

## COMMUNITY ECOLOGY IN STREAMS: EFFECTS OF TWO SPECIES OF PREDATORY SALAMANDERS ON A PREY SPECIES OF SALAMANDER

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**ABSTRACT:** I investigated how density affected the growth and survival of two predatory species (*Gyrinophilus porphyriticus*, *Desmognathus quadramaculatus*) and one prey species (*Eurycea wilderae*) of larval salamanders by manipulating the density of each species in stream enclosures. Survival and growth of *E. wilderae* was independent of density, suggesting a lack of competition. Growth also was not affected by the presence of predator species. However, survival of *E. wilderae* was significantly reduced when exposed to one or both predators. Larvae of *G. porphyriticus* were more effective predators than larval *D. quadramaculatus*, and larvae of *G. porphyriticus* exposed to high prey density grew more than those exposed to low prey density. Prey density had no effect on prey survival. Predator effects on prey survival were additive, indicating neither a mutualistic nor a competitive interaction between the two predators.

**Key words:** Competition; Predation; Mutualism; *Desmognathus quadramaculatus*; *Eurycea wilderae*; *Gyrinophilus porphyriticus*

PREDATORS have significant impacts on the population structure of their prey and the interaction of prey within communities (Ebenman and Persson, 1988; Kerfoot and Sih, 1987). For example, age-specific predation can result in a change in age at maturity of prey (Charlesworth, 1980; Reznick et al., 1990), and predators can enhance species diversity by preying upon superior competitors (Paine, 1966). The interactions between predation and competition are complex and can include both direct and indirect effects (e.g., Fauth and Resetarits, 1991; Martin et al., 1989; Resetarits, 1991; Soluk, 1993; Soluk and Collins, 1988; Van Buskirk, 1988; Werner, 1991; Wissinger and McGrady, 1993).

Experimental studies on amphibians have been instrumental in discovering important interactions between competition and predation. For example, prey species that are competitors in isolation can become mutualists when a predator is added to the system (Wilbur, 1988). In temporary pond communities of tadpoles, the effect of predation can be positive in that the "thinning" of the population releases tad-

poles from competition and allows some to escape (by metamorphosing) from a pond before it dries (Wilbur, 1987, 1988; Wilbur and Fauth, 1990).

However, the effects of predation are typically considered from the standpoint of one species of predator. Because predators can interact, the effects of simultaneous interaction of more than one predator on prey populations may be more complex than the effects of a single predator (Fauth and Resetarits, 1991; Resetarits, 1991; Wilbur and Fauth, 1990).

The purpose of my study was to examine how predator and prey densities affect the interactions of two predatory stream salamanders with their salamander prey. Larval *Gyrinophilus porphyriticus* and *Desmognathus quadramaculatus* prey on invertebrates and salamanders (Beachy, 1993; Bruce, 1979; Davic, 1991; Hairston, 1986), including larval *Eurycea wilderae*, which is the most common salamander in southern Appalachian streams (Bruce, 1985). Larvae of *E. wilderae* feed on invertebrates. These salamanders are members of the family Plethodontidae and form part of the rich salamander fauna of southern Appalachian streams. In headwater streams where fishes are absent, these sal-

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amanders are top predators. I asked these questions: (1) are the effects of predation dependent on prey density, and (2) is the effect of one predator on its prey dependent on the presence of the other predator?

#### MATERIALS AND METHODS

The experiment was carried out July–August 1992 in Mill Branch and Cunningham Creek, Watershed 32 (elevation 915 m) of the Coweeta Hydrologic Laboratory of the United States Department of Agriculture, Forest Service, located in the Nantahala Mountains of North Carolina. These are first-order streams with no fishes. In addition to the three species used in this study, larval *Pseudotriton ruber*, *Desmognathus monticola*, and *D. ochrophaeus* are found in these streams.

