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Effects of combining an intraguild predator with a cannibalistic intermediate predator on a species-level trophic cascade

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Abstract. A greater diversity of natural enemies can in some cases disrupt prey suppression, particularly when natural enemies engage in intraguild predation, where natural enemies compete with and prey upon each other. However, empirical studies have often demonstrated enhanced prey suppression despite intraguild predation. A recent theoretical study proposed the hypothesis that, when the intermediate predator is cannibalistic, intraguild predation can reduce cannibalism within the intermediate predator population, leading to little change in intermediate predator mortality and thus enhanced prey suppression. The goal of this study was to examine this hypothesis empirically. Two summer-long field enclosure experiments were conducted in cotton fields. We investigated the effects of adding an intraguild predator, *Zelus renardii*, on (1) the abundance of a cannibalistic intermediate predator, *Geocoris pallens*, (2) the abundance of a herbivore, *Lygus hesperus*, and (3) cotton plant performance. *G. pallens* adult abundance did not increase, even when food availability was high and natural enemies were absent, suggesting that density-dependent cannibalism imposes an upper limit on its densities. Furthermore, although *Z. renardii* is an intraguild predator of *G. pallens*, *G. pallens* long-term densities were unaffected by *Z. renardii*. In the presence of the intermediate predator, the addition of the intraguild predator *Z. renardii* enhanced suppression of *L. hesperus*, and there were suggestions that *Z. renardii* and *G. pallens* partitioned the *L. hesperus* population. Effects of herbivore suppression cascaded to the plant level, improving plant performance. In conclusion, we provide empirical support for the hypothesis that the addition of an intraguild predator may enhance prey suppression if the intermediate predator expresses density-dependent cannibalism. Intraguild predation and cannibalism co-occur in many communities; thus their joint effects may be broadly important in shaping predator effects on herbivores and plant performance.

Key words: biological control; cannibalism; cotton; generalist predators; Geocoris pallens; *intraguild predation;* Lygus hesperus; *resource partitioning; trophic cascade;* Zelus renardii.

INTRODUCTION

Increasing the diversity of predator communities may disrupt prey suppression if diversity also promotes antagonistic interactions, such as intraguild predation (IGP). IGP occurs when natural enemies that compete for a common prey species also prey on each other (reviewed in Rosenheim et al. 1995). IGP theory suggests that to achieve coexistence at equilibrium, the intermediate predator must be the better competitor for the common prey species (Holt and Polis 1997). In other words, the intermediate predator alone must be able to maintain the prey population at a lower equilibrium density than the intraguild predator can. If so, adding an intraguild predator that consumes the intermediate predator is predicted to disrupt prey suppression and elevate the equilibrium density of the common prey (Fig. 1A). This prediction is supported by a large body of empirical work (meta-analysis: Vance-Chalcraft et al. 2007); however, there are also many examples where the addition of an intraguild predator enhances prey suppression (Janssen et al. 2006, Snyder et al. 2008). These findings imply gaps in our understanding of mechanisms underlying the effects of IGP on prey suppression. In response, ecologists have begun to investigate several factors that can alter IGP outcomes (Straub et al. 2008).

A recent IGP model that incorporated a cannibalistic intermediate predator proposed a new hypothesis to explain improved prey suppression despite IGP (Rudolf 2007). The model suggests that an intraguild predator may reduce cannibalism rates in a population of intermediate predator that expresses density-dependent cannibalism, such that total mortality of the intermediate predator imposed by IGP + cannibalism is little changed compared to mortality expected under cannibalism alone (Rudolf 2007). This could be due to the intraguild predator removing cannibals or suppressing cannibalistic behavior of cannibals (Rudolf 2008). Under this scenario, adding an intraguild predator may contribute directly to prey suppression without decreasing intermediate predator abundance, and may therefore lead to enhanced prey suppression (Fig. 1B).

