



Evidence for intraguild predation by *Podisus maculiventris* on a ladybeetle, *Coleomegilla maculata*: Implications for biological control of Colorado potato beetle, *Leptinotarsa decemlineata*

N. MALLAMPALLI*, I. CASTELLANOS and P. BARBOSA

Department of Entomology, University of Maryland, College Park, Maryland, USA

**Author for correspondence; e-mail: nikhilmmd@hotmail.com*

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Abstract. The potential for intraguild predation (IGP) between larval and adult life stages of two polyphagous arthropod predators common in North American agroecosystems was studied in the laboratory. Predators examined were the spined soldier bug, *Podisus maculiventris* Say, and the twelve-spotted ladybeetle, *Coleomegilla maculata* Leng. A shared prey item, eggs of the Colorado potato beetle (CPB), *Leptinotarsa decemlineata* Say, was also provided to the predators, both to provide an alternate food source and to quantify the impact of IGP on the potential for pest suppression by these two predators. Experiments were conducted on single potato leaves in plastic cup arenas, and, subsequently, in cages enclosing whole potato plants. IGP occurred asymmetrically, with *P. maculiventris* adults and nymphs only attacking *C. maculata* larvae. Even though ladybeetle adults were generally smaller than soldier bug adults, they were never preyed upon. This appears to be the first documented case of a coccinellid showing differential larval and adult immunity to attack by a larger invertebrate predator. The impact of IGP, when it did occur, on CPB egg consumption was equivocal. IGP did not consistently influence levels of predation on the eggs. Conversely, even when IGP did not occur, predation on CPB eggs by both predators together did not increase significantly over levels inflicted by either predator alone. The implications for biological control of CPB by these predators, which are being considered for augmentative release in potato and tomato crops in the United States, are discussed.

Key words: Colorado potato beetle, intraguild predation, predator-prey interactions, Coleoptera, Coccinellidae, Heteroptera, Pentatomidae

Introduction

Generalist insect predators are common in agroecosystems, including cotton, potato, corn, and soybean (Pedigo, 1989; Huffaker and Gutierrez, 1999). Some have been reported as major mortality agents of many pest herbivores (Grodén et al., 1990; Hodek and Honek, 1996; Van Dreische and Bellows, 1996). However, there is growing awareness that polyphagous predators often

include other predators in their diet, a phenomenon often referred to as intraguild predation (IGP) (Polis et al., 1989; Polis and Holt, 1992; Rosenheim et al., 1995). Such behavior is important to biological control if it results in a decrease in predation pressure on a target pest herbivore. It may also impede the goals of biological control if a less effective predator eats another, particularly effective natural enemy. In this context, IGP has often been discussed as an 'antagonistic' interaction between predatory insects (Huang and Sih, 1991; Wissinger and McGrady, 1993; Fagan et al., 1998). Predators may also respond to one another in such a way as to interfere with their potential ability to suppress pest populations even where IGP itself does not occur (Yao and Chant, 1989; Schmitz et al., 1997).

As part of a study of the impact of insect predators in potato agroecosystems in the eastern United States, we investigated the potential for IGP between two common predatory insects, the spined soldier bug, *Podisus maculiventris* Say (Heteroptera: Pentatomidae), and the twelve-spotted ladybeetle, *Coleomegilla maculata* Lengi (Coleoptera: Coccinellidae). *P. maculiventris* has been imported into the US to be used in mass releases against a variety of pests, including the Colorado potato beetle (CPB), *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) (Biever and Chauvin, 1992; Hough-Goldstein and McPherson, 1996), the most economically damaging insect pest of potatoes in North America (Hare, 1990). *P. maculiventris* has been recorded as a predator of all CPB life stages (Hough-Goldstein and McPherson, 1996). It also attacks aphids, larval Lepidoptera, and other heteropteran arthropods (McPherson, 1980). *C. maculata* is native to the eastern US and is abundant in many crop systems, particularly corn (Coll and Bottrell, 1991) and potato (Hilbeck and Kennedy, 1996). It is able to complete its development not only on a wide array of insect eggs, small larvae, and aphids (Hazzard and Ferro, 1991; Phoofolo and Obrycki, 1997), but on pollen as well (Smith, 1960). Groden et al. (1990) reported that *C. maculata* inflicted high rates of mortality (up to 60%) on CPB eggs in Massachusetts potato fields.

