

## THE INFLUENCE OF SIZE-SPECIFIC INDIRECT INTERACTIONS IN PREDATOR–PREY SYSTEMS

VOLKER H. W. RUDOLF<sup>1</sup>

Department of Biology, University of Virginia, 243 Gilmer Hall, Charlottesville, Virginia 22904-4327 USA

**Abstract.** Nonlethal indirect interactions between predators often lead to nonadditive effects of predator number on prey survival and growth. Previous studies have focused on systems with at least two different predator species and one prey species. However, most predators undergo extreme ontological changes in phenotype such that interactions between different-sized cohorts of a predator and its prey could lead to nonadditive effects in systems with only two species. This may be important since different-sized individuals of the same species can differ more in their ecology than similar-sized individuals of different species. This study examined trait-mediated indirect effects in a two-species system including a cannibalistic predator with different-sized cohorts and its prey. I tested for these effects using larvae of two stream salamanders, *Gyrinophilus porphyriticus* (predator) and *Eurycea cirrigera* (prey), by altering the densities and combinations of predator size classes in experimental streams. Results showed that the presence of large individuals can significantly reduce the impact of density changes of smaller conspecifics on prey survival through nonlethal means. In the absence of large conspecifics, an increase in the relative frequency of small predators significantly increased predation rates, thereby reducing prey survival. However, with large conspecifics present, increasing the density of small predators did not decrease prey survival, resulting in a 14.3% lower prey mortality than predicted from the independent effects of both predator size classes. Small predators changed their microhabitat use in the presence of larger conspecifics. Prey individuals reduced activity in response to large predators but did not respond to small predators. Both predators reduced prey growth. These results demonstrate that the impact of a predator can be significantly altered by two different types of trait-mediated indirect effects in two-species systems: between different-sized cohorts and between different cohorts and prey. This study demonstrates that predictions based on simple numerical changes that assume independent effects of different size classes or ignore size structure can be strongly misleading. We need to account for the size structure within predator populations in order to predict how changes in predator abundance will affect predator–prey dynamics.

**Key words:** cannibalism; community structure; *Eurycea cirrigera*; *Gyrinophilus porphyriticus*; higher order interactions; interaction modification; intraguild predation; intraspecific predation; multiple predators; stage structure; stream salamander; trait-mediated indirect interaction (TMII).

### INTRODUCTION

Most predators undergo substantial size changes during ontogeny, and cohorts of different-sized individuals often coexist (Polis 1984, Ebenman and Persson 1988). Body size influences key life history processes, such as growth, mortality, consumption rates, food, and habitat choice (Werner and Gilliam 1984, Persson 1988); thereby size can determine the character and strength of ecological interactions. As a result, the interaction of a size-structured predator and its prey can lead to complex interactions with population dynamics that are not possible in unstructured predator–prey systems (Persson et al. 1998, Wahlstrom et al. 2000, De Roos et al. 2003).

Although there is a large body of research on size-structured predator–prey interactions (Ebenman and

Persson 1988, De Roos et al. 2003), it has been largely overlooked that cohorts of different sizes within a predator population often represent distinct functional groups and could thus create nonlethal (or behavioral) indirect interactions in one predator–one prey systems. These interactions can strongly impact the dynamics of such systems. For example, the attack rate of a small predator on its prey is likely to be lower than that of a larger conspecific (Thompson 1975, Wahlstrom et al. 2000, Aljetlawi et al. 2004). The behavioral response of a prey might differ according to predator size because of variable predation risks. In such cases, the presence of one predator size class might indirectly alter the per capita effect of another size class by changing the behavior of the prey, thereby creating a trait-mediated indirect effect.

Another type of nonlethal indirect interaction can arise within a population of a predator. Size differences between predator cohorts can lead to asymmetric competition or cannibalism, such that individuals respond

Manuscript received 20 June 2005; revised 25 July 2005; accepted 1 August 2005. Corresponding Editor: O. J. Schmitz.

<sup>1</sup> E-mail: vrudolf@virginia.edu

differently towards similarly sized conspecifics than to larger or smaller conspecifics. For example in odonates (Van Buskirk 1992), isopods (Leonardsson 1991), and fish (Greenberg et al. 1997, Biro et al. 2003) individuals change their foraging behavior or habitat use in response to larger conspecifics to avoid cannibalism or aggressive interactions. If the different-sized cohorts share the same prey, such nonlethal, intercohort interactions can lead to behavioral indirect effects that are likely to alter the predator's impact on the population dynamics of its prey.

Empirical studies have shown that in systems with three or more species, behavioral indirect interactions can strongly impact the dynamics of predator-prey interactions and have a similar or stronger impact on prey demographics and trophic cascades than direct effects (Schmitz 1998, Preisser et al. 2005). Such behavioral indirect interactions commonly lead to nonadditive (higher order) effects of multiple predators; when multiple predators are present, prey survival might be lower or higher than expected from their independent effects in the absence of the other predators (reviewed in Sih et al. 1998). Interestingly, all previous studies have focused on systems with three or more species and at least two different predator species. Yet, these interactions may also be important in two-species systems because different-sized individuals of the same species can differ more in their ecology than similar-sized individuals of different species (Wilbur 1980, Polis 1984). This study tests the hypothesis that nonadditive effects can arise in a two-species system through interactions between different-sized cohorts of a predator and between predator cohorts and their prey.