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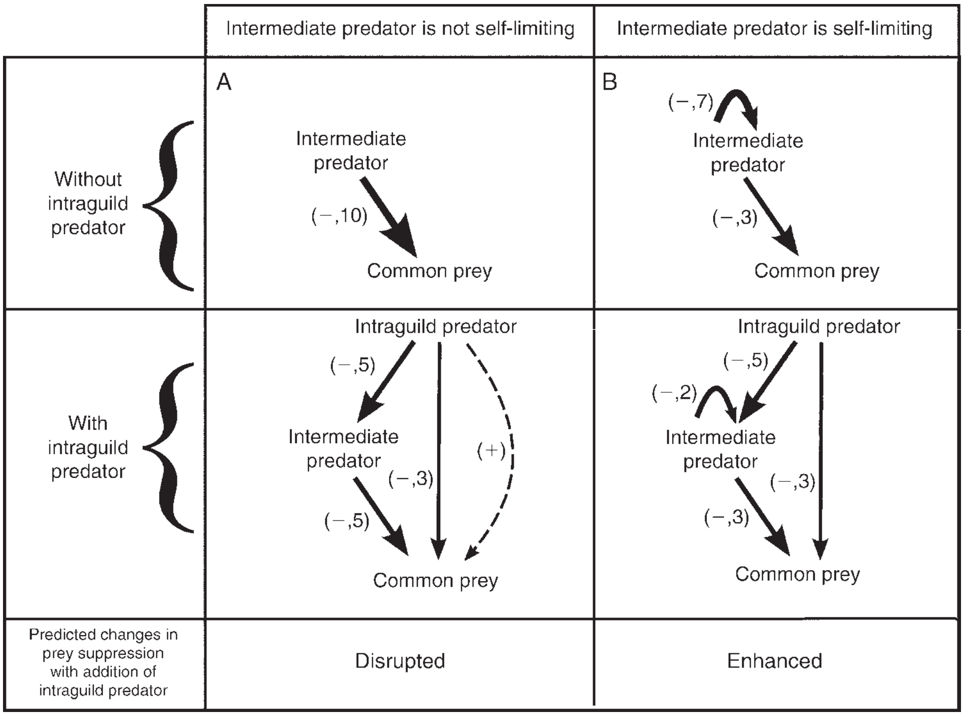

FIG. 1. Conceptual models of intraguild predation and predicted effects on prey suppression in a cotton (*Gossypium hirsutum*) agroecosystem at the University of California–Davis (USA): (A) basic intraguild predation and (B) intraguild predation with a strongly self-limiting (e.g., cannibalistic) intermediate predator (*Geocoris pallens*) and an intraguild predator (*Zelus renardii*) that exerts strong direct predation on the common prey. Signs within parentheses indicate the effect of interaction on the receiver. Numbers within parentheses indicate interaction strength, which is also indicated by arrow widths. Solid arrows indicate direct effects, whereas dashed lines indicate indirect effects. Basic intraguild predation predicts that the intraguild predator will reduce the intermediate predator's consumption of the common prey, thus leading to disrupted prey suppression. If the intermediate predator is self-limiting, the intraguild predator may have little influence on the intermediate predator's consumption of the common prey (see *Introduction* for detailed explanation) and thus exert little indirect benefits to the common prey. In this case, the consequent prey suppression may be enhanced if the direct predatory impact of the intraguild predator on the common prey is strong.

Similar results were obtained in a linear analytical model: removing intraguild predator abundance (by increasing intraguild predator mortality) can disrupt prey suppression if there is strong self-limitation in the intermediate predator (Hart 2002). To date, this hypothesis remains unexamined in the field.

The cotton agroecosystem, with its rich diversity of arthropod predators and herbivores, is a promising setting to study the IGP-cannibalism hypothesis. The cotton plant (*Gossypium hirsutum* L.) is host to spider mites (*Tetranychus* spp.) and plant bugs (*Lygus* spp.) (University of California 1996). The western tarnished plant bug *Lygus hesperus* Knight feeds primarily on flower buds and fruits, resulting in flower bud abscission (University of California 1996). The insect *Geocoris pallens* Stål is a generalist predator of spider mites and *L. hesperus* (University of California 1996, Zink and Rosenheim 2008). The assassin bug, *Zelus renardii* Kolenati, preys on *G. pallens* as well as spider mites and *L. hesperus* (Cisneros and Rosenheim 1998). *Z. renardii* can substantially increase short-term mortality of *G. pallens* adults (Appendix: Fig. A1).

G. pallens expresses cannibalism that is size-structured and positively density dependent. Adult and nymphal *G. pallens* are highly cannibalistic, with all stages consuming eggs and smaller motile stages (Appendix: Table A1). Furthermore, *G. pallens* females are >10-fold more cannibalistic on conspecific eggs in the presence of even a single conspecific female than when they are alone (Y.-H. Law and J. A. Rosenheim, *unpublished data*). A preliminary experiment showed that the strong density-dependent increase in egg cannibalism by *G. pallens* females reduced reproductive recruitment by >75% in the field (Y.-H. Law and J. A. Rosenheim, *unpublished data*), and is thus likely to contribute to the regulation of *G. pallens* populations.

Although IGP has been studied actively over the past two decades, the implications of a cannibalistic intermediate predator for IGP, prey suppression, and plant performance have received little attention (but see Schellhorn and Andow 1999, Hart 2002, Denno et al. 2004, Rudolf 2008). The model introduced by Rudolf (2007) provides a framework within which we can start to investigate the effects of adding an intraguild predator to a cannibalistic intermediate predator–

herbivore module (Fig. 1). Using an ecological community that matches the framework of the model, we ask the following questions: (1) What are the effects of an intraguild predator (*Z. renardii*) on the density of a cannibalistic intermediate predator (*G. pallens*)? (2) What are the effects of an intraguild predator on the population density of an herbivore (*L. hesperus*) that is also consumed by a cannibalistic intermediate predator? (3) What are the cascading effects on the plant due to combined suppression of herbivores by an intraguild predator and a cannibalistic intermediate predator?

