Tadpoles, Predation and Pond Habitats in the Tropics

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ABSTRACT

Tadpoles involved in predator-prey interactions were studied in tropical wet forest in Costa Rica under laboratory and field conditions. Larvae of the frog *Leptodactylus pentadactylus* and naiads of the odonate *Pantala flavescens* are important predators on larvae of several species of frogs. The predators discriminate the prey on the basis of size and species, but not type of habitat in which predation occurs. A graphical model is proposed to illustrate the relationships between species diversity and habitat complexity as they affect the composition of tadpole communities. The model is used to evaluate the relative importance of abiotic and biotic factors in determining the use of specific kinds of aquatic habitats by frogs with larval stages. Predation by permanent aquatic predators (primarily fish) is considered to be the most important biotic factor influencing the temporal and spatial composition of tadpole communities. The development and maintenance of predatory feeding modes, including cannibalism, in certain tadpoles is examined in light of the model.

MOST TADPOLES are generalized herbivores (Jenssen 1967) that either scrape plant material from a substrate or filter planktonic food directly from the water. Only a few species are known to be carnivorous although some instances of cannibalism among tadpoles have been reported (Bragg 1964). We were surprised, therefore, to find a well-developed predator-prey system in which tadpoles of one species were carnivores on other tadpoles. This finding was unusual not only because documented instances of tadpoles feeding on other tadpoles are relatively rare, but also because the carnivorous tadpoles were found in relatively small puddles.

The predator-prey interactions studied occur in small rain-filled tropical puddles characteristically utilized by opportunistic breeders. Experiments were run to study the relative ability of predators to capture prey and their preference for certain prey species, to ascertain the influence of microhabitat on predator-prey interactions, and to evaluate the influence of prey size on their ability to escape predation.

Results of these experiments led to a consideration of tadpole habitats and to those factors controlling the diversity of tadpole communities. A model is used to illustrate the relationship between pond complexity and predation as they affect the species composition of a tadpole community. The predatory feeding mode of tadpoles is considered in light of this model.

METHODS AND MATERIALS

Observations and experiments were made during two weeks in June 1973 (WRH and RWM) and two weeks in August 1973 (DLW and RWM) in the vicinity of the Osa Field Station, Rincón de Osa, Puntarenas Province, Costa Rica. The station is surrounded by the remnants of the lowland wet forests that once covered much of the Golfo Dulce region. This area receives more than 4000 mm of rain each year and is the only remaining large tract of wet forest on the Pacific coast of Middle America. Most of the work was done in the immediate vicinity of the airfield at Rincón, an area of disturbed second-growth vegetation surrounded by relatively undisturbed wet forest.

Our studies were conducted during the rainy season when most of the anuran species known from the area were breeding. Breeding sites used by the various species included very small (less than 1 m diam.) puddles, usually in disturbed areas; small temporary ponds (less than 20 m diam. and 1 m deep); seepage areas along roads; and some sizable (more than 20 m diam. and 1 m deep), more persistent ponds. Larvae of the following species were commonly found in the smallest ponds: *Physalaemus pustulosus, Leptodactylus poecilochilus, Leptodactylus pentadactylus*, and *Smilisca phaeota. Bufo marinus* sometimes used these temporary ponds but usually bred in more permanent sites. *Hyla rosenbergi* called from concealed sites near the puddles but only bred in small mud depressions near seepage areas along roads or near small temporary ponds. Most of the other 37 frog species at Rincón bred in large aquatic sites (permanent ponds, rivers, streams, etc.)

or had some form of terrestrial development.

Observations were made in the field and laboratory, but all experiments conducted at the field station used freshly caught material. The two major tadpole predators used were larvae of *Leptodactylus pentadactylus* and naiads of the odonate *Pantala flavescens* (Libellulidae). Both predator and prey tadpoles and naiads were kept by species in holding trays of plastic bags before each experiment. At the conclusion of the experiments, the predators and the remaining prey were preserved. Later these were staged (Gosner 1960) and measured in the laboratory. All measurements, unless otherwise specified, are in millimeters.

EXPERIMENTAL DESIGN AND RESULTS

CAPTURE ABILITY AND PREFERENCE: The first experiment was designed to test the effectiveness of the predatory tadpole *Leptodactylus pentadactylus* in capturing larvae of two common co-inhabitants of temporary ponds, and its preference for one species over the other, although the experimental design did not specifically test this aspect. Larvae of *Bufo marinus* and *Physalaemus pustulosus* were used as prey. Experiments were run in three plastic trays (19 x 12 x 7 cm) filled with clear water 2.5 cm deep. The first run on 14 June used three experimental units including 12 hatchling *Bufo*, 6 hatchling *Bufo* and 6 small *Physalaemus*, and 12 small *Physalaemus*, respectively. A single *L. pentadactylus* larva was added to each tray and maintained in it for two hours. The experiments were repeated at the same time on 18 and 19 of June so that each individual predator was exposed to all three prey conditions. Sizes of predators and prey and results are listed in table 1. Comparison of the numbers of prey individuals of *Bufo marinus* and *Physalaemus pustulosus* captured by *L. pentadactylus* in the containers of pure prey species indicated that significantly (P=

0.05) more *Bufo* were eaten than *Physalaemus*. In the containers where both prey were offered, again significantly more individuals of *Bufo* were eaten. It is possible that the statistical differences relating to numbers of each type of prey eaten reflect their differential success at avoiding predation rather than predator choice or preference, or perhaps a combination of both. Unequivocally, however, it is biologically significant that the predator ate both types of prey (see discussion).

HABITAT: A second series of experiments, designed to determine the effect of habitat on feeding efficiency, were run using tadpoles of *L. pentadactylus* as the predator and *Bufo marinus, Smilisca phaeota, Physalaemus pustulosus,* and *Hyla rosenbergi* as prey. Four of the same type of trays used in the previous experiment were filled to a depth of 5 cm with clear water, turbid water, clear water over a rocky bottom, or clear water over leafy substrate, respectively, conditions matching the natural habitats used by the larvae. The rocks were sufficiently large and the leaves sufficiently loose so that both predators and prey could hide. Twelve prey of one species and three predators were added to each habitat tray. Each experiment was run for one hour and repeated on three successive days so that each set of predators was exposed to each habitat type. The sizes of the predators and prey, summary of experimental results, and results of an analysis of variance for a three-way factorial experiment are presented in table 2. The groups of predators did not vary in their feeding efficiency from day to day. The type of habitat was not significant with respect to the number of prey consumed by the predators. There were no significant prey by day interactions or day by habitat interactions.

