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Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid

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Abstract

We studied parasitism rates by *Dinocampus coccinellae* (Schrank) of the native species *Coleomegilla maculata* De Geer and the introduced *Harmonia axyridis* (Pallas) in the laboratory and in the field. The rate of successful parasitism for *H. axyridis* was lower than for *C. maculata*, but the proportion of the population that had immature stages of the parasitoid was similar for both species. We used a population dynamics model to predict interactions between *C. maculata*, *H. axyridis*, and *D. coccinellae*, incorporating the differences in suitability we found between the two hosts. In the model, parasitoid attacks on non-suitable hosts contribute to parasitoid egg depletion without causing host death or parasitoid recruitment. Thus, hosts with low suitability could act as sinks for parasitoid eggs. Simulations of this model suggest that there is a critical value of the growth rate (r) for *C. maculata* below which *C. maculata* goes extinct. The critical r value is an increasing function of the attack rate on *C. maculata* (as expected) and a decreasing function of the attack rate on *H. axyridis* because the strength of *H. axyridis* as an egg sink increases with the attack rate on this species. Simulations of the model using experimentally derived parameter values suggest that the presence of *H. axyridis* leads to an increase in equilibrium densities of *C. maculata*. This outcome is due to the wastage of parasitoid eggs in the relatively unsuitable *H. axyridis* hosts.

Keywords: *Coleomegilla maculata*; *Harmonia axyridis*; *Dinocampus coccinellae*; Parasitoids; Apparent competition; Indirect interactions

1. Introduction

The introduction of a new species into a habitat may have consequences for populations of native species. The newly introduced species may interact directly or indirectly with species that were present before. One mechanism of indirect interaction is competition that is mediated by a shared parasitoid or predator, termed apparent competition by Holt (1977). Here, the presence of one species has a negative effect on the population of another species by allowing the population of a shared natural enemy to increase, leading to a higher level of predation on both prey species (Berdegue et al., 1996; Bonsall and Hassell, 1999; Holt, 1977; Holt and Lawton, 1994; Morris et al., 2001; Wootton, 1994; Müller and Godfray, 1997, 1999).

Apparent competition can in principle lead to the displacement of native species by introduced species as described by Settle and Wilson (1990). In their study, populations of the native grape leafhopper (GL), *Erythroneura elegantula* Osborn, declined after invasion of the variegated leafhopper (VL), *Erythroneura variabilis* Beamer, in the San Joaquin Valley, California. The authors concluded that this was due to differential parasitism by a shared parasitoid rather than to direct competition for resources. From experiments that compared the effects of intra- and interspecific competition on fecundity of GL and VL they found that there was no detectable difference in competitive ability. The presence of VL led to an increase in the parasitoid population, and the shared parasitoid attacked the native leafhopper more effectively than it did the introduced one, leading to a lower relative GL abundance.

The introduction of a new prey species might also lead to a decrease in predation on another prey species,

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for instance if the new prey is easier to locate or otherwise preferred by the natural enemy. In this case the introduction of a new species could have a positive effect on population densities of the original prey species (Abrams, 1987, 1993; Abrams et al., 1996; Holt, 1977; Holt and Lawton, 1994; Wootton, 1994). If predator satiation occurs at high densities of prey, two prey species can exhibit short-term apparent mutualism (Holt, 1977). At the predator's equilibrium density, however, its numerical response is expected to cause apparent competition between its prey species (Holt, 1977). Müller and Godfray (1999) also discussed the possibility of short-term apparent mutualism in indirect interactions between two primary aphid parasitoids that share a secondary parasitoid. Under certain circumstances (e.g., if the new host is preferred) the introduction of a new host may lead to a lower rate of parasitism in the host that was present before.

Another mechanism that can cause a positive effect of one prey species on another is switching (Bonsall and Hassell, 1999; Holt, 1977). If a predator forages mainly for the prey that is most abundant, this can positively affect densities of another prey that is present at lower densities. If this species becomes more abundant, the predator may "switch" to feed mainly on this prey, thus relieving predation pressure on the prey that was initially preyed upon more. This way switching can promote coexistence between prey species (Bonsall and Hassell, 1999; Gillis and Hardy, 1998; Hardy and Gillis, 1997). However, a predator's foraging behavior may not just depend on which prey is more abundant. A predator may prefer one prey species to another, leading to a higher level of predation on the preferred species. The prey species that can withstand the highest level of attacks is expected to be the one that persists (Bonsall and Hassell, 1999).

