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Annual activity patterns of anurans in a seasonal neotropical environment

M. Aichinger
Institute of Zoology, University of Viena, Althanstraße 14, A-1090 Vienna, Austria

Summary. At Panguana, a study site in the upper Amazon basin, 7 different aquatic breeding sites of anurans were investigated from Nov. 1, 1981 to Oct. 31, 1982. Rainfall in this area is seasonal. Only 20% of the total annual precipitation was maesured during the dry period, which lasted from mid-March until mid-September 1982. The reproductive periods of the species were highly affected by the rainfall distribution. Calling males and/or gravid females of 46 species were found during the study period. 37.0% of the anuran species were exclusively, and 43.5% predominantly, active during the rainy season. Plots of 100 m^2 were established at 6 aquatic sites in primary rainforest. A total of 2126 frogs was counted; 93.2% of these were made during the rainy season. A maximum of 378 individuals were found during one check in the plot at the permanent pond. At this site high concentrations of individuals and large choruses were found at the beginning of the rainy season. As soon as favourable temporary aquatic sites were established, reproductive activities decreased at the permanent pond and increased at temporary breeding sites.

Key words: Anura – Community structure – Activity patterns – Seasonal dependency

Seventy one anuran species are known from "Panguana", a study site in the upper Amazon basin. Toft and Duellman (1979) stated that the seasonality of rainfall at Panguana affects the reproductive activities of anurans, but no detailed work was carried out. During one year I investigated the activity patterns of the anuran fauna at Panguana. This study deals with 46 species in which calling males and/or gravid females were found. Seven different aquatic breeding sites were studied in order to show the spatial and temporal distribution for each species.

Description of study site

Panguana is located on the south bank of the Río Llullapichis, a tributary of the Río Pachitea, in the upper Amazon basin in eastern Peru (Figs. 1 and 2). The biological field-station is situated at 9°37′ S, 74°56′ W, at an elevation of 260 m. Maximum relief in the investigation area is less than 40 m.

Rainfall was seasonal as shown in Fig. 3. My weather records indicate that for the period November 1981 – October 1982, the driest months were August (24.7 mm), June

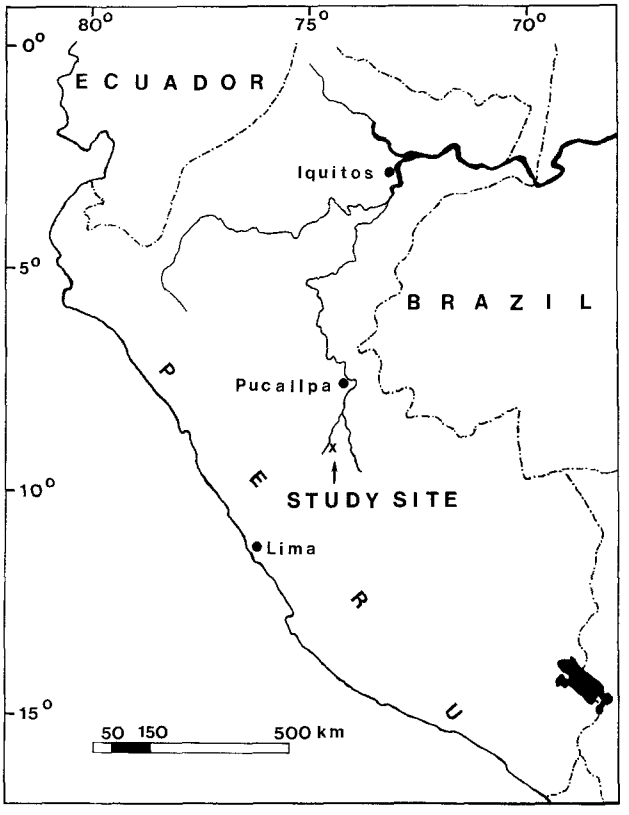

Fig. 1. Map of Peru showing the location of the study site (×)

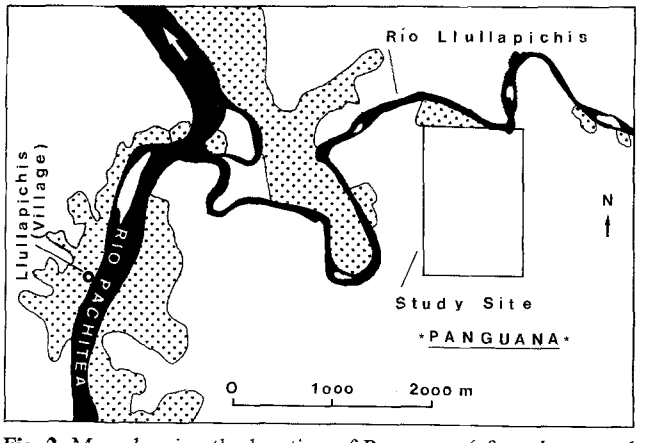

Fig. 2. Map showing the location of Panguana (after photographs taken by the Peruvian air-force-Nr. UAg II3038 16324 in July 1981). *Stipples* area under cultivation

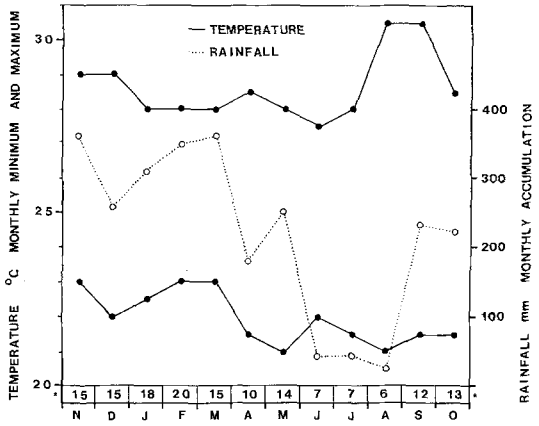

Fig. 3. Monthly minimum and maximum ambient air temperatures (measured in primary rain forest) and monthly rainfall accumulation for the period Nov. 1981 – Oct. 1982. * number of rainy days per month

