Intraguild Predation Between Lady Beetles and Lacewings: Outcomes and Consequences Vary With Focal Prey and Arena of Interaction

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ABSTRACT We examined reciprocal intraguild predation (IGP) and cannibalism among various combinations of *Coleomegilla maculata* DeGeer and *Chrysoperla carnea* Stephens larvae as they developed feeding on greenbugs, *Schizaphis graminum* Rondani, on sorghum plants in microcosms. Pairs of *C. maculata* larvae suppressed aphids better than pairs of *C. carnea* larvae or heterospecific larval pairs and yielded the highest rate of plant survival. IGP by *C. carnea* larvae occurred mostly in the first instar, whereas *C. maculata* larvae were more aggressive in later instars. Although *C. carnea* was the superior intraguild predator, winning 62.7% of contests in microcosms, this value increased to 88.9% when the experiment was repeated in petri dishes without plant material, regardless of whether greenbugs or eggs of *Ephestia kuehniella* Zeller were offered as focal prey. Provision in petri dishes of the sessile, higher quality prey (*Ephestia*) as opposed to greenbugs, improved the survival of solitary larvae and delayed cannibalism and IGP until later developmental stages in both species. Larvae of *C. maculata* that cannibalized took longer to develop and weighed less at pupation, independent of the arena or prey offered. Although larvae of *C. carnea* did not pay a cost for cannibalism or IGP in microcosms, there were some negative developmental effects of IGP in petri dishes, particularly on the *Ephestia* diet. These results illustrate how the plant, as a substrate, can mediate the strength of IGP interactions and how the relative suitability of the focal prey can influence both the timing and consequences of cannibalism and IGP.

KEY WORDS cannibalism, Coccinellidae, Chrysopidae, *Ephestia kuehniella*, *Schizaphis graminum*

Predators that exploit a shared resource, or focal prey, frequently encounter one another in the course of foraging and thus face the prospect of either preying on, or falling prey to, competing species. This phenomenon has been termed intraguild predation (IGP) (Polis and McCormick 1987, Polis et al. 1989). A distinction is often drawn between asymmetric IGP, where one predator preys on another but is not itself vulnerable, and symmetric IGP, where the predation is reciprocal. Because of its ecological implications, IGP has emerged as a topic of interest for both practitioners of biological control in managed agroecosystems (e.g., Rosenheim et al. 1995, Chacon et al. 2008), and those concerned with the conservation of diversity in natural communities in the face of climate change (Barton and Schmitz 2009) or alien species invasions (Mizell 2007, Pell et al. 2008). Many empirical studies have examined IGP among predators of aphids (e.g., Colfer and Rosenheim 2001, Hindayana et al. 2001, Meyhofer 2001, Meyhofer and Klug 2002, Gardiner and Landis 2007). Aside from their economic importance as pests, aphids often form large colonies on plants in exposed locations that serve to attract a range of generalist and specialist predators, thus generating ample opportunities for IGP.

The larval stages of many lady beetles and lacewings are specialized aphid predators that engage in symmetric IGP (sensu Polis et al. 1989). Thus, interactions between these two groups have often been the subject of IGP experiments in both laboratory (Lucas et al. 1997, Phoofolo and Obrycki 1998, Michaud and Grant 2003, Moser and Obrycki 2009) and field cage studies (Costamagna et al. 2007, Gardiner and Landis 2007, Chacon and Heimpel 2010). Aphids are a notoriously ephemeral resource such that the larvae of aphid predators are frequently driven to cannibalism and IGP to obtain resources sufficient for complete development. Hemptinne et al. (2011) reviewed some 70 published studies of IGP in aphidophagous systems and found the majority to be laboratory studies, many conducted without the presence of focal prey, and very few in which the density of focal prey was manipulated. However, even providing prey at different densities does not mimic the natural scenario in which predatory larvae grow in parallel with an aphid colony and experience first an increase, and then a decrease, in prey density during the course of their development. In the current study, we explored IGP outcomes among different combinations of coccinellid and lacewing larvae in laboratory microcosms (consisting of

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live plants with developing aphid colonies) and tracked the consequences of these interactions, not only for the fate of the plant and the aphid colony, but also for the development of surviving predators. Daily observations made it possible to determine the timing of IGP events with respect to both the stage of predator development and the availability of focal prey.

The greenbug, *Schizaphis graminum* Rondani (Hemiptera: Aphididae), is a common pest of wheat and sorghum in the Great Plains of the United States. The important predators of this aphid include the 12-spotted ladybird, *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae), and the green lacewing, *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae) (Rice and Wilde 1988). Our objectives were to 1) determine the frequency and outcome of IGP interactions between *C. maculata* and *C. carnea* on live sorghum plants bearing developing greenbug colonies, 2) assess the impact of IGP on aphid suppression, and 3) determine if the outcomes of IGP interactions would be different in a simplified arena (petri dish) or with a different food source (eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller [Lepidoptera: Pyralidae]). We also wanted to establish the timing of IGP and cannibalism events with respect to developmental stage of both predator and prey.

