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Effect of Predatory Larval *Desmognathus quadramaculatus* on Growth, Survival, and Metamorphosis of Larval *Eurycea wilderae*

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I examined whether predation affects larval life-history parameters of the stream-dwelling salamander *Eurycea wilderae*. In cages placed in a North Carolina stream, I exposed groups of 10 larval *E. wilderae* to 0, 1, or 3 predatory larval *Desmognathus quadramaculatus*. Growth and survival of *E. wilderae* were recorded every two months from August 1991 to June 1992, and metamorphic stage was recorded for all surviving prey at the end of the experiment. Survival rates did not differ among treatments during any of the two-month intervals, but larvae in zero-predator treatments experienced higher survival over the duration of the experiment. Risk of predation caused significant variation in growth rates during the last four months. Larvae in three-predator treatments grew the fastest from February to April but grew more slowly than the zero-predator and one-predator treatments from April to June. Given that many larval amphibians utilize temporary, high productivity habitats, current models predict that variation in growth rate and/or mortality risk should result in variation in metamorphic timing and/or size. However, larval *E. wilderae* that experienced different growth rates and predation risk metamorphosed at the same time. Because southern Appalachian mountain streams are relatively permanent and have low productivity, there may be little or no advantage of maintaining plasticity in time or size at metamorphosis.

THE aquatic larval stage of amphibians has been considered as an adaptation to transient habitats (e.g., temporary ponds) that provide high growth opportunities (Wilbur and Collins, 1973; Wassersug, 1974). Because amphibian larvae should delay metamorphosis when exposed to an opportunity for growth, variation in larval growth rates can generate variation in size and time at metamorphosis (Wilbur and Collins, 1973; Alford and Harris, 1988). In addition, variation in mortality risk relative to growth opportunity may result in variation in metamorphic size (Werner, 1986). Because size and time of metamorphosis are linked to size and time of maturation in some frogs (Smith, 1987) and salamanders (Semlitsch et al., 1988), this developmental event can have direct implications for fitness.

In temporary ponds, predators play a key role in structuring larval amphibian communities by affecting the growth, survival, behavior, and metamorphosis of their prey (Morin, 1981; Wilbur, 1987; Wilbur and Fauth, 1990). By decreasing densities, predators enhance growth opportunities for some amphibian larvae (Morin, 1983a, 1983b; Harris, 1987). In addition, predators can offer benefits to prey populations in a desiccating habitat by reducing densities, enhancing growth, and allowing larvae to metamorphose before the pond dries (Wilbur, 1987, 1988).

The influence of predators on life-history parameters of larval amphibians in streams is only poorly understood. Mechanisms of population regulation in these communities may differ from those in temporary ponds because stream habitats are usually less productive and do not offer the growth opportunities of temporary ponds (Hynes, 1970; Russell-Hunter, 1970; Hairston, 1987).

Resetarits (1991) and Gustafson (1993, 1994) studied the effects of predation in a stream community and found that larval *Gyrinophilus porphyriticus* influenced survival of larval *Eurycea cirrigera*. In addition, *G. porphyriticus* caused reduced growth in *E. cirrigera* relative to controls. Because larval periods in plethodontids are long (9–60 months; Bruce, 1980, 1989) these studies did not evaluate the effect of reduced larval growth on metamorphic timing and size.

I studied whether a predatory larval salamander (*Desmognathus quadramaculatus*) affected the growth, survival, behavior, and time to metamorphosis of a prey species (*Eurycea wilderae*). I tested the hypothesis that variation in predator density will result in different ages and sizes at metamorphosis (Wilbur and Collins, 1973; Werner, 1986). These species have long larval periods and slow larval growth relative to pond-dwelling salamanders. Because *D. quadramaculatus* has a longer larval period than *E. wilderae* (Bruce, 1988a, 1988b), individual *D. quadramaculatus* are sufficiently large to prey on larval *E.*

wilderae and smaller conspecifics (Beachy, 1993, 1994).

Materials and Methods

Study animals.—I collected 300 larval *E. wilderae* (12–19 mm SVL) and 40 large (31–40 mm SVL) larval *D. quadramaculatus* from Mill Branch and Cunningham Creek of the Coweeta Hydrologic Laboratory in Macon County, North Carolina during July 1991. Animals were brought to the laboratory at the Highlands Biological Station where they were anesthetized in a 0.1% solution of MS-222 and were measured for SVL to the nearest 0.1 mm. Individuals were assigned a unique number, placed in separate containers, and revived in stream water.