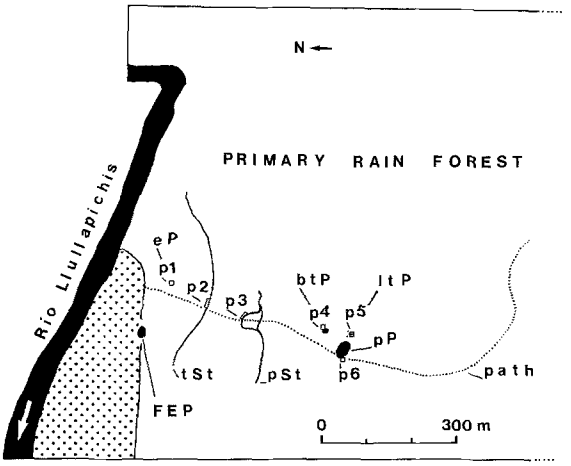

Fig. 4. Panguana with the investigated aquatic breeding sites and the different plots. *eP* ephemeral puddles, *tSt* temporary stream, *ltP* little temporary pond, *btP* big temporary pond, *FEP* forest edge pond, *pSt* permanent stream, *pP* permanent pond, *p1–p6* plot 1 to plot 6, *stipples* area under cultivation

Table 1. Specification of 7 aquatic sites

Aquatic sites	Maximum surface (m^2)	Maximum depth (m)	Maximum No. of days filled with water	1981		1982				M O N T H S						
				N	D	J	F	M	A	M	J	J	A	S	O	
Ephemeral																
1) Puddles (Plot 1)	1	0.3	3	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	
Temporary																
2) Stream (Plot 2)	–	0.4	117	× ×	. .	× ×	× ×	× ×	× ×	. .	. .	. .	. .	. .	. ×	
3) Little Pond (Plot 3)	50	0.5	107	× ×	. ×	× ×	× ×	× ×	× .	× .	. .	. .	. .	. ×	. ×	
4) Big Pond (Plot 4)	200	1.0	262	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	. .	. .	. ×	× ×	
5) Forest-Edge Pond	150	0.8	44	. ×	. ×	. ×	× ×	× .	. .	. .	. .	. .	. .	. .	. .	
Permanent																
6) Stream (Plot 5)	–	1.0	333	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× .	. ×	× ×	
7) Pond (Plot 6)	1,000	1.5	353	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	. ×	× ×	

. . without water, × × filled with water, × . during the first, . × during the second half of month filled with water

(40.8 mm) and July (43.0 mm); the wettest March (362.0 mm) and November (359.1 mm). Total annual rainfall accumulation was 2634.6 mm. During the dry period lasting from mid-March to mid-September 1982 only 20% (543.3 mm) of total precipitation was registered. Local residents confirmed that the wet and dry patterns of that particular year were typical.

The maximum temperature measured in the forest shade during the year was 30.5° C, the minimum temperature 21° C. Mean ambient temperature was 25° C.

Methods

Field work at Panguana was carried out from Nov. 1, 1981 until Oct. 31, 1982. In order to obtain a more accurate annual distribution pattern of anurans, the 12 month investigation was divided into 18 periods of 20 days each (except for the last 25 day period). The dry season lasted from period 8 to 16.

Daily weather data consisted of maximum and minimum ambient temperature measured in primary rain forest shade, and rainfall accumulation.

Species assemblages (composition, abundance, and calling activity of males) of anurans were recorded at certain aquatic breeding sites at regular intervals throughout the year. Observations were made both by day and night. Six plots of 100 m^2 (10 × 10 m and, at two streams, 20 × 5 m) were established at different sites (Fig. 4); trails were cleared outside of them with a machete.

Field work was carried out in 2 km^2 area covered mostly with primary rain forest (Fig. 4). Table 1 shows the 7 aquatic sites which were investigated extensively throughout the study period. Ephemeral puddles were found after heavy rains throughout the primary rain forest area. They were filled with water for a maximum of only 3 days. The calling activities of species which do not lay their eggs in water (dendrobatids and Eleutherodactylus spp.) are shown here. Temporary sites are considered those in which water was present for at least 44 days at a time; all are known to dry up. The permanent environments were filled with water nearly the entire year (except 12 days during August 1982).

The number of individuals in 6 plots was counted. Caught frogs were not marked; therefore it was not possible to determine whether an individual was caught one or more times in a specific plot. The number of anuran species was determined. Four frequencies of calling frogs per species were discerned: a) ≥ 50, b) >10, c) >5, d) ≤ 5 synchronously calling males at the whole breeding site. At least two examinations per 20 day period were made at all 7 sites. Those with the higher number of individuals and the greatest assemblages of calling males per species were chosen for the Figures. In addition, the river bank and the remaining investigation area were studied at regular intervals.

Results

Spatial distribution

Forty six species belonging to 5 families (Bufonidae, Dendrobatidae, Hylidae, Leptodactylidae, Microhylidae) showed reproductive activity during the investigation. These species display six different reproductive modes (according to Crump (1974); Table 4):

Mode 1: Eggs and tadpoles in water (20 species);

Mode 3: Eggs in constructed basins of water on ground; tadpoles in water (1);

Mode 4: Eggs on vegetation above water; tadpoles in water (8);

Mode 5: Eggs in foam nests on or near water; tadpoles in water (5);

Mode 6: Eggs on land; tadpoles carried to water by parent (6);

Mode 7: Eggs in foam nests on land; tadpoles develop in nest (1);

Mode 8: Eggs on land; direct development (5).

Probably Hyla rossalleni lay the eggs on vegetation above water because of the low number of eggs (Salthe and Duellman 1973) but egg-deposition was not observed during the study.

A total of 34 anurans utilize puddles, ponds, streams, and the river for egg-deposition. Tadpoles of 40 species complete their development in water. The spatial utilization of breeding sites was therefore intensively studied in order to determine whether the species demonstrate a regular or a clumped distribution with regard to breeding activities. I considered that egg-deposition took place when calling males and gravid females were observed at an aquatic site.

Figure 5 shows the distribution of species at the different sites. The greatest anuran congregation was observed at the permanent pond. Twenty three species with calling males and 42 species with synchronously calling males were found there. At the little temporary pond only 3 species called synchronously.

The investigated sites were assessed for number of shared species with calling males (Table 2). The forest edge pond had no species in common with the ephemeral puddles in primary rain forest. Except *Osteocephalus leprieurii* and *Phrynohyas coriacea*, only more highly evolved breeding types like the tadpole-carrying dendrobatids and Eleutherodactylus spp. (direct development) showed reproductive activities in this area in primary rain forest. In contrast, the forest edge pond attracted many aquatic breeders (e.g. *Hyla marmorata*, *H. riveroi*, *Ololygon cruentomma*, *O. rubra*) from the adjacent grassland.

The maximum number of shared species between any site was 20, exhibited between the permanent pond and the big temporary pond. The reason for this seems to be the close proximity (60 m) of the two ponds. The temporal utilization by anuran species, however, was considerably different between these two sites.

