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COMPETITION BETWEEN AQUATIC INSECTS AND VERTEBRATES: INTERACTION STRENGTH AND HIGHER ORDER INTERACTIONS[1]

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Abstract. Replicated experiments in artificial ponds demonstrated that an assemblage of aquatic insects competed with tadpoles of the frogs *Hyla andersonii* and *Bufo woodhousei fowleri*. We independently manipulated the presence or absence of aquatic insects, and the abundance of an anuran competitor (0 or 150 *Bufo w. fowleri* per experimental pond), using a completely crossed design for two-factor variance analysis, and observed the responses of initially similar cohorts of *Hyla andersonii* tadpoles to neither, either, or both insect and anuran competitors.

Insects and *Bufo* significantly depressed the mean individual mass at metamorphosis of *Hyla* froglets and the cumulative biomass of anurans leaving the ponds at metamorphosis. Neither insects nor *Bufo* affected the survival or larval period of *Hyla*. Insects also significantly reduced the mean mass of *Bufo*, showing that both anurans responded to competition from insects. The intensity of competition between natural densities of insects and *Hyla* tadpoles was comparable to the intensity of competition between *Bufo* and *Hyla*, at a density of 150 *Bufo*/1000 L.

Key words: anurans; Bufo woodhousei; *competition; higher order interactions;* Hyla andersonii; *insects; interphyletic competition; mesocosms; New Jersey; ponds.*

INTRODUCTION

Recent reviews of field experiments support the belief that interspecific competition influences the distribution and abundance of species (Connell 1983, Schoener 1983). These reviews make equally clear that competition for food between distantly related taxa has received little experimental study, despite the growing awareness among ecologists that many taxonomically disparate species potentially compete. Explicitly experimental studies like that of Brown and Davidson (1977), which demonstrated that granivorous insects and mammals compete for food, are rare, compared with more numerous observations of resource overlap between phylogenetically distant species (e.g., Wright 1979, Hurlbert et al. 1986, Schluter 1986; see Diamond 1987). In contrast to those demonstrating competition for food, there are many experiments demonstrating competition for space among distantly related species of sessile marine organisms (Woodin and Jackson 1979).

The historical disregard for competition among taxonomically disparate species has important consequences for generalizations about community organization. Failure to consider competition between taxonomically different groups would lead to underestimates of the overall frequency of interspecific competition demonstrated in nature (e.g., Schoener 1983). Connectance (sensu May 1975) within trophic webs might also be underestimated. The existence of strong competition between species that are sufficiently different in morphology as to be placed in different phyla would seriously compromise the fundamental assumption underlying the application of the morphological niche in studies of exploitative competition and species packing.

Here we demonstrate that the intensity of competition between two taxonomically distant groups, aquatic insects and anuran tadpoles, rivals the intensity of competition measured between two anuran species. Many anuran tadpoles and herbivorous aquatic insects graze on periphyton (Dickman 1968, Cuker 1983, Hart 1985), the assemblage of sessile algae, bacteria, and animals that adhere to and cover objects submerged in freshwater habitats. If periphyton is a limiting resource, competition can result despite obvious taxonomic and morphological differences between vertebrates and insects, to the extent that insects and tadpoles significantly deplete periphyton abundance.

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Amphibians are particularly well suited for experimental studies of interspecific competition. The well-known density-dependent plasticity of larval growth and development makes size at metamorphosis a sensitive indicator of the intensity of competition experienced by tadpoles (Wilbur and Collins 1973). We show that naturally occurring densities of aquatic insects reduce the size at metamorphosis of tadpoles of two anuran species, the Pine Barrens treefrog, *Hyla andersonii,* and Fowler's toad, *Bufo woodhousei fowleri.* In turn, reduced size can ultimately affect fitness, because the attainment of maturity and subsequent fecundity are size dependent in frogs (Berven and Gill 1983, Smith 1987).

METHODS AND MATERIALS

Manipulations of insects and anurans in artificial ponds

We studied competition between insects and tadpoles in artificial ponds located at the Hutcheson Memorial Forest of Rutgers University. The artificial ponds were 12 cylindrical, galvanized steel tanks (1.52 m in diameter and 0.61 m deep), painted with epoxy enamel, and filled with 1000 L of filtered water pumped from a nearby stream through an 88-μm mesh plankton net. Each tank contained similar amounts of dry grassy litter (14 L, tightly packed), macrophytes (50 stems of *Elodea canadensis*), 50 g of commercial trout food for nutrients, and a standard 0.64-L inoculum of plankton from natural ponds, following the general protocol specified for previous experiments (Morin 1981). Screen lids (7 meshes/cm) placed on six randomly selected tanks immediately after filling excluded ovipositing insects. The other six tanks remained uncovered until the onset of anuran metamorphosis, to permit natural colonization by aquatic insects.