1.1. The system studied

We studied two species of ladybird beetles and a parasitoid that attacks both. *Coleomegilla maculata* De Geer (Coleoptera: Coccinellidae) is native to North America. *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) was introduced into North America from Asia before 1988 (Chapin and Brou, 1991). Its population has since spread widely, and it is thought to have an impact on some native coccinellid species (Colunga-Garcia and Gage, 1998). Although several coccinellid species were present at our field site, we compared *C. maculata* and *H. axyridis* because they were the two most abundant species.

Dinocampus (= *Perilitus*) *coccinellae* (Schrank) (Hymenoptera: Braconidae) is a solitary, koinobiont endoparasitoid that attacks several coccinellid species. It can attack all stages, but prefers, and is most successful, in adults (Balduf, 1926; Obrycki, 1989). It has been reported to attack coccinellids throughout the Holarctic region (Balduf, 1926; Obrycki et al., 1985). In the field, the percentage of a *C. maculata* population that is attacked has been reported to approach 20% (Richerson and DeLoach, 1973; Obrycki and Tauber, 1978). In adult beetles, its development time is approximately four weeks, with the last 9 days spent as a pupa. To pupate, the fourth instar larvae exits the host and spins a cocoon attached to the legs of the host. *D. coccinellae* is a thelytokous species, producing only female progeny.

This study explores the possible outcomes of the parasitoid-mediated interactions between *C. maculata* and *H. axyridis* using a model developed by Heimpel et al. (in review). We also conducted laboratory and field studies to compare actual parasitism rates in both species.

2. Materials and methods

2.1. Parasitism in the field

From to 9 June to 2 September 1999 and from 23 May to 12 September 2000, adult coccinellids were collected in cornfields at the University of Minnesota Experimental Station, Rosemount, MN. Collected beetles were frozen at −20 °C, dissected, and the presence of *D. coccinellae* larvae or eggs was recorded. The dissection of field samples provided us with an estimate of immature stages of the *D. coccinellae* present in the coccinellid population.

To estimate the fraction of beetles from which adult parasitoids emerged (successful parasitism), adult beetles were collected on four dates in 2000: 2, 16, and 28 August and 1 September. Collected individuals were kept in petri dishes at 23 °C, 70% R.H. and 16:8 (L:D) h, and provided with food (diet 7 in Atallah and Newsom, 1966) and water in a 0.5 ml microcentrifuge tube with moist cotton. They were inspected every day for *D. coccinellae* cocoons. After 26 days, at least 5 days after the maximum time it would have taken for the cocoon to appear (Balduf, 1926; Obrycki, 1989; Obrycki et al., 1985), the beetles from which no *D. coccinellae* emerged were frozen at −20 °C. These individuals were then dissected to check for the presence of dead or live parasitoid larvae. Parasitoid larvae that were dead before freezing were brown in color and partially decomposed. Live larvae were white, and remained white after freezing.

2.2. Parasitism in the laboratory

Both *C. maculata* and *H. axyridis* used in the experiments were reared in the laboratory. They were fed an artificial diet (diet 7 in Atallah and Newsom, 1966) that was supplemented with aphids, and they were provided with water from 0.5 ml microcentrifuge tubes with moistened cotton. Parasitoids were reared in the laboratory on *C. maculata* adults.

At the beginning of each experiment, parasitoids were introduced into petri dishes (10 cm diameter) with one adult beetle, either *H. axyridis* or *C. maculata* (1 parasitoid and 1 beetle per arena). If stinging was observed within 20 min, the beetles were kept at 23 °C with food and water for periods of time ranging from 4 to 15 days. After this they were frozen at −20 °C and dissected to check for the presence of *D. coccinellae* larvae or eggs.

2.3. A model for parasitoid-mediated interactions

We used a model (Heimpel et al., in review) to predict interactions among *H. axyridis*, *C. maculata*, and *D. coccinellae*. In this model, the parasitoid's attack rate can be limited by its fecundity. The hosts can have varying susceptibilities for parasitoid attack. A lower susceptibility of the host may be caused by its ability to encapsulate parasitoid eggs or other physiological defense mechanisms. The susceptibility term introduces the possibility of an 'egg sink' (i.e., hosts in which oviposition contributes to parasitoid egg depletion without causing host death or parasitoid recruitment) (Heimpel et al., in review).