Cages.—Thirty cages were constructed of plastic tubs (91 × 61 × 20 cm LWH). Tubs were modified to provide for flow-through of stream water by cutting openings in the front (= entrance; 25 × 15 cm LH) and bottom rear (= exit; 25 × 5 cm LW). Nylon window screening (mesh size = 1.4 × 1.7 mm) over the tops of tubs and over entrance and exit openings prevented escape. The top screen was also equipped with a recloseable slit to facilitate the capture of animals for periodic sampling.

Cages were placed in 10 sets of three cages on two sites on Mill Branch and one site on Cunningham Creek during the last week of July 1991. Each set of three cages contained one replicate of each treatment. Sets experienced different slope and flow rates and constituted the "block" effect in the analysis. Each cage was sunk 3–5 cm into the stream bed. Sand, silt, gravel and approximately 30 kg of large rocks were added to each cage to provide habitat and anchor the cages. To provide initial prey, 350 g of leaf litter (with invertebrates) from the streambed and margin were added to each cage. Leaf litter was searched for other salamanders prior to addition to cages.

Experimental protocol and sampling.—I tested the hypothesis that predation by larval *D. quadramaculatus* affects the larval life-history parameters of larval *E. wilderae* by comparing the growth, survival, behavior, and metamorphosis of 10 *E. wilderae* in the presence of zero, one, or three *D. quadramaculatus*. Ten replicates (blocks) of each treatment were used, for a total of 30 cages with 300 *E. wilderae* and 40 *D. quadramaculatus*. The initial densities used are within the range of natural densities for these species (unpubl.).

Animals were randomly assigned to treatments, and initial mean sizes of larvae did not differ among experimental treatments (ANOVA, $F_{2,27} = 0.86$, $P = 0.43$ for *E. wilderae*; $F_{1,18} = 0.27$, $P = 0.61$ for *D. quadramaculatus*). Larvae were added to the cages on 1 August 1991, and treatments were randomly assigned within individual blocks. Thereafter, I visited cages weekly to clear entrance and exit screens of silt and litter blockage and to maintain stream flow through all cages.

I sampled all cages at the beginning of October, December, February, April, and June. Sampling usually took three days and consisted of removing all rocks and individuals from each cage. Larvae of *E. wilderae* were captured by sucking them into a clear, plastic tube, whereas *D. quadramaculatus* were captured using a small net. Neither capture technique ever killed or injured a larva. Animals were anesthetized, measured for SVL, revived, and returned to their respective cages. Only three times in 146 cage samplings were more individuals found in a cage than in an earlier sample, suggesting that all animals present were usually found and captured. The June sample terminated the experiment.

Because macroinvertebrate prey were excluded from the cages (aside from the initial litter addition), 15.0 g of live *Tubifex* worms were added to each cage on 1 September, 1 January, and 1 May. Few *Tubifex* were observed in the cages 3–4 days after their introduction, suggesting that the salamanders ate them.

At the end the experiment, in addition to recording size and survival, a metamorphic score (Table 1) was given to each surviving *E. wilderae*; the score was assessed by an independent observer unaware of treatments. This provided both an estimate of average metamorphic development in each cage and number of meta-

Table 1. Summary of Metamorphic Scores* ($\bar{x} \pm 1$ SE) of Larval *Eurycea wilderae*. Predators in this experiment were larval *Desmognathus quadramaculatus*. Cages with no surviving prey are not included. *N* refers to the number of cages with metamorphs in the June sample.

Number of predators	Metamorphic score	*N*
0	2.77 (0.22)	6
1	3.17 (0.26)	5
3	2.80 (0.27)	8

* Metamorphic scores were based on characteristics following Wilder (1925) and indicate progress toward metamorphic climax. Scores were: 0 = no metamorphic characters; 1 = two-line pattern formation evident; 2 = formation of nasolabial groove evident and labial fold still visible; 3 = labial fold absent; and 4 = gill loss and gill slit closure are complete. A score of 4 indicated that metamorphosis was completed.

morphs produced at the experiment's completion.

In addition to growth, survival, and metamorphic score, I assayed escape behavior of larval *E. wilderae* during the December and June samples. A significant difference in escape behavior of the prey was interpreted as indicative of a significant threat by the predators. The assay was conducted prior to the removal of the rocks and litter and was conducted on the first *E. wilderae* located in each cage; thus a maximum of 30 observations (10 per predator treatment) per sample. The end of the suction tube was placed next to the larva (within 1 cm), and the time (in seconds) until an escape reponse was elicited was recorded using a stopwatch. The assay was terminated after 15 sec if no escape response occurred, and the response time was recorded as 15 sec.

