

Predator-Prey Relationships Among Larval Dragonflies, Salamanders, and Frogs

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Summary. Tadpoles of the barking tree frog, *Hyla gratiosa*, are abundant in spring and summer in some ponds and Carolina bays on the Savannah River Plant near Aiken, South Carolina. To determine how these tadpoles survive in the presence of predaceous salamander larvae, *Ambystoma talpoideum*, and larvae of an aeshnid dragonfly, *Anax junius*, we determined fields densities and sizes of the predators and the prey and conducted predation experiments in the laboratory. Tadpoles rapidly grow to a size not captured by *Ambystoma*, although *Anax* larvae can capture slightly larger tadpoles. Differing habitat preferences among the tadpoles and the two predator species probably aid in reducing predation pressure. Preliminary work indicates that the tadpoles may have an immobility response to an attack by a predator. In addition, the smallest, most vulnerable tadpoles have a distinctive color pattern which may function to disrupt the body outline and make them indiscernable to predators.

Introduction

Many species of frogs reproduce in temporary pools such as small ponds, Carolina bays (Schalles 1979), and roadside ditches that form in late winter or early spring and persist until midsummer. These pools lack certain kinds of very efficient predators of tadpoles such as fish; however, toward the end of spring, they develop large populations of potential invertebrate predators such as dragonfly and beetle larvae, and vertebrate predators such as salamander larvae. Calef (1973) reported that 95% of a population of tadpoles of the red-legged frog, *Rana aurora*, did not survive to metamorphosis and that 75% of this mortality was due to predation by salamander larvae. Other studies (Neill 1968; Pritchard 1964; Young 1967; Heyer, McDiarmid, and Weigmann 1975; Walters 1975) have shown that a variety of invertebrates prey on certain species of tadpoles.

We observed large populations of tadpoles of the barking tree frog, *Hyla gratiosa* LeConte, in Carolina bays and small ponds in the southeastern U.S.A. from May through August. Because this period coincides with maximum densities of invertebrate and salamander populations in these temporary lentic environments, we asked the following questions concerning survival of *Hyla gratiosa* tadpoles: (1) What are the potential predators of *H. gratiosa* and what are their densities? (2) How does the relationship between tadpole size and predator size change over time?

(3) What are some of the mechanisms used by these tadpoles to escape predation? We designed laboratory experiments to answer some of these questions and attempted to relate these findings to our field observations on densities and sizes of these organisms.

Methods

The primary study area was Pond 9, a large, temporary pond located in the southern portion of the U.S. Department of Energy's Savannah River Plant (SRP) in Barnwell County, South Carolina. Some observations were also made in Morse Code Bay and Carolyn's Bay, located in the eastern part of the SRP in Aiken County. When the study began in June, 1978, Pond 9 was approximately 75 m in diameter with a maximum depth of 1 m. The pond was completely dry by the middle of August. Morse Code Bay was approximately 40 m in diameter, had a maximum depth of 0.5 m, and was dry by the end of June. Carolyn's Bay is similar to Morse Code Bay, but holds water for a longer period of time. All ponds supported large populations of *H. gratiosa* tadpoles.

Field Data. Benthic organisms were sampled quantitatively from 20 June to 21 July at 10-day intervals to determine species composition and density of predators and tadpoles occurring in Pond 9. On each sampling date, 10 samples were taken using a heavy metal drop box covering an area of 0.5 m². Samples were selected in a stratified random fashion with equal numbers taken from vegetated and open areas. After the box was quickly lowered in a particular area, all vertebrates and macroinvertebrates on or above the substratum were removed by sweeping the enclosed area with a dip net until 10 sweeps yielded no additional animals. All organisms collected were immediately preserved in the field in 10% formalin. Densities are expressed as numbers/m².

Hyla gratiosa tadpoles, larvae of the mole salamander, *Ambystoma talpoideum* (Holbrook), and nymphs of an aeshnid dragonfly, *Anax junius* Drury, were identified and measured to the nearest 0.1 mm. The standard measures of total length for tadpoles (Altig 1970) and snoutvent length for salamanders were used. Total length was also measured for *Anax*. The means and standard errors of the abundances and sizes of *Hyla*, *Ambystoma*, and *Anax* were calculated for each sampling date.