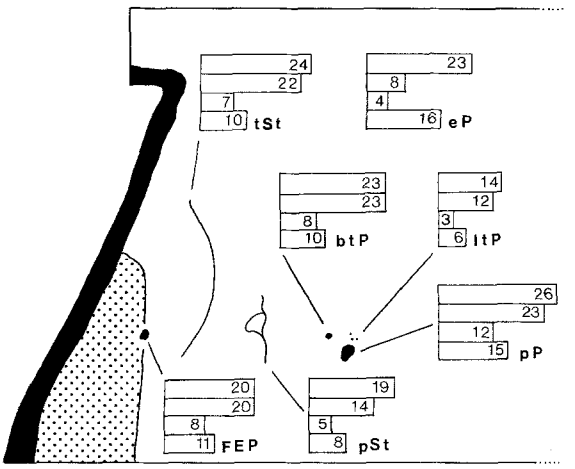

Fig. 5. Number of species at 7 different breeding sites. For site abbreviations see Fig. 4; horizontal bars from top to bottom: Total number of species, number of species with calling males, number of species with synchronously calling males, number of species with gravid females

Table 2. Community matrix of 7 different aquatic sites

	eP (8)	tSt (22)	ltP (12)	btP (23)	FEP (21)	pSt (14)
tSt (22)	6	–				
ltP (12)	5	10	–			
btP (23)	5	14	11	–		
FEP (21)	0	13	7	13	–	
pSt (14)	6	10	8	11	7	–
pP (23)	5	14	11	20	16	11

Numbers in brackets number of species found calling at this site; for site abbreviations see Fig. 4

The different breeding sites for 43 species are listed in Table 3. Not listed are the two species inhabiting the river bank, *Hyla boans* and *Bufo marinus*, and *Ololygon funerea* which was found at another permanent stream in the investigation area.

The number of breeding sites utilized by a species ranges from 1 to 6. The dendrobatids (*Colostethus marchesianus*, *Dendrobates femoralis*, *D. pictus*, *D. trivittatus*) were found at all studied sites except the river bank and the forest edge. Aquatic breeders like *Hamptophryne boliviana* and *Hyla parviceps* also were common at most sites. At the same time certain specialists, such as *Hyla marmorata* (forest edge pond), *Hyla sp.* and *Leptodactylus rhodomystax* (both temporary stream), *Hyla boans* and *Bufo marinus* (both river edge), called at only one site.

Temporal distirbution

The duration and temporal distribution of the reproductive period of the anuran species was studied in order to determine if the patterns corresponds to the extreme seasonality of precipitation at Panguana (Table 4). Of 46 species, only

Table 3. Spatial distribution of 43 species at 7 different sites

Species	eP	tSt	ltP	btP	FED	pSt	pP
Colostethus marchesianus	PDG	PDG	PDG	PDG	---	PDG	PDG
Dendrobates femoralis	PDG	PDG	PDG	PDG	---	PDG	PDG
Dendrobates petersi	XDG	---	---	---	---	---	---
Dendrobates pictus	PDG	PDG	PDG	P--	---	PDG	PD-
Dendrobates quinquevittatus	P-G	---	P--	---	---	---	---
Dendrobates trivittatus	PDG	PDG	PDG	PD-	---	PDG	PD-
Bufo typhonius	X-G	---	---	---	---	P--	---
Dendrophryniscus minutus	X--	---	PDG	PDG	---	---	---
Adenomera hylaedactyla	---	---	---	---	XNG	---	---
Ceratophrys cornuta	X--	---	---	---	XN-	---	XNG
Edalorhina perezi	P-G	---	P--	P--	---	P--	---
Eleutherodactylus carvalhoi	P-G	---	P--	P--	---	---	P--
Eleutherodactylus ockendeni	X-G	---	PN-	---	---	---	P--
Eleutherodactylus peruvianus	PNG	XN-	---	PN-	---	PN-	---
Eleutherodactylus toftae	X-G	P--	---	---	---	P--	---
Ischnocnema quixensis	X-G	---	---	---	---	---	---
Leptodactylus pentadactylus	---	XN-	---	X--	XN-	---	X--
Leptodactylus rhodomystax	X--	XN-	---	---	---	---	---
Leptodactylus wagneri	---	XN-	PNG	XN-	XN-	P--	PNG
Physalaemus petersi	P--	---	---	---	---	PN-	---
Hyla brevifrons	---	PNG	PNG	PNG	XNG	---	PNG
Hyla fasciata	X--	PNG	---	---	XN-	---	PN-
Hyla granosa	---	XNG	PN-	XN-	XNG	---	PNG
Hyla leucophyllata	---	XN-	---	---	XN-	---	---
Hyla marmorata	---	---	---	---	XN-	---	---
Hyla parviceps	---	PNG	PN-	PNG	XNG	XNG	PNG
Hyla rhodopepla	---	---	---	PNG	XNG	---	PNG
Hyla riveroi	---	XNG	---	PNG	XNG	---	PNG
Hyla rossalleni	---	XN-	---	PNG	---	---	---
Hyla sarayacuensis	P--	PN-	---	PNG	XNG	---	PNG
Hyla sp.	---	XN-	---	---	---	---	---
Ololygon cruentomma	---	XN-	---	PN-	XNG	P--	PNG
Ololygon garbei	---	XN-	---	---	XNG	---	---
Ololygon rubra	---	---	---	PN-	XNG	XN-	PN-
Osteocephalus leprieurii	PNG	XN-	---	---	---	PN-	XN-
Osteocephalus taurinus	P--	XN-	---	---	XN-	XNG	---
Phrynohyas coriacea	XN-	---	---	---	---	---	---
Phyllomedusa tarsius	---	---	---	PN-	---	---	PNG
Phyllomedusa tomopterna	---	---	---	PNG	---	---	PN-
Phyllomedusa vaillanti	---	---	PN-	PNG	XN-	XNG	PNG
Chiasmocleis ventrimaculata	---	---	---	PN-	XNG	---	PNG
Ctenophryne geayi	---	---	---	PN-	XN-	XN-	PN-
Hamptophryne boliviana	P--	XNG	PN-	PNG	XNG	PN-	PNG

P found in plot, *X* found at breeding site but not in plot, heard calling by *D* day, *N* night, *G* gravid female, for site abbreviations see Fig. 4

two, *Dendrobates pictus* and *D. trivittatus*, were heard calling every month of the year. The majority of the anurans (74%) showed reproductive activities (calling males and/or gravid females) for no more than 6 months.

In general, the availability of aquatic breeding sites restricted the reproductive activities of anurans to the rainy season. Seventeen species (37.0%) were reproductive exclusively, and 20 species (43.5%) predominantly, during the rainy season. *Hyla boans* and *Bufo marinus* were active only during the dry period, utilizing the low level of the river. These two species stopped calling immediatly after the first overflow of the Río Llullapichis at the beginning of the rainy season.

