

An examination of multiple factors affecting community structure in an aquatic amphibian community

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Summary. The potential effects of multiple factors structuring certain larval amphibian communities were studied using a pen experiment in a natural pond. Potential factors (predation and competition from other species) were allowed to act in a stepwise fashion such that their relative importance could be evaluated. Based on a previous study, it was hypothesized that predation by *Ambystoma* salamander larvae on other larval amphibian species would be the most important factor. Survival of *Ambystoma jeffersonianum* salamander larvae and *Rana sylvatica* tadpoles was significantly depressed only by *Ambystoma opacum* predation. Survival of *Ambystoma maculatum* salamander larvae was significantly greater in the absence of both *A. opacum* and *A. jeffersonianum* predators. The virtual elimination of *Hyla chrysoscelis* larvae in all treatments also can be largely attributed to *Ambystoma* predation. Thus, *Ambystoma* predation was the dominant factor determining larval survival of four amphibian prey species in the experimental communities.

Key words: Multiple factors – Predation – Competition – Community structure – Amphibians

Natural communities can be structured by multiple operating factors. For example, salamander predation can alter the competitive interactions among larval anuran prey (Morin 1983a). However, consideration of multiple factors in designing field experiments can be difficult (Quinn and Dunham 1983). Quinn and Dunham describe three types of problems in multiple factor experiments: (1) where multiple factors operate it is not possible to “distinguish between the ‘truth’ of processes occurring simultaneously;” (2) univariate tests may not estimate the actual contributions of individual factors

if there are strong interactions among factors; and (3) absence-of-effect null hypotheses may be difficult to construct.

A variety of direct and indirect interactions (predation, competition, competitive priority effects, and/or indirect facilitation) may influence the structure of aquatic larval amphibian communities (e.g. Seale 1980; Morin 1983a, b, 1986; Smith 1983; Wilbur 1984; Alford and Wilbur 1985; Wilbur and Alford 1985; Holomuzki 1986). Travis et al. (1985) emphasize the importance of considering multiple factors acting on larval amphibian populations. Previous results suggest that predation by *Ambystoma opacum* (marbled salamander) larvae results in low survivorship of *Ambystoma jeffersonianum* (Jeffer-

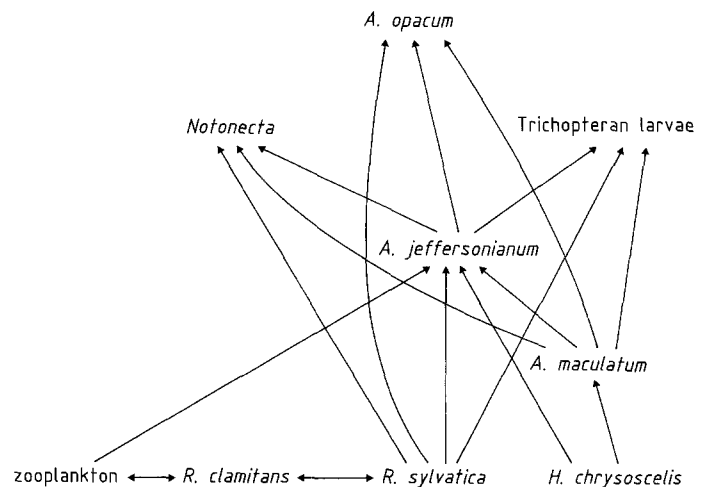


Fig. 1. Trophic interactions studied here. These interactions are those we hypothesized for ponds without abundant adult *Notophthalmus viridescens* (red-spotted newts). Newts probably occupy the same position as *A. opacum*. Some ponds lack certain species depicted here. Proposed interactions are based on known amphibian feeding habits, field observations, and Cortwright (1987). Double-pointed arrows indicate competitive interactions. Salamander larvae probably prey on immature *Notonecta* and Trichoptera, however, direct evidence has not been gathered

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son salamander) and *Rana sylvatica* (wood frog) larvae in both experimental and natural communities (Cortwright 1987). However, these species are embedded in a complex web of trophic interactions (Fig. 1). As a result, other predators and competitors acting over an entire season could also have affected the survivorship of the latter two species. Factors that could have reduced survival of *A. jeffersonianum* larvae included: (1) predation by larval *A. opacum*, (2) predation by aquatic invertebrates, (3) competition between *Rana clamitans* tadpoles (green frog) and the zooplankton prey of *A. jeffersonianum* larvae resulting in reduced availability of zooplankton to *A. jeffersonianum*, and (4) background physical and biological factors. Factors that could have reduced survivorship of *R. sylvatica* tadpoles included: (1) predation by larval *A. opacum*, (2) predation by larval *A. jeffersonianum*, (3) predation by aquatic invertebrates, (4) reduction of suspended particle resource levels by overwintering *R. clamitans* tadpoles to a point where *R. sylvatica* hatchlings starve (cf. Seale 1980) or die due to other causes related to low resource availability, and (5) background physical and biological factors.

The present study examines the impact of these multiple causes on *R. sylvatica* and *A. jeffersonianum* using stepwise addition of factors in a field experimental design. In addition, responses of the other amphibians to

the various treatments were analyzed. Problems (1) and (2) outlined by Quinn and Dunham (1983) were largely obviated in that the design assessed the importance of factors added one at a time while still allowing several combinations of factors to act. Problem (3) is addressed by comparing each added factor to previous treatment(s) which do not include the factor in question. Not all combinations of factors were possible due to limitations on the number of available pens.