Materials and Methods

Insect Colonies. A laboratory colony of *S. graminum* biotype 'I' was established from material collected from sorghum, *Sorghum bicolor* (L.) Moench, at the Agricultural Research Center-Hays (ARCH), Kansas State University, Hays, KS, in the spring of 2010. The colony was maintained on sorghum seedlings (cultivar 'P8500') in a Percival I-36VL growth chamber under 'coolwhite' fluorescent lighting set to a photoperiod of 16:8 (L:D) h and a diurnal temperature cycle of 23/21°C. Sorghum seeds were planted in metal trays (36 × 26 × 8 cm) and watered as required.

Stock colonies of *C. maculata* were established from ≈120 adult beetles collected from fields of cultivated sorghum and sunflower on the grounds of ARCH in Hays, KS, in the summers of 2009 and 2010. Adult beetles were held in a climate-controlled growth chamber set at a 24 (±2) °C and a photoperiod of 16:8 (L:D) h regime, in 1 L wide-mouth glass mason jars containing shredded wax paper as harborage and with water continuously available on a cotton wick. Beetles were fed every second day with 20–30 mg of frozen eggs of the Mediterranean flour moth, *E. kuehniella*, a highly suitable diet for this species (Michaud and Jyoti 2007).

For breeding each new generation, *C. maculata* females were isolated in petri dishes (as above), each with ≈10 mg of *E. kuehniella* eggs added daily and water provided on a small cube of sponge. Egg clusters were laid directly on the surface of the petri dish and were collected daily by transferring the female beetles into clean dishes. After eclosion, larvae were reared in petri dishes (15.0 × 1.5 cm) lined with a piece of paper towel, 10–15 larvae per dish, until pupation. Eggs of *E. kuehniella* were provided ad libitum and a moistened piece of paper towel served as a source of moisture. Eggs and larvae were held under the same environmental conditions as the adults and no experimental insects were more than three generations removed from a field collection.

A colony of *C. carnea* was established from a shipment of second instar larvae obtained by mail order from Koppert B. V. (Berkel en Rodenrijs, South Holland, The Netherlands). On arrival, larvae were isolated in groups of three in petri dishes (5.5 cm diameter) and reared on *Ephestia* eggs under the same physical conditions as described above for the coccinellids. Newly emerged adults were transferred to petri dishes (15 cm diameter), 20–30 per dish, with diluted honey provided on a moistened piece of paper towel and pulverized bee pollen in a 5.5 cm petri dish. Eggs were laid directly on the surface of the dish and were collected daily.

Microcosm Experiment. The sorghum-greenbug microcosm used was the 'conetainer' system first developed by Harvey et al. (1991). Plants were germinated in plastic cones (16.5 × 2.5 cm diameter; Stuewe and Sons, Corvallis, OR) filled with soil. Seeds of sorghum (cultivar P8500) were planted in the soil to a depth of ≈1 cm and the cones arranged in a rack that was then immersed in a water bath until all cones were saturated. In total, 400 cones were planted and, after germination, plants were thinned to three per cone. The best 220 cones were selected for use in the experiment; these were fertilized during the third week of growth then manually infested 30 d postgermination by transferring eight fourth instar apterous *S. graminum* nymphs to each with a fine camel hair brush. A ventilated, clear plastic tubular cylinder (2.5 cm diameter × 30 cm height) was then fitted to the top of each cone to confine insects on the plants. Racks of caged containers were then placed in growth chambers operating at a photoperiod of 16:8 (L:D) h with a diurnal temperature cycle of 23/21°C. Three days later, the required number of first instar predator larvae (<24 h old) were introduced to each microcosm. Larvae were selected based on some evidence of feeding on *Ephestia* eggs (abdominal distension) to minimize the probability of predator mortality before discovery of prey in the microcosm.

Preliminary experiments were conducted to calibrate microcosms (number of insects introduced per cone and timing of infestation relative to plant development) that would minimize premature plant death as a result of aphid feeding while still providing sufficient food resources for the complete development of both predators in at least a portion of replicates, thus permitting opportunity for a wide range of IGP and aphid suppression outcomes. The above microcosm configurations were selected based on these experiments.

The following treatments were established:

1. No predators ($n = 20$).
2. One first instar *C. maculata* larva ($n = 20$).
3. One first instar *C. carnea* larva ($n = 20$).

4. Two first instar *C. maculata* larvae ($n = 40$).
5. Two first instar *C. carnea* larvae ($n = 40$).
6. One first instar *C. maculata* + one first instar *C. carnea* larva ($n = 80$).

Beginning on day 6 of the experiment, each replicate was examined nondestructively at 48 h intervals and the developmental stage and state (alive or dead) of each observed predator was recorded. A predator was considered victorious when its counterpart was either found moribund with signs of predation or cannibalism on the cadaver, or when it had been completely consumed. The larval stage of victor and victim at the time of the event was inferred by counting exuviae and examining remains. In the cases that no cadaver was found, the last recorded larval stage counted as the stage of predation. All pupating predators were removed as either prepupae or pupae within each observation period and their fresh weight determined on an analytical balance. Replicates were terminated when surviving predators pupated, when no predatory larvae remained alive, or when the plant died. All live aphids were counted on the last day of observation (=number of aphids). Aphid colonies that exceeded the carrying capacity of their plants and abandoned them were assigned an arbitrary count of 250. Plant survival and aphid suppression were ranked as binary outcomes. Plant survival was tallied as zero if all three plants in the microcosm died, otherwise one. Aphid suppression was considered successful if predation reduced aphid numbers to fewer than or equal to eight, the number used to infest each microcosm. In many cases, a significant number of early instar aphids remained concealed in leaf sheaths at the last observation. However, because these did not constitute growing colonies and plants were clearly outgrowing any damage they had sustained, aphid suppression was judged to be successful in these cases. In a few replicates, a predator drowned in condensation on the cylinder; these were excluded from analysis. Surviving predators were categorized according to their feeding history; cannibals if they consumed a conspecific, IG predators if they consumed a heterospecific, and focal predators if they did neither. The entire experiment was repeated a second time with half the number of replicates.

