

# Intraguild predation of the aphid parasitoid *Aphelinus certus* by *Coccinella septempunctata* and *Harmonia axyridis*

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**Abstract** Coincidental intraguild predation is expected to be less disruptive to biological control than omnivorous intraguild predation, and strong intraguild predation is not expected to occur in natural systems. Coincidental intraguild predation in a food-web involving introduced pest and natural enemy species was examined to determine whether intraguild predation would be disruptive of biological control services in soybean agroecosystems. Introduced natural enemies are important regulators of soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), populations in North America. Seven-spotted lady beetles, *Coccinella septempunctata* L., and multicolored Asian lady beetles, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), are key predators of soybean aphid in North America while the

chalcidoid wasp, *Aphelinus certus* Yasnosh (Hymenoptera: Aphelinidae), is the most common parasitoid of soybean aphid in Ontario, Canada. Predation of parasitized soybean aphids at two stages (newly parasitized aphids and mummified aphids) by adults and third instar larvae of both *C. septempunctata* and *H. axyridis* was examined in laboratory experiments. In choice experiments, all stages of lady beetles preferred non-parasitized aphids over mummified aphids. In cage experiments, third instar larvae and male and female adults of both lady beetles did not discriminate between newly parasitized and non-parasitized aphids. The influence of coincidental intraguild predation on the efficacy of parasitoids as biological control agents, and implications for soybean aphid management decisions based on natural enemies, are discussed.

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## Introduction

Intraguild predation can strongly influence community structure, diversity, and the efficacy of biological control agents (Arim and Marquet 2004; Pell et al. 2008; Polis et al. 1989; Rosenheim et al. 1995). The influence of intraguild predation may vary depending on the species, sex, developmental stages of predators

and prey, and environmental parameters under which the interaction occurs (Arim and Marquet 2004; Pell et al. 2008; Polis et al. 1989). Intraguild predation can be symmetric when species are mutual predators of one another or asymmetric when one species consistently preys upon the other (Polis et al. 1989). Intraguild predation between predators and parasitoids is typically asymmetrical and favours the predator, where parasitoids are susceptible to predation in all stages that develop within the herbivore host (Brodeur and Rosenheim 2000; Polis et al. 1989). Coincidental intraguild predation (Polis et al. 1989), such as occurs when an intraguild predator consumes a herbivore that is host to a larval parasitoid (i.e. developing intermediate predator), results in mortality of the intermediate predator, but is considered less disruptive of biological control than is omnivorous intraguild predation, where the intraguild predator pursues both the herbivore and intermediate predator as prey (Rosenheim and Harmon 2006; Vance-Chalcraft et al. 2007). Intraguild predation by generalist predatory coccinellids is a widespread phenomenon within food webs (Chacon et al. 2008; Colfer and Rosenheim 2001; Cottrell and Yeagan 1999; Evans 1991; Ferguson and Stiling 1996; Lucas et al. 1998; Meyhofer 2001; Meyhofer and Klug 2002; Pell et al. 2008; Snyder and Ives 2003; Snyder et al. 2004), and has the potential to impact biological control in ecosystems where this taxon is present. This study aims to examine intraguild predation within the predator/parasitoid guild of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae).

The main species in the pest-predator complex of North American soybean ecosystems are introduced species from Europe and Asia. Seven-spotted lady beetles, *Coccinella septempunctata* L., and multicolored Asian lady beetles, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), have been introduced to North America over many decades, and are important predators of the soybean aphid, which was first introduced in 2000 (Costamagna and Landis 2007; Mignault et al. 2006; Rutledge 2004; Rutledge et al. 2004; Xue et al. 2009). In addition, the chalcidoid wasp, *Aphelinus certus* Yasnosh (Hymenoptera: Aphelinidae) (Heraty et al. 2007; Yasnosh 1963), has become the most common parasitoid of soybean aphid in Ontario, Canada since first being recorded in 2007 (Frewin et al. 2010). Natural enemies are important regulators of soybean aphid populations

