

## PREDATION, COMPETITION, AND THE COMPOSITION OF LARVAL ANURAN GUILDS<sup>1</sup>

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**Abstract.** Experimental manipulations of densities of the predatory salamanders *Notophthalmus viridescens dorsalis* and *Ambystoma tigrinum* significantly altered relative abundances of six species of larval anurans in 22 artificial-pond communities. One competitively inferior anuran, *Hyla crucifer*, was virtually excluded from predator-free control communities but survived best and occurred at greater relative abundances in communities containing high densities of *Notophthalmus*. A second competitively inferior species, *Hyla gratiosa*, survived best at intermediate intensities of predation. Each of four competitively superior species (*Scaphiopus holbrooki*, *Rana sphenoccephala*, *Bufo terrestris*, and *Hyla chrysocelis*) exhibited inverse relationships between relative abundance and *Notophthalmus* density. *Ambystoma* eliminated the entire anuran guild from tank communities and had a much greater per capita impact on anuran guild composition than did *Notophthalmus*.

In most anuran species, maximum and mean mass at metamorphosis were positively correlated with predator density, suggesting an inverse relationship between intensities of predation and competition among tadpoles. Low growth rates of most anuran species in the absence of predators were correlated with high abundances of superior competitors. These results indicate that predators mediated interspecific competition among larval anurans.

Intermediate values of *Notophthalmus* density maximized the total production of anuran metamorph biomass. Biomass of metamorphs of each species varied in a species-specific manner with predation. The propensity of *Rana sphenoccephala* for overwintering as tadpoles following a season of growth was also related to predator density. Laboratory feeding experiments demonstrated that at least two competitively superior anurans, *Scaphiopus holbrooki* and *Bufo terrestris*, were especially vulnerable to predation by salamanders. This suggested that *Notophthalmus* may preferentially remove competitively superior anurans from pond communities, allowing competitively inferior anurans to persist and to complete development successfully at moderate to high predator densities.

**Key words:** *Ambystoma*; *Bufo*; community structure; competition; diversity; guild; *Hyla*; *Notophthalmus*; predation; *Rana*; *Scaphiopus*; temporary ponds.

### INTRODUCTION

A general synthesis of the roles of predation, parasitism, mutualism, and competition in determining community structure is a principal goal of community ecology. Predation has received particular emphasis in previous syntheses (Paine 1966, Harper 1969, Connell 1975, Menge and Sutherland 1976, Lubchenco 1978). Predators can enhance prey species richness by limiting abundances of superior competitors, thereby preventing monopolization of critical resources by competitively dominant species and precluding local competitive exclusion of inferior competitors (Paine 1966, Dayton 1971, 1975). Predation also promotes the dominance of species or morphs which are either resistant to or dependent on predation (Paine and Vadas 1969, Dodson 1974, Kerfoot 1975, Paine 1980, Zaret 1980).

The generality of previous syntheses is compromised by their restriction to sessile, space-limited species or aquatic invertebrates of low trophic status. Information from a greater diversity of communities

is needed to determine whether the overriding importance of predation is peculiar to space-limited species, or constitutes a general theme of community organization. In particular, the impact of predation on the structure of guilds (sensu Root 1967) of vertebrates remains largely conjectural. The composition of many guilds of lizards, birds, and mammals has been explained as the outcome of interspecific competition (e.g., MacArthur 1958, Brown and Lieberman 1973, Pianka 1973, Cody 1974, Schoener 1974). However, an experimental study of larval salamanders (Wilbur 1972) and a comparative study of piscine guild composition (Zaret and Paine 1973) suggest that species composition in some vertebrate guilds may also depend on predation.

This paper describes differences in the species composition of larval-anuran guilds caused by experimental manipulations of the abundance of predatory salamanders in artificial-pond communities. These results specifically address how predation and interspecific competition may interact to structure assemblages of mobile vertebrate prey and provide a distinct counterpoint to previous studies of analogous processes in assemblages of sessile invertebrates and plants. Factors previously suggested to influence the species composition of larval-amphibian assemblages include

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interspecific competition (Dumas 1964, Wiltshire and Bull 1977), predation (Heyer et al. 1975, Walters 1975), and interactions between competition and predation (Brockelman 1969, Wilbur 1972, 1980). Preliminary results reported earlier (Morin 1981) for three anuran species in the present study demonstrated that competition and predation interact to produce nonrandom patterns of species composition. This paper extends the effects of predation to three additional species in the anuran guild, documents an inverse relation between the intensities of predation and competition among anurans, and describes alternate patterns of larval development that permit successful metamorphosis at high intensities of competition or predation.

#### THE STUDY SYSTEM: NATURAL TEMPORARY PONDS AND THEIR EXPERIMENTAL ANALOGS

Although my experiments were conducted in artificial ponds, they were inspired by the natural history of temporary ponds in the Sandhills Game Management Area of Scotland and Richmond Counties in south-central North Carolina, USA. The following overview of the natural history of natural ponds identifies potential sources of community organization, specifies the limitations of natural ponds as experimental units, and emphasizes the aspects of natural ponds that could be mimicked in experimental artificial ponds.

The natural ponds are potential breeding sites for  $\approx 25$  species of frogs (Martof et al. 1980), and up to 17 species of frogs may chorus and breed near a single pond during one evening. Consequently, larvae of many species are forced into syntopy after breeding choruses that follow heavy rain, creating rich and varied possibilities for interspecific interactions. There is little evidence for habitat separation among larval anurans in the Sandhills, and aside from patterns of temporal separation that vary greatly among years, mechanisms reducing ecological overlap among these or other larval anurans are not pronounced (Heyer 1974, 1976). In general, tadpoles feed by rasping and filtering bacteria, phytoplankton, periphyton, and detritus (Wassersug 1975). To exploit temporary ponds successfully, tadpoles must garner sufficient resources to metamorphose before ponds dry, while simultaneously evading predators (Wilbur 1980). Successful membership in a tadpole guild is best (and somewhat paradoxically) assayed by the successful metamorphosis and departure of tadpoles from the pond community, while unsuccessful members are those species that fail to complete larval development.

Although most species can chorus and breed in each pond in the Sandhills, species composition of tadpoles and metamorphs varies conspicuously among ponds. This variation may reflect stochastic exploitation of ponds by ovipositing frogs. However, tadpoles of some species often fail to persist in ponds even after the input of thousands of viable eggs. Most of the natural ponds are shallow depressions (maximum depth < 1

m) filled with rainwater. They are acidic (pH = 4.0–6.5) and dilute (conductivity < 40  $\mu\text{S}/\text{cm}$  at 18°C). Many ponds completely evaporate during periods of drought, which tend to occur in late summer and autumn. These episodes of desiccation apparently exclude fish from most ponds.

In the Sandhills, salamanders assume the role of dominant vertebrate predators where fish are absent. Observations of predation by salamanders on amphibian eggs and larvae are frequently correlated with the postbreeding exclusion of species from ponds (Walters 1975, Morin 1983). The broken-striped newt, *Notophthalmus viridescens dorsalis*, enjoys a nearly ubiquitous distribution among 17 frequently observed ponds. Several other salamanders, including *Ambystoma tigrinum*, *Ambystoma mabeei*, and *Siren intermedia*, are less frequently encountered. *Notophthalmus* is a generalist predator that feeds on zooplankton, large aquatic invertebrates, and the eggs and larvae of amphibians (Wood and Goodwin 1954, Christman and Franz 1973, Mellors 1975, Walters 1975, Gill 1978).

Rigorous experimental study of the impact of salamander predation demands control over potentially confounded factors (especially variable colonization and historical differences in species composition) that are difficult to separate, control, or manipulate in natural ponds. Effective removals of *Notophthalmus* are especially difficult in these natural ponds, because these nonmigrating populations of newts cannot be excluded by interception at drift fences (Storm and Pimentel 1954). Homing behavior also compromises the successful augmentation of newt densities (Gill 1979). To overcome the potential limitations imposed on experiments conducted in restricted numbers of highly variable natural ponds, I manipulated salamander densities in artificial-pond communities reconstituted in cattle-watering tanks. These analogs of temporary ponds contained many of the species found in natural ponds but could be controlled, manipulated, and censused better than natural ponds. Reconstructed freshwater communities, ranging from laboratory microcosms (Neill 1974, 1975) to artificial ponds (Hurlbert et al. 1972, Johnson 1973), possess distinct advantages for the empirical study of communities. Construction of initially similar communities eliminates historical differences in species composition. Reconstituted trophic webs can be engineered to contain fewer species than natural webs, thereby revealing details of interspecific interactions. The realism of such reconstituted communities is confirmed by the successful development, persistence, and reproduction of component species (Morin 1983).

Theory suggests that dispersal may influence broad patterns of predator-mediated coexistence of prey species in collections of discrete habitats linked by migration (Caswell 1978). I have focused first on patterns of species composition and community dynamics caused by processes operating strictly within communities.

## MATERIALS AND METHODS

*Artificial ponds*

I reconstructed 22 pond communities in cylindrical, galvanized steel, cattle-watering tanks, which were 1.52 m in diameter and 0.62 m in height. The interior of each tank was painted with white epoxy enamel to retard rusting. Each tank contained  $\approx 1 \text{ m}^3$  of water drawn from the Durham municipal water supply. The tanks were placed in an array of five rows of four tanks and a sixth row of two tanks in the Duke University Botany Plot, located in Durham County, North Carolina. Tightly fitting lids constructed of Fiberglas window screen stapled to hexagonal wooden frames retained experimental organisms and excluded unwanted colonists.

After filling the tanks with water in early March 1980, I added measured amounts of litter, nutrients, and macrophytes to each tank. Each tank received 50 g of Purina trout chow and 550 g of dry litter. Trout chow provided nutrients; grassy litter collected near a pond in Scotland County provided cover, additional nutrients, and infusoria. Fifty washed stems of the aquatic macrophyte *Myriophyllum pinnatum* were planted in the litter in each tank to provide additional spatial heterogeneity.

I reconstituted simple temporary-pond trophic webs by inoculating the tanks with temporary-pond organisms via a repeatable protocol. Successive inoculations of each tank on 14, 20, and 22 March 1980 established phytoplankton, periphyton, zooplankton, and small invertebrates. On each date, an inoculum consisted of 650 mL of a well-mixed suspension of organisms in pond water. Inocula were drawn from a mixture of organisms collected by tows of an 88- $\mu\text{m}$  mesh plankton net through eight natural ponds in the Sandhills. I screened inocula to prevent uncontrolled introductions of large predatory insects or larval amphibians. Tanks were inoculated within 24 h of organism collection. Within 1 mo of inoculation, cladocera and copepods became abundant and cleared much of the phytoplankton and bacteria from the previously green and turbid water. The diversity of common invertebrate taxa that persisted and reproduced (see Appendix I) emphasized the resemblance of tank communities to natural ponds.

I also introduced three taxa of macroinvertebrates as alternate prey for salamanders: 10 adult *Synurella chamberlaini* (Amphipoda: Gammaridae) per tank on 21 March and several adults and freshly deposited eggs of *Hesperocorixa* sp. and *Sigara* sp. (Hemiptera: Corixidae) on 22 March.

