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Reproduction, Tadpoles, and Ecological Aspects of Three Syntopic Microhylid Species from Peru*) (Amphibia: Microhylidae)

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With 10 figures and 2 tables

Summary

Ecological data on the syntopic microhylid species *Chiasmocleis ventrimaculata* (Andersson, 1945), *Ctenophryne geayi* Mocquard, 1904, and *Hamptophryne boliviana* (Parker, 1927) were gathered during several stays in the Peruvian Biological Station Panguana. At a black water pond spawning is coincident with a remarkable increase of precipitation at the beginning of the rainy season and a short rainless period immediately after the first heavy rain. Segregation of calls, calling sites and oviposition sites is remarkable. Reproductive periods, amplexus, clutch and egg sizes, tadpoles, prey selection, predation, and defensive behaviour are described. Associated frog species are indicated.

Key words: Amphibia; Anura; Microhylidae; *Chiasmocleis ventrimaculata*; *Ctenophryne geayi*; *Hamptophryne boliviana*; reproduction; calls; calling sites; tadpoles; prey selection; predation; defensive behaviour; Amazonian Peru.

Resumen

– Reproducción, renacuajos y aspectos ecológicos de tres espécies sintópicas de microhílidos del Perú (Amphibia, Microhylidae) –

Durante varias estadías en la Estación Biológica Panguana se juntaron datos ecológicos sobre las especies sintópicas de microhílidos *Chiasmocleis ventrimaculata* (Andersson, 1945), *Ctenophryne geayi* Mocquard, 1904, y *Hamptophryne boliviana* (Parker, 1927). En el investigado estanque de agua negra toda la reproducción sucede coincidentemente con un aumento evidente de precepitación y una corta época seca inmediatamente después de la primera lluvia fuerte. La segregación de voces, sitios de vocalización y sitios de oviposición es obvidia. Se describe sitios de reproducción, amplexus, tamaño de postura y huevos, renacuajos, selección de presa, predación, y comportamiento defensivo. Se presenta especies asociadas.

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Zusammenfassung

Während mehrerer Aufenthalte im Gebiet der Biologischen Forschungsstation Panguana wurden ökologische Daten über die syntopischen Microhyliden *Chiasmocleis ventrimaculata* (Andersson, 1945), *Ctenophryne geayi* Mocquard, 1904, und *Hamptophryne boliviana* (Parker, 1927) zusammengetragen. An einem Schwarzwassertümpel fiel die Fortpflanzung immer in den Beginn der Regenzeit, und zwar in eine kurze regenfreie Phase unmittelbar nach dem ersten starken Regenfall. Die Abgrenzung der Paarungsrufe, Ruf- und Laichplätze ist deutlich. Fortpflanzung, Amplexus, Laich- und Eigrößen, Kaulquappen, Nahrung, Feinde und Abwehrverhalten werden beschrieben. Weitere, in dem untersuchten Gewässer vorkommende Frosch-Arten werden genannt.

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1. Introduction

The South American microhylids *Chiasmocleis ventrimaculata, Ctenophryne geayi,* and *Hamptophryne boliviana* are sympatric throughout their western range, the upper Amazon Basin of Ecuador and Peru. At Panguana, Peru, they are syntopic (in the sense of Rivas, 1964) at least during the rainy season when they inhabit the leaf litter and reproduce synchronically at the same small blackwater pond. Nearly nothing is known about their habits during the dry season. Observations on calling individuals and chorusing frogs of these species (Nelson, 1973; Schlüter, 1980) gave some information about their ecology. Cocroft & Hambler (1989) examined a commensal relationship between *C. ventrimaculata* and the burrowing spider *Xenesthis immanis.*

Ecological studies on anurans of Panguana were carried out by the senior author during various stays between 1977 and 1988, raising the species-list from 53 (Toft & Duellman, 1979) to 71 species (Schlüter, 1983). In 1988, we made additional observations on the reproduction of *Ctenophryne geayi.* All studies were carried out at a permanent blackwater pond, which is a breeding site of *Chiasmocleis ventrimaculata*, *Ctenophryne geayi*, *Hamptophryne boliviana* and the calling and/or breeding site of more than 30 other frog species (Schlüter, 1979, 1980, 1983)[1]) (Fig. 1, Table 1). Once every year after the first heavy rainfall at the beginning of the rainy season (Figs. 2, 3, 9), thousands of microhylid frogs migrate to the pond giving an ear-deafening mass concert which lasts about 36 hours (Schlüter, 1980, 1983). At

[1]) Aichinger (1987) confirmed these results and others from the same study site.

