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AGGREGATE EFFECTS OF MULTIPLE PREDATOR SPECIES ON A SHARED PREY

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Abstract. We evaluated the potential for emergent nonlinear effects of multiple predators on mortality of a shared prey species by conducting experiments in cages in an old field. We examined interactions among three spider predators, *Pisaurina mira*, *Phidippus rimator*, and *Rabidosa rabida*, and a grasshopper prey *Melanoplus femurrubrum*. The predators have disparate hunting behaviors and are located in different parts of the vegetation canopy used by the grasshoppers, suggesting the potential for nonlinear effects. We examined the effects of spider species singly and in all possible combinations using a substitutive design in each of two years. Multiple predator effects on grasshopper mortality were generally the average of the corresponding single-species effects, indicating that the species effects were largely substitutable. This result indicates that it is reasonable to aggregate these predator species into a single functional unit, despite their disparate individual effects on grasshopper prey, when modeling predator–prey interactions for this system.

Key words: aggregating species by functional group; direct interaction; emergent nonlinear effects; grasshopper prey; hunting spider predators; individual species vs. functional group; multiple predator effects; predation risk enhancement or reduction; predator–prey interactions.

INTRODUCTION

Ecological theory often describes community structure and dynamics by combining species with putatively similar roles (e.g., top predators) into a single functional unit. The rationale for such aggregation is that species belonging to the same organizational unit should have similar effects on communities and thus represent functionally substitutable entities. Ecological models are formalized this way to be mathematically tractable. Models that account for interactions among many species are unwieldy, whereas models that simplify by aggregating species into a few key organizational units (e.g., trophic species, guild, or trophic level) are more resolvable.

Such model simplification may conflict with empirical reality because important mechanistic details tend to be abstracted (Polis and Strong 1996). For example, combining species of predators into a single functional unit ignores the possibility that species differ in their habitat use and hunting capabilities. These differences can translate into differential predator effects in communities with the same prey species (e.g., McIntosh and Peckarsky 1999, Turner et al. 1999, Schmitz and Suttle 2001). Most predators are linked to many species in a community because they are generalists (Hurd and Eisenberg 1990, Sih et al. 1998), possibly causing a host of nonlinear interactions. For instance, a prey species' response to one predator species may change the

nature of its interaction with another predator species (Chang 1996, Losey and Denno 1998). Also, generalist predators interact with other predator species via competition or intraguild predation (Spiller 1986, Rosenheim et al. 1993, Wise 1993, Hodge and Marshall 1996, Moran et al. 1996, Rosenheim 1998). For these reasons, different predator species may not be functionally substitutable when coexisting in communities (Sih et al. 1998).

Simplification is, however, fundamental to developing a general conceptualization of community structure and dynamics (Levin 1992). The key empirical challenge, then, is to identify how natural complexity can be faithfully characterized in ecological models. When examining predator–prey interactions in particular, this requires discerning how predator species combine to influence community interactions and dynamics (Sih et al. 1998).

To this end, we report on experiments that examined effects of multiple predator species on a shared prey species. We build upon previous work (Schmitz and Suttle 2001), which showed that individual hunting spider species have different direct effects on the survival and habitat use of a common grasshopper prey species. This system thus offers the potential to evaluate how predator species with disparate direct effects may combine to influence the abundance of a shared prey species.

Our research was guided by two working hypotheses about mechanisms that may lead to nonlinear effects in multiple predator systems. Multiple predators may have *risk-enhancing* effects (Matsuda et al. 1993, Sih

