Competitive interactions between an exotic and a native ladybeetle: a field cage study

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Abstract

We conducted field-cage studies on the direct interactions between a coccinellid species native to North America, *Coleomegilla maculata* De Geer, and a species introduced from Asia, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). We compared the mortality and weight gain of larvae of both species in field cages that enclosed one or both species with corn plants containing high or low aphid numbers. We did not find a significant effect of the presence of *H. axyridis* on the survival or weight gain of *C. maculata*, but *H. axyridis* larvae weighed more when kept with *C. maculata* for 5 days than when kept with equal numbers of conspecifics. This suggests that intraspecific competition was stronger for *H. axyridis* than the interspecific competition with *C. maculata*. The spatial distribution of *C. maculata* over the plants differed between single-species and two-species treatments in a manner that suggested that this species avoided interactions with *H. axyridis*.

Introduction

Exotic animal species, whether introduced accidentally or deliberately, may impact communities of native species through resource competition, trophic interactions, or indirect interactions. They can lead to environmental damage (the deterioration of native ecosystems, decline in biodiversity), and economic damage (impacts on agricultural yield, impacts on livestock, etc.) in the areas of introduction (Pimentel et al., 2000).

Competition for resources may lead to the competitive exclusion of one or more native species that are utilizing the same resources. For example, native ant species declined after the introduction of the invasive Argentine ant in a reserve in California, both through exploitation and interference competition (Human & Gordon, 1996). In a study conducted in an isolated lake in Finland over a period of 30 years, the displacement of a native crayfish species was attributed to competition with an introduced crayfish species (Westman et al., 2002). The introduction of the coccinellid *Coccinella septempunctata* L. from Europe led to a decrease in the populations of three native coccinellid species in several agricultural systems in North America (Wheeler & Hoebeke, 1995; Elliott et al., 1996). A decrease in two native species was observed after the introduction of *Harmonia axyridis* (Pallas) (Colunga-Garcia & Gage, 1998). Evans (1991) showed that interspecific competition between the larvae of *C. septempunctata* and three native coccinellid species in laboratory assays was as strong as the intraspecific competition in any of the species, and Obrycki et al. (1998a,b) showed that competitive interactions between *C. septempunctata* and the native *Coleomegilla maculata* De Geer were asymmetrical in favor of *C. septempunctata*, especially when prey were limited. The incorporation of *C. septempunctata* into North American coccinellid communities should therefore lead to a population decline in native species, provided that they are food limited (Evans, 1991).

Introduced species can also feed on native species, leading to substantial population reduction, or even local extinction. Examples of these phenomena can be found in the literature on deliberate introductions of exotic organisms for purposes of biological pest control, where both native pests (Hokkanen & Pimentel, 1984, 1989) and native non-target species (Louda, 1998; Boettner et al., 2000; Follett & Duan, 2000) can be impacted. Some coccinellid species can be aggressive predators of the larvae and eggs of other coccinellids (Cottrell & Yeargan, 1998; Schellhorn & Andow, 1999a; Yasuda et al., 2001; Agarwala et al., 2003), and Wheeler & Hoebeke (1995) listed interspecific predation as a possible mechanism by which *C. septempunctata* may have displaced the native *C. novempunctata* from eastern North America.

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Here, we have focused on direct interactions between a coccinellid species that was introduced to North America fairly recently, and a native coccinellid species therein. The multicolored Asian ladybeetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), was first detected in the USA in 1988 (Chapin & Brou, 1991). This species has since invaded large areas of North America (Coderre et al., 1995; Dreisdadt et al., 1995; Hoebeke & Wheeler, 1996; LaMana & Miller, 1996; Brown & Miller, 1998). A few studies have been directed at the direct effects of *H. axyridis* on populations of other coccinellid species (Brown & Miller, 1998; LaMana & Miller, 1996; Colunga-Garcia & Gage, 1998). Colunga-Garcia & Gage (1998) sampled several species of coccinellids before and after the arrival of *H. axyridis*. After the arrival of *H. axyridis*, two coccinellid species typical of arboreal and early successional habitats, *Brachiacantha ursina* (F.) and *Cycloneda munda* (Say) appeared to suffer a decline. *Adalia bipunctata* (L.), an arboreal species, showed a population decline before and after the arrival of *H. axyridis*. Studies by Brown & Miller (1998) and LaMana & Miller (1996) showed that *H. axyridis* became the most abundant coccinellid species in areas it had invaded, and apparently displaced the exotic *Coccinella septempunctata*.