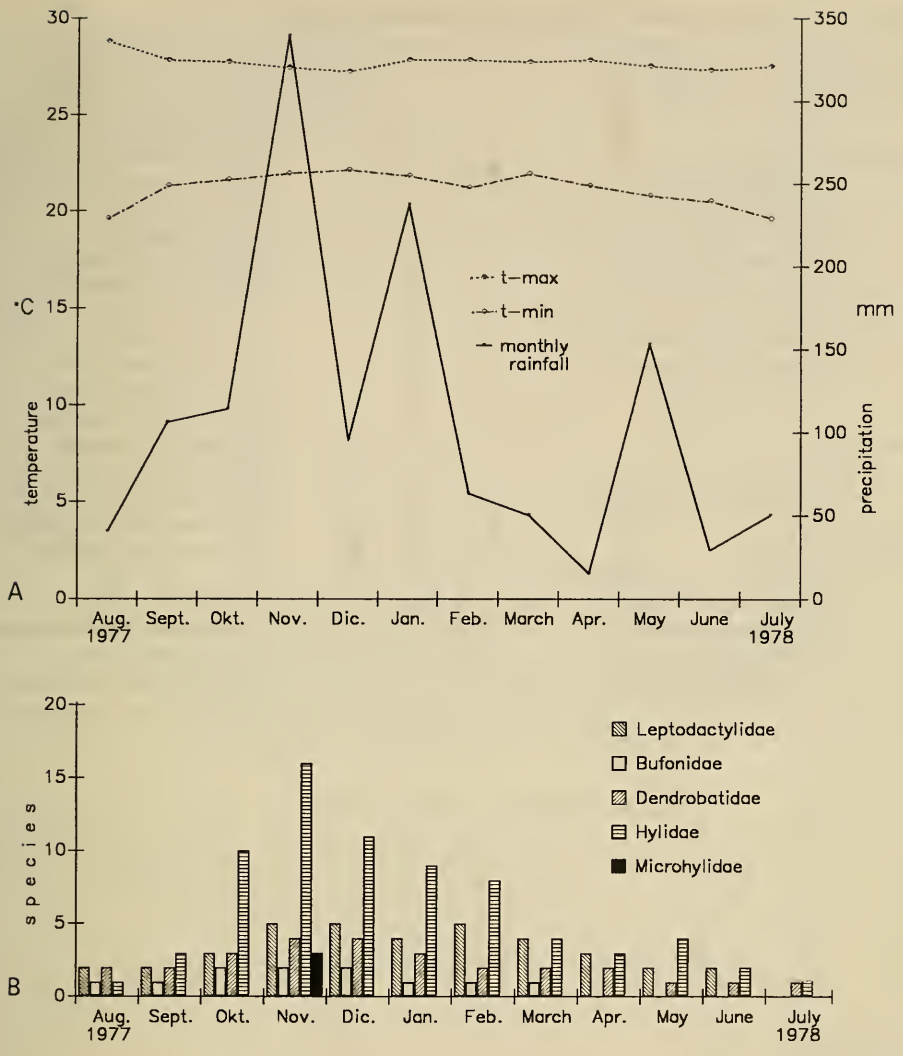

Fig. 1. Investigation-period August 1977 – July 1978. – A. Monthly mean maximum and minimum of air temperatures and monthly rainfall accumulation; – B. Species diversity of frogs at the blackwater pond.

the end of the concert frogs leave the pond which is sewed over with eggs. The development of eggs takes place during a short, rainless period within the rainy season, immediately after the above mentioned heavy rainfall.

This report increases our ecological understanding of sympatric members of the Microhylidae. The following aspects are discussed: reproductive periods, calls, calling sites, amplexus, oviposition sites, clutch and egg sizes, number of eggs in clutches, tadpoles, prey selection, predation, and defensive behaviour.

Table 1. Amphibian species diversity at the blackwater pond.

Caeciliidae
Siphonops annulatus

Leptodactylidae
Ceratophrys cornuta
Edalorhina perezi
Eleutherodactylus peruvianus
Eleutherodactylus toftae
Eleutherodactylus spp.
Leptodactylus pentadactylus
Leptodactylus wagneri
Phyllonastes myrmecoides
Physalaemus petersi

Bufonidae
Bufo marinus
Dendrophryniscus minutus

Dendrobatidae
Colostethus marchesianus
Epipedobates femoralis
Epipedobates petersi
Epipedobates pictus
Epipedobates trivittatus

Hylidae
Hyla brevifrons
Hyla calcarata
Hyla granosa
Hyla parviceps
Hyla rhodopepla
Hyla rossalleni
Hyla sarayacuensis
Ololygon cruentomma
Ololygon funerea
Ololygon garbei
Ololygon rubra
Osteocephalus leprieurii
Osteocephalus taurinus
Phrynohyas coriacea
Phyllomedusa palliata
Phyllomedusa tarsius
Phyllomedusa tomopterna
Phyllomedusa vaillanti

Microhylidae
Chiasmocleis ventrimaculata
Ctenophryne geayi
Hamptophryne boliviana

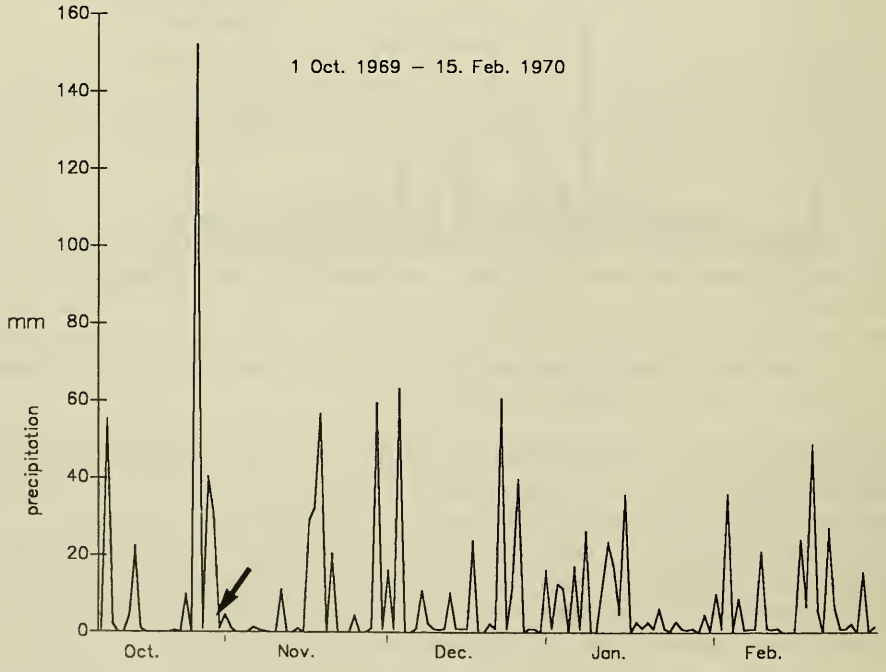

Fig. 2. Values of precipitation during rainy season 1969/70 and spawning (mass concert) of the three microhylid species at the investigated pond (arrow). – From measurements by H.-W. and M. KOEPCKE.

