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## INTERACTIONS BETWEEN INTRASPECIFIC COMPETITION AND PREDATION IN AN AMPHIBIAN PREDATOR-PREY SYSTEM<sup>1</sup>

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**Abstract.** The predatory salamander *Notophthalmus viridescens* indirectly facilitates the growth and survival of herbivorous tadpoles of *Hyla crucifer*, when the latter are embedded in guilds of superior competitors. I used experimental manipulations of *N. viridescens* and *H. crucifer* densities in artificial ponds to explore the dependence of facilitation on guild composition, by testing whether *N. viridescens* facilitated *H. crucifer* when it was the only species in the tadpole guild. I also measured the independent relative contributions of intraspecific competition and predation to tadpole survival and growth, to test whether competition among prey influenced the impact of predation on prey survival. Tadpole survival was independent of intraspecific density and negatively affected by predator density. In communities without predators, increased tadpole densities decreased growth rates, prolonged larval development, and reduced froglet mass at metamorphosis. Predation tended to increase metamorph mass slightly within a given level of initial tadpole density. However, the impact of predators on tadpole survival was independent of density-dependent tadpole growth. Predators failed to reduce competition substantially among larval *H. crucifer*, because tadpoles altered their micro-habitat use to avoid predators. Consequently, tadpole densities and competitive interactions were only slightly moderated by predators. Predator avoidance exacted no cost in terms of reduced mass at metamorphosis or prolonged larval periods. Although predators may greatly reduce the intensity of interspecific competition among prey by reducing densities of particularly susceptible competitively superior species, the intensity of intraspecific competition among remaining predator-resistant species may remain unaffected. The failure of *N. viridescens* to facilitate *H. crucifer* in the absence of other species of competing anurans indicated that previously documented facilitation was indirect and dependent on guild structure.

**Key words:** amphibians; community structure; experimental communities; facilitation; guild; indirect effects; intraspecific competition; mesocosms; New Jersey; ponds; population regulation; predation.

### INTRODUCTION

Complex interactions between competition and predation figure prominently in synthetic theories of population regulation and community structure (Hairston et al. 1960, Menge and Sutherland 1976, Lubchenco and Gaines 1981, Lubchenco 1985). Despite a growing emphasis on interacting mechanisms in current community theory, such interactions are rarely studied in community-level experiments (Connell 1983a, b, Schoener 1983). The continuing absence of such experiments compromises assertions about the general importance of interactions between processes such as competition and predation.

Amphibian predator-prey interactions offer an exceptionally promising model system for the experimental exploration of community dynamics (Wilbur 1972, 1984, Morin 1983a). Intensities of predation and competition can be manipulated independently by stocking artificial ponds with varied but natural densities of predators and prey amphibians (Wilbur et al. 1983). Here I focus on interactions between the predator *Notophthalmus viridescens* (Urodela: Salamandridae), the red-spotted newt, and one of its most abun-

dant anuran prey, the herbivorous tadpoles of *Hyla crucifer* (Anura: Hylidae), the spring peeper. Experiments reported here (1) clarify the role of tadpole guild composition in the previously documented indirect facilitation of *Hyla* by *Notophthalmus* (Morin 1983a), (2) illustrate an unexpected independence of interprey competition and the impact of predation on prey survival, and (3) suggest that predator avoidance can uncouple the consequences of interprey competition and predation.

*Notophthalmus* and *Hyla crucifer* commonly coexist in temporary ponds in eastern North America (Walters 1975, Gill 1978, Morin 1983a, Smith 1983). *Notophthalmus* significantly enhances the growth and survival of *Hyla crucifer* tadpoles competing within a guild of six anuran species (Morin 1983a). I hypothesize that the facilitation of *Hyla crucifer* depends on the particular competitive regime set by guild composition, rather than on a simple release of *Hyla crucifer* from intraspecific competition (see Wilbur 1984). *Notophthalmus* can potentially interact directly and indirectly with *Hyla crucifer*. Predation on *Hyla crucifer* tadpoles is a simple direct negative interaction. Indirect positive interactions result when predation on other competitively superior species releases *Hyla crucifer* from interspecific competition. The net effect of *No-*

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*Notophthalmus* on *Hyla crucifer* survival depends on the relative contributions of direct negative and indirect positive effects.

