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Complementary biocontrol of aphids by the ladybird beetle *Harmonia axyridis* and the parasitoid *Aphelinus asychis* on greenhouse roses

William E. Snyder,* Stacey N. Ballard, Suann Yang,[1] Garrett M. Clevenger,
Terry D. Miller, Jeong J. Ahn, Timothy D. Hatten,[2] and Alan A. Berryman

Department of Entomology, 166 FSHN Building, Washington State University, Pullman, WA 99164-6382, USA

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Abstract

We investigated whether two biocontrol agents, the parasitoid wasp *Aphelinus asychis* Walker and the predatory ladybird beetle *Harmonia axyridis* Pallas, would act in concert to reduce densities of an aphid (*Macrosiphum euphorbiae* Thomas) that attacks greenhouse-grown roses (*Rosa hybrida* L.). We conducted three types of experiments: feeding trials in microcosms that examine predator preference for mummies versus aphids; a longer-term pairing of the two natural enemies and aphids on whole plants in large cages; and a trial release of ladybird beetles into a rose greenhouse infested with the aphid and parasitoid. In the microcosm feeding trials both larvae and adults of *H. axyridis* fed on aphids, but also on parasitoid mummies, raising the possibility that intraguild predation of parasitoids by *H. axyridis* could disrupt aphid control. In cages, ladybird beetles dampened peak aphid densities during an outbreak without altering densities of parasitoid pupae or the ratio of parasitoids to aphids. In our whole-greenhouse release, we saw no evidence that *H. axyridis* disrupted aphid control by resident *A. asychis*. Together, these results suggest that *H. axyridis* can complement aphid biocontrol by the parasitoid *A. asychis*, rather than disrupting control through intraguild predation.

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Keywords: Intraguild predation; Ladybird beetle; Predator; Parasitoid; Aphid; Biocontrol; Greenhouse; *Harmonia axyridis*; *Aphelinus asychis*; *Macrosiphum euphorbiae*

1. Introduction

Specialist natural enemies have often been used successfully to control greenhouse pests. For example, the parasitoid *Encarsia formosa* Gahan has provided biological control of whiteflies on many greenhouse crops (van Lenteren et al., 1997; van Lenteren and Martin, 1999; van Lenteren, 2000). Similarly, the specialist predatory mite *Phytoseiulus persimilis* Athias-Henriot, and several other species of predatory mites, have been successfully used for the control of two-spotted spider mite, *Tetranychus urticae* Koch (Griffiths, 1999). Both *Encarsia* and *Phytoseiulus* are a good fit to the paradigm that specialists provide the most effective biological control (Berryman, 1992; Hassell, 1980; Hassell and May, 1986; Murdoch, 1994; Turchin et al., 1999), because these natural enemies have a high degree of prey specificity, a developmental time less than or equal to their hosts, and are highly fecund. However, specialists by themselves have often proven to be ineffective at controlling aphids in greenhouses (Rabasse and van Steenis, 1999). It appears that aphids are particularly difficult to control biologically because they have a very high reproductive rate in the benign greenhouse environment (Gullino et al., 1999).

Much less is known about the role of generalist predators in greenhouses (Albajes and Alomar, 1999). Generalists have relatively long generation times and do not feed only on a target pest (Chang and Kareiva, 1999; Riechert and Lockley, 1984), and also engage in

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* Corresponding author. Fax: 1-509-335-1009.
E-mail address: wesnyder@wsu.edu (W.E. Snyder).

[1] Present address: School of Biological Sciences, Washington State University, Pullman, WA 99164-4236, USA.

[2] Present address: Division of Entomology, Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, ID 83844-2339, USA.

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intraguild predation (Polis and Holt, 1992; Rosenheim et al., 1995). By preying on other natural enemies, generalists can worsen pest problems (Rosenheim et al., 1993; Snyder and Wise, 2001). When generalists and specialists co-occur, intraguild predation is likely to be unidirectional, with generalists feeding on specialists, but the reverse rarely occurs (Brodeur and Rosenheim, 2000; Lucas et al., 1998). This raises the possibility of relatively ineffective generalists disrupting efficient pest control by specialists (e.g., Snyder and Ives, 2001).