The dynamics of populations can be characterized in at least two ways. Changes can either be "numerical," such that the total numbers of individuals increase or decrease, or the dynamics can be "structural," such that the relative frequency of different size classes changes within the population. Most experimental studies on the effect of a predator on prey dynamics have focused on numerical changes while neglecting structural changes (but see e.g., Rice et al. 1993, Persson et al. 2000, Rettig and Mittelbach 2002). However, intrinsic numerical changes (i.e., population growth) also generally result in structural changes that might alter the effect of numerical changes. For example, when an iteroparous predator experiences conditions favorable for survival and reproduction, there will be an increase in the population density, but only the smallest size class increases while the abundance in the larger size classes remains unchanged or decreases. Previous studies have shown that structural changes within predator populations can have a strong impact on predator-prey dynamics if the survival of one predator size class is affected by other size classes (Persson et al. 2003, Claessen et al. 2004). Nonlethal indirect interactions could be of similar importance. If the effect of increasing the small size class is dependent on the presence

or relative abundance of larger size classes, then predictions based on simple numerical changes that ignore the change in size structure might be erroneous.

I tested for these effects in two species of salamander by altering the densities and presence of two predator size classes in experimental streams. In particular I tested the following hypotheses: (1) the effects of changes in small predator density on prey survival are altered by the presence of large conspecifics predators; (2) large predators alter the behavior of small conspecifics; and (3) prey individuals respond differently to predator cohorts in behavior and growth. Testing these hypotheses allowed me to determine if the effects of different size classes of a predator on their prey are additive and can be predicted by simple numerical changes. My experiment also studied the mechanisms, such as behavioral indirect interactions, that might explain nonadditive effects.

## MATERIALS AND METHODS

### *Study species*

Stream salamanders provide an excellent study system to test if nonadditive effects can arise in a one predator-one prey system through interactions between different-sized cohorts of a predator and its prey. Salamanders are top predators in fishless headwater streams and many species have a long larval period resulting in different size classes that coexist in time and space. The spring salamander *Gyrinophilus porphyriticus* is a common species in the southern Appalachians. Because of its long larval period of typically four years (Bruce 1980), coexisting cohorts can differ by more than four-fold in size (from 15 mm to 65 mm snout-vent length; Bruce 1980; unpublished data). Larvae of *G. porphyriticus* are generalized predators that feed on smaller conspecifics (unpublished data), heterospecific salamander larvae, and invertebrates. The two-lined salamander *Eurycea cirrigera* is the most abundant species in streams at the study site, and its larvae are a common prey of *G. porphyriticus* (Resetarits 1991, Gustafson 1993; see Plate 1). Larvae hatch at 8–10 mm snout-vent length (SVL) and metamorphose at 18–32 mm SVL after a larval period that typically lasts one year (Bruce 1982, 1985).

### *Experimental streams*

The experiment was conducted at Mountain Lake Biological Station (MLBS), Giles County, Virginia, USA, from June to August 2004. Density and size structure of the two species of stream salamanders were manipulated in 16 experimental streams (3.35 m long  $\times$  0.69 m wide  $\times$  0.36 m deep) that mimicked the natural habitat of both species. The stream mesocosms were closely packed in six rows directly on the stream bed of Sartain Branch under natural canopy of *Rhododendron maximum* for shading (see Plate 1; for details see Resetarits [1991]). Water was obtained from

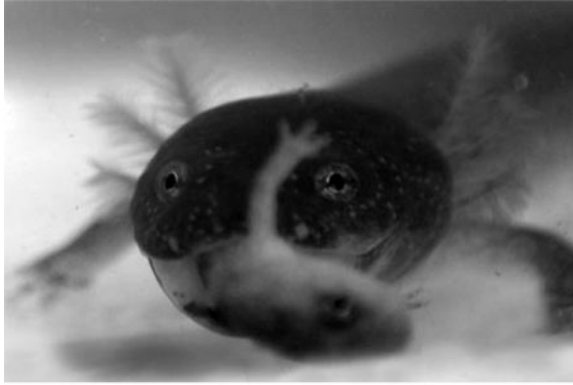


PLATE 1. (Top) *Gyrinophilus porphyriticus* larva consuming a larva of its common prey *Eurycea cirrigera*. (Bottom) Experimental streams placed on the stream bed of Sartain Branch under natural canopy of *Rhododendron maximum*. Photo credit: V. H. W. Rudolf.