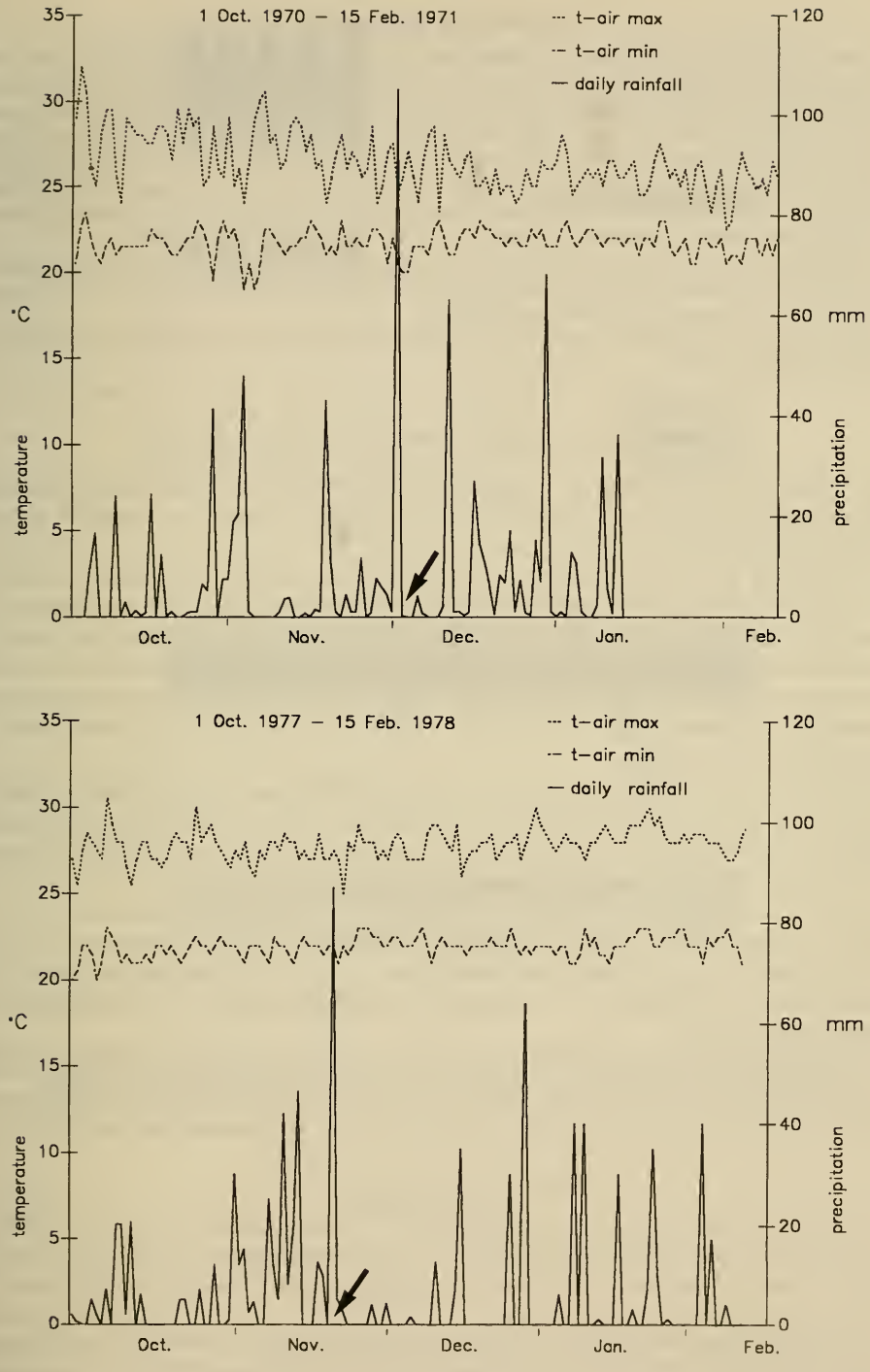

Fig. 3. Values of variables during rainy seasons 1970/71 and 1977/78 and spawning (mass concerts) of the three microhylid species at the pond (arrows). – Values of 1970/71 from measurements by H.-W. and M. Koepcke.

2. Study Site and Methods

The study site was Panguana, a field station in the upper Amazon Basin on the lower Río Yuyapichis (= Llullapichis), about 5 km upstream from its confluence with the Río Pachitea (about 9°35'S, 74°56'W, elevation 220 m; for maps and detailed descriptions see KOEPCKE, 1972; TOFT & DUELLMAN, 1979). The total annual rainfall is about 2000–3000 mm (HANAGARTH, 1981; RÖMBKE & VERHAAGH, 1987). The wet season from October to April comprises 80% of the rainfall; it is followed by a distinct dry season (Fig. 1). The temperature (in shade) is mostly between 22 and 30 °C, but usually once a year, in June or July, cold southerly winds, „friados" or „friajes", can drop the temperature to 12 °C (HANAGARTH, 1981).

Most obsvervations on the microhylids from Panguana were made at the mentioned permanent blackwater pond. During rainless season this pond has a surface of about 2–4 m²; during rainy sesaon it increases to more than 1200 m².

The calls were recorded by means of a tape recorder (SONY-D6C) and analyzed with a Kay DSP Sonagraph 5500.

3. Spatial and Temporal Patterns of Reproduction

During their mating time, *Chiasmocleis ventrimaculata*, *Ctenophryne geayi*, and *Hamptophryne boliviana* are active by day and night. Usually the temporal pattern of their choruses is as follows:

At midday after the first rainfall above average (about 60 mm or more), males of *C. ventrimaculata* and *H. boliviana* appear near the pond, first calling on land from leaf litter, later from their calling sites described below. Females reach the pond by sunset; the oviposition of both species mainly occurs during the night. Chorusing continues throughout the next day and night with a second peak of ovipositions during the following night. On the third morning, the frogs leave the pond which is sewed over with clutches.