Two results were statistically significant. First, the predators ate more of some prey species than others. The mean numbers of each prey eaten were:

TABLE 1. *Predator capture ability and preference experiments.*[a]

	B. marinus	P. pustulosus	
Single-species trays	15 of 36	6 of 36	$\chi^2 = 3.90$[b]
Mixed-species trays	14 of 18	5 of 18	$\chi^2 = 4.32$[b]

	Stage	Body length	Total length	Maximum width	Beak width
Predator—L. pentadactylus	36-39	13.4-16.8	50.0-61.1		1.7-2.0
Prey —B. marinus	20-26	2.4- 5.0	4.7-11.1	1.5-3.5	
Prey —P. pustulosus	24-26	2.1- 4.1	5.9- 9.9	1.5-2.7	

[a] Specimen data (measurements in millimeters).
[b] 0.05 level of significance.

TABLE 2. *Habitat experiments showing total prey consumed over four days by four sets of predatory* Leptodactylus pentadactylus.

	Stage	Total Length	Clear	Turbid	Rocks	Leaves
				Habitat		
Expt. A.						
Predator *L. pentadactylus*	33-36	42.0-53.5				
Prey *Bufo marinus*	26-27	7.9-11.9	28	38	40	40
Expt. B.						
Predator *L. pentadactylus*	31-36	40.7-51.8				
Prey *Physalaemus pustulosus*	25-27	7.9-11.9	16	18	19	25
Expt. C.						
Predator *L. pentadactylus*	34-36	43.0-47.0				
Prey *Smilisca phaeota*	25	8.0-10.5	16	10	20	13
Expt. D.						
Predator *L. pentadactylus*	32-34	44.0-49.0				
Prey *Hyla rosenbergi*	22-25	7.5-12.0	27	29	19	26

Analysis of variance

Source	DF	MS	F Value
Prey	3	87.87	18.85[a]
Day	3	2.29	0.49
Habitat	3	3.12	0.67
Prey by day interaction	9	15.78	3.38[a]
Prey by habitat interaction	9	6.05	1.30
Day by habitat interaction	9	7.30	1.57
Error	27	4.66	

$F_{(3, 27, 5\%)} = 2.96$, $F_{(3, 27, 1\%)} = 4.60$, $F_{(9, 27, 5\%)} = 2.25$, $F_{(9, 27, 1\%)} = 3.15$

[a] 0.01 level of significance.

Bufo marinus, 9.1; *Physalaemus pustulosus*, 4.9; *Smilisca phaeota*, 3.7; *Hyla rosenbergi*, 6.3. All two-species comparisons are significantly different at the 1 percent level (t-test) except for the mean number of *Physalaemus pustulosus* eaten compared with *Smilisca phaeota* and the mean number of *Smilisca phaeota* eaten compared with *Hyla rosenbergi*. This finding supports the results of the first set of experiments in which individual *L. pentadactylus* ate more *Bufo marinus* than *Physalaemus pustulosus*.

The prey by day interaction also was significant as, within certain prey species, there was a day effect which is the same as differential predation by the same set of predators. The mean numbers of prey eaten by prey species by day are given by species in table 3. No statistically significant differences due to day or number of *Smilisca phaeota* eaten were found. More *Physalaemus pustulosus* were eaten at the end of the experiment than at the beginning, but the most striking differences are with *Bufo marinus* and *Hyla rosenbergi*. Significantly more *Bufo* were consumed during the last two days of the experiment than during the first two days; significantly more *Hyla* were consumed during the first two days than the last two days (Duncan's new multiple-range test).

TABLE 3. *Mean number of prey eaten by prey species by day.*[a]

Species	1	2	3	4
		Day		
Bufo marinus	3.5	4.8	8.9	9.5
Physalaemus pustulosus	3.8	3.8	5.5	6.5
Smilisca phaeota	2.0	4.0	4.8	4.0
Hyla rosenbergi	9.0	8.8	4.0	3.5

[a] N = 4 each cell, standard error = 1.08.

PREY SIZE: The third series of experiments was designed to test the effect of prey size on capture by predaceous naiads of the odonate *Pantala flavescens* (Libellulidae). The odonates were collected from the same kinds of habitats as were the prey. The experiments were run in round plastic bowls (22 cm diameter) filled to a depth of 5 cm. Three prey species, *Smilisca phaeota, Physalaemus pustulosus,* and *Bufo marinus,* were divided into three size classes. For each 90-minute trial, 12 individuals of each size class of one of the species were put into the experimental containers with two naiads. The same group of predators was used in each trial, two naiads being selected each day. The results of these tests and an analysis of variance are presented in table 4. Rate of feeding by naiad predators varies significantly with size, but not species, of prey.

TABLE 4. *Dragonfly naiad predation on different-sized tadpole prey.*[a]

| | Number eaten | | |
	Small	Medium	Large
Trial I. *Smilisca phaeota*			
Stage	25	27-28	40-41
Total length	8-10	20.0-22.5	35-38
Number eaten	10	4	1
Trial II. *Physalaemus pustulosus*			
Stage	25	28-29	40-41
Total length	7.5-8.0	11-13	20-22
Number eaten	12	7	3
Trial III. *Bufo marinus*			
Stage	28-29	31-33	39-41
Total length	12-14	18-20	21.0-21.5
Number eaten	9	7	5

Analysis of variance		
Source	DF	F Value
Prey	2	0.46
Size	1	27.97[b]
$F_{(1,5,5\%)} = 6.61$, $F_{(1,5,1\%)} = 16.3$,		
$F_{(2,5,5\%)} = 5.79$		

[a] Predators were large naiads of *Pantala flavescens* (Libellulidae), 21-23 mm total length, with well-developed wing pads and with venation and color pattern beginning to appear.

[b] = 0.01 level of significance.

PREDATOR-PREY BEHAVIOR

Observations of the behavior of the predator and prey larvae were made during the experiments and in the field. Larvae of *L. pentadactylus* generally swallowed their prey entire, starting from the front. When *L. pentadactylus* grabbed a tadpole on the back or side, the predator orally manipulated the tadpole until the prey was oriented head first and then swallowed it. Only one prey was observed eaten tail first. *Leptodactylus pentadactylus* either swam vigorously during capture keeping a constant force on the prey or held the prey against a surface by continuous tail movement. Prey that escaped during this oral manipulation appeared unharmed. Smaller prey items (e.g. mosquito larvae) were swallowed whole without respect to orientation.