Petri Dish Experiment. To contrast IGP outcomes between a seminatural microcosm (the conetainer) and a more simplified arena, an experiment similar to that described above was conducted in 5.5 cm diameter. Petri dishes with similar treatments:

1. One first instar *C. maculata* larva ($n = 40$).
2. One first instar *C. carnea* larva ($n = 40$).
3. Two first instar *C. maculata* larvae ($n = 60$).
4. Two first instar *C. carnea* larvae ($n = 60$).
5. One first instar *C. maculata* + one first instar *C. carnea* larva ($n = 100$).

In addition, the food provided (=diet) was varied to test for possible effects of focal prey quality on the intensity of cannibalism and IGP. Half the replicates in each treatment were fed frozen *Ephestia* eggs ad libitum daily, while the other half were provided with 30–50 *S. graminum* of various developmental stages. It has previously been shown that eggs of *Ephestia* are higher in protein than aphids and may actually be a superior food for some coccinellid species (Specty et al. 2003). Larvae were held in the same dish throughout the duration of the experiment and all dishes were examined daily to record mortality and larval molts. Replicates were terminated either when victorious predators had pupated, or when none remained alive. The fresh weight of all surviving predators was measured on an analytical balance within 24 h of pupation. Surviving predators were categorized according to their feeding history; cannibals if they consumed a conspecific, IG predators if they consumed a heterospecific, and focal predators if they did neither.

Statistical Analysis. Categorical variables (plant survival, aphid suppression, and predator victory in IGP events) were analyzed pairwise using a χ^2 Goodness of Fit test. Scalar variables (aphid numbers, predator fresh weight at pupation, and larval developmental time) were analyzed by one-way analysis of variance (ANOVA) (SPSS 1998). Because there were no significant differences in mean values between the two repetitions of the microcosm experiment ($\alpha > 0.05$ in all cases), results for the pooled data set are reported. A two-way ANOVA was used to test for interactions between effects of diet and treatment on developmental time and pupal weight in the petri dish experiment. One-way ANOVAs were performed on dependent variables if treatment interactions were not significant and means were separated by Tukey's honestly significant difference (HSD) test with false discovery rate control for multiple comparisons (Verhoeven et al. 2005).

Results

Microcosm Experiment. In the treatment with mixed pairs of predators, there were no significant differences in outcomes between the two repetitions of the experiment ($n = 68$ and $n = 34$ usable replicates, respectively) with respect to plant survival (86.8 vs. 79.4%; $\chi^2 = 2.25$; ns), IGP victories for *C. carnea* (66.2 vs. 55.9%; $\chi^2 = 2.92$; ns), or aphid suppression (69.1 vs. 70.6%; $\chi^2 = 0.07$; ns) so the data were pooled for further analysis.

With the exception of one replicate in which an aphid colony failed to establish, all plants in the 'no predator' treatment ($n = 30$), died as a result of aphid feeding. All three plants in each microcosm with a single *C. maculata* larva survived in 92.9% of valid replicates ($n = 28$), whereas those with a single *C. carnea* larva ($n = 15$) survived in 86.7% ($\chi^2 = 0.57$; ns). When two *C. maculata* larvae were present ($n = 53$), all three plants survived in 98.1% of replicates, compared with 81.3% in the treatment with two *C. carnea* ($n = 48$; $\chi^2 = 9.90$; $P < 0.005$). In the treatment with mixed pairs of predators, all three plants survived in 84.3% of replicates, not significantly different from two *C. carnea* larvae ($\chi^2 = 0.63$; ns), but significantly lower than two *C. maculata* ($\chi^2 = 105.25$; $P < 0.001$). There

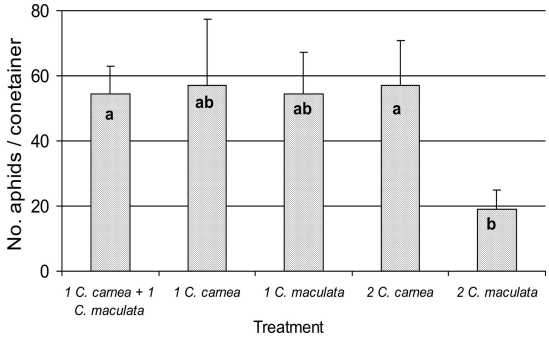

Fig. 1. Mean numbers of aphids per microcosm at end of experiment for greenbug colonies initiated on three sorghum plants with eight fourth instar aphids with various combinations of first instar predatory larvae introduced 3 d later.

was no difference in the rate of plant survival between treatments with single or paired *C. carnea* larvae ($\chi^2 = 1.32$; ns), or between treatments with single or paired *C. maculata* ($\chi^2 = 1.01$; ns).