A total number of 2126 frogs belonging to 35 species were counted in the 6 investigated plots during the year (Table 5). Of these, 1981 frogs (93.2%) were adults and 145 (6.8%) were juveniles. I was unable to catch 69 (3.2%) of the adult frogs. Therefore sex-determination of these 3.2% was impossible. 6.5 times more males than females were found in the plots.

93.2% of the adult individuals were found during the rainy season (corresponding to the breeding period). On the other hand the majority of juvenile frogs (85.5%) were counted during the dry period. Juveniles, especially dendrobatids, preferred the wet areas of the drying streams and ponds.

The number of frogs of 35 species found in 6 different plots are shown in Table 6. A maximum of 1345 countings was made in plot 6 (permanent pond). This exceeds the number of all other plots by far. The bufonid *Dendrophryniscus minutus*, the microhylids *Chiasmocleis ventrimaculata* and *Hamptophryne boliviana*, and the hylids *Hyla parviceps*, *H. rhodopepla* and *Ololygon cruentomma* were most common at the permanent pond. The dendrobatids in contrast,

Table 4. Duration of breeding activities for 46 species

2 months	4 months	6 months	8 months	10 months	12 months
Ceratophrys cornuta (A, 1)	Chiasmocleis ventrimaculata (A, 1)	Hyla brevifrons (A, 4)	Adenomera hylaedactyla (B, 7)	Eleutherodactylus peruvianus (B, 8)	Dendrobates pictus (6)
Dendrobates quinquevittatus (A, 6)	Dendrophryniscus minutus (A, 4)	H. granosa (A, 1)	Colostethus marchesianus (B, 6)	Hyla parviceps (B, 1)	Dendrobates trivittatus (6)
Ololygon funerea (A, 1)	Hyla leucophyllata (A, 4)	H. rhodopepla (A, 1)	Dendrobates femoralis (B, 6)	Osteocephalus leprieurii (B, 1)	
Hyla sp. (A, 1)	Leptodactylus rhodomystax (A, 5)	H. riveroi (A, 1)	Hyla fasciata (B, 1)		
Eleutherodactylus toftae (B, 8)	Ctenophryne geayi (B, 1)	H. rossalleni (A, 4?)	Ololygon rubra (B, 1)		
	Edalorhina perezi (B, 5)	H. sarayacuensis (A, 4)	Phyllomedusa vaillanti (B, 4)		
	Eleutherodactylus carvalhoi (B, 8)	Leptodactylus wagneri (A, 5)	Dendrobates petersi (D, 6)		
	Leptodactylus pentadactylus (B, 5)	Ololygon cruentomma (A, 1)			
	Osteocephalus taurinus (B, 1)	Phyllomedusa tarsius (A, 4)			
	Eleutherodactylus ockendeni (C, 8)	Hamptophryne boliviana (B, 1)			
	Ischnocnema quixensis (C, 8)	Hyla marmorata (B, 1)			
	Physalaemus petersi (D, 5)	Ololygon garbei (B, 1)			
	Bufo marinus (E, 1)	Phrynohyas coriacea (B, 1)			
		Phyllomedusa tomopterna (B, 4)			
		Bufo typhonius (D, 1)			
		Hyla boans (E, 3)			

In brackets: A only during the rainy season, *B* mainly during the rainy season, *D* mainly during the dry season, *E* only during the dry season; *numbers 1 to 8* reproductive modes according to Crump (1974)

Table 5. Number of species and individuals found at 6 plots

	Plot												Total	
Number of	1		2		3		4		5		6			
Checkings	35	(18)	35	(18)	35	(18)	41	(24)	35	(18)	44	(27)	225	(123)
Species	11		12		15		18		13		24		35	
Counts	91	(60)	94	(68)	99	(77)	374	(325)	112	(69)	1,356	(1,310)	2,126	(1,909)
Adults	77	(57)	73	(61)	86	(73)	336	(324)	92	(65)	1,317	(1,308)	1,981	(1,888)
Males	39	(34)	55	(48)	66	(61)	303	(295)	46	(34)	1,150	(1,146)	1,659	(1,618)
Females	19	(11)	7	(4)	9	(6)	27	(25)	25	(18)	166	(165)	253	(229)
Males per female	2.4		1.8		7.4		11.8		1.6		6.8			
Juveniles	14	(3)	21	(7)	13	(4)	38	(1)	20	(4)	39	(2)	145	(21)

In brackets number during the rainy season

with the exception of *Dendrobates quinquevittatus*, were observed more or less regularly at all plots.

Activity patterns of anurans

The calling activity of the 39 anuran species found calling at all investigated breeding sites (including the river bank) are shown in Table 7. The greatest assemblage of calling individuals observed during the 20 day period was chosen. Between 22 and 31 ($\bar{X}=26.4$) species exhibited calling males during each 20 day period during the rainy season. During the dry period the number ranged from 6 to 14 ($\bar{X}=8.9$). Eight species, *Chiasmocleis ventrimaculata*, *Dendrophryniscus minutus*, *Hamptophryne boliviana*, *Hyla parviceps*, *H. rhodopepla*, *H. riveroi*, *Ololygon cruentomma* and *O. rubra* were found calling in assemblages of at least 50 males during the rainy season. No species called at that frequency during the dry period.

For more detailed information, each investigated breeding site is listed seperately:

A) Ephemeral aquatic site

1) Puddles/Plot 1 (Figs. 6, 7). The ephemeral puddles in the primary rain forest were not filled with water for more

