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Estimating the prevalence and strength of non-independent predator effects

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Abstract Understanding whether multiple predator species have independent effects on shared prey is critical for understanding community dynamics. We describe the prevalence and strength of non-independence between predators by quantifying the prey's risk of predation and the degree to which it deviates from the risk predicted from a null model of independent predator effects. Specifically, we document how frequently non-independent effects occur among ten different multiple predator combinations with mayfly larvae as prey. These predator combinations vary both predator density and predator species richness. Overall, the predator effects were non-independent and translated to an average of 27% fewer prey being consumed compared to independent predator effects. Non-independence of this magnitude is likely to have population level consequences for the prey and influence the distribution or prey preference of predators. Closer inspection shows that much of the risk reduction in this system is weak, to the point of being indistinguishable from independent predator effects, while few effects are strong. This pattern of many weak interactions and few strong ones parallels the pattern of interaction strengths documented previously in intertidal communities. Consequently, understanding strong interactors in multiple predator systems may help us understand the importance of a species.

Keywords Effect size · Independent predator effects · Multiple predator species · Risk reduction · Trait-mediated interactions

Introduction

Understanding whether multiple predator species have independent (i.e., additive) effects on their shared prey is critical for understanding community dynamics (Soluk and Collins 1988a; Wilbur and Fauth 1990; Sih et al. 1998). Non-independent (i.e., non-additive) predator effects can raise (risk enhancement) or lower (risk reduction) a prey's risk of predation in the presence of multiple predator species (see review in Sih et al. 1998). Whether non-independent outcomes are present in the form of risk enhancement or risk reduction will influence whether the prey's population growth rates are higher or lower than those predicted by independent predator effects (e.g., Losey and Denno 1998a; Cardinale et al. 2003). Both risk enhancement (Soluk 1993; Swisher et al. 1998; Losey and Denno 1998a) and risk reduction (Rosenheim et al. 1993; Soluk 1993; Crowder et al. 1997) are known to occur in natural and agricultural systems, but risk reduction seems to occur more commonly than risk enhancement when compared across disparate systems (Sih et al. 1998). In this manuscript we focus on the prevalence and strength of risk reduction and risk enhancement among multiple combinations of predators that occur in the same system.

Some factors are known to produce predator effects that are not independent, including trait-mediated interactions (Wissinger and McGrady 1993; Wootton 1993; Abrams 1995; Sih et al. 1998; Bolker et al. 2003), intraguild predation between predators (Gustafson 1993; Rosenheim et al. 1993; Wissinger and McGrady 1993), or predator attack rates on prey that change with predator or prey density (Sih et al. 1998). Furthermore, there are particular conditions under which risk enhancement and risk reduction, specifically, are likely to occur. Risk enhancement occurs when one predator

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species elicits a phenotypic response from prey that increases its overall vulnerability to predation from other species (Rahel and Stein 1988; Soluk and Collins 1988b; Kotler et al. 1992). These effects are most likely in instances where predators put conflicting demands on the prey (spatially, temporally, or behaviorally) such as when predators forage in different microhabitats (e.g., Losey and Denno 1998a; Soluk and Collins 1988c). However, conflicting prey defenses do not always produce risk enhancement (e.g., Krupa and Sih 1998). Risk reduction occurs when one predator species elicits a phenotypic response from the prey or other predator such that the prey is now less accessible to the predators (Soluk and Collins 1988a; Adler and Morris 1994; Wootton 1994; Werner and Peacor 2003). These effects are most likely when: (1) predators directly interfere with each other, (2) there is potential for intraguild predation between the predators, (3) there is substantial exploitative competition between the predators, or (4) when the prey have a generalized response to one predator that is also effective against other predators.

Risk reduction and risk enhancement have the potential to cancel each other. Whether prey's overall risk of predation in a community is enhanced or reduced will depend upon both the prevalence and strength of both kinds of effects. The net strength of risk enhancement and risk reduction can be quantified as the natural log of the ratio of the observed and expected (if predator effects were independent) final densities in a multiple predator treatment. This ratio is a form of the log response ratio (Osenberg et al. 1997; Hedges et al. 1999), and we use it as our measure of the strength of non-independence. Measuring the strength of non-independent effects is important in order to determine if they are likely to be large enough to influence community dynamics (Osenberg et al. 2002; Luttbeg et al. 2003). If these effects are large, then food web models of natural communities need to incorporate these emergent properties (see Schmitz and Sokol-Hessner 2002; Sokol-Hessner and Schmitz 2002).