Materials and Methods

Arthropod collection and maintenance

Tetranychus urticae, the main prey for *G. pallens* in our experiments, was maintained on cotton seedlings in our laboratory colony and transferred to field cages. *L. hesperus* was obtained from both the field and laboratory colonies (fed green beans). *G. pallens* and *Z. renardii* were collected from the field and maintained in the laboratory for several days before use in experiments. *G. pallens* was reared on frozen moth eggs (*Spodoptera exigua* [Hübner] and *Ephestia kuehniella* Zella) and water; *Z. renardii* was fed a variety of field-collected insects. We conducted all our field experiments at the Plant Pathology Experimental Farm at the University of California–Davis (USA). Thrips, mostly *Frankliniella occidentalis*, were prevalent in the field, and we retained them in all our field cages at natural densities.

Experiment 1 (summer 2007)

Experiment 1 was conducted to test the effects of *Z. renardii* IGP on *G. pallens* abundance, overall prey suppression, and plant performance. There were three treatments and one control: treatment 1, herbivores only ($n = 15$ cages); treatment 2, herbivores + *G. pallens* ($n = 32$); treatment 3, herbivores + *G. pallens* + *Z. renardii* ($n = 33$); and the control ($n = 18$), which was the cotton plant caged alone without any arthropods added.

Cages were made from fine mesh (0.14 × 0.14 mm, Econet S; U.S. Global Resources, Seattle, Washington, USA). Each cage had dimensions of 0.6 × 0.6 × 1.9 m (length × width × height) with another 0.2 m buried in the ground to seal the cages. A 1.5 m long Velcro opening on a cage wall allowed access into the cage. Individual cotton plants were caged immediately after seeding.

Cotton was planted 15 May 2007, and arthropods were added thereafter according to treatments. Forty *T. urticae* females and one *L. hesperus* female were introduced to cages on 10 June and 22 June, respectively. Two *G. pallens* females were introduced on 24 June, followed by two more on 5 July. One *Z. renardii* female and two second instar nymphs were introduced on 12 July. The experiment was ended on 23 August. Running the experiment for two months allowed for several generations of *T. urticae* and at least one complete generation of *L. hesperus* and *G. pallens*. *G. pallens* females mate often and remain reproductive for at least several weeks after a single mating (Y.-H. Law, *personal observation*). Reproduction by *Z. renardii* was not expected given its short tenure (six weeks) in the cages. The sequence of arthropod additions deliberately reflected population dynamics in Californian cotton agroecosystems. In cotton fields, *T. urticae* densities are typically very much higher than *L. hesperus* densities. The cages were inoculated with a density of *G. pallens* adults that is frequently observed in the field (Appendix in De Valpine and Rosenheim 2008). At least some treatments within our experiment excluded key constraints that might act on *G. pallens* populations in the field (e.g., prey shortage; parasitoids that attack the egg stage of *G. pallens*; higher-order predators). If *G. pallens* populations are regulated by extrinsic factors, rather than by density-dependent cannibalism, we would expect *G. pallens* populations to grow vigorously in our treatments without *Z. renardii*.

All cages were sampled destructively at the end of the experiment to measure arthropod abundance and plant responses to herbivory. The plant traits that are most reflective of *L. hesperus* herbivory are retention rates and biomass of reproductive structures. Cotton plants were first examined in the field to measure retention rates of reproductive structures (estimated as the proportion of the first node positions on fruiting branches that retained buds/flowers/fruits; hereafter referred to as "fruit retention rates"). Plants were then cut at the soil level and bagged. The insides of cages were visually searched for arthropods after removing all plant material from the cages. Arthropods on plants were collected by washing all plant structures over fine sieves (mesh size = 0.075 mm) in the laboratory. Reproductive structures (buds, flowers, and fruits) of the cotton plants were dried and weighed.

Experiment 2 (summer 2008)

Experiment 2 was similar to experiment 1 but incorporated a full factorial design to examine the interactive effects of *G. pallens* and *Z. renardii* on herbivore suppression and plant performance. The field cages were as described in experiment 1. Experiment 2 had four treatments plus a control: treatment 1, herbivores only ($n = 14$ cages); treatment 2, herbivores + *G. pallens* ($n = 15$); treatment 3, herbivores + *Z. renardii* ($n = 12$); treatment 4, herbivores + *G. pal*lens + *Z. renardii* ($n = 15$); and the control ($n = 13$), which was a cotton plant caged alone without any arthropods added.