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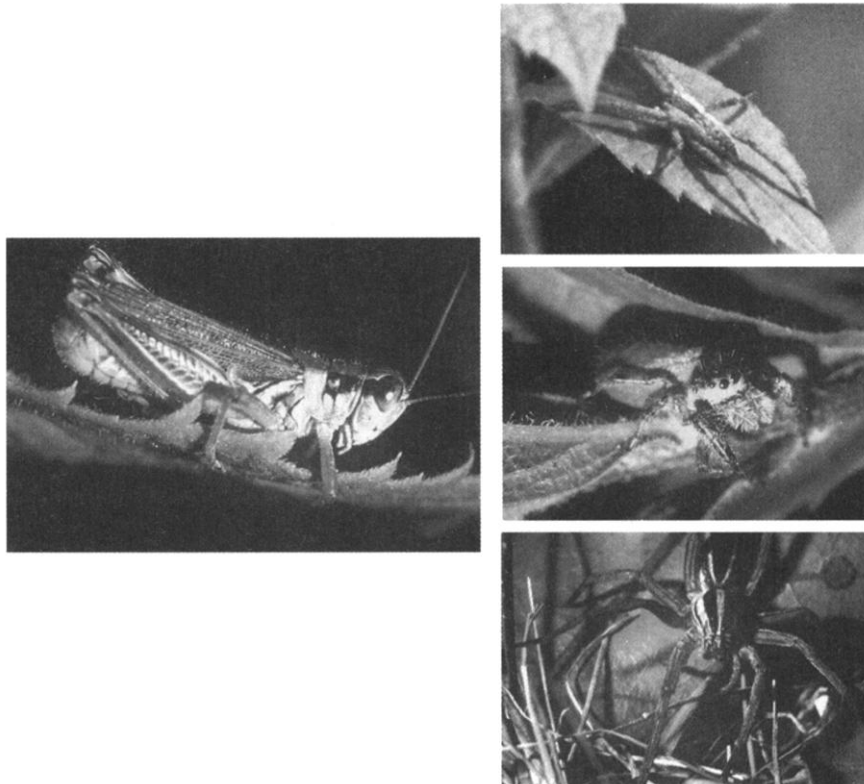


PLATE 1. (Left) The focal grasshopper species *Melanoplus femurrubrum* and (right) its three predator species (in order from the top) *Pisaurina mira*, *Phidippus rimator*, and *Rabidosa rabida*.

et al. 1998) if prey experience higher mortality in multiple-predator communities than in single-predator communities. This can arise when a prey's normal response to one predator species (e.g., habitat shift to avoid the predator) increases its vulnerability to another predator species (e.g., Soluk 1993). Alternatively, multiple predators may have *risk-reducing* effects when prey are less vulnerable to mortality in multiple-predator systems than in single-predator systems (Sih et al. 1998). This occurs when predator species engage in interference competition or intraguild predation.

NATURAL HISTORY

We conducted the research at the Yale-Myers Research Forest, in northeastern Connecticut, USA (see Schmitz and Suttle [2001] for a detailed description). The research was completed in an old field dominated by the herbs *Solidago rugosa*, *Daucus carota*, *Aster novaeangliae*, and *Trifolium* sp., and the grasses

Phleum pratense and *Poa pratensis*. We examined interactions among the grasshopper *Melanoplus femurrubrum* and three numerically dominant hunting spider predators capable of killing grasshoppers in the field (Schmitz and Suttle 2001): *Pisaurina mira*, *Phidippus rimator*, and *Rabidosa rabida* (see Plate 1). *P. mira* is a sit-and-wait predator that resides in the upper canopy. It does not have a significant effect on grasshopper density, but it causes grasshoppers to shift their habitat use to decrease predation risk (Schmitz and Suttle 2001). *P. rimator* is an actively hunting species that resides in the middle of the canopy (Schmitz and Suttle 2001). It significantly reduces grasshopper density but causes only minor if any habitat shifts. Finally, *R. rabida* is a sit-and-pursue predator residing in the lower canopy and on the ground (Schmitz and Suttle 2001). It causes both habitat shifts and significant reductions in grasshopper density. The natural history attributes of these species are summarized in Table 1. These spi-

TABLE 1. Summary of natural history attributes of the three hunting spider species used in the field experiments.

