
<i>Scinax cruentoma</i>	U	x	x	x	x
<i>Scinax garbei</i>	D	x			
<i>Scinax rubra/bosemanni</i>	U	x	x	x	x
<i>Scinax</i> sp. A	D	x		x*	
Microhylidae					
<i>Chiasmocleis shudikarensis</i>	U		x	x	x
<i>Chiasmocleis</i> sp.	U		x	x	x
<i>Ctenophryne geayi</i>	U				x
Microphylidae sp. A	D			x	x
<i>Synapturanus miranderiboi</i>	U				x
<i>Synapturanus salseri</i>	U		x	x	x

TABLE 19.1. (continued) Frog Species Encountered in Each Habitat Type Within the BDFFP Landscape

	Habitat type				
	Survey ¹	Pasture	Cut and burn	Cut only	Continuous forest
Bufonidae					
<i>Atelopus pulcher</i>	U		x		x
<i>Bufo granulosis</i>	D	x	x	x	x
<i>Bufo marinus</i>	D	x	x	x	x
<i>Bufo typhonius</i>	U		x	x	x
<i>Bufo typhonius</i> -like	D		x		
<i>Dendrophryniscus minutus</i>	U		x	x	x
Dendrobatidae					
<i>Colostethus marchesianus</i>	U		x	x	x
<i>Colostethus stepheri</i>	U		x	x	x
<i>Epipedobates femoralis</i>	U	x	x	x	x
Pipidae					
<i>Pipa arrabali</i>	U				x
Centrolenidae					
<i>Centrolenella oyampiensis</i>	U				x
Unknown					
Unknown tadpole sp. A	D		x		
Unknown sp. A	U				x

Notes: ¹U = Species found in undisturbed forest in Zimmerman's (1991) surveys. D = species found in surveys of disturbed, matrix habitat. * = Species recorded less than five times in the respective habitat.

analysis of covariance with pool size as a covariant.

Tadpole survival in matrix and continuous-forest pools. We set up two concurrent experiments to test for differences in tadpole survival as a function of pool location (i.e., in continuous forest or in pasture matrix) and tadpole population (continuous forest versus matrix). Each experiment consisted of raising tadpoles in enclosures in pools in matrix habitat and continuous forest and monitoring survival. In one experiment we used tadpoles from continuous-forest populations, whereas in the other experiment we used tadpoles from matrix populations. To control for phenological effects we ran both experiments concurrently. Enclosures were constructed of fine nylon mesh sewn together in a box shape (Gascon 1995). Each enclosure measured 30 cm × 25 cm × 25 cm and was secured in its pool with wooden stakes. Three pools (replicates) in each habi-

tad type were chosen and two enclosures were placed in each (one enclosure for each population type). In each enclosure, ten stage 25 (Gosner 1960) tadpoles were placed. Experiments lasted for thirty days, at which point all surviving tadpoles were counted. We compared survival between habitat types for each tadpole population using t-tests. The design also allowed for comparison of survival between tadpole populations reared in the same habitat (i.e., matrix and continuous-forest sites separately).

Results

OVERALL COMMUNITY COMPOSITION AND HABITAT TYPE

Sixty-one species of frogs in seven families were observed in the BDFFP landscape (see table 19.1). Two species (Unknown tadpole sp. A and *Osteocephalus buckleyi*) were col-

TABLE 19.2. Number of Species Associated with Open Areas or Closed Forest in Each of the Four Habitat Types Sampled

Habitat type	Number of species		Total
	Open areas	Closed forest	
Continuous forest	5	46	51
Cut	9	32	41
Cut/burn	6	34	40
Pasture	7	17	24

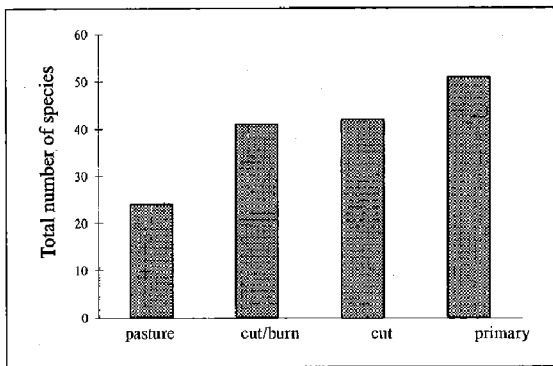


Fig. 19.1. Total number of species of frogs encountered in each habitat type.