Larvae were collected from field sites and anesthetized by immersion in a 0.1% solution of tricane methylsulfonate (MS-222). The snout–vent length (SVL) of each larva was measured to the nearest 0.1 mm, before reviving the larvae in stream water. In addition, the predators were weighed to the nearest 0.01 g.

I collected larval *E. wilderae* (480) and *D. quadramaculatus* (16) from Mill Branch. Larvae of *G. porphyriticus* (16) were collected from Mill Branch and the nearby Wayah Bald area.

#### Cages

Thirty-two cages and lids (1.0 × 0.5 × 0.3 m, LWH) were constructed using PVC pipe and nylon window screening (mesh size = 1.1 × 1.3 mm). The PVC pipe provided the framework, and the screening was wrapped around the frame and secured, with steel wire and rubber silicone sealant around the top margin of the frame.

The cages were placed in four replicate blocks in Mill Branch and Cunningham Creek. Each cage bottom was lined with the sand, gravel, and small and large rocks that occupied the stream where each cage was placed. The screening allowed water and small invertebrates to flow in and out of the cage.

The litter and invertebrates at each cage position were collected, placed in a container, thoroughly mixed, and divided into

32 aliquots that each weighed 143 g. Each cage received one aliquot of litter and invertebrates. Because the screening allowed colonization by only small invertebrates, the cages may have contained an unrealistic ratio of small to large invertebrates compared to that observed in uncaged streams.

Cages within blocks were placed in close association given the spatial limits of the stream (Fig. 1). Three blocks were placed on Mill Branch and one block on Cunningham Creek. The block design was used to account for variation induced by stream position and variation in predator size (see below).

#### Experimental Design

The experiment was a full factorial, randomized complete block design using three species at two densities each (10 and 20 for prey, 0 and 1 for predators). There were four replicates each for a total of 32 experimental units ( $2 \times 2 \times 2 \times 4 = 32$ ). One quarter of the cages contained no predators while one-half of the cages contained one individual of either *G. porphyriticus* or *D. quadramaculatus*. The remaining cages contained both predators.

Larvae of *G. porphyriticus* that were collected ranged in size from 32.2–60.5 mm SVL. The larvae were sorted into four size groups for introduction into each of the blocks. This resulted in non-overlapping size distributions of larval *G. porphyriticus* between blocks. Within a block, larvae were assigned randomly to treatment.

Larval *D. quadramaculatus* that I collected for this experiment ranged from 32.2–43.7 mm SVL. As above, larvae were sorted into four non-overlapping size groups for introduction into each of the blocks. Because the smallest individuals of *G. porphyriticus* were paired with the smallest *D. quadramaculatus* in the same block (and largest with largest, etc.), the possibility of the predators eating one another was reduced.

To ensure that initial prey sizes were similar, prey were ranked by size and assigned to 10 groups of 48 larvae on that basis. Beginning with the smallest group,