a collecting tank fed directly by a natural spring immediately above the experimental units. Each experimental stream received water from the tank independently and was drained through a standpipe covered with plastic window screening to prevent larvae from escaping. The flow rate into each stream was initially adjusted to 3 L/min, but flow regimes varied depending on the natural spring flow and rainfall. Streams were angled by  $2^\circ$  to create a natural gradient of water depth (water depth above substrate was  $\sim 0$  cm at the upstream end and  $\sim 15$  cm at the downstream end). Each stream received sand and river gravel (60 L) plus 11 large flat rocks as cover objects and one large splash stone below the inflow. The top of the experimental units were open to allow arthropods and plant material to fall into the tanks and insects to colonize them. A 10-cm plastic lip attached to all edges of each stream prevented larvae from escaping. Water flow was initiated two weeks prior to the beginning of the experiment to allow accumulation of plant and debris material and to establish a natural invertebrate community. After two weeks, each stream had been colonized by a variety of invertebrate taxa that served as food for

salamanders. These experimental streams adequately represented the spatial heterogeneity present in natural headwater streams with respect to water depth, substrate type, light regime, water flow, and temperature. All study animals were collected in three first-order headwater streams near MLBS.

#### Experimental setup

I used two size classes of *Gyrinophilus porphyriticus* as predators, and larvae of *Eurycea cirrigera* as prey. At the beginning of the experiment, the small predator size class (small GP) ranged between 26 mm and 38 mm snout-vent length (SVL,  $34.7 \pm 4.3$  mm [mean  $\pm$  SD],  $N = 64$ ) with a mean mass of  $0.973 \pm 0.323$  g, and the large size class (large GP) ranged between 57 mm and 63 mm SLV ( $59.7 \pm 2.1$  mm,  $N = 32$ ) with mean mass of  $4.535 \pm 0.564$  g. *Eurycea cirrigera* larvae ranged between 14.0 mm and 18.5 mm SVL ( $16.6 \pm 0.85$  mm,  $N = 224$ ) with a mean mass of  $0.120 \pm 0.003$  g. The experiment was a  $2 \times 2$  factorial randomized complete block design with four replicates per treatment. The relative number of the small predator size class to the prey (low ratio of 2:16 = 0.87 predator individuals/m<sup>2</sup> to 6.5 prey individuals/m<sup>2</sup> and high ratio of 6:12 small *G. porphyriticus* to *E. cirrigera*) was manipulated in the absence (no large GP) or presence (four large GP, or 1.7 individuals/m<sup>2</sup>) of the large predator class. The two ratios simulated an increase in predation pressure by small *G. porphyriticus*, and simultaneously increased the probability of interference between both *G. porphyriticus* size classes relative to the prey. Densities for each species and size class were within the mean natural densities found in headwater streams at MLBS (Resetarits 1991, Gustafson 1993). Small and large *G. porphyriticus* were each ranked by size and then divided into four size groups. All four size classes of small and large *G. porphyriticus* were paired by rank and each pair was randomly assigned to one of the four blocks to keep the size ratio of large to small *G. porphyriticus* equal across treatments ( $\sim 1.75:1$ ) and to prevent cannibalism. Previous laboratory studies have shown that cannibalism is unlikely below a size ratio of 2:1 even under confined conditions (*unpublished data*). Individuals were randomly assigned to treatments within each block. Because of the small variation in size, *E. cirrigera* were randomly assigned across blocks and treatments. The experiment started on 17 July and was terminated after six weeks when the first *E. cirrigera* larvae were close to metamorphosis and had started to leave the water, which strongly reduces their risk of predation and alters densities within streams.

#### Survival and growth

At the termination of the experiment, each stream was searched on three consecutive nights and days for surviving individuals to assure that all survivors were recovered. To test if the effect of an increase in the

density of small predators was independent of the effect of the presence of large conspecifics and to calculate expected survival, I assumed a multiplicative risk model (Soluk and Collins 1988, Wilbur and Fauth 1990, Wootton 1994). Thus, proportional survival was log-transformed to convert the multiplicative risk model into its linear (additive) form in which the model could be tested in a two-way ANOVA (Wilbur and Fauth 1990, Billick and Case 1994, Wootton 1994). Mass and snout-vent length (SVL) of each individual of both species were measured immediately before the start and again after the termination of the experiment. The pattern of the lateral pores on the top of the head of each larva of *G. porphyriticus* was recorded prior to the experiment, because the pattern of these pores is unique for each larvae and permits individual identification. Thus growth of individuals could be calculated. Initial tank means and standard deviation of initial body mass and SVL were not significantly different across treatments for *E. cirrigera* (all  $P > 0.43$ ); thus the analyses were carried out on final measurements to reduce the error variance. Growth for all species was analyzed based on tank means weighted by the number of survivors as the dependent variable. *Eurycea cirrigera* mass was log-transformed to meet normality assumptions.