Because of the hidden existence of *C. geayi*, nothing can be said about its time of appearance at the investigation pond. The calling activity usually begins at sunset after the first rainfall above average, continues throughout the next day and night and ends on the third day before sunrise.

Results on population densities are preliminary. The highest population density has *C. ventrimaculata* (app. 3.000–4.000 individuals; males : females 12 : 1). In *H. boliviana* the population is calculated about 1.500–2.500 individuals (males : females about 6 : 1). Because of its hidden way of life nothing can be said about the density of *C. geayi*.

The oviposition site of all three species is quiet water (Reproductive Mode No. 1 sensu CRUMP, 1974; DUELLMAN, 1985; DUELLMAN & TRUEB, 1986), with differences mentioned below. The observations on the clutches are summarized in Table 2.

4. Life Histories

4.1. *Chiasmocleis ventrimaculata*

4.1.1. Call

The advertisement call (at 26 °C air temperature) (Fig. 4 A; SCHLÜTER, 1980) consists of a series of short pulses. The repetition rate of these pulses is 7–8 per second (pulse length 130–140 ms, mean value 135; 22–63 pulses per call). The dominant frequency range is 5.120–6.960 Hz, e. g. much higher than calls of this species from Vaupes, Colombia (3.350–3.700 Hz after NELSON, 1973).

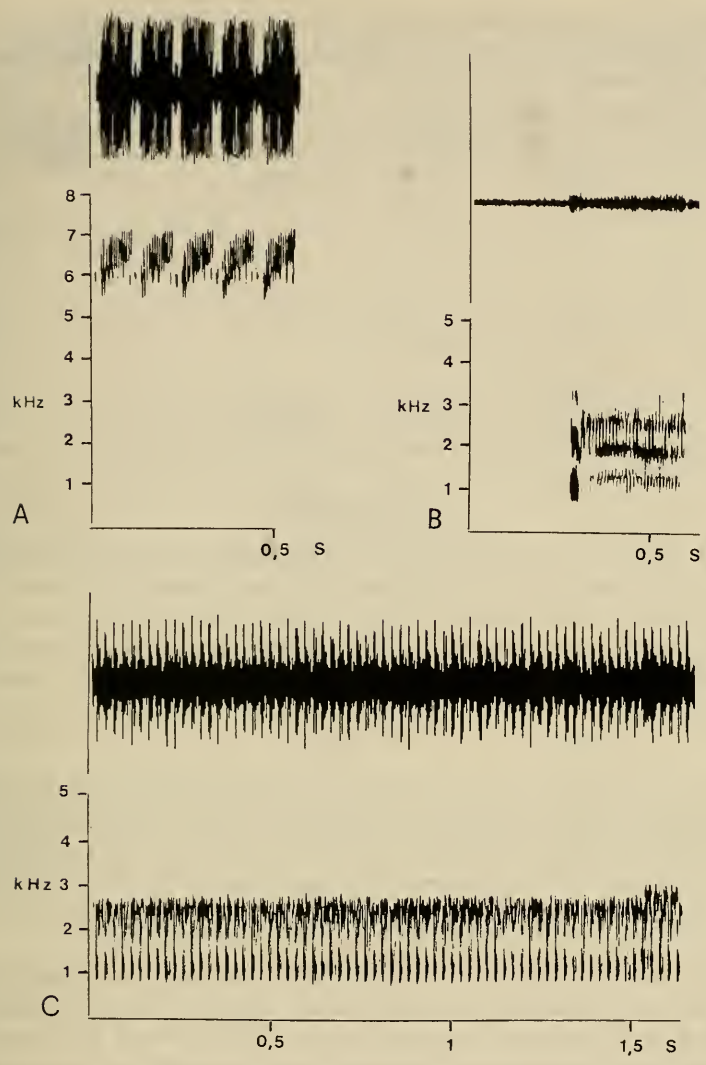

Fig. 4. Sonograms (below) and oscillograms (above) of advertisement calls of the three investigated species; air temperature: 26 °C. – A. *Chiasmocleis ventrimaculata*, – B. *Hamptophryne boliviana*, – C. *Ctenophryne geayi*.

4.1.2. Calling Sites and Amplexus

Males of *C. ventrimaculata* call from floating twigs and leafs, assuming a typical posture of elevating their inflated vocal sacs (SCHLÜTER, 1980). Males calling from underleaf litter (NELSON, 1973) could never be observed at Panguana. Actual mating occurs during day and night, but mainly at night between 20.00 and 4.00 hr. The female, attracted by the male's call, moves floating to the male which jumps into the water, amplecting the female axillary. The male does not vocalize while in amplexus. The amplexus mainly lasts up to 30 minutes.

Table 2. Numbers and measurements of eggs and clutches in *Chiasmocleis ventrimaculata*, *Ctenophryne geayi*, and *Hamptophryne boliviana*. – Numbers in parentheses: extreme values.

	C. ventrimaculata		*C. geayi*	*H. boliviana*	
Year	1977	1978	1988	1977	1978
Clutch number	90	100	4	140	150
Clutch diameter [cm]	23 (18–25)	23 (18–26)	29 (27–31)	10 (9–12)	10 (9–12)
Number of eggs per clutch	389 (282–448)	370 (222–430)	569 (520–610)	233 (182–272)	220 (160–280)

4.1.3. Clutch Size

The entire clutch of *C. ventrimaculata* ist held together by a thin layer of viscous jelly, but it is, like clutches of *Ctenophryne geayi*, less compact than those of *Hamptophryne boliviana*. 90 clutches (in 1977), and 100 clutches (in 1978) were measured. Each egg (diameter 2 mm) is surrounded by a gelatinous capsule of about 6 mm. The numbers and measurements of eggs and clutches are summarized in Table 2.