Orius spp. is one taxon of generalist that has been fairly well studied as a biocontrol agent in the greenhouse (Janssen et al., 1998). Cloutier and Johnson (1993) examined predation of western flower thrips, *Frankliniella occidentalis* Pergande, by *Orius tristicolor* White, and nicely demonstrated some of the difficulties associated with using generalists as biocontrol agents. The authors found that *Orius* would feed on thrips, but also fed heavily on the predacious mite *P. persimilis*, an important biocontrol agent of spider mites. Intraguild predation was reduced, but not eliminated, when the experimental microcosms also included herbivorous mites as alternative prey (Cloutier and Johnson, 1993). While somewhat effective in reducing intraguild predation, addition of herbivorous mites also lowered the rate of *Orius* predation on thrips. This study demonstrates how the lack of prey specificity can detract from the biocontrol effectiveness of generalists. Ladybird beetles are often released into greenhouses to improve aphid biocontrol (Dreistadt and Flint, 1996). However, ladybirds are known to be intraguild predators (Cottrell and Yeargan, 1999; Evans, 1991; Kajita et al., 2000; Obrycki et al., 1998; Snyder and Ives, 2003), which can limit their effectiveness as biocontrol agents if they feed heavily on beneficial specialists (Colfer and Rosenheim, 2001; Ferguson and Stiling, 1996; Snyder and Ives, 2001).

Plants grown in greenhouses for cut flower production are particularly challenging targets for biological control because very low pest densities are permitted. Cut flowers remain in production for a relatively long time compared to other crops, so that there is time for complex communities of pests to develop. Despite these drawbacks, because of the long cropping cycles, there is also ample time for natural enemies to establish self-replicating populations (Hatten, 2002). Also, long re-entry times following pesticide application make it very difficult for growers to complete the time-intensive management that cut flower production requires (van Lenteren, 2000), and so by avoiding human exposure to pesticides, biological control can be very attractive to growers. Still, biological control is rarely used in greenhouse production in North America, apparently at least in part because of the complexity of interactions among multiple pests and natural enemies (Wawrzynski et al., 2001).

We examined the combination of a predator, *Harmonia axyridis*, and a parasitoid, *Aphelinus asychis*, for the biocontrol of the potato aphid, *Macrosiphum euphorbiae*, on greenhouse-grown roses. We hoped that the two natural enemies would complement each other and dampen aphid outbreaks (e.g., Snyder and Ives, 2003). However, *H. axyridis* is a well-known intraguild predator (Cottrell and Yeargan, 1999; Hironori and Katsuhiro, 1997; Kajita et al., 2000; Michaud, 2002; Yasuda and Ohnuma, 1999), and has been reported to feed on parasitoid mummies (Snyder and Ives, 2003). As such, it was possible that the beetles would disrupt biocontrol through intraguild predation on the parasitoid (Brodeur and Rosenheim, 2000).

2. Materials and Methods

We paired *H. axyridis*, *A. asychis*, and their shared aphid prey in arenas of three types: (1) small laboratory microcosms housing single rose stems; (2) larger cages that contained several whole rose plants; and (3) a greenhouse with a hydroponic bent-cane rose production system.

Our *H. axyridis* colonies were started from individuals originally collected near Prosser, WA, USA, in the summer of 2000. Beetles were maintained in 100-mm × 15 mm plastic petri dishes on a mixed diet of pea aphid, *Acyrthosiphon pisum* Harris, Russian wheat aphid, *Diuraphis noxia* Mordvilko, and English grain aphid, *Sitobion avenae* F., at 22–25 °C and a day length of 16:8 (L:D) h. Water was provided using a moistened dental wick. Larvae were separated at hatching and reared individually, on the same diet and under the same environmental conditions as adults.