#### *Activity and microhabitat use*

To determine indirect behavioral effects resulting from different treatments, a day and a night activity census was performed weekly and every two weeks a census of microhabitat use was done starting seven days after the experiment had been initiated (resulting in a total of six and three observations for activity and habitat census, respectively). Individuals were defined as active when they were observed on top of the substrate at first sighting. Day and night censuses were performed at 10:00 and 22:00, respectively, with the order of these censuses being determined randomly. The search order of blocks and units within blocks was determined randomly for each search period. Habitat censuses were done similarly to day activity checks, but each cover stone was carefully lifted. Stones could usually be removed and returned without disturbing individuals. The length of each stream was divided into 14 equal sections of 24 cm, and the position of each individual and its size class and species within sections was recorded. For each stream, all three observations were pooled to calculate the mean proportion of observed individuals in each section.

#### *Statistical analysis*

Treatment effects on survival and growth were analyzed with mixed procedure of SAS (Littell et al. 1996), with both treatment effects as fixed factors and block as a random effect. A one-tailed log-likelihood ratio  $\chi^2$  test was used to determine if the variation due to the random block effect was significantly greater

than zero (Littell et al. 1996). In situations where block effects were not significant (see Appendix A), block degrees of freedom were pooled with the error term degrees of freedom for the final analysis. Early in the experiment, several *E. cirrigera* larvae entered one experimental unit through the water because of a hole in the mesh covering of the pipe that was later repaired. Observations during the experiment and final survival estimates indicated that more individuals were in the unit than initially added. Thus, the initial number was unknown and the unit had to be removed from the survival analysis. However, this unit was only a significant outlier for survival, but not for the other dependent variables, and thus it was included in all other analyses. To account for the missing replicate in the analysis of survival, the degrees of freedom were adjusted using the Satterthwaite procedure (Littell et al. 1996). Proportional activity and microhabitat use were analyzed in a similar manner to survival and growth, but the activity analysis included observation time as a repeated factor and the microhabitat analysis included stream section as repeated factor to account for covariance of observations and stream sections. The appropriate covariance structure for the repeated-measures analysis was determined using the fitted model with the lowest AIC value (Littell et al. 1998).

## RESULTS

### *Survival*

Survival of *Eurycea cirrigera* ranged from 93.8% in treatments with only two small predators present to 50% with both small and large predators present. Both an increase in predation pressure by small *Gyrinophilus porphyriticus* ( $F_{1,7.97} = 9.93$ ,  $P = 0.0136$ ) and the presence of large *G. porphyriticus* ( $F_{1,7.97} = 6.34$ ,  $P = 0.0360$ ) significantly reduced the proportional survival of *E. cirrigera*. The effect of increasing the density of small *G. porphyriticus*, however, was dependent on the presence or absence of large conspecifics (interaction effect,  $F_{1,7.97} = 9.35$ ,  $P = 0.0157$ ; Fig. 1). Without large predators, increasing the number of small predators per prey reduced prey survival, on average, by  $14.1 \pm 2.99\%$  (mean  $\pm$  SE;  $N = 4$ ). When large predators were present, increasing the number of small predators did not lead to a decrease in prey survival ( $-2.1 \pm 6.68\%$ ,  $N = 3$ ), resulting in 14.3% higher average prey survival than expected from treatments without large predators (Fig. 1; one block could not be included because the missing treatment did not allow for calculation of the expected value). Survival for both size classes of *G. porphyriticus* was 100%.

### *Growth*

Final mass of *E. cirrigera* was 17.8% lower in treatments with a higher ratio of small *G. porphyriticus* to *E. cirrigera* ( $F_{1,12} = 18.57$ ,  $P = 0.001$ ) and final mass was 37.3% lower in the presence of large *G. porphy-*

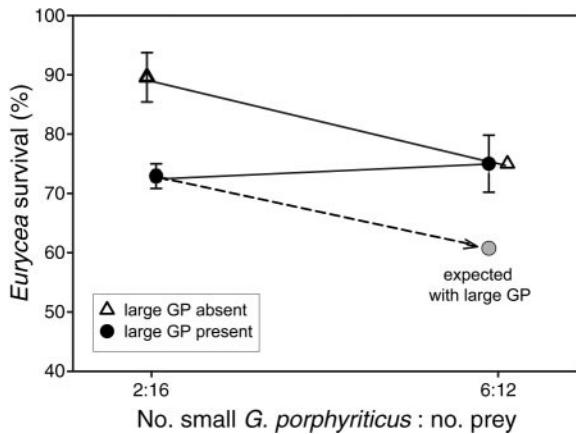


FIG. 1. Test for independent effects of both predator (*Gyrinophilus porphyriticus*) size classes showing the effects of density changes in small predators (predator:prey ratio) on prey (*Eurycea cirrigera*) survival (mean  $\pm$  SE) in the presence and absence of large conspecifics. The dashed arrow indicates the expected value for the treatment with a high density of small predators and large predators present. The expected value was calculated using a multiplicative risk model that assumes that both treatment effects are independent (additive). The effects of both treatments are not independent (for the interaction term,  $F_{1,7.97} = 9.35$ ,  $P = 0.0157$ ). With large conspecifics present, increasing the density of small *G. porphyriticus* (GP) resulted in 14.3% higher survival than expected when assuming independent effects of both predator size classes (dashed arrow).

