PART 3

ANURAN SUCCESSION IN A TEMPORARY POND IN COLIMA, MEXICO

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Introduction

While studying the herpetofauna of the Nevado de Colima, Jalisco, we were able to study anuran succession in a temporary pond in a tropical deciduous forest (Fig. 1). The pond is in the State of Colima on the road from Colima to Tecoman, 2.4 km E. and 9.6 km S. of Colima at 520 m elevation. The dominant plants of the area are legumes (*Acacia* and *Prosopis*), with an occasional larger tree (*Crescentia*) and giant organ cacti (*Lemaireocereus*).

Our first visit to the pond was daytime, of July 11, 1967. We were attracted to the dry bed of the pond by male Leptodactylus labialis calling from hidden burrows in the cracked soil beneath rocks, logs, and debris. Rain began to fall at approximately 0100 hours on July 12 and continued until 0500. By 0800 about 20 cm of water had collected in the pond. Bufo marmoreus and Hypopachus variolosus were calling. We returned the same night and recorded calls of three additional species: Agalychnis dacnicolor, Diaglena spatulata, and Smilisca baudinii. We revisited the site on several days and nights through July 24, to collect tadpoles, adults and to record calls and new anuran visitors to the pond.

MATERIALS AND METHODS

Samples of the adult anuran fauna were taken 8 times in the period from July 11-24. Larval samples were taken at 3-4 day intervals. At-

tempts were made to sample microhabitats and morphologically distinct larvae. Larvae were returned to the laboratory for identification, staged (Gosner, 1960), and gut analyses were made on one or two larvae of three of the species. Only a few gut analyses were made because we were primarily interested in gross differences in feeding habits and had only a small sample of some species.

All specimens of adults and larvae have been deposited in the Los Angeles County Museum of Natural History.

RESULTS

A summary of the visits made to the pond, time of day, choruses, larval stages at time of collecting, and anurans present but not chorusing, are given in Table 1.

Species Accounts

Bufo marmoreus — Most of the breeding activity took place during the day of July 12. Several amplexing pairs were observed and mating calls were recorded. A few calling males were observed on the night of July 12, but none were seen or heard during the remainder of the study.

Agalychnis dacnicolor — Adults were found calling from vegetation in the pond and some distance from the shore on the night of July 12, and individuals continued to call throughout the study period. Several individuals were seen on the retaining wall of the pond on the night of July 12, but none were calling from these positions. Neither amplexus or eggs were observed, nor were tadpoles collected of this species. However, during the study period, egg masses were seen in other areas.

Diaglena spatulata — Adults were calling from rock walls, vegetation, and shoreline only on the night of July 12. Several amplexing pairs were found in the water. One individual was found on the night of July 13, crossing the road near the pond, but heading away from the water. Neither eggs nor tadpoles were collected.

Smilisca baudinii — This species was the most common, both in terms of adults present and number of larvae observed in the water. Adults called on every nightly visit and sometimes during the day. Tadpoles were observed in large swarms at times. Tadpoles were also observed feeding on vegetation on or near the surface of the pond. The anterior portion of the gut of the larvae has a manicotto (stomach-like, thickened walls). The total length of the gut is 12 times body length. The gut of one tadpole (stage 35), was filled with a mucoid-appearing matrix consisting of filamentous algae and diatoms. The larvae appeared to be scraping the algae and diatoms off of vegetation in the water. Adults were breeding thoughout the study period. The last sam-



Figure 1. Photograph of the study site at the termination of the study.

ples of larvae taken from the pond contained three or more temporal lots.

Leptodactylus labialis — Adult males were calling from terrestrial "incubating chambers" both night and day during the entire study. These chambers were found in clay soil, usually beneath rocks, logs, or other debris. Some chambers contained either calling males, foam nests, or were empty. The chambers were usually 30-40 mm in depth, with an entrance 20-30 mm in diameter. (Fig. 2). The main chamber was approximately 50 mm wide and 65 mm long. Some of the chambers contained another opening (probably an escape exit) 90-100 mm in a direction opposite the main entrance, connecting with the chamber by a tunnel about 10 mm below the soil surface.

On one occasion two chambers were found under the same rock, one with foam and eggs, the other empty. The foam was about 20 mm below the surface of the entrance. Yellowish eggs lacking melanophores were located in the lower half of the foam.