We studied two anuran species, the Pine Barrens treefrog, *Hyla andersonii,* and Fowler's toad, *Bufo woodhousei fowleri. Bufo* and *Hyla andersonii* are sympatric in the New Jersey Pine Barrens, and often breed simultaneously in the same temporary ponds. The resulting intimate syntopic association of tadpoles underscores the potential for competition between these anurans. The tadpoles used in this study were the offspring of three female *Hyla* and two female *Bufo.* Tadpoles of each species were pooled and mixed before their introduction into experimental ponds, to homogenize potential genetic differences in tadpole performance over all replicate experimental ponds.

On 19 May 1986, all 12 tanks received 150 hatchling tadpoles of *Hyla andersonii.* Then, three covered and three uncovered tanks, which were selected at random, received 150 *Bufo* hatchlings. Four resulting treatment combinations (hereafter termed: "control" = no *Bufo,* tank covered; "*Bufo*" = 150 *Bufo,* tank covered; "insects" = no *Bufo,* tank uncovered; "insects and *Bufo*" = 150 *Bufo,* tank uncovered) were each replicated three times. This design permitted comparison of the separate competitive effects of insects or 150 *Bufo woodhousei fowleri* tadpoles on *Hyla* tadpoles, by determining whether *Bufo* and insects reduced *Hyla* growth or survival by comparable amounts. All anuran densities were within the range observed in natural ponds for similar species (see Woodward 1982, Morin 1983). Insect densities resulted from natural patterns of colonization.

Colonizing insects could invade the uncovered tanks from 19 May until 4 June 1986, when the open tanks were covered to retain the first metamorphosing anurans. Standard samples taken from the tanks on 27 June 1986 with a 0.5–mm mesh dip net, shortly after the last tadpoles metamorphosed, showed that mean total insect abundance was 39.5 insects/sample in uncovered vs. 1.2 insects/sample in covered tanks (Table 1; ANOVA of $\log_{10}$ transformed total counts of all insects: $F_{1,10} = 10.14$, $P < .01$). Samples consisted of two vertical sweeps of the dip net along the walls of each tank, and all collected insects were identified to family or subfamily. Insects arriving in the tanks as eggs at the earliest possible time, 19 May, would have to have had combined periods of embryonic and larval development of <40 d to have been missed by sampling on 27 June. Only very rapidly developing insects, such as mosquitoes, or transient ovipositing adults of other species, would have left the tanks by this time. Consequently, we feel that our sampling protocol provided a conservative measure of insect abundance in the open and closed tanks. The point of the sampling was to document that the covered and uncovered treatments successfully manipulated insect abundance, rather than to determine the absolute abundance of insects in the open tanks. Sampling of sufficient intensity to estimate absolute insect abundances would have completely mixed and disrupted the artificial pond communities.

The most common insects that colonized the tanks were mosquitoes (Diptera: Culicinae), midges (Diptera: Chironomidae and Chaoborinae), water boatmen (Hemiptera: Corixidae), and mayflies (Ephemeroptera: Baetidae). Percent taxonomic similarity (as defined in Pielou 1984) of insect samples from open tanks ranged from 0.0 to 66.7%, with a mean of only 25.6%. No single insect taxon occurred in samples from more than four uncovered tanks, but all open tanks contained abundant mosquito larvae during the first 2 wk of the experiment. Our daily observations of the tanks indicated that no other potential competitors, including frogs, differentially colonized the uncovered and covered tanks during the experiment.

All metamorphosed froglets were collected daily, identified to species, counted, and weighed to 1 mg precision. From this information we determined survival to metamorphosis, mean mass at metamorphosis, mean larval period, and the cumulative biomass of metamorphs for each experimental population (tank) of each species. In anurans, increased competition reduces mean mass at metamorphosis and/or prolongs larval development (Wilbur and Collins 1973, Wilbur 1976). Consequently, relative intensities of competition experienced by tadpoles can be inferred from interpopulation differences in mean mass at metamorphosis.