Host encounters by the parasitoid are described by an encounter function introduced by Getz and Mills (1996) (1)

$$\varepsilon = \frac{a\beta P}{\beta + aH}, \tag{1}$$

where H is the host density, P is parasitoid density, a is a parameter proportional to parasitoid search, and β is the parasitoid maximum fecundity. Attack rates can become egg-limited at low values of β and when $a \to \infty$, and host-limited at low levels of a and when $\beta \to \infty$ (Getz and Mills, 1996).

The set of equations that describe population growth for the two hosts and the parasitoid (2) is

$$\begin{aligned} H1_{t+1} &= H1_t g(H1_t)[1 - s_1(1 - f[\varepsilon_{1,t}])], \\ H2_{t+1} &= H2_t g(H2_t)[1 - s_2(1 - f[\varepsilon_{2,t}])], \\ P_{t+1} &= s_1 H1_t[1 - f(\varepsilon_{1,t})] + s_2 H2_t[1 - f(\varepsilon_{2,t})], \end{aligned} \tag{2}$$

where $g(H1_t)$ and $g(H2_t)$ are host density dependence terms, $f(\varepsilon_{1,t})$ and $f(\varepsilon_{2,t})$ are the proportions of hosts escaping parasitism, and s_1 and s_2 are the host susceptibilities for host 1 and host 2, respectively. The host density dependence term (3) is

$$g(H_{i,t}) = \exp\left[r_i\left(1 - \frac{H_{i,t}}{K_i}\right)\right], \tag{3}$$

where r_i and K_i are the rate of increase and the carrying capacity, respectively, of host i. The proportion of hosts that escapes parasitism follows a negative binomial distribution, and is described by function (4)

$$f(\varepsilon_{i,t}) = \left[1 + \frac{\varepsilon_{i,t}}{k}\right]^{-k}. \tag{4}$$

The rate at which the parasitoid encounters hosts is described by (5)

$$\varepsilon_{i,t} = \frac{a_i \beta P_t}{\beta + a_1 H1_t + a_2 H2_t}. \tag{5}$$

2.4. Application of the model: estimating parameters

To use this model in describing interactions among *H. axyridis*, *C. maculata*, and *D. coccinellae*, we estimated some parameters from available data. An estimate for maximum fecundity (β) was obtained from a study on the life history of *D. coccinellae* by Balduf (1926). To estimate a measure of susceptibility (s), data from field-collected beetles were used. The number of beetles from which an adult parasitoid emerged (successful parasitism), divided by the total number of parasitized beetles (beetles from which adult parasitoids emerged + number of beetles with immature *D. coccinellae* that did not develop into adults) provided an estimate for s for each species. In the simulations of the model, we varied the values of population growth rate (r_i) for both species, and the values of parasitoid attack rate (a_i) for both species.

3. Results

3.1. Parasitism in the field: dissections of field-collected coccinellids

The number of beetles dissected in both seasons and the number of beetles that were parasitized are shown in Table 1. A nominal logistic regression analysis was used to evaluate effects of species, sample year, and the interaction of these factors on whether individual beetles were parasitized or not. Species by itself had no significant effect on parasitism ($\chi^2 = 1.810, P = 0.178$, df = 1). Parasitism rates were significantly lower in 2000 than in 1999 ($\chi^2 = 15.823$, $P = 0.0001$, df = 1). The interaction of species and sample year had a significant effect on parasitism ($\chi^2 = 8.868$, $P = 0.0029$, df = 1), which reflected the observation that parasitism levels of

Table 1
Number of *C. maculata* and *H. axyridis* dissected and percentage of individuals parasitized

Year	No. dissected	No. parasitized	% Parasitism
C. maculata			
1999	435	79	18.2
2000	110	16	14.5
H. axyridis			
1999	63	15	23.8
2000	282	25	8.9

C. maculata were much higher than those of *H. axyridis* in 2000, but not in 1999. In separate tests for both sample years, in 1999 parasitism levels between the two species did not differ significantly ($\chi^2 = 1.488$, $P > 0.2226$), but in 2000 they did ($\chi^2 = 7.920$, $P > 0.0049$).