This hypothesis implicitly requires the presence of alternate, preferred, competitively superior prey, if indirect positive effects are to outweigh direct negative effects. One test of indirect facilitation involves determining whether newts facilitate *Hyla crucifer* in the absence of interspecific competitors. To this end, I manipulated *Notophthalmus* and *Hyla* densities in artificial ponds without other anurans. I also estimated the relative impacts of predation and intraspecific competition, to determine whether competition exacerbated predation on prey, as proposed elsewhere (Wilbur 1982, Smith 1983, Wilbur et al. 1983). Observations of microhabitat use by tadpoles also documented a behavioral mechanism allowing *Hyla crucifer* to persist with *Notophthalmus*.

## METHODS AND MATERIALS

### *Artificial ponds*

I manipulated densities of *Notophthalmus viridescens* and *Hyla crucifer* in 27 small artificial ponds, similar to those used in my previous studies (Morin 1981, 1983a, b, Morin et al. 1983, Wilbur et al. 1983). The artificial ponds (hereafter referred to as tanks) were cylindrical steel cattle-watering tanks (1.52 m in diameter and 0.61 m deep) within the size range of natural temporary ponds. The tanks were part of a square array of tanks, six tanks on a side, at the W. L. Hutcheson Memorial Forest of Rutgers University (Somerset County, New Jersey, USA). A double coating of epoxy paint on each tank retarded rust and provided an inert barrier on the galvanized surface. Each tank contained  $\approx 1 \text{ m}^3$  of water pumped from Spooky Brook on 11 April 1984, leaf litter (0.6 kg), commercial trout food (50 g), and macrophytes (14 L packed *Sphagnum* spp.). Each tank received a 460-mL inoculum of pond water, algae, and microinvertebrates subsampled from plankton tows taken in three ponds in Ocean County, New Jersey. Lids of Fiberglas screening attached to hexagonal wooden frames retained metamorphosing amphibians and prevented uncontrolled colonization.

### *Experimental design*

All possible combinations of three predator densities (0, 2, or 4 *Notophthalmus* per tank) and three prey densities (100, 200, or 400 *Hyla crucifer* hatchlings per tank) defined nine treatments in a two-factor experimental design for variance analysis. Densities fell within the natural ranges measured for these species (Morin 1983a). The two independently manipulated factors were the potential intensity of intraspecific competition among prey (initial tadpole density) and predation intensity (newt density). I randomly assigned three replicates of each treatment to different tanks, using a total of 27 tanks.

I stocked the tanks on 20 April 1984 with tadpoles hatched from eggs deposited by 19 pairs of amplexant *Hyla crucifer*. I collected the frogs from one pond in Ocean County. The eggs developed and hatched at ambient temperature, yielding abundant hatchling tadpoles of similar size, age, and history. The 19 female *Hyla crucifer* deposited an average of 414.9 eggs per female (SD = 85.96 eggs per female) and weighed an average of 1.515 g (SD = 0.194 g) after oviposition. I pooled hatchlings from different families before adding tadpoles to tanks, to ensure that potential genetic differences in larval performance were randomized (see Travis 1980).

I stocked the tanks on 23 April 1984 with adult newts collected from two ponds in Warren County, New Jersey, where *H. crucifer* also breeds. These *Notophthalmus viridescens viridescens* were larger than the *N. v. dorsalis* used in my previous experiments (Morin 1983a, b, Morin et al. 1983, Wilbur et al. 1983). *N. v. viridescens* had an average snout-vent length of 44.3 mm and a mean wet mass of 2.908 g, compared to a mean of 1.287 g for *N. v. dorsalis* (see Morin 1983b).

On 3 June,  $\approx 1$  wk before the first *Hyla crucifer* metamorphosed, I added 200 hatchling gray treefrog tadpoles, *Hyla versicolor*, to each tank. I appended this manipulation to examine how the prior exploitation of ponds by different densities of tadpoles and newts influenced a species that typically breeds 1–2 mo after *Hyla crucifer*. Responses of *Hyla versicolor* are considered elsewhere, and this manipulation is only mentioned here for completeness. I ignored potential effects of small *Hyla versicolor* hatchlings on much larger pre-metamorphic *Hyla crucifer*. Such effects should have been small, given the competitive advantage of large tadpoles over small ones (Wilbur 1984), and any effects of *H. versicolor* should have been similar among treatments, given the identical number of *H. versicolor* added to all tanks.