4.1.4. Tadpole

Hatching of the tadpoles occurs about 36 hrs after fertilization (water temperature 26 °C). Immediately after hatching the black larvae remain motionless in a vertical position (head up) under the surface. 24 hrs after hatching their position changes from vertical to diagonal (angle to water surface about 45°), remaining motionless. 48 hours after hatching they begin to move. The following description is based on specimen No. SMNS 7117 in Stage 36 (sensu Gosner, 1960) (Fig. 5).

The typical pond tadpole has a total length of 17 mm and a body length of 7 mm. Body depressed and about twice as wide as deep; widest at the level of the eyes. Eyes large, directed laterally, widely separated. Snout in dorsal view broad and bluntly rounded, rounded in lateral view. Nostrils absent. A single, median posterior spiracle; anal tube median. Caudal musculature of xiphicercal tail becomes slender posteriorly and extends beyond caudal fins. Dorsal fin deepest at about two-thirds of tail, not extending on body. Ventral fin uniform in depth on anterior 3/4 of tail. Distal part of tails curves dorsally; both fins narrow distally.

Mouth small, terminal. Upper lip large, fleshy, covering the orifice. Horny mouthparts absent.

The living tadpoles are nearly uniform pale brown, but more heavily pigmented than tadpoles of *Ctenophryne geayi*. The froglets leave the water after three weeks.

4.2. *Ctenophryne geayi*

4.2.1. Call

The advertisement call (at 26 °C air temperature) (Fig. 4 C; Schlüter, 1980) agrees with a call from Vaupes, Colombia (Nelson, 1973). It consists of a long series

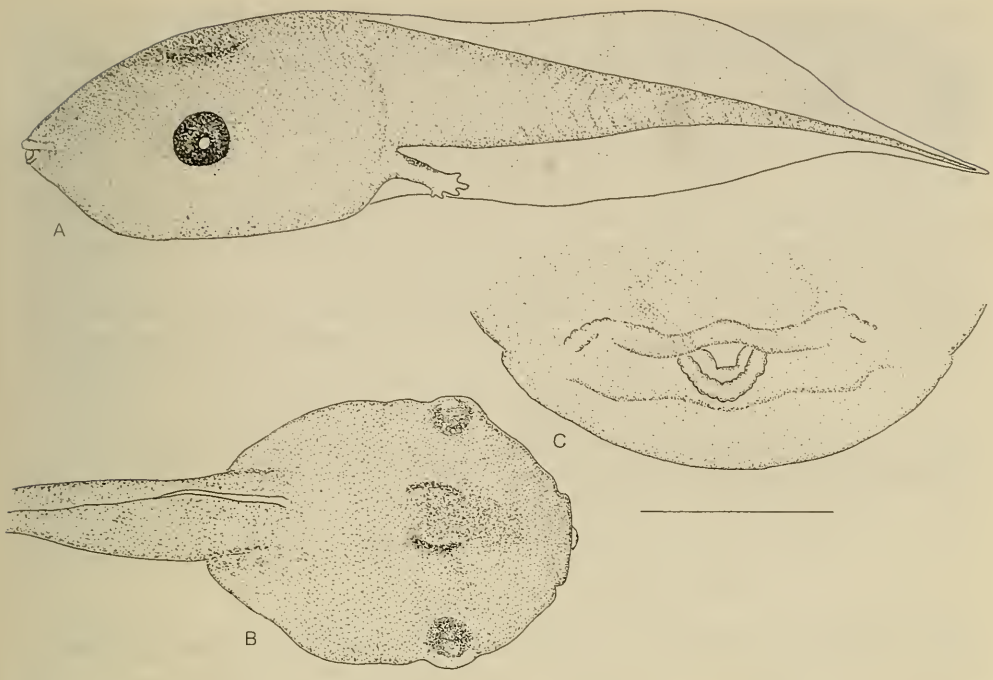

Fig. 5. Tadpole of *Chiasmocleis ventrimaculata* (SMNS 7117) in stage 36; total length = 17 mm. – A lateral view, – B. dorsal view, – C. mouthpart (scale: 1.5 mm).

of short pulses. The repetition rate of these pulses is 40–43 per second (pulse length 9–11 ms, mean value 10; 134–210 pulses per call). The dominant frequency range is 840–2.720 Hz. 98 analyzed calls had durations between 4,2 and 5,2 sec.

4.2.2. Calling Sites and Amplexus

The calling males of *C. geayi* remain under leaf litter at the edge of the pond. Mating occurs between 23.00 and 4.00 hr (only six pairs could be observed). The female, attracted by the male's call, moves to the male under leaf litter, while the male remains in a wet site under leaf litter. The amplexus is axillary; it also happens under leaf litter. The only four clutches which we found were also deposited under leaf litter. Males do not vocalize while in amplexus, which lasts up to three hours.

4.2.3. Clutch Size

Only four clutches were found and measured (in 1988). Each egg (diameter 2 mm) is surrounded by a gelatinous capsule of about 8 mm; the entire clutches are held together by a thin layer of viscous jelly, as in *Chiasmocleis ventrimaculata*. The results are summarized in Table 2.