Given the potential importance of *P. maculiventris* and *C. maculata* as predators of the CPB, we assessed the potential for IGP in this system. It is noteworthy that there is a size difference between these life stages of the predators studied. *P. maculiventris* adults were by far the largest, followed by *C. maculata* adults, which were roughly equivalent in size to *P. maculiventris* nymphs, and lastly, *C. maculata* larvae. Other studies reporting IGP have noted that larger predators attack smaller ones (Polis et al., 1989; Rosenheim et al., 1993; Lucas et al., 1997), and we expected a similar phenomenon in our system. Our studies had the following objectives: 1) to determine whether IGP can occur, in an environment where the predators have a choice between

feeding on one another or upon the shared prey (CPB eggs), 2) to determine the extent to which IGP affects consumption of CPB eggs, and 3) if IGP is absent, to determine whether predation on CPB eggs by both predators is increased significantly over that inflicted by either predator alone.

Materials and methods

C. maculata adults were collected on late-planted corn plots in which corn was still tasselling (producing pollen) in Beltsville, Maryland. They were maintained in the laboratory on a diet of bee pollen and artificial wheat germ diet supplemented with Mexican fruit fly (*Anastrepha ludens* Loew) eggs. Adults used in experiments were separated from the main colony and held without food for 24 h prior to use. *P. maculiventris* adults were obtained from colonies started with field-collected individuals maintained at the Maryland Department of Agriculture, Plant Protection Unit, and maintained on a diet of green beans and mealworm (*Tenebrio molitor* Linnaeus) larvae. Individuals used in experiments were held in containers with only green beans for 24 h, and starved completely for an additional 24 h. Fresh CPB eggs were obtained from the Philip Alampi Biocontrol Laboratory of the New Jersey Department of Agriculture, Trenton, NJ. We measured weights and lengths of a sample ($n = 15$) of these insects, to verify the differences between the predator species and life stages involved. Measurements were made on an Ohaus Analytical Plus AP250D electronic balance.

To examine IGP potential between larval and adult life stages of each predator species, *P. maculiventris* adults were paired with either *C. maculata* adults or with early 4th-instar *C. maculata* larvae, and 3rd-instar *P. maculiventris* nymphs were paired with either *C. maculata* adults or with early 4th-instar *C. maculata* larvae.

Experiments were carried out in two arenas: plastic cups and potted plants. Cup arenas were used initially, to determine whether IGP had any potential for occurring in this system. Subsequently, plant arenas were used to introduce spatial heterogeneity more representative of a natural environment these predators might encounter. In both arenas, combinations involving *P. maculiventris* adults were conducted separately from those involving *P. maculiventris* nymphs. The plant-arena experiments were conducted only for the combinations of *P. maculiventris* adults or nymphs with *C. maculata* larvae. In all experiments, control treatments were also included, in which individuals of each predator species were placed into arenas with CPB eggs. One insect of each species was present per arena in any given arena, except in treatments where both species were assigned to an arena (in that case one individual of each species was placed into each arena). A completely

randomized design was used throughout, and treatments consisted of the type of predator (alone or in combination as described above) placed into an arena. Experiments involving adult predators used a 1:1 ratio of males and females. There were 15–16 replicates per treatment in cup-arena experiments, and 7 replicates per treatment in the plant-arena experiments.

