Guild Structure in Streamside Salamander Communities: A Test for Interactions among Larval Plethodontid Salamanders

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Studies on salamanders of the family Plethodontidae have been instrumental in providing experiment-based research in community theory. For example, in streamside salamanders of the genus *Desmognathus*, there is a correlation between adult body size and habitat use. Large congeners use more aquatic habitats while smaller species are more terrestrial.

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TABLE 1. Summary of responses ($\bar{x} \pm 1$ SE) of larval *Eurycea wilderae* and first-year larval *Desmognathus quadramaculatus*.

Species	Treatment	Growth (mm SVL)	% survival
E. wilderae	1	1.44 ± 0.37	73.09 ± 3.93
E. wilderae	3	1.35 ± 0.61	82.14 ± 7.32
E. wilderae	4	0.93 ± 0.72	10.33 ± 7.26
D. quadramaculatus	2	1.64 ± 0.47	89.67 ± 6.36
D. quadramaculatus	3	1.34 ± 0.17	98.30 ± 2.62
D. quadramaculatus	5	1.05 ± 0.59	14.64 ± 7.37

This assemblage of salamanders was originally interpreted as the result of exploitative competition and niche partitioning (Hairston, 1949). However, experimental manipulation (Hairston, 1986) showed that, in the southern Appalachians, the important interaction was predation. Adults of the largest species, *Desmognathus quadramaculatus*, prey upon the smaller members of the genus, as does the second largest species, *D. monticola* (Hairston, 1986). The result is a community of streamside species that exhibits a correlation between adult body size and habitat use (Hairston, 1987; Roudebush and Taylor, 1987).

The ecology of larval plethodontids has been relatively ignored. However, density-dependent interactions occur often among pond-dwelling salamander larvae (e.g., Scott, 1990), and predation is common among salamanders in pond communities (Morin, 1983). Premetamorphic mortality is an important regulating mechanism in pond-breeding amphibians (Wilbur, 1980) but is an uninvestigated aspect of streamside plethodontid ecology. As noted by Hairston (1987, p. 148), "there have been good analyses of the population ecology of stream-living larvae, . . . and we should not ignore the possibility that interactions among larvae may be crucial to a complete understanding of the community."

I designed an experiment to identify the interactions (predation, competition, both, or neither) among larvae of the two most common species in the southern Appalachian Mountains: *Desmognathus quadramaculatus* (subfamily Desmognathinae) and *Eurycea wilderae* (subfamily Plethodontinae, tribe Hemidactyliini). Both species can occur in high densities (10–80 larvae/m² for *E. wilderae*, 0.25–8 larvae/m² for *D. quadramaculatus* [Beachy, unpubl. data]) and have extended larval periods (12–15 mo for *E. wilderae* [Beachy, unpubl. data], 36–48 mo for *D. quadramaculatus* [Bruce, 1988]). These species differ in mean body size and have distinct size classes: larval *D. quadramaculatus* are larger than larval *E. wilderae*.

The collections and experiment were conducted May–October 1990 in Mill Branch, Watershed 31 (elevation 915 m) of the Coweeta Hydrologic Laboratory of the United States Department of Agriculture, located in the Nantahala Mountains of Macon County, North Carolina. Mill Branch is a first-order stream lacking fish.

Larval salamanders were collected by dipnet and taken to the Highlands Biological Station. During collection and transport, different species and size classes were kept in separate containers. Animals were anesthetized by immersion in a 0.1% solution of tricaine methane sulfonate (MS-222), measured (with calipers) for snout–vent length (SVL) to the nearest 0.1 mm, and revived in stream water. All animals

were returned to Mill Branch following the termination of experiments.

Experimental densities of salamander larvae were greater than those under natural conditions. The maximum density used (four larvae per cage) was approximately twice the highest density of *E. wilderae* that I observed at Mill Branch.

High densities were used in this experiment because this study was designed not to simulate natural conditions, but to identify the interactions that are possible among these larvae. If the null hypothesis of no interaction (i.e., competition or predation) was not rejected at high densities, then it was considered likely that these interactions do not operate in natural populations of larvae.

Five treatments were used to test for the presence of competition and predation between larval *E. wilderae* and larval *D. quadramaculatus*:

(1) single species: *E. wilderae* (4 individuals);
(2) single species: first-year *D. quadramaculatus* (4 individuals);
(3) two species: *E. wilderae* (2 individuals) and first-year *D. quadramaculatus* (2 individuals);
(4) two species: *E. wilderae* (2 individuals) and large *D. quadramaculatus* (1 individual);
(5) single species: first-year *D. quadramaculatus* (2 individuals) and large *D. quadramaculatus* (1 individual).

The different densities assigned among treatments reflect size differences between the species. This is a variation of a substitutive design (i.e., biomass is kept constant across treatments). For *E. wilderae* at Mill Branch, there is only one size class of larvae in summer (Beachy, unpubl. data), while *D. quadramaculatus* is represented by four size classes (Bruce, 1988).

I used different sizes of larvae in this experiment because interference competition in carnivorous amphibians often occurs among similarly-sized animals, while large size differences usually result in predator-prey interactions (e.g., Morin, 1983). The size ranges of animals used in this experiment were first-year *D. quadramaculatus* = 18–24 mm SVL, large *D. quadramaculatus* = 30–45 mm SVL, and *E. wilderae* = 14–18 mm SVL. Twelve blocks were established, for a total of 60 cages and 216 animals.

