

## Linearity in the aggregate effects of multiple predators in a food web

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### Abstract

Theory in community ecology often assumes that predator species have similar indirect effects and thus can be treated mathematically as a single functional unit (e.g. guild or trophic level). This assumption is questionable biologically because predator species typically differ in their effects, creating the potential for nonlinearities when they coexist. We evaluated the nature of indirect effects caused by three species of hunting spider predators, singly and in multiple species combinations, on grass and herb plants in experimental old-field food webs. Despite the potential for nonlinearity, indirect effects in different multiple predator combinations consistently did not differ significantly from the respective means of the single species effects. Thus, for this experimental system, the whole was simply the average of the parts. Consequently, models which abstract predator species as single trophic levels would successfully predict indirect effects in this system regardless of the composition of the predator fauna.

### Keywords

Food web interactions, indirect effects, hunting spiders, grasshoppers, old-field food web, trophic interactions, multiple predators.

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### INTRODUCTION

Understanding the indirect effects of different predator species on food webs is critical to the development of ecological theory (Sih *et al.* 1998) and to forecasting the impacts resulting from predator species loss (Mittelbach *et al.* 1995; Schoener & Spiller 1996; Yodzis 1998). Much of current theory on food web interactions assumes that different predator species can be treated as a single functional unit such as a guild or trophic level (Oksanen *et al.* 1981; Carpenter *et al.* 1986; Menge & Sutherland 1987; Leibold 1989; Schmitz 1992). This assumption has been repeatedly questioned because such simplification tends to abstract important mechanistic details of individual species (Polis & Strong 1996; Polis *et al.* 2000). Thus, current theory may not adequately capture important dimensions of complexity of natural systems.

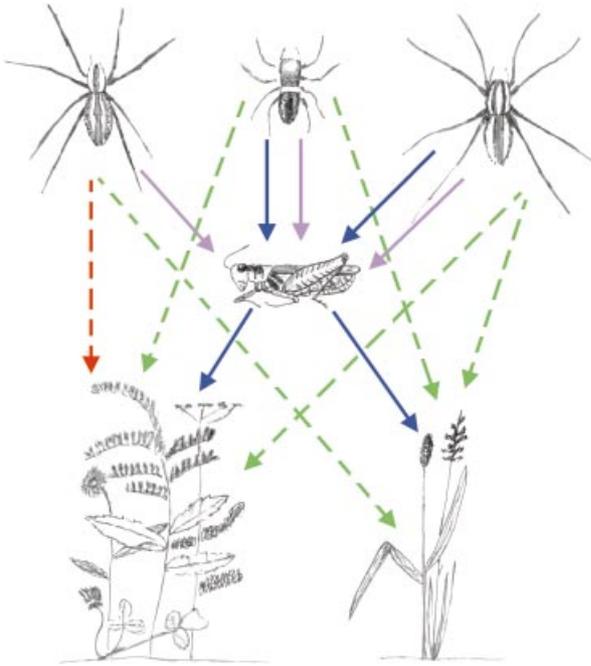
Complexity may arise because individual predator species differ in their habitat use and hunting capabilities, which can translate into differential indirect effects in communities with the same prey species (e.g. McPeck 1998; McIntosh & Peckarsky 1999; Persson 1999; Turner *et al.* 1999; Schmitz & Suttle 2001). These individual differences may lead to emergent nonlinearities when predator species coexist in a

community. This is because a prey species' response to one predator species may change the nature of its interaction with another predator species and consequently its own resources (Chang 1996; Losey & Denno 1998). Also, predators interact not only with their prey but with other predator species via interference competition or intra-guild predation (Spiller 1986; Rosenheim *et al.* 1993; Wise 1993; Moran *et al.* 1996; Rosenheim 1998).

We report on experiments aimed at understanding the emergent indirect effects of multiple predator species in a New England meadow food web. We manipulated combinations of three species of hunting spider predators that individually differ in their food web effects (Fig. 1). We then compared the net indirect effects on grass and herb plants of different predator species combinations with effects emerging in single predator species treatments.