For the cup-arena experiment, a single mature (fully expanded) potato leaf was placed in a 20 ml glass vial filled with water, and placed in 946 ml plastic cups. Moistened dental wicking provided water for predators. Cups were placed in an environmental chamber set at a 16:8 light:dark regime, 24 °C, and 70% RH. For plant-arena experiments, single 2-week-old potato plants (*cv.* 'Atlantic'), in 15 cm plastic pots, were placed into 64 cm × 34 cm plastic cages set in potting trays. Sand was placed around the base of cages to prevent insects from escaping. Experiments were conducted in a greenhouse set at a 16:8 light:dark regime and 24 °C.

A single CPB egg mass containing 40 eggs was fastened to the underside of the single leaf (in the cup experiment) or of a mature upper leaf (in the plant experiment), using an insect pin. Experiments began when individual predators were released into the cages, and were terminated after 48 h. At that point mortality of predators and the number of eggs eaten was recorded. Data on proportion of eggs eaten, and on sizes and weights of predators, were analyzed using PROC GLM in SAS (SAS Institute, 1992). Where needed, data were transformed using either the arc-sine square root or the log (base 10) procedure, to meet assumptions of ANOVA. Pairwise means comparisons were made using Tukey's HSD test (with $\alpha = 0.05$).

Results

Our measurements of predators generally confirmed size differences between the different life stages and species involved. ANOVA showed a significant difference due to predator type for both length ($F = 490.5$, $df = 3,56$, $p < 0.0001$) and weight ($F = 478.3$, $df = 3,56$, $p < 0.0001$). *P. maculiventris* adults had a mean weight of 10.7 ± 0.16 mg, and were 25 ± 1.2 mm in length, while nymphs weighed 5 ± 0.15 mg and were 5.0 ± 0.4 mm long. *C. maculata* adults weighed 5.7 ± 0.1 mg and were 14 ± 1.2 mm long; larvae weighed 2.6 ± 0.2 mg and were 3.5 ± 1.1 mm long. Tukey's HSD test indicated that *P. maculiventris* adults were significantly larger and heavier than any of the other predator types. *P. maculiventris* nymphs were significantly heavier than both *C. maculata* larvae and adults (but were not significantly longer than coccinellid adults). *C. maculata* adults were significantly heavier and longer than *C. maculata* larvae.

There was no predation on either *P. maculiventris* life stage by *C. maculata* larvae or adults in the cup-arena experiments. There was also no predation at all on *C. maculata* adults by *P. maculiventris* adults or nymphs. However, both *P. maculiventris* adults and nymphs preyed heavily on *C. maculata* larvae. *P. maculiventris* nymphs ate $75 \pm 5.5\%$ of all *C. maculata* larvae by the end of all trials, and no *C. maculata* larvae survived at the end of the experiments involving *P. maculiventris* adults (i.e., 100% larval coccinellid mortality at the end of all such trials).

CPB egg consumption data from the cup experiments involving *P. maculiventris* adults and *C. maculata* larvae and adults are presented in Figures 1A and 1B, respectively. There was a significant effect of predator type ($F = 12.5$, $df = 4$, 58 , $p = 0.002$). *P. maculiventris* adults alone ate significantly more CPB eggs than *C. maculata* larvae alone (Figure 1A), but not more than coccinellid adults (Figure 1B). Furthermore, when *P. maculiventris* adults were placed with *C. maculata* larvae (where heavy IGP mortality of coccinellid larvae was observed) predation on CPB remained at a level comparable to that of *C. maculata* larvae alone, but was significantly lower than that observed with *P. maculiventris* alone (Figure 1A). When *P. maculiventris* adults and *C. maculata* adults were placed together, despite the lack of IGP mortality, consumption of CPB eggs did not increase significantly over that of either predator alone (Figure 1B).

In cup-arena experiments involving *P. maculiventris* nymphs and *C. maculata* larvae or adults significant differences due to predator type were again observed ($F = 14.72$, $df = 4, 58$, $p < 0.001$). *C. maculata* larvae ate significantly more than *P. maculiventris* nymphs. When these life stages of the predators were paired together, CPB consumption was reduced significantly compared to *C. maculata* predation (Figure 2A), possibly as a result of the high IGP mortality of coccinellid larvae. *C. maculata* adults alone also ate significantly more CPB eggs than *P. maculiventris* nymphs. When these stages of the predators were paired together, predation on CPB eggs was increased significantly over that inflicted by *P. maculiventris* nymphs alone but remained at a level comparable to that of *C. maculata* alone (Figure 2B), despite the absence of IGP.