3.2. Rearing of field-collected coccinellids: proportion of successful parasitism

From the 57 *C. maculata* individuals collected in the field, 6 *D. coccinellae* cocoons developed. By dissection, 2 dead *D. coccinellae* larvae (2nd–3rd instar) were found inside individuals that were frozen after 26 days. Thus the total proportion that was parasitized was 0.14 (8/57), and the proportion of parasitism that was successful was 0.75 (6/8).

From 84 collected *H. axyridis*, 1 cocoon developed. By dissection, 9 dead larvae (2 of which 1st instar, 7 3rd–4th instar) were inside individuals that were frozen. The total proportion of *H. axyridis* parasitized was therefore 0.12 (10/84), and the proportion of successful parasitism was 0.1 (1/10). The difference in successful parasitism between species was significant ($\chi^2 = 4.183$, $P = 0.0408$).

3.3. Parasitism in the laboratory

Both *H. axyridis* and *C. maculata* were readily attacked by *D. coccinellae* when the parasitoid was introduced into a dish with one of the hosts (apparent stinging attempts were designated as attacks). Of a total of 44 *H. axyridis* individuals, two were not attacked, and out of 23 *C. maculata*, three were not attacked. These individuals were removed from the analysis.

Out of the 20 *C. maculata* that were attacked, 18 were found to be parasitized upon dissection. Of all parasitized individuals, most had more than one egg or larva inside (mean (SE) = 5.1 (1.2)). Of 42 *H. axyridis* attacked, three were found to be parasitized upon dissection (all three individuals were frozen 7 days after stinging). The mean number of eggs in parasitized individuals was not significantly different from *C. maculata* (mean (SE) = 4.6 (2.7)). The large number of eggs that was laid per beetle is possibly an artifact of parasitoids being confined with their hosts, and does not necessarily indicate the number of eggs laid per host in the field.

There was a significant difference between species in the proportion of individuals parasitized ($\chi^2 = 44.764$, $P < 0.0001$). This result suggests that *D. coccinellae* does not often successfully attack adult *H. axyridis* in the laboratory.

3.4. Model simulations

The parameter values we used for s_1 and s_2, based on the proportions of successful parasitism in field-collected *C. maculata* and *H. axyridis*, were 0.75 ($= s_1$) and 0.1 ($= s_2$), respectively. For maximum fecundity (β), we used a value of 100, based on the observation by Balduf (1926) that at least 100 mature eggs were visible in the ovaries of two-day old *D. coccinellae* individuals.

Table 2 gives the results of a sensitivity analysis in which a_1 and a_2 (attack rates of *D. coccinellae* on *C. maculata* and *H. axyridis*, respectively) were varied, keeping the value of r_2 (*H. axyridis*) constant at 1. For different combinations of a_1 and a_2, the critical values of r_1 (*C. maculata*) are shown. These are the lowest possible growth rates of *C. maculata* for which this species reaches a stable equilibrium as opposed to being excluded. As shown in Table 2, these values are dependent on the values of a_1 and a_2. The critical value of r_1 increases with a_1 (as expected), but it also increases with decreasing levels of attack on *H. axyridis* (a_2). This is because the role of *H. axyridis* as an egg sink decreases at lower levels of a_2.

A similar analysis was performed in which a_1 and a_2 were varied, keeping the value of r_1 (*C. maculata*) constant at 1. Critical values for r_2 (*H. axyridis*) varied between 0.05 (for $a_1 = 1$ and $a_2 = 0.1$) and 0.11 (for $a_1 = 0.1$ and $a_2 = 1$). It is unlikely that values of r would be this low in nature, and it seems that invasion of *H. axyridis* is relatively insensitive to the attack rate on *C. maculata*.