*iticus* ( $F_{1,12} = 5.10$ ,  $P = 0.0433$ ). Both treatment effects were additive ( $F_{1,12} = 0.28$ ,  $P = 0.6057$ ; Fig. 2A). This was similar for final SVL, which decreased 11.8% with increasing numbers of small *G. porphyriticus* ( $F_{1,12} = 39.47$ ,  $P < 0.001$ ) and 26.7% when large *G. porphyriticus* ( $F_{1,12} = 6.06$ ,  $P = 0.0216$ ) were present (Fig. 2A). This indicates that growth rates of the prey were significantly reduced by the presence of predators. Individual growth rates of small *G. porphyriticus* were reduced by 33.0% for mass and 25.9% for SVL at a high ratio of small *G. porphyriticus* to *E. cirrigera* (mass,  $F_{1,9} = 8.58$ ,  $P = 0.0168$ ; SVL,  $F_{1,9} = 2.59$ ,  $P = 0.1491$ ). With large *G. porphyriticus* present mass and SVL growth rates of small *G. porphyriticus* were reduced by 36.6% and 5.3%, respectively (mass,  $F_{1,9} = 6.66$ ,  $P = 0.0296$ ; SVL,  $F_{1,9} = 11.17$ ,  $P = 0.0086$ ; Fig. 2B), indicating that large conspecifics reduced growth rates of small conspecifics. There were no significant interaction effects ( $P > 0.05$  for mass and SVL). Growth rates of large *G. porphyriticus* were 45.2% lower for mass and 32.06% lower for SVL at a higher ratio of small *G. porphyriticus* to *E. cirrigera* (mass,  $F_{1,6} = 8.89$ ,  $P = 0.0246$ ; SVL,  $F_{1,6} = 8.26$ ,  $P = 0.0283$ ; Fig. 2C).

#### Activity

Only day activity of *E. cirrigera* was significantly affected by the interaction of the ratio of small *G. porphyriticus* to *E. cirrigera* and large predators ( $F_{1,12} =$

5.45,  $P = 0.0377$ ; see Appendix B for full table for repeated-measures analysis). Increasing the density of small predators increased mean day activity of the prey in the absence of large predators by 11.26%, but decreased prey mean day activity when large predators were present by 7.91% (Fig. 3). The presence of large predators strongly reduced prey night activity, on average, by 40% ( $F_{1,12} = 33.66$ ,  $P < 0.001$ ; Appendix B), while ratio and the interaction of both factors had no effect on night activity (Fig. 3). There were too few individuals of both *G. porphyriticus* size classes observed during the day to allow for statistical analysis. Night activity did not differ between treatments for both predator size classes (Appendix B).

#### Microhabitat use

The repeated-measures analysis (see Appendix C for full table) showed that the proportional abundance of *E. cirrigera* was different across stream sections ( $F_{13,156} = 5.91$ ,  $P < 0.0001$ ), being generally higher in the mid and downstream sections (Fig. 4A). The significant interaction between stream section and ratio treatment ( $F_{13,156} = 3.01$ ,  $P = 0.0006$ ) indicated that *E. cirrigera* shifted its microhabitat use from the downstream end to the mid sections of the stream at a high ratio of small *G. porphyriticus* to *E. cirrigera* (Fig. 4A). None of the other factors or interactions was significant (Appendix C). The relative abundance of small predators differed between stream sections ( $F_{13,156} = 4.39$ ,  $P < 0.001$ ). Microhabitat use was only affected by the ratio of small *G. porphyriticus* to *E. cirrigera* ( $F_{13,156} = 2.1$ ,  $P < 0.0166$ ) and the three-way interaction between section, ratio treatment, and large predator treatment ( $F_{13,156} = 2.55$ ,  $P < 0.0033$ ). The latter three-way interaction shows that the way small predators changed microhabitat use between the low and high ratio of small predators to their prey was dependent on the presence or absence of large conspecifics (Fig. 4B). In the absence of large conspecifics, small *G. porphyriticus* showed an identical microhabitat use compared to large conspecifics and preferred the downstream end. At higher densities of small conspecifics, small predators shifted microhabitat use from the downstream end towards the upstream end (Fig. 4B). With large conspecifics present, small predators were more abundant in the downstream half of the stream at low densities, but shifted their distribution at higher densities toward the upstream end (Fig. 4B).