Apparently males attract females to the chambers, where the eggs are laid. The eggs hatch in the enclosed foam nest and the larvae remain within the foam until the first rain, at which time they float or swim from the nest to the pond. One preserved nest contained 247 larvae at devel-

opmental stage 25. It is possible more advanced stages may be reached before flooding releases the larvae from the nest. A second preserved nest contained 190 eggs. When one nest was uncovered, it flooded with water, and the larvae swam into the pond.

The majority of the tadpoles were observed in very shallow water near the edge of the pond. Three larval guts were examined. The gut is 8-10 times the body length. The largest example (stage 38) has a manicotto; this is not evident in smaller stages (25). The gut contents consist of a mud-silt matrix, with a few plant fibers and seeds, and unidentified debris. The larvae apparently ingest bottom material indiscriminately.

Leptodactylus melanonotus — Adult males and females were first observed on July 17, but none were calling. A large number were seen on July 24, again none were calling. The adults may have moved in for feeding and perhaps establishment of a breeding site. Actual reproduction may have been delayed because rain had not fallen at the pond since July 12, and the water level was receding.

Hypopachus variolosus — Adults were observed calling and in amplexus on July 12. Males were observed calling on July 13 but amplexus was not observed. Adults were not present at any other time during the study. Tadpoles of this species were relatively scarce. Improper sampling techniques or low larval survival rates may have accounted for their scarcity.

One tadpole gut was examined. The gut is 11 times the body length, and contains a homogeneous, silty-appearing matrix. These tadpoles seemingly vacuum the pond bottom, selecting small particles, and pass them to the gut via a mucus cord, as reported by Savage (1955).

Rana pipiens — This ubiquitous frog appeared at the pond on July 20, and was present during the remainder of the study. Never were they observed calling or in amplexus. This species was commonly encountered on the road following every rain, even though permanent water was several miles away.

DISCUSSION

There are definite differences in breeding periods and appearance of larvae. Bufo marmoreus, Diaglena spatulata, and Hypopachus variolosus are early breeders. They called for only a short period of time (24-36 hours), and left the pond by the second day following the first rain. Apparently these three species were less successful in egg laying and had a lower larval survival than the other species. Eggs of B. marmoreus were observed on July 11, larvae on July 14, but larvae were



Figure 2. Photograph of a foam nest of Leptodactylus labialis. Arrow indicates opening of the nest which was beneath a rock.

never collected again. *D. spatulata* eggs and larvae were never found and the adults had the shortest activity period at the site of all the anurans. *H. variolosus* eggs were observed on July 12. Larvae were taken first on July 17, and occasionally in later larval samples, but never in abundance.

Leptodactylus labialis and Smilisca baudinii are early breeders. Eggs and larvae were present on July 11 for L. labialis; eggs of S. baudinii were present on July 12 and larvae on July 14 and later. Adult males of the latter species continued to call throughout the study, and amplexing pairs were observed on at least three different nights. The larvae of these two species made up the bulk of larvae present at any one time in the pond.

Agalychnis dacnicolor appeared on the night of July 12 and called both night and day during the entire period of the study. However, amplexing pairs, eggs, and larvae were not observed. Nest sites may not have been available for this species. A. dacnicolor often lays its eggs in trees or branches overhanging the water. The large shrubs at the side of the pond (Fig. 1) could have provided adequate nesting sites,

but the water level never reached under these large shrubs during the study period. The species may also require a long calling period before breeding is actually achieved.

Both Leptodactylus melanonotus and Rana pipiens arrived at the pond towards the end of the study; no breeding activity was observed.

It is apparent that the number of species of adults breeding at any single time is not indicative of what species of larvae are present in the pond. There may be more species breeding than number of species of larvae using the pond at any one time.

The effect of continual rainfall on anuran succession at this site can only be imagined. Doubtless there would still be a succession, with some species breeding and leaving shortly after initial pond formation. The breeding period of some of these species, such as *H. variolosus*, might be extended, however. With continual rain, breeding would probably take place in the later arriving species, such as *L. melanonotus* and *R. pipiens*. It seems likely that at no time would the species of larvae in the pond exactly coincide with the breeding species.

There is a definite trend towards terrestrial adaptation in *Leptodactylus labialis*, as indicated by the partly terrestrial period of egg and larval development prior to the first rain. The presence of calling males, foam, and eggs and larvae in "incubating chambers" substantiates terrestrial breeding activity prior to the availability of standing water.

Apparently *L. labialis* has a competitive advantage in survival of eggs and young because of the "incubating chambers". Large numbers of metamorphosing larvae were observed on July 24, indicating an aquatic larval life of 13 days. The short aquatic larval life is related to the advanced hatching of the eggs and early larval development in the "incubating chambers".