Suppression of aphids was judged to be successful in 83.0% of replicates with pairs of *C. maculata*, significantly more than the 60.4% observed for pairs of *C. carnea* ($\chi^2 = 11.36$; $P < 0.001$). Aphids were controlled in 69.6% of replicates in the treatment with mixed pairs, significantly less than for pairs of *C. maculata* ($\chi^2 = 13.02$; $P < 0.001$), but significantly more than for pairs of *C. carnea* ($\chi^2 = 7.41$; $P < 0.01$). Two *C. carnea* did not control aphids any more often than did one ($\chi^2 = 3.34$; ns), but two *C. maculata* were more successful than one ($\chi^2 = 14.46$; $P < 0.001$). Single *C. maculata* controlled aphids in 57.1% of replicates, not significantly different from the 66.7% controlled by single *C. carnea* ($\chi^2 = 1.17$; ns).

The mean number of aphids per replicate at the end of the experiment varied among treatments ($F_{4,241} = 2.52$; $P = 0.042$). The treatment with two *C. maculata* larvae finished with fewer aphids per replicate than those in the treatment with mixed pairs and those in the treatment with two *C. carnea* (Tukey's HSD, $\propto = 0.05$), with no other differences among treatments significant (Fig. 1). It should be noted that the majority of aphids remaining in most replicates were scattered among refuges in leaf axils and under leaf sheaths, rather than comprising cohesive colonies. Many predators died of starvation when the aphid colony was suppressed to low levels. This occurred in 1/28 replicates (3.6%) with solitary *C. maculata*, in 3/15 replicates (20.0%) with solitary *C. carnea*, in 14/53 replicates (26.4%) for pairs of *C. maculata*, and in 12/48 replicates (25.0%) for pairs of *C. carnea.* For survivors in the mixed pairs treatment, starvation occurred less often for *C. maculata* (3/38 = 7.9%) than for *C. carnea* (20/64 = 31.3%; $\chi^2 = 9.69$, $P < 0.005$).

Larvae of *C. carnea* were superior to *C. maculata* larvae in IGP interactions in microcosms, winning 64 contests (62.7%) compared with 38 (37.3%; $\chi^2 = 6.62$, $P < 0.025$), respectively. A comparison of the developmental stages of victors and victims by species (Table 1) reveals that *C. maculata* is particularly vulnerable to *C. carnea* in the first instar but has a much higher probability of victory if it can reach the second instar. When two *C. maculata* larvae developed in the same microcosm, cannibalism occurred in 35/53 replications (66%), whereas it occurred in 42/48 replications (87.5%) with pairs of *C. carnea* larvae, suggesting that *C. carnea* was more cannibalistic ($\chi^2 = 22.5$; $P < 0.001$).

Table 1. Distributions of predator life stages and those of their prey in cannibalism and intraguild interactions categorized by species and outcome and expressed in percentages

Instar	1	2	3	4
Percentage of cannibalism events				
C. carnea ($n = 42$)				
Cannibal	71.4	7.1	21.4	—
Prey	71.4	9.5	19.1	—
C. maculata ($n = 35$)				
Cannibal	0.0	5.7	22.9	71.4
Prey	2.9	14.3	17.1	65.7
Percentage of IG predation events ($n = 102$)				
C. carnea				
IG predator	35.3	17.6	9.8	—
IG prey	2.8	5.9	2.9	—
C. maculata				
IG predator	1.0	28.4	3.9	3.9
IG prey	35.3	12.7	12.7	2.0

Experimental units were microcosms each containing three greenbug-infested sorghum plants.

Larvae of *C. maculata* that cannibalized required significantly longer to complete larval development than either IG predators or those that fed only on aphids ($F_{2,111} = 7.63$, $P = 0.001$; Fig. 2) but differences in pupal weight were not significant ($F_{2,110} = 2.56$, $P = 0.082$; Fig. 3). In contrast, larval feeding history had no effect on *C. carnea* developmental time ($F_{2,78} = 1.999$; $P = 0.142$) or fresh weight at pupation ($F_{2,78} = 0.58$; $P = 0.563$).

Petri Dish Experiment. There was no effect of diet on IGP outcomes in petri dishes; larvae of *C. carnea*

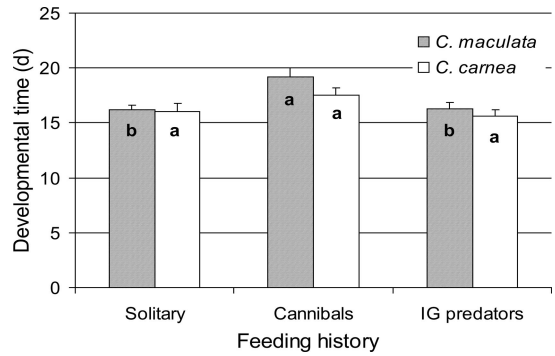

Fig. 2. Mean (+SE) developmental times of *C. maculata* and *C. carnea* larvae that pupated either as focal predators (Solitary), or after acts of cannibalism or intraguild predation when feeding on greenbugs in microcosms. Columns bearing the same letters did not differ significantly among feeding histories within species (Tukey's HSD with FDR test for multiple comparisons, $\alpha = 0.05$).