### *Response variables and statistical analysis*

I censused metamorphosed *Hyla crucifer* froglets in each tank daily, and recorded the wet mass at tail resorption and date of collection of each froglet. Responses for each population (i.e., tank) included survival to metamorphosis (expressed as the percentage of the individuals stocked on 20 April that metamorphosed), mean mass at tail resorption, mean duration of the larval period (mean number of days between stocking and metamorphosis), and mean growth rate (mean mass  $\div$  mean larval period). Relative differences among populations in mass at metamorphosis and larval period provide indirect measures of the intensity of competition experienced during development (Wilbur 1976, Morin 1983a). Intensities of competition are negatively correlated with mass at metamorphosis and positively correlated with length of larval period, ceteris paribus. I inferred that competition was more intense in populations exhibiting

reduced mass at metamorphosis and/or prolonged development relative to populations with larger and/or more rapidly developing metamorphs. These variables can help explain the outcome of size-dependent predator-prey interactions, if slowed growth and development prolongs tadpole vulnerability to size-limited predators (e.g., see Caldwell et al. 1980, Smith 1983).

An appropriate statistical test for treatment effects must: (1) adjust for potential type I errors (Sokal and Rohlf 1981) arising from multiple tests and (2) be robust to potential correlations among variables. A two-factor multivariate analysis of variance (MANOVA) simultaneously tested the overall significance of differences in survival, mean mass, mean larval period, and mean growth rate among treatments. The MANOVA provided a conservative test adjusted for type I error and correlations among variables for three null hypotheses: (1) no effect of initial prey density, (2) no effect of predator density, and (3) no interaction between factors. Rejection of the third hypothesis would indicate that the impact of predation depended on the intensity of competition among prey, or vice versa.

ANOVAs partitioned the relative contributions of competition and predation to total variation in each response. I estimated the fraction of the total sum of squares attributable to (1) initial hatchling density, (2) predator density, (3) a hatchling density  $\times$  predator density interaction, and (4) residual unexplained variation. I assumed that the partitioning of the total sum of squares in the ANOVA described, for each factor, the relative contribution to prey responses. The ANOVAs were used only to partition variance, and overall statistical significance was inferred from the MANOVA. The choice of statistical methods is justified in Morin (1983a).

#### *Measurement of microhabitat utilization*

I also explored whether predator avoidance behavior was correlated with prey persistence at high predator densities. *Hyla crucifer* tadpoles exploit two tank microhabitats: the dense, spatially heterogeneous benthic matrix of litter and macrophytes, and the exposed tank walls, which are covered with periphyton grazed by tadpoles. Unlike other hylids, such as *Hyla gratiosa*, *Hyla crucifer* did not exploit the open-water microhabitat.

I counted all visible tadpoles that were foraging on the tank walls on 5 and 15 May. Before 5 May (for the first 2 wk of development), tadpoles remained hidden in benthic litter. After 5 May, tadpoles in some tanks gradually emerged from benthic cover to graze on the tank walls, where they were easily observed. Tadpoles in the litter could not be counted without disrupting the tanks with destructive sampling. However, abundances on a given date could be standardized against the total number of tadpoles metamorphosing from each tank to provide an indirect measure of the abundance of animals hidden in the litter.

A two-factor ANOVA tested whether visible tadpole abundance depended on hatchling density and predator density. Covariance analysis (ANCOVA) indicated whether the relation between abundances of visible and metamorphosing tadpoles differed among predator density treatments. This analysis pooled results for the three tadpole densities within each level of newt density, and used final numbers of surviving tadpoles as a covariate. The hypothesis tested was equality of slopes among the three linear regressions (one for each newt density) relating the number of surviving tadpoles to the number of tadpoles visible on 15 May. Significantly different slopes would indicate differences in the fraction of surviving tadpoles visible on the tank walls and differences in the relative use of open or concealed tank microhabitats.

Tadpoles that avoid predators may experience restricted foraging opportunities. Consequently, predator avoidance may have costs manifested as reduced growth and prolonged development. Elevated local densities in spatially limited refugia, or exclusion from feeding sites by predators, may reduce growth over and above the effects expected at a given tadpole density. I tested this hypothesis by examining whether mean mass at metamorphosis differed for tadpoles under different predator densities, after adjusting mass at metamorphosis for differences in final tadpole densities among populations with ANCOVA. If the slope and intercept of linear regressions of average mass at metamorphosis against surviving tadpole abundance did not differ among predator density treatments, I inferred that microhabitat shifts correlated with different predator densities had no detectable effects on tadpole growth.