In experiments using plant arenas, *P. maculiventris* adults and nymphs both preyed heavily upon *C. maculata* larvae, as was observed in the cup-arena experiments. *P. maculiventris* nymphs ate an average of $90 \pm 4.5\%$ of coccinellid larvae, while adults ate $55.5 \pm 3.5\%$. The pattern of CPB consumption by *P. maculiventris* adults and *C. maculata* larvae, alone and together (Figure 3A), mirrors that seen in the comparable cup experiments (Figure 1A). Significant differences due to predator type were observed ($F = 4.55$, $df = 2, 19$, $p = 0.02$), and CPB egg consumption by *P. maculiventris*

adults was significantly greater than that of *C. maculata* larvae alone as well as that observed when both predators were together (Figure 3A). In the experiment involving *P. maculiventris* nymphs and *C. maculata* larvae in plant-arenas, predator type was again significant ($F = 5.38$, $df = 2,19$, $p = 0.02$). However, the pattern of CPB consumption by *P. maculiventris* nymphs and *C. maculata* larvae on plants (Figure 3B) was different than that seen in the cup experiments (Figure 2A). In the plant arenas, *C. maculata* alone ate significantly less than *P. maculiventris* nymphs alone; when the predators were placed together in these arenas, predation on CPB eggs dropped relative to that of *P. maculiventris* nymphs, but not significantly (Figure 3B).

Discussion

The results of our experiments document an asymmetric form of IGP between *P. maculiventris* and *C. maculata*, with *P. maculiventris* attacking only the larval form of the ladybeetle. The cup experiments showed that IGP between these predator species was plausible, but only between certain life stages. Even in the comparatively higher spatial complexity of the plant-arena experiments, IGP mortality of coccinellid larvae was observed at a level similar to that seen in the cup arenas. Furthermore, the presence of an alternate food source (CPB eggs) did not eliminate IGP between *P. maculiventris* and *C. maculata*.

At least one other study has reported that *P. maculiventris* feeds on both larvae and adults of another ladybeetle, *Harmonia axyridis* Pallas (Hough-Goldstein et al., 1996), albeit in no-choice tests in Petri dishes. In their study, as in ours, the IGP was asymmetric, in that *P. maculiventris* was never attacked by the coccinellid. In that system, however, the life stages of *P. maculiventris* used were always larger than those of the coccinellid. Lucas et al. (1997) also reported IGP between some larval instars of *C. maculata* and those of the neuropteran predator, *Chrysoperla rufilabris* Burmeister. In that case, IGP was symmetric, with the larger life stage of either predator generally preying on the smaller one. Indeed, across a wide range of taxa, the loser of an IGP bout is almost always the smaller predator (Polis et al., 1989; Diehl, 1993). Our study is the first (to our knowledge) to report differential susceptibility of larval and adult life stages of a coccinellid beetle against a larger invertebrate predator.

The apparent immunity of *C. maculata* adults to IGP may be due to the chemical defenses this species is known to possess, in the form of pyrrolizidine alkaloids (Henson et al., 1975). It is interesting that *C. maculata* larvae do not appear to have the ability to repel *P. maculiventris*. It is not known whether the alkaloids isolated by Henson et al. (1975) vary