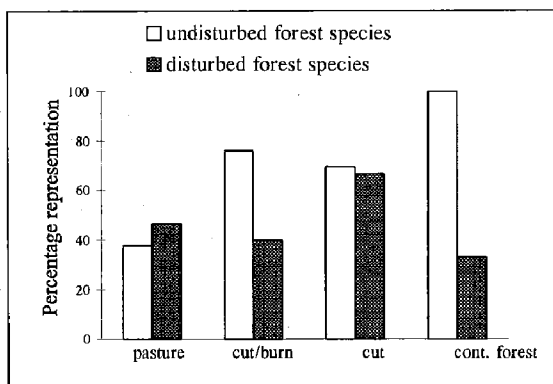


Fig. 19.2. Percentage of total undisturbed and disturbed forest species represented in the total number of species found in each habitat.

lected only as tadpoles. Fifty-one frog species were found in continuous forest (representing 85 percent of the entire assemblage), 41 in second growth that was cut (68 percent), 40 in cut-and-burned second growth (67 percent), and 24 in pasture (40 percent) (table 19.2; fig. 19.1).

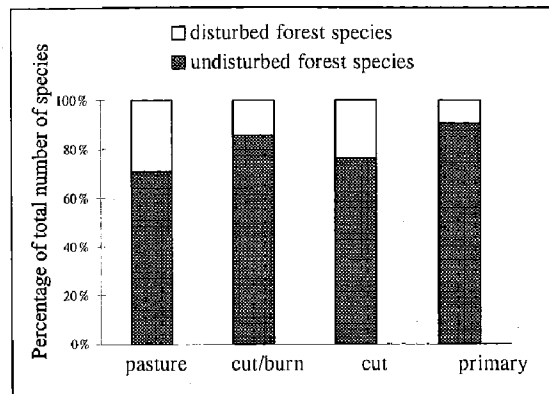


Fig. 19.3. Percentage of total number of species in each habitat that are characterized as undisturbed or disturbed forest species (see table 19.1).

Representation of closed-forest species declined with an increase in disturbance and as numbers of open-area species increased. In both second-growth habitats, closed-forest species occurred in similar numbers, whereas cut second growth had more open-area species than any other habitat (table 19.2; fig. 19.2). Despite the decrease in representation of forest species as disturbance intensity increased, 71 percent of the species present in pasture were closed-forest species (fig. 19.3). Similarly, a high percentage of species encountered in both second-growth types were closed-forest species (76.2 percent and 85.4 percent, cut and cut-and-burned second growth, respectively).

All families had similar representations in both second-growth types (table 19.3). No species of microhylidae, pipidae, or centrolenidae were ever recorded in pasture. Only one species, *Hyla nana* (Hylidae), was found exclusively in pasture (see table 19.1).

POOL-BREEDING SPECIES AT UPLAND FOREST POOLS

Surprisingly, the number of core upland forest-pool breeders that used pools in continuous forest was not significantly different

TABLE 19.3. Representations of Frog Families in Both Second-Growth Forest Types of the BDFFP Landscape

Family	Secondary growth type	
	Cut only	Cut and burn
Leptodactylidae	13	12
Hylidae	16	15
Microhylidae	4	3
Dendrobatidae	3	3
Centrolenidae	0	1
Bufonidae	4	6
Pipidae	0	0

from the number that used these in the two matrix types (fig. 19.1). Fewer species were present at upland forest pools with increasing disturbance, with pasture pools supporting on average only 42 percent of the pool breeders (fig. 19.4). Distance of the upland forest pools from continuous forest was not related to number of species present (fig. 19.5).

POPULATION COMPARISONS—*PHYLLOMEDUSA TARSIVS*

The total number of *P. tarsius* individuals encountered in matrix pools was 150 (of which 141 were males), whereas 48 individuals (of which 45 were males) were recorded at pools in continuous forest. Overall mean population size per pool for males and females was greater in matrix habitat sites (mean 17.0 individuals) compared to continuous forest (mean 3.2 individuals). However, when pool size was taken into account, no differences existed in the number of individuals observed per site in each habitat (analysis of covariance [ANCOVA], $F = 0.360$, $P = 0.557$, $df = 1,15$).