Materials and methods

The study site was a permanent pond (330 m² when full) in Yellowwood State Forest, Brown County, Indiana. Details of pen construction and the study area are given elsewhere (Cortwright 1987, 1988). Each pen (2.5 × 1.0 m) was built directly into the pond bottom thereby offering a natural, leaf and twig covered substrate. Vexar screen (14 × 6 mm mesh) was placed over the pens to control colonization by large insects and a hardware cloth shield (3 mm mesh) was sewn on the walls of each pen so metamorphs could not leave. The Vexar tops reduced sunlight by only ca. 12%. Pen walls were fiberglass window screen (7 meshes/cm) supported by wood poles.

The stepwise experimental design (Table 1) focused on species interactions which may have resulted in the low survivorship of *R. sylvatica*, *A. jeffersonianum*, and, in some habitats, *Ambystoma maculatum* (spotted salamander) previously observed in natural

Table 1. Experimental design in the 1984 pen experiment. Each *Ambystoma* and *Rana* species was added at its hatching time in nature except for *A. opacum* and *R. clamitans*, which hatched the previous October and summer respectively. There were two replicates per treatment

Treatment	Numbers added per pen (date added) ^a							Design factors expected to influence species performance ^c
	<i>A. opacum</i> overwintered larvae	Invertebrate predators ^b	<i>R. clamitans</i> yearling tadpoles	<i>A. jeffersonianum</i> hatchling larvae	<i>R. sylvatica</i> hatchling tadpoles	<i>A. maculatum</i> hatchling larvae	<i>H. chrysosecelis</i> hatchling tadpoles	
1	0	0	0	0	500 (7–11 April)	84 (30 April–7 May)	230 (4–9 June)	Impact of physical and biological background factors on <i>R. sylvatica</i> and <i>A. maculatum</i> . <i>A. maculatum</i> predation on <i>H. chrysosecelis</i> <i>A. jeffersonianum</i> predation on <i>R. sylvatica</i> and <i>A. maculatum</i> . Impact of background factors on <i>A. jeffersonianum</i>
2	0	0	0	84 (60% 11, 12 April 40% 18, 19 April)	500	84	230	Competition of <i>R. clamitans</i> on <i>R. sylvatica</i> and indirectly on <i>A. jeffersonianum</i>
3	0	0	30 (1 April)	84	500	84	230	Invertebrate predation on <i>R. sylvatica</i> and <i>A. jeffersonianum</i>
4	0	12 (4 April)	30	84	500	84	230	<i>A. opacum</i> predation on <i>R. sylvatica</i> and <i>A. jeffersonianum</i>
5	11 (1 April)	12	30	84	500	84	230	

^a 3 ml strained volume of *Chaoborus* larvae (Diptera) were added to each pen on 7, 15 April

^b 7 *Notonecta undulata* adults (hemiptera), 5 Trichoptera larvae

^c The factors operating on *H. chrysosecelis* and *A. maculatum* over treatments 2–5 parallel (except where noted) those on *R. sylvatica* and *A. jeffersonianum* respectively

and experimental communities (Cortwright 1987). The design included amphibian larvae and two predaceous insects common in the study and nearby ponds in 1984. Specific predictions were: (1) *R. sylvatica* and *A. jeffersonianum* survivorship should be least in the presence of larval *A. opacum* predators, and (2) *A. maculatum* larvae should experience their highest survival in pens free of other species of salamander larvae (treatment 1). Both predictions were based on previous results (Cortwright 1987). However, the present design addressed the extent to which low survivorship through an entire growing season should be attributed to *A. opacum* predation, to other interactions (outlined above and see Table 1), or to background physical and biological factors. The design also allowed the examination of predatory impact by *Ambystoma* larvae on *Hyla chrysoscelis* (gray treefrog) tadpoles. All treatments and replicates (2) were randomly applied to 10 pens within a set of 22 (the other 12 pens were used for a separate study).

All amphibian larvae were introduced at their hatching time in nature, except *A. opacum* salamander larvae and *R. clamitans* tadpoles, which hatched the previous autumn and summer respectively. The latter two species were added prior to any other species in order to simulate the natural phenology. Also, *H. chrysoscelis* hatchlings were allowed to grow for a few days until they were too large to pass through the screen wall. Metamorphic amphibians were caught on floating boards, resting under boards on dry pen areas, or climbing on the pen walls at night. All densities used were within the range occurring in nearby natural communities (Cortwright 1987, 1988). Metamorphic individuals were collected daily (between 0100–0500 h 2–3 times per week and after 0500 h other days), weighed in the lab (to the nearest mg), and released the next day.

The three response variables measured for each species in each pen were: 1) number of survivors, 2) mean wet mass at metamorphosis, and 3) mean duration of larval period. Survivorship is most directly related to predation, except where solely competitive and background physical and biological factors operated. Smaller metamorphic body mass and longer larval period primarily reflect competitive and other density dependent processes, especially in permanent ponds where the threat of pond drying is absent. In some situations, slow growth may increase vulnerability to large predators over the larval period (Wilbur 1984). However, the predators used here are only effective on these amphibian prey during the early part of the prey's larval period (Cortwright 1987).

Species responses were analyzed using univariate oneway analysis of variance (ANOVA). Planned comparisons (Lindman 1974) were used to assess statistical significance of the two major predictions (above). When an ANOVA was statistically significant for metamorphic mass or larval period, Student-Newman-Keuls (SNK) a posteriori contrasts were used to assess which treatments differed. In general, examination of statistical significance across treatments allows one to infer which processes contributed to shifts in the response variable. In addition to oneway ANOVAs on mass at metamorphosis, intraspecific density effects were analyzed using linear regression of metamorphic mass on the number of metamorphs (as only one initial hatchling density was used per species).