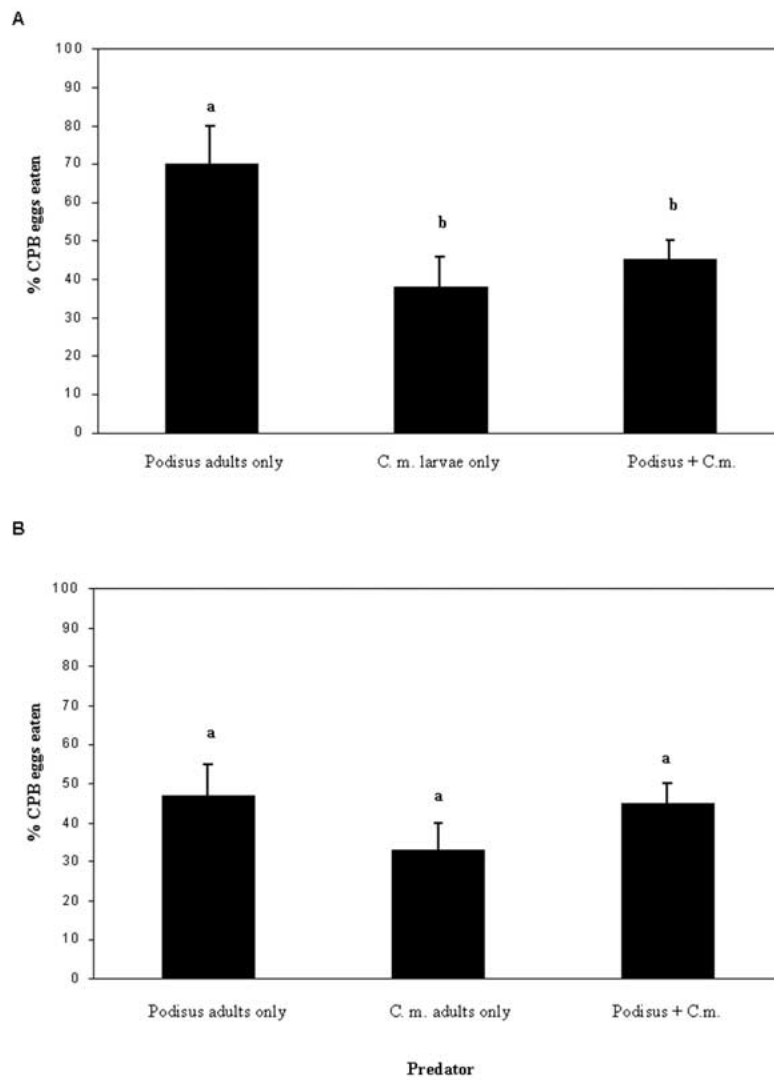


Figure 1A–B. Cup-arena experiments. **A.** Mean (± 1 S.E.) CPB egg consumption by *P. maculiventris* adults and/or *C. maculata* larvae. **B.** Mean (± 1 S.E.) CPB egg consumption by *P. maculiventris* adults and/or *C. maculata* adults. Bars with the same letter are not significantly different ($p > 0.05$).