Predator species	Common name	Location in field	Hunting strategy
<i>Pisaurina mira</i>	nursery web spider	upper canopy	sit-and-wait
<i>Phidippus rimator</i>	jumping spider	throughout middle canopy	active hunting
<i>Rabidosa rabida</i>	wolf spider	lower canopy and ground	sit-and-pursue

der species co-occur in multiple species combinations in the field. The mean density of individual adult spiders, for all three species combined, was 2.5 ± 0.31 spiders/m² (mean \pm 1 SE), $n = 13$ during the months of the study (July and August).

METHODS

Study design

We compared the single and multiple spider species effects on grasshoppers in each of two years (1999 and 2000). We were interested in the substitutability of predator species effects. Thus, we used a substitutive design because it does not confound predator species effects with predator density (Sih et al. 1998). For example, if each predator species has identical but independent effects on prey (i.e., they are substitutable), the combined species effect should be the mean of the individual species effects. Departures from this average would indicate emergent nonlinear effects (Sih et al. 1998).

We stocked grasshoppers and spiders to standard aluminum screening enclosure cages measuring 1 m² (basal area) \times 1 m (height). The protocol for cage construction and placement in the field has been presented elsewhere (Schmitz et al. 1997). The cages were arrayed in a randomized-block design separated by 1.5 m and placed over natural vegetation in the field. To ensure that there was no bias in initial conditions among treatments each year, we sampled initial plant biomass in cage locations. We measured the percentage of area that all dominant plant species (see *Natural history*) covered in each cage location. MANOVAs on arcsine square-root transformed data revealed no significant difference ($P > 0.30$, $df = 35, 315$) in initial abundance of plant species among treatments in each year. We also removed all animals within the cages by carefully hand-sorting through the vegetation and litter in each cage. We removed all the large insects and spiders from the cages. Small spider species could not be removed; although their size and habitat use prevented capture, it also precluded their ability to prey upon the grasshoppers or the treatment spiders.

The experiment consisted of seven treatments, to account for all possible predator species combinations (i.e., three single species, three pairwise combinations, and one three species combination), plus a control containing no spiders. Each treatment and control was randomly assigned to each block: treatments and controls were replicated 10 times in each year. We stocked all the treatment cages at a constant density of three spiders to approximate natural densities (see *Natural history*). However, we could not stock 1.5 spiders of each species to the pairwise treatments. Thus, 5 of 10 replicates received two individuals of one species and one individual of the other species, and vice versa.

In early July of each year, we stocked each control and treatment cage with 14 mid-instar (third) grass-

hopper nymphs, which was ~ 1.5 times natural field densities at the time of stocking. Grasshoppers were intentionally stocked this way to produce a pulse perturbation that allowed their densities to decline toward levels set by local limiting factors in each cage (e.g., food resources, predators, etc.). In some cases, these local levels may be higher than the average density for the whole field (Schmitz et al. 1997, Schmitz and Suttle 2001).

At this time, we also stocked the assigned combination of spider species to the cages. We conducted censuses of enclosure densities of grasshoppers and spiders over the course of the entire experiment. After initial stocking, the first three censuses were performed at two-day intervals to ensure that grasshopper populations did not go extinct due to artifacts of initial conditions (none went extinct). Thereafter, enclosures were monitored every five days until termination of the experiment in late August.

Data analysis

We tested for spider species effects on grasshoppers in two ways. We first determined whether there were significant reductions in prey density among treatments. We also examined whether spiders had substitutable effects on the trajectory of grasshopper mortality over time, irrespective of final density.