Larvae were assigned randomly to cylindrical cages (15 × 15 cm) covered with nylon window screening (mesh = 1.1 × 1.3 mm). Cages were lined with a natural composite of sand, silt, and gravel. A large rock (minimum size = 10 × 10 cm) and 100 g of leaf litter (containing prey and additional cover objects) collected from the stream margin were also included. Cages were then placed in the stream in replicate blocks. Each block was placed in a cell of a hexagonal

array in the stream. Each hexagon was 1 m in diameter, and the center of each hexagon was 1 m from the center of all adjacent hexagons. Treatments were randomly assigned to a position within a block. The cages were removed from the stream after 50 d and survival and growth (in mm SVL) were recorded. Mean growth and percent survival of *E. wilderae* and first-year *D. quadramaculatus* in each cage were used for analysis.

Two comparisons were made: among mean growth and percent survival of *E. wilderae* for treatments (1), (3), and (4); and among mean growth and percent survival of first-year *D. quadramaculatus* for treatments (2), (3), and (5). The percent survival data were arcsine-transformed (Sokal and Rohlf, 1981). The analysis was a randomized complete-block ANOVA (α = 0.05) with the block effect accounting for variation in stream position. Because no significant block effects were detected by ANOVA, I performed three pairwise *F*-tests on survival and growth of each species. Because three hypothesis tests were performed on each data set, I used the Bonferroni method to set α = 0.0167 (Sokal and Rohlf, 1981; Day and Quinn, 1989).

Growth differences were interpreted to represent competitive interactions, whereas differences in survival served as indication of predator-prey interactions. Differences in both variables suggest competition or a complex combination of competition and predation.

Bartlett's test indicated that the variances of data sets were homogeneous, permitting parametric analysis (Sokal and Rohlf, 1981). The responses of larval *E. wilderae* and first-year larval *D. quadramaculatus* are summarized in Table 1.

Growth.—No differences in growth were observed for larval *E. wilderae* in any of the treatments. The same was found for the small *D. quadramaculatus* (Table 2).

Survival.—Significant differences in survival among treatments were found for both *E. wilderae* and small *D. quadramaculatus* (Table 2). A posteriori contrasts indicated that survival of *E. wilderae* was unaffected by the presence of first-year *D. quadramaculatus* but was significantly reduced in the presence of large *D. quadramaculatus*, suggesting that predation may occur and is size-specific (Table 2). The survivorship of first-year *D. quadramaculatus* was also unaffected by the presence of *E. wilderae* but was significantly reduced by larger *D. quadramaculatus* (Table 2).

The results of this experiment suggest that cannibalism of first-year *D. quadramaculatus* by large *D. quadramaculatus* is as frequent as predation on *E. wilderae* by large *D. quadramaculatus*. Furthermore, competitive interactions were not observed, even given that the densities of larvae in the experiments were higher than maximum natural densities. These results suggest that the most important interaction that occurs among plethodontid larvae is predation of small individuals by larger individuals.

Ecologists no longer believe that a single factor, such as competition or predation, controls the development and regulation of communities. There is an increasing appreciation that the factors governing community structure vary temporally (Wiens, 1977) and spatially (Mittlebach, 1988).

The purpose of this experiment was to examine the relative effects of predation and competition in two common cooccurring species of larval plethodontid

TABLE 2. Results of pairwise *F*-tests between treatment groups after ANOVA. Refer to Table 1 for treatment group labels. Data for percent survival were arcsine transformed. Zero survival resulted in empty cells in the growth analyses. The Bonferonni method was used to set α = 0.0167.

Comparison	df	MS	F	P
Growth				
Eurycea wilderae				
1 vs. 3	1,24	0.042	0.015	0.902
1 vs. 4	1,24	0.748	0.276	0.604
3 vs. 4	1,24	0.503	0.186	0.670
First-year *Desmognathus quadramaculatus*				
2 vs. 3	1,26	0.555	0.355	0.556
2 vs. 5	1,26	1.227	0.785	0.384
3 vs. 5	1,26	0.228	0.184	0.672
Survival				
Eurycea wilderae				
1 vs. 3	1,33	234.375	0.307	0.583
1 vs. 4	1,33	9600.000	12.590	0.001
3 vs. 4	1,33	12,834.375	16.832	<0.001
First-year *Desmognathus quadramaculatus*				
2 vs. 3	1,33	759.375	1.134	0.295
2 vs. 5	1,33	14,259.375	21.286	<0.001
3 vs. 5	1,33	21,600.000	32.244	<0.001

salamanders. Competition and predation have been documented in pond-dwelling guilds of larval salamanders (Wilbur, 1972; Morin, 1983; Stenhouse et al., 1983; Stenhouse, 1985; Walls and Jaeger, 1987), but little is known about the interactions among stream-dwelling larval salamanders. Bruce (1979) found larval stream salamanders in the stomachs of the larval plethodontid, *Gyrinophilus porphyriticus*. Resetarits (1991) found that larval *Eurycea cirrigera* avoided larvae of *G. porphyriticus*. This anti-predator behavior resulted in reduced growth rates compared to *E. cirrigera* that were not exposed to predation.

Competition was not detected given the confines of the experimental design, suggesting that competition among larvae may not be an effective mechanism of population regulation. Predation may be an important interaction among larval plethodontids, and may serve a role in population regulation among these stream-dwelling salamanders.

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