#### DISCUSSION

This study presents the first empirical test of whether the effect of numerical changes within one stage of a predator population can be predicted from the combined independent effects of numerical changes in other stages, or if behavioral indirect interactions lead to nonadditive effects in stage-structured predator-prey dynamics. With large conspecifics present, increasing

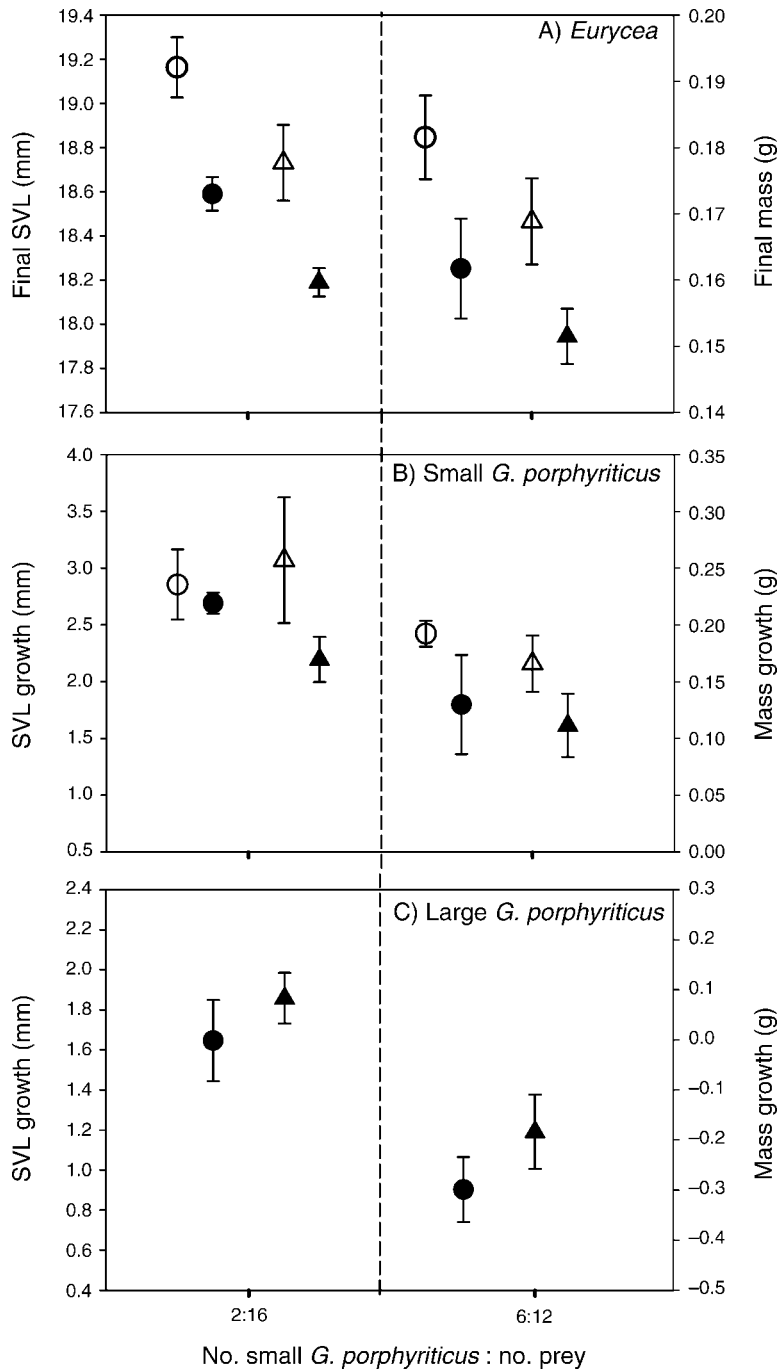


FIG. 2. (A) Final mean mass and snout-vent length (SVL) for prey *E. cirrigera*, and mean growth rates of mass and SVL for (B) small predators and (C) large predators (*G. porphyriticus*) for each of four treatments. For both sizes of predators, growth is given by the difference between final and initial mass or SVL of each individual. Circles represent mass, triangles represent SVL, solid symbols indicate the presence of large predators, and open symbols indicate the absence of large predators. Values represent means  $\pm$  SE.

the relative frequency of small predators resulted in significantly lower mortality of the prey than expected from trials without large predators present. The results clearly demonstrate that the impact of a density increase in one predator size class on prey survival can

be significantly altered by the presence of large conspecific predators through behavioral indirect interactions. Such behavioral indirect effects are documented in three-species systems; however, this study is the first to demonstrate that behavioral-mediated indirect ef-

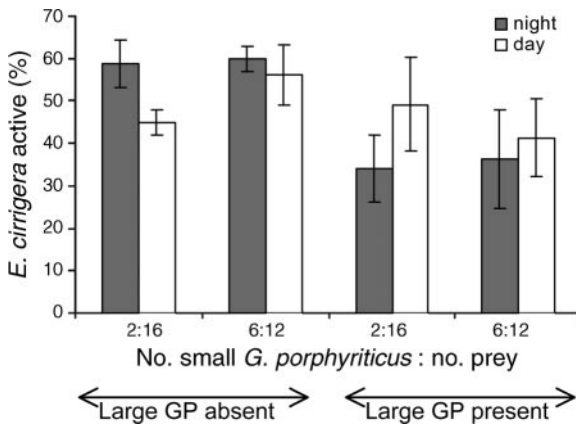


FIG. 3. Night and day activity of *E. cirrigera* (the percentage of individuals active, mean  $\pm$  SE) for each predator (*G. porphyriticus*, GP) treatment. Analysis was carried out as repeated measures using each of six observation events per tank with observation time as the repeated factor to account for covariance of observations.

fects can also strongly impact the dynamics of a system with only one predator and its prey.