There was a definite maximum size of prey that *L. pentadactylus* larvae could swallow. In two instances in which predators were unsuccessful in swallowing prey and the individual predators could be associated with individual prey, the maximum body width of the prey was about twice the beak width of the predator. For most experimental animals the predator beak-prey width ratio fell below this value (table 1). Groups of *L. pentadactylus*, however, were able to eat prey too large for individual predators. When larger prey were introduced into a container of about 25 predators, several predators tore the prey apart. This group activity probably is not

a natural phenomenon as *L. pentadactylus* larvae generally tend to be dispersed in ponds and puddles and to feed as individuals. However, when ponds begin to dry and tadpole density increases, group predation may occur.

In the experimental trays, the *L. pentadactylus* larvae tended to lie on the bottom as did those of *Physalaemus* and *Smilisca*. The *Bufo* larvae tended to swim around in the container usually near the surface. *Bufo* larvae also behaved this way in the field and were the only tadpole commonly active during the day. In trays with clear water, the *Physalaemus* larvae swam away from the *L. pentadactylus* larvae when about one *Physalaemus* body width separated them. In contrast, the *Bufo* did not attempt to swim away from the *L. pentadactylus* until the predator was very near or actually touching.

The naiads and *L. pentadactylus* larvae foraged differently. The naiads waited until prey came within range, and grabbed it without pursuit. *Leptodactylus pentadactylus* larvae used both waiting and pursuit to capture larvae. A prey animal that came close was grabbed; however, if the predator missed it chased the prey. In the trays, the *L. pentadactylus* sporadically changed waiting locations. If this behavior occurs in nature, it should stimulate prey swimming and increase the probability of encounter and capture.

DISCUSSION

The experimental results, combined with field observations, indicate that in certain kinds of tropical habitats larval *Leptodactylus pentadactylus* are potentially important aquatic predators (also see Heyer 1970, for evidence from field-collected larvae). However, larval *L. pentadactylus* are facultative predatory carnivores and may function and grow to metamorphosis as substrate-scrapers (Vinton 1951). None of the morphological characteristics usually associated with predaceous tadpoles of *Scaphiopus* (e.g. greatly hypertrophied jaw muscles, enlarged mouthparts, notched beaks, etc., Orton 1954, Bragg 1964) are found in *L. pentadactylus* larvae. However, some larval characteristics that may be related to predatory habitats are: a relatively long tail (about 70% of body length), the shape and terminal position of the mouth and oral disc, and a well-developed lateral line system (Heyer 1970). A long muscular tail to provide strong thrust during swimming would be useful in open water in keeping constant pressure on struggling prey during oral manipulation and also in increasing speed during pursuit of prey. Many of the puddles and small ponds that served as natural habitat for *L. pentadactylus* larvae

were turbid from frequent rains and influx flowing over disturbed ground, yet our results (table 2) show no significant difference in prey capture among the four habitats. We suggest that the well-developed lateral line system of *L. pentadactylus* as compared to other *Leptodactylus* tadpoles is important in prey detection and capture.

Significant differences were obtained in comparing results of the *L. pentadactylus* and *Hyla rosenbergi* experiments depending on the day, and hence stage of the prey species (table 2, D). The prey were in stages 22-23 at the beginning of the experiment and in stage 25 by the end of the experiment. It is during this period that the developing larvae undergo transition to free-swimming tadpoles. *Hyla rosenbergi* oviposits in a mud depression nest hollowed out by the males. The eggs and early larval stages are black and float in the surface film. Noble (1927) suggested that the enormous external gills of this species allow the tadpole to hold onto the surface film. During the early, external-gilled stages (stages 20-23), the larvae are ineffective swimmers and easy prey for most aquatic predators. Once the gills are covered (stage 25), the tadpoles are free-swimming and better able to avoid predation. Our results show that the early developmental stages of *H. rosenbergi* are more susceptible to aquatic predation than other species of comparable age or than later stages of the same species. The significance of the mud depression nests is thus apparent. Spatial isolation of the eggs and early larval stages of *Hyla rosenbergi* in a depression that fills primarily by seepage will isolate the larvae from aquatic predators. In addition, the later breeding of *Hyla rosenbergi* (first clutches found in August) as compared to the predator *L. pentadactylus* (tadpoles and nests first collected in June) increases their temporal susceptibility to predation. Thus isolation of eggs and early larval stages in mud depressions potentially decreases mortality from aquatic predators such as *L. pentadactylus* during the more susceptible early stages.

Wassersug (1971) demonstrated the relative unpalatability of larval *Bufo marinus* to man, i.e. a vertebrate predator, as compared to larvae of seven other species from the Osa. Later (1973), he argued that the black larvae of *Bufo* form conspicuous aggregates for greater visibility to predators than those of non-aggregating, cryptically colored larvae of other species. Unpalatability then is an adaptive response of larval *Bufo* which affords some protection from potential predators. Wassersug (1973) suggested that this unpalatability would not be very effective against invertebrate predators that suck body fluids from their prey (e.g. belostomatids,

most predaceous beetle larvae) or vertebrate predators that swallow their prey indiscriminately (some salamanders). The present study demonstrates that both *Leptodactylus pentadactylus* larvae and *Pantala flavescens* naiads feed readily on *Bufo marinus* larvae. The results of the experiments in which *L. pentadactylus* ate more larvae of *Bufo marinus* than of any other prey tested (tables 1, 2) suggest that in some situations *Bufo* larvae were more vulnerable to predation. At the same total length *Bufo* larvae are bulkier and darker than the other species tested including *Physalaemus* larvae. The results of the habitat experiments argue against visual hunting by *L. pentadactylus*. The relatively well-developed nature of the lateral line system indicates a reliance on cues (e.g. movement, olfaction, etc.) other than shape, color, etc. for prey detection. Why were the *Bufo* tadpoles more vulnerable to predation? The constant but relatively slow swimming mode of highly visible *Bufo* tadpoles, usually in aggregations, makes them easy prey to aquatic predators that are not deterred by unpalatability. In contrast, *Physalaemus* larvae are generally nocturnal, spend more time on the bottom (exploiting their cryptic coloration), and respond sooner to the approach of a predator. Wassersug (1971) reported that when larvae of *P. pustulosus* are disturbed, they burrow into the mud bottom of a pond.