4.2.4. Tadpole

Hatching of the tadpoles occurs about 36 hrs after fertilization (water temperature 26 °C). Immediately after hatching the black larvae remain motionless in a vertical position (head up) under the surface. 12 hrs after hatching their position changes

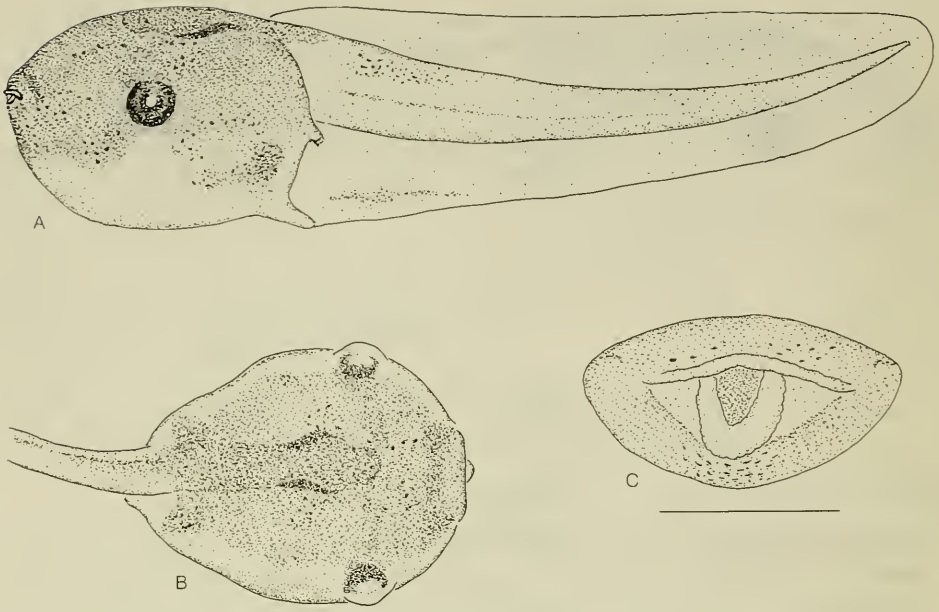

Fig. 6. Tadpole of *Ctenophryne geayi* (SMNS 7118) in stage 25; total length = 12 mm. – A. lateral view, – B. dorsl view, – C. mouthpart (scale: 1.5 mm).

from vertical to diagonal (angle to water surface about 45°), remaining motionless. 24 hrs after hatching the larvae are agile, moving mainly in a horizontal position. The following description is based on specimen No. SMNS 7118 in Stage 25 (sensu Gosner, 1960) (Fig. 6).

The typical pond tadpole has a total length of 12 mm and a body length of 5 mm. Body depressed, about twice as wide as deep; widest at level of eyes. Eyes large, directed laterally, widely separated. Snout in dorsal view broad and bluntly rounded, round in lateral view. Nostrils absent. A single, median posterior spiracle; anal tube median. Caudal musculature slender, equal in depth to dorsal fin at midlength of tail. Ventral fin half as deep as dorsal fin. Dorsal fin not extending on body. Dorsal and ventral fins extending to tip of tail. Tip of tail round.

Mouth small, terminal. Fleshy upper lip nearly covering orifice. Horny mouthparts absent.

Living tadpoles are pale brown, body and tail brown with darker brown mottlings dorsally and laterally; one pair of S-shaped dark brown patches on dorsum. The froglets begin to leave water after three weeks.

4.3. *Hamptophryne boliviana*

4.3.1. Call

The advertisement call (at 26 °C air temperature) (Fig. 4 B; Schlüter, 1980) consists of a note of 0,33 and 0,47 sec. The dominant frequency range is between 520 and 2.040 Hz (cf. Nelson, 1973, for Iparía, Peru). 200 analyzed calls had durations between 250 and 300 ms (mean value 280).

4.3.2. Calling Sites and Amplexus

Males of *H. boliviana* mainly call from floating structures (e. g. trunks) which are bigger than the floating calling sites of *Chiasmocleis ventrimaculata*. Actual mating occurs during day and night, but mainly at night between 20.00 and 4.00 hr. The female, attracted by the male's call, moves floating to the male which jumps into the water, amplecting the female axillary. The male does not vocalize while in amplexus. During the amplexus the female holds on to a trunk with its hands. Though some clutches are laid in free water, most amplecting pairs and clutches of *H. boliviana* were found in small depressions near the pond, e. g. waterfilled trails of mammals like Peccary (*Tayassu p. pecari*), Tapir (*Tapirus t. terrestris*) and Jaguar (*Panthera onca peruvianus*) (SCHLÜTER, 1983). The amplexus observed lasted up to four hours.

4.3.3. Clutch Size

The clutches of *H. boliviana* are smaller and more compact than those of *C. ventrimaculata* and *C. geayi*. 140 clutches (in 1977), and 150 clutches (in 1978) were measured. Each egg (diameter 1.5 mm) is surrounded by a capsule of about 4 mm. Results are summarized in Table 2.

4.3.4. Tadpole

Hatching of the tadpoles occurs about 36 hrs after fertilization (water temperature 26 °C). Immediately after hatching the black larvae remain motionless in a vertical position (head up) under the water surface. 24 hours after hatching some individuals