In January 2000, we established 45 pots, each containing three rose bushes (*Rosa hybrida*, variety Kardinal) in a 46-m^2 greenhouse on the campus of Washington State University in Pullman, WA, USA. Temperatures in the greenhouse averaged 22 °C, with a 16:8 (L:D) h cycle. Our cultural practices generally followed those of commercial growers, with the major exception that we did not apply any pesticides; a full description of our cultural practices is presented in Hatten (2002). Four common greenhouse pests colonized the roses almost immediately: potato aphid, *M. euphorbiae*, two-spotted spider mite, *Tetranychus urticae*, greenhouse whitefly, *Trialeurodes vaporariorum* Westwood, and western flower thrips, *Frankliniella occidentalis* (Hatten, 2002). The pests likely arrived either on rootstock or moved in from surrounding greenhouses. As each pest arrived, we released a specialist natural enemy into the greenhouse that attacked that pest: the parasitoid wasp *A. asychis* for potato aphid, the predatory mite *Galendromous occidentalis* Nesbitt for two-spotted spider mite, the parasitoid wasp *Encarsia formosa* for greenhouse whitefly, and the predatory mite *Amblyseius cucumeris* Oudemans for western flower thrips (Hatten, 2002). It is important to note that after initial release, no additional releases of any arthropod were made. Thus, both the pests and natural enemies maintained self-sustaining populations (Hatten, 2002). Each week since 3 January 2000, we have counted densities of pests and natural enemies on 160 randomly selected rose leaflets.

Our *A. asychis* were from a self-sustaining feral population (our greenhouse complex is never sprayed with insecticides) that colonized the roses following *M. euphorbiae* infestation. All aphids and *A. asychis* mummies used in the experiments were collected from the roses in our greenhouse. The parasitoid has become established in the greenhouse, but the aphid population has continued to cycle through outbreak and crash phases (J. Ahn, A. Berryman, and W. Snyder, unpublished data). The work presented here examines whether adding predators to the system can help to stabilize aphid–parasitoid population dynamics.

2.1. Microcosm aphid–mummy choice experiments

We conducted feeding trials in microcosms to examine predator preference for mummies versus aphids. We looked at two stages: (1) fourth instar *H. axyridis* larvae, and (2) *H. axyridis* adults. We placed twenty 20-cm long rose stems individually into 9-dram vials containing water and sealed the lids with parafilm. We attached 10 *A. asychis* mummies to each stem using a small drop of Elmer's glue (Borden, Columbus Ohio, USA). The glue droplet was entirely covered by the mummy, and did not alter predator behavior (Snyder and Ives, 2001, 2003). Each stem was then placed into a separate 18 cm diameter × 30 cm tall mylar tube, with the vial buried to the mouth in potting soil. We added 10 aphids, *M. euphorbiae*, to each microcosm, and covered the top of each mylar tube with fine mesh screening. After 24 h we counted aphids and mummies, and then added predators to half of the tubes. We added single fourth instar *H. axyridis* larvae and adults. After 24 h of exposure to the predators, we counted mummies and aphids.

2.2. Cage experiment

We conducted an experiment to examine aphid–parasitoid population dynamics in the presence and absence of *H. axyridis*. Our experimental units were 1 m^3 cages covered with 52 × 52 Lumite screening (Sante Traps, Lexington, KY, USA). Cages were covered on all sides, including the bottom, by screening; a zippered flap on the front face of each cage allowed access. These cages were large enough to house two pots containing 3 rose (*R. hybrida*, variety Kardinal) bushes each ($N = 6$ bushes per cage). Inside the cages, the roses were infested with 50 aphids per cage. We did not add *A. asychis* adults; however, some of the aphids had been parasitized while in the greenhouse. We left aphids on the plants for 7 days, and then visually counted all aphids and mummies on each plant; this sample was day 0 of the experiment.

We established two treatments: (1) Pred + Para—ladybird predators added to cages containing plants, aphids, and parasitoids; and (2) Para—no predators added to the cages. There were six replicates of each treatment, for a total of 12 cages. Twenty-four second instar *H. axyridis* larvae were added to each of the Pred + Para cages on day 0, after aphids and mummies were counted. We then censused aphid and parasitoid densities on days 5, 12, 17, 24, 33, and 45, using the same methodology as on day 0. Thus, we were able to follow the impact of the ladybird beetle on both aphid and parasitoid through time. All censuses were made with a sheet of dark cloth draped over the cage door to darken the background, and with the cage doors pulled close to the census taker's body, to minimize parasitoid escape. We never observed any parasitoids flying out of the cages during census, although we cannot be certain that this never occurred.

