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Is prey predation risk influenced more by increasing predator density or predator species richness in stream enclosures?

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Abstract The direct lethal impacts and the indirect effects predators have on prey characteristics, such as behavior, have fitness consequences for the prey. Whether the level of predation risk that prey face in the presence of multiple predator species can be predicted from a null model that sums the risk from each predator species in isolation is unclear. In field enclosures, we tested whether the predation risk experienced by *Stenonema* mayfly larvae from a dragonfly larva (*Boyeria vinosa*) and a hellgrammite (*Corydalus cornutus*) together matched the predictions of the multiplicative risk model. We then compared whether any deviations from the model's predictions were larger in the presence of two predator species than in the presence of an equivalent density of individuals from either predator species alone, to determine if unique effects arise for the prey in the presence of multiple predator species. We also determined if prey moved preferentially into predator-free refuge spaces or decreased their movement in the presence of predators. *Stenonema*'s risk of predation was reduced compared to the model's prediction, but no unique multiple predator species effects were present because this risk reduction was comparable in magnitude to the level exhibited in the presence of each predator species alone. The prey did not move into predator-free refuge spaces in the presence of predators in the field enclosures. Thus, these predators appear to interfere interspecifically and intraspecifically, which may facilitate the coexistence of the predators and the prey.

Keywords Dragonfly · Hellgrammite · Mayfly · Multiple predator species · Non-additive

Introduction

Predation is one of the major forces influencing population dynamics and community structure (Paine 1966; Connell 1975; Sih et al. 1985; Sih 1987). Predators can have direct lethal effects and important indirect effects on prey, influencing the abundance, species diversity, morphology, physiology, chemistry, life history, and behavior of prey (Sih 1987; Martin et al. 1989; Lima and Dill 1990). For example, stream predators can cause prey to increase their use of a refuge, decrease their movement, or shift habitats (Stein and Magnuson 1976; Peckarsky and Dodson 1980; Werner et al. 1983; Rahel and Stein 1988; Huang and Sih 1990; Forrester 1994; Kirk and Smock 2000). These behavioral shifts may cause the prey to decrease their foraging efficiency or to increase their risk of running into other predators.

Most predation studies look at the effect of one predator species on a prey assemblage. However, in nature, most prey face multiple predator species simultaneously (Soluk 1993; McIntosh and Peckarsky 1999; Eklov and Van Kooten 2001). To understand natural communities it is important to study the responses of prey to multiple predators and investigate the mechanisms determining the outcome of interactions involving multiple predators (McIntosh and Peckarsky 1999; Eklov and Van Kooten 2001). We are interested in determining whether we can sum (using a null model) the risk of predation from each predator species in isolation to predict the risk of predation when multiple predator species are together. If the prey's risk of predation is additive, experiments examining the

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prey's risk of predation from one predator species at a time are adequate to predict the risk of predation when multiple predator species are present. Some experiments have shown that the risk of predation for prey is additive (Van Buskirk 1988a; Wilbur and Fauth 1990; Sokol-Hessner and Schmitz 2002).

Non-additive predation risk indicates that predicting a prey's risk of predation in multiple predator species systems is more difficult. Non-additivity can occur as risk enhancement or risk reduction for the prey. Risk enhancement indicates facilitation among the predators, and/or changes in prey microhabitats or behaviors that increase their risk of predation (Soluk and Collins 1988; Martin et al. 1989; Losey and Denno 1998; Sih et al. 1998). Risk reduction for the prey indicates negative interactions among predators (interference, intraguild predation), exploitation, and/or changes in prey microhabitats or behaviors that reduce their risk of predation (Soluk and Collins 1988; Huang and Sih 1990; Wissinger and McGrady 1993). Both risk enhancement and risk reduction could potentially influence the distribution and stability of prey populations, but this influence is dependent on characteristics of the prey such as their life history and behavior. Although risk enhancement and risk reduction have been discussed as a consequence of multiple predator species, they can also occur as a consequence of multiple individuals of the same species. It has long been recognized that predators' feeding rates may be positively or negatively influenced by intraspecific density (Schoener 1971; Van Buskirk 1988b; Evans 1991; Peckarsky 1991a; Resetarits 1995; Nilsson 2001). However, the resulting risk enhancement or risk reduction for prey has rarely been discussed in the same context as interspecific non-additivity (Sih et al. 1998). Both types of non-additivity are important for the prey, but non-additivity can only be termed an emergent multiple predator species effect if the magnitude of interspecific non-additivity is larger than the magnitude of non-additivity that occurs due to an increase in intraspecific density (hereafter called intraspecific density-dependence).