Cotton was planted on 12 May 2008. Based on our experiences in experiment 1, we used lower initial densities of *T. urticae*: only 10 *T. urticae* females and two *L. hesperus* females were added to each cage on 26 June. Another two *L. hesperus* females were added on 11 July. Two *G. pallens* females were added on 3 July, 12 July, and 15 August for a total of six *G. pallens* females. One *Z. renardii* female and two first or second instar nymphs were introduced on 12 July. Despite a lighter inoculation of *T. urticae*, by mid-July *T. urticae*

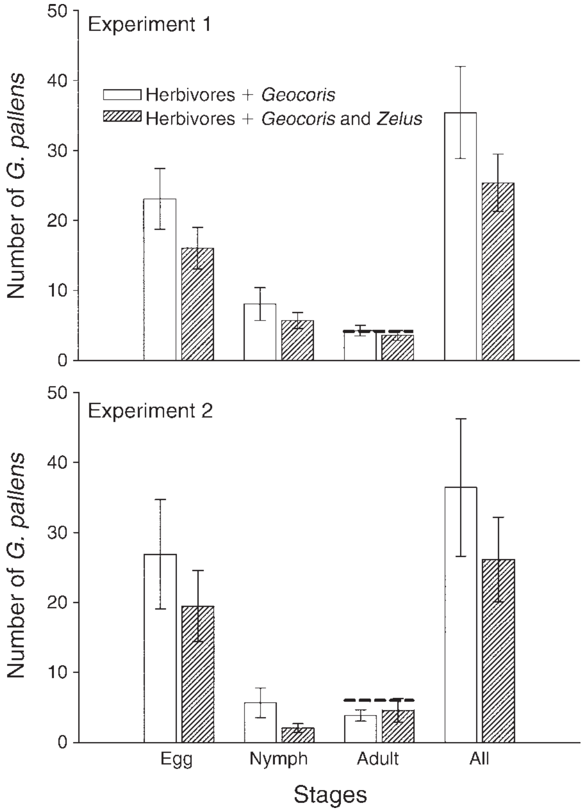

FIG. 2. Abundance of *Geocoris pallens* (mean ± SE) in different life stages at the end of experiments 1 and 2 in the absence or presence of the assassin bug *Zelus renardii*. The insect *G. pallens* is a generalist predator of spider mites and *Lygus hesperus*, the western tarnished plant bug. Dashed lines indicate the total number of *G. pallens* females introduced into treatments. In no case did *G. pallens* abundance differ significantly between treatments ($P > 0.05$).

populations were growing very rapidly and appeared likely to overwhelm treatments without predators; we therefore added ~100 predatory mites (*Galendromus occidentalis* [Nesbitt]) to all treatments except the control, which lacked *T. urticae*. *G. occidentalis* is a specialist consumer of spider mites. The experiment ended on 27 August, with all cages destructively sampled as in experiment 1.

Statistical analysis

Nonparametric Wilcoxon or Kruskal-Wallis tests were used to compare treatment effects because data did not meet assumptions for parametric tests even after several transformations were explored. We used the adjusted rank transform method to test for interactions between factors in experiment 2 (Sawilowsky 1990). The relationship between plant performance and herbivore densities was analyzed using a Spearman rank correlation. All values reported in this paper are mean ± standard error. An α value of 0.05 is used for all tests. Statistical analyses were done with JMP 7.0 (SAS Institute 2007).

RESULTS

Response of the intermediate predator, G. pallens

Experiments 1 and 2 produced similar responses in *G. pallens* population densities. First, in the absence of the intraguild predator *Z. renardii*, final *G. pallens* adult (males + females) densities were either lower than or similar to the total number of females added over the course of the experiments (Fig. 2). Thus, the abundance of adult female *G. pallens* failed to increase in both experiments, despite the absence of natural enemies and the presence of abundant prey (see *Response of the herbivores*). Second, the addition of *Z. renardii* did not affect the long-term, final density of *G. pallens* (eggs and all mobile stages combined; experiment 1, $\chi^2 = 0.96$, $P = 0.34$; experiment 2, $\chi^2 = 0.72$, $P = 0.40$; Fig. 2), although there were modest and nonsignificant trends toward lower *G. pallens* egg and nymph densities in the presence of *Z. renardii*.

Response of the herbivores

T. urticae, the primary prey for *G. pallens* in our experiments, reached high densities in all treatments where they were introduced (final abundance per plant: experiment 1, 5481 ± 507 spider mites/plant; experiment 2, 1095 ± 242 spider mites/plant; Y.-H. Law and J. A. Rosenheim, *unpublished data*). Thrips densities were modest in the cages (final abundance per plant: experiment 1, 84.9 ± 15.6 thrips/plant; experiment 2, 348.1 ± 72.5 thrips/plant).

There were significant treatment effects on *L. hesperus* densities (nymphs + adults) in both experiments 1 and 2 (Fig. 3; experiment 1, $\chi^2 = 8.71$, $P = 0.033$; experiment 2, $\chi^2 = 8.02$, $P = 0.045$). In treatments with either *G. pallens* or *Z. renardii* as the sole predator species, *L. hesperus* adult densities were not significantly suppressed. However, a combination of both predators strongly suppressed *L. hesperus* adults (experiment 1, $\chi^2 = 8.55$, $P = 0.004$; experiment 2, $\chi^2 = 4.67$, $P = 0.031$); *L. hesperus* nymph densities remained unaffected (experiment 2, $\chi^2 = 3.48$, $P = 0.062$). Furthermore, adding *Z. renardii* as a second predator to the *G. pallens*–*L. hesperus* module consistently reduced *L. hesperus* adult densities compared to densities observed in the presence of *G. pallens* alone (experiment 1, $\chi^2 = 4.88$, $P = 0.027$; experiment 2, $\chi^2 = 6.34$, $P = 0.012$).