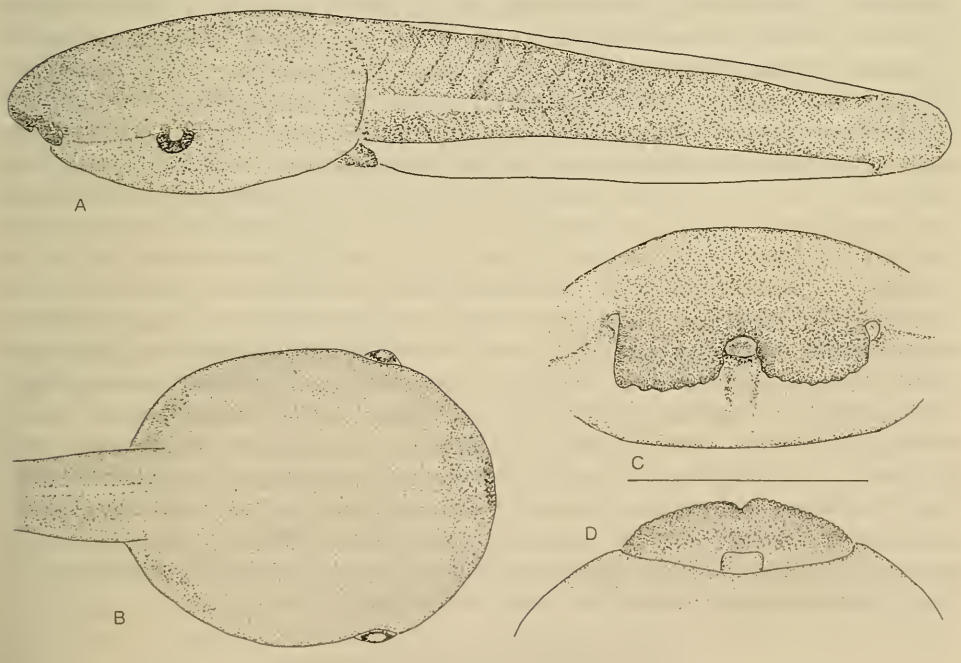

Fig. 7. Tadpole of *Hamptophryne boliviana* (SMNS 7119) in stage 25; total length 13 mm. – A. lateral view, – B. dorsal view, – C. mouthpart in frontal view (scale: 1.5 mm), – D. mouthpart in ventral view.

begin to move, but always return to the surface. 48 hrs after hatching their position changes from vertical to diagonal (angle to water surface about 45°), remaining motionless under the surface. 70 hrs after hatching about 60% of the larvae remain motionless under the surface in a horizontal position, while 40% are spread at different levels. Active individuals always move down diagonally and up passively in a horizontal position. From the ninth day after hatching, larvae move into different directions. The tadpole (SMNS 7119; Fig. 7; stage 25; total length 13 mm, body length 5 mm) agrees with the description given by DUELLMAN (1978).

5. Ecological Aspects

5.1. Prey Selection

At Panguana, *C. ventrimaculata* and *H. boliviana* are ant specialists in the sence of TOFT (1976, 1980). 220 stomachs of adult *C. ventrimaculata* were examined. Most of them were empty but 39 contained small ants (1–5 mm). Two individuals were observed feeding on mites at night. 160 stomachs of *H. boliviana* were examined. Most of them were empty, but 16 stomachs contained ants (2–10 mm). One contained parts of a dipteron, another remains of a juvenile frog. *C. geayi* seems to feed on different types of prey. Most of the investigated 52 stomachs were empty, but the stomachs of 12 individuals contained ants (3–5 mm) and beetles (5–9 mm).

5.2. Predation

The three microhylid species, their eggs, and tadpoles are picked up by a lot of predators. Tadpoles of *C. ventrimaculata* and *H. boliviana* could be observed being caught by Malacostraca (*Dilocarcinus* sp., *Goyazana* sp.). In captivity, an adult *C. ventrimaculata* was picked up by a *Goyazana* sp.; also larvae of Odonata fed on tadpoles of *Chiasmocleis* and *Hamptophryne*. Spiders (Avicularidae) which could be observed attacking tree frogs (hylids) are also suspected to feed on microhylids. In one case, a giant ant (*Dinoponera longipes*) was observed transporting a juvenile microhylid frog (not identified). Fishes like *Hoplias malabaricus* (Erythrinidae) and *Synbranchus marmoratus* (Synbranchidae) which live in the pond are known to feed on frogs and their larvae. Turtles (*Phrynops gibbus* and *Podocnemis unifilis*) fed on tadpoles. Caimans (*Paleosuchus trigonatus*), which were observed at the pond, are known to feed on frogs. Snakes seem to be the main predators of frogs (and sometimes of their larvae and eggs). We found the following frog-feeding snakes at the pond: *Chironius multiventris, Drymarchon poecilonata, Helicops angulatus, Imantodes lentiferus, Oxybelis argenteus* (Colubridae), *Micrurus s. surinamensis* (Elapidae), and *Bothrops atrox* (Crotalidae). Capped Herons (*Pilherodius pileatus*) could be observed catching frogs (and probably tadpoles). Sunbitterns (*Eurypyga h. helias*) and Double-toothed Kites (*Harpagus bidentatus*), also found at the investigated pond, are known to feed on frogs. Bats, probably *Trachops cirrhosus*, could be observed diving to the water level, especially during mass concerts. At Panguana, this frog-feeding bat was recorded by KOEPCKE (1987).

5.3. Defensive Behaviour

Besides their cryptic appearance, *Chiasmocleis ventrimaculata* and *Ctenophryne geayi* have a defensive behavior which enhances their resemblance to fallen leaves.

Fig. 8. Stiff-legged posture as a defensive behaviour of *Ctenophryne geayi*.

When *C. geayi* is threatened, it makes a short leap and lands with its legs stretched backwards in a stiff-legged posture (Fig. 8), just as described for the microhylid *Stereocyclops parkeri* (SAZIMA, 1978) and the leptodactylids *Proceratophrys appendiculata* and *P. moehringi* (SAZIMA, 1978; WEYGOLDT, 1986). This posture could be observed to last up to 4 minutes. Stiff-legged postures could also be seen in amplectant pairs of *C. ventrimaculata*. Males assume a posture of stretching their legs sidewards (SCHLÜTER, 1983).

5.4. Larval Habitat Partitioning

The tadpoles of *C. ventrimaculata* could be observed at different levels of the peripheral shallow water (depth of water about 60 cm) forming big, nearly motionless aggregations, in which each individual is positioned in the same direction. Aggregations of *H. boliviana* tadpoles, remaining motionless at the surface during the first four days, could mainly be found in waterfilled depressions (e. g. trails) near the pond, but also at the surface of the extreme peripheral shallow water (depth of the water about 20 cm). From the fifth day they began to occupy different water levels becoming more agile than tadpoles of *C. ventrimaculata*. Nothing can be said about the habitat preference of *C. geayi* tadpoles (the larvae described above were raised from eggs collected under leaf litter at the edge of the pond). It is supposed, that they either move into the pond when the water level increases or that metamorphosis takes place within waterfilled depressions under leaf litter.