We tested for spider treatment, and block effects using ANOVA. We used density data from the last census date for comparison. ANOVA was followed by Tukey tests whenever a significant effect was detected. We tested for substitutability of spider species effects over time by comparing grasshopper mortality rates in single vs. multiple predator treatments. We estimated grasshopper mortality rates (m) for each enclosure population by fitting the function $\ln(N_t) = \ln(N_0) - mt$ to natural logarithm-transformed time series data. In this model $\ln(N_t)$ is the natural logarithm of population density at time t and $\ln(N_0)$ is the natural logarithm of initial population density, which is a fixed constant. We tested the hypothesis that the combined predator species effects deviated from the predicted average of the single-species effects, thereby indicating risk enhancement or risk reduction, using the following comparisons:

- 1) predicted average of *P. mira* and *P. rimator* vs. observed *P. mira* + *P. rimator* combined;
- 2) predicted average of *P. mira* and *R. rabida* vs. observed *P. mira* + *R. rabida* combined;
- 3) predicted average of *P. rimator* and *R. rabida* vs. observed *P. rimator* + *R. rabida* combined;
- 4) predicted average of *P. mira*, *P. rimator*, and *R. rabida* vs. observed *P. mira* + *P. rimator* + *R. rabida* combined.

To guard against a high likelihood of committing Type II errors (i.e., failing to detect risk enhancement or risk reduction when we should have), we employed a randomized resampling test (Manly 1997) using the

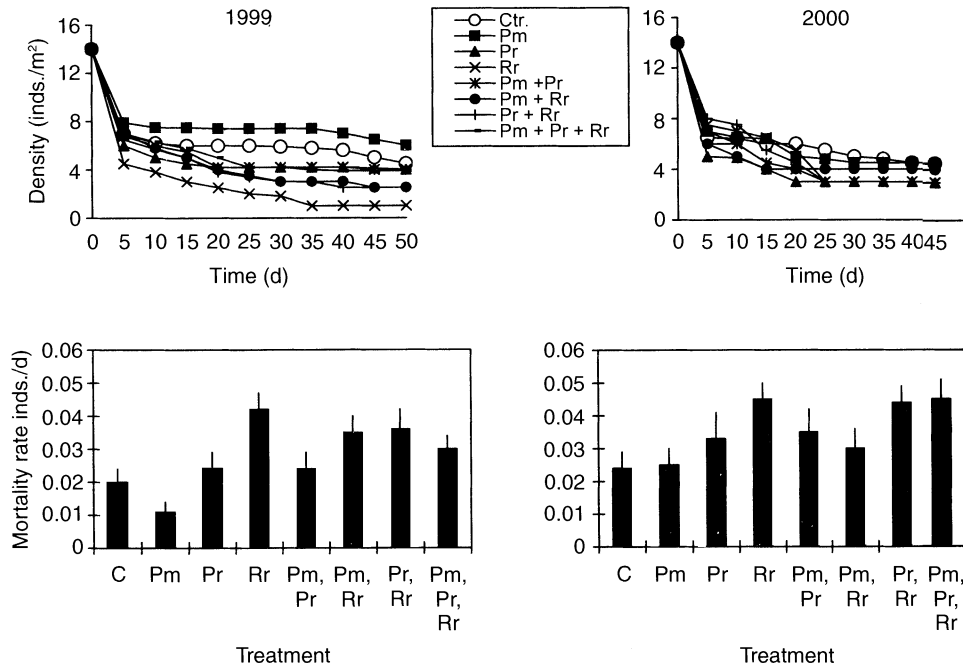


FIG. 1. Effects of spider species on grasshopper populations in experimental enclosures in each of two study years (1999 and 2000). (Top) Time series of grasshopper densities alone (Ctr.) or in combination with different single and multiple spider species combinations (Pm = *Pisaurina mira*, Pr = *Phidippus rimator*, Rr = *Rabidosa rabida*). The lines for Pr + Rr and Pm + Pr + Rr are indistinguishable from one another in the graph because the effects of the two spider species treatments essentially duplicate each other. (Bottom) Mean and standard errors in mortality rates estimated from each of the time series for different predator-species combinations.

program Resampling Stats 4.0.9 for Macintosh (Resampling Stats, Arlington, Virginia USA). We randomly picked, with replacement, density measures from the time series of the 10 enclosures within a treatment to generate a new data set, upon which to run a regression and extract an m value. This procedure was repeated 1000 times to generate an observed mean and standard error in m values. We then compared the observed and predicted mean values using a t test with $\alpha = 0.05$. Because we conducted multiple comparisons within a year, we used the Bonferroni corrected level of significance $\alpha' = \alpha/4$ where 4 is the number of comparisons conducted in the analysis within a year. This method ensured that the probability of a Type II error was < 0.01.