Results

Predation

We predicted that *Ambystoma opacum* salamander larvae should produce a marked reduction (beyond all prior factors) in the survivorship of *R. sylvatica* and *A. jeffersonianum*. No *R. sylvatica* tadpoles survived in the presence of predatory *A. opacum* larvae (Table 2), although large numbers survived (15.0 to 58.4%) in all other pens. The unequal variances among treatments for the number of surviving *R. sylvatica* were removed

Table 2. Summary of mean responses at metamorphosis for the one-way pen experiment with two replicates

	Treatment				
	1	2	3	4	5
<i>A. opacum</i> salamander larvae					
Initial density	0	0	0	0	11
Mean no. survivors	–	–	–	–	10.5
Mean % survivorship	–	–	–	–	95.5
Mean mass (mg)	–	–	–	–	1286.6
Mean larval period (days) ^a	–	–	–	–	69.6
<i>R. clamitans</i> yearling tadpoles					
Initial density	0	0	30	30	30
Mean no. survivors	–	–	24.5	27.5	29.0
Mean % survivorship	–	–	81.7	91.7	96.7
Mean mass (mg)	–	–	2249.5	2029.2	2144.6
Mean larval period (days) ^a	–	–	104.8	101.0	105.4
<i>A. jeffersonianum</i> salamander larvae					
Initial density	0	84	84	84	84
Mean no. survivors	–	40.5	36.0	23.0	4.0
Mean % survivorship	–	48.2	42.9	27.4	4.8
Mean mass (mg)	–	898.2	792.6	655.5	1099.0
Mean larval period (days)	–	119.6	125.0	127.2	101.0
<i>R. sylvatica</i> tadpoles					
Initial density	500	500	500	500	500
Mean no. survivors	283.0	172.0	156.0	107.5	0
Mean % survivorship	56.6	34.4	31.2	21.5	0
Mean mass (mg)	234.8	287.7	298.8	273.6	–
Mean larval period (days)	72.0	83.7	72.8	73.8	–
<i>A. maculatum</i> larvae					
Initial density	84	84	84	84	84
Mean no. survivors	67.5	0	2.5	4.0	7.0
Mean % survivorship	80.4	0	3.0	4.8	8.3
Mean mass (mg)	427.6	–	930.4	731.8	959.8
Mean larval period (days)	103.2	–	129.0	119.6	102.8
<i>H. chrysoscelis</i> tadpoles					
Initial density	230	230	230	230	230
Mean no. survivors	0	0	0	0	0.5
Mean % survivorship	0	0	0	0	0.2

^a calculated from 1 April

Table 3. One way ANOVAs on the number of surviving *A. jeffersonianum*, *R. sylvatica*, and *A. maculatum* and the duration of the larval period for *A. jeffersonianum*. Ln X and Ln X + 1 transformations were required for the number of surviving *A. jeffersonianum* and *R. sylvatica*, respectively

Source of variation	df	MS	F	P
1. <i>A. jeffersonianum</i> number surviving				
Between treatments	3	2.238	10.833	0.022
Error	4	0.207		
2. <i>R. sylvatica</i> number surviving				
Between treatments	4	10.459	36.316	0.0007
Error	5	0.288		
3. <i>A. maculatum</i> number surviving				
Between treatments	4	5.001	9.195	0.016
Error	5	0.544		
4. <i>A. jeffersonianum</i> larval period				
Between treatments	3	284.46	9.63	0.027
Error	4	29.54		

using a ln (x + 1) transformation (1 was added because ln 0 is undefined when there are no survivors-treatment 5). The ANOVA was highly significant (Table 3) and the only significant treatment effect was from *A. opacum* predation (treatment 5 differs from each of 1–4, a priori contrast $T = -11.9$, d.f. = 5, $P < 0.001$). Similarly, only 3.6 or 6.0% of *A. jeffersonianum* survived in the presence of *A. opacum* while many more (20.2 to 65.5%) survived in each of the other pens. A ln transformation of number surviving was required to meet the homogeneity of variance assumption. The ANOVA was significant (Table 3) and again, the only significant treatment effect was from *A. opacum* predation (treatment 5 differs from each of 2–4, a priori contrast $T = -5.6$, d.f. = 4, $P = 0.005$).

As predicted, the number of surviving *A. maculatum* salamander larvae decreased dramatically in the presence of *A. jeffersonianum* or *A. opacum* larvae as only 0 to 9.5% survived, while 60.7 or 100% survived in the treatment lacking these predators (Tables 2, 3). The reduction of *A. maculatum* survivorship when both predatory salamander larvae were present (treatment 5) was probably due largely to predation by *A. opacum* larvae as an average of only four *A. jeffersonianum* larvae survived per pen (Table 2). The predator-free treatment differed significantly from the others (treatment 1 differs from each of 2–5, a priori contrast $T = 5.3$, d.f. = 5, $P = 0.003$).

Only one *H. chrysoseleis* tadpole survived to metamorphosis. Survivorship in a small cage containing only *H. chrysoseleis* tadpoles showed that these tadpoles can survive well (42/50) in this pond in the absence of other species. Most *A. opacum* larvae were at or near metamorphosis upon addition of *H. chrysoseleis* tadpoles and feeding activity decreases at this time (Walters 1975). One of us (SAC) has directly observed larval *A. jeffersonianum* feeding on *H. chrysoseleis* tadpoles in both natural settings and containers. Hence, the low survival of *H. chrysoseleis* was probably due to strong predatory

pressure by larvae of *A. maculatum* (in all treatments) and/or *A. jeffersonianum* (in treatments 2–5).