We measured the impact of insect and anuran consumers on periphyton on 7 June 1986 by comparing the amount of periphyton chlorophyll *a* harvested from 75 × 25 mm glass microscope slides suspended at middepth adjacent to the walls of each tank. We used the trichromatic method of Strickland and Parsons (1968) to estimate chlorophyll concentration, and converted this estimate to micrograms of chlorophyll per slide. We only sampled chlorophyll from the side of the slide facing the center of the tank, which received unrestricted grazing by tadpoles and insects.

Our experimental protocol mimicked the vernal patterns of insect and anuran colonization in natural ponds that dry during summer or autumn, and subsequently refill in late winter or early spring. Overwintering competitors and predators, such as tadpoles and insects that fail to complete development in a single season of growth, are eliminated when ponds dry. Anurans and insects subsequently recolonize refilled ponds only after it becomes sufficiently warm for adults to become active and breed. Because large overwintering predatory insects are absent from such sites, these predators cannot reduce abundances of early-colonizing insects or tadpoles. For example, in New Jersey, odonates only begin to fly and oviposit in numbers during the first 2 wk of June, at about the same time that early cohorts of transforming tadpoles are leaving temporary ponds. Consequently, early-breeding frogs that exploit ponds that have recently dried and refilled avoid late-arriving predatory insects, but they may face increased competition from the other herbivores that simultaneously colonize the ponds. We expect that predator densities would gradually increase as the season wears on. Seasonal predator avoidance may be an important selective factor underlying the early spring, cold-weather breeding of many amphibians (Morin 1987).

Statistical analyses

We used a two-factor multivariate variance analysis (MANOVA) to assess the impact of insects (covered vs. uncovered tanks) and *Bufo* on the survival, mean mass at metamorphosis, mean larval period, and cumulative biomass of *Hyla andersonii.* We analyzed population means, rather than individual metamorph values, because the latter are not independent measures of the treatment effects. The analysis permitted direct tests of three hypotheses: (1) no effect of insects, (2) no effect of *Bufo,* (3) no interaction between the effects of insects and *Bufo.* We inferred that competition occurred if insects or *Bufo* reduced *Hyla* mass at metamorphosis relative to the controls. Relative intensities of competition exerted by insects and *Bufo* could be inferred by comparing the reductions in mean mass caused by the respective treatments. A significant interaction term in an ANOVA of any index of competition would indicate the existence of a higher order interaction arising from the interdependence of density-dependent competitive effects exerted by insects and *Bufo* tadpoles (sensu Wilbur 1972; contra Pomerantz 1981).

TABLE 1. Abundance of insects in dip net samples from tanks open to insect colonization (open tanks) or closed to insects (closed tanks). Each mean (±SE) is based on samples from six tanks.

Taxon	Open tanks	Closed tanks
Hemiptera		
Corixidae	5.83 ± 3.18	0.33 ± 0.21
Diptera		
Chaoborus	17.17 ± 11.29	0.17 ± 0.17
Culicinae	5.83 ± 5.64	0.00 ± 0.00
Chironomidae	3.17 ± 1.45	0.17 ± 0.17
Coleoptera		
Hydrophyllidae	0.33 ± 0.21	0.00 ± 0.00
Laccophilus	2.00 ± 0.93	0.00 ± 0.00
Other	0.83 ± 0.83	0.33 ± 0.21
Ephemeroptera		
Caenis	0.00 ± 0.00	0.17 ± 0.17
Cloeon	4.17 ± 3.43	0.00 ± 0.00
Odonata		
Zygoptera	0.17 ± 0.17	0.00 ± 0.00
Total	39.50 ± 16.40	1.17 ± 0.54

We also tested for competitive effects of insects on *Bufo* by comparing the mean masses of *Bufo* froglets that metamorphosed from tanks with and without insects. Insect abundance was independent of *Hyla* density, since *Hyla* were initially present at identical densities in all tanks and survived equally well in all treatments. Single-factor ANOVAs (factor = insects present or absent) tested the hypothesis of no effect of insects on *Bufo* survival, mean mass, larval period, and cumulative biomass. The small total number of replicates (six tanks) with *Bufo* precluded the use of a MANOVA, but Bonferroni adjustments of significance levels (see Timm 1975) rendered these tests appropriately conservative.