In Fig. 1, a simulation of the model is shown, with the values of r_1 and r_2 both at 1.5, comfortably above the critical value for both species. Upon introduction of *H. axyridis* into a situation, where *C. maculata* and *D. coccinellae* are at their 2-species equilibrium levels, this species soon reaches an equilibrium density close to the carrying capacity, while equilibrium densities of both *C. maculata* and *D. coccinellae* increase when compared to their levels in the absence of *H. axyridis*. While this may seem to be a mutually beneficial situation, Fig. 2 shows that this is not actually a case of apparent mutualism. Fig. 2 shows the hypothetical situation where *H. axyridis* is present first, and *C. maculata*

Table 2
Results of a sensitivity analysis in which the values of a_1, a_2, and r_1 are varied

Attack rate on		Critical r_1	*C. maculata* equilibrium density
C. Maculata (a_1)	*H. axyridis* (a_2)		
0.1	1.0	0.35	4.6
0.3	1.0	0.65	3.3
0.5	1.0	0.80	3.6
0.7	1.0	0.90	5.1
0.9	1.0	1.00	11.9
1	1.0	1.00	7.3
1	0.9	1.00	3.9
1	0.7	1.05	5.6
1	0.5	1.10	6.6
1	0.3	1.15	6.5
1	0.1	1.20	7.1

$r_2 = 1$, $\beta = 100$, $s_1 = 0.75$, $s_2 = 0.1$, $K_1 = K_2 = 500$, and $k = 0.75$.

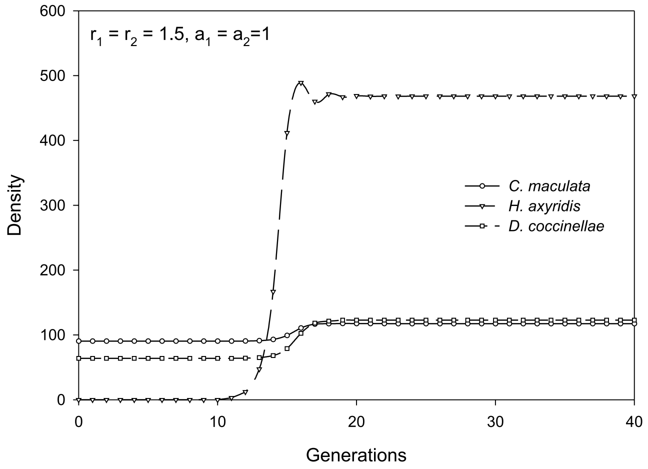

Fig. 1. A simulation using the model with $\beta = 100$, $s_1 = 0.75$, $s_2 = 0.1$, $K_1 = K_2 = 500$, and $k = 0.75$. At $t = 0$, *C. maculata* and *D. coccinellae* are at their equilibrium densities. The value of 1.5 is chosen for r_1, because this is above the critical value found in the sensitivity analyses. Given these parameter values, *H. axyridis* would reach its carrying capacity within 20 generations after introduction, while population densities of both *C. maculata* and *D. coccinellae* increase compared to their levels before introduction.

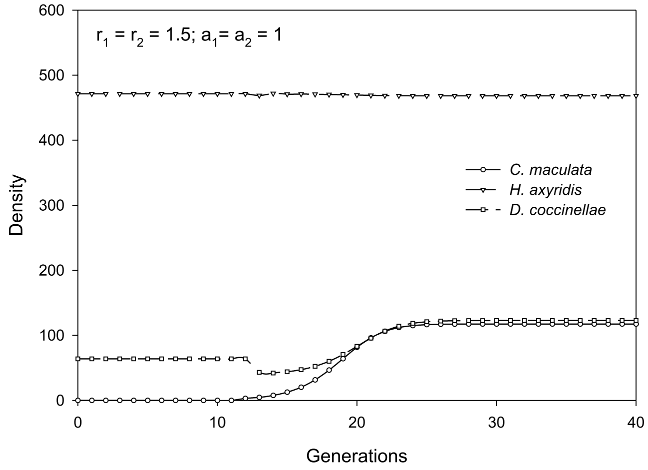

Fig. 2. A simulation of the hypothetical situation in which *H. axyridis* is present first, and *C. maculata* invades. Parameter values are the same as in Fig. 1. At $t = 0$, *H. axyridis* and *D. coccinellae* are at their equilibrium densities. The equilibrium density of *H. axyridis* is slightly lower in the presence of *C. maculata* than when it is by itself, which indicates that the relationship between *H. axyridis* and *C. maculata* is not a case of apparent mutualism.

is introduced. Although the effect is small, the equilibrium density of *H. axyridis* is lower in the presence of *C. maculata* than when by itself. The indirect interaction between *H. axyridis* and *C. maculata* is therefore of the +,− type ("apparent predation," Holt, 1977), where *C. maculata* benefits from the egg sink formed by *H. axyridis*, and *H. axyridis* suffers a slight negative effect of an increase in parasitism caused by the presence of *C. maculata*.