Most of the previous experimental work on tadpole palatability used fish or aquatic salamanders as predators (see Wassersug 1973). Both of these predators are likely to "chew" or bite their prey. The species tested avoided *Bufo* when given the opportunity to feed on other species (Wassersug 1973). When tadpoles of several species, including *Bufo*, were put into aquaria with certain fishes from the Osa, the *Bufo* larvae were generally avoided or grabbed and rejected, whereas those of other species often were eaten. It would appear that vertebrates (fish, and possibly birds and mammals) may be the major predators attuned to aposematic color and behavior and hence avoid *Bufo* larvae. Our results indicate that *L. pentadactylus* larvae and certain odonate naiads are exploiting the *Bufo* behavioral mode (slow but continuous movement in aggregations). The results (table 3) suggest that the predators may have learned to feed on *Bufo* more efficiently during the course of the experiments. We would not expect taste receptors to be well developed in predatory organisms that are evolutionarily derived from essentially indiscriminate herbivores (most tadpoles). Likewise, it appears that many invertebrate predators (particularly odonate naiads) feed indiscriminately on tadpole larvae (Wager

1965, Young 1967, Brockelman 1969, Heyer and Bellin 1973).

Another aspect of predator-prey interactions involving *Bufo* larvae that needs consideration is the possibility of ontogenetic change in palatability. All of Wassersug's *Bufo marinus* larvae (1971) were more advanced (stage 30-32 vs. 20-26) and much larger (head-body length greater than 8 mm vs. less than 5 mm) than those we used. One of us (WRH) tasted small and large *Bufo marinus* larvae. The small larvae were of the same size range as those *eaten by L. pentadactylus* in our experiments and did not have an unpleasant taste. The large larvae comparable to those used by Wassersug did taste badly. Thus there may be an ontogenetic change in palatability with older tadpoles (larger doses) becoming more unpalatable. Licht (1968, 1969) demonstrated that the eggs of several species of *Bufo* are toxic and unpalatable. We would not expect unpalatability to characterize eggs and late larval stages without being present in the early larval stages also. However, the degree of unpalatability in terms of amount of toxin ingested probably would increase with increasing size of the larvae and may account for the apparent ontogenetic change in taste. This possibility should be studied in more detail. Predation studies using large *B. marinus* tadpoles and *L. pentadactylus* are needed. It may be that palatability is unimportant to *L. pentadactylus* larvae in terms of prey selection and that size and relative availability are the important criteria.

The odonate experiments indicate that naiads of *Pantala flavescens* may be important predators on tadpoles in puddles at the Osa. *Pantala flavescens* is a cosmopolitan species that characteristically exploits exposed water in temporary pools and has very rapid growth (Needham and Westfall 1955). The naiads used in this study were collected from temporary pools that were built on 14 July; the predation experiments were run between 20 and 24 August. The maximum possible age of the naiads was 40 days, which is within the time required for tadpole development. It is clear that odonate predation decreases with increasing tadpole size (table 4). Pritchard (1965) demonstrated that odonates are prey-size limited and that moving or recently moved prey are required to elicit an attack. He also pointed out that neither color nor olfaction is an important criterion in prey selection. Although there is some indirect evidence that naiads can discriminate prey on the basis of taste, *Pantala flavescens* appears to be primarily a vision-oriented predator. From these data and our results, we conclude that odonate naiads are important tadpole predators that select prey by size, not by taste.

This study again demonstrates the importance of prey size in naturally occurring predator-prey interactions. The larger the tadpole, the lower its probability of being eaten by *Pantala flavescens* naiads or *Leptodactylus pentadactylus* larvae. For predator and prey species that have coexisted over evolutionary time, one predator-escape mechanism would be for the prey to grow large quickly. Another would be for the prey to start growing before the predator so that the prey species are relatively larger. For opportunistic breeders, these cases may be relatively few (see below).

Results of this study indicate that predation upon tadpoles (and probably other organisms as well, e.g. mosquitoes) by tadpoles and by naiads is an important component of the ecology of species using small puddles and ponds at the study site. Small puddles are characteristically used by opportunistic breeders. One reproductive pattern of opportunistic breeders is to lay numerous clutches in small, ephemeral habitats; due to the number of reproductive attempts, some will be successful. Biological factors (e.g. competition, predation) probably play a lesser role in determining reproductive success of opportunistic frogs breeding in small, ephemeral puddles than the abiotic factor of the puddles drying up. As ephemeral puddles and ponds are short-lived phenomena and frequently unpredictable in time and space, not all will be utilized by frogs. In certain instances the number of reproductively active frogs may be fewer than the number of available ephemeral ponds; in other instances a very ephemeral pond may not be found by reproductively active frogs. Thus one would predict that many of the very ephemeral habitats would have very few (1-2) or no species of tadpoles. At the study site, most of the ponds sampled had tadpoles of one to several prey species, together with predatory *L. pentadactylus* larvae, naiads, belostomatids, and other aquatic organisms. Because the apparently ephemeral aquatic sites at the Osa support several species including a well-developed predator-prey system involving tadpoles, we pose two questions which invite speculation: 1) are the situations described at the study site common or rare? 2) why do so few tadpoles eat other tadpoles?

We expect that the situation described at the Osa site is relatively rare for the following reasons. Frogs that are opportunistic breeders are adapted to exploit short-lived aquatic habitats characteristic of dry or very seasonal environments. Tadpoles of predatory species are much larger than tadpoles of the prey species that they eat, so, given equal growth

rates, they need a relatively longer time to grow. The average length of time that *L. pentadactylus* needs to metamorphose probably is longer than the average duration of ephemeral ponds utilized by opportunistic species in tropical dry environments, areas characterized by marked seasonality in abundance and distribution of rainfall and many ephemeral habitats. The reason that these two usually exclusive situations can coexist at the Osa (a tropical wet forest site) is the extended period during which many seemingly ephemeral ponds, such as roadside puddles, are renewed by almost daily rain. The opportunistic breeders utilize these small, aquatic sites. Since many of these sites exist for a longer period than expected, they also are able to support more species including those interacting as predator prey. This situation would be found only in seasonal but relatively wet environments, such as the Osa Peninsula in Costa Rica.