Field experiments have been conducted in a wide variety of aquatic systems (Peckarsky 1979; Morin 1981; Walde and Davies 1984; Martin et al. 1989; Resetarits 1991; Eklov and Diehl 1994; Dahl 1998). Methodological differences that might affect interactions between predators and prey, including whether the experiment involves enclosures or exclosures, differences in enclosure size, mesh/fence size, the presence of refuges, the ability of organisms to immigrate/emigrate, the time of year, and the length of the experiment all potentially influence the outcome (Connell 1975; Diamond 1986; Cooper et al. 1990; Peckarsky 1991b; Dahl and Greenberg 1996; Englund and Olsson 1996; Dahl 1998). However, altering predator species composition in enclosures has been useful in evaluating the effects of predation and competition on distribution patterns (Peckarsky 1979).

This paper describes a short-term stream enclosure experiment which examined the level of predation risk mayfly larvae (*Stenonema* sp.) faced from dragonfly larvae (*Boyeria vinosa*) and hellgrammites (*Corydalus cornutus*) alone and together. We asked three main questions:

1. Is the risk of predation to *Stenonema* reduced, enhanced, or additive when faced with a dragonfly larva and a hellgrammite together in the field? These predator species use the same microhabitats on which to feed (rock or wood surfaces), which provides the potential for interference competition between the predators, resulting in risk reduction for the prey.
2. Is any interspecific non-additivity larger in magnitude than any intraspecific density-dependence? If the magnitude of non-additivity and density-dependence are the same, then the risk to the prey is similar in the presence of single and multiple predator species. This result would indicate that no unique properties arise in the presence of multiple predator species.
3. Do *Stenonema* respond to the predators by moving into predator-free refuge spaces when predators are present?

Methods

Study species

The prey used in this study were larvae of the mayfly *Stenonema* (Ephemeroptera: Heptageniidae) in the size range of 7.4–11.4 mm total length. The predator species were *Boyeria vinosa* dragonfly larvae (Odonata: Aeshnidae) and *Corydalus cornutus* hellgrammites (Megaloptera: Corydalidae). These species naturally co-occur and the predators regularly consume mayfly larvae (Evans and Neunzig 1996; Westfall and Tennessen 1996; Kirk and Smock 2000). We used dragonflies with head widths of 6.1±0.15 mm (mean±1 SE) and hellgrammites with head widths of 8.2±0.27 mm (mean±1 SE) because preliminary work showed that individuals of these sizes are unlikely to consume each other (Vance-Chalcraft, unpublished data). All mayflies, hellgrammites, and some dragonflies were collected from Jordan Creek (Vermilion County, Ill.). The remaining dragonflies were collected from Shivering Sands Creek (Door County, Wis.). The predators were held for at least 24 h before being used in an experiment and were not fed for 24 h before being used in an experiment. If held longer than 24 h, the predators were fed live mayflies, oligochaetes, and zooplankton. The prey were held in aquaria with algae-covered rocks as food sources.

Design and methods

Each treatment was run in an independent, randomly selected stream enclosure (40.9×30.3×20.05 cm). The enclosures were placed in Jordan Creek in east-central Illinois, a warm-water stream with predominantly bedrock and coarse gravel as bottom materials. The outside of each enclosure was made of 6.35-mm hardware cloth lined with 800-µm Nitex mesh. This mesh size allowed water and chemical cues to pass through the cage, but constrained the study species within the enclosure. Each enclosure was comprised of three sections of equal size: a center section, an upstream section, and a downstream section. The sections were separated by 6.35-mm hardware cloth lined with 4.8-mm plastic screening. This plastic screening allowed the prey to pass between sections, but not the predators. To deflect debris away from the enclosures and slow the clogging process, we anchored a V-shaped structure made of 25.4-mm hardware cloth, 6.35-mm plastic screening, and re-bar approximately 1 m upstream of each enclosure. To anchor the enclosures in the stream, we placed each enclosure in a PVC frame anchored to re-bar.

We used six experimental treatments: one dragonfly, two dragonflies, one hellgrammite, two hellgrammites, one dragonfly + one hellgrammite, and a no predator control. Each treatment contained 14 *Stenonema* as prey. These densities reflected natural field densities (Vance-Chalcraft, unpublished data). Each treatment was represented once in each of five temporal blocks, for a total of five replicates during July 2002.