Twenty-two percent of all captures were previously marked individuals. Only 16 percent of all individuals marked in matrix habitat were recaptured at least once, compared to 18.8 percent for individuals

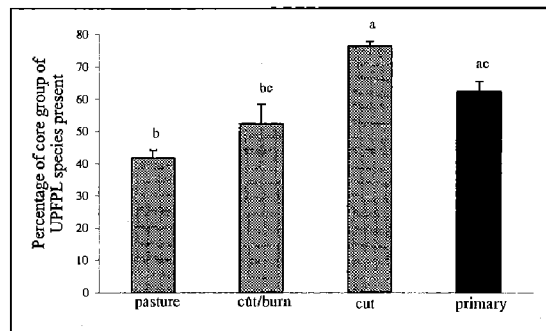


Fig. 19.4. Percentage of the core group of upland forest-pool species encountered in each habitat type. Only data from the aquatic sites surveys were considered here.

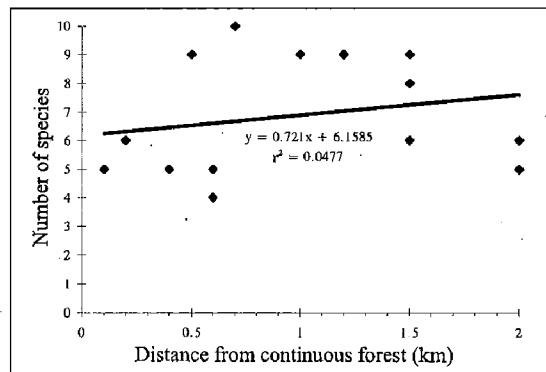


Fig. 19.5. Number of species encountered in upland forest pools in all types of matrix habitat as a function of distance of pool to continuous forest.

marked at continuous-forest sites (table 19.4). Considering only individuals that were recaptured at least once, the mean number of recaptures per individual was very similar for the two habitats (1.38 for matrix habitat versus 1.33 for continuous forest). Finally, only 24 percent and 17 percent of all recaptures, for matrix habitat and continuous forest sites, respectively, were at different pools than those where the individual had been marked. No across-habitat movement was observed.

TADPOLE SURVIVAL AND HABITAT TYPE

Survival was high in both habitat types for both tadpole populations (table 19.5). Al-

TABLE 19.4. Mark-Recapture and Movement Characteristics of Populations of *Phyllomedusa tarsius*

	Matrix habitat	Continuous forest
Total number of individuals marked	150	48
Total number of recaptures	33	12
Total number of recaptured individuals	24	9
Proportion of individuals marked that were recaptured	0.16	0.188
Total number of movements	8	2
Mean number of recaptures (per recaptured individuals only)	1.38	1.33
Proportion of total recaptures at different pools (number of movements/total number of recaptures)	0.24	0.17
Mean distance of movements (m)	216	364

TABLE 19.5. Survival of *Phyllomedusa tarsius* Tadpoles in Enclosures in Open-Area Habitat and Continuous Forest Habitats.

Source of tadpoles	Mean survival in	
	Open-area habitat	Continuous forest
Open-area habitat	9.05 (0.83)	7.00 (3.40)
Continuous forest	7.35 (1.35)	8.50 (0.71)

Notes: Mean survival values are numbers of tadpoles out of the original ten that were alive at the end of the experiment. Numbers in parentheses are one standard deviation of the mean.

though there was a tendency for tadpoles of matrix habitat and continuous forest to have higher survival in their "native" habitats, an analysis of variance (ANOVA) showed the difference was not significant ($F = 0.007$, $P = 0.937$). Likewise, no difference in mean survival was found between tadpole populations reared in the same habitats ($F = 0.166$, $P = 0.694$).

Discussion

Frog species composition varied considerably between open-area habitats and continuous forest sites. This has also been shown for other faunal groups, such as ants (Chapter 16). In this study, which covered the entire BDFFP landscape, we recorded

seventeen frog species that were not found in previous surveys of continuous forest (Zimmerman 1991; Gascon 1991). We noted a decrease in total number of species as the level of disturbance increased (the human-induced processes of deforestation that result in alteration of pristine forest), in particular a drop in representation of closed-forest species, especially those associated with streams or specialized breeding habitat. Despite this, closed-forest species still made up half the total number of species present in the most disturbed habitat. Furthermore, surveys of calling males and determination of breeding patterns of wallow and upland forest-pool breeders showed that matrix is exploited as a quality breeding habitat, and in some cases frogs appear to be more successful in matrix habitat.