(Costamagna et al. 2007, 2008; Desneux et al. 2006; Donaldson et al. 2007) and have the potential to maintain aphid populations below economic action thresholds (Costamagna et al. 2008, Fox et al. 2004, Hallett et al., unpublished data). Accurate assessments of the impact of natural enemies on soybean aphids is important in developing decision-making practices for soybean aphid management based on natural enemy numbers (Hallett et al., unpublished data), as is an understanding of potential intraguild interactions that may affect the level of biological control services they provide. Theory suggests that strong intraguild predation cannot (or can only rarely) occur in natural systems or it will result in extirpation of the intermediate predator (also referred to as the intraguild prey) (Janssen et al. 2006). However, it is possible that strong intraguild predation could be observed when the intraguild prey is prone to re-introduction after local extinction, either by re-colonization, movement of commodities, or intentional release.

By feeding on parasitoids, generalist predators may disrupt the ability of specialist parasitoids to control pest populations (Brodeur and Rosenheim 2000; Ferguson and Stiling 1996; Snyder and Ives 2001). Several studies have demonstrated the occurrence of non-additive effects by multiple natural enemies on aphid populations (Ferguson and Stiling 1996; Wheeler et al. 1968), and coccinellids are known to exhibit varying degrees of intraguild predation intensity. When given a choice between mummified and non-parasitized aphids, larval and adult coccinellids have either preferred non-parasitized aphids (Meyhofer and Klug 2002; Snyder and Ives 2003) or exhibited no preference (Bilu and Coll 2009; Snyder et al. 2004). In two studies that examined intraguild responses by coccinellids to newly parasitized aphids (i.e. aphids not yet showing signs of mummification), the lady beetles either preferred newly parasitized aphids over non-parasitized aphids (Meyhofer and Klug 2002) or exhibited no preference (Bilu and Coll 2009). There were no consistent patterns observed between larval and adult stages of coccinellids. Lack of preference in *Coccinella undecimpunctata* resulted in a lower parasitism rate in the presence of predators due to intraguild predation and interactions (Bilu and Coll 2007). Although preference for pea aphids over mummies parasitized by *Aphidius ervi* Haliday resulted in an increased ratio of mummies to aphids in a laboratory study, in field experiments *H. axyridis*

did not change the ratio of parasitoids to pea aphids and the impact of the two natural enemies was additive (Snyder and Ives 2003). Similarly, generalist predators (mainly Coccinellidae) did not disrupt soybean aphid parasitism by *Lysiphlebus testaceipes* Cresson in the field (Costamagna et al. 2007, 2008).

The purpose of this study was to investigate predation preferences of two generalist coccinellid predators, *C. septempunctata* and *H. axyridis*, for soybean aphids at two stages of parasitism by *A. certus*, in order to assess the compatibility of these natural enemies in providing biological control services. Though intraguild predation has been studied for both of these coccinellid species in other systems (e.g. Meyhofer and Klug 2002; Snyder and Ives 2003), the interactions of these species with *A. certus* parasitizing *A. glycines* has not been quantified. Both *A. certus* and lady beetles have been observed on the same soybean plants in our field studies of this system, indicating the potential for intraguild predation to occur. Specifically we determined feeding preferences of adult and larval lady beetles between non-parasitized and mummified aphids, and between non-parasitized and newly parasitized aphids. To our knowledge this is the first study to examine intraguild predation amongst natural enemies of the soybean aphid, which is now the most serious economic pest of soybeans in North America. This study indicates that, although coincidental intraguild predation does occur, these natural enemies are compatible biological control agents for soybean aphid population control.