One of the native species that may be affected by the invasion of *H. axyridis* is *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae). Like *H. axyridis*, *C. maculata* is a polyphagous predator that feeds mainly on aphids, but also on insect eggs, pollen, and other prey (Hodek & Honek, 1996). Schellhorn & Andow (1999a) conducted field studies investigating the effects of crowding and prey density on cannibalism and intraguild predation in three coccinellid species: *C. maculata*, *A. bipunctata*, and *Hippodamia convergens* (Guerin). They found that cannibalism and interspecific predation occurred more frequently at low aphid densities. *Coleomegilla maculata* was the least aggressive of the three species, and most often fell prey to interspecific predation. Despite this, they found that in general, interspecific interactions were weaker than intraspecific interactions, and they demonstrated that *C. maculata* should be able to coexist with the other species.

When 3rd or 4th instar *C. maculata* and *H. axyridis* larvae were confined together in a small arena in the laboratory, *H. axyridis* often preyed upon the smaller and less voracious *C. maculata* larvae. Both species showed cannibalism, but the rate of cannibalism in *H. axyridis* was higher than in *C. maculata* (Cottrell & Yeargan, 1998).

We investigated the impact of *H. axyridis* on *C. maculata* larvae and vice versa at low and high prey densities in a field-cage setting. We evaluated intra- and interspecific competition by comparing weight gain, survivorship, and the prevalence of aphid parts within the guts of both coccinellid species at low and high aphid densities. Intraspecific predation and cannibalism were evaluated by comparing survivorship and the prevalence of coccinellid parts in the guts of both species.

Methods

Experimental design

Five plantings each of two rows of sweet corn (*Zea mays* L., var. Jubilee [Poaceae]) were located at the University of Minnesota Experiment Station in Rosemount, MN, during spring and summer in 2001. Each planting took place 2 weeks from the previous, with the first planting on May 29. When plants reached a height of approximately 1 m and tassels appeared, six plants were caged individually in fine mesh (±0.5 mm) cages, measuring 0.5 × 0.5 × 1 m. This was repeated five times throughout the summer, as plants that had been planted on the different dates reached the desired height. The cages were supported by PVC frames. The bottom of each cage was covered with white sand to make it easier to see larvae that were located on the soil surface. Each cage had a velcro closure on one side.

The cage experiment consisted of five replicates, each with six cages (three low and three high prey density), conducted consecutively from late July to early September in 2001. Start dates for the five experimental runs were July 25, August 4, August 15, August 17, and September 7. Each experimental run lasted 5 days. Prior to each experimental run, the contents of the cages were inspected for insects, especially coccinellids, which were removed. Corn leaf aphids, *Rhopalosiphum maidis* (Fitch) (Homoptera: Aphididae), were added to each cage 2 days prior to an experiment. These aphids occurred naturally in the surrounding cornfields (sweet corn and field corn), and were located mainly in the developing tassels of the plants. At the start of each experimental run, the tassels and most of the aphids were removed from three of the six cages, leaving fewer than 50 detectable aphids in these cages. To the other three cages, tassels and leaves with aphids were added, collected from the surrounding corn fields. At the beginning of each experimental run, the number of aphids in the high density cages exceeded 200, and depending on the time of the season, densities were higher. Aphids were shaken into the whorls and leaf axles of the plants, and tassels (that had not yet developed pollen) with high numbers of aphids were propped in the leaf axles of the plants. These high-prey density cages contained at least 200 detectable aphids (determined by a visual inspection of all areas of the plants) at the onset of each experiment. The plants were approximately the same height, but the number of leaves varied between plants. The addition of tassels or leaves with aphids also added a small amount of leaf surface to these cages, but this addition was deemed negligible. At the onset of each experimental run, caged plants had just developed tassels but were not yet shedding pollen. However, the field corn plants in nearby fields were shedding pollen from late July, and during all the experimental runs pollen from nearby fields was found in our cages.

Coleomegilla maculata larvae were obtained from a laboratory colony. Adults were kept individually in 5 cm diameter Petri dishes at 23 °C, 70% r.h., and L16:D8, fed an artificial diet based on chicken liver (diet 7 in Atallah & Newsom, 1966), and provided with water from a moist strip of tissue in a 0.5 ml microcentrifuge tube. When an egg mass was found in a Petri dish, it was separated from the adult female to prevent cannibalism. *Harmonia axyridis* egg masses were provided by Dr J. Luhman of the Minnesota Department of Agriculure. *Harmonia axyridis* were kept in cages on fava bean plants containing pea aphids, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae).

At the start of each experimental run, 1st instar larvae of one or both coccinellid species were introduced into each of the cages. The total number of larvae was the same for all cages within each experimental run, but differed between runs, because of a variability in the number of larvae that were available from laboratory colonies of *C. maculata* and *H. axyridis.* The total number of larvae present in each cage varied between 22 and 30 (in runs one through five, each cage contained 30, 22, 30, 22, and 26 larvae, respectively). Treatments were: (1) only *H. axyridis*, (2) only *C. maculata*, and (3) equal numbers of *H. axyridis* and *C. maculata*, all at high and low prey densities.