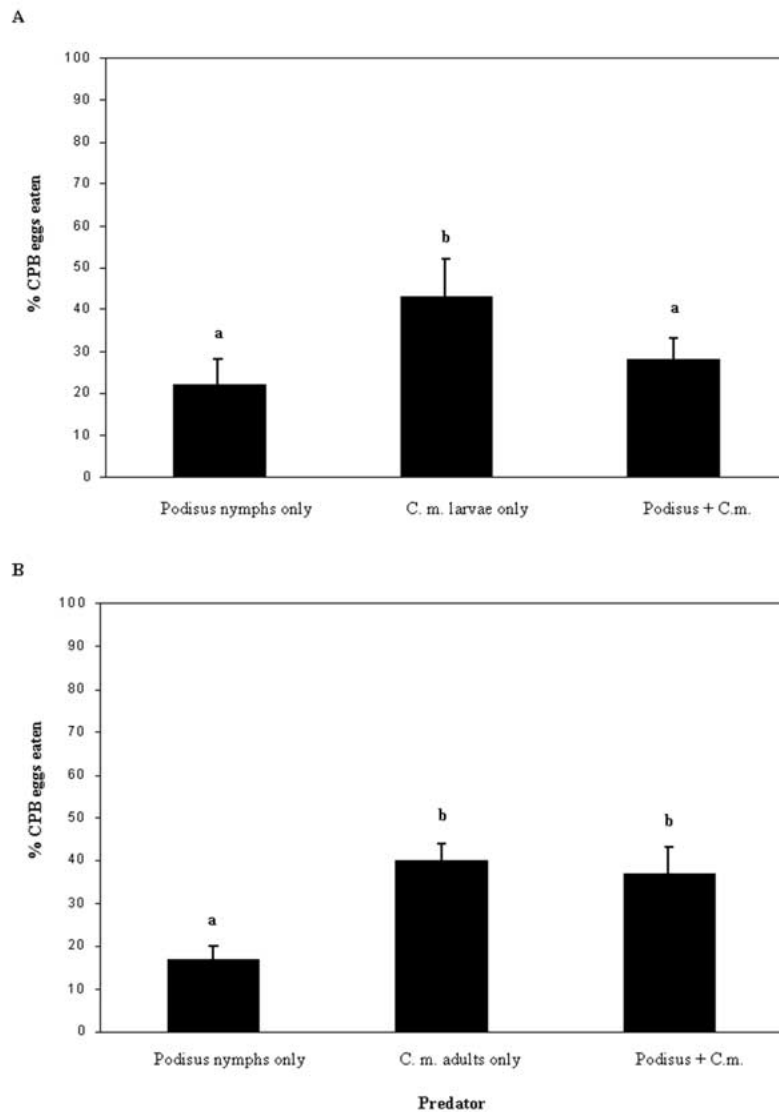


Figure 2A–B. Cup-arena experiments. **A.** Mean (± 1 S.E.) CPB egg consumption by *P. maculiventris* nymphs and/or *C. maculata* larvae. **B.** Mean (± 1 S.E.) CPB egg consumption by *P. maculiventris* nymphs and/or *C. maculata* adults. Bars with the same letter are not significantly different ($p > 0.05$).