Before initiating a block, we added two rocks and one stick to each section of each enclosure. The rocks and sticks were approximately the same size and were haphazardly chosen from a pool of approximately 40 natural stream rocks and 15 sticks that had been in a container with stream water. All invertebrates were removed from the rocks and sticks before being added to enclosures. We added 14 *Stenonema* to the center section of each enclosure. After approximately 10 min, we added 0, 1, or 2 predators to the center section of the appropriate enclosures and sealed each enclosure with cable ties, modeling clay, and duct tape. Hence the predators were constrained to the center section, while the prey could move freely among all three sections of an enclosure. After placing the enclosures in the stream, we recorded the flow rate, water depth, and water temperature approximately 0.5 m upstream of each enclosure. After 2 days, we again recorded the flow rate, water depth, and water temperature approximately 0.5 m upstream of each enclosure, and then inside the center section of each enclosure. We then removed the predators, prey, rocks, and sticks from each enclosure. The number of mayflies remaining, and the section in which they were recovered (upstream, downstream, or center), was recorded. We measured the total length, head width, and wet mass of the predators. Each enclosure was cleaned before being used in another temporal block. All experimental animals were only used once; the rocks and sticks were cleaned and then returned to the container with stream water to be used again.

Statistical analysis

Block effects were included in all analyses. Using ANOVA, we tested whether there were significant differences among the treatments in the environmental conditions present at the beginning or end of each block. To determine whether the predator treatments caused significant prey mortality, we used ANOVA on the proportion of prey missing at the end of the experiment, followed by planned comparisons to determine which treatments significantly differed from the control. We used a two-way ANOVA to determine whether the observed proportion of prey eaten in single predator species treatments was dependent on the identity of the predator species present and/or predator density (one or two individuals present). To account for the loss of individuals not due to predation, the actual proportion of prey eaten within each block in the *x*th treatment (p_x) was calculated as:

$$p_x = (n_c - n_f)/n_c \qquad (1)$$

where n_c is the average final number of prey recovered in the control enclosures (with no predators) and n_f is the final number of prey found in the *x*th experimental enclosure.

To test for non-additivity, we compared the observed predation risk to the predicted values generated by a null model. The null model of additivity that is used to predict the predation risk when two predator species are together and prey depletion occurs is the multiplicative risk model (Soluk and Collins 1988; Soluk 1993; Sih et al. 1998). The multiplicative risk model predicts that the expected proportion of prey killed by a dragonfly larva and a hellgrammite together (p_{DH}) is:

$$p_{DH} = p_D + p_H - p_D p_H \qquad (2)$$

where p_D is the probability of being consumed by a dragonfly in isolation, and p_H is the probability of being consumed by a hellgrammite in isolation. The $p_D p_H$ term in the model accounts for the fact that as prey are eaten by one predator they are no longer available to other predators. We calculated an expected proportion of prey eaten for each enclosure having two predator individuals present by substituting the observed proportion of prey eaten in enclosures with one predator individual into the multiplicative model (Eq. 2). The expected proportion of prey eaten in a particular enclosure was always based on observed proportions of prey eaten that were recorded in enclosures in the same block. Thus, we had an observed and expected proportion of prey eaten for each enclosure with two predator individuals in each block.

We simultaneously determined (1) if non-additivity occurred among the three treatments with two predator individuals, and (2) whether the magnitude of non-additivity was similar across all three treatments by using a two-way ANOVA. The three predator treatments with two predator individuals represent one factor and the categories “observed” and “expected” represent different levels of the second factor. The response variable for each enclosure was proportion of prey eaten (both observed and expected values). The observed and expected proportion eaten for each enclosure are independent of each other because the expected values were derived from information collected from different independent experimental units. If the observed and expected proportions eaten are equivalent, the prey’s risk of predation is additive. A larger observed risk than expected risk would indicate risk enhancement for the prey, while a smaller observed risk than expected risk would indicate risk reduction for the prey. In the case of the single species treatments, additivity can be interpreted as a lack of density-dependence in the predators’ feeding rate. A larger observed rate than expected rate would indicate positive density-dependence, while a smaller observed rate than expected rate would indicate negative density-dependence in the predators’ feeding rates. Although interpretation of the treatment effect is meaningless (as it pools both observed and predicted values within a treatment), a non-significant interaction between the factors “treatment” and “observed versus expected” would indicate that the magnitude of non-additivity does not differ among treatments. In this case, any between-species non-additivity could not be larger than any within-species density-dependence, indicating that no unique properties arise in the presence of multiple predator species. However, if a significant interaction occurred, we used one-way ANOVA to compare the magnitude of the deviation between the observed and expected proportion eaten for the dragonfly + hellgrammite combination to the magnitude of the combined deviations for the two intraspecific combinations (two dragonflies, two hellgrammites) to determine if unique properties arose in the presence of multiple predator species.