2.3. Greenhouse release of H. axyridis

Before beginning the work reported here, we had collected ca. 12 months of data on the population dynamics of the herbivores and their specialists (Hatten, 2002; T. Hatten, J. Ahn, A. Berryman, and W. Snyder, unpublished data), a period that encompasses >5 generations of each arthropod. We made two *H. axyridis* releases (24 January and 29 March 2001). Both releases were of mixed groups of first and second instar larvae, and were at a rate of 6 larvae/pot. Two, 4, 6, 7, 8, 10, 11, and 13 weeks after the first release we searched four randomly selected pots per row (total $N = 20$) for 1 min each, recording all *H. axrydis* larvae, pupae, and adults that we observed.

2.4. Statistics

In the small microcosm studies, we compared the change in the relative densities of mummies and aphids using paired *t* tests. In the cage experiment we followed aphid–parasitoid population dynamics through time, and so analyzed the data using repeated measures MANOVA with initial densities (at day 0) included as a covariate (von Ende, 1993). Our greenhouse release was not replicated, and so statistical analysis is not possible.

3. Results

3.1. Mummy–aphid choice tests

Harmonia axyridis larvae and adults had similar feeding rates on mummies, but larvae ate more aphids

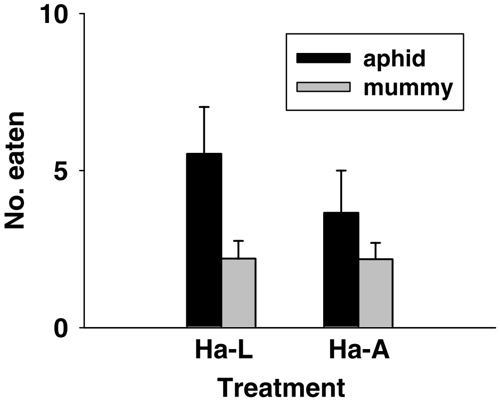

Fig. 1. Per capita feeding rates of *H. axyridis* larvae ("Ha-L") and adults ("Ha-A"). Feeding rates are corrected for mortality in the controls using the formula: (final mean aphid and mummy densities in predator arenas) − (final densities in control arenas). Error bars are ± 1 SE.

(Fig. 1). *Harmonia* larvae significantly increased the ratio of mummies to aphids ($F_{1,17} = 5.57$, $P = 0.035$; Fig. 2A), but adults did not ($F_{1,13} = 1.79$, $P = 0.198$; Fig. 2B).

3.2. Cage experiment

We examined aphid–parasitoid population dynamics, in large cages in a greenhouse, in the presence and absence of *H. axyridis*. For aphids, treatment differences were consistent through time (treatment × time interaction; Wilks' $\lambda = 0.31$, $F_{5,5} = 2.24$, $P = 0.20$; Fig. 3A). Initial aphid densities significantly influenced later aphid densities ($F_{1,9} = 11.65$, $P = 0.008$). Peak aphid densities were 75% lower in cages with both ladybird beetles and parasitoids, compared to cages with just parasitoids ($F_{1,9} = 2.17$, $P = 0.014$; Fig. 3A). For mummies, treatments were consistent through time (Wilks' $\lambda = 0.28$, $F_{5,5} = 2.63$, $P = 0.16$; Fig. 3B); initial mummy densities did not influence later densities ($F_{1,9} = 1.48$, $P = 0.26$),