RESULTS

Grasshopper densities declined over the course of the season in both years (Fig. 1). ANOVA on final grasshopper density for both years combined revealed no significant block effects ($P > 0.40$, $df = 9, 142$), but there was a significant year effect ($P < 0.05$, $df = 1, 142$) due possibly to differences in weather conditions between years (1999 was a dry summer, 2000 was a rainy summer). We therefore report results for 1999 and 2000 separately. ANOVA revealed that there were significant treatment effects in both 1999 and 2000 ($P < 0.05$, $df = 7, 63$). Tukey tests revealed that in 1999,

grasshopper densities in all treatments containing *R. rabida* were significantly lower than the no-predator control (all $P < 0.05$). In 2000, all treatments containing *P. rimator* and *R. rabida* were significantly different from the control (all $P < 0.05$). In all other treatments, there were no significant differences between treatments and the control (all $P > 0.15$).

Regression R^2 for all fits of $\ln(N_t) = \ln(N_0) - mt$ used to estimate mortality rate m were on the order of 0.80 or higher. Grasshopper mortality rates tended to be higher in 2000 than in 1999 (Fig. 1). For all combinations, the mortality rates in the multiple predator species treatments were not significantly different from the respective predicted average of the individual species mortality rates (Table 2). This conservative conclusion is based on a high level of power ($\beta = 0.99$).

DISCUSSION

This study was designed to test whether or not the effects of three hunting spider species on mortality rates of experimental grasshopper populations were substitutable. Previous research revealed that the effects are not expected to be substitutable because each species individually has a different direct effect on *Melanoplus femurrubrum* grasshoppers (Schmitz and Suttle 2001). The nursery web spider *Pisaurina mira* causes habitat shifts by grasshoppers but it has no significant density effect (Beckerman et al. 1997, Schmitz

TABLE 2. Pairwise comparisons testing the hypothesis that the combined predator species effects observed in the experiments deviated from the predicted average of the single-species effects.

Species combination	Predicted mortality rate (individuals/d) [†]	Observed mortality rate (individuals/d) [‡]	<i>t</i>	Conclusion [§]
1999				
<i>P. mira</i> and <i>P. rimator</i>	0.018	0.024 ± 0.005	1.2	not significant
<i>P. mira</i> and <i>R. rabida</i>	0.027	0.035 ± 0.005	1.6	not significant
<i>P. rimator</i> and <i>R. rabida</i>	0.033	0.036 ± 0.006	0.5	not significant
<i>P. mira</i> , <i>P. rimator</i> , and <i>R. rabida</i>	0.026	0.030 ± 0.004	1.0	not significant
2000				
<i>P. mira</i> and <i>P. rimator</i>	0.029	0.035 ± 0.004	1.5	not significant
<i>P. mira</i> and <i>R. rabida</i>	0.035	0.030 ± 0.006	0.8	not significant
<i>P. rimator</i> and <i>R. rabida</i>	0.039	0.044 ± 0.005	1.0	not significant
<i>P. mira</i> , <i>P. rimator</i> , and <i>R. rabida</i>	0.036	0.043 ± 0.007	1.0	not significant

Note: A significant deviation from the predicted value would indicate risk enhancement or risk reduction.

[†] Values were estimated by taking the average of the respective single-species mean effects reported in Fig. 1.

[‡] Values are means ± 1 SE.