*Additions of anurans and experimental manipulations of salamanders*

I experimentally manipulated one factor, the initial densities of adult *Notophthalmus viridescens* and larval *Ambystoma tigrinum* established in each tank. Six treatments were defined by different initial densities

of salamanders. Four treatments constituted an experimental gradient in predator density and consisted of the addition of 0, 2, 4, or 8 *Notophthalmus* to each tank, with a sex ratio of 1:1 in each population. Each treatment was replicated in four tanks. Two additional treatments consisted of the addition of either both four *Ambystoma* larvae and four *Notophthalmus* or only four *Ambystoma* to remaining tanks. These two treatments were each replicated in three tanks. Individual salamanders and replicates of each treatment were randomly assigned to tanks, in accord with a randomized design for variance analysis.

*Notophthalmus* and *Ambystoma* were collected from "Grassy Pond" in Scotland County. *Notophthalmus* were dipnetted on 19 March 1980. Developing *Ambystoma* embryos were collected in February 1980. Hatchling *Ambystoma* were reared in the laboratory on a diet of zooplankton, amphipods, and isopods. *Notophthalmus* with a mean mass of 1218 mg were added to appropriate tanks on 22 March. *Ambystoma* with a mean mass of 979 mg were added to tanks on 27 March, before the addition of tadpoles. *Ambystoma* of this size were invulnerable to predation by *Notophthalmus*.

Initially identical tadpole guilds were established in all tanks by adding hatchlings of six species of anurans to the tanks on three successive dates in 1980. Hatchlings were obtained by collecting egg masses or amplexant frogs in the Sandhills and Durham County. Numbers of each species added to each tank were: 100 *Rana sphenoccephala*, 200 *Scaphiopus holbrooki*, and 300 *Hyla crucifer* on 27 March, 300 *Bufo terrestris* on 2 May, and 150 *Hyla chrysocelis* and 150 *Hyla gratiosa* on 24 May. Three successive introductions corresponded to the natural phenology of breeding choruses in the Sandhills. Rather than artificially contrive additions of all species on 1 d, I preserved the natural phenology and potential advantages and disadvantages conferred by the natural timing of breeding. These six species were the most abundant species breeding in the Sandhills in 1980 and were assumed to be the major potential members of the larval-anuran guild.

Hatchlings from multiple clutches of a species were mixed before addition to randomize potential effects of genetic variation among sibships (Travis 1980). Counted hatchlings were randomly assigned to each tank, and all introductions on each date were made within 1 h. This protocol ensured that initial intraspecific densities did not vary among tanks or treatments.

Interspecific differences in initial anuran densities arose from unavoidable differences in availabilities of viable hatchlings; however, experimental densities of salamanders and tadpoles were well within the range of densities estimated in natural ponds. Amphibian densities were sampled with a screen drop box sampler similar to that used by Turnipseed and Altig (1975). Densities of representative species in the Sandhills in April 1979 (Table 1) indicate that initial experimental

TABLE 1. Mean densities ( $\pm$  standard error) of common amphibians sampled in natural ponds during late April and early May 1979. Units of density are the number of individuals per cubic metre; 1 m<sup>3</sup> is the average volume of a cattle tank. Means are based on six haphazard samples per pond. The sampler enclosed an area of 0.5 m<sup>2</sup>, and samples were taken at several depths within each pond. Experimental densities established in the cattle tanks are given at the bottom of the table for comparison.

Pond	Mean density ( $\pm$ SE)		
	<i>Notophthalmus</i>	<i>Hyla crucifer</i>	<i>Rana</i> spp.
Wagram	1.9 $\pm$ 1.3	11.9 $\pm$ 4.9	14.5 $\pm$ 7.4*
Jog 1	2.2 $\pm$ 2.2	24.0 $\pm$ 14.9	0.0 $\pm$ 0.0
Jog 2	0.0 $\pm$ 0.0	362.6 $\pm$ 126.4	278.4 $\pm$ 135.6*
Mistletoe	6.3 $\pm$ 4.2	464.0 $\pm$ 126.4	0.0 $\pm$ 0.0
Deep	10.4 $\pm$ 3.9	0.0 $\pm$ 0.0	79.2 $\pm$ 15.8†
Sandbowl	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	13.3 $\pm$ 4.5†
Ditch 1	1.7 $\pm$ 1.7	78.4 $\pm$ 45.2	0.0 $\pm$ 0.0
SWT	2.2 $\pm$ 2.2	49.2 $\pm$ 24.1	0.0 $\pm$ 0.0
NET	0.0 $\pm$ 0.0‡	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
PAEOR	0.0 $\pm$ 0.0‡	319.4 $\pm$ 44.2	21.0 $\pm$ 7.1*
Grassy	15.5 $\pm$ 2.5	37.2 $\pm$ 23.5	0.0 $\pm$ 0.0
Weed	0.0 $\pm$ 0.0‡	255.7 $\pm$ 70.2	0.0 $\pm$ 0.0
Slimington	4.0 $\pm$ 2.3	130.1 $\pm$ 70.8	0.0 $\pm$ 0.0
Square	8.0 $\pm$ 2.9	28.4 $\pm$ 18.5	0.0 $\pm$ 0.0
Cattle tanks	0, 2, 4, 8	300	100

\* Tadpoles of *Rana sphenoccephala*.

† Overwintering tadpoles of *Rana clamitans*.

‡ Known to be present in pond but not found in six samples.

densities of tadpoles and newts were not excessive. Counts of *Ambystoma tigrinum* eggs in a small pond ("NET") of known area yielded an estimate of 8 hatchlings/m<sup>2</sup> of benthos in 1980. In comparison, *Ambystoma* densities in the tanks corresponded to  $\approx$ 2.2 larvae/m<sup>2</sup>.

I completely censused the final species composition of each tadpole guild by daily collecting all metamorphosed froglets from each tank. Metamorphosis was defined by the emergence of at least one forelimb. Because surviving anurans were completely censused, rather than incompletely sampled, measured attributes of anuran populations (such as mean mass at metamorphosis) were described by complete distributions and were therefore not subject to sampling error. I interchangeably use the terms abundance and density to describe total numbers of anurans censused from each tank, because tanks were similar in volume and area.

Captured froglets were taken to the laboratory, where the towel-dried wet mass of each frog was measured to the nearest milligram. Metamorphs were retained until tail resorption was completed, when each frog was weighed again and released in Durham or Scotland County.

I terminated the tank experiments on 28 November 1980,  $\approx$ 1 mo after anuran metamorphosis ceased. Many, but not all, natural ponds had dried by this date, indicating that the experiment's duration correspond-

ed to the time available for larval development in the Sandhills. At termination, six tanks still contained populations of large overwintering *Rana* tadpoles that exhibited no indication of imminent metamorphosis. Amphibians, large arthropods, litter, and macrophytes were harvested from the tanks with a large dip net. Arthropods were preserved for later enumeration. *Rana* tadpoles were counted, and their towel-dried wet mass was determined to the nearest milligram.

#### Laboratory predation experiments

I used laboratory trials to detect interspecific differences among tadpoles in vulnerability to predation by *Notophthalmus* and *Ambystoma*. Experimental arenas were covered polyethylene pans (30 cm long  $\times$  24 cm wide  $\times$  12 cm deep) containing a 2 cm deep layer of washed sand, 7 L of water, and a plastic aquarium plant for cover. In each experimental replicate, 20 similarly sized tadpoles of each of two or three species were added to a pan. Tadpoles were sorted into size-classes with sieves, and tadpoles of a single size-class were used to remove biases caused by interspecific differences in size. Small, recently hatched tadpoles were used in all experiments, because predator-related mortality in natural populations is greatest shortly after hatching (Herreid and Kinney 1966, Calef 1973, Licht 1974). After tadpole addition, a single predator was added to each pan. Predators fed for 2 h and were then removed. Surviving tadpoles were identified to species and counted. Frequencies of predation on each species were determined by subtraction. Prey densities and the duration of feeding trials ensured that predators could feed to satiation on a single prey species. Salamanders were haphazardly selected from laboratory stocks maintained on diets of Purina trout chow (Ralston-Purina, Saint Louis, Missouri) and aquatic invertebrates. Salamanders were not fed for at least 24 h before each feeding trial. Tadpoles of nine species (*Rana sphenoccephala*, *Scaphiopus holbrookii*, *Bufo terrestris*, *B. quercicus*, *Pseudacris triseriata*, *Hyla crucifer*, *H. gratiosa*, *H. chrysocelis*, and *H. andersoni*) were obtained by collecting eggs and tadpoles from natural ponds in Scotland and Durham Counties, North Carolina. Combinations of species used in different trials were determined by the availability of species of similar size.

Results of differential predation experiments were analyzed with standard techniques for frequency analysis (Sokal and Rohlf 1981). Numbers of consumed tadpoles were summed separately by species over all independent replicates of each experiment. These sums defined frequencies of predation on each species in a given experiment. Significant deviations (tested with a chi-square statistic) of observed frequencies of predation from frequencies expected under the null hypothesis of indiscriminant predation on all species were used to infer species-specific differences in vulnerability to predators.

## HYPOTHESES AND STATISTICAL TESTS

This section briefly identifies the main hypotheses tested to detect and describe the effects of salamander predation on both the entire anuran guild and its component populations. Specific hypotheses and statistical tests are justified and detailed further in Appendix II.

1) Do salamander treatments alter the final composition of anuran guilds? Guild composition in each tank was defined by the vector  $P_j = (p_{1j}, p_{2j}, p_{3j}, p_{4j}, p_{5j}, p_{6j})$ , where  $p_{ij}$  is the fraction (or relative abundance) of all surviving anurans censused from tank  $j$  belonging to species  $i$ . A single-factor MANOVA was used to detect whether  $P_j$  differed significantly among predator treatments, and a discriminant function analysis identified species whose relative abundances contributed to differences among treatments. Because the relative abundances ( $p_{ij}$ ) in each tank sum to one (and thus are linearly dependent), the MANOVA was performed on vectors of five rather than six species.

2) Do salamanders alter the combined density of all surviving tadpoles? An ANOVA of the total number of anurans censused from each tank tested whether salamander treatments influenced the total density of tadpoles surviving and presumably competing throughout the experiment.

3) Do salamanders affect the survival of each anuran species? Separate ANOVAs for the effects of salamander treatments on the survival of each species illustrated the basis for changes in the relative abundance or dominance of species.

4) Does salamander predation alter aspects of the larval development of each species that normally reflect the intensity of competition experienced during development? Separate MANOVAs for each species tested whether combined patterns of mean mass at metamorphosis (in milligrams), mean larval period (in days), and mean growth rates (in milligrams per day) differed among treatments for populations of each species. These measures are fitness components of larval frogs (Wilbur 1972, Smith-Gill and Gill 1978); reductions in mean mass or mean growth rates or increases in mean larval periods indicate increased intensities of competition.