6. Discussion

Southamerican lowland frog communities can present more than 80 species. Long-term studies on the ecology of Amazonian anuran communities are known from Belém, Brazil (CRUMP, 1971), Santa Cecilia, Ecuador (CRUMP, 1974; DUELLMAN, 1978), Manaus, Brazil (HÖDL, 1977), and Panguana, Peru (SCHLÜTER, 1983; AICHINGER, 1987). WEYGOLDT (1986, 1989) studied the ecology of a stream frog community in the Atlantic Mountains of Brazil during 15 years. Basic ecological principle, shown in all these works, is that two species cannot coexist occupying the same ecological niche.

More than 70 anuran species are known from Panguana. Of the more than 34 species which could be observed at the blackwater pond, the microhylids *Chiasmocleis ventrimaculata*, *Ctenophryne geayi*, and *Hamptophryne boliviana* have the shortest time of appearance. Their hidden way of life impedes field investigations, and notes on their ecology are very rare (NELSON, 1973; COCROFT & HAMBLER, 1989). The remarkable appearance of thousands of microhylid frogs during an extreme short period per year seems to be the only possibility to recognize some ecological differenciations in the field.

The advertisement calls of the three species are very distinct (NELSON 1973); SCHLÜTER 1980), and the calling site segregation is remarkable (SCHLÜTER 1980). A segregation of the oviposition sites is visible: periferal shallow water in *C. ventrimaculata*, mainly small waterfilled depressions at the edge of ponds in *H. boliviana*, and under leaf litter in *C. geayi*.

Amphibian larvae may partition their habitat in terms of space, time, or food (e. g. HEYER, 1973, 1976; WEYGOLDT, 1986). Primary plant production is not visible in the

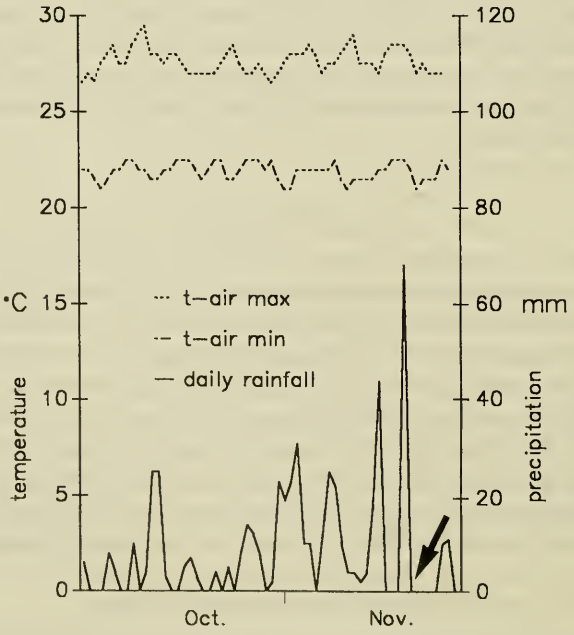

Fig. 9. Daily precipitation from 1 October 1978 to 28 November 1978 and spawning (mass concert) after the first rainfall above 60 mm.

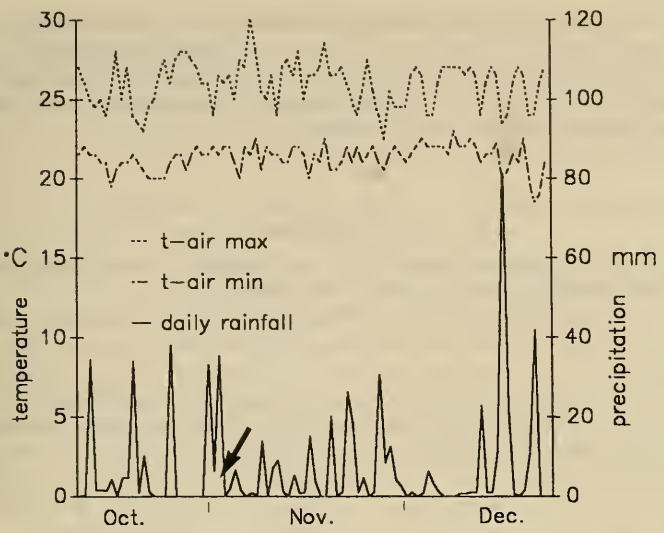

Fig. 10. Daily precipitation from 1 October to 28 December 1971 and spawning (mass concert) after two short rainfalls (arrow). – From measurements by H.-W. and M. Koepcke.

mainly overshadowed acid pond. Algae and submerge higher plants could not be found. Allochthone material, mainly from decomposing litter and insects, seems to be the main food of the tadpoles. Differences in food selection are not clear whereas habitat partitioning is obvious. The concentration of tadpoles (as well as spawning) in the periperal parts of the pond are interpreted as a protection from aquatic predators.

Of the environmental variables, only precipitation seems to guide the onset of reproduction. At the investigation pond, reproduction is coincident with a remarkable increase of precipitation and a short rainless period, immediately after the first heavy rain (Figs. 2 and 9). Changes in maximum and minimum air temperatures do not seem to trigger reproduction. Atmospheric pressure was not measured.

The rainy season 1971/72 was unusual regarding the amount of precipitation, and the spawning period of the frogs (Fig. 10). The oviposition started after two short rainfalls (32 mm on 25. X. and 33 mm on 27. X. 1971).

At other calling sites, e. g. temporary ponds („aguajales") and relatively permanent pools at the edge of streams, choruses were not synchronized with those of the investigated pond. Further studies are necessary to recognize the parameters of microhylid appearance and oviposition at different ponds in the investigated area and to recognize valid results on population densities.

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