Statistical analyses.—Data used for analyses were percent survival, mean size (per cage), mean metamorphic score (per cage), and time until an escape response was elicited in each cage. Data on mean size and metamorphic score met the assumptions for analysis of variance. Survival data were arcsine transformed to reduce skewness. Data on time until an escape response was elicited were not normally distributed and were analyzed with a nonparametric procedure. Analyses were performed using SYSTAT, version 3.2 (Wilkinson, Evanston, IL, 1989, unpubl.). Where applicable, I report type III mean squares. Predator level and blocks were considered as main effects, with no interaction (Sokal and Rohlf, 1981). The significance criterion was set as $\alpha = 0.05$, and Wilks' lambda was used as the multivariate test statistic (Green, 1978).

Data for growth, survival, and metamorphic score were analyzed in two ways: (1) a multivariate analysis of variance (MANOVA); and (2) a profile analysis. The MANOVA tested the effect of block and predator treatment on final mean size, survival, and mean metamorphic score. This analysis ignored growth and survival history and examined only the final data set (i.e., the June sample). Univariate results were then analyzed only if the MANOVA indicated significant differences in response vectors among predator treatments.

The profile analysis of variance (Morrison, 1976; Simms and Burdick, 1988) was performed to evaluate the effects of predator treatment on the growth and survival trajectories that were recorded from August 1991 to June 1992. The profile analysis of growth tested three hypotheses: (1) treatments differed in height of the growth trajectory (referred to in Results as "treatment effect"); (2) individuals grew over time (referred to as "time effect"); and (3) treatment growth profiles were not parallel (referred to as "time × treatment effect"). The first hypothesis was tested by performing an ANOVA on the sums of the mean SVLs measured for each cage. Testing the second two hypotheses involved a MANOVA on a five-value response vector that consisted of differences between SVLs on adjacent sampling dates. If significant effects of treatment were found on slope of growth profiles, I performed univariate contrasts between adjacent sampling dates to determine when the growth trajectories diverged. This procedure was repeated on the survival trajectories.

The behavioral assays of December and June were examined in two Kruskal-Wallis tests. Due to the likelihood that escape responses were correlated between samples, I reduced α to 0.025 in both tests.

Results

Four cages (one each from the zero- and three-predator treatments, two from the one-predator treatment) failed before the experiment ended. Another zero-predator cage was dropped from analysis because larvae were overanesthetized accidentally during the October sample.

June was an appropriate time to terminate the experiment. Most of the larvae of *E. wilderae* were undergoing metamorphosis, and all cages with surviving larvae had at least one larva with a metamorphic score less than 4. The larvae of *D. quadramaculatus* had not yet initiated metamorphosis.

Responses of Eurycea wilderae.—The number of predators present did not appear to influence the metamorphic parameters (i.e., mean metamorphic score, mean size, and percent survival) of the prey (MANOVA on June data: Wilks' $\lambda = 0.72$, $F_{6,28} = 0.84$, $P = 0.55$, Table 1, Fig. 1). In addition, the number of metamorphs produced (individuals with a score of 4) did not differ significantly among treatments ($\bar{x}_{0\ \text{pred}} = 1.0$, $\bar{x}_{1\ \text{pred}} = 0.88$, $\bar{x}_{3\ \text{pred}} = 0.89$; $F_{2,22} = 0.02$, $P = 0.98$).

Two of the three profile analyses on growth trajectories were significant. The treatment effect was nonsignificant ($F_{2,15} = 0.28$, $P = 0.76$), which indicates that the heights of trajectories were not different among treatments. The significant Time effect (Wilks' $\lambda = 0.05$, $F_{5,11} = 45.48$, $P < 0.0001$) simply indicates that animals grew during the experiment. The time × treatment effect was also significant (Wilks' $\lambda = 0.24$,

