Notes on Tadpoles as Prey for Naiads and Turtles

W. Ronald Heyer and Miriam H. Muedeking

Amphibians and Reptiles, Smithsonian Institution, Washington, D. C. 20560

Although there is a large literature on predator-prey interaction theory, there are still some specific interactions for which there is little or no information. Naiads and turtles are known predators on tadpoles, but nothing is known concerning feeding rates involved. In order to gather some basic information on these specific interactions, we ran some simple, straightforward experiments while on Barro Colorado Island, Canal Zone, in July 1975.

Naiad-Tadpole Experiments

The purpose of the experiments was to determine the maximum feeding rate of naiads, using tadpoles as prey. All experimental animals, plants and water came from a cement pond in the living compound built by A. S. Rand for his studies on *Physalaemus pustulosus*.

Holding and experimental containers were square or round plastic containers approximately 9 cm across, filled with pond water 4 cm deep. Large naiads (Family Libellulidae, *Orthemis* sp. prob. *ferruginea*) were isolated for 1 or 2 days prior to introducing them to the prey. Each experimental tray had 1 naiad, some water weed (*Hydrella*), and a superabundance of prey, either 30 or 50 individuals, depending on prey type. Three types of prey were used: 30 small *Agalychnis callidryas* tadpoles, 50 small *Physalaemus pustulosus* tadpoles, or 30 large *Physalaemus pustulosus* tadpoles. Experiments were run from 22-¾ to 26-⅔hr. Other projects did not allow exact 24-hr experimental runs in all cases. All tadpole larvae were well within the size range on which the naiads could feed. At the end of each experiment, the naiad and remaining prey were preserved together in a vial containing 10% formalin. Five replicates of small *Agalychnis*, 10 replicates of small *Physalaemus*, and 12 replicates of large *Physalaemus* were run. In one of the small *Agalychnis* runs, several tadpoles died in handling; the results of this particular run are not included in the analyses.

In the laboratory, the following data were taken from specimens in each experimental vial: 1) the number of tadpoles left after the experiment; 2) the volume of the tadpoles left after the experiment, 3) the volume of the naiad. Volumes were determined by formalin displacement in a 10-ml graduated cylinder. Excess surface moisture was removed by paper towelling before volume determination. From these data, the following were determined: 1) the number of tadpoles consumed during the experiment (initial number minus number left), 2) the volume of tadpoles eaten per predator adjusted to 24 h. The assumption used in determing this last value is that the sizes of the tadpoles consumed were the same as the sizes of the tadpoles left in each experiment. As post-hatchling *Agalychnia* and large premetamorphic *Physalaemus* were used, the size variances in experiments using these prey were not great. The greatest size variance was in the experiments run with small *Physalaemus* as prey.

The data were analyzed using the UCLA Biomedical 10V program (Dixon, 1974), general linear hypothesis without and with a covariate, testing numbers of prey and volumes of prey consumed separately.

The results of the analysis testing kinds of prey based on numbers of prey eaten are presented in Table 1. There is a signif-

TABLE 1.—Analysis of number of prey types eaten with no covariate. P1 = *Agalychnis*, P2 = Small *Physalaemus*, P3 = Large *Physalaemus*. SS = sums of squares, DF = degrees of freedom, MS = mean squares, * = significant at the 5% level, ** = significant at the 1% level.

Source	SS	DF	MS	F
Prey	221.86145	2	110.93072	4.92604*
P1 = P2	31.77779	1	31.77779	1.41114
P1 = P3	27.75521	1	27.75521	1.23251
P2 = P3	221.79206	1	221.79206	9.84900**
Error	517.94317	23	22.51926	

icant difference in the number eaten among the 3 prey types and the difference is between the number of small *Physalaemus* vs. large *Physalaemus* eaten.

The results of the analysis testing kinds of prey based on volumes of prey eaten are presented in Table 2. There are no significant differences among the volumes eaten of the 3 prey types.

Large naiads were purposely chosen to minimize the variation in the experiments due to predator differences. Predator-prey size relationships are very important, however (e.g. Heyer *et al.*, 1975), so the data were tested to see if the results were affected by differences in sizes among the predators. To test, volume of predator was used as the size factor and included as a covariate with the data as analyzed in Tables 1 and 2. The results with the covariate added are presented in Tables 3 and 4. The results are exactly the same as in Tables 1 and 2; size differences among the predators used had no effect on the experiments.

The average number of *Agalychnis* consumed per naiad over 24 h is 5.7 with an average volume of 0.038 ml/tadpole. The average number of small *Physalaemus* consumed per naiad over 24 h is 9.0 with an average volume of 0.027 ml/tadpole. The average number of large *Physalaemus* consumed per naiad over 24 h is 2.63 with an average volume of 0.109 ml/tadpole. An individual naiad consumed 0.77 of its volume in prey tadpoles per 24 h on the average.