## Materials and methods

### Insect cultures

Soybean aphids were collected from a soybean field near Guelph, Ontario, Canada. Adult *C. septempunctata* and *H. axyridis* lady beetles and *A. certus* mummies were obtained from ten soybean fields in Kent and Lambton counties, Ontario. Soybean aphids were reared on soybean cv. Colby in a growth room held at  $24 \pm 2^\circ\text{C}$  and 16:8 L:D. Cereal aphids (a mixture of *Rhopalosiphum padi* (L.) and *Rhopalosiphum maidis* (L.)) (Aphid banker system, Plant Products, Brampton, Ontario, Canada) were reared on barley and held within a large mesh enclosure in a greenhouse at  $23 \pm 3^\circ\text{C}$  and 16:8 L:D.

Beetles were held in mesh cages in a growth room held at  $24 \pm 2^\circ\text{C}$  and 16:8 L:D, and fed a diet of soybean and cereal aphids. Age cohorts of lady beetles were reared in separate cages, with new aphids introduced twice weekly. All lady beetle eggs found in cages containing adults were removed every 2–3 days and reared separately on a fresh supply of aphids.

Parasitoids that emerged from collected mummies were used to establish laboratory colonies (Frewin et al. 2010). Colonies were maintained in mesh-sided acrylic chambers at  $26 \pm 2^\circ\text{C}$ , 65–75% RH, and 16:8 L:D. Each chamber was provided with a soybean plant infested with soybean aphid once per week. Under these conditions, parasitized aphids turn black and develop into mummies 6–7 days after parasitization, and parasitoids emerge as adults after a further 5–6 days (Frewin et al. 2010). At 3–4 days post oviposition by *A. certus*, aphids are considered newly parasitized and do not exhibit visible signs of parasitism or mummification.

### Choice tests

Choice tests were conducted in order to assess preference for non-parasitized and mummified soybean aphids by lady beetles. One unifoliate leaf of soybean was placed on a layer of wet cotton in a 90 mm Petri dish. Twenty mummies and twenty aphids of similar size were transferred to the abaxial leaf surface and spaced evenly. After 1 h, a single third instar or a 1–3 week old female or male adult lady beetle was introduced into each Petri dish. Third instars were obtained by collecting late second instars (which had ceased to feed and were preparing to moult) from colony plants, and holding them individually in small containers without food. Twenty four hours after moulting to the third instar, larvae were used in experiments. Adults were starved for 24 h before being introduced to the Petri dishes. Petri dishes were sealed with Parafilm to prevent the escape of aphids during the trial, and held in a controlled environment chamber at  $26^\circ\text{C}$ . After 1 h the number of aphids and mummies killed by the predator was recorded. The choice test was replicated 24 times for each of the larvae and male and female adults of both *C. septempunctata* and *H. axyridis*. In cases where the predator did not eat any aphids during the test period, they were excluded from analyses (resulting in 19–23

replicates per treatment). Preference of prey type was evaluated by calculating Manly's index of preference (Manly 1974; Meyling et al. 2004) for each replicate:

$$\beta_1 = \frac{\log(e_1/A_1)}{\log(e_2/A_2) + \log(e_1/A_1)}$$

where  $\beta_1$  is the preference for type 1,  $e_i$  is the number of prey remaining after experimentation,  $A_i$  is the number of prey offered. An index value close to 0.5 indicates that the predator shows no preference for a given prey type, a value close to 1 indicates preference for prey type 1, and a value close to 0 indicates preference for prey type 2 (Meyling et al. 2004). Manly's index applies to experimental situations where killed prey are not replaced (Manly 1974; Meyling et al. 2004; Sherrat 1993). One-sample  $t$  tests were used to compare the experimentally observed Manly's index for non-parasitized aphids and a value of 0.5 to test the null hypothesis that the predator selected prey at random.