5) Is an index of the intensity of competition (mean growth rate) correlated with the abundances of surviving, potential competitors in each tank over all treatments? A canonical correlation analysis tested whether the mean growth rate =  $G_{ij}$  of species  $i$  in tank  $j$  was correlated with a canonical variable  $V_{ij} = c_1N_{1j} + c_2N_{2j} + c_3N_{3j} + c_4N_{4j} + c_5N_{5j} + c_6N_{6j}$ , where  $N_{ij}$  is the density of species  $i$  in tank  $j$  and the coefficients  $c_i$  are chosen to maximize the correlation between  $G_{ij}$  and  $V_{ij}$  within tanks over all communities. This analysis is directly analogous to multiple regression techniques for estimating multispecies competitive relations (Emlen 1981), but it relies on a correlative approach because abundances of potential

competitors were not experimentally manipulated. Species correlated in abundance with  $G_{ij}$  are identified as probable competitors by negative product moment correlations between values of  $V_{ij}$  and densities of surviving potential competitors.

6) Does predation influence the total production of metamorph biomass? An ANOVA of the effects of predator treatments on the combined biomass of all anurans censused from each tank tested whether predators influenced the export of secondary production from tanks and suggested whether thinning by predators reduced competition and enhanced production.

7) Does predation alter the distribution of guild biomass among species? The relative distribution of biomass among species in each tank defined a vector  $M_j = (m_{1j}, m_{2j}, m_{3j}, m_{4j}, m_{5j}, m_{6j})$ , where  $m_{ij}$  is the fraction of total guild biomass collected from tank  $j$  contributed by species  $i$ . A MANOVA on  $M_j$ , analogous to the analysis of relative abundance described above, indicated whether guild biomass was distributed differently among species in different treatments, providing an alternate measure of the dominance of species based on their ability to extract nutrients from tank communities.

All statistical analyses were performed with procedures of the Statistical Analysis System (Helwig and Council 1979).

## RESULTS

*Predator density and patterns of anuran relative abundance*

Predation by larval *Ambystoma* essentially deleted the entire anuran guild from tank communities. Tadpoles failed to survive through metamorphosis in half of the tanks containing *Ambystoma*. In the remaining three tanks, two, three, and eight tadpoles survived and metamorphosed. These tadpoles included 10 *Hyla gratiosa*, 1 *Rana sphenoccephala*, 1 *Hyla crucifer*, and 1 *Hyla chrysocelis*. The presence or absence of four *Notophthalmus* in addition to four *Ambystoma* was not related to complete exclusion of tadpoles. Because few or no tadpoles survived in these tanks, they were not included in the analysis of remaining treatments, which comprised a salamander density gradient from predator-free tanks to tanks containing eight *Notophthalmus*. Hereafter, differences among treatments ascribed to salamander density refer only to differences in *Notophthalmus* density.

Differences in salamander density produced striking differences in the final species composition of the anuran guild (Fig. 1). Metamorphs of *Scaphiopus holbrookii* predominated in salamander-free tanks. *Rana sphenoccephala* (combined metamorphs and overwintering tadpoles), *Bufo terrestris*, and *Hyla chrysocelis* also persisted at moderate relative abundances in the absence of salamanders. Metamorphs of *Hyla crucifer* and *Hyla gratiosa* were notably rare in predator-free

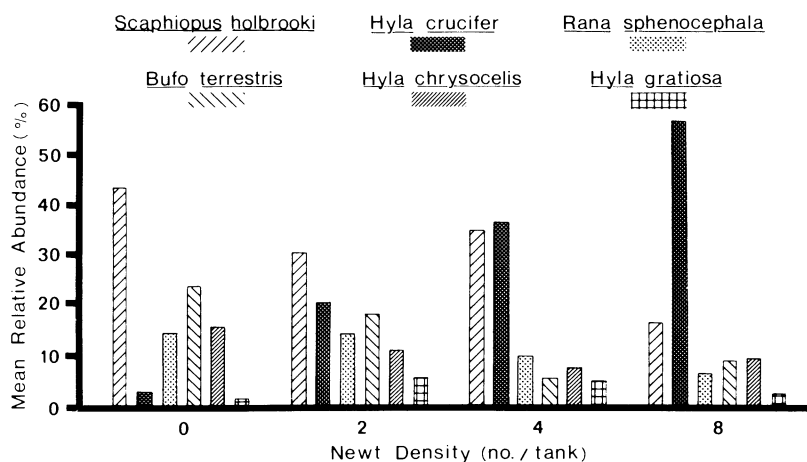


FIG. 1. Mean relative abundances of surviving censused anurans at each level of *Notophthalmus* density. Relative abundances indicate the percent of the total number of surviving anurans in each tank corresponding to each species. Relative abundances of *Rana* include combined abundances of metamorphs and overwintering tadpoles. Histograms for each species are identified by the key at the top of the figure. All means are based on four replicate communities at each level of *Notophthalmus* density.

tanks, despite moderate initial relative abundances as hatchlings (25 and 12.5%, respectively, of all introduced hatchlings).

In tanks containing eight *Notophthalmus*, anuran relative abundances differed greatly from the pattern observed in the predator-free tanks (Fig. 1). Metamorphs of *Hyla crucifer* predominated. Species metamorphosing at high to moderate relative abundances in the predator-free tanks (*S. holbrooki*, *R. sphenoccephala*, *B. terrestris*, and *H. chrysocelis*) were relatively rare at high salamander densities. Relative abundances of metamorphosing *H. gratiosa* were consistently low at all *Notophthalmus* densities.

Differences in species composition between extremes of the newt density gradient did not correspond to alternate discrete states of guild structure. Instead, there was a continuum of guild structure. With in-

creasing salamander density, numerical dominance by *Scaphiopus holbrooki* gradually shifted to numerical dominance by *Hyla crucifer*. This shift was accompanied by declining relative abundances of *R. sphenoccephala*, *B. terrestris*, and *H. chrysocelis* in response to increased salamander density.

A MANOVA of vectors of angularly transformed relative abundances demonstrated that predator-mediated differences in anuran guild composition were statistically significant ( $P < .01$ , Tables 2 and 3). Hence, variation in *Notophthalmus* density significantly influenced overall patterns of anuran species composition. The discriminant function analysis of anuran relative abundances (Table 3) indicated that differences in species composition detected by the MANOVA corresponded to differences among treatments in relative abundances of *H. crucifer*, *S. holbrooki*, *R.*

TABLE 2. Newt density and error matrices of sums of squares and cross products for the MANOVA of final anuran relative abundances. Diagonal elements running from upper left to lower right correspond to univariate sums of squares for separate ANOVAs of the relative abundances of each species.

Matrix (df)	Species	Sums of squares or cross products				
		<i>Scaphiopus holbrooki</i>	<i>Hyla crucifer</i>	<i>Rana sphenoccephala</i>	<i>Bufo terrestris</i>	<i>Hyla gratiosa</i>
Error (12)	<i>S. holbrooki</i>	1362.92	-1139.49	142.76	394.99	-253.09
	<i>H. crucifer</i>	...	1866.34	-83.63	-1447.28	226.32
	<i>R. sphenoccephala</i>	...	...	151.17	-5.32	-118.54
	<i>B. terrestris</i>	...	...	...	1628.52	-51.33
	<i>H. gratiosa</i>	...	...	...	...	210.46
Newt density (3)	<i>S. holbrooki</i>	947.75	-1662.68	315.71	533.45	-110.57
	<i>H. crucifer</i>	...	3804.81	-725.97	-1646.54	487.78
	<i>R. sphenoccephala</i>	...	...	166.19	340.68	-13.92
	<i>B. terrestris</i>	...	...	...	892.10	-224.56
	<i>H. gratiosa</i>	...	...	...	...	340.61

TABLE 3. Multivariate test criterion and summary of discriminant function analysis for differences in anuran relative abundances among newt treatments. Wilk's Criterion = .011769;  $P < .01$ . Discriminant function coefficients and correlations between discriminant function scores and transformed relative abundances of anurans are given.

Species	Coefficients	Correlations
<i>S. holbrooki</i>	.05239	-.60
<i>H. crucifer</i>	.09898	.81
<i>R. sphenoccephala</i>	-.06428	-.74
<i>B. terrestris</i>	.06855	-.51
<i>H. gratiosa</i>	-.05961	.10

*sphenoccephala*, and *Bufo terrestris*. Relative abundances of these species were significantly correlated with values of discriminant function scores for each tank and therefore were primarily responsible for differences in species composition among treatments.

The total number of surviving anurans of all species censused from each tank was inversely related to *Notophthalmus* density (Fig. 2;  $F_{3,12} = 9.27$ ,  $P < .002$ ). High newt densities significantly reduced total abundances and densities of potentially competing tadpoles comprising the anuran guild.

Intermediate densities of predators maximized the total production of metamorph biomass in anuran guilds (Fig. 3;  $F_{3,12} = 5.61$ ,  $P < .01$ ). Guild biomass was greater at moderate predator densities than in predator-free tanks, despite the survival of greater total numbers of metamorphs in the absence of newts.

Predator treatments also altered relative contributions of each species to guild biomass (Fig. 3). A MANOVA of vectors of angularly transformed relative biomass demonstrated that these differences were significant (Tables 4 and 5). A discriminant function analysis indicated that relative biomasses of *S. holbrooki*, *H. crucifer*, and *R. sphenoccephala* were significantly correlated with scores for the discriminant

function that maximized differences among treatments (Table 5). These species contributed to significant differences in relative biomass among predator treatments. *S. holbrooki* accounted for most of the anuran biomass harvested from predator-free tanks, but guild biomass at greater predator densities was the product of more equitable contributions by metamorphs of all species.

Biomasses of *S. holbrooki* and *B. terrestris* were inversely related to newt density. Biomasses of *R. sphenoccephala* and *H. gratiosa* were maximized at intermediate densities of newts. Biomass of *H. crucifer* was positively related to newt density, while biomass of *H. chrysocelis* was unaffected by salamander density. The interplay between mean abundance and mean mass generating these species-specific patterns of biomass is summarized in Fig. 4. For some species, predator-mediated decreases in abundance were offset by predator-mediated increases in mean mass, producing constant or increasing biomass despite lower abundances of metamorphs in the presence of predators. Predator densities that maximized total guild biomass did not simultaneously maximize the biomass of each species (Fig. 3).

Predator density significantly influenced the survival of all species except *H. chrysocelis* (Table 6). Survival of *S. holbrooki*, *R. sphenoccephala*, and *B. terrestris*, three species predominating in the predator-free tanks, was inversely related to predator density. Reductions in relative abundances of these species corresponded to low survival where newts were abundant. In contrast, survival of *H. crucifer* was very low in predator-free tanks but significantly greater and similar in tanks containing two, four, or eight *N. viridescens*. Its relative abundance increased despite moderate but constant survival in the presence of newts, because survival of other guild members declined precipitously with increasing predator density.