### MATERIALS AND METHODS

The research was completed in a meadow at the Yale–Myers Research Forest in north-eastern Connecticut (see Schmitz & Suttle 2001). The meadow was dominated by the herbs *Solidago rugosa*, *Daucus carota*, *Aster novaeangliae*, and *Trifolium* sp., and the grasses *Phleum pratense* and *Poa pratensis* (Fig. 1).



**Figure 1** Interactions among spiders (from left: *Pisaurina mira*, *Phidippus rimator*, and *Rabidoso rabida*), *Melanoplus femurrubrum* grasshoppers and herbs and grasses in an experimental old-field food web. Blue solid lines indicate direct effects of individual spider species on the numerical abundance of grasshoppers and direct effects of grasshoppers on the numerical abundance of plants. Purple solid lines indicate direct effects of spiders on grasshopper foraging behaviour (feeding time and selection of grasses vs. herbs). The figure illustrates that *P. mira* causes only shifts in grasshopper foraging behaviour whereas *P. rimator* and *R. rabida* cause both behavioural shifts and numerical effects. These direct effects on grasshoppers cause predator species-specific indirect effects on plants (dashed lines). *P. mira* individually has a net negative indirect on herbs (red dashed line) and a net positive indirect effect on grass (green dashed line). *P. rimator* and *R. rabida* each have a net positive indirect effect (green dashed lines) on grasses and herbs. The aim of the research presented here is to discern whether there are predictable changes in net indirect effects of predators on plants when different combinations spider species coexist in experimental food webs.

We examined interactions among those plants, the grasshopper herbivore *Melanoplus femurrubrum*, and three important predators of the grasshopper (Schmitz & Suttle 2001): the hunting spiders *Pisaurina mira*, *Phidippus rimator* and *Rabidoso rabida*. *Pisaurina mira* is a sit-and-wait predator that resides in the upper canopy of the field, *P. rimator* is an actively hunting species that resides in the middle of the canopy, and *R. rabida* is a sit-and-pursue predator residing in the lower canopy and on the ground (see Table 1).

Previous research showed that grasshoppers preferentially exploit nutritionally superior grasses, and can inflict considerable damage to them when predators are absent

(Schmitz & Suttle 2001). Predator presence causes grasshoppers to forego feeding on grasses and to seek refuge in leafy herbs, resulting in high damage levels to herbs (Schmitz & Suttle 2001). The extent to which this trade-off behaviour alters damage levels to plants depends on the nature of the predator's hunting behaviour. Individually, the sit-and-wait *P. mira* spiders have little success capturing grasshopper prey, yet they have a profound effect on trade-off behaviour by grasshoppers, resulting in a positive indirect effect on grasses but a detrimental, negative indirect effect on herbs (Schmitz & Suttle 2001). Individually, the sit-and-pursue *R. rabida* has a strong effect on trade-off behaviour by grasshoppers but the actively hunting *P. rimator* has only a minor effect (Schmitz & Suttle 2001). Both predators, however, reduce grasshopper densities to levels where they cannot inflict significant damage to herbs or grasses. This results in a net positive indirect effect of spiders on both grasses and herbs (Fig. 1).

We evaluated the indirect effects of predator species combinations in each of two years (1999 and 2000). We used a substitutive experimental design because it does not confound predator species effects with predator density and the combined species effects should be the mean of the corresponding individual species effects, if multiple predator effects are linear (Sih *et al.* 1998). Departures from this average would indicate emergent nonlinear effects (Sih *et al.* 1998).