A two-factor ANOVA tested the following hypotheses regarding effects of experimental treatments on periphyton chlorophyll: (1) no effect of insects, (2) no effect of *Bufo,* and (3) no interaction between the effects of insects and *Bufo.* Differences in chlorophyll among treatments measured the relative impact of insects and *Bufo* tadpoles on periphyton. Reductions in both periphyton standing crop and anuran growth in tanks with insects would suggest an exploitative, consumptive mechanism of competition between insects and tadpoles.

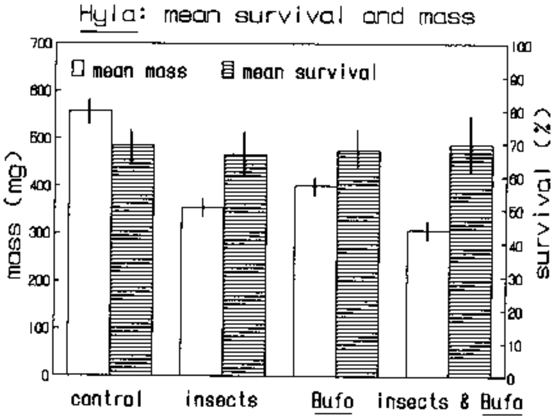

FIG. 1. Mean mass and survival to metamorphosis of *Hyla* froglets in the four treatments. Insects reduced the mass at metamorphosis of *Hyla*. Each bar represents the mean of three replicate artificial ponds; vertical lines denote ±1 SE.

RESULTS

Hyla andersonii

Aquatic insects and *Bufo* tadpoles, separately and together, significantly reduced the mean mass at metamorphosis of *Hyla* (Fig. 1, Table 2). Insects also reduced the mean total biomass of *Hyla*, while *Bufo* generated a nonsignificant trend in the same direction. Insects without *Bufo* reduced the mean mass of *Hyla* metamorphs by the about same amount as 150 *Bufo* without insects. The combined impact of insects and *Bufo* on *Hyla* growth was only slightly greater than the separate impact of either group alone. The significant interaction term in the ANOVA for *Hyla* mean mass (Table 2) underscored the reduced aggregate effect of insects and *Bufo* on *Hyla*.

None of the treatments affected the duration of larval development for *Hyla* (Table 2), which averaged 30.3 d over all treatments. Treatments also had no effect on *Hyla* survival, which averaged 68.5 % over all treatments (Fig. 1). Consequently, variation in final *Hyla* density was not a source of variation in mean mass. Differences in mean mass at metamorphosis following similar periods of larval development in all treatments mean that tadpoles differed in their growth rates, since hatchlings of the same initial size metamorphosed at different sizes after similar periods of growth.

Bufo woodhousei fowleri

Insects significantly reduced the mean individual mass of *Bufo* froglets, and exerted a similar but nonsignificant effect on total *Bufo* biomass (Figs. 2, 3; Table 3). Insects did not significantly affect the mean survival

TABLE 2. Summary of MANOVA and univariate variance analyses for responses of *Hyla andersonii* tadpoles to *Bufo* tadpoles and insects. For these contrasts the multivariate test criterion, Wilks' λ, has an exact relation with an *F* statistic, given below.

Source	df	Sum of squares	*F*	*P**
ANOVA: Survival				
Insects	1	0.00003333	0.00	.9637
Bufo	1	0.00030000	0.02	.8915
Insects × *Bufo*	1	0.00133704	0.09	.7738
Error	8	0.12103704		
ANOVA: Mean mass				
Insects	1	65 578.8675	112.71	.0001
Bufo	1	31 079.5408	53.42	.0001
Insects × *Bufo*	1	9201.9408	15.82	.0041
Error	8	4654.7000		
ANOVA: Larval period				
Insects	1	2.707500	2.38	.1612
Bufo	1	4.440833	3.91	.0834
Insects × *Bufo*	1	0.187500	0.17	.6952
Error	8	9.086666		
ANOVA: Total froglet biomass				
Insects	1	722 181 360	13.09	.0068
Bufo	1	313 466 830	5.68	.0443
Insects × *Bufo*	1	135 619 719	2.46	.1556
Error	8	441 513 316		

MANOVA: Survival, mean mass, larval period, biomass

Source	Wilks' λ	*F*	Numerator df	Denominator df	*P*
Insects	0.03884525	30.92	4	5	.0010
Bufo	0.06100348	19.24	4	5	.0031
Insects × *Bufo*	0.31098179	2.76	4	5	.1468

* Probabilities for the univariate tests should be compared against the Bonferroni adjusted significance level for four variables, which is 0.0127.