Interestingly, *L. pentadactylus* larvae at the Osa show a remarkable resistance to drying. Valerio (1971) observed many tadpoles in a puddle which dried up for a day. During this period, the tadpoles clustered in groups of up to 20 individuals in holes in the mud under stones and grass. The next day the puddle filled with rain, and the tadpoles swam actively. In the laboratory, Valerio (1971) showed that some *L. pentadactylus* remained alive on moist filter paper for more than 156 hrs., longer than six other species tested. Two other species, *Leptodactylus poecilochilus* and *Smilisca phaeota*, that lived for a considerable time under these conditions also are opportunistic breeders that use these temporary breeding sites. This resistance to desiccation by *L. pentadactylus* larvae supports our findings and suggests that small puddles susceptible to drying are typical habitats for certain frog species. A similar response to desiccation has been reported recently for larvae of *Scaphiopus bombifrons* (Black 1974).

Tadpoles that prey on other tadpoles are relatively rare. The best-known cases are of species occupying ephemeral situations, especially temporary rain pools in arid environments (*Ceratophrys*, Noble 1927; *Lepidobatrachus*, Parker 1931; *Lechriodus*, Moore 1961; *Scaphiopus*, Bragg 1965; *Pyxicephalus*, Burton 1972) or bromeliads (*Anotheca*, Taylor 1954; *Hyla*, Laessle 1961). In some of these situations, the predatory tadpole mode seems to be an extreme specialization ensuring that some larvae will metamorphose. This condition is especially true with regard to *Scaphiopus* larvae which often become cannibalistic (Bragg 1965). It appears then that predatory tadpoles are found primarily in small, non-permanent aquatic situations. The question

arises as to why they are not found in more permanently aquatic habitats? We suggest that the reason no predatory tadpoles apparently occur in permanent ponds is the increased probability of fish utilizing the aquatic habitat. Many fishes are efficient aquatic predators, and the predatory tadpoles would be as susceptible to predation as other tadpoles, or perhaps more susceptible because of their presumed longer larval life and larger size.

The interactions among the major variables influencing the composition and evolutionary patterns of a tadpole community, including the development or maintenance of predatory modes among tadpoles, can be expressed in a graphical, heuristic model (fig. 1). Our model is based on the following assumptions: 1) that tadpole mortality and ulti-
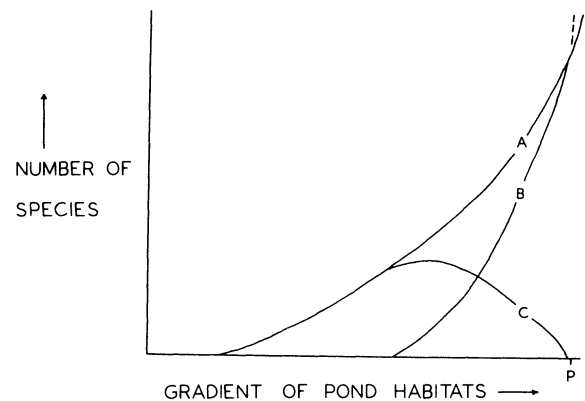

FIGURE 1. Predicted occurrence of numbers of species of tadpoles in a generalized environment. Horizontal axis represents ordination of ponds based on a combination of four factors: 1) size, 2) duration, 3) kind, amount, and seasonal distribution of primary productivity, 4) structural complexity. Curve A is the potential number of species of tadpoles that could be supported in various kinds of ponds. Curve B is the number of species of tadpoles removed by fish predation. Curve C is the expected number of species of tadpoles to be found in various ponds as an interaction between curves A and B (C=A–B). Point P represents the kinds of ponds expected to be able to support tadpoles that eat other tadpoles (see text).

mately species occurrence in any habitat is the result of the interactions of both physical and biotic parameters, 2) that tadpoles occurring in small ponds of shorter duration are more likely to be affected by abiotic factors (e.g. ponds dry up) than tadpoles occurring in larger, permanent ponds, where biotic factors (e.g. predation) may be more important, and 3) that under most natural conditions interspecific competition among tadpoles is not a major factor determining community composition. While some authors (e.g. Savage 1961, Brockelman 1969) have suggested that competition might be an important

component of anuran larval ecology, De Benedictis (1974) was unable to show interspecific competition for food in an experimental field study of two species of *Rana.* The few data available (Martin 1967, Heusser 1970, Heyer 1973) show that tadpoles may partition ponds effectively both spatially and temporally. This finding suggests that competition has been important over evolutionary time, and the present patterns of distribution may represent an evolutionary response to competition. It is possible, however, that part of the larval partitioning patterns is a passive reflection of spatial or temporal premating isolating mechanisms operating at the adult stage. Until interspecific competition is shown to be an ecological factor important in dynamics of larval communities we prefer not to consider it in our model.

The number of species of tadpoles able to metamorphose are plotted along the vertical axis in figure 1. The horizontal axis represents the spectrum of pond types found in a given environment. The spectrum ranges from puddles that last less than a day on the left, through ponds of increasing size, duration, habitat complexity, probable productivity, etc. to permanent bodies of water on the right. Curve A is the maximum number of species of tadpoles potentially able to metamorphose in the various kinds of ponds. Thus, a complex pond (to the right of fig. 1) would be expected to support a more diverse (species number) tadpole fauna than a simpler one (to the left). This correlation of diversity and complexity is expected because the relationship appears to be a general one based on studies of other groups of organisms (e.g. Sanders 1969). Curve B is defined as the number of species removed through fish predation. We think that fish (here restricted to predaceous forms which likely co-occur with tadpoles) are the only purely aquatic predators capable of eliminating species of tadpoles from pond systems. Many fishes that eat tadpoles actively search for their prey and easily overpower them. For this reason, fish probably are able to seek out and eliminate the entire breeding effort of some frogs. Thus, curves A and B cross in figure 1 indicating that at a certain degree of pond complexity, fishes always will be present and eliminate any tadpoles in these ponds (see also Scott and Starrett 1974). We think this is generally true for tropical situations (see exceptions below).