We used one-way ANOVAs to determine if the treatments (including the control) differed in the proportion of the final number of surviving prey that moved out of the center away from the predator(s), moved into the upstream section, or moved into the downstream section. Systat version 10.0 (SPSS) was used for all statistical analyses.

Results

There were no significant differences among the treatments in the environmental conditions (flow rate, water depth, and temperature) present at the beginning or the end of each block (all $P>0.05$). All predator treatments caused a significant amount of prey mortality, compared to the control (all $P<0.05$). The two predator species consumed similar proportions of prey ($F_{1,4}=1.513$; $p=0.286$), and there were no differences in the observed proportions of prey consumed by one or two predator individuals ($F_{1,4}=0.126$; $P=0.740$). There was no significant interaction between predator species identity and predator density ($F_{1,4}=0.736$; $P=0.439$).

The observed and expected proportions of prey eaten did significantly differ ($F_{1,4}$=9.876; P=0.035). Specifically, the observed proportion of prey eaten was significantly less than the model's predictions. There was no significant interaction between the "treatment" and "observed versus expected" factors ($F_{2,8}$=0.363; P=0.706), indicating that the strength of the non-additivity did not differ among the treatments and the between-species non-additivity was not larger than the within-species density-dependence. Thus, the prey experienced risk reduction in all three treatments in which two predators were present (Fig. 1) and no unique properties arose in the presence of multiple predator species (Fig. 2). With the two dragonfly and the two hellgrammite combinations, the non-additivity can be interpreted as negative density-dependence in the predators' feeding rates.

The predator treatments did not differ from the control in the proportion of the final number of surviving prey that moved out of the center (regardless of direction) ($F_{5,20}$=0.109; P=0.989; Fig. 3), moved upstream ($F_{5,20}$=0.698; P=0.631), or moved downstream ($F_{5,20}$=0.394; P=0.847). Thus, the prey did not appear to increase use of the predator-free sections in the presence of predators. The prey in this system exhibited no behavioral shift that we could detect by looking only at their position at the end of the experiment.

Discussion

The prey's risk of predation was strongly reduced with the combination of a dragonfly and a hellgrammite together compared to the model's predictions, but this risk reduction was not significantly larger in magnitude than the negative intraspecific density-dependence. Thus, there is no evidence that unique properties arise when these predator species are combined that do not occur by merely increasing predator density (Sih et al. 1998). Other studies that have compared intraspecific interactions to interspecific interactions have found similar results (Evans 1991; Peckarsky 1991a; Vance-Chalcraft 2003).

However, unique properties will sometimes be associated with the presence of multiple predator species. Losey and Denno (1998) demonstrated risk enhancement for pea aphids in the presence of foliar-foraging and ground-foraging predators together. The mechanism for this risk enhancement was a "dropping" behavior of the aphid in the presence of the foliar-foraging predator that increased its risk of predation from the ground-foraging predator (Losey and Denno 1998). Increasing the number of foliar-foraging predators in isolation would not be expected to influence the prey's risk of predation to the same degree as adding the presence of the ground-foraging predators. Likewise, Soluk and Richardson (1997) found that, in the presence of trout and predaceous stoneflies,

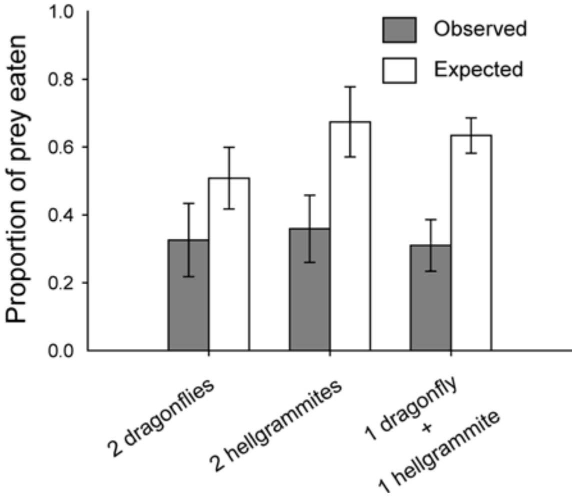

Fig. 1 Mean (±1 SE) observed and expected proportion of *Stenonema* mayfly larvae eaten for each predator combination with two predator individuals present. The observed − expected predation risk was, on average, −0.18 for the two dragonfly (*Boyeria vinosa*) combination, −0.32 for the two hellgrammite (*Corydalus cornutus*) combination, and −0.32 for the dragonfly + hellgrammite combination