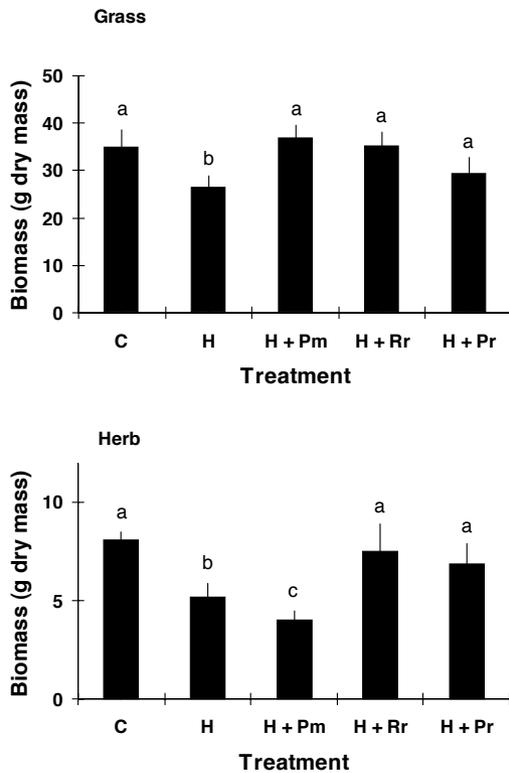
We conducted the experiments in standard (Schmitz & Suttle 2001)  $1 \text{ m}^2$  (basal area)  $\times$   $1 \text{ m}$  (height) aluminium screening enclosures arrayed in a randomized-blocks design separated by  $1.5 \text{ m}$  and placed over natural vegetation in the field. This method of enclosure placement does not bias the initial plant abundance among experimental treatments (Schmitz & Suttle 2001). The experiment consisted of eight treatments, to account for all possible predator species combinations (i.e. no predators, three single species, three pair-wise combinations, and one three-species combination), plus a control containing neither grasshoppers nor predators. Each treatment and control was randomly assigned to each block. Blocks were replicated six times in each of 2 years.

In early July of each year we stocked all the treatment cages at a constant density of three spiders to approximate natural densities of  $2.5 \pm 0.31$  (1 SE)  $\text{m}^{-2}$ ,  $n = 13$ . However, we could not stock 1.5 spiders of each species to the pair-wise treatments. Thus, half of the replicates received two individuals of one species and one individual of the other species and vice versa. We also stocked each treatment enclosure with 14 mid-instar (3rd) grasshopper nymphs with the assigned combination of spider species. We monitored animal densities by conducting censuses of enclosure densities of grasshoppers and spiders every 5 days over the course of the entire experiment. The experiments were run for most of the generation time of the grasshoppers and

Predator species	Location in field	Hunting strategy	Direct effect on grasshopper prey
<i>Pisaurina mira</i>	Upper canopy	Sit-and-wait	Diet shift in response to predation risk
<i>Phidippus rimator</i>	Middle canopy	Active hunting	Reduction in density; minor diet shift in response to predation risk
<i>Rabidosia rabida</i>	Lower canopy & ground	Sit-and-pursue	Reduction in density; diet shift in response to predation risk

**Table 1** Natural history attributes of the three hunting spider species used in the field experiments

spiders each year. They were terminated just before the seasonal onset of frosts that kill the arthropod community and cause the herbaceous plant community to senesce. At this time, all plants in the enclosures were clipped to the soil surface, sorted by class (grass and herb), dried at 60 °C for 48 h and weighed. Data for both years were pooled in statistical analyses.



**Figure 2** Effect of predator species and trophic level manipulations on grass and herb biomass in experimental old-field food webs. C represents 1-trophic-level webs containing plants only, H represents 2-trophic-level webs containing grasshoppers and plants, and H + \_\_ represents 3-level webs composed of plants, grasshopper and natural field densities of one spider species. Pm, Rr and Pr are, respectively, 3-level webs containing *Pisaurina mira*, *Rabidosia rabida* and *Phidippus rimator*. Bars with different lower-case letters identify treatments that were statistically significantly different at the  $P = 0.05$  level (ANOVA followed by a Tukey Test, d.f. = 4, 55). Values are mean  $\pm$  1 SE.

**RESULTS**

A positive indirect effect of predators on plants can be detected whenever predator addition to food webs results in lowered damage to plants (i.e. a net increase in plant biomass) relative to food webs containing only herbivores and plants. A negative indirect effect occurs whenever predator addition to food webs causes herbivores to inflict more damage to plants (i.e. a net decrease in plant biomass) than in food webs containing only herbivores and plants.

We found that effects of individual spider species on plants differed by species. ANOVA followed by a Tukey test revealed that *P. mira* had a significant positive effect on grass biomass and negative effect on herb biomass (Fig. 2); *R. rabida* and *P. rimator* both had significant positive effects on grass and herb biomass (Fig. 2), entirely consistent with a previous independent study (Schmitz & Suttle 2001).