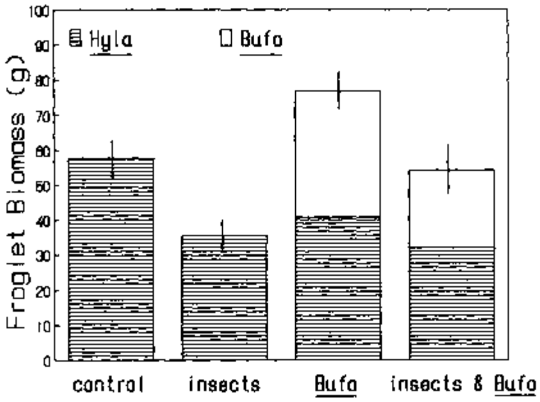

FIG. 2. Mean total biomass of froglets emerging from the four experimental treatments. Vertical lines denote ±1 SE for total biomass of both frog species.

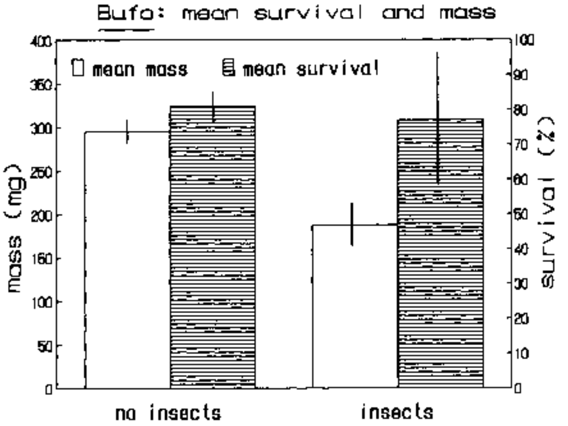

FIG. 3. Mean mass and survival to metamorphosis of *Bufo* froglets in the six tanks with *Bufo* (three replicates with insects, three replicates without insects). Insects reduced the mass at metamorphosis of *Bufo*. Format as in Fig. 1.

(mean over both treatments = 79.0%) or larval period (mean over both treatments = 24.8 d) of *Bufo* (Table 3). The smaller size of *Bufo* in tanks with insects may have contributed to the nonadditive competitive impact of insects and *Bufo* on *Hyla* mean mass (indicated by the significant interaction in Table 2). Nonadditivity, the significant interaction term in the two-factor ANOVA for *Hyla* mean mass (Table 2), means that the reduction in mass caused by *Bufo* and insects in sympatry was not the sum of the independently measured reductions in allopatry. Small *Bufo* tadpoles could be weaker competitors than their larger counterparts in tanks without insects.

Periphyton

Insects significantly reduced the standing crop of periphyton available to tadpoles (Fig. 4, Table 4). We observed larval chironomid midges (Diptera: Chironomidae) and mayflies (Ephemeroptera: Baetidae) feeding directly on periphyton during the experiment. Larval midges cleared small areas of periphyton immediately around their tubes on the tank walls and on the slides used to sample periphyton. We also observed that diurnally inconspicuous larval mayflies moved up onto the tank walls at dusk from their locations in the benthic litter and grazed on periphyton.

Bufo also tended to reduce periphyton abundance (Fig. 4), but this trend was not statistically significant. Previous transient reductions in periphyton caused by *Bufo* grazing may have disappeared by the time we sampled the slides. The sampling date coincided with the onset of metamorphosis by *Bufo*, and would have been preceded by a period of reduced feeding when tadpoles remodeled their mouthparts before assuming a terrestrial carnivorous lifestyle.

DISCUSSION

Competition between distantly related taxa

Much of the evidence for consumptive competition (sensu Schoener 1983) between distantly related taxa is observational or correlative. This evidence usually takes the form of overlap in resource use among dissimilar taxa (e.g., Wright 1979, Eadie and Keast 1982, Hurlbert et al. 1986, Schluter 1986). Unfortunately, overlap alone is insufficient evidence for competition (MacArthur 1972). More direct evidence involves observations of interference between dissimilar taxa during foraging (Carpenter 1979, Shields and Bildstein 1979). Such interactions illustrate that the potential for competition exists, but they fail to demonstrate that interference affects growth, survival, or other fitness components.