In sum, all of the significant treatment effects were due to salamander predation (severe reductions down to 0–10% in survivorship). Thus, the prediction of strong predation by *Ambystoma* larvae was amply supported, especially for *A. opacum*. However, it should be noted that the estimated mean survival of *A. jeffersonianum* and *R. sylvatica* decreased as each potential species interaction was added across treatments. This suggests that some of the species interactions other than salamander predation may have had small, but not statistically detectable, effects on prey survival.

Interspecific competition

No *A. jeffersonianum* response variables were significantly different between treatments 2 and 3, those which tested competitive effects of *R. clamitans* on the prey of *A. jeffersonianum* (SNK $P > 0.05$). Similarly, no *R. sylvatica* response variables were significantly different between treatments 2 and 3, those which tested direct competition of *R. clamitans* on *R. sylvatica* (SNK $P > 0.05$).

If larvae of *A. maculatum* grow beyond a size vulnerable to *A. jeffersonianum* predation, then these two species might compete for resources, especially since ambystomatid larvae are typically generalist predators (Dodson and Dodson 1971; Wilbur 1972; Licht 1975; Walters 1975; Sever and Dineen 1977; Freda 1983; Collins and Holomuzki 1984; Taylor 1984). If *A. jeffersonianum* competition on *A. maculatum* was strong, then *A. maculatum* body mass should have increased markedly from treatments 3 and 4 to treatment 5, where few *A. jeffersonianum* survived. *A. maculatum* body mass increased (Table 2), but not significantly so ($F_{2,3} = 1.69$, $P > 0.30$). However, *A. opacum*, which may also compete with *A. maculatum* (see Stenhouse et al. 1983), was present in treatment 5.

Intraspecific competition

Although increased density did not have a large direct impact on survivorship of the amphibian prey species tested (in the absence of salamander predators larval survival was generally high), density could affect larval growth. Specifically, the number of survivors to metamorphosis could produce density-dependence in mass at metamorphosis or length of larval period.

The relation between *A. jeffersonianum* metamorphic body mass and number surviving to metamorphosis was not statistically significant ($r^2 = 0.37$, $P = 0.11$). However, pen 15 (treatment 2) exhibited a strongly bimodal distribution of body masses (Fig. 2) with 11 individuals considerably larger than the rest. All other pens had a unimodal or bimodal distribution with only 1–3 large individuals. In some local ponds, large *A. jeffersonianum* larvae (> 1.5 g) consumed *R. sylvatica* tadpoles nearly as wide as the salamander's jaws, and exhibited bimodal

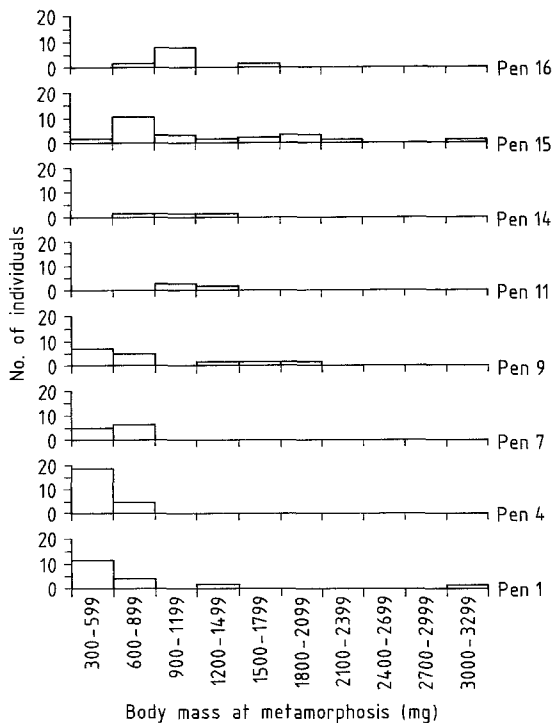


Fig. 2. Metamorphic *A. jeffersonianum* body mass distributions from each experimental pen

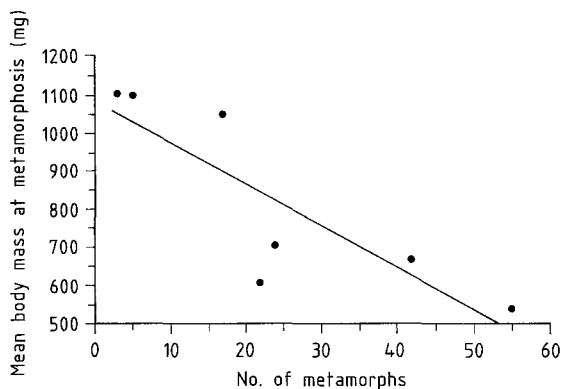


Fig. 3. Regression of metamorphic *A. jeffersonianum* body mass on number of *A. jeffersonianum* metamorphs. The regression equation is: Mean mass at metamorphosis = -11.053 (number of *A. jeffersonianum* metamorphs) + 1088.153 . ($P=0.016$, $r^2=0.72$)

size distributions (Cortwright 1987). We suspect that in pen 15 a high number of *A. jeffersonianum* differed in resource utilization by preying on *R. sylvatica* tadpoles (this pen had only 76 *R. sylvatica* metamorphose). If pen 15 is excluded from the analysis, there is a significant inverse relationship between metamorphic *A. jeffersonianum* body mass and the number surviving (Fig. 3). This suggests that intraspecific density had a strong effect on metamorphic body size.