If predator species have nonlinear effects on food webs, the net indirect effect of multiple predator treatments on plants should be significantly different from expectation, determined by averaging the single species treatment effects (Fig. 2) for each predator species combination. We predicted the effects of multiple predator treatments on plant biomass by averaging the mean grass and mean herb biomass in the corresponding single species treatments. We then compared the predictions against grass and herb biomass observed in multiple predator treatments. *T*-tests revealed a strong congruence between predicted and observed average effects of multiple predators (Table 2), indicating consistent *linearity* in spider species effects in the different experimental food webs. The maximum difference between predicted and observed values in Table 2 is of the order of 22%. We consider a nonlinear effect to occur when there is a difference of 25% or greater. Given our level of replication, the likelihood of making a Type II error (failing to detect a 25% difference) is 6% at  $\alpha = 0.05$ .

**DISCUSSION**

The emergence of linear effects in the complex system (Fig. 1) is particularly intriguing because such linearity does not arise in experiments in which the spider species

**Table 2** Comparisons of observed multiple predator species effects and the predicted average of the respective single species effects. Lack of a significant deviation from the predicted effect indicates linearity in multiple predator effects. Values are means  $\pm$  1 SE

Predator species combination	Predicted effect (biomass/plot) <sup>†</sup>	Observed effect (Biomass/plot)	<i>t</i>	d.f.	<i>P</i>
Grass					
<i>P. mira</i> & <i>R. rabida</i>	36.2	32.4 $\pm$ 3.01	1.26	11	0.20
<i>P. mira</i> & <i>P. rimator</i>	33.2	33.4 $\pm$ 3.43	0.06	11	0.95
<i>P. rimator</i> & <i>R. rabida</i>	32.3	29.3 $\pm$ 2.99	1.00	11	0.26
<i>P. mira</i> , <i>P. rimator</i> & <i>R. rabida</i>	33.9	32.9 $\pm$ 3.39	0.47	11	0.79
Herb					
<i>P. mira</i> & <i>R. rabida</i>	6.1	7.3 $\pm$ 1.26	0.95	11	0.34
<i>P. mira</i> & <i>P. rimator</i>	5.8	7.4 $\pm$ 1.16	1.37	11	0.20
<i>P. rimator</i> & <i>R. rabida</i>	6.4	6.0 $\pm$ 0.68	0.59	11	0.67
<i>P. mira</i> , <i>P. rimator</i> & <i>R. rabida</i>	5.7	5.4 $\pm$ 0.63	0.47	11	0.73

<sup>†</sup>Values were estimated by taking the average of the respective single species mean effects reported in Fig. 2.

*P. rimator* and *R. rabida* exist singly in treatments (Schmitz & Suttle 2001). In these cases, each spider species, especially *R. rabida*, cause both density reductions and behavioural shifts of grasshoppers, but the density effects swamp out behavioural effects at the food web level (Schmitz & Suttle 2001). Such nonlinearity does not carry over to the community level when predator species that cause density reductions of grasshoppers coexist with predator species that merely cause grasshopper behavioural shifts. The implication from this study is that the whole can be predicted simply by averaging the contribution of the parts.

The complexity of food webs is seen as a major obstacle to the development of effective ecological theory (Polis & Strong 1996). Because food webs contain species with widely different biological properties that interact at different spatial scales and organizational hierarchies, it is not clear how to construct mathematical frameworks that provide a general, mechanistic understanding of ecological interactions and dynamics. One challenge, in particular, is deciding on the relative weighting to assign to species that have different mechanisms and strengths of food web effects when including them in dynamical systems models (Schoener 1993; Yodzis 1995, 1998). The results of this study show that, in some cases, we may be able to use the average of the individual species effects, even where individual species differ strongly in their direct and indirect effects. This result means that it may be premature to discount a large part of ecological theory (Oksanen *et al.* 1980; Carpenter *et al.* 1986; Menge & Sutherland 1987; Leibold 1989; Schmitz 1992), simply on the assertion that species specificity ought to prevent aggregation into trophic levels (Polis & Strong 1996). An immediate challenge is to determine the prevalence of such trophic homogenization in field systems using multiple species manipulations (Sih *et al.* 1998).

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