Experimental evidence for interphyletic competition

TABLE 3. Summary of univariate variance analyses for responses of *Bufo w. fowleri* tadpoles to presence vs. absence of aquatic insects. The Bonferroni adjusted significance level for four tests is 0.0127.

Variable	Source	df	Sum of squares	*F*	*P*
Mean mass	Insects	1	17 273.15	43.96	.0027
	Error	4	1 571.55		
Mean survival	Insects	1	4.1902	0.05	.8397
	Error	4	359.8345		
Mean larval period	Insects	1	0.0840	0.07	.8050
	Error	4	4.8316		
Biomass	Insects	1	281 090 747.39	8.53	.0432
	Error	4	131 789 270.78		

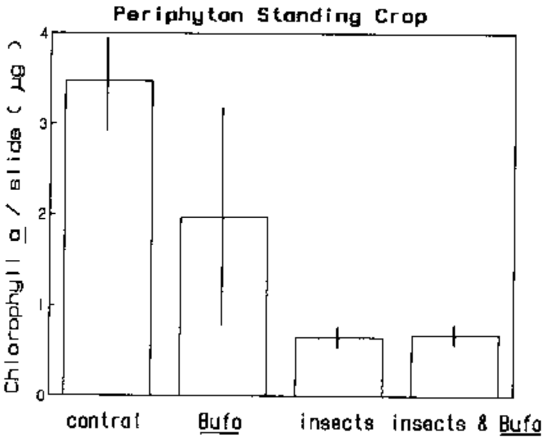

FIG. 4. Mean amount of chlorophyll *a* extracted from periphyton on microscope slides exposed to grazers in the artificial ponds. Periphyton chlorophyll *a* was significantly depressed in tanks with insects on 7 June 1986, 4–8 d before the onset of metamorphosis in *Hyla,* and during the metamorphosis of *Bufo.*

for food is rare. Important studies include the work summarized by Brown et al. (1986) for desert granivores, Karban et al. (1987) on herbivores and pathogens, and Cuker (1983) on periphyton-grazing invertebrates. Although ecologists have recently increased their awareness of potential competition between phyla, they have done little to experimentally explore the consequences of interphyletic competition for community organization. For instance, the relative intensities of interspecific competition between closely and distantly related species are seldom measured. Without such information it is difficult to assess the relative importance of competition between species of different taxonomic affinity.

Our study allowed us to calibrate the competitive effects of a diverse assemblage of aquatic insects against the intensity of competition exerted by a known density of *Bufo* tadpoles. The density of *Bufo* tadpoles used was well within the natural density range observed for the genus (Brockelman 1969, Wilbur 1977, Woodward 1982). From this we conclude that the strength of competitive effects exerted by an assemblage of aquatic insects on *Hyla andersonii* tadpoles was comparable to the strength of the effects exerted by a conservative natural density of *Bufo* tadpoles. The impact of interphyletic competition was not trivial.

Mechanisms of competition between insects and tadpoles

The reduced abundance of periphyton in ponds with abundant insects provided circumstantial evidence for a consumptive (exploitative) mechanism of competition between insects and tadpoles. Negative effects of insects on tadpole size need not result only from direct competition for periphyton. Indirect effects mediated through the food web are also plausible (see Bender et al. 1984). Insects that did not directly graze on periphyton might still reduce the standing crop of periphyton by depleting nutrients. Because the experimental ponds were essentially closed systems with respect to nutrients, nutrients tied up in larval insects or exported by metamorphosing insects represent a loss to the whole system. Reduced amounts of nutrients cycling through the pond food web might then limit periphyton abundance, and in turn depress tadpole growth. Our experimental design could not separate these direct and indirect effects, but they are interesting topics for future research.

TABLE 4. ANOVA of periphyton chlorophyll *a* standing crop on 7 June 1986.

Source	df	Sum of squares	*F*	*P*
Bufo	1	1.62	1.27	.2932
Insects	1	12.64	9.83	.0139
Bufo × insects	1	1.77	1.38	.2732
Error	8	10.28		

We feel that our interpretation of the open/closed tank manipulation as a competitive effect of insects is parsimonious. We have difficulty reconciling our results with some kind of positive shading effect on tadpole resources. The photosynthetic component of periphyton should respond positively to light, but was nonetheless more abundant in screened, potentially shaded, tanks without insects. This means that if anything, our measure of the impact of insects is conservative, since periphyton abundance and subsequent tadpole growth would be expected to be even greater than observed in our insect-free controls if it were possible to exclude insects without the slight shading imposed by screen lids.

