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Natural Enemies of Woolly Apple Aphid (Hemiptera: Aphididae) in Washington State

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ABSTRACT Woolly apple aphid, *Eriosoma lanigerum* (Hausmann), has become a pest of increasing importance in Washington apple orchards in the past decade. The increase in aphid outbreaks appears to be associated with changes in pesticide programs and disruption of biological control. We sampled woolly apple aphid colonies in central Washington apple orchards for natural enemies of this pest from 2006 to 2008. The most common predators encountered were Syrphidae (*Syrphus opinator* Osten Sacken, *Eupeodes fumipennis* Thomson, and *Eupeodes americanus* Wiedemann); Chrysopidae (*Chrysopa nigricornis* Burmeister); and Coccinellidae (*Coccinella transversoguttata* Brown and *Hippodamia convergens* Guérin-Méneville). The specialist syrphid *Heringia calcarata* Loew was recorded for the first time occurring in Washington apple orchards. The only parasitoid found in aerial colonies of woolly apple aphid was *Aphelinus mali* Haldeman; root colonies, however, were not parasitized. Identification of important natural enemies provides a better basis for conservation biological control of this pest.

O pulgão lanígero *Eriosoma lanigerum* (Hausmann) tem SE tornado uma praga de grande importancia econômica nos pomares de maçã do estado de Washington nos Estados Unidos. Acredita-SE que o aumento das infestações está relacionado a mudanças no programa de inseticidas utilizados e disrupção do controle biológico. Porém, SE sabe que existe um grande potencial para o estabelicimento do controle biológico desta praga tanto em pomares convencionais como em pomares orgânicos. Durante este trabalho inimigos naturais do pulgão lanígero foram coletados em vários pomares da região central do estado de Washington desde 2006 a 2008. Os principais grupos de predadores encontrados foram sirfídeos (*Syrphus opinator* Osten Sacken, *Eupeodes fumipennis* Thomson and *Eupeodes americanus* Wiedemann), crisopídeos (*Chrysopa nigricornis* Burmeister) e coccinelídeos (*Coccinella transversoguttata* Brown and *Hippodamia convergens* Guérin-Méneville). Pela primeira vez o predator especialista *Heringia calcarata* Loew foi encontrado nos pomares do estado de Washington. O único parasitoide encontrado parasitando o pulgão lanígero foi *Aphelinus mali* Haldeman; porém, este parasitoide não SE mostrou capaz de parasitar colônias do pulgão que estavam abrigadas nas raízes das macieiras. A identificação dos inimigos naturais mais importantes do pulgão lanígero proporciona a formação de uma base mais integrada para o controle biológico por conservação.

KEY WORDS *Eriosoma lanigerum*, natural enemies, biological control, survey, apple

Woolly apple aphid, *Eriosoma lanigerum* (Hausmann), has been a pest of apple orchards in Washington State for over 100 yr, but since ≈2000, there has been an increase in the incidence and severity of outbreaks (S.D.C., personal communication). This increase is likely associated, to some extent, with changes in pesticide programs. Broader spectrum pesticides such as the organophosphates that used to keep this pest in check gradually are being displaced by pesticides with reduced mammalian toxicity, and theoretically, a higher degree of pest specificity. Surprisingly, outbreaks of woolly apple aphid also have been noted in organic orchards, where approved pesticides tend to be more benign to natural enemies (E.H.B., personal communication).

Woolly apple aphid is native to eastern North America and originally was a holocyclic, heteroecious aphid species that used the American elm tree, *Ulmus americana* L., as the winter host and one of several woody plants (*Crataegus* or *Sorbus*) as summer hosts. After the introduction of cultivated apples *Malus domestica* (Borkhausen) by European settlers, this aphid began using apple as its summer host. This pest subsequently was spread to apple-growing areas around the world, and in areas where *U. americana* was absent, it adapted to survive on apple throughout the year. Sexual reproduction occurs on the winter host (Patch 1913),

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but reproduction on apple generally is regarded to be asexual only (Sandanayaka and Bus 2005).