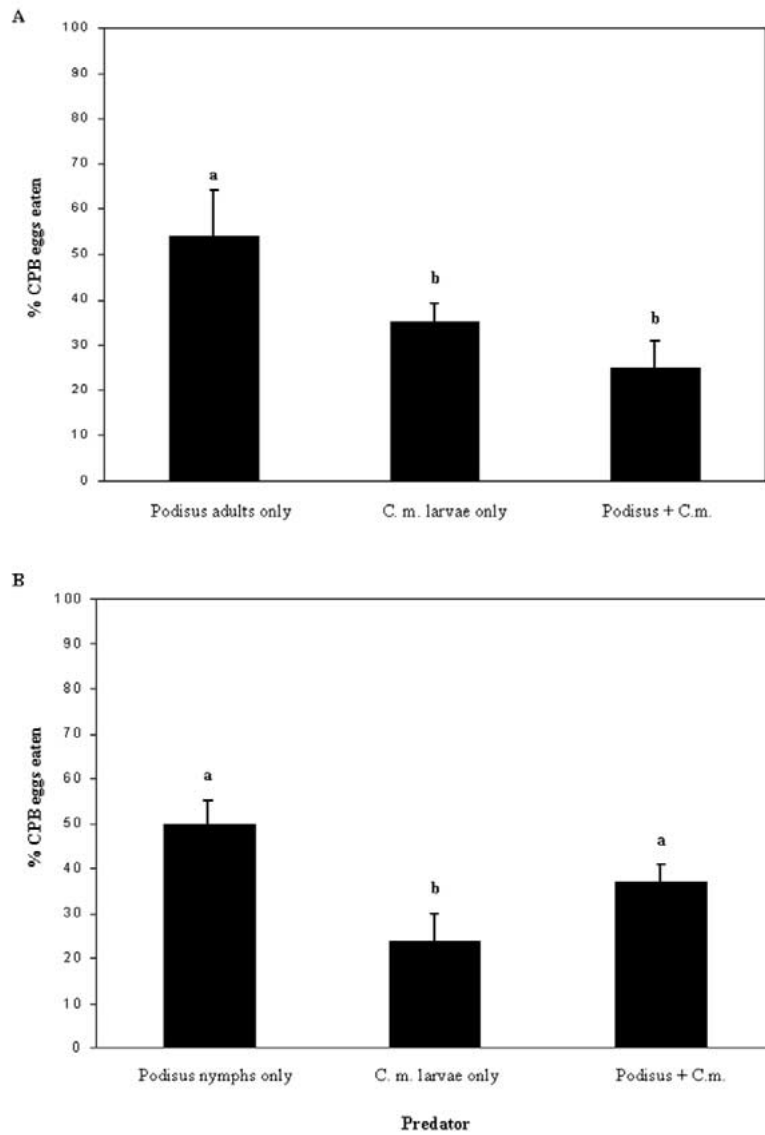


Figure 3A–B. Plant-arena experiments. **A.** Mean (± 1 S.E.) CPB egg consumption by *P. maculiventris* adults and/or *C. maculata* larvae. **B.** Mean (± 1 S.E.) CPB egg consumption by *P. maculiventris* nymphs and/or *C. maculata* larvae. Bars with the same letter are not significantly different ($p > 0.05$).

in concentration or expression over the life stages of this species, but the results from our study suggest this is a possibility. We have conducted similar experiments with another coccinellid, *Coccinella septempunctata* Linneaus, substituted for *C. maculata* (data not shown). In those studies, *P. maculiventris* readily consumed both larvae and adults of the ladybeetle. *C. septempunctata* is known to produce alkaloids similar (but not identical) to those of *C. maculata* (Tursch et al., 1971). However, there was no apparent repulsion of *C. septempunctata* by *P. maculiventris* in our study. This suggests that *P. maculiventris* may be sensitive only to specific alkaloids in specific concentrations.

The consequences of IGP (when it did occur) for CPB egg consumption by *P. maculiventris* and *C. maculata* are not straightforward. In both the cup and plant experiments, CPB consumption remained at a relatively high level, even when IGP occurred. Since we did not attempt to distinguish between CPB predation by *P. maculiventris* or *C. maculata*, it is possible that *P. maculiventris* fed upon the CPB eggs after killing coccinellid larvae. Alternatively, the coccinellids may have consumed appreciable amounts of CPB eggs before being attacked.

In the case of *P. maculiventris* adults paired with *C. maculata* larvae, the plant-arena experiment suggests that this combination may even disrupt the biological control of CPB egg populations exerted by either predator alone. In this case, the fact that predation of the CPB eggs in the combination treatment was significantly lower than that of *P. maculiventris* alone also suggests that soldier bug adults, in using coccinellid larvae as alternative food, were distracted from egg prey. Thus, at the very least, our results indicate that it is unlikely that the presence of *P. maculiventris* (adults or nymphs) in combination with *C. maculata* larvae will result in increased mortality of CPB. A more effective strategy might be to utilize *P. maculiventris* with a predominantly adult population of *C. maculata*, since IGP does not occur in that situation. However, our results also suggest that, even with this combination (a situation where IGP did not occur) predation on CPB may not increase significantly over that inflicted by both predators separately. This may be due to behaviorally mediated interference between these predators. This type of interference has been demonstrated for other predator systems (Yao and Chant, 1989; Schmitz et al., 1997).

Our experiments were conducted in relatively artificial arenas over a short time scale. Field-level studies examining the longer-term effects of IGP between these predators on CPB populations may reveal a magnified positive impact on CPB numbers (i.e. an overall increase in CPB populations). This effect has been observed in the relatively few field studies of this type that have been conducted thus far (Cisneros and Rosenheim, 1997; Rosenheim et

al., 1993; Croft and Macrae, 1992). There may also be a negative impact on *C. maculata* reproductive recruitment, due to IGP by *P. maculiventris*, which only a long-term field experiment would reveal.

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