#### RESULTS

Both the initial density of hatchling tadpoles and predator density significantly affected the survival, growth, and development of *Hyla crucifer* (mean responses, Table 1; MANOVA, Table 2). There was no significant interaction between tadpole density and newt density when all variables were analyzed simultaneously. However, separate ANOVAs (Table 3) indicated marginally significant interaction effects for mass at metamorphosis and growth rate.

#### *Mass at metamorphosis*

Initial tadpole density determined most of the variation in mass at metamorphosis (Table 3). Predator density explained only a small additional fraction of the total sum of squares. Without predators, quadrupling the initial density decreased mean mass by  $\approx 55\%$  (Table 1). Predators slightly moderated these density effects. Increased predator density slightly increased mean mass at metamorphosis in tanks with initially moderate or high tadpole density (200 or 400 hatchlings per tank), but not in low-density tanks (100 hatchlings per tank) (Table 1). The significant interaction in the ANOVA for mean mass reflected this weak de-

TABLE 1. *Hyla crucifer* population responses to levels of density and predation. Each treatment mean ( $\pm$  one standard error of the mean) is based on three population means for three replicates of each treatment combination. There were 42–341 metamorphosed tadpoles per population.

Initial density (no./tank)		Survival	Mass (mg)	Larval period (d)	Growth rate (mg/d)
Tadpole*	Newt†				
100	0	0.68 $\pm$ 0.03	384.6 $\pm$ 3.2	52.9 $\pm$ 0.2	7.28 $\pm$ 0.09
100	2	0.60 $\pm$ 0.08	360.5 $\pm$ 14.2	53.2 $\pm$ 0.3	6.78 $\pm$ 0.09
100	4	0.48 $\pm$ 0.04	370.4 $\pm$ 3.6	54.4 $\pm$ 0.2	6.81 $\pm$ 0.08
200	0	0.73 $\pm$ 0.06	268.6 $\pm$ 3.6	54.8 $\pm$ 0.3	4.91 $\pm$ 0.09
200	2	0.64 $\pm$ 0.04	294.5 $\pm$ 9.9	55.4 $\pm$ 0.5	5.32 $\pm$ 0.22
200	4	0.44 $\pm$ 0.06	314.6 $\pm$ 1.9	56.7 $\pm$ 0.1	5.55 $\pm$ 0.03
400	0	0.79 $\pm$ 0.04	173.3 $\pm$ 8.3	56.3 $\pm$ 1.2	3.09 $\pm$ 0.19
400	2	0.59 $\pm$ 0.09	215.6 $\pm$ 5.9	56.8 $\pm$ 1.4	3.80 $\pm$ 0.19
400	4	0.48 $\pm$ 0.10	235.9 $\pm$ 16.3	58.1 $\pm$ 1.1	4.05 $\pm$ 0.25

\* The prey, *Hyla crucifer*.

† The predator, *Notophthalmus viridescens*.

pendence of predator effects on initial hatchling density. Invariantly large size at metamorphosis at low tadpole densities, regardless of predator density, was consistent with the hypothesis that tadpoles at low densities experienced little competition even in predator-free tanks. Reductions in tadpole densities by predation would not be expected to further increase prey growth in these low-density prey populations.

*Hyla crucifer* tadpoles metamorphosed over a range of 10.75% (at 400 hatchlings per tank) to 25.72% (at 100 hatchlings per tank) of mean adult female mass. Different larval densities clearly imposed substantial differences in the amount of subsequent terrestrial growth required for metamorphs to reach average adult size.

The slight increases in mean mass caused by predators arose either from real increases in tadpole growth or from selective predation on small tadpoles. Correlations between mean and maximum mass within populations were used to decide which alternative best explains observed shifts in size. Positively correlated means and maxima would indicate that entire size-frequency distributions had shifted toward larger sizes, as expected if all tadpoles grew larger with predators present than without predators. Uncorrelated means

and maxima would indicate that predators truncated the smaller size classes from initially similar size distributions, without increasing maximum size. This criterion suggested that predators facilitated tadpole growth at moderate densities (200 tadpoles per tank:  $r = 0.85$ ,  $P < .01$ ), while at high densities (400 tadpoles per tank) there was a similar but nonsignificant trend ( $r = 0.60$ ,  $P > .05$ ).