Higher order interactions between insects and tadpoles

Higher order (nonadditive) interactions among competitors result when the nature of density-dependent competition between two species is influenced by additional species (Wilbur 1972, Neill 1974, Abrams 1983). There have been remarkably few experimental efforts to detect such effects (Vandermeer 1969, Wilbur 1972, Neill 1974, Case and Bender 1981), and their results have been subject to different interpretations (see Roughgarden and Diamond 1986). Higher order interactions vastly complicate the prediction of aggregate multispecies competitive effects from knowledge of pairwise interspecific interactions, since aggregate density-dependent effects are not simply the sum of pairwise density-dependent effects, as proposed in some early versions of competition theory (e.g., Levins 1968).

The significant statistical interaction between the effects of insects and *Bufo* on *Hyla* provides a clear example of a higher order interaction (sensu Wilbur 1972). Specifically, the aggregate competitive impact of *Bufo* and insects was less than the sum of the separately measured effects of both groups of competitors. One mechanism underlying this interaction may have been a reduction in the per capita competitive impact of *Bufo*. This reduction could be caused by insects competing with and reducing the size of *Bufo* tadpoles. Small tadpoles tend to be weaker competitors than their larger counterparts (Wilbur 1984).

Our operational definition of higher order interactions, a change in the density-dependent interspecific interactions between two species caused by other species, is consistent with previous definitions (Wilbur 1972, Abrams 1983). This definition is also similar to the definitions of behavioral or chemical response indirect effects proposed by Miller and Kerfoot (1987). The important point here is that we are assuming that changes in the joint impact of two manipulated groups, *Bufo* and insects, result from changes in their per capita effects, rather than from changes in the densities of *Bufo* and insects in allopatry and sympatry.

Much confusion has arisen over what constitutes evidence for higher order interactions (e.g., Pomerantz 1981), and how important such interactions are (Vandermeer 1981). We address these issues here. Criticisms raised by Pomerantz (1981) and echoed by others (Case and Bender 1981) that are relevant to this study are (1) the kind of data required to test for higher order interactions, (2) the primacy of intraspecific nonlinear density-dependence as an explanation for nonadditive effects, and (3) statistical evidence required to document that nonadditive effects exist.

First, the data used to measure interspecific competition need not be restricted to changes in population size. Certainly this is the unit of measure used in many simple models of interspecific competition, but it does not logically preclude the use of other measures, such as mean mass, for inferring competitive effects in long-lived organisms. Pomerantz (1981) suggests that measures of competition based on size or growth rates do not address higher order interactions, because the Lotka-Volterra equations model population growth rather than somatic growth. This distinction arbitrarily redefines higher order interactions, and restricts their study to competitive effects measured by changes in population size predicted by the Lotka-Volterra model for interspecific competition. We see no logical reason for this restriction.

Second, we can also eliminate intraspecific nonlinear density dependence as a source of nonadditive competitive effects. Neither the initial nor final intraspecific density of *Hyla* varied among treatments, consequently the final departures from additive effects of *Bufo* and insects cannot be attributed to intraspecific nonlinear density dependence of *Hyla*. The same point can be made for the invariant final densities of *Bufo* and insects in sympatry and allopatry. Insects did not affect the final survival and density of *Bufo* (see Table 3), and analysis of insect samples also showed that *Bufo* did not affect the total abundance of insects in open tanks on 27 June (ANOVA of $\log_{10}$ insect abundance: $F_{1,4} = 7.54$, $P > .05$). Differences in the impact of *Bufo* and insects in allopatric and sympatric treatments cannot be attributed to changes in their density.

Third, in his critique of Wilbur's (1972) study of higher order interactions in amphibian communities, Pomerantz (1981) apparently misunderstood the statistical evidence presented for higher order interactions. The existence of such interactions in Wilbur's study was based not on simple inspection of irregularities in the response surface that described size as a function of competitor densities (as implied by Pomerantz), but on the statistical significance of the interaction terms in a variance analysis. Reference to any basic statistics text (e.g., Timm 1975) will show that the meaning of the interaction term in a two-way ANOVA is that the joint impact of two factors on the mean response is not predicted by their separate impacts. When the two factors in question are the abundances of two competitors, and the response is the size or growth rate of a third species, the ineluctable conclusion is that their joint density-dependent competitive effects differ from the sum of their separate density-dependent effects. Note also that these changes occurred without changes in the densities of *Bufo* or insects in our experiment.