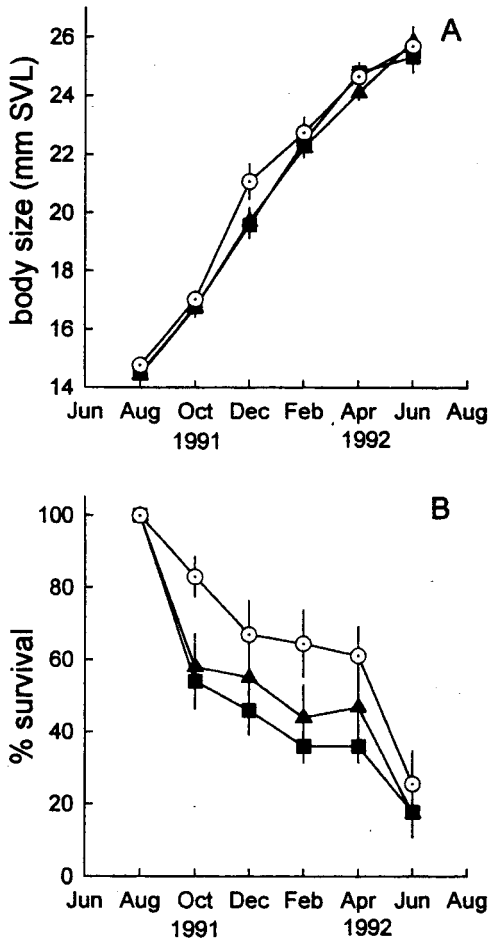

Fig. 1. (A) Growth and (B) survival trajectories of larval *Eurycea wilderae* in experimental cages. Points represent means on each sample date, bars are ± 1 SE. Circles = zero predators, triangles = one predator, squares = three predators.

$F_{10,22} = 2.32$, $P < 0.05$), indicating that growth trajectories were not parallel. Univariate ANOVAs on differences between dates indicated that slopes of the growth curves differed during the two intervals between February and June 1992 (Fig. 1A). Between February and April, larval *E. wilderae* in the three-predator treatment grew at a faster rate than larvae in either the one- or the zero-predator treatments ($F_{2,15} = 3.74$, $P < 0.05$). However, from April to June, larvae in the three-predator treatment experienced significantly reduced growth rates. Those in the zero-predator treatment grew slightly slower, whereas those in the one-predator treatment maintained consistent growth ($F_{2,15} = 5.72$, $P < 0.05$). Unexpectedly, variation among treatments in growth rate from February to June did not result in differences in metamorphic score (MANOVA result on final size, survival, and metamorphic score). Block effects were not significant.

All larvae of *E. wilderae* grew well in cages. Although amphibian larvae typically do not grow as they overwinter, larvae in cages grew during this period (Fig. 1A). Maximum metamorphic size of larvae at Mill Branch in other years has been 25 mm SVL (unpubl. data), slightly below the average size of metamorphosing animals in this experiment. This suggests that these larvae were not metamorphosing at a minimum-size threshold (Wilbur and Collins, 1973).

Two of the three profile analyses on survival trajectories were significant. The treatment effect indicates that sums of values along the trajectories were different; larvae in cages with no predators experienced higher survival ($F_{2,13} = 3.85$, $P < 0.05$). The time effect indicates that the animals in all treatments suffered mortality during the experiment (Wilks' $\lambda = 0.01$, $F_{5,9} = 125.27$, $P < 0.0001$). The time × treatment effect was not significant (Wilks' $\lambda = 0.44$, $F_{10,18} = 0.93$, $P = 0.78$), suggesting that the survival trajectories were parallel. Visual inspection of the survival curves (Fig. 1B) suggests that most of the predator-induced mortality occurred early in the experiment. Because the slope of the zero-predator survival curve is not different from the predator treatments, I interpret the mortality across all treatments between April and June as deaths due to the stress of metamorphosis. Block effects were not significant.

Significant differences occurred among treatment groups in escape behavior (December sample: $H = 13.73$, df = 2, $P = 0.001$; June sample: $H = 4.65$, df = 2, $P = 0.098$). In December, those larvae in zero-predator cages were less likely to show an escape response to a capture attempt than were larvae in cages with predators (Fig. 2). Antipredator behaviors can result in a decrease in foraging time and hence in growth (Lima and Dill, 1990). No such differences in growth rates were observed, however, in the December sample. Growth rates were different at the June sample, but escape responses were uniform across treatments (Fig. 2). Growth rates were lowest during this time in three-predator cages but were highest in one-predator cages. The intermediate growth rates of larvae in zero-predator cages may reflect a balance of predator density and conspecific density.