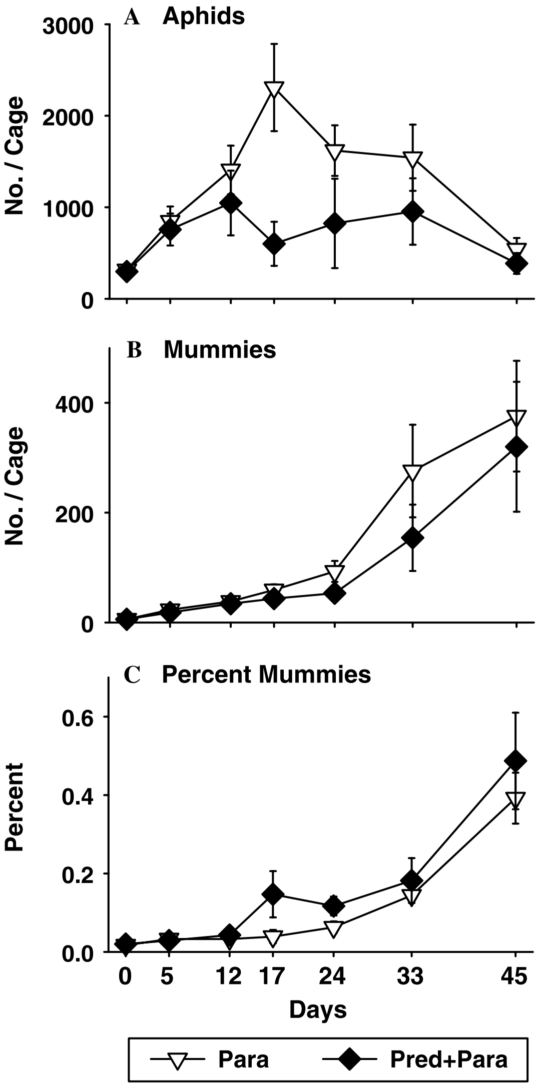

Fig. 3. (A) Aphid and (B) mummy population dynamics, and (C) parasitism (mummy/(mummy + aphid density)) through time from the cage experiment. Treatments: parasitoids present, no predators added (Para); both predators and parasitoids present (Pred + Para). Error bars are ± 1 SE.

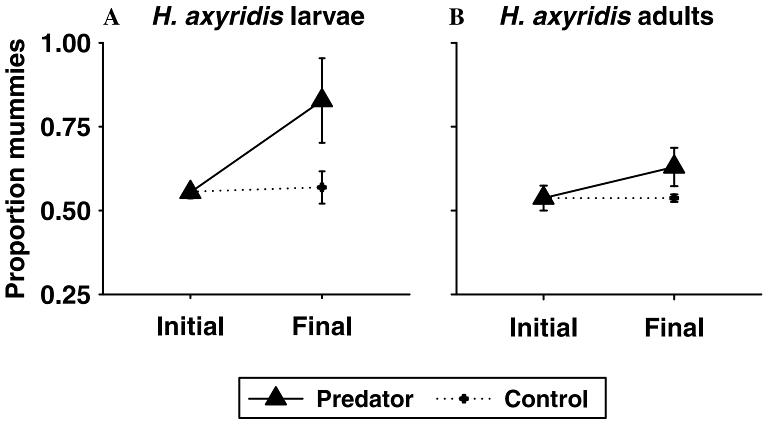

Fig. 2. Densities of aphids and mummies before ("Initial") and after ("Final") a 1-day exposure to (A) a fourth instar *H. axyridis* larva, and (B) a *H. axyridis* adult. Each trial included an equal number of controls, where no predator was present. Error bars are ± 1 SE.

and *H. axyridis* did not alter the number of parasitoid pupae ($F_{1,9} = 2.51$, $P = 0.15$; Fig. 3B). Ladybird beetles also did not alter the ratio of mummies to aphids ($F_{1,9} = 1.18$, $P = 0.31$; Fig. 3C).

3.3. Greenhouse releases of *H. axyridis*

At the time of our *H. axyridis* release, we had been measuring population dynamics of the arthropods in this greenhouse for >1 year; dynamics for 15 weeks before and after beetle introduction are shown in Fig. 4. Beetle densities declined rapidly after the first introduction (Fig. 4), and we realized that adult beetles were escaping through a poorly fitting screen over the main exhaust fan; the screen was replaced and a second release was made (arrow after week 40 marks this release; Fig. 4). Following this release, beetle densities increased, reaching >5 per pot on week 45 (Fig. 4). The increase was due, in part, to beetle reproduction. We saw *H. axyridis* eggs and newly hatched larvae at all sample dates once beetles from the first release had completed development ($\geqslant$2 weeks).