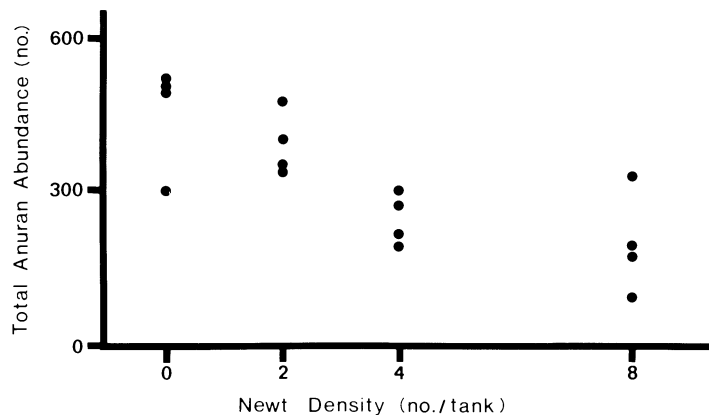


FIG. 2. Relation between final abundance of all censused anurans (including overwintering *Rana*) and initial density of predatory *Notophthalmus* in each of four tanks. Final densities of surviving anurans declined significantly in response to experimental increases in *Notophthalmus* density.

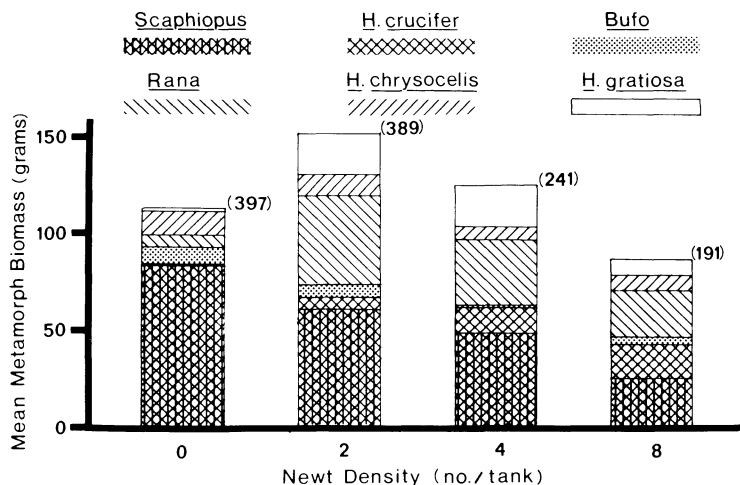


FIG. 3. Mean biomass of metamorphs of each species censused from four replicates of each *Notophthalmus* density treatment. Biomass of each species is stacked to reflect the sequence of metamorphosis in each treatment (species metamorphosing first at the base, species metamorphosing last at the top). Numbers in parentheses indicate the mean number of metamorphs contributing to total guild biomass in each treatment.

Survival of *H. gratiosa* was maximal at intermediate levels of newt density (Table 6). A combination of density-dependent and density-independent factors apparently caused its low survival in predator-free tanks. *H. gratiosa* larvae grew slowly in predator-free tanks (Table 6) but persisted at high densities through early October. However, floundering, dying tadpoles of *H. gratiosa* appeared at the water surface in late October, coincident with a drop in water temperature to below 10°C. All tadpoles of *H. gratiosa* died within several days of this observation. Overwintering tadpoles of *R. sphenoccephala* in the same tanks showed no signs of distress. *H. gratiosa* tadpoles from less dense populations with more rapid growth and development metamorphosed long before the onset of declining water temperature; however, few escaped predation at high densities of newts.

Patterns of survival in response to newt density de-

fining two groups of anuran species. One group tended to survive best in the absence of *Notophthalmus* and included *S. holbrookii*, *R. sphenoccephala*, *B. terrestris*, and *H. chrysocelis*. The second group of species survived best at moderate or high newt densities and included *H. crucifer* and *H. gratiosa*.

Mean mass at metamorphosis increased significantly in response to increasing newt density, for all species except *S. holbrookii* (Table 6). Marked depressions of mean mass at metamorphosis of *H. crucifer* and *H. gratiosa* in predator-free tanks coincided with their reduced survival in the absence of predators.

Frequency histograms of mass at metamorphosis in populations of *H. crucifer* (Fig. 5) unambiguously illustrate that increases in mean mass at metamorphosis at greater predator densities correspond to increases in minimum, mean, and maximum mass in each population. Differences among replicates simply reflect the

TABLE 4. Newt density and error matrices of sums of squares and cross products for the MANOVA of relative biomass of anuran metamorphs. Format as in Table 2.

Matrix (df)	Species	Sums of squares or cross products				
		<i>Scaphiopus holbrookii</i>	<i>Hyla crucifer</i>	<i>Bufo terrestris</i>	<i>Rana sphenoccephala</i>	<i>Hyla gratiosa</i>
Error (12)	<i>S. holbrookii</i>	1585.50	-875.38	323.13	-450.55	-347.76
	<i>H. crucifer</i>	...	720.93	-408.34	115.26	279.84
	<i>B. terrestris</i>	...	...	421.58	-143.83	-53.87
	<i>R. sphenoccephala</i>	...	...	...	611.63	-185.08
	<i>H. gratiosa</i>	...	...	...	...	483.59
Newt density (3)	<i>S. holbrookii</i>	2472.79	-1871.69	651.61	-1554.71	-906.45
	<i>H. crucifer</i>	...	1560.75	-527.03	1403.63	529.11
	<i>B. terrestris</i>	...	...	281.10	-451.95	-341.02
	<i>R. sphenoccephala</i>	...	...	...	1153.86	815.76
	<i>H. gratiosa</i>	...	...	...	...	693.90



TABLE 5. Multivariate test criterion and summary of discriminant function analysis for differences in relative biomass of anuran metamorphs among newt density treatments. Wilk's Criterion = .011676;  $P < .01$ . Discriminant function coefficients and correlations between discriminant function scores and transformed relative biomass of each species are given.

Species	Coefficients	Correlations
<i>S. holbrooki</i>	.07964	-.80
<i>H. crucifer</i>	.15906	.86
<i>B. terrestris</i>	.11088	-.48
<i>R. sphenoccephala</i>	.07319	-.69
<i>H. gratiosa</i>	.01443	.41

error variance associated with responses to each treatment. There was little or no overlap between distributions of mass at metamorphosis at low and high predator densities. Nonoverlapping size distributions showed that increases in mean mass at metamorphosis could not arise from size-dependent truncations of a common underlying distribution that would exist in the untruncated form in the absence of predators. Rather, predator-mediated increases in mean mass occurred because survivors at high predator densities attained greater sizes than did most survivors at low predator densities.

There was a strong positive correlation between mean and maximum mass measured for *H. crucifer* in each tank ( $r = .99$ ,  $P < .01$ ), demonstrating that mean mass accurately reflected differences in maximum mass among populations. Mean and maximum masses were significantly and positively correlated in populations of all remaining species (*S. holbrooki*:  $r = .94$ ,  $P < .01$ ; *R. sphenoccephala*:  $r = .80$ ,  $P < .01$ ; *B. terrestris*:  $r = .61$ ,  $P < .05$ ; *H. chrysocelis*:  $r = .84$ ,  $P < .01$ ; *H. gratiosa*:  $r = .92$ ,  $P < .01$ ), underscoring the interspecific generality of this predator-mediated pattern. These correlations demonstrated that differences in mean mass among treatments corresponded to differences in maximum mass and shifts in entire size distributions in response to predation.

Mean developmental periods of three species (*R. sphenoccephala*, *H. chrysocelis*, and *H. gratiosa*) were shortened significantly at high salamander densities (Table 6). Larval periods of the three remaining species exhibited a similar though nonsignificant trend.

Mean growth rates of *S. holbrooki* were consistently high and varied little in response to predator density (Table 6). Mean growth rates of *H. crucifer* were consistently less than growth rates of other species at each level of salamander density. Mean growth rates of *H. gratiosa* ranged from low values in the predator-free tanks to the highest rates observed at the highest newt densities. Mean growth rates of all species except *Scaphiopus* indicated that tadpoles metamorphosed at larger sizes and after shorter periods of development as densities of *Notophthalmus* increased. MANOVAS

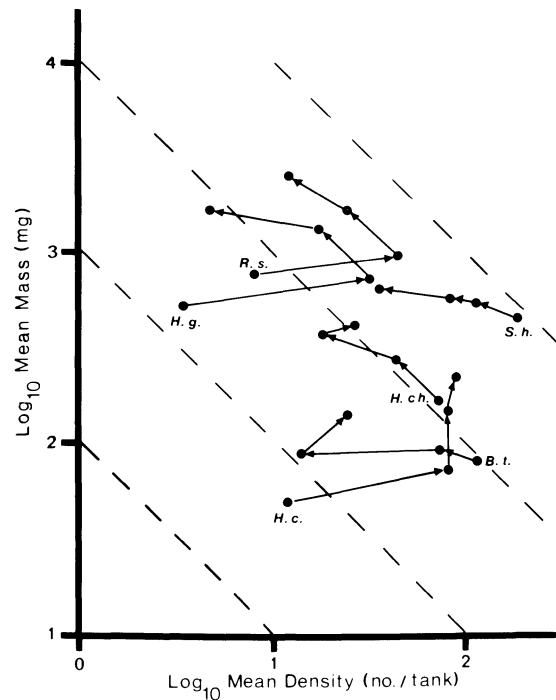


FIG. 4. Relations between the logarithm of mean metamorph abundance (number per tank) and the logarithm of mean metamorph mass (in milligrams) for each anuran species at each level of *Notophthalmus* density. Trajectories for each species originate at mean values for the predator-free tanks and proceed through respective values for densities of two, four, and eight newts per tank. Dashed lines indicate combinations of abundance and mean mass yielding equal values of biomass. *R.s.* = *Rana sphenoccephala*; *H.g.* = *Hyla gratiosa*; *S.h.* = *Scaphiopus holbrooki*; *H.ch.* = *Hyla chrysocelis*; *B.t.* = *Bufo terrestris*; *H.c.* = *Hyla crucifer*.

for mean mass at metamorphosis, mean larval period duration, and mean growth rate indicated that predator-mediated differences described above were significant for all species except *S. holbrooki*. Thus, univariate trends suggested in Table 6 were confirmed by more conservative multivariate tests.

Newt density also influenced the likelihood of overwintering by tadpoles of *Rana sphenoccephala* (Table 7). *Rana sphenoccephala* was the only species with overwintering tadpoles. All other species completed development before the termination of the experiment in November. Overwintering *Rana* tadpoles were restricted to tanks containing two or no newts. Overwintering tadpoles were more abundant and of smaller mean mass where newts were absent than in tanks containing two newts. All *Rana* populations in predator-free tanks contained some overwintering individuals, while only half the populations in tanks containing two newts had overwintering tadpoles. Approximately 1 mo elapsed between the collection of the last *Rana* metamorph and the termination of the

TABLE 6. Means of population means for statistics measured at each level of newt density. The ANOVA column indicates approximate levels of significance from univariate tests for effects of newt density on population means. The MANOVA column gives conservative levels of significance ( $P$ ) for simultaneous differences among treatments in mean mass at tail resorption, length of larval period, and mean growth rate of each species.  $N$  indicates the number of populations producing survivors.