We weighed the larvae of each species introduced into each cage in batches of 15, 11, or 13 on the start day of each experimental run. After 5 days, larvae were collected from the cages by carefully inspecting and dissecting the corn plants, and by checking the bottom and sides of the cages. The number of recovered larvae was recorded for each cage, as was their position on the plant or in the cages. We differentiated between the top, middle, and lower third of the plant, and the bottom and sides of the cage. The larvae that were collected were frozen, and each individual larva was weighed. Larvae were prepared for gut content analysis by dissecting-out the entire alimentary canal (foregut, midgut, and hindgut), using dissecting needles in a drop of distilled water on a microscope slide under a dissecting microscope (magnification ×20), and then covering the samples with a cover glass. Gut contents were viewed using a compound microscope at a magnification of ×100.

Data analysis

Experimental run was analyzed as a variable in all analyses in order to account for any environmental variability occurring over the season. Prey density (high or low), species (*H. axyridis* or *C. maculata*), and whether the cage contained one or two species were the three factors of interest, each with two levels. Multifactor analyses of variance (ANOVA) were used to analyze the influence of these factors on the fraction of larvae recovered and on larval weight. The weights of the two species were analyzed separately, because *H. axyridis* larvae were much larger than *C. maculata* larvae. The influence of prey density and single or two species treatments were the factors of interest in the analysis of the weights. Prior to the analyses, data were checked for equal variances and normality, and were transformed if necessary.

Five categories were distinguished in the distribution of larvae: the sides of the cage, bottom of the cage, and the lower, middle, and top thirds of the plants. The distribution of larvae was analyzed using a χ^2 test for likelihood ratios. Pair-wise comparisons were made between species, within treatments, and between treatments within species. Before using these tests, we first determined that we could pool across dates by testing whether there was an effect of date on any of the observed categories by using a multifactor ANOVA including date. We also did this for gut fullness and content.

Likelihood ratio tests were also used to analyze the gut contents and fullness. Gut content (or type of prey present in the gut) could be placed in general categories based on fragments of legs, exoskeleton, etc. (Powell et al., 1996), and was classified as aphids alone, aphids and pollen, or pollen alone (individuals with empty guts were not included in this analysis). Other prey was rarely found in the dissections, and was excluded form our analysis. Aphid parts were recognized by comparing dissected individuals from this experiment to several previous dissections that were known to contain aphid parts, and to slides of corn leaf aphids. Aphids were the main prey available in the cages, other than the other coccinellid larvae, and aphid parts could be recognized by their color, size, shape, and lack of hairs and spines. *Harmonia axyridis* larvae have large spines, and *C. maculata* larvae have hairs. Gut fullness was rated as empty, less than half full, or more than half full. Again, pair-wise comparisons were made between treatments, species, and treatments within species.

Results

Proportion of larvae recovered

The proportion of larvae of both species that was recovered was significantly higher at the high prey density than at the low prey density (Table 1, Figure 1). Proportions recovered did not differ between species or between the single- and two-species treatments (Table 1, Figure 1). The proportion of larvae that was recovered varied between experimental runs. In the analysis, we corrected for this by including experimental run as one of the factors.

Table 1 Multifactor analysis on the proportion of larvae recovered. Prior to the analysis, data were transformed using arcsine transformation. Only main effects are shown (none of the factor interactions was significant). d.f. error = 32, d.f. model = 7

Source	d.f.	F ratio	Prob>F
Exp. date	4	12.2776	<0.0001
Prey density	1	31.3167	<0.0001
Species	1	0.2086	0.6514
Mix/single species	1	2.1115	0.1573

Weight of recovered larvae

The combined weights of the first instar larvae at introduction into the cages was always less than 0.01 g per 15 larvae for both species, and was often less than the detection limit of our scale. At recovery after the 5-day experimental period, individual *C. maculata* larvae weighed between 0.1 and 6.7 mg, with an overall mean weight (across all treatments) of 2.31 mg, and *H. axyridis* weighed between 0.5 and 33.5 mg, with an overall mean weight of 6.50 mg (Figure 2). Neither prey density nor the presence of *H. axyridis* affected the weights of recovered *C. maculata* larvae (Table 2, Figure 2). However, the recovered *H. axyridis* larvae were slightly heavier in the high-prey treatments than in the low-prey treatments (the treatment effect was marginally significant, see Table 2). *Harmonia axyridis* appeared heavier in the presence of *C. maculata* larvae than in the presence of conspecifics alone (Figure 2), but this difference was not significant (Table 2).