The pattern of interaction strengths in communities is thought to be skewed toward many weak interactions and few strong ones (Paine 1992). Non-independent predator effects, however, cause the value of interaction strengths to change. Consequently, it is important to know whether most multiple predator effects are weak and have little influence on interaction strengths or whether most multiple predator effects have strong effects that could alter the way in which interaction strength values are distributed among community members. This question has received little attention in the multiple predator literature.

Although examination of the independence of predator effects has recently focused on interactions between multiple predator species (Sih et al. 1998), non-independence between individuals of the same species also occurs (Hassell 1978; Van Buskirk 1989; Resetarits 1995; Nilsson 2001). In a review of emergent multiple predator effects, Sih et al. (1998) describe the importance of

determining if non-independent predator effects between species are different from those within species. Thus, one can discover whether predator effects are substitutable such that their effects can be predicted on the basis of the number of "predator functional units" (Sih et al. 1998). However, most multiple predator studies have used designs that confound the presence of multiple predator species with increased predator density (but see Evans 1991; Vance-Chalcraft et al. 2004). In this manuscript, we avoid this confounding factor by including both inter- and intra-specific combinations of predators at the same density to evaluate whether non-independent interactions between multiple predator species differ from those between conspecifics.

In this study, we quantified the net strength of risk enhancement and risk reduction for ten pairwise combinations of four predator species that occur in a common system, determined if the magnitude of non-independence differed for inter- and intra-specific predator combinations, and tested whether risk enhancement would result when predators foraged in different microhabitats (creating the potential for conflicting prey defenses) and risk reduction would result when predator-predator interactions were present. The predators were selected to represent a range of phenotypic characteristics (e.g., microhabitat use and foraging modes) thought to influence the likelihood of risk enhancement and risk reduction for prey (mayfly larvae) (Sih et al. 1998). By making these comparisons, we address some of the most important gaps in our understanding of the nature of multiple predator effects and their influence on both prey populations and the structure of natural communities.

Study system and a priori expectations

We used a diverse array of stream predators that are widespread in distribution, common, co-occur in many streams in the Midwestern USA, and regularly include mayflies in their diets: dragonfly larvae (*Boyeria vinosa*), hellgrammites (dobsonfly larvae: *Corydalus cornutus*), greenside darters (*Etheostoma blennioides*), and young creek chubs (*Semotilus atromaculatus*). Dragonfly larvae and hellgrammites typically forage on benthic rock surfaces (Roell and Orth 1991; Galbreath and Hendricks 1992; Kirk and Smock 2000); greenside darters and creek chubs typically take prey either off the top surfaces of stones or from the drift (Smith 1979; Magnan and FitzGerald 1984; Welsh and Perry 1998). *Stenonema* mayfly larvae (Ephemeroptera: Heptageniidae) (5.4–11.4 mm total length) were used as prey. They graze on benthic periphyton, crawl to change microhabitats, and typically reduce their movement, and rely on cryptic coloration when predators are near (Peckarsky 1980; Jacobi and Benke 1991; Peckarsky and Cowan 1995). When preying on *Stenonema*, the dragonflies and hellgrammites are primarily ambush predators while the darters and creek

chubs are actively searching predators (Vance-Chalcraft and Soluk, unpublished data). Based on these foraging characteristics and the mechanisms leading to risk enhancement and risk reduction described above, we had a priori expectations for the type of multiple predator effects produced by each predator combination (Table 1).

Methods

We ruled out intraguild predation in our study by limiting predator sizes to large dragonfly (mean head width = 6.1 ± 0.15 mm) and hellgrammite larvae (mean head width = 8.2 ± 0.27 mm) and relatively small fish (mean mass = 3.3 ± 0.2 g for darters and 9.8 ± 1.2 g for creek chubs). Preliminary experiments (Vance-Chalcraft, unpublished data) showed that individuals of these sizes were unlikely to consume each other and none of the predators were consumed in this study. Thus, any non-independence in this system cannot be due to density-mediated effects. However, the predators could still perceive intraguild predation as a threat, even if it was unlikely to occur, and could therefore still cause trait-mediated effects.