The duration of larval period for *A. jeffersonianum* larvae differed statistically among treatments (Table 3). In most treatments, *A. jeffersonianum* larvae took 119 to 127 days to complete metamorphosis. However, in treatment 5, where by far the fewest survived, only 101 days were required (Treatment 5 versus each of 2–4,

SNK $P<0.05$). This suggests an appreciable (18–26%) increase in larval period as a result of intraspecific competition at higher densities. Overall, for *A. jeffersonianum* there was a significant difference among treatments in larval period (Table 3, treatments account for 88% of the variance) and also in number surviving (Table 3, treatments account for 89% of the variance). Further, metamorphic mass was related to the number surviving (with pen 15 excluded-Fig. 3). Thus all three response variables were influenced by treatment conditions. However, the drastic reductions in survival should have the greatest influence on adult population size.

A linear regression of *A. maculatum* metamorphic mass on the number of metamorphs was not possible since the values of the independent variable were clumped (few survivors predominated). A oneway ANOVA of *A. maculatum* body mass (without treatment 2 with no survivors) showed that metamorphic mass varied among treatments ($F_{3,4}=13.81$, $P=0.014$). In treatment 1, where *A. maculatum* was the only *Ambystoma* and survived in high numbers, the metamorphic mass was significantly (SNK $P<0.05$) smaller than each of treatments 3–5 by a factor of two (Table 2). This result suggests that intraspecific competition occurred. However, *A. maculatum* larval period did not vary significantly among treatments ($F_{2,3}=3.0$, $P=0.19$) and formed no consistent pattern.

No other analyses of the response variables for *R. sylvatica* or *R. clamitans* (ANOVA) were statistically significant.

Discussion

Naturalness of pens

Before evaluating the major experimental results, it is important to assess the similarity of experimental and natural conditions. The pens used in this study were similar in size to pens or reconstructed habitats used in other studies (e.g. Wilbur 1972; Wilbur et al. 1983; Morin 1986). Doty's (1978) pens were larger, but the water level rapidly drew down in his pond. Larval salamander predators are basically sit and wait foragers (Smith and Petranks 1987; Cortwright pers obs). Thus, 2.5 m² pens should not restrict their behavior during periods of foraging. Since the pens had natural pond bottoms, all foraging options were available to larvae except the shore line, which was available only when the water level dropped during summer. We have observed (night and day observations) both salamander and frog larvae utilizing all parts of pens (leaf litter, mud-water interface, open water, pen walls, patches of duckweed).

Growth of larvae in pens was generally similar to that in LJ pond (Table 4, compare with Table 2). Larval period and metamorphic mass for *A. maculatum* overlapped widely among pens and the pond (LJ has *A. opacum* and *A. jeffersonianum* predators so treatments 2–5 are most applicable). *A. jeffersonianum* larval period and metamorphic mass (only slightly) also overlapped (treatment 5 most applicable – *A. opacum* present in

Table 4. Range of larval period and metamorphic mass for free-living amphibian larvae in LJ pond (1984). A few extreme values for either variable were omitted (ranges are otherwise based on a complete capture of all individuals at a drift fence)

Species	Larval period (d)	Metamorphic mass (mg)
<i>A. opacum</i>	55–75 ^a	1470–2600
<i>A. jeffersonianum</i>	71–194	1090–2000
<i>A. maculatum</i>	61–170	430–1300
<i>R. sylvatica</i>	64–81	425–750

^a from 1 April (same as stocking time in pens)

pond). Perhaps some crowding effects on *A. jeffersonianum* occurred in pens (however, we have sampled ponds with high densities of *A. jeffersonianum* that were targeted for metamorphosis in the range of 400–800 mg).

A. opacum in pens cannot be compared directly with *A. opacum* in the surrounding (LJ) pond. The initial *A. opacum* pen density was an estimate of what larval density would have been if raccoons had not destroyed 75% of *A. opacum* nests the previous autumn. (Many salamanders laid eggs under boards I had previously used around the pond. Raccoon(s) took advantage of this arrangement one night, thus producing atypically high mortality.) Consequently, we used about 3 times the density of *A. opacum* larvae observed in March (this assumed that in the absence of 75% mortality there would have been no major density dependent mortality over winter). As a result, *A. opacum* density was higher in the pens than the pond (Table 4 growth data reflect this). Data from another year, suggest at the very least that pens were not overly restrictive [1983–ME pit \bar{x} = 1694 mg metamorphic mass, range 1320–1960 (a low density pond); Op pit \bar{x} = 1254 mg, range 1150–1430; LJ pond \bar{x} = 1227, range 950–1575].

A direct comparison of *R. sylvatica* data from the pond with that from the pens is not reasonable either, since the remaining *A. opacum* in the pond consumed virtually all *R. sylvatica* (0.15% survived to metamorphosis). *R. sylvatica* only survived in the pens that lacked *A. opacum*, which resulted in much higher densities. A nearby pond that lacked *A. opacum* and had dense *R. sylvatica*, had a range of larval period (66–100 d) and metamorphic mass (170–400 mg) that overlapped widely with the means from the pens.

Taken together, these comparisons suggest that growth of larvae was fairly natural. Further, we have observed that initial growth in pens was similar to free-living populations (it is during this time that vulnerability to predators is greatest). Individuals in pens with high density appeared to show reduced growth in the second half of their larval period; a time when they were less vulnerable to predators.

Experimental results

The stepwise comparison of several factors that may influence community structure of certain larval amphibian

communities confirmed our prediction that predation by salamander larvae is a much stronger influence on prey survival than either predation by invertebrates or competition from other amphibians. In the absence of *A. opacum*, survival of *A. jeffersonianum* larvae ranged from 27.4–48.2%. This exceeds survivorship both for *A. jeffersonianum* in nature (Cortwright 1987, unpub data, \bar{x} = 4.1%, range 0.2–10.8%, n = 15) and for other aquatic amphibian larvae (Petranka and Sih 1986). However, in the presence of *A. opacum*, survivorship of *A. jeffersonianum* was markedly reduced to 4.8%. This is well within the range commonly observed in nature both for *A. jeffersonianum* and other species (Cortwright 1987, unpublished data; Petranka and Sih 1986).

