SIZE-LIMITED PREDATION ON LARVAL
RANA AREOLATA (ANURA: RANIDAE)
BY TWO SPECIES OF BACKSWIMMER
(INSECTA: HEMIPTERA: NOTONECTIDAE)

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ABSTRACT: Size-limited insect predators can act as agents of selection for tadpole growth rate and body size. We designed an experiment to test for size-limited predation on larval *Rana areolata* by adults of two species of notonectid insects. An individual insect, either *Notonecta indica* or *N. undulata*, was exposed to 21 tadpoles from one of four tadpole size classes. Predation rate of *N. undulata* decreased continuously with increasing tadpole size. By contrast, *Notonecta indica* did not attack newly hatched tadpoles but consumed considerable numbers of tadpoles in the second size class. The subsequent rate of *N. indica* predation was a decreasing function of increasing tadpole size. These daily rates of predation were comparable to those displayed by other insect predators of tadpoles, although the size range of tadpoles attacked is narrower for notonectids than for other insect predators.

Key words: Larval mortality; Notonectids; *Rana areolata*; Size-limited predation

MANY anurans exploit temporary ponds for breeding sites. Such ponds offer an advantage to the tadpoles, because they lack efficient predatory fish (Grubb, 1972). One disadvantage of temporary ponds is the abundance of predaceous insects, many of which are effective predators of tadpoles (Brockelman, 1969; Caldwell et al., 1980; Calef, 1973; Formanowicz and Brodie, 1982; Heyer et al., 1975; Smith, 1983). In most of these cases, predation is size limited: predation rate decreases with increasing tadpole size, and once beyond a critical maximum size, the tadpoles are invulnerable. Size-limited predation on anuran larvae can influence species-abundance patterns (Morin, 1983), and such predators can select for increased larval growth rate (Travis, 1983a; Travis et al., 1985).

Adult notonectid hemipterans have been implicated as agents of selection on tadpole growth rate (Travis, 1983a), but experimental support for that role is only suggestive (Licht, 1974). In north Florida, adult notonectids are particularly common in temporary ponds during the late winter and early spring, when the ponds are used by breeding *Hyla crucifer*, *Pseudacris ornata*, *Rana sphenocephala*, and *R. areolata*. If notonectids are significant size-limited predators, then they could be selective agents of mortality for all four species. We report experimental results on the effect of tadpole body size on notonectid predation rate, using tadpoles of *R. areolata* and adult *Notonecta indica* and *N. undulata*.

MATERIALS AND METHODS

Experimental Design and Procedure

Our experiments were designed to test for size-limited predation by two different species of *Notonecta*. We exposed 21 tadpoles from one of four size classes to one individual adult insect for 24 h. We used 10 replicates per size class per insect species. Individual *N. indica* were held without food for 24 h before each trial, while individual *N. undulata* were held for 48 h before each trial. This difference was caused by practical constraints on repeated collecting and culturing of insects and tapoles and precludes our making any direct inferences about differences between the species.

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We divided two thousand hatchling tadpoles from one egg mass into 20 containers for culturing. Each container held approximately 4 liters of well water. We reared tadpoles under uniform conditions to minimize body size variance among individuals at any given time (see Travis, 1981, 1983b, for descriptions of rearing techniques). Adult insects were collected from the same pond as the egg mass, typically from shallow areas amid vegetation.

Individual insects were placed in separate containers in the laboratory with 4 liters of well water. After the acclimation period, 21 tadpoles were removed from culture conditions and were placed in each of the 10 containers holding the insects. An additional sample of 20 tadpoles was frozen for later assay of dry weight for that trial. After 24 h, the containers were censused and the number of tadpoles eaten was recorded. This entire procedure was repeated every seven days, although tadpoles were continually cultured, resulting in four tadpole size classes for each species of insect predator. Frozen tadpoles were dried for 48 h at 60 C at 22 mm Hg vacuum and weighed to 0.01 mg precision.

We made no attempt to control the sex of insect, the age of insect, or any other factor that may influence the predation rate (Cockrell, 1984). Any effects of these factors served to increase the residual variance of our statistical model and thereby reduced the power of our tests. Our method of testing the effects of tadpole body size confounded body size with time: size classes were tested in sequence from smallest to largest. The only viable alternative method, culturing tadpoles under variable temperature or food regimes to obtain all size classes simultaneously, would confound tadpole size with vigor, responsiveness, and energetic content of the tadpoles (Crump, 1981; Travis et al., 1984).