All species used in this experiment naturally co-occur and were collected from the Vermilion River drainage system (Vermilion County, IL) or Shivering Sands Creek (Door County, WI). Before being used in an experiment, invertebrates were held in a cold room for at least 24 h and fish for at least 1 week. *Stenonema* were held in aquaria with algae-covered rocks as food and the predators were fed live mayfly larvae, oligochaetes, or zooplankton. Fish diets were supplemented with frozen mosquito larvae. All predators were starved for 24 h before being used in an experiment.

Multiple predator experiment

We used 15 experimental treatments (Table 2) to: (1) measure the impact of each predator species in isolation to predict the combined impact of two predators assuming independent effects, (2) measure the strength of non-independence between predators and determine if the direction of that non-independence matches our expectations (Table 1), and (3) determine if the magnitude of non-independence between multiple predator species is larger than that between conspecifics. Each treatment consisted of 30 *Stenonema* mayfly larvae (161.5 larvae/m²) and 0, 1, or 2 predator individuals (0 , 5.4 , and 10.8 individuals/m²) of 0, 1, or 2 species (Table 2). These densities reflected natural field densities (Vance-Chalcraft, unpublished data). Each treatment was represented once in each of nine temporal blocks, for a total of nine replicates.

Within each temporal block, each of the 15 treatments was randomly assigned to an independent, recirculating 30.48 cm \times 30.48 cm \times 60.96 cm stream tank (Soluk and Collins 1988a) with an average current velocity of 0.12 m/s. Barriers between stream tanks prevented visual interactions between organisms in different aquaria. Stream tanks were located in a controlled environmental chamber at 17°C , with a 12 h light:12 h dark cycle to approximate natural spring conditions. Room lighting was broad-spectrum fluorescent.

Before each temporal block, reconditioned deionized water (approximately 56 l), an air diffuser, and nine large rocks were added to each stream tank. Rocks were haphazardly chosen from a pool of approximately 300 natural stream rocks kept for at least 2 weeks in a tank illuminated with a broad-spectrum actinic algae growth lamp to encourage algae and periphyton growth. After 24 h, we added 30 *Stenonema* mayfly larvae to each

Table 1 A priori expectations for the type of multiple predator effects produced by each multiple predator combination

Treatment	Risk enhancement	Risk reduction			Outcome expected
	Different foraging microhabitats	Interference competition	Threat of IGP	Generalized prey defenses	
BH	No	Yes	No	Yes	Risk reduction (mainly from interference)
BD	Yes	No	Yes	Yes	Risk reduction (mainly from threat of IGP)
BC	Yes	No	Yes	Yes	Risk reduction (mainly from threat of IGP)
HD	Yes	No	Unlikely	Yes	Risk enhancement
HC	Yes	No	Unknown	Yes	Risk enhancement
DC	No	Yes	Yes	Yes	Risk reduction
BB	No	Yes	No	Yes	Risk reduction (mainly from interference)
HH	No	Yes	No	Yes	Risk reduction (mainly from interference)
DD	No	Yes	No	Yes	Risk reduction (mainly from interference)
CC	No	Yes	No	Yes	Risk reduction (mainly from interference)

Some mechanisms producing risk enhancement and risk reduction are listed as columns (IGP, intraguild predation). Whether we found each of the mechanisms likely for each treatment (B, *Boyeria* dragonfly; H, hellgrammite; D, darter; C, creek chub where each letter stands for one predator individual) is shown along with our conclusion about which outcome was most likely based on what we hypothesized to be the relative strengths of the varying

mechanisms. These expectations were based on our knowledge of the system, not any specific experiments. Interference competition was thought to be most likely when predators foraged in similar microhabitats. Actual IGP was prevented in the experiment reported here by using predators of a size that were unlikely to consume each other, but the threat from IGP was still present.

treatment. Two hours after adding the mayflies, we haphazardly chose predators from a holding tank and added them to the appropriate treatments. Lids were placed on each tank to prevent escape by any experimental organisms. After 4 days, the predators and surviving mayfly larvae were removed and each tank was drained. Predator and prey individuals were used only once.

Statistical analysis

We tested whether each predator treatment caused significant prey mortality using ANOVA on the proportion of prey missing at the end of the experiment, followed by multiple comparisons with Bonferroni adjustments which contrasted the effect of each predator treatment to the control treatment with no predators.