Species	Variable	<i>Notophthalmus</i> density (no. per tank)				$P$	
		0	2	4	8	ANOVA	MANOVA
<i>S. holbrooki</i>	Survival (%)	93.3	57.6	42.6	18.0	.0005	
	Mass (mg)	466	552	577	650	.0538	
	Larval period (d)	38	37	36	35	.9218	.4453
	Growth rate (mg/d)	11.9	15.5	16.5	18.4	.0750	
	$N$	4	4	4	3		
<i>H. crucifer</i>	Survival (%)	4.0	27.6	27.1	30.3	.0086	
	Mass (mg)	49	72	148	211	.0021	
	Larval period (d)	68	66	63	56	.1043	.0434
	Growth rate (mg/d)	0.7	1.1	2.5	3.8	.0044	
	$N$	3	4	4	4		
<i>R. sphenoccephala</i>	Survival (%)	62.5	57.6	24.0	12.0	.0001	
	Mass (mg)	781	989	1637	2457	.0220	
	Larval period (d)	135	127	98	85	.0011	.0074
	Growth rate (mg/d)	5.9	7.8	17.7	30.5	.0200	
	$N$	4	4	4	4		
<i>B. terrestris</i>	Survival (%)	38.0	23.8	4.8	8.0	.0494	
	Mass (mg)	80	92	88	135	.0093	
	Larval period (d)	37	34	31	32	.1113	.0535
	Growth rate (mg/d)	2.2	2.8	2.8	4.3	.0082	
	$N$	4	4	3	2		
<i>H. gratiosa</i>	Survival (%)	2.3	20.6	11.7	3.2	.0096	
	Mass (mg)	524	724	1337	1685	.0190	
	Larval period (d)	128	91	59	51	.0001	.0001
	Growth rate (mg/d)	4.1	8.4	23.1	33.9	.0270	
	$N$	3	4	4	4		
<i>H. chrysocelis</i>	Survival (%)	48.3	29.5	12.0	17.2	.1208	
	Mass (mg)	167	273	372	402	.0014	
	Larval period (d)	63	52	46	41	.0018	.0036
	Growth rate (mg/d)	2.7	5.3	8.3	9.9	.0004	
	$N$	4	4	4	4		

experiment. At lower newt densities, the distribution of larval period duration for *Rana* would have been bimodal, with peaks of metamorphosis in 1980 and 1981 separated by a winter hiatus in development.

*Correlations among mean growth rates and final densities of potential competitors*

Mean growth rates of most species were negatively correlated with final censused abundances of surviving

species. Canonical correlation analyses summarized in Table 8 describe correlations between mean growth rates of each species and densities of potential competitors measured in each tank. For example, a significant canonical correlation indicated that mean growth rates of *H. crucifer* in each tank were positively correlated with values of a canonical variable, which was a linear combination of the final abundances of potential competitors. In turn, values of the

TABLE 7. Effects of *Notophthalmus* density on overwintering tadpoles of *Rana sphenoccephala*. Surviving *Rana* columns indicate mean numbers of metamorphs and tadpoles censused from each tank summed through the termination of the experiment. Entries in tadpole statistics columns refer only to cohorts of overwintering tadpoles. Columns headed  $N$  denote the number of *Rana* populations included in each tabulation.

<i>Notophthalmus</i> density (no. per tank)	Surviving <i>Rana sphenoccephala</i>			Tadpole statistics		
	$N$	Metamorphs per tank	Tadpoles per tank	$N$	No. per tank	Mean mass (mg)
0	4	8.0	54.5	4	54.5	1755
2	4	34.3	12.3	2	25.0	2718
4	4	24.0	0.0	0	...	...
8	4	12.0	0.0	0	...	...
$F_{1,4}$	...	...	...	...	8.14	14.71
$P$	...	...	...	...	.05	.02

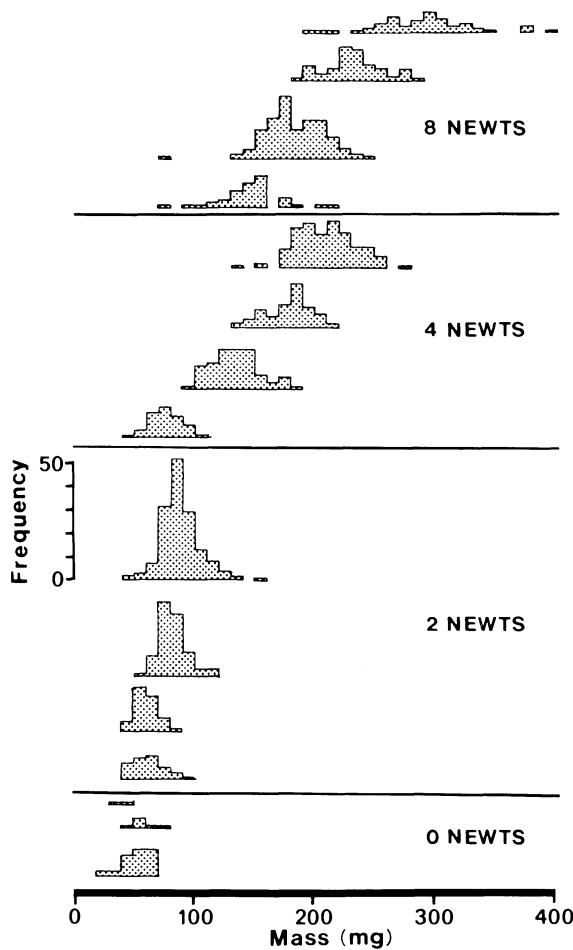


FIG. 5. Frequency histograms of mass at tail resorption in all populations of *Hyla crucifer* that produced metamorphs. One population in the predator-free treatment produced no metamorphs.

canonical variable were correlated strongly and negatively with densities of surviving *R. sphenoccephala* and *S. holbrookii*. Values of the same canonical variable were correlated moderately and negatively with densities of surviving *B. terrestris* and *H. chrysocelis*. The latter two species were added to the community after *R. sphenoccephala* and *S. holbrookii* and potentially interacted with *H. crucifer* for less time. The canonical variable was not negatively correlated with intraspecific density, despite considerable variation in density of *H. crucifer* among tanks. Thus, mean growth rates of *H. crucifer* were negatively correlated with final densities of four species. These four species also survived best in the same predator-free tanks where *H. crucifer* survived poorly.

Similarly, mean growth rates of *H. gratiosa* were correlated negatively with densities of surviving *S. holbrookii*, *R. sphenoccephala*, *B. terrestris*, and *H. chrysocelis*. As with *H. crucifer*, mean growth rates of *H. gratiosa* were not significantly negatively correlated with final intraspecific density. Mean growth rates of both *H. gratiosa* and *H. crucifer* were negatively correlated with densities of anurans that predominated in the same predator-free tanks from which *H. gratiosa* and *H. crucifer* were essentially excluded.

Growth rates of the four remaining species were negatively correlated with both intraspecific and interspecific densities, in contrast to the preceding pattern. Mean growth rates of *S. holbrookii* and *R. sphenoccephala* were highly correlated with respective intraspecific densities and were also moderately correlated with densities of *B. terrestris* or *H. chrysocelis*. Mean growth rates of *H. chrysocelis* were correlated strongly with densities of *R. sphenoccephala* and *S. holbrookii* and more moderately correlated with intraspecific density. Mean growth rates of *B. terrestris*

TABLE 8. Correlations between final densities of anurans and canonical variables best correlated with mean growth rates of each species. Entries in each column are product-moment correlations between censused anuran densities and values of canonical variables best correlated with growth rates of species heading each column. *N* indicates the number of surviving populations available for each analysis. \* indicates correlations significant at the .05 level.

Density of	Canonical variable best correlated with mean growth rates of					
	<i>Scaphiopus holbrookii</i>	<i>Hyla crucifer</i>	<i>Rana sphenoccephala</i>	<i>Bufo terrestris</i>	<i>Hyla chrysocelis</i>	<i>Hyla gratiosa</i>
	Correlation between anuran density and canonical variable					
<i>S. holbrookii</i>	-.94*	-.88*	-.85*	-.85*	-.93*	-.77*
<i>H. crucifer</i>	.85*	.45	.37	.76*	.59*	.40
<i>R. sphenoccephala</i>	-.57*	-.93*	-.88*	-.69*	-.88*	-.91*
<i>B. terrestris</i>	-.26	-.61*	-.55*	-.52*	-.62*	-.69*
<i>H. chrysocelis</i>	-.28	-.58*	-.60*	.17	-.74*	-.71*
<i>H. gratiosa</i>	.34	-.28	-.23	.21	-.10	-.40
Canonical correlation	.93	.94	.89	.88	.96	.92
Significance	.0026	.0016	.0089	.0595	.0001	.0046
<i>N</i>	15	15	16	13	16	15

TABLE 9. Differential vulnerability of tadpoles to salamander predation. Combinations of anuran species offered to predators in separate experiments are listed in the column headed prey. Frequency indicates the number of each species consumed in *N* replicates of each experiment. Deviations from equal predation on available prey species are evaluated with the accompanying  $\chi^2$  statistics. \*\* indicates significant deviation ( $P < .01$ ). NS indicates not significant ( $P > .05$ ).

Prey	Frequency	<i>N</i>	$\chi^2$	df	<i>P</i>
(predator = <i>Notophthalmus viridescens</i> )					
<i>R. sphenoccephala</i> : <i>H. crucifer</i> : <i>P. triseriata</i>	12 : 13 : 22	10	3.9	2	NS
<i>R. sphenoccephala</i> : <i>H. crucifer</i>	73 : 96	15	3.2	1	NS
<i>R. sphenoccephala</i> : <i>P. triseriata</i>	30 : 35	10	0.4	1	NS
<i>R. sphenoccephala</i> : <i>B. terrestris</i> : <i>S. holbrooki</i>	24 : 64 : 110	15	59.3	2	**
<i>R. sphenoccephala</i> : <i>B. terrestris</i>	27 : 82	15	27.7	1	**
<i>R. sphenoccephala</i> : <i>S. holbrooki</i>	12 : 132	15	100.0	1	**
<i>B. terrestris</i> : <i>S. holbrooki</i>	27 : 87	15	31.6	1	**
<i>H. chrysocelis</i> : <i>H. gratiosa</i> : <i>H. andersoni</i>	95 : 129 : 105	15	5.6	2	NS
<i>R. sphenoccephala</i> : <i>H. gratiosa</i>	110 : 135	15	2.6	1	NS
<i>R. sphenoccephala</i> : <i>H. chrysocelis</i>	80 : 86	10	0.2	1	NS
<i>B. terrestris</i> : <i>H. gratiosa</i>	78 : 89	15	0.7	1	NS
<i>B. quercicus</i> : <i>H. gratiosa</i>	208 : 218	15	1.9	1	NS
(predator = <i>Ambystoma tigrinum</i> )					
<i>R. sphenoccephala</i> : <i>H. crucifer</i> : <i>P. triseriata</i>	3 : 34 : 32	10	26.1	2	**
<i>R. sphenoccephala</i> : <i>B. terrestris</i> : <i>S. holbrooki</i>	9 : 33 : 43	8	21.5	2	**
<i>R. sphenoccephala</i> : <i>H. gratiosa</i>	30 : 47	7	3.8	1	NS

tended to be negatively correlated with densities of species that survived best in the absence of newts, but this trend was marginally nonsignificant. Mean growth rates of these four species were not negatively correlated with densities of *H. crucifer* or *H. gratiosa*. Over all tanks, mean growth rates of all species were negatively correlated only with final densities of the species that survived best in predator-free tanks.