Predation Experiments. Laboratory experiments were conducted to determine the relative efficiency of predation of *A. talpoideum* larvae and *A. junius* nymphs on *H. gratiosa* tadpoles. Experimental containers were green plastic buckets with a diameter of 27 cm. Each bucket contained water 12 cm deep and approximately 5 g

(wet weight) of an aquatic grass, *Hydrochloa carolinensis*, for cover. In each experiment five tadpoles were tested from each of 4 size classes (0–29 mm, 30–39 mm, 40–49 mm, and 50+ mm). Tadpoles were added to each bucket and allowed to acclimate for at least 1 h before a predator (either a salamander or a dragonfly) was added. Buckets with tadpoles but no predators served as controls. Predators were measured as described previously and were starved for 48 h before being used in experiments. The number of surviving and injured tadpoles was recorded after 24 h. Predators were used only once.

A nonparametric test, the Mann-Whitney U-statistic, was used to examine the effects of the two predators on the number of tadpoles eaten or wounded as a function of prey size. Kendall's coefficient of rank correlation was employed to test the effects of predator size and prey size on the number of tadpoles eaten or wounded.

Linear and non-linear models were constructed in an attempt to predict the effects of predator size, predator type, tadpole size, and the interaction of predator and tadpole sizes on the number of tadpoles eaten and the percent wounded. Programs for the regression models were part of the General Linear Model (GLM) package of the Statistical Analysis System (Barr et al. 1976). In all tests the percent of tadpoles wounded was corrected to reflect the maximum number of tadpoles which were available for wounding after the original complement of prey had been reduced by predation. The following correction factor was used:

$$\% \text{ wounded} = 100 \times \frac{\text{no. wounded}}{5 - \text{no. eaten}}.$$

An alpha level of 0.05 or less was used for significance in all experiments.

Immobility Experiments. Many animals become immobile if touched or approached very closely by a predator, a behavior thought to reduce the probability of an attack (see review of literature in Brodie, Johnson and Dodd 1974). To determine if *H. gratiosa* tadpoles have an immobility response, experiments were conducted in the field at Pond 9 and at Carolyn's Bay on the SRP. Twenty-five tadpoles in each of the four size classes described above were tested in 2.5 l of pond water in a glass aquarium (14 × 2.5 cm base). For each replicate, a tadpole was netted, immediately placed in the aquarium, and allowed to acclimate for 2 min. The tadpole was then prodded at the base of the tail to simulate an attacking predator. After an initial quick movement, the tadpole became immobile. This period of quiescence was timed with a stop-watch. After the tadpole moved, its total length was measured and it was then released. For each of the 4 size classes the mean and standard deviation were calculated for the time of immobility. An analysis of variance was used to detect significant differences among size classes.

Results and Discussion

Predator and Prey Sizes and Densities. The average size of barking tree frog tadpoles and mole salamander larvae remained nearly constant during the course of the study, whereas the mean length of individuals of the dragonfly nymph, *A. junius*, increased considerably in early July (Fig. 1). The mean length within cohorts of tadpoles from each sampling date remained constant over the study period because of continual egg-laying for several months by the adults; thus, each sample was composed of a variety of

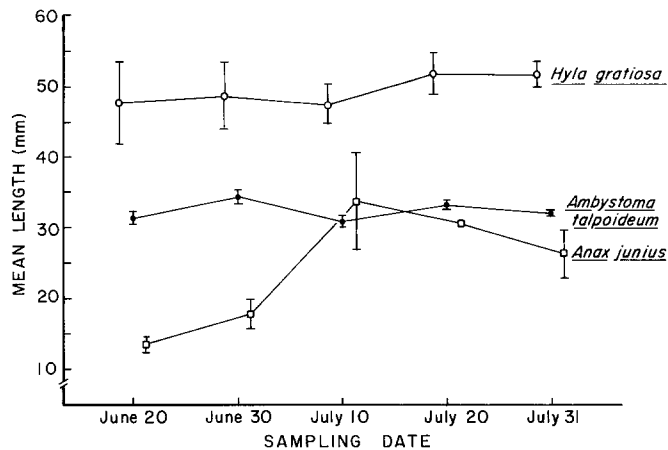


Fig. 1. Changes in mean length and standard errors of populations of barking tree frog tadpoles, *Hyla gratiosa*, larvae of the mole salamander, *Ambystoma talpoideum*, and larvae of an aeshnid dragonfly, *Anax junius*, for five sampling dates in Pond 9 on the SRP. Ten subsamples were taken on each sampling date