The factorial design of experiment 2 allowed us to test for main effects and interactions of *G. pallens* and *Z. renardii*. The presence of *G. pallens* decreased *L. hesperus* nymphs ($\chi^2 = 4.98$, $P = 0.026$) without any significant impact on *L. hesperus adults* ($\chi^2 = 0.06$, $P = 0.81$). In contrast, the presence of *Z. renardii* reduced *L. hesperus* adults ($\chi^2 = 8.29$, $P = 0.004$) but not *L. hesperus* nymphs ($\chi^2 = 0.33$, $P = 0.56$). The interaction terms were nonsignificant for effects on *L. hesperus* nymphs ($F_{1,52} = 0.84$, $P = 0.37$) and adults ($F_{1,52} = 0.18$, $P = 0.67$).

The absence of *L. hesperus* nymphs at the end of experiment 1 could have been caused by intense

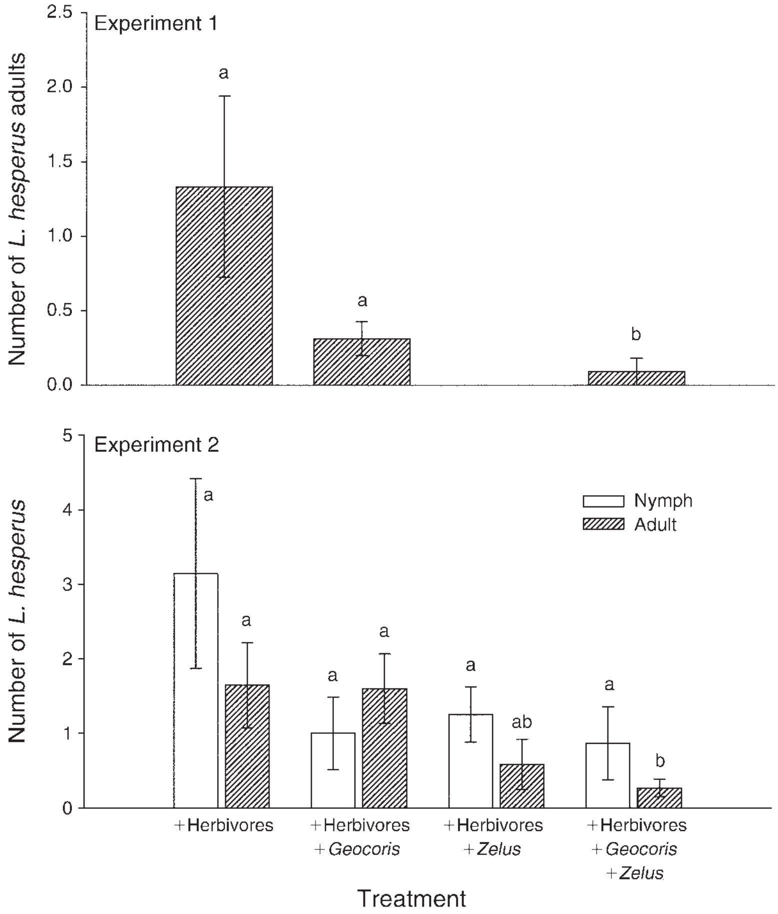

FIG. 3. Abundance of *L. hesperus* (mean ± SE) at the end of experiments 1 and 2. No *L. hesperus* nymphs were found at the end of experiment 1. There was no "+ herbivores + *Zelus*" treatment in experiment 1. Treatments not sharing the same letter have significantly different means ($P < 0.05$).

competition from the extremely high *T. urticae* densities. Cotton plants were visibly malnourished and covered with abundant spider mite webbing, which may have impeded *L. hesperus* foraging. In experiment 2, spider mite densities were moderated by changes in our protocols, and we found *L. hesperus* nymphs at the end of the experiment.

Responses of the host plant

Herbivory significantly diminished cotton plant performance in both experiments 1 and 2. Adding herbivores only to cotton plants decreased reproductive biomass of cotton plants by >80% (Fig. 4; experiment 1, $\chi^2 = 17.9$, $P < 0.0001$; experiment 2, $\chi^2 = 12.2$, $P = 0.0005$) and decreased fruit retention rates by ~50% (Fig. 4; experiment 1, $\chi^2 = 14.8$, $P = 0.0001$; experiment 2, $\chi^2 = 10.6$, $P = 0.001$). Cotton reproductive biomass was not significantly correlated with either *L. hesperus* adult or *L. hesperus* nymph densities. Fruit retention rates were negatively correlated with *L. hesperus* adult densities (Spearman's rho, experiment 1, $\rho = -0.43$, $P < 0.0001$; experiment 2, $\rho = -0.35$, $P = 0.0091$) but were uncorrelated with *L. hesperus* nymphs (experiment 2, $\rho = 0.058$, $P = 0.67$).