Turtle-Tadpole Experiment

A single 49.5-mm-carapace-length juvenile turtle, *Chrysemys scripta*, was found in Rand's pond. After isolating the turtle for 24 h, it was placed in a plastic container of the same size as used in the naiad experiments, without water weed, and with 30 large *Physalaemus*. After 26-⅔ h, all of the tadpoles had been killed and at least partially consumed. The water was turbid. After isolating the turtle for 24 h, it was placed in the bottom of a plastic Chlorox bottle from which the top half had been cut off. The bottle was 15 cm in diameter and water was placed 4 cm deep. Some *Hydrella* was added along with 30 large *Physalaemus*. We were interested in knowing if giving the prey a better opportunity to hide from the predator would make a difference in the results. After 26.5 h, only 1 tadpole was left alive. The water was clear. The turtle was isolated for another 24 h. The experimental setup was the same as the previous run except 100 large *Physalaemus* were added. After 27 h, 1 *Physalaemus* was left alive. The water was relatively clear. The turtle was isolated for 48 h. The next experiment differed only in adding 200 large *Physalaemus*. After 25-⅓ h, 71 *Physalaemus* were alive, but the water was dark brown as in the first run. As turtles are largely visual feeders,

TABLE 2.—Analysis of volume of prey types eaten with no covariate. See Table 1 for explanation of abbreviations.

Source	SS	DF	MS	F
Prey	0.08021	2	0.04011	0.63027
P1 = P2	0.07498	1	0.07498	1.17833
P1 = P3	0.06235	1	0.06235	0.97984
P2 = P3	0.00173	1	0.00173	0.02726
Error	1.46360	23	0.06363	

TABLE 3.—Analysis of number of prey types eaten with naiad volume as a covariate. See Table 1 for explanation of abbreviations.

Source	SS	DF	MS	F
Prey	211.99865	2	105.99932	4.52292*
P1 = P2	32.59413	1	32.59413	1.39077
P1 = P3	29.91784	1	29.91784	1.27657
P2 = P3	211.99650	1	211.99650	9.04575**
Covariate	2.35026	1	2.35026	0.10028
Error	515.59291	22	23.43604	

the limits of the experimental design had been reached.

Discussion

A model has been proposed recently which attributed a limiting factor of tadpole diversity to fish predation (Heyer *et al.*, 1975). The same authors commented that other vertebrate predators may also control tadpole diversity through completely eliminating tadpole populations in given ponds. Such invertebrate predators as dragonfly larvae were considered not to be able to eliminate tadpole populations, although tadpole populations could be markedly reduced. The critical aspect is elimination, not reduction of tadpole populations.

Although Rand's pond from which all experimental animals were taken is artificial, the assemblage of species in it probably is not. For purposes of discussion, then, only the species populations in this pond will be examined. There are two aspects to eliminating tadpole populations; eliminating the tadpoles from a single clutch of eggs and eliminating the total tadpole population, which would result from 1 or more clutches of eggs. The average of 16 *Agalychnis* egg clutches

TABLE 4.—Analysis of volume of prey types eaten with naiad volume as a covariate. See Table 1 for explanation of abbreviations.

Source	SS	DF	MS	F
Prey	0.08164	2	0.04082	0.63759
P1 = P2	0.08159	1	0.08159	1.27454
P1 = P3	0.03877	1	0.03877	0.60558
P2 = P3	0.01371	1	0.01371	0.21413
Covariate	0.05517	1	0.05517	0.86185
Error	1.40843	22	0.06402	

counted was 53.4; of 3 *Physalaemus* nests counted, 216.7.

The turtle, *Chrysemys scripta*, could possibly eliminate the tadpoles from a clutch of *Agalychnis* eggs in about 0.5 day, and the tadpoles of a *Physalaemus* clutch in somewhat more than 1 day. By remaining in a pond for a few days, *Chrysemys scripta* could theoretically eliminate the tadpole population from the pond, assuming moderate anuran reproductive output. Whether turtles remove entire tadpole populations in nature remains to be determined, however. There is at least one reason to believe that turtles would not eliminate tadpoles. Turtles are mobile feeders; as the tadpole population is reduced, the energy spent in capture becomes greater. There is likely a point where the energy expenditure per capture becomes so great that the turtle switches to another prey, if available. The experimental evidence presented here suggests that turtles can be effective tadpole predators, even if turtles do not completely eliminate tadpole populations.

If the average consumption rates of the large naiads are used together with average clutch size, it takes A) 9.4 large naiad days to consume the small tadpoles from a single *Agalychnis* clutch; B) 24.1 large naiad days to consume the tadpoles from a single *Physalaemus* clutch if the tadpoles are consumed when small; C) 82.4 large naiad days to consume the tadpoles from a single *Physalaemus* clutch if the tadpoles are consumed when large. These are probably maximal rates, as the experiments were designed to saturate the predators with prey.