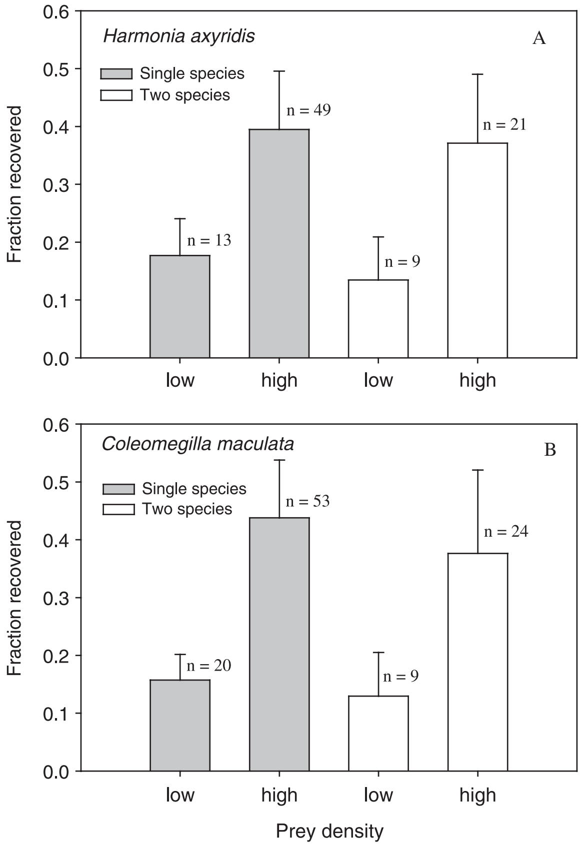

Figure 1 The fractions of larvae recovered from the cages after 5 days for (A) *H. axyridis*, and (B) *C. maculata*. Average fractions are given for single- and two-species cages, and low- and high-prey treatments. Fractions recovered differed between prey densities, but did not differ between species. The fractions are the number of larvae found, divided by 130 for the single-species treatments, and divided by 65 for the two-species treatments.

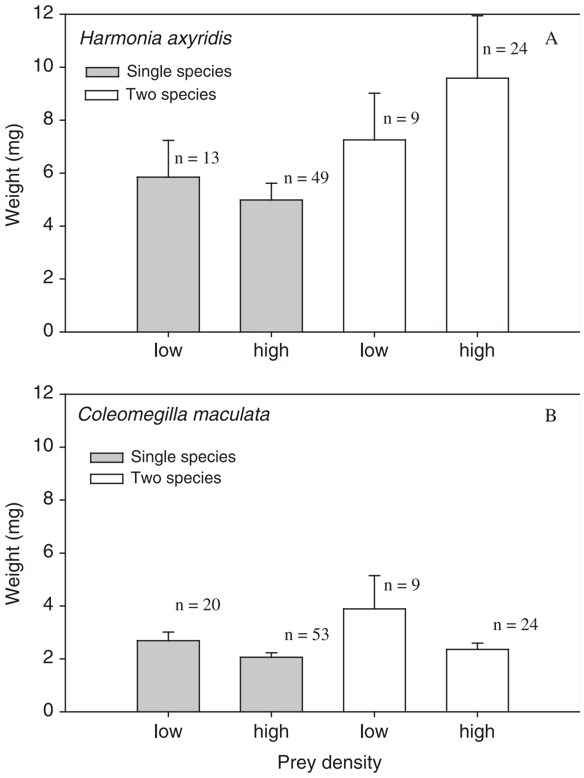

Figure 2 Weight in mg of the recovered larvae for (A) *H. axyridis*, and (B) *C. maculata*. Prey density or number of species in the cage did not influence the weights of recovered *C. maculata* larvae, but *H. axyridis* larvae recovered from the two-species treatments weighed more than larvae recovered from single-species treatments.

Position of larvae on the plants

Prey density did not influence the distribution of larvae over the plants in either *H. axyridis* ($\chi^2 = 1.56$, d.f. = 3, P = 0.67) or *C. maculata* ($\chi^2 = 5.0$, d.f. = 3, P>0.15). Figure 3 shows the distribution of larvae for both species in the single-species and the mixed treatments, pooled for

Table 2 Multifactor analysis on the weights of recovered larvae. The two species were analyzed separately. For both analyses data were transformed using Box-Cox best transformations (for *H. axyridis*: ln(averageweight) × 3.40076; for *C. maculata*: (averageweight) – 1)