#### *Differential vulnerability of anuran species to salamander predation*

Anuran species differed in vulnerability to predation by *Notophthalmus* and *Ambystoma* (Table 9). When confronted with various combinations of equally abundant *S. holbrooki*, *R. sphenoccephala*, and *B. terrestris*, *Notophthalmus* consistently consumed more *S. holbrooki* than either *B. terrestris* or *R. sphenoccephala* and consumed more *B. terrestris* than *R. sphenoccephala*. This pattern held whether the three species were presented simultaneously to *Notophthalmus* or in pairwise combinations. Feeding trials using other prey indicated that various hylid tadpoles (*Hyla* and *Pseudacris* spp.) did not differ in vulnerability to *Notophthalmus* predation. Similarly, hylid tadpoles did not differ from *Rana sphenoccephala* in vulnerability. In general, *Notophthalmus* selectively preyed on tadpoles of *Scaphiopus holbrooki* and *Bufo terrestris* under most circumstances and indiscriminately preyed on tadpoles of other species as they were encountered.

Patterns of vulnerability to predation by *Ambystoma* were similar to patterns described for *Notophthalmus* (Table 9). Unlike *Notophthalmus*, *Ambystoma* discriminated against tadpoles of *R. sphenoccephala* when they were presented with *Pseudacris* and *Hyla* tadpoles. I observed that *Ambystoma* frequently rejected tadpoles of *Rana sphenoccephala* after they were

captured and held in the buccal cavity for several seconds. Rejected *Rana* tadpoles usually swam away from these encounters with *Ambystoma* and were apparently unharmed by aborted attacks.

#### DISCUSSION

Experimental manipulations of predator density in tank communities dramatically altered the final species composition of larval-anuran guilds. Direct negative effects of predators on the persistence to metamorphosis of four species caused part of the difference in guild composition among treatments. Reduced relative abundances of *S. holbrooki*, *R. sphenoccephala*, *B. terrestris*, and *H. chrysocelis* at high newt densities were the direct results of increased consumption by predators. However, enhanced survival and relative abundances of *H. crucifer* and *H. gratiosa* in the presence of newts could not be reconciled with direct negative effects of predators. Similarly, the nearly complete exclusion of *H. crucifer* and *H. gratiosa* from predator-free tanks could not be attributed to predation. Ample evidence indicated that predator-mediated shifts in anuran dominance were consequences of inverse relations between intensities of salamander predation and competition among tadpoles, and complementary interspecific differences among anurans in the ability to exploit communities successfully under extremes of competition and predation. First I discuss the statistical and biological evidence for predator-mediated competition among larval anurans. I then consider the relevance of predator-mediated competition among anurans to emerging theories of community structure. Finally, I describe patterns of larval development that may allow some species to tolerate competition, and I suggest constraints making other anurans either predator-dependent or fugitive species.

*Evidence for interactions between competition and predation*

Evidence presented above for an inverse relation between salamander density and competition among tadpoles is indirect but compelling. A rich literature documents that competition among tadpoles is density dependent and illustrates that increased competition depresses mean mass at metamorphosis while prolonging periods of larval development (Brockelman 1969, Wilbur 1972, 1976, 1977a, b, 1980, 1982, Wilbur and Collins 1973, DeBenedictis 1974, Wiltshire and Bull 1977, Smith-Gill and Gill 1978, Steinwascher 1979a, b, Travis 1980). I inferred that intraspecific differences in mass at metamorphosis, larval period, and growth rate among predator treatments were manifestations of predator-mediated differences in the intensity of anuran competition. Density-dependent competition among tadpoles is expected to be less intense where fewer tadpoles escape predation and survive to compete. The interpretation of reduced intensities of anuran competition at high salamander densities is consistent with the inverse relationship found between densities of surviving, potentially competing tadpoles and predators.

Hypotheses that do not invoke variable intensities of competition among tadpoles cannot adequately account for observed predator-mediated differences in anuran growth and development. For example, increases in mean mass at metamorphosis might result from selective predation by newts on smaller tadpoles and increasingly extreme truncations of potentially identical size distributions. The crucial difference between this size-dependent predation hypothesis and the predation-dependent competition hypothesis is that size-dependent truncations will result in broad overlap among populations in frequency distributions of mass, and will not increase maximum mass. In contrast, if tadpoles are released from competition at high predator densities, most individuals should grow to a larger size than their counterparts at low predator densities. Distributions of *H. crucifer* mass at low and high predator densities barely overlapped. Truncation of *H. crucifer* size distributions in the predator-free tanks could not produce shifts in maximum mass observed at high newt densities. Thus, increases in mean mass were assumed to reflect a predator-mediated release from intense competition in the predator-free tanks. I analyzed population means instead of maxima because means contained information on all survivors, while maxima reflected the performance of single individuals, depended on sample size, and thus constituted rather biased measures of average larval attributes. Means accurately reflected differences in maxima among populations, given the positive correlations between means and maxima.

Because competition among tadpoles is density dependent, I inferred that competing species could be

rigorously identified by negative correlations between densities of surviving anurans (potential competitors) and mean growth rates of species responding to competition. Tadpole densities were not directly manipulated by experiment, but predation and other factors generated considerable variation in final anuran densities among tanks. Relative strengths of correlations between intra- and interspecific densities and mean growth rates were assumed to correspond to relative strengths of competition exerted by each species. Strong negative correlations indicated high covariance between densities and growth rates.

The negative correlation between mean growth rates of *H. crucifer* and *H. gratiosa* and densities of surviving *S. holbrooki*, *R. sphenoccephala*, *B. terrestris*, and *H. chrysocelis* indicates that these latter four species were the source of intense competition contributing to the demise of *H. crucifer* and *H. gratiosa* in predator-free tanks. The fact that mean growth rates of *H. crucifer* and *H. gratiosa* were not negatively correlated with their respective intraspecific densities suggests negligible intraspecific competition in these two species. Mean growth rates of the four species that survived best in predator-free tanks were negatively correlated both with respective intraspecific densities and densities of other members of this group but were not correlated with densities of *H. crucifer* or *H. gratiosa*. I suggest that the two groups of species distinguished by high survival or near exclusion in the absence of newts correspond to competitively superior species (*S. holbrooki*, *R. sphenoccephala*, *B. terrestris*, and *H. chrysocelis*) capable of high survival or successful development despite high tadpole densities and competitively inferior species (*H. crucifer* and *H. gratiosa*) incapable of persisting to metamorphosis at high tadpole densities. The assumption of poor competitive ability of *H. crucifer* and *H. gratiosa* was supported by the absence of negative correlations between their densities and growth rates of any anurans, by their near exclusion from predator-free tanks where competition appeared to be most intense, and by their dramatically enhanced growth where predators reduced the densities of other anurans.

Mean growth rates of *H. chrysocelis* and *H. gratiosa* were negatively correlated with densities of *S. holbrooki*, even though *S. holbrooki* metamorphosed from all tanks several weeks before hatchlings of these late-breeding *Hyla spp.* were added to the communities. This relation might be explained as a statistical artifact, but it might also reflect an intriguing effect of early-breeding *S. holbrooki* on the growth of late-breeding species.

The statistical artifact hypothesis invokes the positive correlation between final densities of *S. holbrooki* and *R. sphenoccephala*. This hypothesis also recognizes that larval periods of *R. sphenoccephala* were much longer than those of *S. holbrooki*, resulting in extensive temporal overlap between *R. sphenocceph-*

*ala* and late-breeding species. Negative correlations between densities of *R. sphenoccephala* and mean growth rates of *H. gratiosa* and *H. chrysocelis* suggest that *R. sphenoccephala* may have competed with late-breeding species. In this case, densities of *S. holbrookii* would be negatively correlated with mean growth rates of late-breeding *Hyla* simply because densities of *S. holbrookii* and *R. sphenoccephala* were positively correlated. A more speculative alternate hypothesis is that early-breeding species may have a lingering impact on resource availability, subsequently influencing the growth of species exploiting a pond later in the same year (Seale 1980). Such priority effects are an interesting topic for future research.

Previous studies have demonstrated that larval density may have nonadditive and nonlinear effects on intensity of competition among tadpoles (Wilbur 1972, 1976, 1977a, b, Wilbur and Collins 1973, Smith-Gill and Gill 1978). Such effects have been cited as evidence for the inadequacy of simple additive linear models of density-dependent competition, but this interpretation has been questioned by others (Pomerantz 1981, Vandermeer 1981). In tank communities, canonical correlations between mean growth rates and simple linear functions of anuran abundances ranged between .88 and .96. These high correlations indicated that simple linear functions of competitor densities described much of the variance in mean growth rates among tanks. My analysis did not include tests for the presence of nonlinear or nonadditive effects, but even if such effects occurred, simple linear functions of final anuran abundances satisfactorily accounted for most of the observed variation in inferred competition.

Canonical correlation analyses also suggested that interspecific competition among tadpoles was strongly asymmetrical. Growth rates of *H. crucifer* and *H. gratiosa* were strongly depressed by high abundances of four competitively superior species, but growth rates of the four competitively superior species appeared unrelated to abundances of *H. crucifer* and *H. gratiosa*. Similar instances of unequal competition among anurans have been described in other studies (Wiltshire and Bull 1977, Wilbur 1982). The apparent absence of intraspecific density dependence in growth rates of *H. crucifer* and *H. gratiosa* also suggests that interspecific competition may outweigh the effects of intraspecific competition in weak competitors.

The restriction of overwintering tadpoles of *Rana sphenoccephala* to tanks containing low densities of predators and high densities of tadpoles also supports predator-mediated competition. Collins (1979) suggested that the likelihood of overwintering by *Rana catesbeiana* tadpoles may be influenced by climate, timing of breeding, and resource availability. The first two factors did not vary among tank communities, leaving predator-mediated differences in resource availability as a likely source of variation in overwintering by *Rana sphenoccephala* tadpoles. Overwinter-

ing tadpoles and other potential competitors were most abundant in predator-free tanks where reduced growth rates prevented *Rana* from attaining minimum metamorphic size in a single season. At high predator densities, *Rana* exhibited enhanced growth and easily attained minimum metamorphic size. Predation apparently influenced competition among *Rana* tadpoles to the extent that cohorts with initially similar density required different numbers of years to complete larval development.