[§] Based on $\alpha' = 0.012$.

et al. 1997, Schmitz and Suttle 2001). The jumping spider *Phidippus rimator* has a strong density effect on grasshopper populations but it causes little or no habitat shift (Schmitz and Suttle 2001). Finally, the wolf spider *Rabidososa rabida* causes grasshopper density reductions and habitat shifts.

In treatments containing individual spider species, we found that mortality rates of grasshoppers facing the sit-and-wait *P. mira* were not statistically different from mortality in no-spider controls, but *P. rimator* and *R. rabidososa* (depending on year) caused significant increases in mortality rate (Fig. 1). This is consistent with a previous independent study (Schmitz and Suttle 2001). However, grasshopper mortality rates under all multiple spider species combinations were not significantly different from the expected mean of the respective single-species effects. The conservative interpretation for the outcome of this study is that the net effects of the multiple predator treatments could be predicted simply by averaging the single-species effects. In other words, there appeared to be some degree of substitutability of spider species effects on grasshopper density.

We feel that our conclusion is robust within the scope of this experiment. First, the high power afforded by the randomization test (Manly 1997) gives us confidence that we are not falsely concluding a lack of nonlinear effect (i.e., likelihood of Type II errors is <0.01). Our natural history observations on spider hunting mode and spider–grasshopper interactions, which were completed in a natural setting (Schmitz and Suttle 2001), corroborate observations from the enclosure experiments. Predation rates of the spiders on grasshoppers in unenclosed field conditions match the predation rates in experimental enclosures (Schmitz and Suttle 2001). Finally, we see the same qualitative effect of spider treatments on grasshopper density and mortality rates between years.

Although other multiple predator studies have dem-

onstrated risk enhancement and risk reduction (i.e., nonlinear effects), consistent with complex mechanistic models of species interaction (Sih et al. 1998), our work shows that multiple predator systems can also conform to assumptions of simple models (i.e., substitutable or linear effects). This result arose despite ecological conditions that usually favor risk enhancement or risk reduction—namely complementarity in predator habitat use and hunting mode (Sih et al. 1998).

Risk enhancement is theoretically likely under these conditions because a prey species, in attempting to avoid one predator species by moving to other parts of its habitat, becomes more vulnerable to other predator species in other locations of its habitat (Chang 1996, Losey and Denno 1998). Our particular system provides limited possibilities for this to happen. *P. rimator* and *R. rabida*, which occupy the middle and lower parts of the canopy, respectively, cause the same level of mortality risk to grasshoppers (Fig. 1; see also Schmitz and Suttle [2001]). Thus, switching habitat locations under this condition will have no net effect on mortality risk. There is the potential for risk enhancement when grasshoppers, in attempting to avoid *P. mira* in the upper canopy, move to the middle canopy only to encounter *P. rimator* (Fig. 1). However, this should be regarded as a trivial effect (Fauth 1990, Sih et al. 1998), because even minor, positive mortality levels would be considered infinite enhancement, since *P. mira* has no significant direct effect on grasshopper mortality relative to nonpredator control conditions. Risk reduction is also theoretically possible because intraguild predation between spider species (Wise 1993) lowers the density of predators hunting prey. However, we were able to recover all individual predators at the end of our experiments, indicating that intraguild predation was not a factor in our system.

In conclusion, this study shows that we may be able to use the average of the individual predator species effects, to predict the net effects of multiple predator

species on a shared prey. Thus, the three species can be effectively treated in the aggregate as a single functional group when modeling multiple predator effects on prey population mortality. This means that it may be premature to discount a large part of ecological theory simply on the assertion that species specificity ought to prevent aggregation into guilds or trophic levels (Polis and Strong 1996). An immediate challenge is to determine the general prevalence of substitutability in multiple predator species effects in other field systems (Sih et al. 1998), especially when there is complementarity in habitat use among predator species that theoretically could lead to risk enhancement or risk reduction.

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