Responses of Desmognathus quadramaculatus.—Mortality of predators resulted in several empty cells in the profile analysis. To facilitate the profile analysis, block effects were assumed to be nonsignificant, and the *D. quadramaculatus* re-

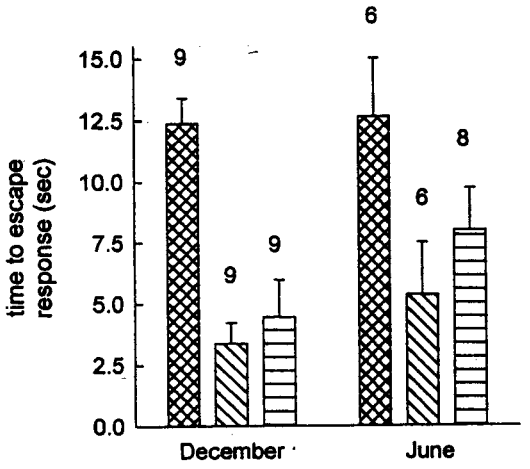

Fig. 2. Amount of time before escape response was elicited during a capture attempt. Behavioral samples were taken in December and June. Cross-hatched bars = zero-predator treatment, diagonally hatched bars = one-predator treatment, horizontally hatched bars = three-predator treatment. Numbers above bars are sample sizes.

sponses were analyzed as a fully randomized design.

Of the three profile analyses on growth trajectories, only the time effect was significant (Wilks' $\lambda = 0.12$, $F_{5,5} = 7.40$, $P < 0.05$). That is, salamanders grew during the study. The *P*-value for the time × treatment effect (Wilks' $\lambda = 0.17$, $F_{5,5} = 4.75$, $P = 0.056$) suggests that density may have made the growth curves nonparallel. However, univariate ANOVAs did not detect any differences among the five contrasts ($P > 0.25$ for all intervals). For this reason, the result for time × treatment was considered to be nonsignificant. The treatment effect was also nonsignificant ($F_{1,9} = 0.20$, $P = 0.67$). The nonsignificant results for the treatment and time × treatment effects indicate that the variation in conspecific density did not influence growth of larval *D. quadramaculatus* (Fig. 3A).

Of the three profile analyses on survival, only the time effect was significant, indicating that some animals died during the experiment (Wilks' $\lambda = 0.32$, $F_{5,13} = 5.43$, $P < 0.01$). The nonsignificant results for the treatment ($F_{1,17} = 0.02$, $P = 0.89$) and date × treatment (Wilks' $\lambda = 1.837$, $F_{5,13} = 1.84$, $P = 0.18$) effects indicate that the effect of density did not influence survival of larval *D. quadramaculatus* (Fig. 3B).

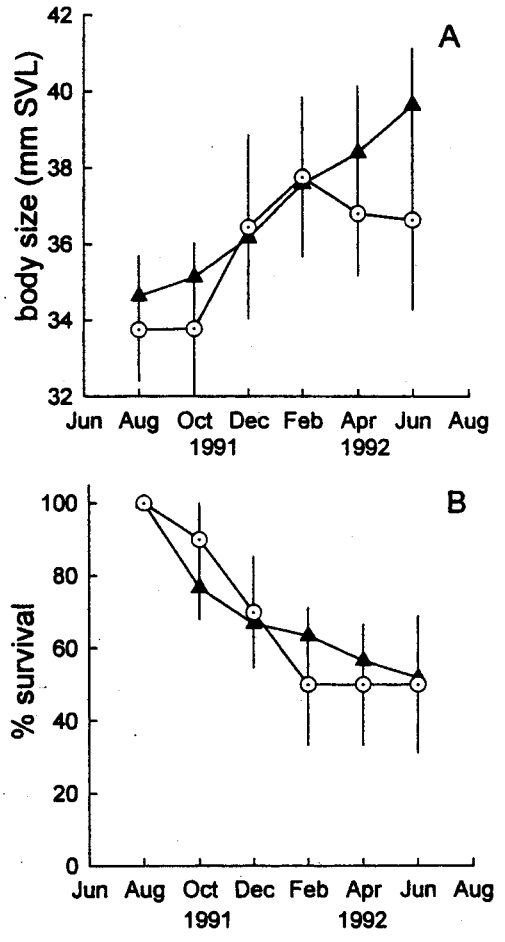

Fig. 3. (A) Growth and (B) survival trajectories of larval *Desmognathus quadramaculatus* in experimental cages. Points represent means on each sample date, bars are ± 1 SE. Circles = one *D. quadramaculatus* per cage, triangles = three *D. quadramaculatus* per cage.