We calculated the predicted survival when interactions between predators were independent for each replicate with two predator individuals present ($\bar{\sigma}_{A+B}$) as:

$$\bar{\sigma}_{A+B} = \frac{(\sigma_A)(\sigma_B)}{(\sigma_{NP})} \tag{1}$$

where σ_A is the proportion of prey that survive in the presence of one predator, σ_B is the proportion of prey that survive in the presence of the other predator, and σ_{NP} is the proportion of prey that survive when no predators are present (Vonesh and Osenberg 2003). The expected proportion of prey surviving in a particular tank was always based on observed proportions of prey surviving in tanks in the same block. Thus, we had an observed and expected proportion of prey surviving for each tank with two predator individuals in each block (Table 2). The observed and expected proportion surviving for each replicate are independent of each other because the expected values were derived from information collected from different independent experimental units.

We estimated the strength of non-independence between predators on the per-capita rate of prey population growth by calculating the log response ratio of observed and expected proportions of survivors for each tank having two predator individuals present for each block as:

$$\ln \left[\frac{\sigma_{A+B}}{\bar{\sigma}_{A+B}} \right] \tag{2}$$

where σ_{A+B} and $\bar{\sigma}_{A+B}$ are the observed and expected proportion of prey surviving, respectively. We used this log response ratio as our measure of the strength of non-independence because it has a clear biological meaning: it is the change in the instantaneous mortality rate due to non-independent predator effects. If it is equal to zero, then interactions between predators are independent. A positive strength of non-independence would indicate risk reduction for the prey, while a negative strength of

Table 2 The mean observed and expected proportions of prey surviving for all 15 experimental treatment species combinations (see “Methods” for description of calculations). The standard errors are in parentheses

	Treatments														
	One dragon-fly	One hellgram-mite	One darter	One creek chub	Two dragon-flies	Two hellgram-mites	Two darters	Two creek chubs	One dragon-fly, one hellgram-mite	One dragon-fly, one darter	One dragon-fly, one creek chub	One hellgram-mite, one creek chub	One hellgram-mite, one darter	One darter, one creek chub	No predators
Observed	0.789 (0.025)	0.726 (0.048)	0.581 (0.051)	0.693 (0.055)	0.748 (0.024)	0.644 (0.060)	0.593 (0.059)	0.674 (0.055)	0.674 (0.057)	0.604 (0.046)	0.659 (0.054)	0.637 (0.066)	0.537 (0.069)	0.478 (0.046)	0.985 (0.006)
Expected	N/A	N/A	N/A	N/A	0.638 (0.041)	0.551 (0.066)	0.365 (0.063)	0.511 (0.075)	0.580 (0.041)	0.464 (0.040)	0.555 (0.050)	0.517 (0.055)	0.423 (0.042)	0.407 (0.044)	N/A

non-independence would indicate risk enhancement for the prey. This measure of the strength of non-independence has desirable statistical properties: it is affected equally by changes in either the numerator or denominator, its sampling distribution is approximately normal, and it is one of the least biased effect size metrics (Osenberg et al. 1997; Hedges et al. 1999). This effect size is also related to those used in reviews of the effects of predation in streams (Cooper et al. 1990; Englund et al. 1999) and to quantify the effects of treatments on per-capita rates of change (Osenberg et al. 1997, 1999).

We estimated the strength of overall non-independence by calculating the mean strength of non-independence for all treatments combined that consisted of two predator individuals (i.e., all single and multiple predator species combinations) and then used a one-sample *t*-test to determine if this mean strength of non-independence significantly differed from zero. We determined whether the magnitude of non-independence was similar across all ten treatments with a one-way ANOVA. If the magnitude of non-independence did not differ among treatments, any interspecific non-independence could not be larger than any intraspecific non-independence, indicating that no unique properties arose in the presence of multiple predator species. If the treatments differed in their magnitude of non-independence, we used one-way ANOVAs to compare the strength of non-independence for each multiple predator species combination (e.g., the darter+creek chub combination) to the mean strength of non-independence of the two corresponding intraspecific combinations (e.g., the combined deviations of the two darter combination and the two creek chub combination) to determine whether non-independence was stronger when conspecifics or heterospecifics were together.