In the absence of *A. opacum*, survival of *R. sylvatica* was 21.5–56.6%. The only natural *R. sylvatica* survival I found this high was 35.1% for the predator-free first season in a newly-enlarged roadway depression (previously too temporary). Survivorship can be in the range of 7.4–19.3% from ponds in which *A. opacum* have been killed overwinter. Survivorship of 0% (or very nearly so) is common in many ponds with either *A. opacum* or *Notophthalmus viridescens* (red-spotted newt) present (Cortwright 1987, unpub data). In the presence of salamander predators, *A. maculatum* survivorship dropped an order of magnitude from 80.4% to 0–8.3%. Again, survivorship in the presence of predators is comparable to that in nature (Cortwright 1987, unpub data, \bar{x} = 0.8%, range 0–3.6%, n = 20). Based on observed and box sample tadpole density estimates, similar arguments can be made for *H. chrysosealis* (it is difficult to get total egg input into ponds and as a result % survivorship is unknown).

In sum, the presence of salamander predators in experimental pens at natural densities resulted in prey survival very similar to that found in nature. The other potential species interactions resulted in species survival much higher than natural. Thus, their relative impact on natural survivorship appears to be very small.

Even though the other factors tested were not statistically significant, there was a tendency for mean survival of both *A. jeffersonianum* and *R. sylvatica* to decrease as each potential interaction was added across treatments. Variance among replicates was high enough to preclude statistical significance. This suggests that some or all of these other species interactions may have small effects which might be statistically detectable with a design featuring more replicates. For example, field observations of *A. jeffersonianum* consuming *R. sylvatica* tadpoles show a definite predator-prey interaction. However, *A. jeffersonianum* is not capable of consuming whole *R. sylvatica* until both species are moderately large. Although *A. jeffersonianum* does prey on *R. sylvatica* in these communities, the rate was very low under the present experimental conditions.

Although only one density of each species was used here, a previous experiment that used various density combinations also indicated that predation was an important mechanism for structuring communities (Cortwright 1987). Larval *A. opacum* overwinter in the pond and their relatively large size in most ponds by the spring

hatching of *A. jeffersonianum* and *R. sylvatica* often results in strong predation. *A. opacum* (if present) and *A. jeffersonianum* larvae drastically reduced larval *A. maculatum* survivorship. *A. opacum* larvae also prey heavily on *A. maculatum* larvae elsewhere (Doty 1978, Stenhouse 1985, Stenhouse et al. 1983). *A. jeffersonianum* hatch about 2–3 weeks before *A. maculatum*, usually grow quickly, and can prey on *A. maculatum* (Wacasey 1961; Walters 1975; Thompson and Gates 1982; Cortwright 1987). Also, *A. jeffersonianum* and *A. maculatum* larvae were large enough to virtually eliminate all *H. chrysosecelis* tadpoles.

Although *H. chrysosecelis* survivorship was extremely low, this does not mean this species cannot coexist with ambystomatid predators. *H. chrysosecelis* has an extended breeding period (maximum length May through early August) and survivorship could improve later in the breeding season in ponds where most *Ambystoma* have already metamorphosed. In addition, the presence of preferred alternate prey or increased habitat structure (Stenhouse 1985) could improve *H. chrysosecelis* survivorship.

Invertebrate predation did not have strong effects in these communities possibly because larval odonate predators were not abundant in the pond (nor in nearby ponds) in 1984 and were therefore not part of the experimental design. A naturally occurring average of 2.5 (2.5 sd) *Platthemis* sp and 0.5 (0.8 sd) *Aeschna constricta* odonates metamorphosed from each pen. However, previous predator experiments showed *A. constricta* to have a relatively small influence on larval amphibian survivorship (Cortwright 1987). *Platthemis* naiads are smaller in size and presumably even less of a threat to larval amphibians. Strong invertebrate predators such as leeches, large odonates (e.g. *Anax junius* and *Tramea lacerata*), and large *Dytiscus* larvae (Coleoptera) (Brockelman 1969; Gill 1978; Caldwell et al. 1980; Formanowicz and Brodie 1982; Brodie and Formanowicz 1983; Smith 1983; Travis et al. 1985) were not present in the study pond (nor in others nearby).

Seale (1980) suggested that massive mortality of some anuran species due to competitive preemption of resources by *Rana catesbeiana* tadpoles occurred in a Missouri larval amphibian community. The addition of 30 large *R. clamitans* tadpoles per pen in treatment 3 addressed this phenomenon in the present study. No effects of *R. clamitans* on *A. jeffersonianum* and *R. sylvatica* (treatment 2 versus 3) were statistically detectable. At the density we used, massive mortality clearly did not occur from preemption of resources.

Intraspecific density effects, resulting in a density-dependent decrease in metamorphic body size, were evident for *A. jeffersonianum* larvae (Fig. 3), and for *A. maculatum* larvae in the absence of *A. opacum* and *A. jeffersonianum*. In other studies, a similar increase in intraspecific (and interspecific) competition occurs among larval anurans (Morin 1981, 1983a; Wilbur et al. 1983) and among salamanders (Wilbur 1972; Morin 1983b) in the absence of predators. However, if density-dependent effects on growth are most important early in the larval period, then reduced early larval growth may pro-

long the period of susceptibility to salamander predators. This could be an interaction of factors where single factor tests might fail (Quinn and Dunham 1983). A negative density effect may be most important for highly vulnerable prey that are typically susceptible to predation for a short time. Morin (1986) suggested no enhanced predation due to negative density effects among *Pseudacris crucifer* tadpoles (to newt predators), a prey species which has low vulnerability and a relatively long susceptible period.