#### Larval period

The length of the larval period of *H. crucifer* depended weakly on densities of hatchlings and newts. The small range of larval periods among treatments (52.6–60.0 d) argued against attaching great significance to these results (Tables 1–3). Experimental manipulations explained most of the variation among replicates, but there was little variation to explain. Minor differences in larval periods might occasionally be important in ponds that dry rapidly near metamorphic climax.

#### Mean growth rate

Effects of predator and hatchling densities on mean tadpole growth rates mirrored the results for mean mass (Tables 1 and 2). This confirmed that tadpoles metamorphosed at different sizes as a consequence of different growth rates during similar larval periods.

#### Survival

Survival to metamorphosis was independent of hatchling density, and inversely related to predator density (Tables 1 and 2). Predator density accounted for about half of the total variation in survival (Table 3).

Tadpole survival was a simple negative exponential function of predator density. A least squares linear regression of the natural logarithm of survival on predator density ( $r^2 = 0.81$ ;  $P < .05$ ) yielded the relation:

$$S = e^{-0.207P}, \quad (1)$$

where  $S$  is the probability that a hatchling tadpole

TABLE 2. Summary of MANOVA results for the effects of initial tadpole density, newt density, and a tadpole density  $\times$  newt density interaction on four population responses of *Hyla crucifer* tadpoles.

Source	Parameter*			Wilks' lambda†	P
	$v_H$	$v_E$	$u$		
Tadpole density	2	18	4	0.00637	.0001
Newt density	2	18	4	0.17855	.0004
Tadpole $\times$ Newt density	4	18	4	0.27874	.1382

\* The parameters  $v_H$ ,  $v_E$ , and  $u$  identify, respectively, the degrees of freedom for the hypothesis sum of squares and cross products (SSCP) matrix ( $H$ ), the degrees of freedom for the error SSCP matrix ( $E$ ), and the number of variables analyzed.

† Wilks' lambda = [determinant( $E$ )]/[determinant( $E + H$ )].

TABLE 3. Partitioning of variation (total sums of squares) in separate ANOVAs for each of four *Hyla crucifer* population response variables. Approximate significance levels are indicated as follows: NS,  $P > .05$ ; \*,  $.05 > P > .01$ ; \*\*,  $.01 > P > .001$ ; \*\*\*,  $.001 > P > .0001$ .

Variables	ANOVA statistics	Factors			
		Tadpole density	Newt density	Interaction	Residual
Survival	% variation	1.0	56.1	3.7	39.2
	<i>F</i>	0.2 NS	12.9***	0.4 NS	
	df	(2,18)	(2,18)	(4,18)	
Mass	% variation	89.3	3.3	4.3	3.1
	<i>F</i>	254.6***	9.4**	6.1**	
	df	(2,18)	(2,18)	(4,18)	
Larval period	% variation	55.9	14.2	0.2	29.8
	<i>F</i>	16.9***	4.3*	0.02 NS	
	df	(2,18)	(2,18)	(4,18)	
Growth rate	% variation	92.1	1.2	3.7	2.9
	<i>F</i>	281.9***	3.8*	5.6**	
	df	(2,18)	(2,18)	(4,18)	

survives to metamorphose,  $e$  is the base of the natural logarithms, and  $D$  is predator density (newts/m<sup>3</sup>).

Negative effects of intraspecific density on larval growth failed to exacerbate the impact of predation on survival (Table 1). The product-moment correlation between mean growth rate and survival for all 27 populations was negative and not statistically significant ( $r = -0.22$ ,  $P = .28$ ), suggesting no obvious advantage of rapid growth. The evidence for predator-dependent microhabitat selection described below suggests why slowly growing *Hyla crucifer* were not at greater risk to predation than their rapidly growing counterparts.

#### Habitat use and predator avoidance

During the first 14 d of development, *H. crucifer* tadpoles remained hidden in benthic refugia. On 5 May, a few foraging tadpoles were visible on the tank walls, well above the benthic mat of litter and *Sphagnum* (Table 4). After 25 d of development (on 15 May), greater numbers of tadpoles foraged on the tank walls, especially in tanks without predators (Table 4). I restrict the following analysis to data from 15 May, which reflects the behavior of the greatest number of observed tadpoles.