Adding predators increased reproductive biomass of cotton plants in experiment 2 (Fig. 4; $\chi^2 = 8.0$, $P = 0.046$) but not in experiment 1 (Fig. 4; $\chi^2 = 0.76$, $P = 0.68$). Adding both predator species produced trends of higher plant reproductive biomass compared to single predator species treatment, but the improvement was not statistically significant. The presence of *G. pallens* increased plant reproductive biomass by 126% ($\chi^2 = 7.71$, $P = 0.06$). The presence of *Z. renardii* increased plant reproductive biomass by 48% ($\chi^2 = 4.04$, $P = 0.045$).

Adding single predator species did not produce significant increases in fruit retention (Fig. 5). A combination of both predators, however, significantly improved fruit retention (experiment 1, $\chi^2 = 4.2$, $P = 0.041$; experiment 2, $\chi^2 = 5.1$, $P = 0.025$). In experiment 2, the combination of both predators even produced fruit retention levels similar to herbivore-free plants ($\chi^2 = 3.0$, $P = 0.084$; Fig. 5). A full factorial analysis of experiment 2 suggested that fruit retention was not

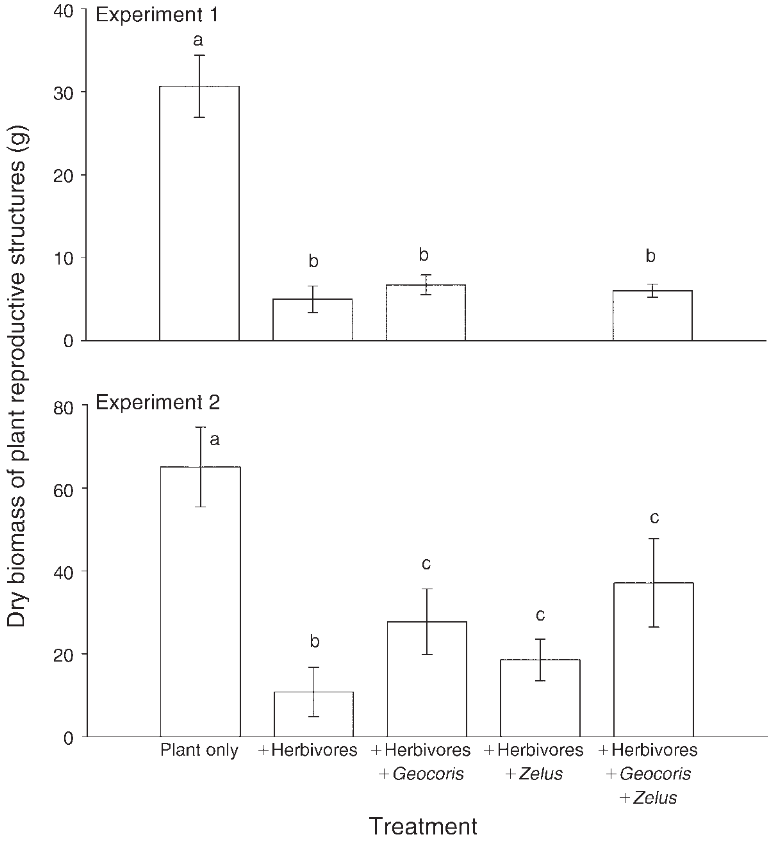

FIG. 4. Dry biomass of cotton plant reproductive structures (mean ± SE) at the end of experiments 1 and 2. There was no "+ herbivores + *Zelus*" treatment in experiment 1. Treatments not sharing the same letter have significantly different means ($P < 0.05$).

increased by *G. pallens* ($\chi^2 = 2.1$, $P = 0.15$) but was significantly enhanced by *Z. renardii* (+35%, $\chi^2 = 4.1$, $P = 0.043$).

DISCUSSION

Here we compare our results to the predictions of the IGP-cannibalism model introduced by Rudolf (2007). First we discuss *G. pallens* as a cannibalistic intermediate predator and the effects that *Z. renardii* has on *G. pallens* populations, and then we focus on the predators' impacts on prey suppression and plant performance.

G. pallens populations appear to be self-limiting. In both experiments the final densities of *G. pallens* adults did not exceed the number of females introduced to each cage (Fig. 4), despite ample time for reproduction across at least one full generation of *G. pallens*. Furthermore, the final densities of *G. pallens* adults in our experiments were similar to densities commonly found in cotton fields. In the field, *G. pallens* population growth might be constrained by several factors, including food scarcity or the presence of higher-order predators. Our experimental design allowed us to alleviate these extrinsic constraints on *G. pallens* populations by providing high food availability (*T. urticae*, thrips and cotton extrafloral nectaries) and excluding natural enemies, yet *G. pallens* adult abundance did not increase as one might have expected. The results reported here, together with our observations of density-dependent cannibalism in *G. pallens* and its effects on reproductive recruitment by *G. pallens* (Y.-H. Law and J. A. Rosenheim, *unpublished data*), are consistent with the hypothesis that density-dependent cannibalism plays a central role in the regulation of *G. pallens* populations.