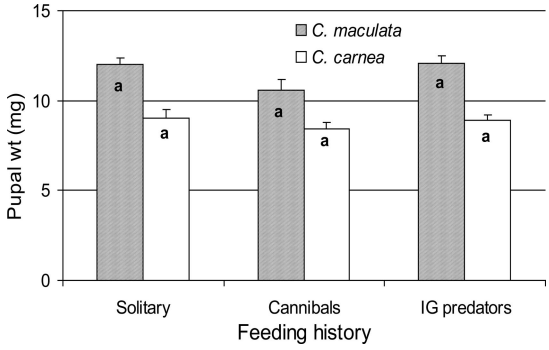

Fig. 3. Mean (+SE) fresh pupal weights of *C. maculata* and *C. carnea* larvae that pupated either as focal predators, or after acts of cannibalism or intraguild predation when feeding on greenbugs in microcosms. Columns bearing the same letters did not differ significantly among feeding histories within species (Tukey's HSD with FDR test for multiple comparisons, $\alpha = 0.05$).

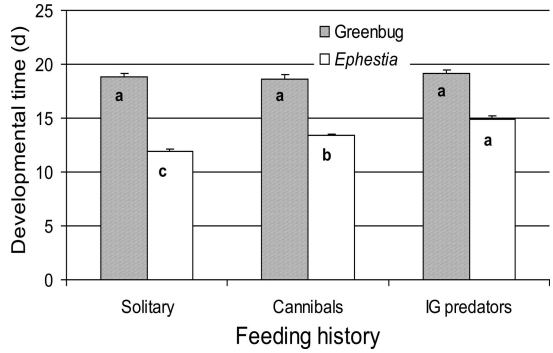

Fig. 4. Mean (+SE) developmental times of *C. carnea* larvae that pupated either as focal predators, or after acts of cannibalism or IGP when reared on each of two diets in petri dishes. Columns bearing the same letters did not differ significantly among feeding histories within diets (Tukey's HSD with FDR test for multiple comparisons, $\alpha = 0.05$).

won 44/49 (89.8%) contests on the greenbug diet, excluding one case of mutual elimination, versus 44/50 (88.0%) contests on *Ephestia* eggs ($\chi^2 = 0.16$; ns). Again, comparison of the developmental stages of winners and losers by species revealed the vulnerability of *C. maculata* to *C. carnea* while in the first instar (Table 2). In contrast with the microcosm experiment, most *C. maculata* victories were achieved in the first instar rather than the second. Only 8/20 (40%) solitary *C. maculata* survived on a diet of greenbug, compared with 17/20 (85%) on a diet of *Ephestia* eggs ($\chi^2 = 31.8$; $P < 0.001$), and for solitary *C. carnea*, survival was also greater on the latter diet (15/20 = 75% vs. 19/20 = 95%; $\chi^2 = 16.8$, $P < 0.001$). Paired *C. maculata* cannibalized in 29/29 (100%) on the aphid diet (including two cases of mutual elimination) and in 24/30 replications (80%) on the *Ephestia* egg diet ($\chi^2 = 7.25$; $P < 0.01$). Larvae of *C. carnea* cannibalized in 100% of replicates with paired larvae, regardless of diet (Table 2).

Table 2. Percentages of cannibalism and intraguild predation events occurring in various larval stages among pairs of predators feeding on either greenbugs or *Ephestia* eggs in petri dishes

Instar	1	2	3	4
Cannibalism (diet = greenbugs)				
C. carnea ($n = 29$)				
Cannibal	13.8	37.9	48.3	—
Prey	13.8	55.2	31.0	—
C. maculata ($n = 29$)				
Cannibal	20.7	24.1	31.0	24.1
Prey	27.6	24.1	34.5	13.8
Cannibalism (diet = *Ephestia* eggs)				
C. carnea ($n = 30$)				
Cannibal	0.0	3.3	96.7	—
Prey	0.0	10.0	90.0	—
C. maculata ($n = 24$)				
Cannibal	4.2	25.0	4.2	66.7
Prey	20.8	8.3	25.0	45.8
IG predation (diet = greenbugs, $n = 49$)				
C. carnea				
IG predator	65.3	24.5	0.0	—
IG prey	10.2	0.0	0.0	—
C. maculata				
IG predator	8.2	2.0	0.0	0.0
IG prey	75.5	12.2	2.0	0.0
IG predation (diet = *Ephestia* eggs, $n = 50$)				
C. carnea				
IG predator	12.0	32.0	44.0	—
IG prey	10.0	2.0	0.0	—
C. maculata				
IG predator	4.0	2.0	6.0	0.0
IG prey	16.0	38.0	26.0	8.0

The two-way ANOVA of developmental time for *C. carnea* was significant overall ($F_{5,162} = 73.31$; $P < 0.001$), with a significant diet*larval feeding history interaction ($F_{2,162} = 6.47$; $P = 0.002$). There was a significant effect of diet ($F_{1,162} = 335.91$; $P < 0.001$) and larval feeding history ($F_{2,162} = 10.57$; $P < 0.001$). Larvae of *C. carnea* that survived to pupate on the *Ephestia* egg diet developed faster than those on the greenbug diet (13.8 ± 0.19 vs. 18.8 ± 2.1 d; $F_{1,166} = 272.31$, $P < 0.0001$). Larval feeding history did not affect the developmental time of lacewing larvae on the greenbug diet ($F_{2,74} = 0.36$; $P = 0.702$), but did affect those on the *Ephestia* diet ($F_{2,88} = 28.69$; $P < 0.001$). On *Ephestia* eggs, focal predators developed faster than cannibals that, in turn, developed faster than IG predators (mean ± SE, 11.9 ± 0.19 vs. 13.4 ± 0.13 vs. 14.9 ± 0.28 d, respectively; Tukey's HSD, $P < 0.01$ in all cases; Fig. 4).