In tanks without predators, visible tadpole abundance on 15 May was directly proportional to the abundance of metamorphosing froglets (Fig. 1, Table 4). The least squares linear regression ( $P < .0001$ ) of visible tadpoles ( $V$ ) against metamorph abundance ( $M$ ) in tanks without newts was

$$V = 0.73(M) - 4.95, \quad (2)$$

confirming that most surviving tadpoles foraged in open locations when predators were absent. In contrast, the corresponding regressions for tanks with two or four newts were

$$\text{two newts: } V = 0.23(M) + 10.87 \quad (3)$$

and

$$\text{four newts: } V = 0.04(M) - 0.58. \quad (4)$$

The slopes of these three lines (Eqs. 2–4) were significantly heterogeneous ( $F_{2,21} = 22.73$ ,  $P < .0001$ ). Inspection of Fig. 2 confirms that for tanks with similar numbers of survivors (metamorphs), tanks with predators had far fewer visible tadpoles than tanks without predators. I attribute this difference to the increased utilization of benthic refugia by tadpoles in response to predators.

Tadpoles restricted to refugia by predators potentially experienced greater crowding than similar numbers of tadpoles foraging throughout the entire tank. Consequently, expressing tadpole densities as numbers per tank may not adequately represent realized intensities of competition, if greater crowding in refugia and restricted foraging further increased competition. Additional competition resulting from differences in dispersion within tanks, a potential cost of predator avoidance, should be detectable as reduced growth in tanks with predators after the effects of tadpole density (number of survivors per tank) are statistically controlled by ANCOVA. However, an ANCOVA indicated that linear regressions of mass at metamorphosis against survivor density for different predator densities (Fig. 2) had statistically indistinguishable slopes ( $F_{2,21} = 0.26$ ,  $P > .77$ ) and intercepts ( $F_{2,23} = 0.77$ ,  $P > .473$ ). Tadpoles that hid in the litter metamorphosed at the same size as their widely foraging counterparts from tanks without newts, when size was adjusted for differences in tadpole densities among tanks.

#### DISCUSSION

##### *The relative impacts of competition and predation on prey populations*

Did intraspecific competition or predation have the greater impact on *Hyla crucifer* population dynamics? The answer depends on the response considered. The ANOVA decomposition of variance in survival un-

TABLE 4. Counts of tadpoles seen foraging at exposed locations on tank walls at 16 (5 May) and 26 (15 May) days of larval development. Each mean is based on three counts from three different replicate populations.

		Initial <i>Hyla crucifer</i> density (no./tank)					
		100		200		400	
		5 May	15 May	5 May	15 May	5 May	15 May
0 newts/tank	Mean	5.6	40.3	33.6	104.0	54.6	228.0
	Range	5–7	33–48	22–40	92–121	16–99	216–242
2 newts/tank	Mean	1.0	29.6	1.0	43.3	4.6	56.6
	Range	1–1	23–41	0–3	8–86	1–7	24–104
4 newts/tank	Mean	0.0	2.6	0.3	1.0	0.3	9.3
	Range	0–0	2–3	0–1	1–1	0–1	1–14
		ANOVA for 5 May			ANOVA for 15 May		
Source	df	F	P	df	F	P	
Newt density	2,18	13.18	.0003	2,18	76.14	.0001	
Tadpole density	2,18	3.40	.0561	2,18	28.36	.0001	
Interaction	4,18	2.71	.0629	4,18	17.38	.0001	

derscored the overriding impact of predation. In contrast, intraspecific competition had an equally lopsided effect on mass at metamorphosis and growth rate.