Examples of multiple factors operating in other systems

Predation and competition often interact in natural communities as (reviewed in Sih et al. 1985). For aquatic larval amphibian communities, Wilbur (1984) proposed a model and presented evidence that salamander predation acts first on hatchling tadpole species, and that subsequent competition occurs only if enough prey survive. Increased densities of salamander predators lessen the competitive interactions among tadpole species (Morin 1981, 1983a). Further, predation sometimes may be strong enough to eliminate or reduce tadpole populations to a point where competition is unimportant (Wilbur et al. 1983). Adult newts (*Notophthalmus viridescens dorsalis*) and larval tiger salamanders (*Ambystoma tigrinum*) interact in a complex way. Predation by newts depresses larval tiger salamander survival and mean metamorphic mass while predation by surviving tiger salamander larvae on newt larvae released adult and larval newts from intraspecific competition (Morin 1983b).

Other biotic factors sometimes interact with predation in structuring natural communities. Two examples are (1) immigration abilities by small mammals on to islands can determine which mammal species are present (predators restricted to closer islands – Lomolino 1984) and (2) habitat selection and resource use in desert rodents can influence which species are most vulnerable to predation (Kotler 1984).

Abiotic factors sometimes affect the extent to which predation structures communities. For example, in stream insect communities, Peckarsky (1985) found that siltation can override the effect of predation on community structure. Flood disturbance can alter predator-prey interactions between mosquitofish and topminnows (Meffe 1984) and between fish and larval *Ambystoma texanum* (Petranka and Sih 1986). Winter oxygen stress can eliminate dominant predators, and possibly competitors as well, in lake fish assemblages (Tonn 1985, Tonn and Magnuson 1982).

Abiotic factors have also been studied in relation to competition. Disturbance and habitat duration influenced the structure of a benthic stream community (McAuliffe 1984). One species of caddisfly competitively dominated the community on stable rocks. More equitable species distributions occurred on more disturbed (overturned) rocks. In temporary stream areas, a second species with a shorter generation time dominated the community. Schoener's (1983) review of competition provides several other examples (the most common abiotic factor was variable intensity of drought).

Multiple factors operating in this study

The above studies emphasize that communities are often structured by several interacting factors. Yet, the experiment presented here suggests that one factor, predation by salamander larvae, largely determined structure (relative abundance) in certain larval amphibian communities. Intraspecific competition is enhanced when predators are absent. However, the large reduction in numbers surviving when predators are present is probably more important to population size than is the shift in body size of the few that escape predation. Further, in the absence of predators, no treatments significantly affected growth (metamorphic mass or larval period). This suggests that other factors probably did not enhance predation by depressing prey growth.

However, environmental factors inherent in the experimental design do play a role in determining community structure. For example, winter harshness determines overwintering survival of predatory species. In two nearby small ponds the 1983–84 and 1984–85 overwintering populations of *A. opacum* larvae were eliminated, probably by prolonged ice cover resulting in anoxia (strong hydrogen sulfide odor under the ice—Cortwright pers obs). In subsequent summers, *A. jeffersonianum* and *R. sylvatica* larvae dominated. *A. maculatum* larvae were eliminated (no metamorphs were caught using standard drift fence techniques, e.g. Stenhouse 1985), probably by *A. jeffersonianum* predation. This situation is similar to treatments 2–4. *A. opacum* larvae were again killed during the winter of 1985–6. In addition, in one of the two ponds, most *A. jeffersonianum* embryos were killed by a March 1986 freeze. For the first time since at least 1983, *A. maculatum* successfully produced metamorphs from this pond (Cortwright unpublished data). This second situation is similar to treatment 1. In a mild winter (1982–83), *A. opacum* salamander larvae were the dominant species, and acted as strong predators on *A. jeffersonianum*, *A. maculatum*, and *R. sylvatica* (Cortwright 1987). This third situation is similar to treatment 5. Thus, in these ponds winter harshness strongly affects which alternative community structure is realized.

A second environmental factor was inherent in the experimental design. Since the experiment used a permanent pond, species such as *R. clamitans*, which requires a year long tadpole period, and *A. maculatum*, which metamorphoses in late summer or early fall, were members of the community. In other nearby ponds, the species composition may be largely determined by the shorter pond duration (Cortwright 1987, c.f. Semlitsch 1983).

Thus, our ability to detect which factors are important in structuring a community depends in part on the level at which we study the community. The study presented here compared species interactions operating simultaneously and found vertebrate predation to predominate. Another important factor, winter harshness, operated outside the temporal scope of the experiment but was reflected in the treatments selected (e.g. the presence or absence of *A. jeffersonianum* and/or *A. opacum*). Another important factor affecting the natural commu-

nities modeled is habitat duration, which was held constant across all treatments and was not a factor in this experimental design. Thus, multiple factors do operate in structuring the communities examined here. One of these is the strong species interaction which the experiment documented.