The two-way ANOVA of *C. carnea* pupal weight was also significant overall ($F_{5,162} = 16.15$; $P < 0.001$) and there was a significant diet*feeding history interaction ($F_{2,162} = 8.36$; $P < 0.001$). Pupal weight was significantly affected by both diet ($F_{1,162} = 61.04$; $P < 0.001$) and feeding history ($F_{2,162} = 7.72$; $P = 0.001$). Larvae of *C. carnea* that survived to pupate on the *Ephestia* egg diet weighed more than those on the greenbug diet (8.7 ± 0.13 vs. 7.6 ± 0.12 mg; $F_{1,166} = 272.31$, $P < 0.0001$). One-way ANOVA tests revealed that feeding history affected pupal weight on both the greenbug ($F_{2,74} = 3.84$; $P = 0.026$) and *Ephestia* ($F_{2,88} = 12.87$; $P < 0.001$) diets. On the greenbug diet, cannibals

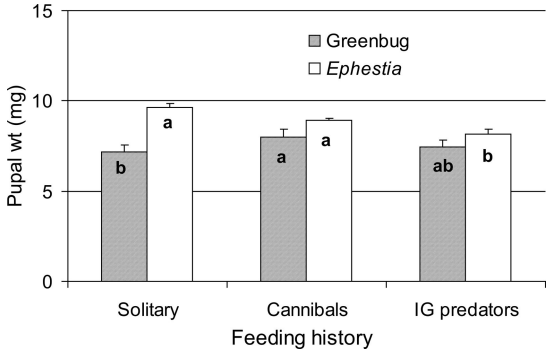

Fig. 5. Mean (+SE) fresh pupal weights of *C. carnea* larvae that pupated either as focal predators, or after acts of cannibalism or IGP when reared on each of two diets in petri dishes. Columns bearing the same letters did not differ significantly among feeding histories within diets (Tukey's HSD with FDR test for multiple comparisons, $\alpha = 0.05$).

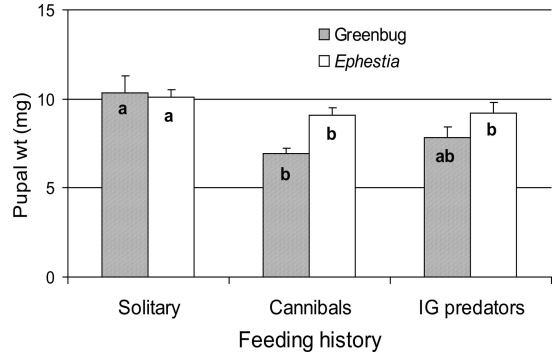

Fig. 7. Mean (+SE) fresh pupal weights of *C. maculata* larvae that pupated either as focal predators, or after acts of cannibalism or IGP when reared on each of two diets in petri dishes. Columns bearing the same letters did not differ significantly among feeding histories within diets (Tukey's HSD with FDR test for multiple comparisons, $\alpha = 0.05$).

weighed significantly more than focal predators (Tukey's HSD, $P = 0.037$), with IG predators not significantly different from cannibals (Tukey's HSD, $P = 0.084$) or focal predators (Tukey's HSD, $P = 0.688$; Fig. 5). However, on the *Ephestia* egg diet, IGPs weighed less on average (8.2 ± 0.18 mg) than cannibals (8.9 ± 0.20 mg; Tukey's HSD, $P = 0.014$) or focal predators (9.6 ± 0.21 mg; Tukey's HSD, $P < 0.001$), the latter being not significantly different (Tukey's HSD; $P = 0.078$).

The two-way ANOVA of developmental time for *C. maculata* was significant overall ($F_{5,71} = 11.04$; $P < 0.001$) but the interaction between diet and larval feeding history was not ($F_{2,71} = 0.39$; $P = 0.682$). Larvae of *C. maculata* that were focal predators of greenbug developed faster than cannibals on the greenbug diet, but IG predators on this diet were not different from either ($F_{2,25} = 4.40$, $P = 0.023$; Fig. 6). Larvae feeding only as focal predators on *Ephestia* eggs developed faster than either IGPs or cannibals on this diet, with the latter two groups not significantly different ($F_{2,46} = 3.84$; $P = 0.029$).

The two-way ANOVA for pupal weight was also significant overall ($F_{5,71} = 9.16$; $P < 0.001$), and the interaction term between the two factors was not ($F_{1,71} = 1.10$; $P = 0.340$). Larvae of *C. maculata* feeding as focal predators on greenbugs pupated at heavier weights than cannibals ($F_{2,25} = 10.43$; $P = 0.001$) with IGPs not significantly different from either, whereas for larvae feeding exclusively on *Ephestia* eggs, focal predators were heavier than both cannibals and IGPs ($F_{2,46} = 7.11$, $P = 0.002$; Fig. 7). Disregarding treatments, *C. maculata* larvae fed *Ephestia* eggs developed faster (19.8 ± 0.59 vs. 25.5 ± 0.71 d; $F_{1,63} = 39.49$, $P < 0.001$) and weighed more at pupation (9.1 ± 0.3 vs. 8.0 ± 0.43 mg; $F_{1,63} = 4.56$, $P = 0.037$) than larvae fed greenbug.