Source	d.f.	F ratio	Prob>F
H. axyridis (d.f. error = 7, d.f. model = 8)			
Exp. date	4	19.1708	0.0004
Prey density	1	4.3544	0.0704
Mix/single species	1	0.6061	0.4587
Preydens*mix/single	1	0.9629	0.3552
C. maculata (d.f. error = 9, d.f. model = 7)			
Exp. date	4	18.4113	0.0002
Prey density	1	0.3173	0.5870
Mix/single species	1	0.0122	0.9143
Preydens*mix/single	1	0.0030	0.9576

high- and low-prey densities. The distributions differed significantly between species in the two-species treatments ($\chi^2 = 27.4$, d.f. = 3, $P<0.0001$) and in the single-species treatments ($\chi^2 = 8.1$, d.f. = 3, $P<0.05$). A greater proportion of *C. maculata* was recovered on the lower and middle parts of the plants, while *H. axyridis* larvae were mainly present on the upper parts of the plants (Figure 3).

The distribution of *C. maculata* differed between the two-species and single-species treatments ($\chi^2 = 11.5$, d.f. = 3, $P<0.01$). A greater proportion of larvae was recovered from the middle and upper parts of the plants in the single-species treatment, and more were present on the lower parts of the plants in the two-species treatments. The distribution of *H. axyridis* did not differ between two-species and single-species treatments ($\chi^2 = 4.4$, d.f. = 3, $P>0.20$).

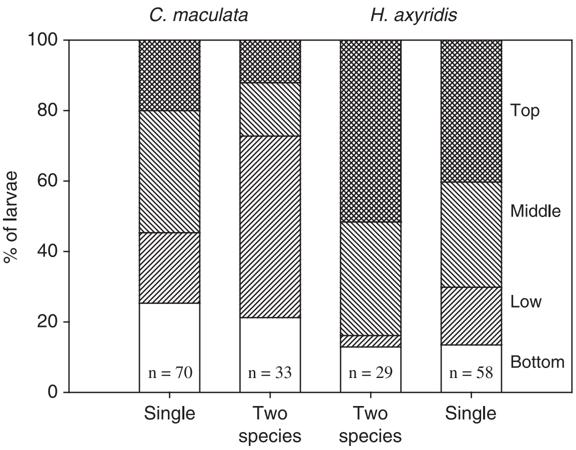

Figure 3 Position of *C. maculata* and *H. axyridis* larvae on the plants in single-species and two-species treatments. A larger proportion of *C. maculata* was recovered from the bottom and middle parts of the plants, while *H. axyridis* larvae were mainly recovered from the top parts.

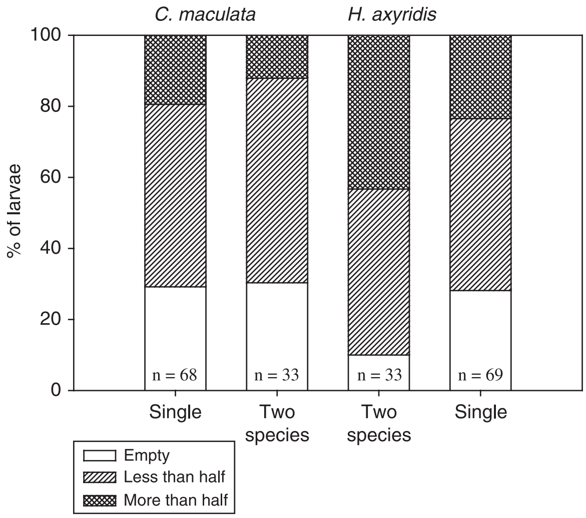

Figure 4 Gut fullness of *C. maculata* and *H. axyridis*. In the two-species treatments, a smaller proportion of *H. axyridis* had empty guts than in the single-species treatment. There was no difference between treatments in *C. maculata*.

Gut fullness

Gut fullness did not differ significantly between low- and high-prey densities in *C. maculata* ($\chi^2 = 0.8$, d.f. = 2, $P = 0.66$) or in *H. axyridis* ($\chi^2 = 4.3$, d.f. = 2, $P>0.1$) (Figure 4). For *C. maculata*, gut fullness also did not differ between the two-species and single-species treatments ($\chi^2 = 0.9$, d.f. = 2, $P = 0.63$). However, for *H. axyridis*, there was a significant difference between mix- and single-species treatments ($\chi^2 = 6.0$, d.f. = 2, $P<0.05$). In the single-species treatment, a larger proportion of individuals of this species had an empty gut. There was a significant difference in gut fullness between *C. maculata* and *H. axyridis* in the two-species treatment ($\chi^2 = 9.6$, d.f. = 2, $P<0.01$). Compared to *H. axyridis*, a larger proportion of *C. maculata* had an empty gut when the other species was present. In the single-species treatments, there were no differences in gut fullness between *C. maculata* and *H. axyridis* ($\chi^2 = 0.33$, d.f. = 2, $P = 0.85$).