#### *Relevance to community theory*

Alternate responses of anuran guild composition to experimentally varied intensities of predation support theories of community organization that invoke complementary effects of inversely varying intensities of competition and predation (Brooks and Dodson 1965, Paine 1966, Connell 1975, Menge and Sutherland 1976, Lubchenco 1978). High premetamorphic mortality of two species (*H. gratiosa* and *H. crucifer*) apparently resulted from intense competition in the absence of predators. These competitive exclusions would not be predicted by community theories based only on predation (e.g., Heyer et al. 1975 for anurans; Dodson 1974, Zaret 1980 for aquatic invertebrates) and illustrate that competition can effectively structure guilds when predators are absent.

Predator-mediated changes in anuran guild composition provided an equally important demonstration of predation's efficacy in structuring guilds of vertebrate prey. Patterns of anuran relative abundance arising from competition in predator-free tanks bore little resemblance to patterns observed at moderate to high predator densities. Complete shifts in the identity of dominant species among treatments emphasized that persistence in the presence of predators was unrelated to competitive ability. It was unlikely that interspecific competition determined predation's influence on species composition (Wilbur 1980, 1982), because competitively superior species failed to maintain their dominance at high predator densities. On the contrary, competition's impact on guild composition was conditional on the intensity of predation on tadpoles. Predation on hatchling tadpoles ameliorated interspecific competition by reducing the densities of anurans that survived to compete. Further, at least two competitively superior species (*S. holbrookii* and *B. terrestris*) were more vulnerable to predators than were competitively inferior species. Differentially severe predation on competitively dominant species can selectively reduce their abundance in the guild and simultaneously release inferior competitors from competitive limitation. This mechanism's importance has been previously recognized and emphasized in other communities (Brooks and Dodson 1965, Lubchenco 1978), since it can shift dominance from predator-vulnerable, competitively superior species in predator-free habitats to less vulnerable, competitively inferior species at high

intensities of predation. However, poor survival of apparently unpreferred *Rana* tadpoles at high predator densities suggests that reduced vulnerability to predators provides an imperfect refuge at best.

Inversely varying intensities of competition and predation have been suggested to control species composition in various communities of sessile space-limited organisms (Paine 1966, 1980, Harper 1969, Connell 1975, Menge and Sutherland 1976, Lubchenco 1978). Such communities differ greatly in taxonomic composition, spatial complexity, and general habitat features from temporary-pond communities and their experimental analogs. Convergent responses of such disparate assemblages to manipulations of predator abundance provide strong support for the generality of predation's impact on species composition over a variety of habitats and organisms. The structuring of anuran guilds by predation demonstrates that such effects are not limited to communities dominated by sessile species or invertebrates.

Previous studies have suggested several factors that may determine the relative impact of competition and predation on species composition in a given locale. In intertidal communities, prey often tolerate harsh environments better than do predators (Connell 1961, 1975; Menge and Sutherland 1976). Where environmental stress more readily excludes predators than prey, competition may predictably influence prey species composition. Predator limitation by environmental stress may be less important in pond communities. Adult *Notophthalmus* easily withstand the physiological stress imposed by the drying of temporary ponds, while their larval amphibian prey are excluded from ponds by desiccation. Adult *Notophthalmus* retire beneath moist litter in the bottom of drying ponds, while larval amphibians must metamorphose or perish under identically harsh conditions. When ponds refill, adult newts persist at predrought densities and pose an unmoderated threat to larval amphibians entering the community via renewed anuran breeding. The apparent harshness of ephemeral ponds creates a refuge for tadpoles from predatory fish (Heyer et al. 1975, Wilbur 1980), but this reduction in the intensity of predation is relative rather than absolute, because predatory salamanders and insects abound in fish-free ephemeral ponds (Walters 1975).

The classic proposition of Hairston et al. (1960) and its extension by Menge and Sutherland (1976) suggests that abundances of species in all but the highest trophic levels are potentially limited below carrying capacity by predators. It is consistent to expect that competition occurs among predatory salamanders occupying the top trophic levels in temporary ponds (Wilbur 1972, Morin 1983), or among predatory starfish in intertidal communities (Menge 1972), while predation controls the species composition of their respective prey. In qualitative agreement with Menge and Sutherland (1976), the impact of competition on

anuran guild composition clearly depended on whether anurans constituted the top trophic level (predator-free tanks) or a subordinate trophic level (tanks containing salamanders). Factors favoring dense populations of *Notophthalmus* in natural ponds remain speculative. *Notophthalmus* density in natural ponds may not be predictable from in situ pond conditions, and immigration may primarily influence the local abundance of adult newts (Gill 1978, 1979), but the potential importance of newts as keystone predators is unambiguous where populations become established.

The specific impact of predators on anuran guild composition depended on the density and species of salamander. *Notophthalmus* shifted dominance from competitively superior to competitively inferior anurans, without altering anuran diversity within tanks (Morin 1982). In contrast, *Ambystoma* deleted the anuran guild, obviously reducing anuran diversity. Similar events are frequently observed in two ponds in the Sandhills where *A. tigrinum* regularly occurs. Many anurans oviposit in these ponds, but large tadpoles and metamorphs are seldom subsequently collected. Different short-term vulnerabilities of anurans to *Ambystoma* in the laboratory (Table 9) did not provide an effective refuge from this rapidly growing predator. This suggests that *Ambystoma* can overcome their apparent dislike for *Rana* tadpoles when other preferred prey are absent. *Ambystoma* attain a much larger size than *Notophthalmus* (10–20 vs. 2–4 g for *Notophthalmus*), and most tadpoles, with the occasional exception of *H. gratiosa*, cannot attain a refuge in body size from this large predator. Four *Ambystoma* per tank had a far greater per capita impact on tadpole guild composition than four *Notophthalmus*. This result clearly demonstrated that top predators, at least among salamander species, may differ drastically in their effects on community organization. In the Sandhills, the small number of ponds successfully exploited by *Ambystoma* probably limits its global importance. Its potentially extreme impact is moderated further because drought and predation by *Notophthalmus* on eggs and small larvae (Morin 1983) readily excludes *Ambystoma* from natural ponds.

Theories relating predation to community organization often specify relations between predation intensity and univariate measures of species composition, especially species richness and species diversity (Paine 1966, Addicott 1974, Lubchenco 1978). Other theories are framed in terms of predator-mediated changes in the dominance or relative abundance of prey species (Brooks and Dodson 1965, Zaret 1980) without specific reference to species richness or diversity. Different measures of community composition used in previous studies complicate comparisons of predator effects among communities. Specifically, alternate measures of species composition (dominance, diversity, and richness) differ substantially in their resolution of dif-

ferences among communities. In tank communities, manipulations of predators reversed patterns of anuran relative abundance, but neither species diversity nor species richness differed among treatments (Morin 1982).

This failure illustrates one serious shortcoming of univariate indices of community structure (also see Hurlbert 1971). Species diversity and species richness obscure simple but important shifts in dominance among species. In contrast, vectors of relative abundance preserve this information by linking relative abundance to the identity of each species. Multivariate analyses of vectors of relative abundance remain sensitive to shifts in dominance of species, regardless of changes in species number or diversity. Multivariate analyses are also sensitive to correlated changes in relative abundances of two or more species. Thus a single MANOVA can detect complex differences in the composition of entire multispecies assemblages that might easily be missed by univariate tests and measures.

*Predation, competition, and anuran  
life history variation*

Interspecific differences in larval growth and development illustrated various mechanisms that permit anuran persistence under high intensities of competition. These mechanisms include low sensitivity to tadpole density, plastic size at metamorphosis, and the ability to overwinter as larvae under conditions unfavorable to rapid growth.

*Scaphiopus holbrooki* survived well at high competitor densities because of its unparalleled competitive ability, illustrated by rapid growth and development that responded only slightly to competitor densities. This pattern was consistent with a high efficiency of resource utilization and low sensitivity to competitor density and contrasted with the great range of density-dependent growth rates of the other five species. Rapid larval growth is a hallmark of this genus (Richmond 1947, Bragg 1965) and represents an adaptation for exploiting highly ephemeral but productive ponds (Wassersug 1975, Wilbur 1980). Intense selection for rapid growth in ephemeral ponds might effectively preadapt *Scaphiopus* as a superior competitor by selecting for high efficiencies of resource utilization. However, the high vulnerability of *Scaphiopus* to predators suggests its susceptibility to exclusion from natural ponds by salamanders. Superior competitive ability and low sensitivity to density argue against competitive exclusion of *Scaphiopus* from natural ponds by any of the anurans considered in this study.

*Hyla chrysocelis* and *Bufo terrestris* exhibited greater sensitivity to tadpole density than *S. holbrooki*, yet both did metamorphose in numbers from predator-free tanks where competition was intense. In these species, plastic size at metamorphosis permitted successful

metamorphosis at reduced size where competition reduced growth rates. These species retained the ability to capitalize on resources and metamorphose at increased size where predators were abundant and competition was less intense, but also appeared quite vulnerable to predators.

*Rana sphenoccephala* displayed density-dependent growth and development coupled with a relatively large minimum size at metamorphosis. Overwintering in the tadpole stage permitted persistence in tanks where competition was so intense that larvae could not attain minimum size for metamorphosis in a single season of growth. In many years, natural ponds exploited by *Rana sphenoccephala* dry in late summer or autumn, illustrating a major shortcoming of overwintering. Overwintering is clearly dangerous, unless tadpoles overwinter in more permanent ponds, or unless stochastic events, such as occasional autumn storms, prevent ponds from drying.

*Hyla crucifer* and *Hyla gratiosa* may both rely on predators to reduce competition among tadpoles and ensure their larval success. In the Sandhills, spring-breeding *H. crucifer* and summer-breeding *H. gratiosa* are the most abundant anurans metamorphosing from Grassy Pond, which contains high densities of salamanders (Table 1). *Rana sphenoccephala* consistently fails to metamorphose from the same pond, despite the annual input of roughly equivalent numbers of eggs. These observations are consistent with patterns in tank communities. *Hyla crucifer* is broadly distributed among natural ponds, perhaps reflecting the distribution of *Notophthalmus* among ponds. *H. crucifer* might also persist as a fugitive species in predator-free ponds if other superior competitors are absent by chance. Comparison of growth rates among species suggests that *H. crucifer* has a low efficiency of resource utilization, even under reduced competitor density.

*H. gratiosa*, like *R. sphenoccephala*, had a large minimum size at metamorphosis that was not readily attained at high intensities of competition. However, it grew rapidly in tanks where predators were abundant and readily attained a refuge in size from *Notophthalmus*. The apparent failure of *H. gratiosa* to overwinter corresponds to the observation that small, stunted tadpoles of this species can be collected in some natural ponds in autumn, but are never subsequently collected from the same ponds in winter or early spring. *H. gratiosa*, like *H. crucifer*, is predicted to be most successful in natural ponds where predators limit abundances of superior competitors.