Table 6. Distribution of 35 anuran species in 6 different plots

Species	Plot 1	2	3	4	5	6	Total
Colostethus marchesianus	41 (23)	30 (18)	26 (17)	30 (11)	26 (14)	9 (4)	157 (87)
Dendrobates femoralis	18 (14)	9 (6)	8 (7)	7 (6)	19 (14)	11 (6)	72 (53)
Dendrobates pictus	10 (9)	18 (13)	4 (3)	4 (3)	45 (28)	2 (2)	83 (58)
Dendrobates quinquevittatus	1 (1)	–	1 (1)	–	–	–	2 (2)
Dendrobates trivittatus	8 (7)	3 (3)	3 (2)	1 (1)	4 (4)	1 (1)	21 (18)
Bufo typhonius	–	–	–	–	1 (1)	–	1 (1)
Dendrophryniscus minutus	–	–	29 (11)	16 (7)	–	304 (21)	339 (39)
Edalorhina perezi	1 (1)	1 (1)	–	–	1 (1)	–	3 (3)
Eleutherodactylus carvalhoi	–	3 (3)	4 (4)	–	–	1 (1)	8 (8)
Eleutherodactylus ockendeni	–	–	–	–	–	1 (1)	1 (1)
Eleutherodactylus peruvianus	8 (8)	1 (1)	2 (2)	1 (1)	3 (3)	–	15 (15)
Eleutherodactylus toftae	–	1 (1)	–	–	2 (2)	–	3 (3)
Ischnocnema quixensis	1 (1)	–	–	–	–	–	1 (1)
Leptodactylus pentadactylus	–	–	–	–	–	1 (1)	1 (1)
Leptodactylus rhodomystax	–	1 (1)	–	–	–	–	1 (1)
Leptodactylus wagneri	–	–	4 (2)	10 (6)	6 (6)	26 (15)	46 (29)
Physalaemus petersi	1 (1)	–	–	–	1 (1)	–	2 (2)
Hyla brevifrons	–	2 (1)	5 (2)	35 (6)	–	69 (5)	110 (14)
Hyla fasciata	–	13 (10)	–	–	–	6 (5)	19 (15)
Hyla granosa	–	–	1 (1)	–	–	13 (9)	14 (10)
Hyla parviceps	–	11 (6)	7 (3)	17 (6)	–	179 (9)	214 (24)
Hyla rhodopepla	–	–	–	49 (7)	–	153 (11)	202 (18)
Hyla riveroi	–	–	–	–	–	21 (3)	21 (3)
Hyla rossalleni	–	–	–	59 (8)	–	–	59 (8)
Hyla sarayacuensis	–	1 (1)	–	53 (15)	–	34 (7)	88 (23)
Ololygon cruentomma	–	–	–	–	1 (1)	159 (2)	160 (3)
Ololygon rubra	–	–	–	–	–	68 (3)	68 (3)
Osteocephalus leprieurii	–	–	–	–	1 (1)	2 (1)	3 (2)
Osteocephalus taurinus	1 (1)	–	1 (1)	–	–	–	2 (2)
Phyllomedusa tarsius	–	–	–	4 (4)	–	2 (1)	6 (5)
Phyllomedusa tomopterna	–	–	–	4 (4)	–	1 (1)	5 (5)
Phyllomedusa vaillanti	–	–	1 (1)	11 (8)	–	–	12 (9)
Chiasmocleis ventrimaculata	–	–	–	50 (1)	–	144 (1)	199 (2)
Ctenophryne geayi	–	–	–	–	–	4 (1)	4 (1)
Hamptophryne boliviana	1 (1)	–	3 (3)	15 (4)	1 (1)	144 (6)	164 (15)

In brackets number of checks in which individuals were observed

than 3 days; they were formed after heavy rains. Species with egg-deposition in water did not utilize these puddles. Nevertheless, two aquatic breeders, *Osteocephalus leprieurii* and *Phrynohyas coriacea*, were heard calling far away from ponds and streams on trees at a height above 5 meters. Calling frequencies of species which do not need aquatic sites for egg-deposition, like the dendrobatids and *Eleutherodactylus peruvianus*, are included only in Fig. 6. In general, abundance of calling males was higher at the beginning of the rainy season. *Colostethus marchesianus* was the only species observed with more than 10 synchronously calling males at this breeding site.

The maximum number of individuals caught in the 100 m^2 plot did not exceed 7. During the 7th period (early March) the first juvenile frogs were found and the number of adults decreased.

B) Temporary aquatic sites

1) Temporary stream/Plot 2. Hyla fasciata and *H. granosa* were found largely, *Leptodactylus rhodomystax* and *Hyla sp.* exclusively calling in the dense vegetation along this temporary stream: A maximum of 12 different species was observed calling during the 4th 20 day period (early January). The number then decreased rapidly until mid-May. Males were heard calling again at the 18th period (mid-October).

A maximum of 8 individuals was counted during a check in plot 2 during the 2nd period (end of November). During the 9th and 14th period (mid-April and end of July) no individuals were found in the entire 100 m^2 area despite 2 checks in each 20 day period.

2) Little temporary pond/Plot 5. Although this aquatic site was filled with water for more than 3 months, only a few species called here. Typical at this pond was *Leptodactylus wagneri.* This foam nest-building leptodactylid is one of the first frogs to come to a newly developed water site after heavy rains at the beginning of the rainy season in September. The white foam nests of *L. wagneri* were first found at the nearby permanent pond and shortly afterwards at the little temporary pond.

The maximum number of individuals (11), mostly the little bufonid *Dendrophryniscus minutus*, was found during the 2nd period (end of November). After the little tempo-

Table 7. Calling patterns for 39 species

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Colostethus marchesianus	3	2	2	2	2	1	2	–	–	–	–	–	–	–	–	2	3	3
Dendrobates femoralis	2	2	2	2	1	1	–	–	–	–	–	–	2	2	2	2	2	2
Dendrobates petersi	–	–	–	–	–	–	–	–	1	1	2	2	2	1	1	–	–	–
Dendrobates pictus	–	3	1	3	2	2	2	2	2	1	1	2	2	1	–	1	2	2
Dendrobates trivittatus	2	2	2	2	2	1	1	2	2	2	2	2	1	2	1	2	2	2
Bufo marinus	–	–	–	–	–	–	–	–	–	1	1	1	1	–	–	–	–	–
Bufo typhonius	3	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1	–	–
Dendrophryniscus minutus	4	3	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Adenomera hylaedactyla	2	2	2	2	2	2	1	1	–	–	–	–	–	–	–	–	2	2
Ceratophrys cornuta	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1
Eleutherodactylus peruvianus	1	1	1	1	1	1	1	1	1	–	–	–	–	–	2	2	2	2
Leptodactylus pentadactylus	–	1	–	–	–	1	–	–	–	–	–	–	–	–	1	1	1	1
Leptodactylus rhodomystax	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Leptodactylus wagneri	2	2	2	2	2	–	–	–	–	–	–	–	–	–	–	–	1	3
Physalaemus petersi	1	–	–	–	–	–	–	–	–	–	–	3	2	–	–	3	1	–
Hyla boans	–	–	–	–	–	–	–	1	1	2	2	2	2	2	1	1	–	–
Hyla brevifrons	3	3	2	3	3	3	–	–	–	–	–	–	–	–	–	–	–	3
Hyla fasciata	2	1	3	1	2	2	3	2	1	–	–	–	–	–	–	–	–	–
Hyla granosa	3	3	2	2	3	2	2	–	–	–	–	–	–	–	–	–	–	2
Hyla leucophyllata	–	2	–	1	2	2	2	–	–	–	–	–	–	–	–	–	–	–
Hyla marmorata	3	2	3	2	2	3	2	2	–	–	–	–	–	–	–	–	–	–
Hyla parviceps	2	3	3	2	3	4	3	2	2	1	2	–	–	–	–	–	4	3
Hyla rhodopepla	3	3	–	3	3	3	2	–	–	–	–	–	–	–	–	–	4	4
Hyla riveroi	3	2	2	3	4	4	3	–	–	–	–	–	–	–	–	–	4	3
Hyla rossalleni	3	3	2	3	1	–	2	–	–	–	–	–	–	–	–	–	–	2
Hyla saraycuensis	3	3	3	3	3	2	2	–	–	–	–	–	–	–	–	–	2	2
Hyla sp.	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ololygon cruentomma	4	2	3	2	3	2	–	–	–	–	–	–	–	–	–	–	–	4
Ololygon garbei	2	2	–	2	–	1	1	2	1	–	–	–	–	–	–	–	–	1
Ololygon rubra	4	4	4	3	4	4	4	3	–	–	–	–	–	–	–	1	–	2
Osteocephalus leprieurii	1	1	1	1	1	1	1	1	1	–	–	–	–	–	2	2	2	2
Osteocephalus taurinus	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	3	2	–
Phrynohyas coriacea	–	1	1	1	–	–	1	–	–	–	–	–	1	1	–	–	1	1
Phyllomedusa tarsius	1	1	1	1	1	1	–	–	–	–	–	–	–	–	–	–	2	2
Phyllomedusa tomopterna	–	1	1	1	1	1	1	1	–	–	–	–	–	–	–	–	1	–
Phyllomedusa vaillanti	1	1	1	1	1	1	1	1	–	–	–	–	1	1	–	–	1	1
Chiasmocleis ventrimaculata	4	–	–	4	2	3	–	–	–	–	–	–	–	–	–	–	–	4
Ctenophryne geayi	2	–	–	1	2	–	1	–	–	–	–	–	–	–	–	1	1	1
Hamptophryne boliviana	4	1	2	3	2	3	–	–	–	–	–	–	–	–	–	1	4	4