Gut contents

Of the 217 larvae that were recovered, four individuals contained remains of coccinellid larvae. Of these individuals, two were *C. maculata* containing *C. maculata* parts, one *H. axyridis* containing *C. maculata* parts, and one *H. axyridis* containing *H. axyridis* parts. Two other types of prey were found in *C. maculata* and *H. axyridis* guts: aphids and pollen. The types of other prey that were present in the guts

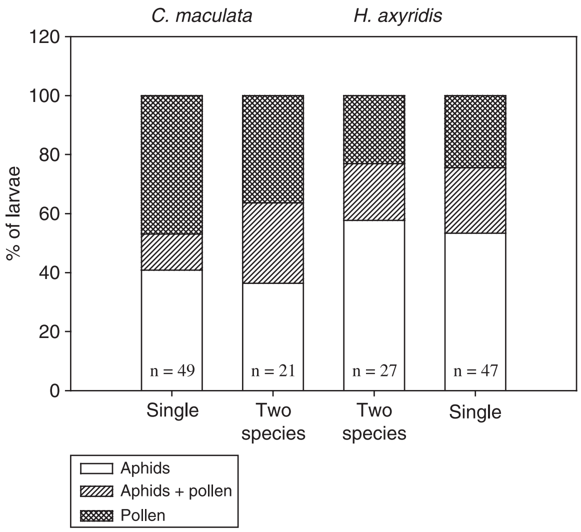

Figure 5 Gut contents of *C. maculata* and *H. axyridis*. There were no significant differences between treatments, but there was a trend towards more aphid parts in *H. axyridis* guts and more pollen in *C. maculata* guts.

did not differ between high- and low-prey treatments in either species (*C. maculata*: $\chi^2 = 0.7$, d.f. = 2, P = 0.69; *H. axyridis*: $\chi^2 = 0.5$, d.f. = 2, P = 0.79). There were no significant differences in gut content between the mixed- and single-species treatments in *C. maculata* ($\chi^2 = 2.4$, d.f. = 2, P = 0.31) or in *H. axyridis* ($\chi^2 = 0.1$, d.f. = 2, P = 0.93). There was no significant difference between species regarding the types of prey that were present in the gut in the two-species treatments ($\chi^2 = 2.2$, d.f. = 2, P = 0.33). However, in the single-species treatments, a marginally significant difference in the types of prey present in the gut ($\chi^2 = 5.5$, d.f. = 2, P = 0.063) reflected a trend towards a higher proportion of *C. maculata* with guts containing pollen, and a higher proportion of *H. axyridis* with aphids (Figure 5).

Discussion

We found an asymmetry in the interaction between *H. axyridis* and *C. maculata*. We found no adverse effects of the presence of *H. axyridis* on the weight gain, mortality rate, or gut fullness of *C. maculata*. The lack of adverse effects of *H. axyridis* on *C. maculata* may be in part due to the short duration of our experiment, but also by differences between the two species in their distributions over the plants. Because *H. axyridis* larvae tended to be present on the upper parts of the plants, and *C. maculata* larvae mainly on the lower parts of the plants, they may not have encountered each other very often. The larvae went through at least two molts during the experiment, which would have made them particularly vulnerable to predation and cannibalism. Lucas et al. (2000) found that the majority of molts of *C. maculata* were found on microsites that were also occupied by foraging larvae, increasing the risk of predation on molting larvae. The results of a cage experiment by Obrycki et al. (1998b) indicated that interactions between *C. maculata* and another introduced coccinellid species, *Coccinella septempunctata* L., reduced larval survival and adult weight in *C. maculata* at low prey densities. *Coccinella septempunctata* is similar in size to *H. axyridis*, and was also reported to be a more voracious species than *C. maculata*. In another cage experiment (Obrycki et al., 1998a), no effect by *C. septempunctata* on survival of *C. maculata* was found, but *C. maculata* weight was affected by the presence of *C. septempunctata*.

Proportion of larvae recovered

We recovered equal proportions of *C. maculata* and *H. axyridis* in two-species as well as in single-species treatments (Table 1, Figure 1). For both species, the proportion of larvae recovered was higher in the high-prey densities than in the low-prey densities. Cottrell & Yeargan (1998) found from laboratory experiments that in almost all cases the larvae of *H. axyridis* preyed upon *C. maculata* larvae. They also found that *H. axyridis* had a higher cannibalism rate than *C. maculata*. The results from our cage study differ from their observations. If *H. axyridis* predation rate upon *C. maculata* had exceeded the cannibalism by *C. maculata*, we would have to have recovered a lower fraction of *C. maculata* in the two-species treatment than in the single-species treatment. Instead, we found no difference in the fraction of *C. maculata* larvae recovered in the absence or presence of *H. axyridis*. Similarly, if *H. axyridis* had a higher rate of cannibalism than *C. maculata*, we would expect to recover fewer *H. axyridis* individuals compared to *C. maculata* individuals in the single-species treatments. However, it was possible that *H. axyridis* had a higher cannibalism rate than *C. maculata*, and that this cannibalism rate resulted in an increase in survival of the remaining population.