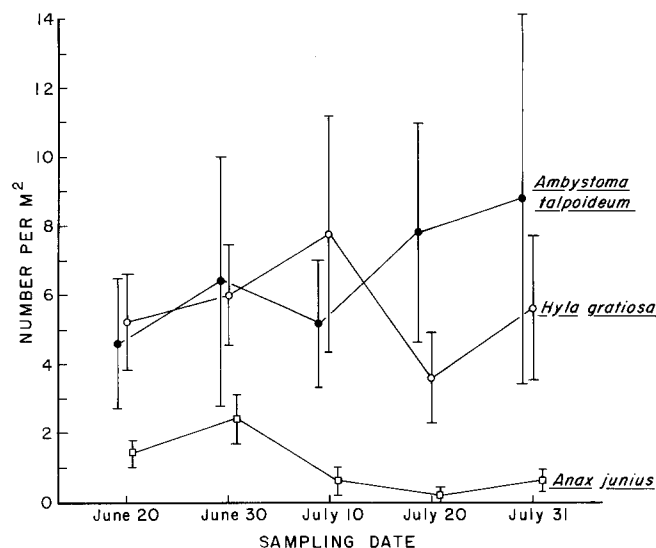


Fig. 2. Changes in mean number/m² and standard errors of populations of barking tree frog tadpoles, *Hyla gratiosa*, larvae of the mole salamander, *Ambystoma talpoideum*, and larvae of an aeshnid dragonfly, *Anax junius*, for five sampling dates in Pond 9 on the SRP. Ten subsamples were taken on each sampling date

sizes of tadpoles. The mole salamander larvae remained constant in size during the study because breeding occurs over a relatively short period in late winter (Patterson 1978) and most larvae had reached their maximum size when the study began. These size relationships are also evident from a comparison of the standard errors of the mean sizes of these tadpoles and salamanders (Fig. 1); the size variation of *Ambystoma* was much smaller than that of *Hyla*. By contrast, *Anax* nymphs showed an increase in size as the summer progressed. Egg-laying also begins in the spring and continues throughout the summer in this dragonfly species (Calvert 1934), but larval growth is slow and a gradual increase in size can be seen throughout the sampling period. The average size for *Anax* in the July 10 sample may have been inflated by one very large nymph.

Hyla gratiosa tadpoles and *Ambystoma* larvae were more abundant throughout the study than *Anax* nymphs (Fig. 2). *Ambystoma*

was most abundant although the high standard errors indicate that salamander distribution was patchy. Initially, *H. gratiosa* tadpoles were as abundant as *Ambystoma* larvae but became less abundant later in July as the tadpoles began undergoing metamorphosis earlier than the salamander larvae. In contrast, the density of *A. junius* nymphs remained at a constant low level throughout the summer.

Predation Experiments. *Anax* nymphs are able to catch and consume tadpoles larger than those caught by *Ambystoma*. Table 1 shows that in the smallest size class of tadpoles (0–29 mm) there was no significant difference between the two predators in the number of tadpoles eaten. However, *Anax* ate significantly more tadpoles of the two largest size classes than did *Ambystoma*. Pritchard (1965) states that dragonfly larvae only will attack prey which fall between certain size limits. For *Aeshna interrupta*, a species similar to *Anax junius*, the largest disc most animals (10 of 12) would attack was 20 mm². This figure corresponds closely to the body size of the largest size class of tadpoles we tested.