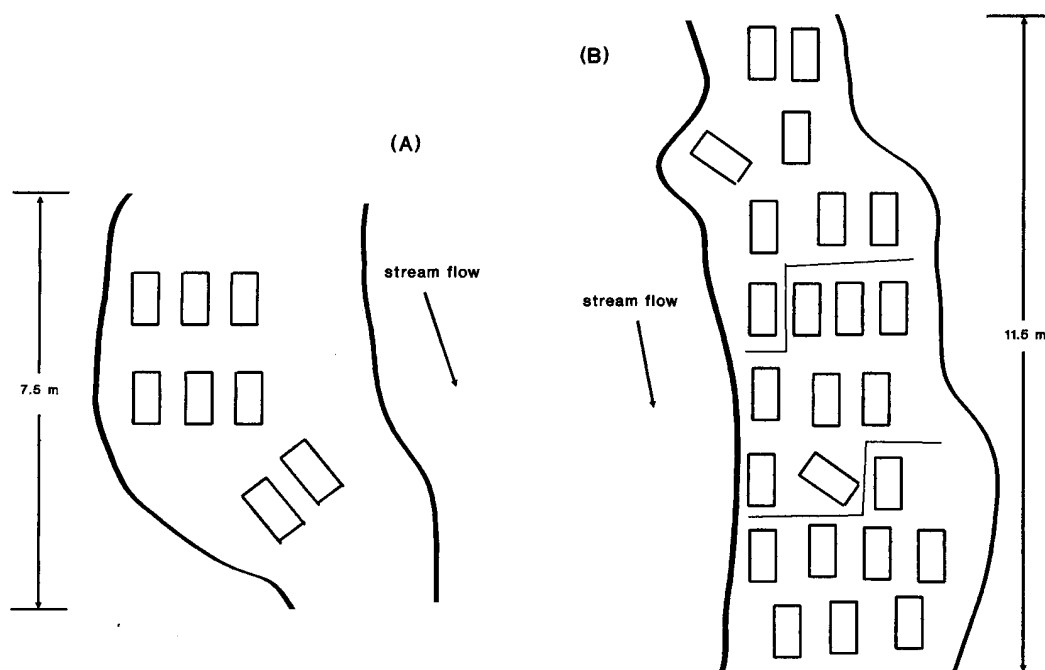


FIG. 1.—Schematic diagram of placement of cages in (A) Cunningham Creek and (B) Mill Branch. Placement of cages is irregular due to the nature of the stream: e.g., fallen logs, immovable boulders, ephemeral margins. The lines between cages in (B) indicate the blocks. Each cage is  $1.0 \times 0.5$  m (L  $\times$  W).

I randomly assigned one larva to each low density cage and two larvae to each high density cage. I repeated this procedure with each size group.

On 31 July 1992, I began the experiment by adding all larvae to their respective cages. Lids were placed on cages, and the borders between lids and cages were sealed with silicone rubber sealant. The experiment was conducted for 30 days. On 31 August and 1 September, I carefully searched each cage and removed all surviving larvae. Larvae were returned to the laboratory, anesthetized, and measured to the nearest 0.1 mm. In addition to SVL, I measured mass of predators to the nearest 0.01 g.

#### *Statistical Analyses*

Statistical analyses of final size (for prey), growth (for predators), and survival (for prey) were performed using SYSTAT, version 3.2 (Wilkinson, 1989). Wilks' lambda was used as the multivariate test statistic (Green, 1978), and the significance criterion

was set at  $\alpha = 0.05$ . Survival data were arcsine transformed (Sokal and Rohlf, 1981), and growth data met the assumptions of the analysis of variance. Where applicable, SYSTAT uses type III mean squares for hypothesis tests.

I analyzed final size (in SVL) and survival of prey using a multivariate analysis of variance (MANOVA) testing the effects of density of each species in a three-way MANOVA. Whenever the multivariate analyses were significant, I performed univariate analyses on each variable (final size and survival). Initial analyses indicated that block effects were not significant, and they were not included in further analyses. The model statement in this analysis included the three main effects and the four interaction terms.

Growth data for each species of predator were analyzed with separate MANOVA's testing the effects of prey density and density of the other predator on two aspects of growth: change in SVL (mm) and change in mass (g). Initial analyses indicated that

TABLE 1.—Treatment means (and 1 SE) for the size and survival responses of prey (*Eurycea wilderae*) and growth responses of the predators (*Gyrinophilus porphyriticus* and *Desmognathus quadramaculatus*).