No one habitat was found to have the full complement of frog species present in the BDFFP landscape. However, continuous forest had more than twice the number of species found in pasture, and it is clear that disturbance results in a decrease in the overall number of frog species. This agrees with a general pattern of faunal response to disturbance in the BDFFP landscape for ants (Chapter 16), small mammals (Malcolm 1991), and birds (Borges 1995; Chapter 20).

Many of the open-area frog species (e.g., *Scinax rubra*) are now known to be present

in continuous forest (see table 19.1). Some of these species (e.g., *Adenomera hyalaedactyla*) may have migrated into the BDFFP landscape from areas closer to Manaus, where disturbance has a longer history.

Although strong evidence is presented for a decrease in species richness with increasing disturbance, very few species were found exclusively in continuous forest. In fact, we found 82 percent of all species recorded in continuous forest in one or more of the open-area habitats. Other taxonomic groups also show similar high proportions of forest species using matrix habitats (Gascon et al. 1999). For frogs, notable exceptions have specific breeding requirements or are rare in the BDFFP landscape. For example, although *Phrynohyas resinifictrix* is a common species in forest reserves in the area, it has specialized breeding requirements. *P. resinifictrix* breeds only in large water-filled tree holes (B. Zimmerman, pers. comm.), which are rare in matrix forest and pasture. Consequently, *P. resinifictrix* was never recorded in either of the two matrix types or pasture. Similarly, *Osteocephalus* sp. A is rare in matrix forest and absent from pasture where its preferred breeding habitat, water-filled bromeliads and palm axles (Jungfer, pers. comm.), is also rare. Thus species with very specialized breeding habitats are unlikely to be present in the matrix as true residents.

The high representation of closed-forest species in the most disturbed habitat-pasture needs further explanation. Many frogs are known to return to their natal breeding pools (see review in Sinsch 1990) regardless of how the surrounding area has been disturbed. But due to the likely longevity of many of the frog species in the BDFFP, relative to the time pools have been surrounded in pasture, a more likely explanation is that some frog species show remarkable plastic-

ity in reproductive behavior, allowing them to adapt to different ecological conditions for breeding.

Cases in point are the two species of *Phyllomedusa* (*P. tarsi* and *P. tomopterna*) that were commonly found in open-area habitats. As with most species of this genus, females will lay eggs in broad leaves of plants at the pool margin that are either folded over (*P. tomopterna*) or joined together (*P. tarsi*) to surround the eggs. In many open-area sites that were surveyed, no such plants existed at the pool margins. Eggs were laid in clumps of grass blades at the water margin, leaving much of the egg mass exposed to desiccation or predation. Regardless, juveniles of both *P. tarsi* and *P. tomopterna* were discovered in the pasture. Further, neither measure of reproductive success for *P. tarsi* (chorus size or larval survival) differed between open-area habitats and continuous forest, indicating that not only is this species capable of using open areas but that it does so successfully.

Certainly, species-specific differences in behavioral plasticity can explain some of the observed distributions, but not all forest species that were found in pasture were necessarily breeding successfully. For some closed-forest species, adults may be attracted to pasture pools, which are not suitable for their breeding. As a result, pasture pools may act as a breeding sink, robbing the local population of breeding individuals.

Both second-growth forests were equally "permeable" to wallow and upland forest-pool breeding species. However, repeated burning, such as that inflicted on pasture habitat, has a greater impact on the frog community than does the lessened burning regime of the cut-and-burned matrix surveyed here. In general, pasture sites were found to be depauperate in closed forest species in comparison to cut-and-burned

areas, which offer more physical cover (vegetation) to resident frogs than the more open pasture habitat.

Physical cover offered by cut-and-burned matrix may also explain the difference in species composition found between pasture and second-growth forests. These data are similar to Tocher's (1998) findings for the entire frog assemblage of the BDFFP (i.e., not just frogs that utilize upland forest pools and wallows). In contrast Phelps and Lancia (1995) showed less impact of forest loss on an amphibian assemblage in South Carolina. Although many species decreased in abundance in cleared areas, relatively few frog species were lost completely. Our results are in sharp contrast, however, with those studies showing more serious impacts of landscape changes on amphibians (Corn and Bury 1989; Petranka, Eldridge, and Haley 1993; Grant et al. 1994; Dupuis, Smith, and Bunnell 1995). Thus predictions as to the effects of forest loss on the resident frog community appear site specific.