There is a trend for *Ambystoma* to wound more tadpoles than *Anax* does, but the relationship may be an indirect consequence of the efficiency of *Anax* in capturing their prey; few tadpoles are wounded by *Anax* because most prey, if caught, are eaten. Unlike *Anax*, *Ambystoma* is unable to seize and devour large tadpoles, but many are wounded as a result of being pursued by salamanders.

Predator size and number of tadpoles eaten was significantly correlated for *Ambystoma* but not for *Anax* (Table 2). As the size of *Ambystoma* increased, the number of tadpoles eaten increased, whereas *Anax* of all sizes ate the same number of tadpoles. As tadpole size increased, fewer were eaten by *Ambystoma*, whereas there was no relationship between tadpole size and the number eaten by *Anax*.

Relationships between predator length, tadpole length, and either the number of tadpoles eaten or the percent wounded varied with predator type (Fig. 3a–d). The linear equation (Fig. 3a) best describing the number of *Hyla* eaten by *Ambystoma* (No. eaten = $-8.51 + 0.33$ (PS) + 0.17 (TS) + 0.01 (PS \times TS); where PS = predator size in mm length, TS = tadpole size in mm length, and PS \times TS = the interaction of the two sizes) was significant for all factors ($P < 0.001$, 0.021 , and 0.003 , respectively). But, the equation which best described the relationship between the number of *Hyla* eaten by *Anax* (No. Eaten = $2.96 + 0.06$ (PS) + (-0.12) (TS) + 0.0007 (PS \times TS)) was not significant (Fig. 3c) possibly because of the manner in which each predator attacked the prey. *Ambystoma* swallows its prey whole, whereas *Anax* grasps the tadpole anywhere on its body, and holds on with its labium eventually consuming the tadpole. Thus, the ease with which *Ambystoma* swallows a tadpole is inversely proportional to the tadpole's cross-sectional area. *Anax*, by contrast, is not as size-limited because of its ability to hold on to large struggling prey. All relationships between percent of *Hyla* wounded by *Ambystoma* and *Anax* which used the same independent variables as for number eaten were non-significant. The lack of significant predictability of these equations may have resulted from the ability of both types of predators to wound most tadpoles regardless of relative size between predator and prey (Figs. 3b and 3d).

Immobility Experiments. *Hyla gratiosa* tadpoles showed an average immobile response in excess of 4 min when predation was simulated (Fig. 4). There was no significant difference, however, in the length of time tadpoles in four size classes remained immobile (ANOVA, $F = 0.0663$; $P > 0.05$).

Table 1. Comparison of the effects of predator type (*Ambystoma talpoideum* or *Anax junius*) and tadpole size class on the number of tadpoles eaten and on the percent wounded using the Mann-Whitney U-test

Size classes	\bar{X} <i>Amby.</i>	\bar{X} <i>Anax</i>	U	n_1/n_2	Prob. > U
0–29 mm					
No. eaten	2.00	2.17	35.5	13/6	0.20
% wounded	37.50	20.83	74.0	13/6	0.005**
30–39 mm					
No. eaten	0.67	2.15	154.0	15/13	0.01**
% wounded	42.11	40.38	103.5	15/13	0.20
40–49 mm					
No. eaten	0.20	1.10	117.5	15/10	0.02*
% wounded	42.67	28.33	94.0	15/10	0.20
Pooled					
No. eaten	0.51	1.86	984.5	36/36	0.001**
% wounded	41.41	30.24	799.0	36/36	0.10–0.05

* $p < 0.05$

** $p < 0.01$

Table 2. The effects of predator size and tadpole size on the number of tadpoles eaten and wounded by *Ambystoma talpoideum* and *Anax junius* using Kendall's coefficient of rank correlation

	τ (tau)	St. Dev. units	n	Prob.
Predator Size				
<i>A. talpoideum</i>				
No. eaten	0.279	2.89	51	0.0038**
% wounded	0.227	2.35	51	0.0188*
<i>A. junius</i>				
No. eaten	0.222	1.78	32	0.0750
% wounded	0.333	2.68	32	0.0074**
Tadpole Size				
<i>A. talpoideum</i>				
No. eaten	-0.386	-4.00	51	0.0002**
% wounded	0.033	0.35	51	0.7264
<i>A. junius</i>				
No. eaten	-0.225	-1.93	36	0.0536*
% wounded	0.086	0.74	36	0.5592