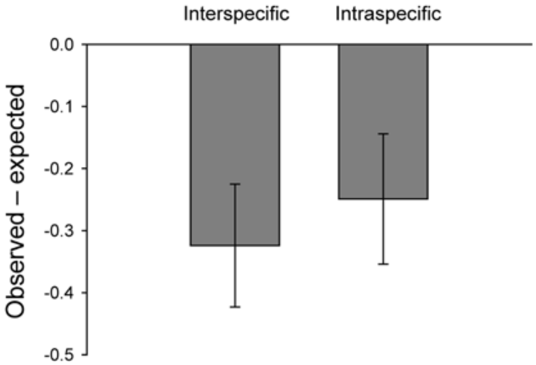

Fig. 2 Mean (±1 SE) deviations from expected (observed − expected proportion eaten) for the dragonfly + hellgrammite combination and both intraspecific pairs combined

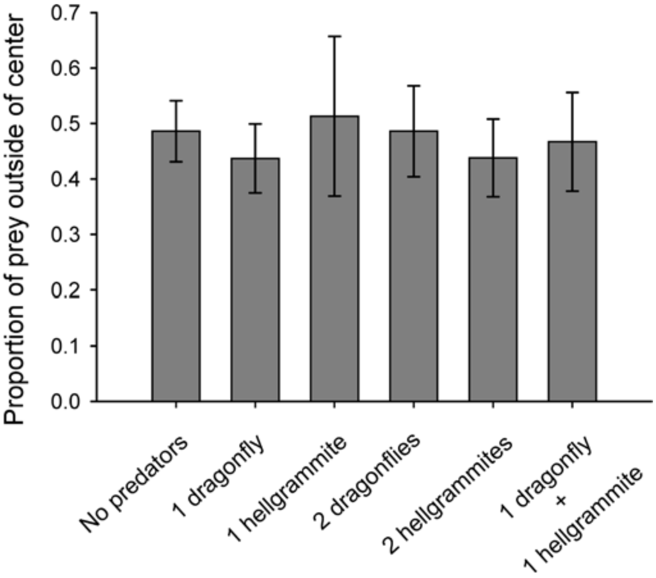

Fig. 3 Mean (±1 SE) proportion of the final number of surviving prey that moved out of the center section of the field enclosures, into a predator-free section (regardless of direction)

mayflies more frequently moved into areas where they were at a greater risk from trout than they did when stoneflies were not present. The mayflies' risk of predation was likely enhanced more in the presence of these two predator species together than they would have been from higher numbers of either predator species alone (Soluk and Richardson 1997). More studies examining the relationship between increasing predator density and increasing the number of predator species would help elucidate other potential mechanisms producing emergent properties in the presence of multiple predator species.

Intraspecific density-dependence in predators' consumption rates has been widely reported (Schoener 1971; Nilsson 2001). In many cases, intraspecific interactions appear to be as important as interspecific interactions (Evans 1991; Peckarsky 1991a), so a term accounting for predator density-dependent interactions (e.g., Hassell et al. 1976) may need to be added to models predicting the combined consumption rates of multiple predators whether or not they belong to multiple species. This term would provide a "correction" for predator density-dependent interactions. For our system, focusing on density-dependent interactions would lead to a more predictive model than focusing on the number of predator species present.

For many aquatic organisms, the survival of an individual depends critically on its success in obtaining a refuge (Connell 1975; Sih et al. 1985; Peckarsky and Penton 1989; Eklov and Diehl 1994; Diehl 1995; Kirk and Smock 2000). Likewise, stream prey often move or drift in response to predators (Walton 1980; Peckarsky and Penton 1989; Rader and McArthur 1995). The combination of refuge use and prey movement typically reduces the predator-prey encounter rate, and thus the prey's risk of predation (Walton 1980). In contrast, prey movement can attract the attention of a visually-orienting predator, such as a dragonfly (Folsom and Collins 1984; McPeek 1990), and decreasing activity can be an effective anti-predator behavior in the presence of these predators (Folsom and Collins 1984). However, in our experiment the prey did not preferentially move into the predator-free sections in the presence of predators. In fact, the prey exhibited no behavioral response at all that we could detect by looking only at the section in which they were located at the end of the experiment. Thus, the prey either shifted microhabitats within the enclosures at smaller scales than we could detect, used defenses that do not rely on movement, or exhibited no anti-predator defenses.

In summary, the prey experienced strong risk reduction in the presence of a dragonfly and a hellgrammite together in the field. In this system it appears that the strength of risk reduction with an increased predator density is similar regardless of whether predator individuals are of the same or different species. Thus, future experiments should examine whether the distribution of these predators and prey is influenced more by the number of predators in an area or the number of species in an area. The prey did not preferentially move into predator-free sections of the enclosures in treatments where predators were present. Instead, it is likely the prey relied on smaller-scale movements and cryptic coloration as defenses against these predators.

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