From these data, it would appear that

a small population of large naiads could eliminate *Agalychnis* tadpoles from a pond. The experiments did not take habitat differences into account, however. The experimental trays were small enough that the naiad could sample tadpoles from the entire water volume, as there was enough *Hydrella* in the trays to allow this. In the pond from which the experimental animals were taken, the naiads were either sitting camouflaged on the cement edge or in *Hydrella* mats. The *Agalychnis* were in the open water; the *Physalaemus* appeared to be everywhere. Thus, the naiads and *Agalychnis* tadpoles were effectively spatially isolated. Another factor contributing to the likelihood that naiads would not eliminate *Agalychnis* tadpoles from ponds relates to size. *Agalychnis* hatchlings are large and the tadpoles become much larger than *Physalaemus* tadpoles. Large *Agalychnis* tadpoles are too large for the size naiads used in the experiments to feed upon (also see Heyer *et al.*, 1975). Thus, in nature, we would not expect naiads to regularly eliminate *Agalychnis* tadpoles from ponds.

The *Physalaemus* larvae are always within the size range of prey items for the size of naiad used in the experiments, and the tadpoles and naiads occur in the same pond habitats. The ingestion rates suggest that the *Physalaemus* tadpoles would not be eliminated by naiads, however. The duration of the *Physalaemus* larval stage probably does not exceed 30 days and small *Physalaemus* larvae would grow to large larvae within 2 to 3 weeks. In terms of a clutch, then, even with maximum naiad predation, some larvae would avoid predation and become large larvae; once the *Physalaemus* larvae are large, the rate of predation falls markedly, such that some larvae would make it through to metamorphosis.

The naiad evidence presented here, while not conclusive, is consistent with the hypothesis that under usual conditions, naiads will reduce—not eliminate—tadpole populations. This was certainly true in the pond from which the experimental animals were taken. There was a noticeably present naiad population, many *Agalychnis* tadpoles and an abundance of *Physalaemus* tadpoles. Assuming that naiads were consuming tadpoles in the pond, the tadpoles were not eliminated; many made it through to metamorphosis during the time we observed the pond.

Under unusual conditions, when the numbers of naiads per volume water is greater than usual, and pond microhabitat differences disappear, the data presented here suggest that naiads could eliminate tadpole populations. Such conditions can occur when temporary ponds dry up as have been reported from field situations (Heyer, 1973).

Another important factor to consider is the nutritive value of tadpoles. Tadpoles are feeding machines, and an unusually large part of the volume of a tadpole is gut. The gut contents, usually algae and diatoms, are not digestible by many tadpole predators, so the total food value of a tadpole to its predator is effectively much less than of a similar sized fish, for example (R. T. Lovell, pers. comm.). Thus, particularly for vertebrate predators, tadpoles may be consumed only when they are very abundant relative to other prey items. The avoidance of tadpoles as prey might involve a tast preference as the gut contents of the tadpole may be distasteful.

One aspect of the experiments invites speculation. The results indicate that naiads feed until they are full, irrespective of the number of prey items it takes to fill them. It would be interesting to know the relative energy costs of naiads catching 9 small *Physalaemus* vs. 3 large *Physalaemus* per day. There are two energy costs to a naiad in consuming prey: 1) the cost of discharing the catching apparatus and trapping the prey (fixed energy cost due to the mechanism involved), 2) the cost of manipulating the struggling prey back into the mouth to be eaten (variable cost). If the latter energy cost is the same for small and large *Physalaemus*, then a naiad would clearly benefit energywise by concentrating on larger prey items. If large struggling tadpoles take much more energy to manipulate into the mouth than small tadpoles, then a naiad would benefit in an energy budget by concentrating on smaller prey items. To our knowledge, the relative energy budgets involved in prey capture by naiads are unknown.

Acknowledgments

Oliver S. Flint and George R. Zug, Smithsonian Institution, carefully read the manuscript. Dr. Flint also identified the naiads. Charles D. Roberts, Smithsonian Institution, provided statistical analyses and interpretations of the data. Susan Arnold took the laboratory data and prepared the data for statistical analysis. George Folkerts, Auburn University, discussed some of the results with us and told us of the work of R. T. Lovell. Laura and Elena Heyer assisted with the experiments. Financial support from the Environmental Sciences Program, Smithsonian Institution, made the study possible.

References Cited

Dixon, W. J. [ed.]. 1974. BMD Biomedical Computer Programs. Univ. California Press, Berkeley. 773 pp.

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

———, **R. W. McDiarmid, and D. L. Weigmann.** 1975. Tadpoles, predation and pond habitats in the tropics. Biotropica 7: 100–111.