* $p < 0.05$

** $p < 0.01$

Brodie et al. (1974) and Dodd and Brodie (1976) defined an immobility response in terrestrial salamanders as the absence of motion when uncovered or prodded. In contrast, tadpoles, when frightened or prodded, initially dart off and then slowly sink a short distance as they become immobile. The difference in the immobility response between salamanders and tadpoles may relate to habitat because one group is terrestrial and the other aquatic. An aquatic predator, such as the dragonfly nymph *Anax*, hunts visually so that it would be advantageous for a tadpole to escape a short distance and then stop. Werschkul and Christensen (1977) reported an immobility response in tadpoles of *Rana sphenoccephala* and *Rana areolata*, although they did not elaborate on the specific details of the response.

An alternative explanation for an immobility response in tad-

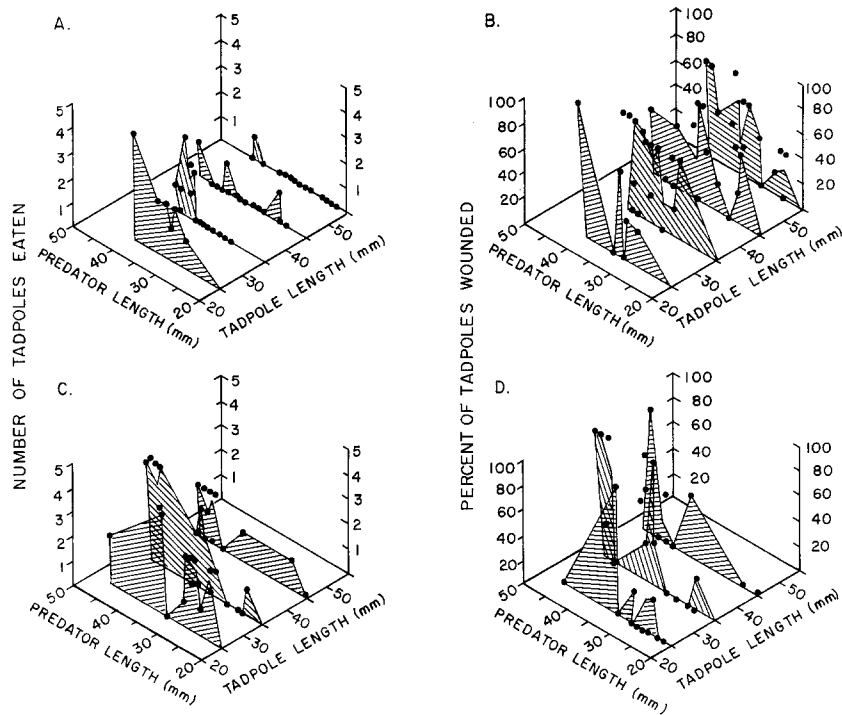


Fig. 3 A-D. Relationships between predator length, tadpole length, and number of tadpoles eaten or wounded. *Ambystoma talpoideum* is the predator in A and B, *Anax junius* in C and D

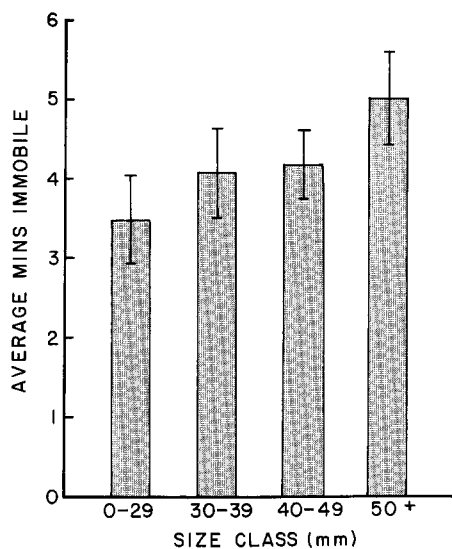


Fig. 4. Mean length of time (in min) that four size classes of *Hyla gratiosa* tadpoles remained immobile after predator attack was simulated. Bars represent one standard error on either side of the mean

poles is that the quick dart they exhibit when frightened might be an escape response, and the immobility observed is due to exhaustion. Additional work on the anaerobic capacity of these tadpoles is currently underway to distinguish between these hypotheses.