These results agree with patterns described previously for another larval anuran, *Rana sphenoccephala* (Wilbur et al. 1983), insofar as the primacy of predation's influence on survival is concerned. However, marked intraspecific competition among *Hyla crucifer* persisted despite predation, while Wilbur et al. (1983) found that similar densities of the same predator obliterated competition among *Rana sphenoccephala*. To account for this difference, I emphasize that *Hyla crucifer* and *Rana sphenoccephala* differed importantly in their susceptibility to newt predation. Greater susceptibility to predators creates a greater potential for the density reductions that moderate density-dependent competition. Wilbur et al. (1983) showed that newts consistently reduced *Bufo woodhousei*, *Bufo terrestris*, and *Rana sphenoccephala* to <10% of their initial hatchling density. In comparison, *H. crucifer* survival in the present study ranged from 35 to 77% of hatchling densities at similar newt densities (for means, see Table 1). Such species-specific idiosyncracies indicate that broad generalizations about the relative contributions of predator and prey densities to prey dynamics must be made cautiously, and should incorporate information about the differential susceptibility of prey to predators.

Inverse relations between intensities of interspecific competition and predation are a common theme in synthetic theories of community organization (e.g., Menge and Sutherland 1976). This study suggests that predator-resistant prey species may be special cases where analogous inverse relations between intraspecific competition and predation do not occur. Resistant species that endure high predation intensities, such as *Hyla crucifer* (Morin 1983a), experience greatly reduced intensities of interspecific competition after predators eliminate other competitively dominant

species, while intensities of intraspecific competition remain undiminished.

#### Interactions between competition and predation

Interactions between *Hyla crucifer* and *Notophthalmus* departed from some expectations about how competition and predation interact in size-dependent predator-prey systems. Previously proposed hypotheses invoke two different temporal sequences of competitive and predatory effects. One scenario suggests that intense early predation may rapidly reduce prey densities to the point where prey are simply too sparse to compete (Morin 1983a, Wilbur et al. 1983). Competition among young tadpoles never materializes, and initial hatchling densities, because they are reduced rapidly and drastically, are poor predictors of subsequent growth and survival. However, final densities of tadpoles that successfully evade predators are frequent-

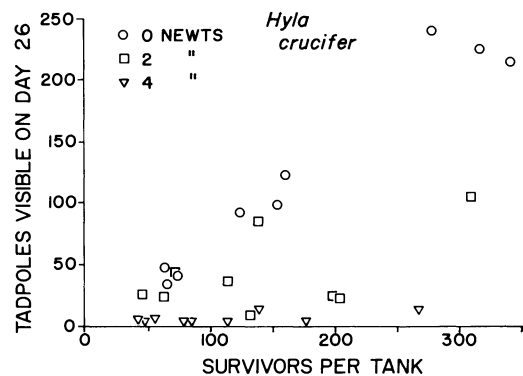


FIG. 1. Relations between counts of *Hyla crucifer* tadpoles visible in each tank on 15 May 1982 (day 26) and the number of tadpoles eventually metamorphosing from those tanks (survivors). Different symbols indicate populations exposed to different densities of predators. No distinction is made among populations with different initial densities of tadpoles.

ly negatively correlated with mass at metamorphosis (e.g., Morin 1983a, Wilbur et al. 1983).

A second scenario holds that early strong density-dependent competition will retard growth, prolong susceptibility to predators, and thereby exacerbate mortality caused by size-limited predation (Wilbur 1982, Smith 1983, Travis 1983, Wilbur et al. 1983). This scenario seems plausible only if tadpoles hatch during seasonal episodes of low predation pressure that are followed by periods of increasing predation intensity. Lags between hatching and the onset of intense predation might result where predators migrate seasonally into ponds after pulses of anuran breeding (e.g., Gill 1978), or where invertebrate predators require long periods of growth to attain sizes permitting successful attacks on tadpoles.

Tank communities mimicked natural situations where prey hatch and are immediately exposed to the predators that can rapidly reduce prey densities and density-dependent competition. However, predators only slightly reduced intraspecific competition among *Hyla* tadpoles. This persistent intraspecific competition also failed to exacerbate effects of predators on prey survival. Predator avoidance can explain these seemingly paradoxical departures from the scenarios outlined above.

Tadpoles persisted at substantial fractions of initial densities by selectively exploiting microhabitats that reduced encounters with predators. This explains why predators had little effect on intraspecific competition among prey. Predator avoidance also explains the absence of the expected relation between density-dependent prey growth and susceptibility to predators. Reduced prey growth had little effect on size-dependent predator-prey interactions, given that even the most stunted prey effectively evaded predators. This also explains the absence of a positive correlation between prey growth rate and survival, such as that previously demonstrated for *Hyla gratiosa* (Travis 1983). *H. gratiosa* typically forages in exposed midwater microhabitats, and may lack the behavioral plasticity to reduce encounter rates with predators.