Initial density			Prey		Predators	
<i>Eurycea wilderae</i>	<i>Gyrinophilus porphyriticus</i>	<i>Desmognathus quadramaculatus</i>	Final size (mm SVL)	% survival	Change in SVL (mm)	Change in mass (g)
10	0	0	16.71 (0.38)	90.00 (4.08)	—	—
20	0	0	17.13 (0.26)	71.25 (10.28)	—	—
10	1	0	16.59 (0.08)	25.00 (12.58)	0.73 (0.43)	0.02 (0.044)
20	1	0	17.38 (0.34)	27.50 (14.79)	2.13 (0.47)	0.16 (0.173)
10	0	1	16.76 (0.37)	55.00 (11.90)	0.10 (0.92)	−0.07 (0.046)
20	0	1	17.18 (0.22)	47.50 (11.64)	2.45 (0.15)	0.10 (0.090)
10	1	1	16.78 (0.15)	15.00 (8.66)	1.68 (0.75) <sup>a</sup>	0.15 (0.060) <sup>a</sup>
					−0.05 (0.65) <sup>b</sup>	−0.11 (0.092) <sup>b</sup>
20	1	1	16.83 (0.51)	26.25 (6.88)	3.40 (0.79) <sup>a</sup>	0.29 (0.110) <sup>a</sup>
					1.00 (1.39) <sup>b</sup>	−0.04 (0.210) <sup>b</sup>

<sup>a</sup> Response of *G. porphyriticus*.<sup>b</sup> Response of *D. quadramaculatus*.

the block effects were not significant, and they were not included in further analyses. The model statement in these analyses included two main effects and the interaction between them. As above, I performed univariate analyses on each variable only when a significant multivariate result was found. This procedure yields conservative hypothesis tests (Morrison, 1976).

## RESULTS

### The Prey

The responses of prey to the treatments are summarized in Table 1. Initial density did not affect growth or survival (Table 2).

Both species of predator significantly reduced the survival of prey (Table 2). However, effects on final size of prey were not

detected. Both predators were equally effective in preying upon larval *E. wilderae* at either high or low density (non-significant density × predator interactions: Table 2).

The interaction of the two predators was not significant. A significant interaction could result from mutualism (a more than additive result) or competition (a less than additive result) between the predators (Wilbur and Fauth, 1990). The non-significant result suggests the hypothesis that neither process occurred between the predators.

### The Predators

Because survival of predators was nearly 100%, the most informative assay was growth of individuals.

TABLE 2.—Summary of multivariate analysis of final size and survival of larval *Eurycea wilderae*. Univariate statistics are only presented for significant multivariate results. Degrees of freedom are 2,19 and 1,20 for multivariate and univariate statistics, respectively.

Treatment	Multivariate statistic			Univariate statistic	
	Wilks' $\lambda$	F	P	Final size (MS × 10 <sup>−2</sup> )	Survival (MS × 10 <sup>−2</sup> )
<i>Eurycea</i>					
density	0.880	1.299	0.291		
<i>Gyrinophilus</i>	0.405	13.944	<0.001	1.61	3.375***
<i>Desmognathus</i>	0.680	4.478	0.024	3.07	1.006*
<i>Eurycea</i> density × <i>Gyrinophilus</i>	0.963	0.398	0.672		
<i>Eurycea</i> density × <i>Desmognathus</i>	0.974	0.255	0.773		
<i>Gyrinophilus</i> × <i>Desmognathus</i>	0.851	1.669	0.211		
Three-way term	0.890	1.177	0.332		
Residual				43.11	0.172

\* P &lt; 0.05, \*\*\* P &lt; 0.001.

TABLE 3.—Summary of multivariate analysis of change in size (SVL and mass) of larval *Gyrinophilus porphyriticus*. Univariate statistics are only presented for significant multivariate results. Degrees of freedom are 2,9 and 1,10 for multivariate and univariate statistics, respectively. Univariate statistics report mean squares.

Treatment	Multivariate statistic			Univariate statistic	
	Wilks' $\lambda$	F	P	Change in SVL	Change in mass
<i>Eurycea</i> density	0.521	4.135	0.053	8.371*	0.068
<i>Desmognathus</i>	0.644	2.490	0.138		
<i>Eurycea</i> density $\times$ <i>Desmognathus</i>	0.091	0.055	0.819		
Residual				1.644	0.038

\*  $P < 0.05$ .