Salamanders, in contrast, usually forage slowly, often sitting and waiting for prey rather than chasing them. Salamanders usually will not remove entire tadpole populations although they may significantly reduce them (Heusser 1971, Calef 1973,

Cooke 1974). Arthropods, especially some species of odonates, that feed on tadpoles usually are sit and wait predators (Pritchard 1965) and probably have lower hunting efficiencies than fishes. Again, these predators may reduce populations (Savage 1961, Bragg 1965), but probably rarely eliminate them. Many (perhaps most) predaceous aquatic insects are larvae or immatures and, as with many salamanders, will metamorphose and leave the pond thus reducing the predatory pressure on tadpole populations. In contrast, fish are permanent residents of ponds and will maintain a more constant predator pressure. We recognize that other aquatic or semiaquatic predators (turtles, caecilians, birds, etc.) also are important, but their impact and efficiencies are unknown. For purposes of this discussion we assume that in tropical situations, long-lived, complex ponds will have predatory fish, and that these fish will eliminate tadpoles. Note that in curve B there is a difference in the complexity of pond type that will support fish in contrast to tadpoles. Curve C is defined by the equation C=A–B. It represents the number of species of tadpoles that actually do metamorphose in different kinds of ponds in a given environment. From left to right, curve C is defined by decreasing importance of abiotic and increasing importance of biotic factors.

Using the model of figure 1 as a general explanation, the point P indicates the sort of aquatic habitat (a relatively permanent pond) that would be expected to support most predatory tadpoles. Point P lies on the far right because of the long period needed for growth and metamorphosis of these large larvae. As indicated in figure 1, these ponds will be of the same complexity that consistently will support fishes which will remove the tadpoles through predation. Thus point P often lies to the right of curve C and accounts for the general rarity of predatory tadpoles.

Variations in curves A and B result in greater realism of the model. The general shape of curve B and the point of intersection with the horizontal axis will be expressed by the ability of fish to colonize newly established, long-lived habitats or to withstand the stressful conditions characteristic of ponds in the highly seasonal tropical and subtropical areas or actually to exploit ephemeral habitats in these areas. Certain species of fishes that live in wet tropical areas are highly mobile. During one two-day rainy period at the Osa, we collected several adult specimens of the catfish, *Rhamdia wagneri,* and the characin, *Astyanax fasciatus,* swimming in about eight centimeters of water across a gravel air strip and road some 50 meters from a permanent pond which

was overflowing. Several species of fish are noted for their ability to cope with seasonal fluctuations in water level. The best-known examples are lungfish and annual fishes of the family Cyprinodontidae (including species of Cynolebias, Pterolebias, Aphyasemion) which are found in small accumulations of water caused by flooding or prolonged rainfall and subject to drying. The cyprinodontid fishes are well adapted to these conditions and survive the long, dry season as resting eggs. All are active predators.

The effects of fish predation can be reduced by modifications of tadpole morphology and behavior. In stream habitats, larvae of frogs of the genus Centrolenella are buried among the leaves and organic debris in stream bottoms. Similar behavior is characteristic of stream larvae of frogs of the families Bufonidae, Hylidae, and Ranidae. In permanent bodies of water (e.g. rivers, lakes, etc.) two kinds of tadpole adaptations appear to reduce fish predation. The first, not fully documented, is size. For example, bullfrog tadpoles (Rana catesbeiana) are so large that many fish cannot eat them. The scanty evidence suggests that bullfrogs require a predator-free nursery in which to grow to a size sufficient to avoid most fish predation. A second effective adaptation is better documented and utilized by toads of the genus Bufo. Bufo larvae taste bad to fish (Voris and Bacon 1966, Wassersug 1973, authors' personal observation). The bad larval taste is part of an adaptive pattern that includes high visibility and frequent aggregations of larvae in the pond habitat. Interestingly, the Bufo mode (Wassersug 1973) is widespread and remarkably constant in pond systems. A brief literature survey reveals the presence of usually one or two species of Bufo in any given area just about any place in the world where frogs occur, except the Australian region.

Because adaptations of pond larvae to avoiding fish predation seem to be either widespread and constant (Bufo) or relatively rare (Rana catesbeiana), we think curve B1 in figure 2 approximates most tropical situations in nature. The right end of curve C1 is represented almost always by Bufo and, in some cases in North America at least, by Rana. For completeness, curve B2 has been added to figure 2 and shows the result of reducing the effects of fish predation: more species of tadpoles should be found in permanent water (as indicated by line C2). Variations in predator curves and concomitant changes in tadpole curves might be due to differential fish predation, e.g. bottom-feeding catfish might eliminate from a pond only those frog species that lay their eggs on the pond bottom or that have
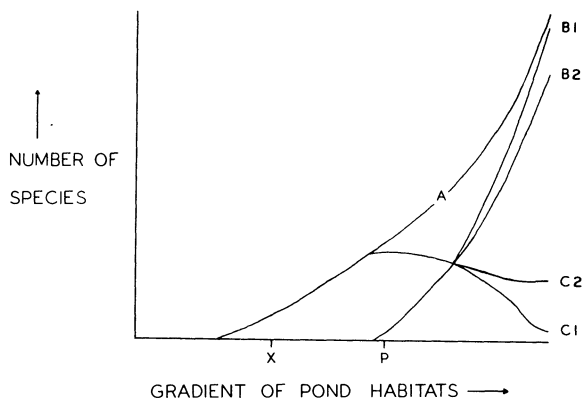

FIGURE 2. Predicted occurrence of numbers of species of tadpoles in a generalized environment as a function of variations of curve B, which represents fish predation. Point X is the location of puddles in seasonal environments along the horizontal axis, point P is the location of the same sized puddles (as at point X) at the Osa site. See legend of figure 1 and text for further explanation.

benthic tadpoles.

The shape, slope, and intercept of curve A may be determined by spatial and temporal fluctuations in rainfall and the nature of the primary productivity. An extreme case, shown in figure 3, describes the kind of breeding habitat used by Scaphiopus in Oklahoma. There are primarily two kinds of natural
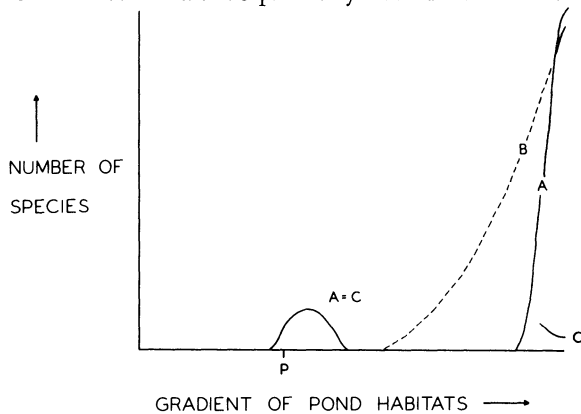

FIGURE 3. Predicted occurrence of numbers of species of tadpoles in the specialized environment of Oklahoma (U.S.A.). Point P is the location of kinds of puddles characteristic of predatory (cannibalistic) Scaphiopus larvae. See the legend of figure 1 and the text for further explanation.

ponds available to Oklahoma frogs, ephemeral, thundershower-filled pools and permanent, spring-fed pools. It is interesting to note that the majority of tadpoles found in the permanent pools appear to be using bad taste (Bufo) or large size (Rana) to reduce the effects of fish predation.