Relationships Between Field Observations and Laboratory Experiments. Heyer and Muedeking (1976) conducted experiments to determine the maximum number of *Agalychnis callidryas* tadpoles, a tropical hyliid similar in habits to *Hyla gratiosa*, that could potentially be eaten by a large dragonfly naiad of the libellulid genus *Orthemis*. By calculating the number of tadpoles in their

study pond using the number of egg clutches found, they concluded that a small population of large naiads could theoretically eliminate all *Agalychnis* tadpoles from the pond. Their observations indicated that this did not happen and they concluded that habitat differences and rapid growth of the tadpoles prevent this occurrence.

The *Anax-Hyla* interactions discussed herein are probably similar to the *Orthemis-Agalychnis* situation described above. Our laboratory experiments were designed to show what size classes were most vulnerable to predation whereas Heyer and Muedeking (1976) determined how many tadpoles a dragonfly naiad could eat under saturated conditions. We used a smaller number of tadpoles in a larger volume of water, and thus our experiments were probably more representative of actual field densities. The results of our experiments compared to those of Heyer and Muedeking were that fewer tadpoles were eaten within a 24-h period. Although other factors cannot be eliminated, a rough comparison of these two experimental approaches indicates that when density is lower fewer tadpoles are eaten, probably because of the greater search time per tadpole. Our field density data showed that *Anax* was not abundant during the study period and, therefore, probably did not regulate the density of the tadpole population.

Field data indicate that both salamander (*A. talpoideum*) larvae and tadpoles (*H. gratiosa*) were present at the same time in the ponds. But observations and a literature report (Anderson and Williamson 1974) show that salamanders are found on the pond bottom during the day, whereas the tadpoles, especially the small ones, occur in midwater (Altig 1972). This diurnal separation probably helps to prevent a heavy predation rate on the tadpoles.

Anderson and Williamson (1974) reported that *A. talpoideum* larvae move up the water column and feed near the surface at night. Altig (1972) found that in the laboratory larger tadpoles have a tail-darkening reaction at night. However, it is unlikely that this reaction is an antipredator response to salamanders, since our laboratory data showed that salamanders did not feed on the larger size class of tadpoles.

Our laboratory data showed that the size class most susceptible to predation was the smallest one used in our experiments (up to 29 mm in total length). It is noteworthy that these tadpoles have a different color pattern than the older tadpoles (above 30 mm in length). The small tadpoles are white or translucent except for the eyes and gut and have a sharply defined black saddle midway on the tail musculature. Altig (1972) presented a diagram showing the color pattern of these small tadpoles and noted that they often hang head-high in midwater. Our laboratory experiments lend credence to Altig's (1972) hypothesis that the saddle serves as a disruptive color pattern by breaking up the body lines against a background of plant stems and shadows.

The field data presented herein show that the density of the tadpoles remained fairly constant, and that a variety of sizes of tadpoles were present at all times in the ponds. Perhaps the strategy of laying eggs throughout the summer has evolved in this species as a response to an ever-present, though low, predation pressure. In addition, *Hyla gratiosa* lays single eggs which may help to disperse the younger, more vulnerable tadpoles. In other species which lay their eggs in clumps (e.g., *Rana utricularia*) the newly hatched tadpoles cling to the jelly mass for a period of time and are more easily eaten by a single predator.

In summary, survival of *Hyla gratiosa* tadpoles appears to be a result of several factors: (1) continual deposition of eggs so that predators are constantly saturated by the small, vulnerable size class, (2) a distinctive color pattern in the small tadpole, (3) habitat separation of the tadpoles and the dragonfly and salamander larvae, (4) rapid growth to a less vulnerable size, and (5) a potential immobility response. At present, work is underway to learn more about the immobility response. Work should also be undertaken to discover if the growth rate of tadpoles is a function of predation pressure.

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