**Responses of *Gyrinophilus*.**—The growth responses of larval *G. porphyriticus* are summarized in Table 1. MANOVA indicated a strong, but non-significant, effect of density of prey. Given the low  $P$ -value in the MANOVA, I have included the univariate results for this effect (Table 3). The univariate result for SVL suggests that, given a longer experimental period, larval *G. porphyriticus* could have significantly increased their growth by preying heavily upon larval *E. wilderae* at high densities.

The presence/absence of larval *D. quadramaculatus* had no effect on the growth of larval *G. porphyriticus*, indicating that no interspecific interaction was present, at either density (Table 3).

**Responses of *Desmognathus*.**—The growth responses of larval *D. quadramaculatus* are summarized in Table 1. In contrast to the trend indicated for *G. porphyriticus*, density of prey had no influence on growth of larval *D. quadramaculatus* (Table 4).

The presence/absence of *G. porphyriticus* had no effect on the growth of larval *D. quadramaculatus*, again indicating that no interspecific interaction was present, at either density (Table 4). This result corroborates the non-significant effect of interaction between predators on final size and survival of prey (Table 2).

**Comparison of predators.**—I conducted an ANOVA comparing the survival of *E. wilderae* in the three different predator treatments to evaluate the relative predatory abilities of *G. porphyriticus* and *D. quadramaculatus*. The analysis included

density of *E. wilderae*, predator treatment, their interaction, and the block effect.

Density and its interaction with predator treatment had no effect on survival of prey (Table 5). The block contributed significantly to this analysis (Table 5), possibly indicating the effects of different sizes of predators among blocks. The prey in the block containing the largest predators had the lowest survival, and the prey in the block containing the smallest predators had the highest survival.

The predator treatment result (Table 5) shows that there were significant differences in abilities of the predators to reduce the survival of the prey. A posteriori multiple  $F$  contrasts indicated that *G. porphyriticus* was a better predator of larval salamanders than was *D. quadramaculatus* (Fig. 2).

## DISCUSSION

The lack of a density effect on growth and survival of the prey, coupled with the non-significant interaction among the predators, suggests that competition and mutualism among larval salamanders may not be viable mechanisms of population regulation in this community. This result

TABLE 4.—Summary of multivariate analysis of change in size (SVL and mass) of larval *Desmognathus quadramaculatus*.

Treatment	Wilks' $\lambda$	df	F	P
<i>Eurycea</i> density	0.749	2,8	1.340	0.315
<i>Gyrinophilus</i>	0.939	2,8	0.262	0.776
<i>Eurycea</i> density $\times$ <i>Gyrinophilus</i>	0.959	2,8	0.180	0.838

TABLE 5.—Results of ANOVA comparing survival of larval *Eurycea wilderae* in the three predator treatments.

Source	df	MS	F	P
<i>Eurycea</i> density	1	80.264	0.524	0.480
Predator treatment	2	1128.128	7.366	0.006
<i>Eurycea</i> density × predator treatment	2	152.037	0.993	0.394
Block	3	1026.533	6.702	0.004
Residual	15	153.157		

is consistent with experiments that were conducted on longer time scales (2–10 mo), and at higher and lower densities (Beachy, 1992, 1993).

In this experiment, I used densities of larval salamanders that were within the range of naturally occurring densities to gain insight to processes that occur in real communities of plethodontid larvae. The density of prey in this study was either 20 or 40 individuals/m<sup>2</sup>, whereas larval *E. wilderae* can be found at densities up to 80 individuals/m<sup>2</sup>. The highest density of either predator that I have found is eight individuals/m<sup>2</sup>; I used densities of two and four individuals/m<sup>2</sup>.

On the other hand, predation may play a significant role in this community. The predators in this experiment had a straightforward effect on the prey: they ate them. No injured salamanders were found, corroborating the suggested lack of competition and indicating that the predators' primary effect on the prey was consumption, not injury.