In addition to the similar recovery rate of both species, evidence of predation and cannibalism from dissections was rare in both species (four out of 217 dissected individuals, three contained *C. maculata* parts and one contained *H. axyridis* parts). The low number of individuals containing conspecific or heterospecific remains suggested that neither cannibalism nor predation was an important factor in the interaction between the species in this experimental setting. It is however, possible that a higher level of mortality through predation or cannibalism would occur over a longer time scale, or at higher densities of larvae. Moreover, it is possible that not all events of intraspecific predation or cannibalism were detected in our gut content analysis because the prey remains were not recognizable (if prey fragments were too small), or had passed through the digestive system.

Weight of recovered larvae

Weight was used as an indicator of the fitness of the surviving larvae that were recovered. If the weight of *C. maculata* larvae were negatively influenced by the presence of *H. axyridis* larvae, this could indicate a decrease in the fitness of this species caused by *H. axyridis*. However, we found that the weight of *C. maculata* larvae in the two-species treatment did not differ from the weights of larvae in the single-species treatment (Table 2, Figure 2). Thus, in this experiment we found no negative effect of the presence of *H. axyridis* on the fitness of *C. maculata*. These results are in contrast to the results of the studies by Obrycki et al. (1998a,b), who found that the weight of *C. maculata* larvae was negatively affected by interspecific competition with *C. septempunctata*.

Prey density also had no influence on the weight of *C. maculata*, suggesting that even in the low-prey density treatments, individuals of this species were able to locate enough prey to sustain themselves. This finding is in accordance with the observations by Schellhorn & Andow (1999a,b) where *C. maculata* larvae were very slow to leave plants without aphids, suggesting that this species is adapted to low aphid densities. However, Smith (1965) showed that prey density can affect larval survival and adult weight in *C. maculata*. We did retrieve fewer larvae from low-prey density treatments, indicating a lower larval survival rate in these treatments. It is possible that in the low-prey density treatments, more first instar larvae died of starvation soon after introduction into the cages because they could not locate prey, leaving sufficient prey for the remaining larvae to sustain themselves.

Prey density did have a significant effect on the weight of *H. axyridis*, suggesting that this species either required more food, or was less successful in finding prey at low densities. This may be an indication that intraspecific competition in *H. axyridis* is stronger than in *C. maculata*. Furthermore, *C. maculata* appeared to avoid interactions with *H. axyridis* (see next section).

Position of larvae on the plants

Predation by *H. axyridis* on *C. maculata* appeared to be low, possibly because *C. maculata* and *H. axyridis* do not encounter each other as much as they would in a laboratory experiment where they are confined together in a small arena, as in the experiments by Cottrell & Yeargan (1998). The distribution of *C. maculata* over the plant differed from the distribution of *H. axyridis*. More *C. maculata* larvae were found on the lower part of the plants and on the bottom of the cages, while more *H. axyridis* larvae were found on the top part of the plant. This was also found in observations by Musser & Shelton (2003), who studied the spatial and temporal distributions of both species in cornfields for 3 consecutive years. The difference in distribution was more pronounced in the cages where both species were present. Although the distribution of *H. axyridis* did not change with the presence of *C. maculata*, the distribution of *C. maculata* differed significantly between the single-species and the two-species treatment (Figure 3). A larger proportion of *C. maculata* larvae was present on the lower part of the plant, and a smaller proportion on the top of the plant in the two-species treatment. (Larvae were very rarely found on the sides of the cages, and this category was left out of the analysis shown here.) In a previous study, Schellhorn & Andow (1999b) found that *C. maculata* adults searched throughout the plant for prey, and oviposited near the bottom, far from aphid colonies. Ewert & Chiang (1966) also observed that *C. maculata* was often found lower on the plant, possibly because of their oviposition behavior. It appears from our observations that the larvae followed a similar distribution.

The change in distribution in the presence of *H. axyridis* may indicate a behavioral response of *C. maculata*. Among the species in which some kind of predator avoidance behavior has been shown experimentally, are larval anurans (Richardson, 2001), pea aphids (Roitberg et al., 1979), herbivorous mites (Bernstein, 1984; Magelhães et al., 2002), lepidopteran larvae (Stamp & Bowers, 1993), spotted cucumber beetles (Snyder & Wise, 2000), and coccinellid larvae (Völkl & Vohland, 1996), and ovipositing females (Agarwala et al., 2003). Simple prey behavioral responses to predators have been incorporated into Lotka–Volterra models (Sih, 1979; Ives & Dobson, 1987), and under certain conditions they can stabilize interactions. However, Luttberg & Schmitz (2000) argued that a flexible prey response to predators may also lead to higher predator–prey oscillations, thus destabilizing the interactions.