Our statistical analysis of the effects of *Bufo* and insects on the growth rates of *Hyla andersonii* is equivalent to the following statistical model:

$$\text{mass}_j = \mu + \alpha(B) + \beta(I) + \gamma(B \times I) + e_j,$$

where mass_j is the observed average froglet mass in tank j, μ is the mean in the absence of *Bufo* or insects, α is the reduction in μ caused by the addition of 150 *Bufo*, β is the reduction in μ caused by ad libitum insects, γ describes the departure of the simultaneous effects of *Bufo* and insects from that predicted by $[\mu + \alpha(B) + \beta(I)]$, and e_j is an error term. The values of B and I are either 1 or 0, when *Bufo* or insects are present (1) or absent (0). Our a priori hypothesis tests in the ANOVA tested whether α (the *Bufo* effect), β (the insect effect), and γ (the interaction effect) were nonzero. There is an obvious analogy between this statistical model and models of interspecific competition evaluated at a constant intraspecific density of the species whose mass has been measured.

How important was the observed higher order interaction? Vandermeer (1981) has implied that while such interactions may be statistically detectable, they may not explain much of the total variation among communities. We can provide one estimate by measuring the total fraction of the variability among experimental communities that is described by the interaction. We do this by partitioning the total sum of squares for mean mass of *Hyla* in Table 2 into components due to *Bufo*, insects, the interaction, and residual unexplained variation. The result is that the interaction effect accounts for 8.33% of the total variation in growth rate, which is substantially less than the 59.34% accounted for by insects and the 28.12% accounted for by *Bufo,* but greater than the remaining 4.21% residual unexplained variation. The higher order interaction is significant, but explains less variation than either of the main effects.

Consequences of interphyletic competition for anuran assemblages

Competition from nonanuran taxa has been virtually ignored in previous studies of the organization of anuran assemblages (see Wilbur 1980, 1984 for reviews), despite the fact that such interactions are implicit in the trophic links of temporary pond food webs (see Wilbur 1972). Given that the intensity of competition from natural densities of insects can rival that of modest densities of tadpoles, it seems imperative to reevaluate the identities of species likely to compete with anurans, regardless of their taxonomic affinity. Many aquatic invertebrates consume periphyton. Consequently the guild of periphyton grazers in any pond may also include gastropods, crustaceans, and insects, which all potentially compete with tadpoles and each other.

Periphyton consumers are not the only potential competitors of anuran tadpoles. Tadpoles can also filter bacteria and phytoplankton directly from the water column (Wassersug 1972, Seale and Bekvar 1980), and consequently may compete with herbivorous zooplankton that also consume this resource. Previous experiments have failed to document a competitive effect of tadpoles on zooplankton (Morin et al. 1983), but the reciprocal experiment required to detect effects of zooplankton on tadpoles has not been done.

We suggest that in natural ephemeral ponds without vertebrate predators, a situation roughly comparable to our experimental ponds, the competitive effect of natural densities of insects on tadpoles may rival the intensity of competition exerted by different anuran species. We also infer that the intensity of competition from natural densities of insects in our study was not as great as that exerted by tadpoles in other experiments that have resulted in the competitive exclusion of certain anuran species (Wiltshire and Bull 1977, Morin 1981).

Interphyletic competition further complicates considerations of the already complex web of size- and stage-dependent interactions among animals with complex life cycles, such as insects and frogs. The well-known changes in habitat and diet that accompany anuran metamorphosis result in a shift from aquatic herbivory to terrestrial carnivory. Thus, it is conceivable that larval anurans can compete with aquatic insects before metamorphosis, and after metamorphosis prey on the same insect species (and perhaps the same individuals) that competed with them as larvae. For interactions between anurans and insects with predatory larvae, metamorphosis can also reverse the roles of predator and prey (Jackman et al. 1981). It remains unclear whether predators (fish, salamanders, and some insects) that accumulate in greater densities in less ephemeral ponds can moderate the intensity of competition between tadpoles and insects. Other studies show that predators can potentially moderate the intensity of density-dependent interactions among tadpoles or insects (Crowder and Cooper 1982, Morin 1983). Additional experiments are needed to determine how disturbance regimes and the impact of predation interact to influence the outcome of competition between disparate taxa in this and other systems.

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