We used one-tailed *t*-tests to determine if the strength of non-independence of each treatment differed from zero in the direction (risk reduction vs risk enhancement) predicted (Table 1). In eight of the ten multiple predator treatments the prey were predicted to experience risk reduction; in the other two multiple predator treatments (i.e., one hellgrammite and one darter, one hellgrammite and one creek chub), the prey were predicted to experience risk enhancement (Table 1). Block effects were included in all analyses, except the *t*-tests.

Results

There were significant treatment effects ($F_{14,112} = 5.899$; $p < 0.001$) on the proportion of prey missing at the end of the experiment. All predator treatments significantly reduced prey survivorship relative to the control (all $p < 0.05$).

The overall predator effects were not independent and resulted in risk reduction for the prey (strength of non-independence = 0.243; $t_{89} = 5.128$; $p < 0.001$). The overall ANOVA detected no significant difference in the

magnitude of non-independence among treatments ($F_{9,72} = 0.884$; $p = 0.544$), indicating that the strength of risk reduction was similar among treatments (Fig. 1). Thus, the predators had non-independent effects when multiple predator species or multiple individuals of the same species were present.

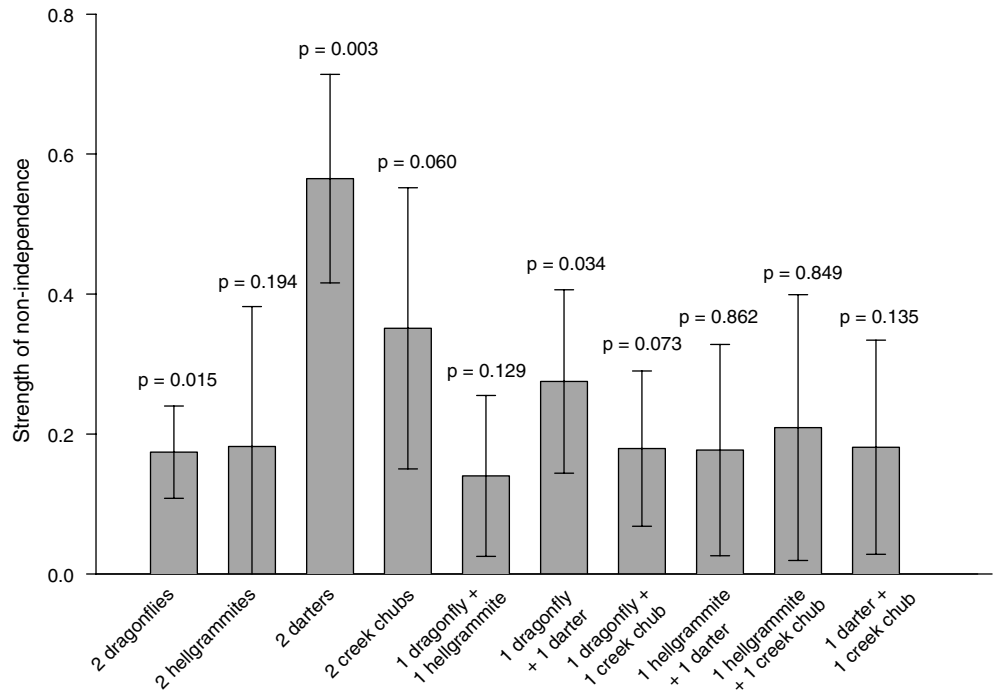
Three of the eight treatments where prey were predicted to experience risk reduction (Table 1) had significant risk reduction (two dragonflies, two darters, one dragonfly and one darter; Fig. 1), and another two of those treatments had marginally significant risk reduction (two creek chubs, one dragonfly and one creek chub; Fig. 1). Neither of the treatments predicted to experience risk enhancement (Table 1) had significant risk enhancement (Fig. 1). A test of combined independent probabilities (Sokal and Rohlf 1981) using the results for each multiple predator combination confirmed the earlier *t*-test results that there is a significant pattern of overall risk reduction in this system ($p < 0.005$). Thus, we have further evidence for a pattern of overall risk reduction, where the risk reduction is weak (i.e., strength of non-independence < 0.2) in six of ten treatments (including some instances where it is not significantly different from zero) and stronger (i.e., strength of non-independence > 0.2) in the other four treatments.