The intraguild predator *Z. renardii* did not have a substantial effect on *G. pallens* population abundance over the six-week duration of their interaction within our cages (experiments 1 and 2). How could this be when *Z. renardii* inflicted strong mortality on *G. pallens* adults in a five-day assay (Appendix: Fig. A1)? A possible explanation, as proposed by Rudolf (2007, 2008), is that the addition of the intraguild predator relaxed cannibalism rates within the intermediate predator population. One plausible scenario is that *Z. renardii* increased predation mortality on all *G. pallens* stages, resulting in a lower abundance of all *G. pallens* stages and thereby triggering a decrease in the density-dependent expression of cannibalism. The combination of increased IGP and decreased cannibalism could therefore produce lower numbers of *G. pallens* eggs and nymphs but higher survival and recruitment of these stages to adults. In

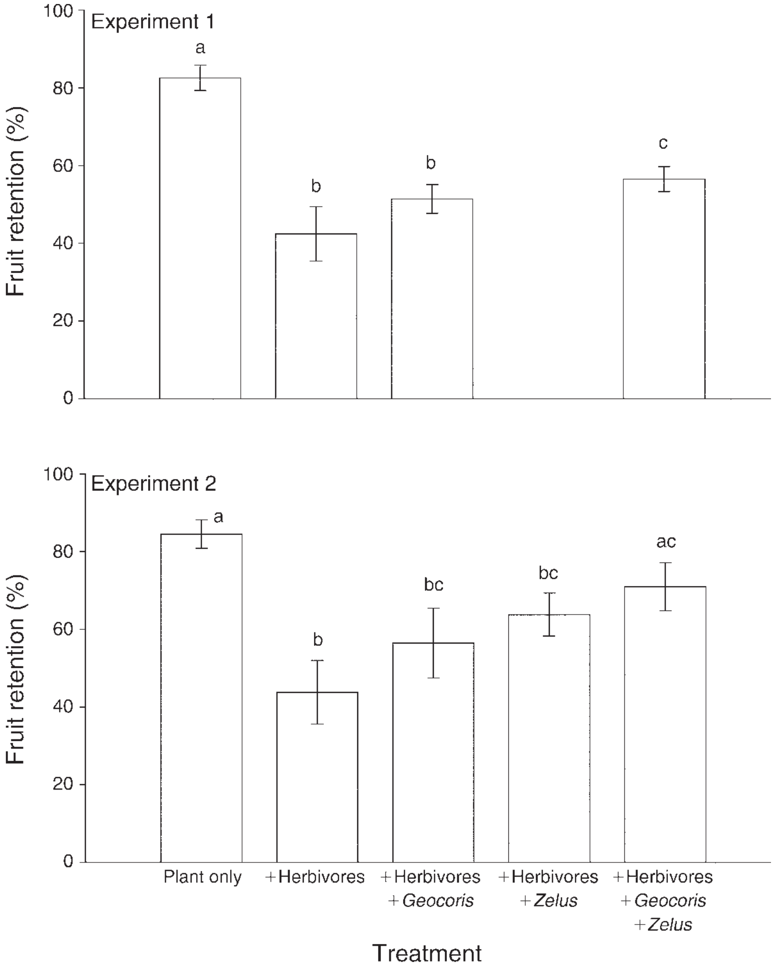

FIG. 5. Cotton fruit retention (mean ± SE) at the end of experiments 1 and 2. There was no "+herbivores+*Zelus*" treatment in experiment 1. Treatments not sharing the same letter have significantly different means ($P < 0.05$).

short, the predation mortality imposed by *Z. renardii* on *G. pallens* could have been compensated for by the gain in survival due to reduced cannibalism, resulting in little net impact of *Z. renardii* on *G. pallens* abundance. It should be noted, however, that our experiments cannot identify cannibalism as the sole explanation for these observations. Any form of strong self-limitation within the *G. pallens* populations that is relaxed by the addition of an intraguild predator could produce the same density responses, although cannibalism seems to be the most likely candidate in our study. Further work is required to confirm density-dependent cannibalism as the self-limiting mechanism that is relaxed by intraguild predation. One potentially useful approach would be to conduct a factorial experiment with IGP as one factor and cannibalism rates in *G. pallens* as another.

Predator diversity increased herbivore suppression in our study: suppression of *L. hesperus* was strongest when both predator species were used instead of single predator species. There are two possible explanations for this positive relationship between predator diversity and prey suppression. The first and most trivial explanation is that if the predator species do not produce net negative effects on each other, then adding new predator species can only be expected to increase herbivore suppression. This scenario applies to our study, because the two predator species have negligible net effects on the abundance of the other. This scenario also matches the prediction of Rudolf's (2007) IGP-cannibalism model.