### Cage experiments

Cage experiments were conducted to evaluate the intraguild predation by lady beetles on newly parasitized aphids not yet showing visible signs of parasitism (3–4 days after exposure to adult parasitoids). In order to simulate the population structure of aphids on plants in the field, soybean plants with three nodes and two unrolled trifoliate leaves (i.e. V2 stage; Pedersen 2009), one plant per pot, were infested with 100 mixed-stage aphids on day 0. In order to achieve a uniform parasitism rate for control and treated plants, eight infested plants were put into a single  $30 \times 38 \times 30$  cm cage. After 48 h (i.e. day 2) 15 *A. certus* adult females were introduced into the cage. After 48 h, each plant was removed and isolated in a separate  $9 \times 30$  cm cylindrical plastic cage. Two plants were used for each of the control, third instar, adult female, or adult male lady beetle treatments. On day 6 (4 day post oviposition by *A. certus*), a single third instar, adult female, or adult male lady beetle was introduced into each of two cages and left for 24 h. The number of aphids remaining and the number of mummies that developed from parasitized aphids were enumerated on days 7 and 11, respectively. This experiment was replicated six times. In these experiments, if predators showed preference for

non-parasitized aphids over newly parasitized aphids, the parasitism rate would be higher in predator-treated than control cages, while if predators preferred newly parasitized aphids, the parasitism rate would be lower. If predators did not discriminate between newly parasitized and non-parasitized aphids, the parasitism rate in control and predator treatments would be the same. Analysis of variance (ANOVA) was used to determine the difference between the control and predator treatments for parasitism rates and numbers of aphids at day 7. A normality test indicated that the data did not deviate significantly from the normal distribution, so untransformed data were used in analyses. Fisher's least significant difference (LSD) was used for post-hoc multiple comparisons of treatments to the control when a significant difference was found. All analyses were performed using SPSS for Windows, version 15.0 (SPSS Inc., Chicago, IL, USA).

### Results

In Petri-dish choice tests, third instar larvae, female and male adults of both *C. septempunctata* and *H. axyridis* were found to prefer non-parasitized aphids over mummified aphids parasitized by *A. certus* (Table 1). Lady beetles consumed 150–187% more non-parasitized aphids than mummified aphids.

In cage experiments, neither *C. septempunctata* nor *H. axyridis* larvae nor adults exhibited a preference between newly parasitized aphids and non-parasitized aphids, as parasitism rates did not differ between treatments (*C. septempunctata*:  $F = 0.271$ ,  $df = 3, 20$ ,  $P = 0.846$ ; *H. axyridis*:  $F = 0.411$ ,  $df = 3, 20$ ,  $P = 0.747$ ) (Table 2). For both *C. septempunctata* and *H. axyridis*, the numbers of aphids in treatments with larvae, female or male adults at day 7 were significantly lower than that in control (*C. septempunctata*:  $F = 12.249$ ,  $df = 3, 20$ ,  $P < 0.001$  for all post-hoc paired comparisons of larvae, female and male adult to control; *H. axyridis*:  $F = 10.255$ ,  $df = 3, 20$ ,  $P = 0.001$ ,  $< 0.001$  and  $0.009$  for post-hoc paired comparisons of larvae, female and male adult, respectively, to control). Female adults of *H. axyridis* killed significantly more aphids than male adults (LSD,  $P = 0.022$ , Table 2). Similar results have been reported in previous research (Xue et al. 2009).

**Table 1** Numbers of soybean aphids, *A. glycines*, consumed and Manly's index of preference for *C. septempunctata* and *H. axyridis* lady beetles given a choice of non-parasitized soybean aphids and mummified aphids parasitized by *A. certus*,

in Petri dish assays (One-sample *t* tests by comparing Manly's index for non-parasitized aphids and 0.5 under the null hypothesis that the predator selected prey at random)