Behavioral indirect interactions can either lead to reduction or enhancement of prey mortality risk. Risk reduction is frequently observed in intraguild predation systems, when one predator changes its behavior to avoid being consumed by the other predator (e.g., Soluk and Collins 1988, Huang and Sih 1990, Wissinger and McGrady 1993, Crumrine and Crowley 2003). Risk enhancement usually results when antipredator behavior of the prey induced by one predator increases prey vulnerability to the other predator (e.g., Soluk and Collins 1988, Losey and Denno 1998). In this study, several possible mechanisms could explain why prey mortality was lower than expected. First, the presence of large predators altered how small conspecifics changed microhabitat use at different ratios. While cannibalism was unlikely, due to the size difference between size classes (see *Introduction*), one small *Gyrinophilus porphyriticus* had lost a front leg, a typical injury in natural populations that can result from a failed predation event by a larger conspecific (*unpublished data*). Thus, small *G. porphyriticus* might have switched microhabitats at high densities to avoid aggressive interactions with large conspecifics. Such behavior has been observed in other cannibalistic species (Van Buskirk 1992, Greenberg et al. 1997). It is possible that the effect of larger predators on change in microhabitat use of small conspecifics reduced predation rates of small predators at high densities by decreasing microhabitat overlap of small predators and their prey.

The second important indirect effect was that larger predators reduced prey night activity, resulting in more time spent in refuges. Increase in refuge use and reduced activity are common antipredator behaviors and decreases probability of encounter with predators

(Huang and Sih 1990). *G. porphyriticus* mostly forage at night and reduction in prey activity during that time could have significantly reduced predation rates of small predators.

It is interesting that changes in the density of small predators had no effect on prey activity. This suggests that the prey discriminated between size classes and adjusted behavior accordingly. In turn, this implies that different-sized predators can have very different effects on their common prey. Laboratory experiments have shown that an increase in size difference between *G. porphyriticus* and *Eurycea cirrigera* is positively correlated with predation rates (*unpublished data*), which might partly explain why *E. cirrigera* responded stronger to the presence of the larger more voracious size class. The correlation between body size and foraging rates has been recorded for many predators (Werner and Gilliam 1984, Persson 1988). This suggests that the observed disparity in the effects of predator size classes on prey behavior might be a common phenomenon in predator-prey systems.

In contrast to survival, effects of both size classes on prey growth were additive. In salamanders, lower growth rates often lead to smaller size at metamorphosis and maturity, lower juvenile and adult survival, and reduced fecundity (Bruce 1978, Semlitsch et al. 1988, Scott 1994). Thus, the additive negative effects of both predator size classes on *E. cirrigera* growth rates are likely to have important implications for population dynamics. Despite lower prey densities, prey growth rates were reduced at high densities of small predators. Since the prey behavior was not different between both ratio treatments, this suggests that small predators compete with their prey for shared food sources. Such interspecific competition has been observed in other stream salamanders (Hairston 1986). With respect to large predators, the experiment does not separate the effects of exploitative competition from behavioral changes that might affect foraging rates (activity changes). In future studies it will be interesting to determine whether the additive effect of both size classes resulted from the combination of two different mechanisms, each imposed by different size classes, or resulted from simple resource competition with both predator size classes.

The substitutive design (decreasing prey density while increasing predator density simultaneously) could have created confounding effects on prey growth. However, if density had been the driving force, then prey mass should have gone up and not down with decreasing density as observed in the experiment. This indicates that density was not the major factor, but that changes in the ratio of predator and prey and the resulting indirect effects were the driving factors.

Small predators were negatively affected by the presence of large predators, as well as fewer prey individuals per small predator. Similarly, large predators showed reduced growth rates at high densities of small