The core group of upland forest-pool breeders identified by Zimmerman (1991) all had one thing in common—they most often bred at upland forest pools. Interestingly, although fewer of these species were present at pasture pools, well over half of them were. It is difficult to know whether they were resident in the pasture, or whether they returned to breeding pools from surrounding forest (Sinsch 1990). No relationship was found between the number of species present at pools and the distance to the nearest continuous forest, so these data provided no clues to resolving this issue. However, although no individuals were found to move between habitat types, some individuals were recaptured at different breeding sites within the same habitat types, suggesting that movement is possible.

There was a high presence of upland forest-pool species in second-growth forest, and on

average more species were present at cut second-growth forest pools than were present in continuous-forest pools (although breeding success of all of these species in open areas was not evaluated).

These findings, in particular the demonstrated ability of upland forest-pool species to move through open cleared areas, including pasture, have obvious management implications. Some frog species are able to alleviate the negative effects of fragmentation, such as reduced and isolated populations, because of their ability to permeate, or disperse into, and exploit the cleared areas. In fact, many species of different taxonomic groups are capable of using the matrix habitat, and this ability is strongly correlated to their persistence probability in forest fragments (Laurance 1991b; Gascon et al. 1999). Furthermore, many species of frogs can use and move along linear forest remnants along streams in open areas, further increasing their chances of surviving in a modified landscape (Lima and Gascon 1999).

It is not surprising that cut (but not burned) second-growth forest has high species richness and a high permeability to upland forest-pool breeding species, considering its relatively moderate disturbance history and structural similarity to continuous forest (Williamson, Mesquita, et al. 1998; Chapter 24). However, with respect to community composition, and also when all breeding groups were investigated independently, no real differences in composition, abundance, or breeding success were found between the two types of second growth (in stark contrast with birds [Chapter 20] and ants [Chapter 16]). It therefore seems that regardless of burning history, the eventual frog community in established second-growth forests will be similar.

In maintained pasture the scenario is very different; fewer frogs are present due to the extreme lack of cover and perhaps the oc-

currence of repeated burnings. The implications of these joint findings for conservation are huge. When continuous forest is cut and burned, as was the case for the BDFFP landscape, all frogs, with the exception of fossorial species, must surely be killed. Individuals encountered in each habitat type (excluding continuous forest) in this study have certainly moved into these areas from surrounding continuous forest. This suggests that many frog species have the capacity to respond to loss of primary habitat, at least in the short term, using a modified, disturbed landscape. It is important, however, to emphasize that more severe disturbances, such as repeated cutting and burning over decades, may result in an overall impoverished frog community. Results presented here portray but one possible scenario of tropical deforestation with moderate to low levels of disturbance and should not be extrapolated to areas where the geographical extent and intensity of disturbance are greater.

Conservation Lessons

1. Although more detailed surveys are needed in open-area habitat of all types, it is clear from these data that continuous-forest (including primary forest and second growth) loss will result in an impoverished amphibian fauna in cleared areas. Many of the continuous-forest species were not observed outside continuous forest.
2. Species found exclusively in open-area habitats are capable of reaching these disturbed areas from source populations in relatively short periods of time. In our study areas the forest had been cleared for less than thirteen years. Species now associated with these open areas were never encountered in continuous forest (Zimmerman and Rodrigues 1990; Gascon 1991) and so are hypothesized to be immigrating from other disturbed areas, probably close to Manaus. Disturbed areas along the main highway probably serve as corridors for these species to invade new matrix habitat.
3. Many species previously characterized as primary-forest species (Zimmerman and Rodrigues 1990; Gascon 1991) are capable of using other types of habitats for reproduction (see also Gascon 1993). This capacity does not seem to be restricted to certain taxonomic or ecological groups because most genera in table 19.1 have representatives in all types of habitats. However, forest destruction will have overall negative effects on the full complement of primary forest species as many are not capable of using open-area habitats and are thus at risk in fragments (Gascon et al. 1999).
4. These results have clear implications for population dynamics and conservation biology. The differential response of amphibian species to landscape changes precludes any generalizations as to the effects of habitat loss or fragmentation. Rather, species-specific requirements seem to dictate how individual species respond to habitat changes (also see Gascon 1993; Tocher, Gascon, and Zimmerman 1997). The presence of calling individuals of *P. tarsius*, among others, and the observed movement of individuals between pools in matrix habitat is indicative of some potential for dispersal through open-area habitat to other patches of primary forest. For such species there may be a lesser need for corridors linking patches of forest as the populations in open-area habitats can act as stepping stones or sources of colonists for dispersal.

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