Biotic Interactions: There appears to be both adult and larval ecological segregation. The calling sites of the adults (Fig. 3) are separated both horizontally and vertically. D. spatulata and S. baudinii are found most often associated with one another in similar calling sites. They occupy the same emergent plant tops in the pond, and call from the shore beneath low lying vegetation, and from open spaces along the shore. The mating calls of these two species are very different and effectively serve as a premating isolating mechanism (see sonagrams of D. spatulata in Porter, 1962; S. baudinii in Duellman and Trueb, 1966). Hypopachus variolosus are found in similar habitats but spacially segregated from the former two species. That is, all three species might be expected to call in certain similar situations, but H. variolosus are never in close proximity to calling males of D. spatulata or S. baudinii.

Bufo marmoreus calls while floating on the open surface of the pond and occasionally calls from the periphery of weeds protruding from the water. Most of the B. marmoreus breeding activity was also temporally isolated from that of the other species. A. dacnicolor were found in the tops of tall plants extending 0.67 to 1 m above the pond's surface. Leptodactylus labialis called only from terrestrial burrows along the shore of the pond, often as high as 0.5 m above and 3 m back from the water's edge.

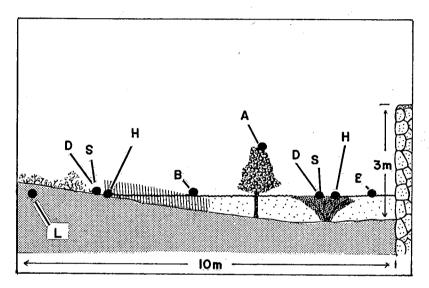


Figure 3. Schematic diagram of the calling sites of anurans on 12 July 1967; $A = Agalychnis\ dacnicolor$, $B = Bufo\ marmoreus$, $D = Diaglena\ spatulata$, $H = Hypopachus\ variolosus$, $L = Leptodactylus\ labialis$, $S = Similisca\ baudinii$.

The larvae are active both day and night. S. baudinii tadpoles were found in open water feeding from vegetation, and sometimes were seen in large swarms. Leptodactylus labialis larvae were in shallower water near the edge of the pond, and appeared to be feeding on the bottom. Upon being approached, they darted to deeper water or potholes in the pond. H. variolosus tadpoles were usually not observed except in the actual sample sweeps taken from the pond. We assume the majority of the H. variolosus tadpoles were feeding in deeper water and on the bottom.

Food analyses of the three above species indicate that they all feed upon organic detritus and/or plant matter. Their gut lengths are comparable but definite segregation in choice of food is evident. *H. vario*-

losus are microphagous feeders, S. baudinii feed on diatoms and algae, and L. labialis feed on dead organic and bottom debris.

Actual predation on tadpoles was not observed, but large bellostomatid Hemiptera and dragonfly larvae were present. Other predators, such as snakes, were not seen.

We do not know the fate of *Bufo marmoreus* larvae or of the *Diaglena spatulata* eggs. These could have been eaten by a predator or we could have overcollected the adults. The absence of *Agalychnis dacnicolor* eggs and larvae remains unanswered. Perhaps suitable nest sites were not available, or the males call for a long period before females arrive. The absense of larvae may be because the eggs remain in the nest for a long period of time. Another rain may have been necessary to induce *Rana pipiens* and *Leptodactylus melanonotus* breeding.

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Anuran Succession

TABLE 1
Summary of anuran activity at the site July 11-24, 1967

Species	Time and Date*									
		D	D/N 12	N 13	D 14	D/N 17	D 18	N 20	D 21	D 24
Bufo marmoreus	Adult Larvae		C,A		23					
Agalychnis dacnicolor	Adult Larvae	•	С	Ċ	С	С	С	C.	C	C .
Diaglena spatulata	Adult Larvae		C,A	P		-				
Smilisca baudinii	Adult Larvae		C,A	С	C 20	C 25-26		С		25-26, 29-31,35
Leptodactylus labialis	Adult Larvae	C 25	С	С	_	C 31-3	C 5	_	C 39	C 42M
Leptodactylus melanonotus	Adult Larvae			-	-	P	P	P	Р	P
Hypopachus variolosus	Adult Larvae		C,A	С		25		27	29	25,28, 29,33
Rana pipiens	Adult Larvae							P	P	P

^{*}Abbreviations: D = day; N = night; A = amplexing pairs; C = chorus; M = metamorphosing tadpoles; P = present but not calling; number indicates tadpole stage.