The amount and distribution of primary productivity in ponds may have the following effects (as yet untested) on curve A. Frequently, the ephemeral habitats (smaller, shorter-lived, etc.) initially have higher nutrient levels from decaying terrestrial vegetation and other organic material than do the more permanent ponds (larger, longer-lived, etc.). They also are warmer. The initial high nutrient level and warmer temperature probably enhance the primary productivity of these ephemeral habitats for a short time (Brylinsky and Mann 1973). Usually the producers in these ephemeral ponds are predominantly planktonic while in more permanent ponds they frequently are rooted. Heyer (1973) found that beakless, plankton-eating tadpoles of the family Microhylidae had faster development rates than did periphyton-eating tadpoles (scraping and chewing mouthparts) of the families Ranidae, Rhacophoridae, and Bufonidae. Developmental rates and hence duration of larval life apparently are functions of water temperature and food availability and type (plankton or periphyton). Thus, small, ephemeral ponds in warm environments should have tadpoles of more species than the same kind of ponds in cooler environments.

Because this paper focuses on predatory tadpoles, their occurrence will be explained in terms of the proposed model. If curve C1 (fig. 2) is assumed to represent the tadpole community at the Osa study sites, then the types of puddles in which we found *L. pentadactylus* tadpoles would be represented by point P (fig. 2). The puddles are relatively small, structurally simple, and not permanent. The same size puddles occurring in a more seasonal environment would be shorter lived (probably lying near point X of fig. 2) and not support a predatory tadpole like *L. pentadactylus*. However, the relatively regular rains at the Osa replenish the puddles and increase their longevity, giving them a greater stability. For this reason point P lies to the right of point X. In some characteristics (predictability, duration, etc.) the small puddles at the Osa are similar to ponds found at point P on figure 1, that is, they are long lived. Their small size excludes fishes, while their long life allows the development of the predatory tadpole habit. We think the occurrence of predatory tadpoles in bromeliads is the same, i.e. presence in long-lived, small ponds which are fish free.

A second kind of predatory mode in tadpoles occurs in *Scaphiopus, Pyxicephalus, Lechriodus, Lepidobatrachus,* and other species that breed in arid areas. In these species the developmental rates of the tadpoles are increased by their predatory or can-

nibalistic behavior so that time to metamorphosis is decreased. Larvae of some species (*Scaphiopus*, Bragg 1965, *Pyxicephalus,* Burton 1972) that develop in ponds containing remains of tadpoles that died in previous years when the same ponds dried metamorphosed earlier than larvae in ponds without such remains. This phenomenon may be due to increased availability of food (Burton 1972) or to the concentration of a substance such as iodine or thyroxine directly influencing metamorphosis (Bragg 1965). *Scaphiopus,* for example, are sporadic breeders that deposit their eggs in transient pools formed by heavy rains even when permanent ones are available (Bragg 1965). In these ephemeral habitats the tadpoles form very active schools which, in concert with the warm water temperatures, apparently allow for maximum growth over short periods of time (Wassersug 1973). Under certain poorly understood circumstances, larval dimorphism develops among siblings. A scraping and chewing tadpole changes both morphologically and behaviorally into a predaceous form, frequently indulging in cannibalism (Bragg 1965). Interestingly, as a result of the breeding behavior of *Scaphiopus,* all larvae are essentially the same age and begin as nonpredatory individuals. Bragg (1964, 1965) has shown that increased growth and developmental rates are characteristic of the predaceous morphs. The shift to a predatory mode in some species of *Scaphiopus* involves differential beak development, modifications of labial teeth, and enlarged jaw muscles. Energetically this change must be a costly switch as it is made only under stressful situations. Fish predation on these tadpoles is not a factor because of the very ephemeral nature of the habitat. In addition, the eggs and hatchling *Scaphiopus* are too large to be eaten by any aquatic, non-vertebrate predators other than fairly larger, aquatic tadpoles, none of which are present because the ponds have just recently filled. Similar predatory modes have been reported for other anuran species breeding in ephemeral puddles in arid areas of Argentina (A. Hulse, pers. comm.), Brazil and Paraguay (Parker 1931), Australia (Moore 1961), and Africa (Burton 1972).

Not enough data are available in the literature (e.g. Orton 1954, Starrett 1973, etc.) to evaluate the nature of the habits of tadpoles reported to be carnivorous. It appears that several are facultative while others are obligate carnivores. Facultative carnivory is a feeding mode intermediate between herbivory (most tadpoles) and obligate carnivory and is advantageous under certain stressful situations (*Scaphiopus*) or in very small ponds (some brome-

liad dwellers). In both of these situations facultative carnivory or cannibalism may have evolved in response to high larval density in habitats of relatively low productivity. Very little is known about obligate carnivory, but it apparently occurs in habitats not generally available to fish. Situations such as that at the Osa where a facultatively carnivorous tadpole, *L. pentadactylus*, is so successful in the small pond system probably are rare. We suggest that the difficulties of being a predatory tadpole are so great that a strictly predatory tadpole has not been able to evolve in tropical environments represented by the Osa Peninsula. *Leptodactylus pentadactylus* breeds along forest edges and does very well in recently disturbed and second-growth areas. It is clear that man's activities in the wet tropics are providing more habitat for *L. pentadactylus* and thus contributing to its success. Perhaps this circumstance will provide a more suitable habitat for the evolutionary development of a strictly predatory mode.

A final comment on the proposed model relates to its testability. To test the model, data defining the nature of the habitats on the horizontal axis must be gathered independent of curve A. At present, no data are available to determine the relationship between the horizontal axis and curve A. It appears that a combination of four pond parameters, 1) size, 2) duration, 3) kind, amount, and seasonal distribution of primary productivity, and 4) structural complexity, will allow for pond ordination along the horizontal axis. To generate curve A, it will be necessary to sample pond environments to determine tadpole species (curve C) and fish predators. Experimental manipulations of fish predator populations and tadpole populations will allow for the estimation of curve A. The number of species which could be added to the pond in the absence of predatory restraints, plus curve C, will give curve A ($A = B + C$). Once C values and experimentally produced A values are determined for a few environments, the nature of the interactions between and within tadpole communities, expressed in numbers of species, the kinds of habitats used, and the role of fish predation can be established, the model will have predictive value and then can be tested in a variety of different habitats.