1 = ≤ 5, *2* = > 5, *3* = > 10, *4* = ≥ 50 synchronously calling males

rary pond dried up (7th period, end of February) juveniles and adult dendrobatids were observed.

3) Big temporary pond/Plot 4 (Figs. 8 and 9). Calling males of 23 species were found at this aquatic breeding site which was filled with water throughout the rainy season. During the 4th period (January) the highest number of species (11) called. A chorus of 8 synchronously calling species was observed. Two microhylids, *Chiasmocleis ventrimaculata* and *Hamptophryne boliviana* were heard calling with at least 50 males. *C. ventrimaculata* is an extremely expolsive breeder, calling a few days a year in great choruses at certain ponds. *H. boliviana*, on the other hand, is an explosive breeder with many synchronously calling males; but a few individuals were observed calling over a longer period.

Corresponding to peak of breeding activity, the highest number of individuals was registered in the 4th period (January). Eighty males and only 5 females were located in the 100 m^2 plot. After January the number of adult individuals decreased rapidly. During the 8th period (end of March until early April) the first juvenils appeared in the wet area of the drying pond.

4) Forest edge pond. Twenty species were calling at this temporary pond although it was filled with water for a maximum of only 44 days. The life span of this pond may have been too short for some species to complete larval development; however, it was, the only pond situated at the forest edge and attracted frogs living in the area under cultivation. The highest number of species with synchronously calling males at this site was 9. The most common species was *Ololygon rubra*. It was found 10 times in choruses with at least 50 males. *Hyla riveroi* and *Hyla parviceps* were also found in such high concentrations.

Males of *Ololygon rubra* and *Hyla marmorata* were calling on March 22 and 28 although the pond had dried up. On March 28 an amplectant pair of *O. rubra* and a gravid female of *H. marmorata* also were found. The next aquatic environment, the temporary stream, was about 120 m away from the forest edge pond.