The performance of the predators in this experiment agrees well with earlier natural history observations that *G. porphyriticus* is a predatory specialist on salamanders. In gut analyses of larval *G. porphyriticus*, Bruce (1979) found an average of 9–15% of gut contents were sal-

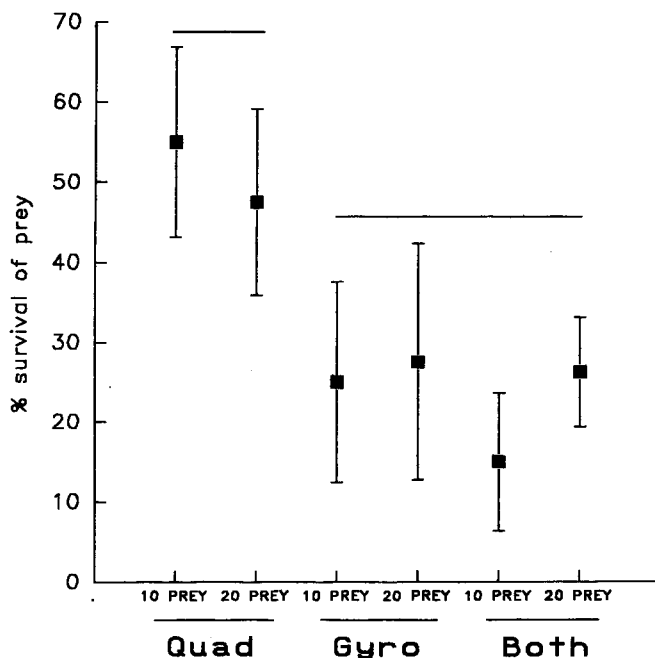


FIG. 2.—Mean survival ( $\pm 1$  SE) of larval *Eurycea wilderae* in the presence of larger predatory larval salamanders. Horizontal bars indicate means not significantly different at  $P < 0.0083$  using multiple  $F$  contrasts.

amanders. Davic (1991) found no salamanders in the guts of larval *D. quadramaculatus*. Guts of adult *G. porphyriticus* also contained a higher proportion of salamanders than the guts of adult *D. quadramaculatus* (Bruce, 1979; Davic, 1991). Formanowicz and Brodie (1993) observed that adults of *G. porphyriticus* are more efficient at capturing salamanders than adults of *D. quadramaculatus*. Because both predators are gape-and-suck feeders as larvae, this suggests that the higher propensity of *G. porphyriticus* to eat salamanders is associated with something other than the differences in adult feeding morphology (Lombard and Wake, 1986).

In addition, other long-term (2–10 mo) experiments that used larval *D. quadramaculatus* as predator have failed to find differences in growth of this predator regardless of predator or prey density (Beachy, 1992, 1993). Thus, the trend suggested for increased growth of larval *G. porphyriticus* in response to high prey density (Table 3) in this 30 day experiment is noteworthy.

The primary purpose of this experiment was to gain insights into the interactions of the two predators. The two could have been competitors if their foraging success (as indicated by a decrease in prey survival or an increase in growth of predators) were decreased when together. The two could have been mutualists if their foraging success were increased when together. Such a result could be obtained if the two predators together cause behavior modifications of prey that expose the prey to high predation risk. The non-significant interaction of the two species on survival of prey suggests that larval *G. porphyriticus* and *D. quadramaculatus* may be neither competitors nor mutualists when acting as predators together.

In summary, the salamander densities were within the range of naturally observed densities. Effects of variation in prey density were not found among the prey and were also not observed among the predators. Predators had significant influences on survival, but not growth, of prey. Further, the predators did not appear to interact. The effect of predators in this

system is simple and suggests the hypothesis that the primary interaction among stream-dwelling salamanders is direct removal of prey salamanders by those salamanders that can have larger body sizes via longer larval periods.

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