We suspect that, in our experiment, *C. maculata* moved to areas on the lower part of the corn plants in response to the presence of *H. axyridis* on the upper parts of the plant, thus exhibiting a predator-avoidance response. Depending on the effect of this response on food availability, the cannibalism rate in both species, and the predation rate by *H. axyridis* on *C. maculata*, this may promote coexistence. Because we found no difference in the number of *C. maculata* larvae that was recovered in the absence or presence of *H. axyridis*, it is unlikely that the difference in distribution over the plants was due to the *C. maculata* on the upper parts of the plants being eaten by *H. axyridis*.

Gut content and fullness

In the two-species treatment, a significantly higher proportion of *H. axyridis* had fed when compared to *H. axyridis* in the single-species treatment or when compared to *C. maculata*. Because *H. axyridis* larvae are much more concentrated on certain plant parts (the tops), the effects of conspecific crowding potentially have a greater effect on this species than on *C. maculata*.

The contents of the gut did not differ significantly between species or between high- and low-prey treatments, with comparable proportions feeding on aphids, pollen, or both. There was a trend towards more feeding on pollen in *C. maculata*, and more feeding on aphids in *H. axyridis*. Although the tassels had been removed from low prey treatments, a similar number of larvae had fed on pollen in these cages, probably because pollen from nearby corn fields could enter the cages.

From the results of this study, it appears that the invasion by *H. axyridis* may not negatively impact the survival and food intake of *C. maculata*. We only used larvae in our study, and interactions between other stages (predation by adults, predation on eggs) should also be considered to gain more insight into the impact of *H. axyridis* on *C. maculata*. The apparently low food requirements of *C. maculata* (Schellhorn & Andow, 1999a), and its avoidance of interactions with *H. axyridis*, may help this species in maintaining its population levels after the invasion of *H. axyridis*. As reported by Musser & Shelton (2003), asynchronies in the temporal and spatial distributions of both species in the field are also likely to limit the effects of *H. axyridis* on *C. maculata* populations. On the other hand, *C. maculata* may also facilitate the invasion by *H. axyridis*. Shea & Chesson (2002) discussed invasions in relation to resource opportunities. Resource opportunities arise not only when resources are supplied at a high rate, but also when resident species that compete for these resources with the invader do not greatly reduce the resource densities. The low food requirements of *C. maculata* may help to create an environment that is easy for *H. axyridis* to invade.

From previous field observations, it appears that *C. maculata* is not among the species that is strongly affected by introductions of other coccinellids, possibly because their distribution is not closely associated with aphids, making them less vulnerable to intraguild predation (Schellhorn & Andow, 1999b). Colunga-Garcia & Gage (1998) did not find changes in populations of *C. maculata* after the introduction of *H. axyridis*, although three other species appeared to be adversely affected by its invasion. Elliot et al. (1996) observed an increase in *C. maculata* after the invasion and establishment of the European coccinellid species *C. septempunctata*. Two other species, *Coccinella transversoguttata richardsoni* Brown and *Adalia bipunctata*, declined in abundance.

In conclusion, we found no increase in the larval mortality of *C. maculata* in the presence of *H. axyridis* larvae, nor did we find negative effects on *C. macutata* larval weight gain and food intake in our experiment, suggesting that larval interactions will not negatively affect *C. maculata* populations. One possible mechanism that may be responsible for the lack of a negative effect of *H. axyridis* is the avoidance of individuals of this species by *C. maculata*. However, interactions between *C. maculata* and *H. axyridis* are not limited to the direct interactions discussed in this and previous papers. Indirect interactions between *H. axyridis* and *C. maculata* may also influence their populations in the field. Both species are attacked by the parasitoid *Dinocampus coccinellae* (Schrank), introducing the potential for apparent competition between the two coccinellid species mediated by this parasitoid (Holt, 1977; Holt & Lawton, 1994; Bonsall & Hassell, 1999). However, *C. maculata* is a more suitable host than *H. axyridis* for *D. coccinellae* (Hoogendoorn & Heimpel, 2002), and this decreases the strength of the apparent competition between these species. Indeed, the presence of *H. axyridis* may indirectly benefit *C. maculata* if *D. coccinellae* wastes sufficient eggs and/or time on *H. axyridis* (Hoogendoorn & Heimpel, 2002; Heimpel et al., 2003).

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