4. Discussion and conclusions

4.1. Levels of parasitism in *H. axyridis* and *C. maculata*

Parasitism rates in the field, although different between sample seasons, were similar for *C. maculata* and *H. axyridis*. There was a discrepancy between parasitism rates observed by dissection and rearing, which was found earlier in a study by Cartwright et al. (1982) on *D. coccinellae* parasitism of several coccinellid species. They used this discrepancy as an indication of larval mortality in *D. coccinellae*. Interestingly, of the five species they analyzed, *D. coccinellae* had the lowest level of larval mortality in *C. maculata*. *H. axyridis* was not included in their study, but they did observe that in another species, *Adalia bipunctata* (L.), larval mortality was 100%, which is in accordance with earlier observations that this is not a suitable host for *D. coccinellae* (Hodek, 1973; Richerson and DeLoach, 1972). Cartwright et al.'s (1982) results suggest that *D. coccinellae* adults are not able to discriminate between suitable and unsuitable hosts. This was also found by Richerson and DeLoach (1972), who found that *D. coccinellae* is mainly attracted by movement and color, and would even attack models made of paper, wood, or metal.

The discrepancy we found between total parasitism and successful parasitism in *H. axyridis* is thus in accordance with earlier studies, and suggests that *D. coccinellae* is not able to recognize *H. axyridis* as a marginal host. We found in our laboratory experiment that *D. coccinellae* attacks both hosts readily although all *D. coccinellae* individuals were reared on *C. maculata*, indicating that the parental host does not influence the parasitoid's willingness to attack another host species. Because *D. coccinellae* is a generalist that is known to attack several native and exotic coccinellid species in North America (Balduf, 1926; Cartwright et al., 1982; Obrycki, 1989; Richerson and DeLoach, 1972), it is reasonable to assume that the parental host does not greatly influence larval development of the parasitoid.

We found *D. coccinellae* eggs in only three *H. axyridis* individuals out of 42 that were observed to attack hosts in the laboratory, which suggests that the other individuals were not successfully stung. This is not in accordance with the relatively high level of parasitism in field-collected *H. axyridis*. In *C. maculata*, *D. coccinellae* is most successful when it attacks adults (Obrycki et al., 1985). To our knowledge, parasitism of *H. axyridis* by *D. coccinellae* has not been studied closely, and it is possible that *D. coccinellae* is more successful when it attacks larval stages of *H. axyridis*. It is also possible that conditions in the field differ from laboratory conditions in a way that makes successful oviposition by *D. coccinellae* in *H. axyridis* more likely.

4.2. Model simulations: parameter values and indirect effects

We did not perform exhaustive sensitivity analyses of all possible combinations of parameters, but instead we used parameter values that were relevant for the interaction among the three species considered in this study. For a more theoretical analysis of parasitoid-mediated indirect interactions among host species, using this model, we refer readers to Heimpel et al. (in review).

From the analyses we performed, it was apparent that under most circumstances *H. axyridis* can invade, and that this has a positive effect on the equilibrium densities of *C. maculata* and *D. coccinellae*. *C. maculata* is more susceptible to parasitism than *H. axyridis*, which serves as an egg sink for *D. coccinellae* eggs. However, even *C. maculata* is not completely susceptible to parasitism ($s = 0.75$). This makes the model more stable, because a fraction of the population of *C. maculata* always escapes parasitism, even in the absence of *H. axyridis* (for similar results using two-species models, see Godfray and Hassell, 1991). Therefore, there is only a small range of parameter values (combinations of a_1 and a_2, and r_1 and r_2) in which *C. maculata* goes extinct. Heimpel et al. (in review) consider the scenario where one host is completely susceptible, and the second is partially susceptible. They find extinction over a wider range of parameter values.

We did not include direct competition between the two host species in this model, because our goal was to investigate if indirect interactions alone could lead to changes in the populations of *C. maculata* after the introduction of *H. axyridis*. However, in the field these two species may compete for resources directly. A laboratory study by Cottrell and Yeargan (1998) indicates that *H. axyridis* larvae may also prey upon *C. maculata* larvae. Further studies into the direct interactions between *C. maculata* and *H. axyridis* are currently being conducted.

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