To further examine the trend of greater risk reduction in the intraspecific predator combinations than in the interspecific predator combinations, we used a post hoc ANOVA to determine if the magnitude of the risk reduction (i.e., the strength of non-independence) was significantly greater for all intraspecific predator combinations combined than all interspecific predator combinations combined. We found that the difference in the magnitude of risk reduction between these two groups was marginally significant ($F_{1,8} = 3.805$; $p = 0.087$), with a higher magnitude of risk reduction in the intraspecific combinations than the interspecific predator treatments (Fig. 2).

Discussion

Our study demonstrates that multiple predator combinations within a common assemblage of predators frequently have unexpected effects on their prey with respect to a null model of independent predator effects. Overall in our system, prey's risk of predation was reduced by the presence of multiple predator species such that 27% fewer prey died (i.e., $e^{\text{strength of non-independence} - 1}$) compared to independent predator effects. Consequently, non-independent predator effects can cause dramatic shifts in the prey's risk of mortality and food web models that assume independence between predators will often predict outcomes that differ substantially from reality. Risk reduction of this magnitude seems likely to have "biologically important" consequences if maintained for prolonged periods of time. For example, if we assume no recruitment, non-independent predator effects may cause prey population abundance to be

Fig. 1 Strength of non-independence (mean \pm ISE) for each treatment containing two predators. The numbers above each bar are the p -values of the individual one-tailed t -tests evaluating whether each treatment's strength of non-independence differed from zero in the direction predicted (Table 1). All the treatments were tested for a positive deviation from zero except the treatments with one hellgrammite and one darter and those with one hellgrammite and one creek chub, which were tested for a negative deviation from zero



substantially larger over the course of a summer because many fewer individuals would be removed from the prey population than would be predicted from independent predator effects. Moreover, the predators would either consume considerably fewer prey than they would if other predators were not present in the area, be forced to switch to a different prey type, or move to a different area. Thus, there may be important implications for the distribution and prey preference of predators, including potentially strong advantages for the predators that space themselves widely to avoid strong negative effects.

While risk reduction was generally prevalent in this system, the strength of these effects with some predator

combinations was too small to be classified as statistically significant. The basic pattern of the strength of risk reduction in this system parallels the distribution of interaction strengths reported for the intertidal zone (Paine 1992) with many weak interactions and few strong ones. This pattern suggests that the distribution of interaction strength values in a community may not be greatly effected if strong non-independent effects are not common. If this pattern holds for other multiple predator systems, identifying “strong interactors” may provide insight into the potential “importance” of a species. This view may then allow us to better understand the complexity that arises from the presence of multiple predator species in a system.

Although we could not detect significant risk reduction in all of the multiple predator combinations, we found no evidence of risk enhancement. This is surprising because we expected to find risk enhancement when a hellgrammite and a fish (either darter or creek chub) were present together. In these situations, we thought the prey would potentially face conflicting defenses if they moved off of the rocks to avoid the hellgrammites. Instead, these treatments had independent predator effects. The prey may have avoided having their risk enhanced by using a generalized prey response that involved a decrease in movement and a reliance on cryptic coloration, if they used this defense in an amount relative to predator density.

The non-independence between some of the predators was most likely due to trait-mediated interactions instead of intraguild predation between predators or changes in predator attack rates on prey with changes in prey density (i.e., non-linearities in predator-prey

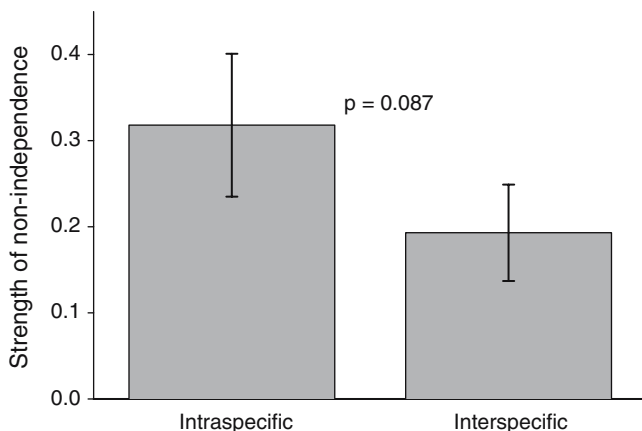


Fig. 2 Strength of non-independence (mean \pm ISE) for all treatments containing one predator species with two individuals (intraspecific) vs those containing two predator species (interspecific)

interactions). We sized our predators such that intraguild predation was not likely. Moreover, we previously tested for non-linearities in two separate experiments with these same predator species. One experiment verified that the instantaneous rate of prey consumption (i.e., \ln [proportion of prey consumed]/unit time) by a predator species is constant for the length of the experiment (Vance-Chalcraft 2003). The other experiment found that neither predation rates nor the magnitude of non-independence between predator effects was influenced by prey density (Vance-Chalcraft and Soluk 2005). This indicates that non-linearities with prey density likely do not explain the risk reduction in this system.