Predator	Stage	No. replicates	No. of non-parasitized aphids consumed (mean $\pm$ SE)	No. of mummified aphids consumed (mean $\pm$ SE)	Manly's index of preference			
					Non-parasitized aphids (mean $\pm$ SE)	<i>t</i>	<i>df</i>	<i>P</i>
<i>C. septempunctata</i>	3rd instar	23	11.48 $\pm$ 1.02	7.48 $\pm$ 1.15	0.67 $\pm$ 0.03	5.177	22	<0.001
	♀	23	10.44 $\pm$ 1.20	7.52 $\pm$ 1.42	0.66 $\pm$ 0.04	4.294	20	<0.001
	♂	19	9.26 $\pm$ 1.15	7.63 $\pm$ 1.43	0.60 $\pm$ 0.04	2.798	17	0.012
<i>H. axyridis</i>	3rd instar	22	9.09 $\pm$ 0.70	5.64 $\pm$ 0.73	0.66 $\pm$ 0.03	5.653	21	<0.001
	♀	22	11.14 $\pm$ 0.95	6.91 $\pm$ 1.18	0.68 $\pm$ 0.04	4.928	21	<0.001
	♂	22	9.64 $\pm$ 0.94	6.55 $\pm$ 1.09	0.64 $\pm$ 0.04	3.662	21	0.010

**Table 2** Populations and rates of parasitism of *A. glycines* by *A. certus* on soybean plants in the presence or absence (control) of *H. axyridis* or *C. septempunctata* lady beetles

Predator species	Stage	Initial no. of aphids	No. of aphids at day 7 (mean $\pm$ SE)*	% parasitism (mean $\pm$ SE)*
<i>C. septempunctata</i>	Control	100	241 $\pm$ 7.8 <sup>a</sup>	13.2 $\pm$ 2.4 <sup>a</sup>
	3rd instar	100	171 $\pm$ 7.8 <sup>b</sup>	14.1 $\pm$ 2.5 <sup>a</sup>
	♀	100	183 $\pm$ 8.0 <sup>b</sup>	15.1 $\pm$ 2.4 <sup>a</sup>
	♂	100	187 $\pm$ 11.2 <sup>b</sup>	12.0 $\pm$ 2.7 <sup>a</sup>
<i>H. axyridis</i>	Control	100	245 $\pm$ 15.0 <sup>a</sup>	11.8 $\pm$ 3.1 <sup>a</sup>
	3rd instar	100	178 $\pm$ 14.7 <sup>bc</sup>	14.6 $\pm$ 1.8 <sup>a</sup>
	♀	100	152 $\pm$ 7.5 <sup>c</sup>	16.0 $\pm$ 2.1 <sup>a</sup>
	♂	100	195 $\pm$ 10.2 <sup>b</sup>	15.3 $\pm$ 3.9 <sup>a</sup>

\* Numbers of aphids at day 7 or percentage parasitism with different letters differ significantly for the comparisons between the four treatments of the same predator (post-hoc LSD multiple comparisons, *P* < 0.05)

## Discussion

In this study both *C. septempunctata* and *H. axyridis* preferred non-parasitized *A. glycines* to mummified aphids and the ratio of consumption was  $\sim 1.7:1$ . Therefore, it is unlikely that intraguild predation will disrupt biological control of the soybean aphid. Similar results have been found in other parasitoid-coccinellid systems (Meyhofer and Klug 2002; Snyder and Ives 2003; Snyder et al. 2004). Our study may have underestimated the bias in consumption of non-parasitized prey by coccinellids that would be observed under field conditions, by restricting avoidance behaviours, and effects of habitat structure (Janssen et al. 2007), that typically would be present at larger spatial and temporal scales. Parasitoids have

evolved antipredator behaviours to minimize risk of predation by intraguild predators and minimize their co-occurrence: a number of studies have been conducted on chemical cues used by parasitoid species such as *Aphidius ervi*, *Aphidius eadyi*, and *Praon volucre* to avoid coccinellid predators (Nakashima and Senoo 2003; Nakashima et al. 2004, 2006). It may also be advantageous for predators to avoid parasitized prey: Takizawa et al. (2000) showed that coccinellids feeding on mummies had reduced larval development rates and survival compared to coccinellids feeding on non-parasitized aphids. However, the specific mechanisms governing selection of prey (parasitized or non-parasitized) by coccinellids is not known.