Following peak *H. axyridis* densities at week 45, aphid densities declined >90% during the next 5 weeks (Fig. 4A). Mummy densities only slowly declined, so that the ratio of mummies to aphids increased (Fig. 4A). Densities of spider mites slowly decreased, and densities of predatory mites increased, following the first *H. axyridis* release in week 35 (Fig. 4B). The slow decrease in mite densities continued for the remainder of the observation period, while predator mite densities peaked at week 38 and then gradually declined (Fig. 4B).

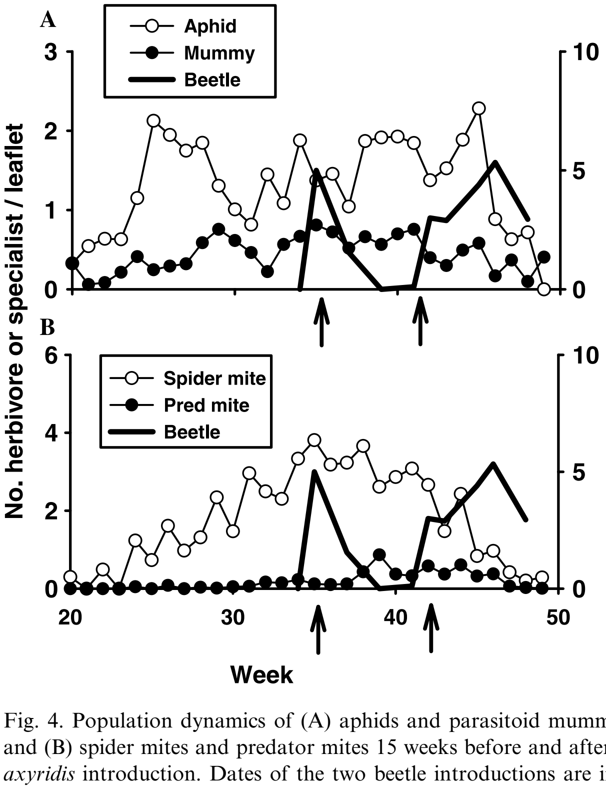

Fig. 4. Population dynamics of (A) aphids and parasitoid mummies, and (B) spider mites and predator mites 15 weeks before and after *H. axyridis* introduction. Dates of the two beetle introductions are indicated by the arrows along the *x*-axes.

4. Discussion

We investigated the combination of a parasitoid wasp, *A. asychis*, and a predatory beetle, *H. axyridis*, for control of a common greenhouse pest, the potato aphid, *M. euphorbiae*. In laboratory feeding trials, *H. axyridis* adults and larvae fed readily on *A. asychis* mummies, although both predator stages also fed heavily on aphids (Fig. 1). Ladybird beetle larvae, for example, when offered both aphids and mummies, ate nearly twice as many of the former, and so significantly increased the ratio of mummies to aphids (Fig. 2). Overall, our laboratory feeding trials revealed that *H. axyridis* would feed on parasitoid mummies, so that intraguild predation of the parasitoid by the predator could weaken overall biocontrol when both were together. Intraguild predation of parasitoids by predators has disrupted, or has been posited to disrupt, biocontrol by parasitoids in a variety of systems (reviewed in Brodeur and Rosenheim, 2000), including greenhouses (Harizanova and Ekbom, 1997). However, the ladybirds either preferred to feed on aphids and so increased the ratio of mummies to aphids, in the case of larvae, or had no preference for mummies or aphids, in the case of adult beetles, which suggests biocontrol might be improved by the ladybird's addition to the community.

In our experiment in large cages containing whole plants, we examined parasitoid–aphid dynamics in cages with and without *H. axyridis*, and found that the combination of predator and parasitoid resulted in the lowest peak aphid densities. Densities of mummies, and the ratio of mummies to aphids, were not significantly altered in the presence of *H. axyridis* over a 45-day period. Thus, results in our cages were consistent with what we found in our microcosms, where intraguild predation may have occurred but because predators fed more heavily on aphids (*H. axyridis* larvae) or had no preference (*H. axyridis* adults), biocontrol was improved with both predator and parasitoid present. However, parasitism rates were initially low in our cages (<10% over the first 10 days). It is possible that, with a higher initial parasitoid density, *H. axyridis* would have been forced (through aphid scarcity) to feed more heavily on mummies, disrupting future aphid control. Still, in our microcosm trials the ratio of mummies to aphids was 1:1 and beetles did not feed more heavily on mummies, suggesting that this scenario is unlikely.