The fact that risk reduction was prevalent may be simply explained if *Stenonema's* generalized defenses (decreased movement and cryptic coloration) (Peckarsky 1980; Jacobi and Benke 1991; Peckarsky and Cowan 1995) were effective against all these predators simultaneously and if the prey decreased movement as a function of predator density. Results of an experiment with these predator combinations and a different mayfly type (*Isonychia* spp.) support this idea. *Isonychia* have a very different antipredator response (they actively flee or drift in response to a threat) and multiple predator experiments using them as prey have found risk enhancement and additivity instead of risk reduction with the same predator combinations (Vance-Chalcraft 2003). Thus, in order to determine how frequently risk enhancement vs risk reduction occurs, it may be necessary to understand how commonly prey use generalized defenses, and how often these generalized defenses are effective against a diverse suite of predators (Sih et al. 1998).

Although having generalized defenses may explain the prevalence of risk reduction, it does not explain the variation in the strength of risk reduction. The risk reduction was only strong when two dragonflies, two darters, or a dragonfly and a darter were together. The intraspecific risk reduction likely was caused by interference between conspecifics. The risk reduction with the dragonfly and darter combination (and marginal risk reduction with the dragonfly and creek chub combination) may have been due to the threat of intraguild predation even though intraguild predation itself was not possible (e.g., Wissinger and McGrady 1993). The dragonflies and darters (or creek chubs) may have viewed each other as intraguild prey and predators, respectively, even though the dragonflies were extremely large in comparison to the darters' typical prey items.

Irrespective of the mechanism behind the risk reduction, it is clear that in this system increasing the number of predators can produce non-independent effects of a magnitude similar to that produced by increasing the number of predator species. This might seem to suggest that all multiple predator effects are simply density effects. However, other studies have identified unique mechanisms for non-independence with multiple species combinations that are not present with single species combinations. For example,

conflicting predator-specific defenses (Soluk and Richardson 1997; Losey and Denno 1998a, b) are unlikely to occur when multiple individuals of the same species are present, but may occur in the presence of multiple predator species. Thus, prey risk enhancement may be more likely when multiple predator species are present, whereas risk reduction may be equally likely when conspecific or heterospecific predators are present. Since generalized prey defenses can be effective against predators comprised of one or multiple species, there may be a selective advantage to these generalized defenses over predator-specific defenses. Consequently, one would expect generalized defenses to be more prevalent than predator-specific defenses.

Although this is a short-term lab experiment, we believe that our results reflect outcomes in natural systems. This experiment incorporated aspects of natural diversity by using predator combinations that are extremely similar (intraspecific combinations) and those that are very diverse (interspecific combinations) in terms of their behaviors, microhabitat use, and foraging modes (Vance-Chalcraft and Soluk, unpublished data). In addition, we previously found strong non-independence between dragonflies and hellgrammites in a stream enclosure experiment (Vance-Chalcraft et al. 2004). Thus, the non-independence we saw in our lab experiment was still easily detectable in a natural stream where there is certainly greater environmental heterogeneity than in our lab experiment. However, we know that structural habitat complexity is important because it influences the encounter rates between predators and prey, as well as between different predator individuals (Swisher et al. 1998). Consequently, our results could change in a habitat with more structural complexity than our stream tanks provided.

In summary, our results indicate that risk reduction may be prevalent for prey in the presence of multiple predators whether these predators are from the same or different species. However, frequently the strength of the risk reduction may be weak to the point of being indistinguishable from independent predator effects. This system contains many weak examples of risk reduction and a few strong ones. Overall, these create a general risk reduction effect that is not trivial and may be sufficient to have important population level consequences for the prey and predators. The risk reduction in our system is likely caused by trait-mediated indirect effects. Since most prey are faced with many competitors and predators in nature, experiments using many predator and prey species are now fundamental to obtaining an accurate understanding of the processes structuring natural and agricultural food webs.

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