Although salamanders reduce the probability that hatchlings of most species will survive to metamorphose, these predators also appear to enhance the fitness of the tadpoles that survive. Fitness is enhanced because mass at metamorphosis is negatively correlated with tadpole density, and tadpole density is a decreasing function of predator density. Large size at



metamorphosis may be advantageous, because large metamorphs have an initial growth advantage that may lead to early attainment of reproductive size (Wilbur 1972). Large size may also enhance reproductive output, given the positive correlation between adult size and fecundity in anurans (Salthe and Duellman 1973, Berven 1981). Furthermore, abbreviated periods of larval development in the presence of predators make mortality by drought less likely, since tadpoles spend less time in unpredictably ephemeral ponds. Density dependence and the plasticity of amphibian development permit competition and predation to influence patterns of offspring number and quality above and beyond the evolutionary constraints imposed by the inverse relation between the initial size and number of propagules (Wilbur 1977c). In addition to controlling anuran guild composition, competition and predation interact to generate intraspecific differences in offspring number and quality within generations that rival the magnitude of interspecific differences in life history parameters ascribed to long-term evolutionary pressures.

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## APPENDIX I.

List of common invertebrate taxa observed in the array of 22 cattle-watering tanks.

Porifera	Cladocera
<i>Spongilla lacustris</i>	<i>Simocephalus serrulatus</i>
Cnidaria	<i>Simocephalus exspinosus</i>
<i>Hydra oligactis</i>	<i>Eurycerus lamellatus</i>
Platyhelminthes	<i>Acantholeberis curvirostris</i>
<i>Mesostoma ehrenbergii</i>	<i>Daphnia laevis</i>
Mollusca	<i>Diaphanosoma brachyurum</i>
<i>Laevapex</i> sp.	<i>Scapholeberis kingi</i>
Ectoprocta	<i>Acroperus harpae</i>
<i>Plumatella repens</i>	<i>Bosmina longirostris</i>
Insecta	<i>Chydorus sphaericus</i>
<i>Hesperocorixa</i> sp.	<i>Alona guttata</i>
<i>Sigara</i> sp.	<i>Ceriodaphnia pulchella</i>
<i>Buena</i> sp.	<i>Moina micrura</i>
<i>Gerris</i> sp.	Copepoda
<i>Tendipes</i> sp.	<i>Diaptomus spatulocrenatus</i>
<i>Laccophilus</i> sp.	<i>Macrocyclus fuscus</i>
<i>Thermonectus basilaris</i>	<i>Macrocyclus albidus</i>
<i>Microvelia</i> sp.	<i>Mesocyclops edax</i>
Amphipoda	<i>Cyclops vernalis</i>
<i>Synurella chamberlaini</i>	<i>Tropocyclops prasinus</i>
	Ostracoda

## APPENDIX II

## Statistical methods

*Parametric vs. nonparametric tests.*—Parametric techniques for variance analysis (ANOVA, MANOVA) are robust to heteroscedasticity (inequality of variances) and departures from normality (Scheffé 1959). This property has been overlooked by many ecologists. Scheffé (1959) points out that assumptions of normality and homoscedasticity were originally made to ease the derivation of statistical theory, but moderate departures from these assumptions have little impact on the ability of the analysis to detect differences among treatment means. Parametric techniques are more powerful than analogous nonparametric tests (i.e., they can resolve smaller differences among treatments at a given level of replication) and can test a greater diversity of a priori hypotheses. For analogous reasons, transformations of original data are usually unnecessary and have been used sparingly in my analysis.

*Multivariate analysis of guild composition.*—A multivariate description of anuran guild composition offered obvious advantages over a brute-force species by species analysis of changes in guild structure. Anuran guild composition was represented by the vector  $P_j = (p_{1,j}, p_{2,j}, \dots, p_{i,j}, \dots, p_{6,j})$ , where  $p_{i,j}$  was the fraction of all surviving anurans censused from tank  $j$  belonging to species  $i$ . Guild composition can be geometrically idealized as a directional vector in a six-dimensional space delimited by axes denoting the relative abundance of each anuran species. The central hypothesis was tested with a single MANOVA, which indicated via one test whether vectors of anuran relative abundances differed among tanks containing different densities of salamanders. Relative abundances were angularly transformed, to reduce further the likelihood of multicollinearity. A univariate approach would require several separate ANOVAs (one for each species), increasing the likelihood of type I error accumulating from multiple tests. The univariate approach was also insensitive to correlated changes in relative abundances of different species, while correlated differences can be detect-

ed with MANOVA. Finally, the multivariate approach emphasizes that the entire guild, with its potential for correlated responses of species, was the unit of study.

Timm (1975) or Morrison (1976) provide detailed descriptions of the MANOVA analysis. Significance was assessed by Wilks' Criterion, defined by  $[\text{determinant } (E)] / [\text{determinant } (E+H)]^{-1}$ , where  $H$  is the matrix of sums of squares and cross products calculated among treatment means of all variables, and  $E$  is the matrix of sums of squares and cross products calculated within treatments.  $H$  and  $E$  are analogous to hypothesis and error sums of squares in a univariate ANOVA. Detection of a significant treatment effect with a MANOVA indicates that differences exist among treatments but does not indicate which variables in the analysis contribute to differences. Variables contributing most to differences among treatments can be identified by a discriminant function analysis of anuran relative abundances in different treatments. Coefficients of each original variable in the discriminant function are given by the eigenvector corresponding to the largest eigenvalue of  $E^{-1}H$ . This function maximizes differences among treatments and minimizes differences among replicates within treatments. Variables (i.e., relative abundances of species) contributing to significant differences among treatments are identified by evaluating product moment correlations between values of the discriminant function calculated from anuran relative abundances in each tank, and original anuran relative abundances (Timm 1975). This approach is preferable to the inspection of discriminant function coefficients, because the coefficients are also sensitive to the magnitude and variance of original variables (Timm 1975).

*Analysis of population statistics.*—Causes of differences in relative abundances of species among treatments were inferred from effects of predator density on four statistics measured for each population of each anuran species: survival, mean mass at tail resorption (in milligrams), mean larval period (in days), and mean growth rate (in milligrams per day) defined by mean mass at tail resorption divided by mean larval period duration. Analyses were performed on population means, which will tend to be normally distributed even if the original data were not, via the central limit theorem. Because exact normality is not required for the analysis of variance (Scheffé 1959), these data were not transformed.

Overwintering tadpoles of *Rana sphenoccephala* presented special problems for the analysis of population statistics. Larval period distributions in six populations with overwintering tadpoles were potentially bimodal (cohorts metamorphosing in 1980 and potentially also in 1981). Only the 1980 cohort was used to estimate larval period duration, providing a consistent comparison with the other species. Numbers of overwintering tadpoles and metamorphs were summed to describe relative abundance at the end of the experiment, accurately reflecting the number of *Rana* surviving to interact with other species. Abundances and mean masses of overwintering tadpoles were also analyzed separately to document effects of predation.

Population statistics described above have been argued to reflect fitness components of larval anurans (Wilbur 1972, 1980, Smith-Gill and Gill 1978). Although mean growth rate was completely specified by mean mass at tail resorption and mean larval-period duration, its presentation and analysis had heuristic value in describing interactions between these aspects of larval development. Survival was known in all populations and was angularly transformed before analysis. Analysis of survival demonstrated whether changes in relative abundance of a species corresponded to changes solely in its survival or also reflected changes in survival of other species. For example, a species may increase in relative abundance, without its survival increasing, if survival of all other species in the guild declines. Conversely, equivalent differences in survival of all species among treatments will not generate differences in relative abundance. Both survival

and relative abundance are required to describe effects of treatments on anuran species composition adequately.

Populations with zero survival had missing values for other statistics. Thus, survival was analyzed separately from remaining population statistics. Because mean growth rate, mean mass at tail resorption, and mean larval period were potentially correlated, a MANOVA simultaneously tested for effects of predator density on these statistics. Missing values for different species did not coincide in the same tanks, necessitating separate MANOVAs for each species. Univariate results suggested which variables contributed to significant multivariate tests but were not used to infer statistical significance.

Differences in growth and development among treatments were used to infer differences in the intensity of competition experienced by tadpoles. Mass at metamorphosis and growth rate are negatively correlated with the intensity of interanuran competition, while larval period duration is positively correlated with intensity of competition (Brockelman 1969, Wilbur 1972, 1976, 1977*a, b*, 1980, Wilbur and Collins 1973, Wiltshire and Bull 1977, Travis 1980). I have used significant depressions in mean mass at tail resorption or mean growth rate, and significant increases in mean larval period duration, to infer greater intensities of competition in some treatments.

*Inference of competitive relations among tadpoles.*—I used canonical correlation analysis to describe patterns of correlation concisely between final abundances of potential intra- and interspecific competitors and mean growth rates of each species. Canonical correlation analysis is a computational analog of multiple regression that is specifically designed for evaluating patterns of multiple correlation between two groups of variables (see Timm [1975] and Morrison [1976] for further details of the analysis). Like multiple regression, canonical correlation establishes a linear combination of "independent" variables (in this case, the final densities of each species of anuran in each tank) that covaries best with values of a "dependent" variable (in this case, the mean growth rate of a particular species). The difference between the two approaches is one of interpretation. Multiple regression is interpreted by examining the coefficients of the "independent" variables in the regression equation. However, if two or more "independent" variables are highly correlated and are also related to a "dependent" variable, only one "independent" variable will tend to carry heavy weight in the regression equation (Sokal and Rohlf 1981). This is an artifact of the orthogonalization of "independent" variables in multiple

regression and arbitrarily obscures other correlations between "independent" and "dependent" variables. In contrast, canonical correlation is interpreted by examining correlations between "independent" variables and their linear combination (the canonical variable) best correlated with the "dependent" variable. This approach preserves patterns of correlation between variables, without arbitrarily eliminating variables from the analysis. A correlative approach is also more appropriate than multiple regression when "independent" variables are not experimentally manipulated (Sokal and Rohlf 1981).

In my analysis of density-dependent growth of each species, a linear combination of final densities of six anuran species (the canonical variable) maximized correlations between values of the canonical variables and mean growth rate over all tanks. The correlation between values of canonical variables and mean growth rate is called the canonical correlation, and is analogous to  $R^2$  in a regression analysis. A significant canonical correlation (as evaluated with Bartlett's chi-square approximation [Timm 1975]) confirmed correlations between final tadpole densities and mean growth rates. Product moment correlations between values of the linear combination of anuran abundances best correlated with growth rates and final densities of anuran species in each tank identified species whose densities strongly covaried with growth rates. Significant negative correlations between densities and canonical variables identified potential competitors, i.e., species whose densities were negatively correlated with growth rates. Approximate intensities of competition exerted by each species were inferred from the strength of negative correlations between anuran densities and canonical variables.

This use of canonical correlation was directly analogous to multiple regression techniques proposed for the inference of interspecific competition (Hallett and Pimm 1979, Emlen 1981). These approaches assume that interspecific competition can be inferred by regressing the abundance of a particular species against abundances of potential competitors in many sampled habitats. Multiple regression can be used to infer the existence of negative correlations between the abundances of one species and its potential interspecific competitors, but it is obviously impossible to detect intraspecific competition by regressing intraspecific density against itself. By using mean growth rate as an index of competitive stress, it was possible to detect negative correlations between an index of competitive stress and both intraspecific and interspecific density.