Reduced larval growth is not without other consequences, especially in the little-studied terrestrial phase of the life cycle. *Ceteris paribus*, smaller metamorphosing froglets will still require more terrestrial growth, and perhaps more time, to attain adult size. The need for additional growth may be a considerable disadvantage, especially if terrestrial habitats are less productive than aquatic ones (Wassersug 1975, Wilbur 1980) and offer few opportunities for rapid growth.

#### *Prey guild complexity and indirect effects*

This study and previous experiments (Morin 1983a) show that the predator *Notophthalmus* can either increase or decrease the survival of *Hyla crucifer*. I attribute this apparent paradox to different net contributions of direct negative and indirect positive effects

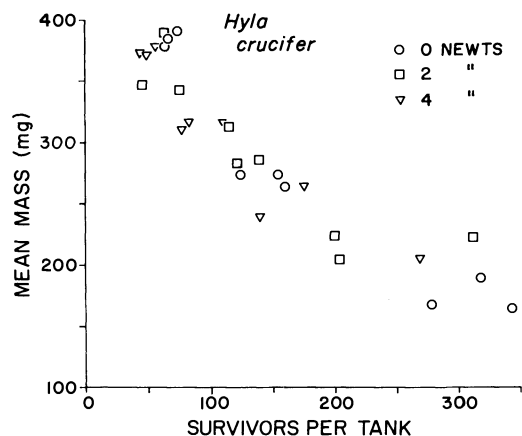


FIG. 2. Relations between the number of *Hyla crucifer* tadpoles eventually metamorphosing from each tank (survivors) and their mean mass at metamorphosis. Different symbols indicate tadpoles exposed to different intensities of predation; greater predator density resulted in greater restriction of tadpoles to refugia.

of newts in the two experiments, which in turn depended on whether *Hyla crucifer* was embedded in a guild of several strongly competing species.

In multispecies guilds (Morin 1983a), selective predation on competitively dominant species released *Hyla crucifer* tadpoles from interspecific competition. The benefits of reduced interspecific competition apparently outweighed the concomitant increased risk of predation, since a net positive effect of predation resulted.

In guilds containing only *Hyla crucifer*, only direct negative effects of predators on survival were possible. Observed negative effects were relatively weak when compared to the impact of newt predation on other anuran species under comparable conditions (Morin 1983a, Wilbur et al. 1983). These modest reductions of intraspecific density slightly increased size at metamorphosis. It also appears that density-dependent intraspecific competition among *H. crucifer* was detectable where interspecific competitors were absent, but its effects were swamped by strong interspecific competition in multispecies experiments (Morin 1981, 1983a). Differences in the densities of surviving *H. crucifer* cannot account for these differences in intraspecific density-dependence, since metamorph densities in single- and multispecies experiments overlapped broadly (42–341 metamorphs per tank and 0–244 metamorphs per tank, respectively).

#### *The noncost of predator avoidance*

Optimal foraging theory emphasizes that foraging behavior represents a compromise between the conflicting demands of maximizing feeding rates and minimizing encounters with predators (Sih 1982, Werner et al. 1983). Predator avoidance costs can be measured as reductions in feeding or growth rates where preda-



tors are present. Predator avoidance costs for *Hyla crucifer* tadpoles failed to materialize.

Absence of predator avoidance costs cannot be simply dismissed by suggesting that tadpoles were too sparse to compete, regardless of differences in dispersion. Density-dependent growth documented ongoing competition. Rather, growth did not depend on whether a given number of tadpoles were crowded into benthic refugia or foraged widely throughout tank microhabitats. One possible reason for the noncost of predator avoidance is that competition may be mediated by diffusible growth inhibitors (see Steinwascher 1978). If growth inhibitors are homogeneously distributed through the water column, competition might not depend on tadpole dispersion.

More subtle costs of predator avoidance remained undetected, and might explain why all *Hyla crucifer* tadpoles didn't selectively forage in the litter, regardless of predator density. Such undetected costs, and the proximal cues for predator avoidance, are unknown and deserve additional attention. What is clear is that complex interactions between competing prey and predators, including indirect facilitation, may depend on frequently ignored aspects of the behavioral ecology of predator-prey interactions.

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