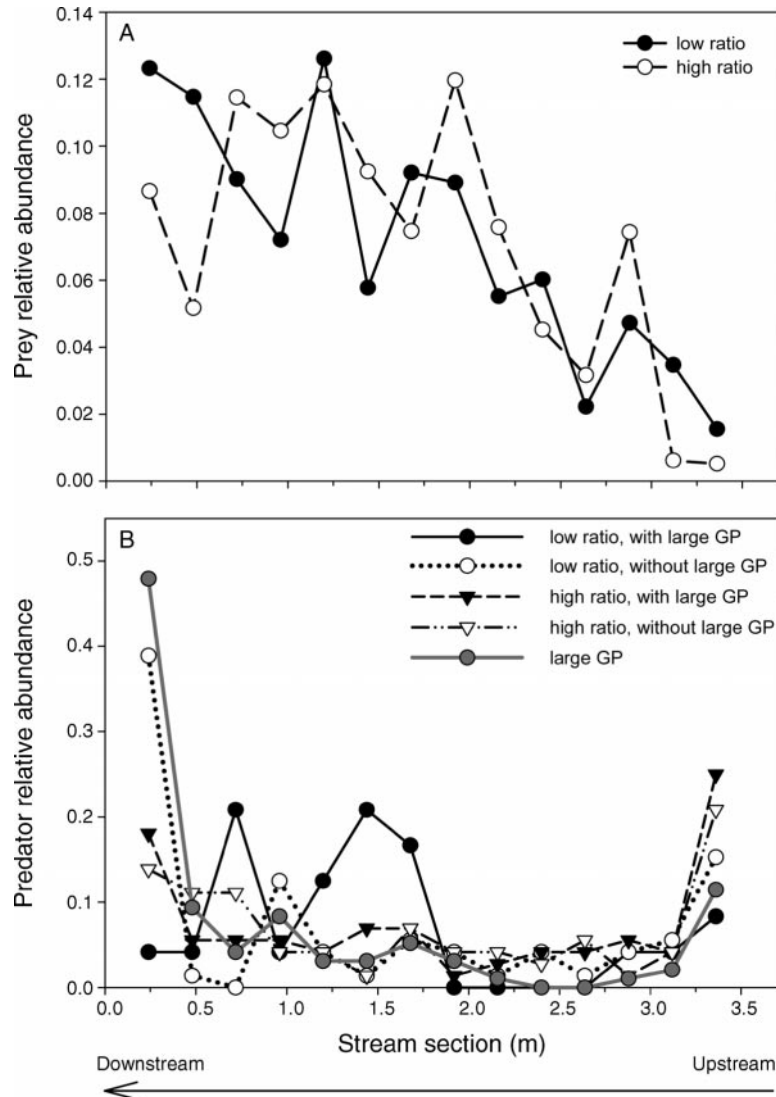


FIG. 4. Microhabitat use by (A) prey (*E. cirrigera*) at different ratios of small predators to prey (low vs. high) and by (B) small predators (*G. porphyriticus*) for each predator treatment. Relative abundance was calculated as the number of individuals in each of 14 stream sections divided by the total number of individuals in the stream averaged across streams for each treatment. Shown are the means ( $\pm$ SE) of three observations grouped by treatment.

conspecifics and fewer prey individuals. This indicates that *E. cirrigera* was an important food source and that there was competition within and between cohorts in the population of the predator. This is consistent with previous studies in which growth rates of small *G. porphyriticus* were increased by densities of *E. cirrigera* and reduced by large conspecifics (Gustafson 1994). Theoretical studies suggest that such intercohort competition in the predator can strongly impact predator-prey population dynamics (review in De Roos et al. 2003).

In the current literature, behavioral indirect interactions are usually termed "trait-mediated indirect interactions" (hereafter TMII; Abrams 1995). This term

has usually been used in systems with at least three species. However, as demonstrated in this study, different size classes within a population often represent distinct functional units and can create nonlethal indirect interactions in two-species systems that are similar to what has been observed in systems with three species. Since the term TMII refers to a similar mechanism, it should be extended to include interactions between distinct functional groups.

Previous studies on TMII have focused on three or more species systems. This study demonstrates that TMII can also strongly affect the dynamics of size-structured predator-prey systems with only two species. Recent observations have indicated that in can-

nibalistic systems, density-mediated indirect effects can lead to increased heterospecific prey abundances (Persson et al. 2003). This study represents a next step towards understanding how the effect of numerical changes on a predator–prey population depends on the population structure. It demonstrates that the impact of a predator can be significantly altered by TMII between different-sized cohorts and between different cohorts and prey. Other studies have shown that large individuals can lead to strong changes in behavior of smaller conspecifics (Greenberg et al. 1997, Biro et al. 2003), suggesting that trait-mediated indirect effects, as observed in this study, are likely to be common in other systems. This suggests that we need to account for the size structure within predator populations to make reliable predictions on how changes in predator abundance affect prey populations. This study focused on within-generation effects. Theoretical models have been very useful in understanding and predicting how direct interactions and density-mediated indirect interactions between cohorts affect long-term population dynamics (e.g., Gurney et al. 1983, Briggs et al. 2000, De Roos and Persson 2003). Future models that account for TMII in size-structured predator–prey systems could give valuable insight into the long-term effects on population and community dynamics.

#### ACKNOWLEDGMENTS

I thank Amy E. Dunham for help in the field, and Henry M. Wilbur, Deborah Roach, Amy E. Dunham, and two anonymous reviewers for their helpful comments on earlier versions of the manuscript, and David Carr for his statistical help. This study was supported by a Mountain Lake Biological Station fellowship.

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#### APPENDIX A

Test of random block effects for survival, growth, activity, and microhabitat variables for prey (*E. cirrigera*) and both predator size classes (*G. porphyriticus*) (*Ecological Archives* E087-021-A1).

#### APPENDIX B

Repeated-measures analyses on treatment and time effects on relative activity of prey (*E. cirrigera*) and both predator size classes (*G. porphyriticus*) (*Ecological Archives* E087-021-A2).

#### APPENDIX C

Repeated-measures analyses on proportional microhabitat use of prey (*E. cirrigera*) and small predators (*G. porphyriticus*) (*Ecological Archives* E087-021-A3).