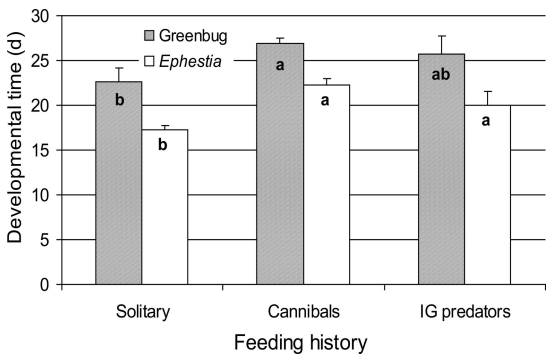

Fig. 6. Mean (+SE) developmental times of *C. maculata* larvae that pupated either as focal predators (Solitary), or after acts of cannibalism or IGP when reared on each of two diets in petri dishes. Columns bearing the same letters did not differ significantly among feeding histories within diets (Tukey's HSD with FDR test for multiple comparisons, $\alpha = 0.05$).

Discussion

The primary difference between the microcosm and petri dish experiments was the presence of growing plants in the former arena, which provided a more complex, three dimensional foraging environment and a natural substrate for predator interactions. Another important contrast is that food was provided ad libitum in petri dishes and was never limiting, whereas predators in microcosms sometimes eliminated their aphid colony and either starved or survived by virtue of IGP. On the plant substrate, *C. carnea* larvae were highly aggressive toward both conspecific and heterospecific competitors in the first instar, whereas larvae of *C. maculata* became more aggressive in later instars (Table 1). Thus, *C. carnea* was prone to attack competitors in the first instar, independent of the availability of prey, whereas *C. maculata* became increasingly prone to attack competitors in later instars. The latter trend may reflect either an intrinsic tendency, or the fact that food became more limiting with the passage of time for this species. Along similar lines, Lucas et al. (1997) showed that the defensive behavior of *C. macu-*

lata larvae against *Chrysoperla rufilabris* (Burmeister) was least effective in the earliest instars.

The treatment with paired *C. maculata* larvae finished the experiment with the highest probability of plant survival, better aphid suppression than paired *C. carnea* larvae, and with fewer aphids, on average, than any other treatment. Thus, *C. maculata* appeared to provide better aphid suppression than did the superior IG predator *C. carnea*, a situation that theoretically favors continued coexistence of both as opposed to mutual exclusion or niche differentiation (Borer et al. 2007). The early elimination of competitors by *C. carnea* larvae may also have reduced aphid suppression in treatments that paired this species with either conspecifics or heterospecifics.

In petri dishes, the nature of the diet appeared to affect the onset of IGP and cannibalism, as well as the survival rates of solitary predators. The provision of sessile prey (*Ephestia* eggs) as opposed to mobile prey (*S. graminum*) not only resulted in higher baseline survival of solitary larvae, but appeared to delay a larger proportion of cannibalism events until later instars in both species, and a larger proportion of IGP events on the part of *C. carnea* (Table 2). It seems likely that predators foraging on wandering aphids had much higher rates of encounter with their competitors compared with those harvesting moth eggs. Conspecific encounter rates are an indication of population density and both parameters are linked to the frequency of larval cannibalism in coccinellids (Michaud 2003, Pervez et al. 2006) and in lacewings (Duelli 1981, Costa et al. 2003).

Larvae of *C. maculata* were almost three times more successful in IGP interactions in microcosms than they were in petri dishes. This result supports the general conclusions of others (Finke and Denno 2006, Janssen et al. 2007) that habitat structure tends to increase the survival of intraguild prey by decreasing the strength of interaction with the intraguild predator. The petri dish arena disadvantaged *C. maculata* relative to *C. carnea* because the coccinellid appeared less able to avoid conflict until the second instar when its probability of success improved (Table 2). Either evasive maneuvers by first instar *C. maculata* were more effective on plants than on the plastic substrate, or the artificial arena lacked refuges that were available on the plants. Lucas et al. (1997) noted that evasive behaviors of young *C. maculata* larvae included fleeing and dropping from the plant when confronted by a lacewing larva. It is well recognized that substrate (e.g., plant architecture or species) can have a strong influence on predator foraging and functional responses to prey (da Silva et al. 1992, Grevstad and Klepetka 1992, Heidari 1999, De Clercq et al. 2000, Khan and Matin 2006, Mahdian et al. 2007), and similar effects on IGP outcomes have been observed. For example, Lucas et al. (2009) obtained highly disparate results between laboratory cages and live plants in tests of IGP between two species of omnivorous mirid bugs. Madadi et al. (2008) demonstrated that IGP interactions between *Orius albidipennis* (Reuter) (Hemiptera: Anthocoridae) and the predatory mite *Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae) while feeding on thrips were strongly affected by host plant species. Similarly, Shakya et al. (2009) showed that both food supplementation (pollen availability) and the arena of interaction could alter the intensity of asymmetric IGP by *Orius laevigatus* Fieber (Hemiptera: Anthocoridae) on predatory mites when thrips were the focal prey.