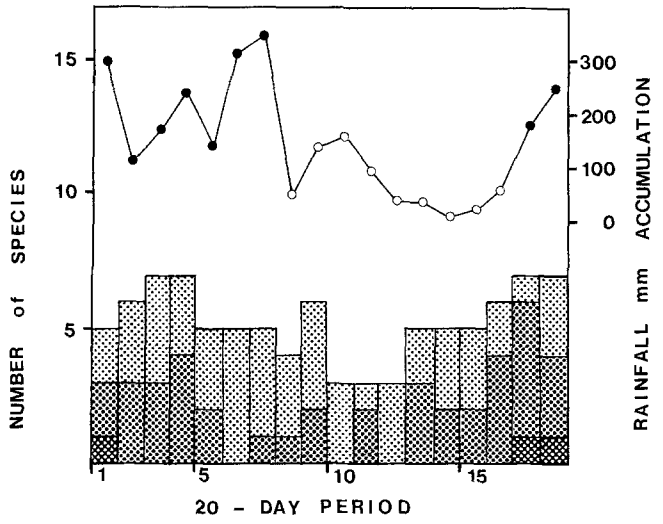

Fig. 6. Calling patterns of 8 species at the ephemeral puddles

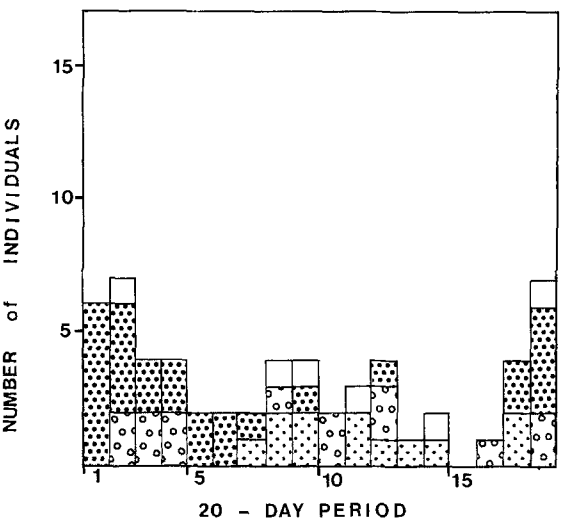

Fig. 7. Number of individuals found at plot 1

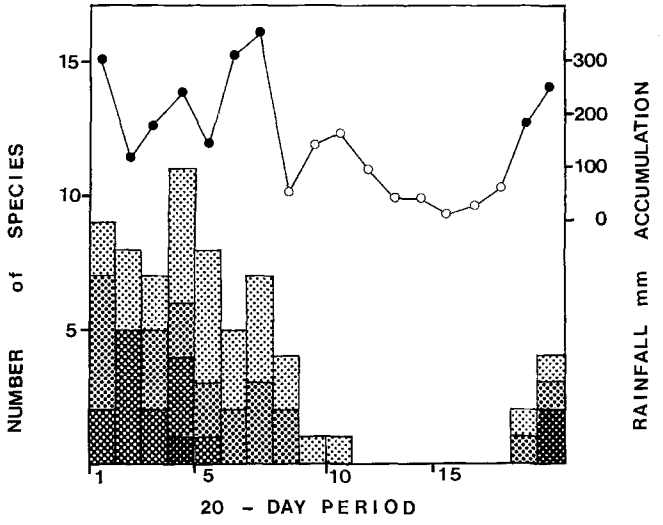

Fig. 8. Calling patterns of 23 species at the big temporary pond

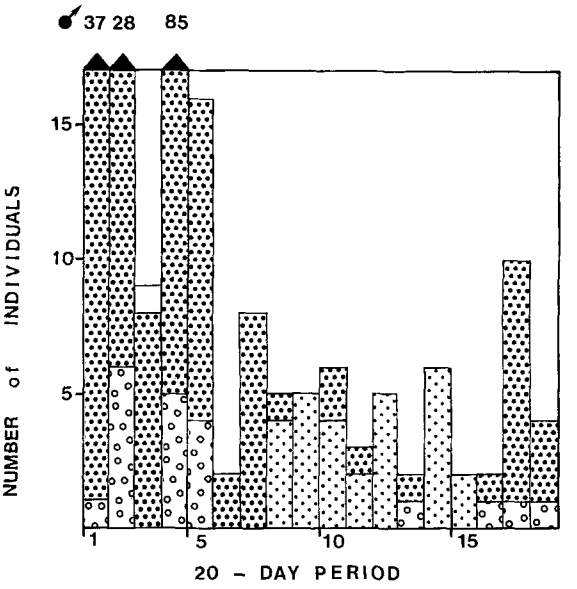

Fig. 9. Number of individuals found at plot 4

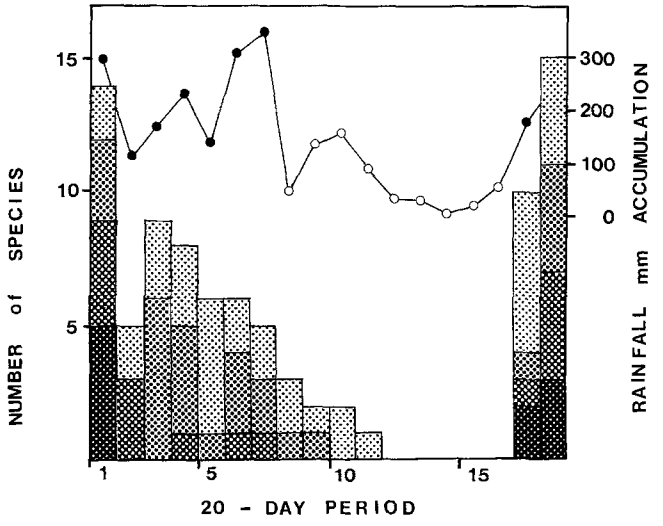

Fig. 10. Calling patterns of 23 species at the permanent pond

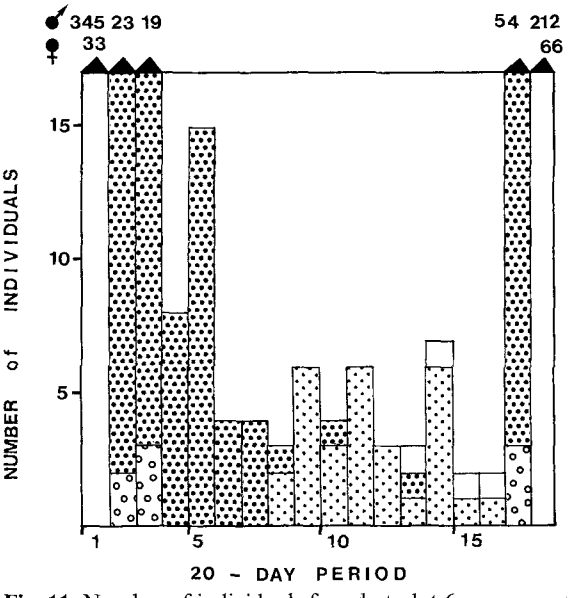

Fig. 11. Number of individuals found at plot 6

Explications to:

Figs. 6, 8, 10: Vertical bars = 4 frequencies of calling males from light to dark: ≤ 5, > 5, > 10, ≥ 50 synchronously calling males
Figs. 7, 9, 11: *Open bars* adult but sex unknown, *bars with circles* females, *bars with broad stipples* males, *bars with light stipples* juveniles

C) Permanent aquatic sites

1) Permanent stream/Plot 3. The most common frog was *Dendrobates pictus*, which called nearly throughout the year. In June and July the current of the stream nearly stopped; a number of deep depressions remained filled with water. Calling males and foam nests of the leptodactylid *Physalaemus petersi* were observed in those depressions.

At the beginning of the rainy season, after a heavy rain on the morning of September 14 (32.9 mm precipitation), about 25 *Osteocephalus taurinus* males were calling at 21:00 from water-filled depression at the permanent stream. Such a great assemblage of this large hylid was observed only once. On September 19, *Hyla riveroi* called in a chorus of at least 50 males. This was the only species that called at such a high frequency at that site.

The number of individuals found in plot 5 never exceeded 7. Most of the specimens captured were dendrobatids.

2) Permanent Pond/Plot 6 (Figs. 10 and 11). Reproductive activities of anurans were concentrated at this site. Calling males of 23 species were observed here. A maximum of 12 species called synchronously. Six species, *Chiasmocleis ventrimaculata*, *Hamptophryne boliviana*, *Hyla parviceps*, *H. rhodopepla*, *Ololygon cruentomma*, and *O. rubra* called at frequencies with more than 50 males. Such high concentrations of frogs were only observed on 7 days during the year. Reproductive activities were highest at the beginning of the rainy season but decreased rapidly after the end of November (even though the pond's maximum extension was measured in January). From June until mid-September no frog was found calling at this site.

The highest concentration of individuals was observed in November. 378 adult anurans were registered in the 100 m^2 plot. Ten times more males (345) than females (33) were counted during a period of about 2 h. After November, adult individuals diminished rapidly. Juveniles appeared during the 8th period (end of March).

Discussion

The single physical factor rainfall distribution regulates anuran reproductive patterns in tropical areas characterized by a pronounced dry season (Heusser 1969; Heyer 1973). The tropical study site Panguana has a pronounced dry season (20% of annual rainfall accumulation) lasting from mid-March until mid-September. Neotropical anurans are extremely dependent on rainfall. This may be shown by a comparison with Santa Cecilia, a study site in the upper Amazon basin (Ecuador) where rainfall distribution is aseasonal (Duellman 1978).