Perhaps too often, observations of intraguild predation in very simple laboratory arenas have been presumed to give evidence that combinations of predators will lead to disruption of biological control on a larger, more realistic scale (e.g., many of the examples in Rosenheim et al., 1995). However, two recent studies suggest that, even when rampant intraguild predation does occur in the field, biocontrol can still be improved by the inclusion of generalists. Lang (2003) examined intraguild predation among a guild of ground dwelling lycosid (wolf) spiders and carabid (ground) beetles in dryland wheat. Ground beetles fed heavily on wolf spiders, but the predator guild still suppressed aphid pests and thus increased crop yields. Similarly, Snyder and Ives (2003) investigated interactions among pea aphids, a specialist parasitoid of the aphids, and a community of generalist predators (which included *H. axyridis*). These authors found that intraguild predation of parasitoids by predators was common; mummy densities were halved in the presence of predators. However, predators did not alter the percentage of aphids parasitized, and aphid densities were lowest when both predators and parasitoid were present. Subsequent modeling work suggested that predators and parasitoids complement one another despite frequent intraguild predation by the former on the latter, as long as predators do not selectively prey upon parasitoids in preference to herbivores (Snyder and Ives, 2003). It appears that predator–parasitoid interactions in our greenhouse community are similar to those in Snyder and Ives' alfalfa system, with *H. axyridis* feeding on aphid mummies, but also feeding heavily on aphids, so that percent parasitism was not altered and biocontrol was improved by the inclusion of *H. axyridis*.

Our greenhouse release was unreplicated (and did not include a control where *H. axyridis* was not released), and so our results must be interpreted with considerable caution. Aphid densities began to decrease after *H. axyridis* densities peaked, with no alteration of mummy densities. Similarly, we did not see any obvious alteration of spider mite–predator mite dynamics once *H. axyridis* was added to the system. Spider mite densities increased and then slowly decreased, followed by a similar increase and then decrease in densities of predator mites. Because there was no control, we cannot attribute aphid or spider mite decline to *H. axyridis*. Still, it is encouraging that we did not notice any obvious disruption of aphid or spider mite biocontrol in the presence of the beetle.

Ladybird beetles have proven difficult to integrate into greenhouse biocontrol (Dreistadt and Flint, 1996), although release of these beetles appears to be one of the more commonly attempted forms of biological control in commercial greenhouses in North America (Wawrzynski et al., 2001). However, the majority of studies have examined releases of adults of the convergent ladybird beetle, *Hippodamia convergens* (reviewed in Dreistadt and Flint, 1996). The adult *H. convergens* available from suppliers generally have been collected from large overwintering aggregations. When the beetles come out of diapause, they immediately enter a dispersal phase and leave the release site (Hagen, 1962, 1974; Packard and Campbell, 1926). However, Dreistadt and Flint (1996) found that even adult *H. convergens* could provide good inundative control of aphids if the beetles were allowed to go through the dispersal phase prior to release. Clearly, more research is needed on the effectiveness of non-dispersing stages of coccinellids. Supporting the effectiveness of less-mobile ladybird beetles as biocontrol agents, Ferran et al. (1996) found that *H. axyridis* larvae remained in outdoor rose beds after release and achieved good control of the rose aphid (*Macrosiphum rosae* L.). We found that *H. axyridis* persisted in our greenhouse for at least 15 weeks, although we noticed that teneral adults seemed to enter a dispersal phase where they would fly against the glass and attempt to emigrate from the greenhouse. However, the adults seemed to eventually pass through this dispersal phase, and if contained within the greenhouse soon settled into feeding, and began to lay eggs.

Biological control in greenhouses has had many successes (van Lenteren, 2000), but aphids remain difficult to control without pesticides (Rabasse and van Steenis, 1999). We found that a predator and parasitoid could successfully be combined to improve aphid control. The common occurrence of intraguild predation in simple laboratory arenas did not mean that biocontrol was disrupted on a larger spatial and temporal scale. We suggest caution in extrapolating from the results of petri dish pairings demonstrating that intraguild predation is possible.

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