In our cage experiments, coccinellids did not preferentially prey upon 3–4 day old parasitized



aphids or non-parasitized aphids, and subsequently did not change the ratio of mummies to aphids. Meyhofer and Klug (2002) found that predation by coccinellids may enhance the ratio of mummies to aphids when parasitized aphids were exposed to predators very soon after parasitization: they observed that *C. septempunctata* larvae killed more non-parasitized black bean aphids, *A. fabae* (Scop.), than aphid mummies parasitized by *Lysiphlebus fabarum* (Marshall), and killed more 2-day old parasitized aphids than non-parasitized aphids. However, their study showed a similar result to our cage experiments when parasitized aphids were exposed to predation at a later time: larvae of *C. septempunctata* showed no preference between 4-day old parasitized aphids and non-parasitized aphids (Meyhofer and Klug 2002). The lack of altered parasitism ratios seen in our cage study was also observed for *H. axyridis* in larger spatial experiments on greenhouse roses (Snyder et al. 2004) and for *Hippodamia convergens* in cotton fields (Colfer and Rosenheim 2001). Snyder and Ives (2003) developed a stage-structured model of aphid, parasitoid, and predator interactions which suggested that the effects of predators and parasitoids will be additive as long as predators do not selectively prey upon parasitoids. Theory suggests that intraguild predation will result in higher populations of the shared herbivore prey compared to systems involving only the prey and one predator when the intraguild prey is the superior natural enemy (Janssen et al. 2006; Rosenheim and Harmon 2006; Vance-Chalcraft et al. 2007). However, in our study, aphid populations were higher in the presence of the intraguild prey alone than with both the intraguild predator and the intraguild prey (Table 2). In this regard, our study concurs with the majority of examples where intraguild predation did not result in reduced control (Janssen et al. 2006, 2007), and demonstrates that low levels of coincidental intraguild predation do not reduce biological control, at least in the short-term (Rosenheim and Harmon 2006). Costamagna et al. (2007, 2008) also reported that generalist predators (mainly Coccinellidae) did not disturb parasitism of soybean aphids by *Lysiphlebus testaceipes* (Cresson) in fields. When predators show a preference for non-parasitized aphids, we may expect that the predator does not disrupt aphid biological control by the parasitoid regardless of intraguild predation.

Although aphid populations increased in all treatments, this is not unexpected given that aphids in cage

experiments were exposed to predators and parasitoids for only 24 h and 48 h, respectively. The parasitism rates and apparent predation rates over these periods of time are consistent with the functional responses of these species at the aphid densities employed in this study (Frewin et al. 2010; Xue et al. 2009).

Our results suggest that *C. septempunctata* and *H. axyridis* prefer to feed on aphids that do not exhibit strong indications of parasitism by *A. certus*. Additional field study is required to elucidate the occurrence and intensity of intraguild predation in this system, however, effects of intraguild predation are expected to be weaker in complex agroecosystems than in simple laboratory contexts (Janssen et al. 2006, 2007). If antipredator behaviours of parasitoids and actual parasitism in soybean fields are accounted for, the influence of intraguild predation by *C. septempunctata* and *H. axyridis* on *A. certus* should be limited. Thus, this parasitoid and these lady beetles species are likely to be compatible biological control agents in soybean fields, with additive effects on soybean aphid populations. Both the introduced parasitoid, *A. certus*, and the introduced lady beetle species, *C. septempunctata* and *H. axyridis*, are therefore expected to persist and co-occur in soybean agroecosystems in North America. The lack of strong intraguild predation between these key species of natural enemies of the soybean aphid should allow natural enemies to limit soybean aphid population growth effectively and will simplify the development of decision-making practices for soybean aphid management based on natural enemy numbers.

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