Of 46 species showing reproductive activities during the study at Panguana, only 7 (*Adenomera hylaedactyla*, *Dendrobates petersi*, *D. trivittatus*, *Eleutherodactylus carvalhoi*, *E. peruvianus*, *E. toftae*, *Hyla sp.*) do not occur at Santa Cecilia. There, 16 species were observed breeding throughout the year (Crump, 1974). Of these species, 9 (*Bufo typhonius*, *Dendrophryniscus minutus*, *Hyla fasciata*, *H. parviceps*, *Ololygon rubra*, *Ischnocnema quixensis*, *Colostethus marchesianus*, *Dendrobates femoralis*, *D. pictus*) occur also at Panguana; where their reproductive patterns are all seasonal.

Seven different reproductive modes, according to Crump (1974), occurred (p 5, Table 4). Twenty one species (45.7%) have the primitive mode of reproduction with egg-deposition and development in water (Crump 1974; Duellman and Trueb 1986). The development of 40 species (87.0%) depends on aquatic sites; eggs are laid on vegetation above water (8 species), in foam nests (5), or carried on the back of a parent to a water site (6). Therefore reproductive periods of 40 anuran species must be closely related with the availability of aquatic sites. The reproduction of most of these species is more or less restricted to the 6 month rainy season. Some species apparently avoided high concentrations of frogs at certain breeding sites. *Hyla boans* and *Bufo marinus* were found calling during the dry period at the river bank when the current of the Rio Llullapichis was slow. *Physalaemus petersi* was found reproductive at deep, water-filled depressions at the permanent stream which was slowly drying up during July. The foam nests of this species protect the larvae from desiccation and accelerate development because of higher temperatures within the foam nest (Lamotte and Lescure 1977; Dobkin and Gettinger 1985). At the beginning of the rainy season in September 1982, *Leptodactylus pentadactylus* started calling at the river bank. After the first major inundation of the river, calling males were heard only in primary rain forest.

Reproductive activities of anurans were not distributed regularly over the 6 months of the dry season. After heavy rains (more than 50.0 mm) at the beginning of the wet period, thousands of frogs migrated to the permanent pond. Choruses of at least 50 males (up to approximately 1,500) were observed here. Only *Chiasmocleis ventrimaculata* was an explosive breeder in the sense of Wells (1977). It was found only a few days a year but with hundreds of individuals. On the other hand, high densities of *Dendrophryniscus minutus* were observed for two months (Nov. to Dez. 1981) at the permanent pond. Up to 70 specimens (64 males and 6 females) were caught in the corresponding plot. Males, calling during day-time, seemed to stay at the breeding site. Gravid females were found regularly after heavy rains in the afternoon. Egg-deposition, especially on mossy tree-trunks (about 30 cm above water), was observed only during the night. Females apparently left the breeding site shortly after spawning because no females were found in the morning. In my opinion, this is the only possible interpretation of the male-female ratio (86.6% more males) for all species found in 6 different plots.

Colostethus marchesianus, *Dendrobates femoralis*, *D. pictus* and *D. trivittatus* started calling at the end of the dry period. After the first heavy rains at the beginning of the rainy season, many tadpole-carrying parents came to the permanent pond.

Even species that prefer temporary aquatic sites (e.g. *Hyla riveroi*, *Ololygon cruentomma*, *O. rubra*, *Phyllomedusa tarsius*, *Leptodactylus wagneri*) appeared first at the permanent pond, but could be observed only once or twice. As soon as temporary breeding sites were available for reproduction (end of December) these species migrated to temporary sites.

Characteristic of the anuran distribution at the permanent pond are the high densities at the beginning of the rainy season. Up to 378 individuals were counted in the corresponding plot. Calling males advertise a breeding area to females, and greater choruses attract females from longer distances (Wells 1977); but predators are also attracted (Ryan et al. 1981). I observed that the number of predators

at the permanent pond such as crocodiles (*Palaeosuchus trigonatus*), snakes (e.g. *Helicops angulatus*), and large spiders increased with the number of anurans. Ryan et al. (1981), however, calculated that for the individual frog a lower predation risk is associated with larger choruses.

A few weeks after the beginning of the rainy season (January) the breeding activities of anurans changed from the permanent pond to temporary aquatic environments. The high density of tadpoles in the permanent pond after the spawning of a great number of frogs must be taken into consideration. Inter- and intraspecific competition influences growth and survival of tadpoles (Wilbur 1972, Woodward 1982) Besides, larvae of naiads, waterbugs (*Lethocerus delpontei*), crabs (*Goyazana sp.*), fish (*Hoplias marabaricus*, *Aequidens sp.*), and turtles (*Phrynops nasutus wermuthi*, *Platemys platycephala*) live in the permanent pond (Schlüter 1984). They are possible predators and major factors controlling tadpole populations (Macan 1966; Seigel 1983). I assume that the reproductive patterns of the predators are correlated with the amount of tadpoles during the rainy season. Therefore it seems reasonable to move to temporary aquatic sites as soon as they are available even though larvae may be threatened by desiccation (Heyer et al. 1975). *Leptodactylus wagneri* was one of the first frogs to come to temporary aquatic environments. This broad-niched species (Heyer and Belin 1973) constructs foam nests which protect the tadpoles from a possible desiccation of the temporary breeding site. With the high amount of rainfall during January, these sites became more stable. This development is correlated with the peak of breeding activities of anurans at temporary environments. At the same time only a few males were calling at the permanent pond.

A special breeding site was the forest edge pond, which attracted many hylids from the nearby grassland. Although 20 species (especially *Hyla marmorata*, *H. riveroi*, *Ololygon cruentomma* and *O. rubra*) and great choruses of frogs were observed, this pond was only filled a few days (a maximum of 44) with water. Water was probably not present long enough for successful reproduction. Nevertheless the forest edge pond exerted a great attraction to frogs because, after a short rainshower in March, calling males and gravid females of *H. marmorata* and *O. rubra* were found although the pond was not filled with water.

The reproduction of 6 species (13%) is completely independent of aquatic breeding sites. The juveniles develop within a foam nest (*Adenomera hylaedactyla*) or within the egg-capsule (Eleutherodactylus spp.). But even these species were not active continuously throughout the year. Calling males of *A. hylaedactyla* and of *Eleutherodactylus peruvianus* were heard predominantly during the rainy season. Gravid females of Eleutherodactylus spp. were found especially during the wet period.

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