ACKNOWLEDGEMENTS

LITERATURE CITED

BLACK, J. H. 1974. Larval spadefoot survival. J. Herpetology 8: 371–373.

BRAGG, A. N. 1964. Further study of predation and cannibalism in Spadefoot tadpoles. Herpetologica 20: 12–24.

———. 1965. Gnomes of the night: The Spadefoot Toads. Univ. Pennsylvania Press, Philadelphia. 127 pp.

BROCKELMAN, W. Y. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. Ecology 50: 632–644.

BRYLINSKY, M., AND K. H. MANN. 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnol. Oceanogr. 18: 1–14.

BURTON, J. 1972. Animals of the African year. The ecology of East Africa. Peter Lowe, Netherlands. 173 pp.

CALEF, G. W. 1973. Natural mortality of tadpoles in a population of *Rana aurora*. Ecology 54: 741–758.

COOKE, A. S. 1974. Differential predation by newts on anuran tadpoles. Br. J. Herpet. 5: 386–389.

DE BENEDICTIS, P. A. 1974. Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica*: an experimental field study. Ecol. Monogr. 44: 129–151.

GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183–190.

HEUSSER, H. 1970. Laich-Fressen durch Kaulquappen als mögliche Ursache spezifischer Biotoppräferenzen und kurzer Laichzeiten bei europäischen Froschlurchen (Amphibia, Anura). Oecologia 4: 83–88.

———. 1971. Differenzierendes Kaulquappen-Fressen durch Molche. Experientia 27: 475.

HEYER, W. R. 1970. Studies of the genus *Leptodactylus* (Amphibia, Leptodactylidae). II. Diagnosis and distribution of the *Leptodactylus* of Costa Rica. Revta Biol. trop. 16: 171–205.

———. 1973. Ecological interactions of frog larvae at a seasonal tropical location in Thailand. J. Herpetology 7: 337–361.

—————, AND M. S. BELLIN. 1973. Ecological notes on five sympatric *Leptodactylus* (Amphibia, Leptodactylidae) from Ecuador. Herpetologica 29: 66–72.

JENSSEN, T. A. 1967. Food habits of the green frog, *Rana clamitans*, before and during metamorphosis. Copeia 1967: 214–218.

LAESSLE, A. M. 1961. A micro-limnological study of Jamaican bromeliads. Ecology 42: 499–517.

LICHT, L. E. 1968. Unpalatability and toxicity of toad eggs. Herpetologica 24: 93–98.

—————. 1969. Palatability of *Rana* and *Hyla* eggs. Am. Midl. Nat. 82: 296–298.

MARTIN, A. A. 1967. Australian anuran life histories: some evolutionary and ecological aspects. *In* A. H. Weatherley (Ed.), Australian inland waters and their fauna. Australian Nat. Univ. Press, Canberra. 287 pp.

MOORE, J. A. 1961. The frogs of eastern New South Wales. Bull. Am. Mus. nat. Hist. 121: 149–386.

NEEDHAM, J. G., AND M. J. WESTFALL, JR. 1955. A manual of the dragonflies of North America (Anisoptera). Univ. California Press, Berkeley and Los Angeles. 615 pp.

NOBLE, G. K. 1927. The value of life history data in the study of the evolution of the Amphibia. Ann. N. Y. Acad. Sci. 30: 31–128.

ORTON, G. L. 1954. Dimorphism in larval mouthparts in Spadefoot Toads of the *Scaphiopus hammondi* Group. Copeia 1954: 97–100.

PARKER, H. W. 1931. Reports of an expedition to Brazil and Paraguay in 1926-1927, supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland. Amphibia and Reptilia. J. Linn. Soc. (Zool.) 37: 285–289.

PRITCHARD, G. 1965. Prey capture by dragonfly larvae (Odonata; Anisoptera). Can. J. Zool. 43: 271–289.

SANDERS, H. L. 1969. Benthic marine diversity and the stability-time hypothesis. *In* Brookhaven Symposia in Biology No. 22, Diversity and Stability in Ecological Systems. Brookhaven National Laboratory, Upton, New York. 264 pp.

SAVAGE, R. M. 1961. The ecology and life history of the common frog. Sir Isaac Pitman and Sons, Ltd. London. 221 pp.

SCOTT, N. J., AND A. STARRETT. 1974. An unusual breeding aggregation of frogs, with notes on the ecology of *Agalychnis spurrelli* (Anura: Hylidae). Bull. Sth. Calif. Acad. Sci. 73: 86–94.

STARRETT, P. H. 1973. Evolutionary patterns in larval morphology. *In* J. L. Vial (Ed.). Evolutionary Biology of the Anurans. Univ. Missouri Press, Columbia. 470 pp.

TAYLOR, E. H. 1954. Frog-egg eating tadpoles of *Anotheca coronata* (Stejneger) (Salientia, Hylidae). Kans. Univ. Sci. Bull. 36: 589–595.

VALERIO, C. E. 1971. Ability of some tropical tadpoles to survive without water. Copeia 1971: 364–365.

VINTON, K. W. 1951. Observations on the life history of *Leptodactylus pentadactylus*. Herpetologica 7: 73–75.

VORIS, H. K., AND J. P. BACON. 1966. Differential predation on tadpoles. Copeia 1966: 594–598.

WAGER, V. A. 1965. The frogs of South Africa. Purnell & Sons, Pty., Ltd., Cape Town, Johannesburg. 242 pp.

WASSERSUG, R. J. 1971. On the comparative palatability of some dry season tadpoles from Costa Rica. Am. Midl. Nat. 86: 101–109.

—————. 1973. Aspects of social behavior in anuran larvae. *In* J. L. Vial (Ed.). Evolutionary Biology of the Anurans. Univ. Missouri Press, Columbia. 470 pp.

YOUNG, A. M. 1967. Predation in the larvae of *Dytiscus marginalis* Linnaeus (Coleoptera: Dytiscidae). Pan-Pacif. Ent. 43: 113–117.