The potential developmental costs of IGP for arthropods have only received attention quite recently (Agarwala and Dixon 1992, Hemptinne et al. 2000, Michaud 2002). For example, Lawson-Balagbo et al. (2008) observed neither costs nor benefits of symmetric IGP between *Neoseiulus paspalivorus* DeLeon (Acari: Phytoseiidae) and *Proctolaelaps bickleyi* Bram (Acari: Ascidae) as they developed feeding on the coconut mite *Aceria guerreronis* Keifer (Acari: Eriophyidae). Sato et al. (2008) showed that IGP on *Propylea japonica* Thunberg by *Coccinella septempunctata brucki* Mulsant (Coleoptera: Coccinellidae) reduced larval survival by more than half. Similarly, costs of coccinellid larval cannibalism in terms of delayed development and reduced adult body weight have been demonstrated by Michaud (2003) and Pervez et al. (2005). Other studies have found negative effects on development for larval coccinellids when they consume aphid parasitoids in immatures stages within their hosts (Royer et al. 2008, Bilu and Coll 2009) or heterospecific eggs (Cottrell 2004, Ware et al. 2008). However, coccinellid eggs contain species-specific alkaloids that may function specifically to deter IGP (Hemptinne et al. 2000, Kajita et al. 2010) and although costs may be associated with the consumption of heterospecific larvae, they are sometimes more acceptable than heterospecific eggs (e.g., Michaud 2002). In the microcosm experiment, *C. maculata* cannibals had delayed development and reduced pupal weight relative to noncannibals, costs not shared by IG predators (Figs. 2 and 3). In petri dishes, the greenbug diet produced effects largely similar to those in microcosms for *C. maculata* larvae, except that IG predators were intermediate to, and not significantly different from, cannibals and noncannibals in both developmental time and pupal weight (Figs. 6 and 7). However, on the diet that enabled faster development (*Ephestia*), both cannibals and IG predators had delayed development and lower pupal weights relative to individuals that did not consume competitors. Thus, both cannibalism and IGP entailed costs for *C. maculata* larvae, although the magnitude of the cost varied with diet. In nature, such costs may be offset by the benefits of reduced local competition for focal prey.

Overall, *C. carnea* larvae appeared more adapted to cannibalism than *C. maculata* larvae in that they incurred lower costs for the behavior; no negative effects were evident in the microcosm experiment, and there was only slightly extended development on the *Ephestia* diet in petri dishes (Fig. 4), and cannibals actually weighed more than solitary individuals on the inferior greenbug diet (Fig. 5). This benefit of cannibalism was not observed in microcosms and may have arisen only because the suitability of aphids in petri

dishes was lower, such that cannibalism provided a more significant food supplement in that setting. The high mortality of solitary *C. maculata* larvae on greenbugs in dishes (that was not observed on plants) further supports this inference. The costs of IGP for *C. carnea* tended to be greater than those associated with cannibalism; longer development and significantly lower pupal weights, but were only evident on the *Ephestia* egg diet that was clearly superior to greenbugs, fostering faster development and heavier pupation weights. Thus, costs of IGP and cannibalism for *C. carnea* were only apparent in the simplified habitat and were more pronounced on the superior diet.

The study by Buitenhuis et al. (2010) demonstrated benefits of IGP on *N. cucumeris* by the predatory mite *Amblyseius swirskii* (Athias–Henriot) (Acari: Phytoseiidae) in terms of faster development and higher oviposition rate when thrips were the focal prey. Although highly suitable nutritionally, the effort expended in capturing thrips reduced the benefits of feeding on them. In the current study, costs of IGP and cannibalism were more pronounced than benefits. According to the general theory of IGP (Polis et al. 1989), when direct costs exceed direct benefits the behavior is best interpreted as interference competition, that is, its selective advantage lies in securing access to the focal prey, rather than in nutritional supplementation. This appears to be the case for symmetric larval IGP between aphidophagous coccinellids and lacewings, where demise of the aphid colony before completion of predator development is a significant risk. In a recent paper, Hemptinne et al. (2012) argued for a distinction between interspecific predation and 'true' IGP on the grounds that the latter implies some top-down control of the focal prey population. They argue further that true IGP (sensu Polis and Holt 1992) is rare in aphidophagous communities because there is little evidence for top-down control of aphids by any IG prey species and most evidence suggests that aphidophagous species pay a cost for consuming IG prey rather than obtaining any nutritional benefit. We view the primary function of IGP by aphidophagous larvae to be interference competition and the primary benefit to be the conservation of focal prey to support development of the IG predator, with dietary supplementation a possible secondary benefit under conditions of prey depletion. Hemptinne et al. (2012) contend that most IGP among aphidophages occurs well after the collapse of aphid colonies, but the studies they cite address interspecific predation on eggs rather than among developing larvae, a distinction we feel is important. The vast majority of IGP events in our microcosm experiments occurred long before the supply of aphids became limiting to predators. Most cannibalism by *C. carnea* also occurred very early in microcosms, consistent with our interpretation that the primary fitness benefit of both IGP and larval cannibalism is the preservation of a local supply of focal prey. In our study, the direct costs of IGP tended to be higher on the nutritionally superior *Ephestia* diet, which also presumably required less energy to harvest than greenbugs. Thus, whether the consequences of IGP are positive or negative for predatory larvae, and the magnitude of the effect, can vary according to the nature of the focal prey and its relative suitability for the IG predator.

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