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References

- Alford RA, Wilbur HM (1985) Priority effects in experimental pond communities: competition between *Bufo* and *Rana*. *Ecology* 66:1097–1105
- Brockelman WY (1969) An analysis of density effects and predation in *Bufo americanus* tadpoles. *Ecology* 50:632–644
- Brodie ED Jr, Formanowicz DR Jr (1983) Prey size preference of predators: differential vulnerability of larval anurans. *Herpetologica* 39:67–75
- Caldwell JP, Thorp JH, Jervey JO (1980) Predator-prey relationships among larval dragonflies, salamanders, and frogs. *Oecologia* 46:285–289
- Collins JP, Holomuzki JR (1984) Intraspecific variation in diet within and between trophic morphs in larval tiger salamanders (*Ambystoma tigrinum nebulosum*). *Can J Zool* 62:168–174
- Cortwright SA (1987) Impacts of species interactions and geographical-historical factors on larval amphibian community structure. PhD thesis. Indiana University, Bloomington, p 226
- Cortwright SA (1988) Intraguild predation and competition: an analysis of net growth shifts in larval amphibian prey. *Can J Zool* 66:1813–1821
- Dodson SI, Dodson VE (1971) The diet of *Ambystoma tigrinum* larvae from western Colorado. *Copeia* 1971:614–624
- Doty TL (1978) A study of larval amphibian population dynamics in a Rhode Island vernal pond. PhD thesis. University of Rhode Island, Kingston, p 132
- Formanowicz Dr Jr, Brodie ED Jr (1982) Relative palatabilities of members of a larval amphibian community. *Copeia* 1982:91–97
- Freda J (1983) Diet of larval *Ambystoma maculatum* in New Jersey. *J Herpetol* 17:177–179
- Gill DE (1978) The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecol Monogr* 48:145–166
- Holomuzki JR (1986) Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. *Ecology* 67:737–748
- Kotler BP (1984) Risk of predation and the structure of desert rodent communities. *Ecology* 65:689–701
- Licht LE (1975) Growth and food of larval *Ambystoma gracile* from a lowland population in southwestern British Columbia. *Can J Zool* 53:1716–1722
- Lindman HR (1974) Analysis of variance in complex experimental designs. W.H. Freeman and Co, San Francisco, California, USA
- Lomolino MV (1984) Immigrant selection, predation, and the distributions of *Microtus pennsylvanicus* and *Blarina brevicauda* on islands. *Am Nat* 123:468–483
- McAuliffe JR (1984) Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65:894–908

- Meffe GK (1984) Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology* 65:1525–1534
- Morin PJ (1981) Predatory salamanders reverse the outcome of competition among three species of anurans. *Science* 212:1284–1286
- Morin PJ (1983a) Predation, competition, and the composition of larval anuran guilds. *Ecol Monogr* 53:119–138
- Morin PJ (1983b) Competitive and predatory interactions in natural and experimental populations of *Notophthalmus viridescens dorsalis* and *Ambystoma tigrinum*. *Copeia* 1983:628–639
- Morin PJ (1986) Interactions between intraspecific competition and predation in an amphibian predator-prey system. *Ecology* 67:713–720
- Peckarsky BL (1985) Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? *Can J Zool* 64:1519–1530
- Petranka JW, Sih A (1986) Environmental instability, competition, and density-dependent growth and survivorship of a stream-dwelling salamander. *Ecology* 67:729–736
- Quinn JF, Dunham AE (1983) On hypothesis testing in ecology and evolution. *Am Nat* 122:602–617
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Seale DB (1980) Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. *Ecology* 61:1531–1550
- Semlitsch RD (1983) Structure and dynamics of two breeding populations of the eastern tiger salamander *Ambystoma tigrinum*. *Copeia* 1983:608–616
- Sever DM, Dincen CF (1977) Reproductive ecology of the tiger salamander, *Ambystoma tigrinum*, in northern Indiana. *Proc Indiana Acad Sci* 87:189–203
- Sih A, Crowley P, McPeck M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. *Ann Rev Ecol Syst* 16:269–311
- Smith CK, Petranka JW (1987) Prey size-distributions and size-specific foraging success of *Ambystoma* larvae. *Oecologia* 71:239–244
- Smith DC (1983) Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology* 64:501–510
- Stenhouse SL (1985) Interdem variation in predation on salamander larvae. *Ecology* 66:1706–1717
- Stenhouse SL, Hairston NG, Cobey AE (1983) Predation and competition in *Ambystoma* larvae: field and laboratory experiments. *J Herpetol* 17:210–221
- Taylor J (1984) Comparative evidence for competition between the salamanders *Ambystoma gracile* and *Taricha granulosa*. *Copeia* 1984:672–683
- Thompson EL, Gates JE (1982) Breeding pool segregation by the mole salamanders, *Ambystoma jeffersonianum* and *Ambystoma maculatum*, in a region of sympatry. *Oikos* 38:273–279
- Tonn WM (1985) Density compensation in *Umbra-Perca* fish assemblages of northern Wisconsin lakes. *Ecology* 66:415–429
- Tonn WM, Magnuson JJ (1982) Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63:1149–1166
- Travis J, Keen WH, Juliana J (1985) The effects of multiple factors on viability selection in *Hyla gratiosa* tadpoles. *Evolution* 39:1087–1099
- Wacasey JW (1961) An ecological study of two sympatric species of salamanders, *Ambystoma maculatum* and *Ambystoma jeffersonianum*, in southern Michigan. PhD thesis. Michigan State University, East Lansing, p 117
- Walters B (1975) Studies of interspecific predation within an amphibian community. *J Herpetol* 9:267–279
- Wilbur HM (1972) Competition, predation, and the structure of the *Ambystoma-Rana sylvatica* community. *Ecology* 53:3–21
- Wilbur HM (1984) Complex life cycles and community organization in amphibians. In: Price PW, Slobodchikoff CN, Gaud WS (eds). *A New Ecology*. John Wiley and Sons, New York, pp 195–224
- Wilbur HM, Alford RA (1985) Priority effects in experimental pond communities: responses of *Hyla* to *Bufo* and *Rana*. *Ecology* 66:1106–1114
- Wilbur HM, Morin PJ, Harris RN (1983) Salamander predation and the structure of experimental communities: anuran responses. *Ecology* 64:1423–1429