The second, and non-mutually exclusive, explanation for the improved suppression of *L. hesperus* is resource partitioning between *G. pallens* and *Z. renardii.* Our results show that *G. pallens* suppressed *L. hesperus* nymphs but not adults, whereas *Z. renardii* suppressed *L. hesperus* adults but not nymphs. This suggests that these predators impose predation risk on different subsets of the *L. hesperus* population. The partitioning is most likely caused by differences in prey size/stage exploited and microhabitat use. *G. pallens*, a relatively small predator (body length = 3–5 mm), can only subdue *L. hesperus* eggs and early instars (Zink and Rosenheim

2008). *Z. renardii*, a substantially larger predator (body length = 15 mm), is capable of consuming all mobile stages of *L. hesperus*, yet surprisingly they did not affect *L. hesperus* nymph densities. It is possible that *L. hesperus* nymphs utilize refuges from *Z. renardii* predation. Compared to adults, *L. hesperus* nymphs spend more time on cotton reproductive structures (Rosenheim et al. 2004), where the complexity of the microhabitat could potentially protect them from *Z. renardii*, which uses motion cues and ambush foraging to capture prey (Cisneros and Rosenheim 1998). These microhabitat refuges should be less effective against *G. pallens*, due to the latter's active foraging and smaller size. Spatial resource partitioning can improve prey suppression (Tylianakis et al. 2008), as could have been the case in our study system. Furthermore, the strong intraspecific interference within *G. pallens* can also promote positive effects of resource partitioning on prey suppression (Griffin et al. 2008). On the other hand, mathematical modeling has suggested that partitioning of prey by developmental stage alone cannot allow coexistence of predator species (Briggs 1993), and prey suppression may not always be improved. Further work needs to be done before we can draw conclusions regarding the contribution of resource partitioning to improved suppression of *L. hesperus* in our study system.

Ecologists strive to understand how ecological interactions affect community dynamics and individual behaviors, yet the complexity of interactions presents a huge challenge (Polis and Strong 1996, Bruno and Cardinale 2008). In response, ecologists sometimes divide the interactions into simpler modules and study them independently; IGP and cannibalism are two such modules. This practical approach has developed our understanding of these two interactions substantially (Rosenheim et al. 1995, Holt and Polis 1997, Schausberger 2003, Arim and Marquet 2004, Wise 2006, Vance-Chalcraft et al. 2007), yet many outstanding questions remain. For example, we are just beginning to account for the importance of individual traits in IGP (Schmitz 2007), where the conventional focus has been on the community level, and cannibalism studies are starting to extend beyond individuals and populations (Claessen et al. 2004). IGP and cannibalism also very likely co-occur in many communities (Polis 1981, Arim and Marquet 2004), and may have nontrivial combined effects on these communities. By addressing these interactions separately, we may be neglecting important and integral dynamics of these communities. Marrying interaction modules may help us to address longstanding questions in ecology. For instance, despite the large amount of research on cannibalism, no solid conclusion can be drawn on the effects of cannibalism within predators on prey suppression (Wise 2006). Although our results do not tell us what influence *Geocoris* alone might have on *Lygus* in the absence of cannibalism, our experiments do suggest that cannibalism in *Geocoris* populations enables this predator to be combined with a population of an intraguild predator (*Zelus*) to enhance total suppression of an herbivore prey population, thereby enhancing plant performance. This is also an example of predator biodiversity enhancing total prey suppression when intraspecific interference (here, likely cannibalism) is strong, and more important than interspecific interference (Aquilino et al. 2005, Griffin et al. 2008, Letourneau et al. 2009).

In conclusion, we have reported here a case where prey suppression is enhanced despite the presence of potentially disruptive IGP, ultimately leading to improved plant performance. The enhancement of prey suppression was likely due to a relaxation in density-dependent cannibalism within the intermediate predator population that was caused by IGP, although a complementary role for resource partitioning cannot be excluded. Our findings provide support for a model of IGP with cannibalism (Hart 2002, Rudolf 2007) and demonstrate empirically the possibility for IGP to enhance prey suppression when the intermediate predator is cannibalistic. Although both IGP and cannibalism are common trophic interactions in predator communities (Polis 1981, Arim and Marquet 2004), little is known about their combined effects because IGP and cannibalism have been studied extensively as isolated interaction modules. IGP and cannibalism are processes that affect interspecfic and intraspecific interference—two key factors in predicting the predator diversity–prey suppression relationship (Schmitz 2007, Letourneau et al. 2009). As such, studying both processes simultaneously is likely to further our understanding of predator richness effects on prey suppression and warrants more attention. Future work should explicitly examine interactions of IGP and intraspecific regulation (e.g., cannibalism), paying particular attention to mechanisms that determine the strength of intraspecific regulation and are also affected by IGP.

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APPENDIX

Laboratory and field data on cannibalism in *Geocoris pallens*, and predation rates of *Zelus renardii* on *G. pallens* (*Ecological Archives* E092-029-A1).