Discussion

Predation and competition among larval salamanders in streams.—When predation lowers prey density, opportunities for growth of prey can exist. In contrast, predators may limit the foraging time of prey, thus restricting these opportunities. Resetarits (1991) and Gustafson (1993) noted that larvae of *E. cirrigera* grew less when exposed to predators, apparently because of predator avoidance. The predator effect on larval *Eurycea* in my experiment was more complex. Larvae in the three-predator treatment grew significantly more than larvae in the other treatments from February to April then experienced a significant decrease in growth relative to the other treatments. The increase may have been a result of low density; larvae in three-predator cages were at lower densities than other treatments. Predator activity may have been lower during winter, accounting for the flat slope of the prey survival curves from October

1991 to April 1992. The consequent decrease in growth in three-predator cages from April to June may have been the result of the increased predator activity with increasing temperature during the April–June period. Perhaps because of fewer predators than the three-predator cages, and lower densities of conspecifics than the zero-predator cages, larvae in one-predator cages were able to maintain consistent growth. These results suggest a complex relationship among density of prey, density of predators, and the growth responses of prey.

Conspecific density did not significantly affect growth and survival of larval *D. quadramaculatus*. Densities used in this experiment were in the upper end of the range of natural densities of this species (1.8/m^2 and 5.4/m^2), and larval growth in this experiment was similar to that in nature (Bruce, 1988a).

Effects of predators on the metamorphosis of prey.— There are several models that have been developed to predict size at and/or time of metamorphosis (Wilbur and Collins, 1973; Travis, 1984; Werner, 1986). All suggest that growth rate can influence the timing of metamorphosis. Wilbur and Collins (1973) suggested that, once a minimum size threshold has been achieved, metamorphosis will be initiated when growth rate drops below a specified level. This signals a deteriorating larval habitat (e.g., threat of desiccation or starvation). In view of the growth responses that Resetarits (1991) and Gustafson (1993, 1994) observed in the stream-dwelling larvae they studied, they suggested that predation could result in delayed time and/or decreased size at metamorphosis. In my experiment, larvae of *E. wilderae* from different predator treatments experienced different growth rates over the last four months of the experiment. Yet no differences in size or time at metamorphosis (measured as "metamorphic score" in this experiment) were found.

Werner (1986) extended the Wilbur-Collins hypothesis by suggesting that an assessment of mortality risk, in addition to growth opportunity, in the larval habitat should lead to an optimal size (not age) at metamorphosis. Werner predicted that, as the ratio of mortality risk to growth opportunity is increased, there should be a decrease in metamorphic size. The converse is predicted as the ratio decreases. Individuals from the three-predator treatment experienced lower growth than larvae from the one-predator treatment over the last sample period, but mortality risk, as assessed by survival curves and escape behavior, was not different. Thus, the mortality risk/growth opportunity ratio was higher in the three-predator treament, but no differences were manifested in size (or age) at metamorphosis. This analysis assumes that Werner's model, which was generated to predict an evolutionarily stable stategy, can be used on an ecological time scale. Further, whether the predators posed a strong enough mortality risk to prey to alter the timing of metamorphosis is not known.

There are several explanations for discrepency between theory and my observations. First, growth trajectories may need to diverge early or throughout the larval life to influence metamorphic parameters, and one of the models predicts that development is set early in the larval period (Travis, 1984). After an analysis of metamorphosis in the frog, *Pseudacris crucifer*, Hensley (1993) suggested that the Wilbur-Collins hypothesis may better predict metamorphosis if developmental timing is viewed as fixed at some point of the larval period (although that point need not be early sensu the Travis model). However, the stream-dwelling plethodontid *Desmognathus ochrophaeus* failed to show variation in metamorphic timing despite early divergence in larval growth trajectory (Beachy, 1995).

Second, Juterbock (1990) suggested that most of these models are not successful for predicting metamorphic parameters in stream-dwelling plethodontids. Growth-based models developed to predict metamorphosis in amphibians using high productivity, temporary ponds as a larval habitat may have little value in predicting metamorphosis for amphibians using low temperature and low productivity southern Appalachian streams as larval habitats.

No response of *E. wilderae* in terms of length of larval period or body size at metamorphosis was elicited by predator treatment in my experiment. Furthermore, when larval growth history is manipulated in the stream-dwelling amphibian *D. ochrophaeus*, no response in metamorphic timing is elicited (Beachy, 1995). It may be that populations in habitats that do not pose a desiccation risk, and/or a significant opportunity for growth, may have little to gain by maintaining a plastic metamorphic response.

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