Statistical Analysis

The number of animals eaten may be a poor statistic for the analysis of predation rate (Travis et al., 1984; Trexler, 1982). The number eaten is a discrete binomial variable whose distribution is normal only when the number of potential prey is large and the probability of an individual predation event is small. In cases, such as ours, that do not exhibit these properties, the data must be transformed. The log odds transformation (natural $\log\{0.5 + [p/(1 - p)]\}$ where p is the proportion eaten) converts the number eaten into a continuous, normally distributed random variable.

The transformed data on the predation rate by each species of insect were analyzed as separate one-way randomized designs. All possible pairwise comparisons among the size classes were tested using Dunn's procedure at the 0.05 error rate (Kirk, 1982). The dry weights of tadpoles from the four trials for each species of notonectid were analyzed as separate one-way randomized designs. Dry weight data were subjected to a logarithmic transformation before analysis, and Dunn's procedure was used for testing all possible pairwise comparisons.

Results

Tadpoles grew between successive trials (Table 1). Analyses of variance and multiple comparisons among the four groups confirmed that each successive trial contained tadpoles significantly larger than those in previous trials.

One *N. indica* from each of trials 2 and 3 and two from trial 4 died during the experiment. These replicates were deleted from the analyses (Table 1). The number of tadpoles eaten increased dramatically between trials 1 and 2, and then decreased steadily to an average of less than one tadpole per replicate in trial 4 (Table 1). Analysis of variance and multiple comparisons suggested that the average predation rate in trial 1 was less than the rate in trial 2, but not different from trials 3 and 4. Trial 2 significantly exceeded trial 3 in predation rate, and in turn trial 3 exceeded trial 4.

One *N. undulata* died during each of trials 1 and 3. The average number of tadpoles consumed in a trial decreased continuously as tadpole size increased (Table 1). Analysis of variance and multiple comparisons indicated that trials 1 and 2 were indistinguishable from each other in pre-

TABLE 1.—Summary of results. Underscore connects indistinguishable averages; n = sample size.

Predator species	Variable (statistic)		Trial number 1	2	3	4
Notonecta indica	Tadpole size (mg)	n	21	21	21	21
	$F_{(3,76)} = 241$	$\bar{x}$	0.85	1.43	3.76	7.32
	$P < 0.0001$	s_x	0.12	0.23	1.02	3.19
	Number eaten	n	10	9	9	8
	$F_{(3,32)} = 14.76$	$\bar{x}$	2.6	7.0	3.3	0.5
	$P < 0.0001$	s_x	1.90	3.28	1.22	0.53
Notonecta undulata	Tadpole size (mg)	n	20	20	20	20
	$F_{(3,76)} = 313$	$\bar{x}$	0.87	1.61	3.63	8.44
	$P < 0.0001$	s_x	0.13	0.29	0.87	3.87
	Number eaten	n	9	10	9	10
	$F_{(3,34)} = 21.75$	$\bar{x}$	7.2	6.8	1.9	0.3
	$P < 0.0001$	s_x	3.27	1.93	1.05	0.48

dation rate, as were trials 3 and 4, but that trials 1 and 2 were significantly greater than trials 3 and 4 in predation. The predation rate in trial 4 was less than one tadpole per predator per 24 h.

DISCUSSION

Although *N. indica* did not prey on hatchlings, predation rates on larger tadpoles diminished dramatically for both species, falling below one tadpole per predator per 24 h for the largest size class. We cannot infer from these data whether this decline reflects a reduced ability to capture large prey or a greater satiation of the predator by larger prey items. Travis et al. (1984) showed that both mechanisms operate in dragonfly predation on tadpoles, but the two mechanisms operate over different size ranges of prey. Whatever the mechanism, tadpole size does appear to limit the extent of notonectid predation. Licht (1974) appears to have obtained similar results with tadpoles of *R. aurora* and *R. pretiosa*, but his sample sizes appear very small, and his size classes of tadpoles appear to have been crudely defined.

The size range of tadpoles taken by these notonectids is narrower than that taken by other insect predators (Travis et al., 1984). Within that range, however, the maximum predation rates displayed are comparable to those displayed by other insect predators of tadpoles (Caldwell et al., 1980; Formanowicz and Brodie, 1982). The per capita impact of notonectid predators can be substantial, although that impact would occur only over a short duration of the larval period. Notonectids were implicated in Travis' (1983a) demonstration of selective mortality among full sib families, and our results demonstrate that these insects are size-limited predators that can play such a selective role. As a result, notonectids can also play an important role as mediators of competitive interactions among species whose tadpoles grow at different rates (Morin, 1983). Their importance under field conditions remains to be investigated.

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