Woolly apple aphid feeding causes hypertrophic gall formation on the roots and aerial parts of the trees (Brown et al. 1991), which can restrict sap flow and rupture plant tissues, thereby providing further feeding sites and allowing the invasion of fungal diseases (Weber and Brown 1988). In addition, the wax and honeydew produced by the colonies are a nuisance to pickers, and aphids found on packed apples are a quarantine concern in countries such as China and Taiwan, which are major importers of Washington apples (Warner 2006).

Nevertheless, woolly apple aphid is likely an induced pest, and susceptible to biological control at a commercially acceptable level. This species is attacked by a large natural enemy complex, including aphidophagous predators such as ladybird beetles, lacewings, syrphids, earwigs, and predatory bugs (Walker 1985, Asante 1997, Mueller et al. 1988, Short and Bergh 2004). In addition, this aphid is also attacked by a specialized hymenopterous endoparasitoid, *Aphelinus mali* Haldeman (Mueller et al. 1992, Brown and Schmitt 1994, Asante 1997). *Aphelinus mali* was introduced into many regions throughout the world (Howard 1929) in one of the early examples of classical biological control, and has shown satisfactory results in many of those regions (McLeod 1954, DeBach 1964, Brown and Schmitt 1994).

The objective of this work was to conduct a survey to identify the key natural enemies of woolly apple aphid occurring in central Washington apple orchards, providing a better foundation for an integrated biological control program of this pest.

Materials and Methods

The natural enemies of woolly apple aphid were surveyed during a 3-yr period (2006–2008) in central Washington State. The orchards sampled during that period had a previous history of woolly apple aphid infestation. Predators were collected between 9:00 a.m. and 4:00 p.m., and physically were associated with the woolly apple aphid colonies. Presence of *Aphelinus mali* was shown by the presence of mummies found in the aphid colonies, and adults parasitoids in the sticky bands (see below).

During 2006, six conventional orchards located in the counties of Okanogan (2), Kittitas (1), Grant (2), and Douglas (1) were sampled for woolly apple aphid natural enemies throughout the apple growing season (April through late October). Up to five woolly apple aphid colonies were collected on a weekly basis in each orchard. The sample unit consisted of a 10-cm section of shoot containing an aphid colony. Colony size varied from a few to hundreds of aphids. Each aphid colony first was inspected in situ for motile predators, which then were collected for species identification. After visual inspection, each sample unit was removed from the tree and placed in a self-sealing plastic bag. All of the colonies collected were brought to the laboratory and kept cool until immersion in 70% ethanol to remove wax filaments, then inspected for predators under a binocular microscope.

In 2007, eight conventional orchards located in the counties of Okanogan (3), Kittitas (1), and Grant (4) were sampled for woolly apple aphid natural enemies at the same time frame described above. At this time, up to 10 aphid colonies per orchard were collected weekly and inspected for predators as described above. In addition to the random sample of colonies mentioned above, we also performed a more specific search targeting syrphids only in five of the orchards, the adults via netting and larvae via manual collection. AQ: 3
The larvae were reared to the adult stage by providing them with shoots infested with woolly apple aphid every 3 d. Adults reared from larvae and field-collected adults were killed and pinned for species identification.

In late March and early April of 2006 and 2007, overwintering aphid colonies were collected from superficial roots as well as from the aerial parts of the trees to assess parasitism by *A. mali.* Up to five aphid colonies per orchard were collected during each visit, with one to two samples per month in two to three different conventional apple orchards located in eastern Washington. The colonies collected were brought to the laboratory and the number of *A. mali* mummies was recorded. In addition, in 2006 and 2007 we also assessed the relative abundance of *A. mali* by counting the number of adult parasitoids caught on the sticky bands used to assess woolly apple aphid crawler movement (Beers et al. 2010). These bands were placed on three trees in each of the three weekly sampled orchards during 2006 and 2007. The bands were collected and replaced weekly. The collected bands were placed individually in a clear plastic bag to facilitate handling, and adult *A. mali* were counted using a binocular microscope. In addition, we also measured the average percentage parasitism of woolly apple aphid by *A. mali.* AQ: 4

In 2008, a more extensive survey of woolly apple aphid natural enemies was conducted. This survey had a broader geographical distribution in Washington, from Bridgeport in the north to the Tri-Cities in the south. In total, 20 orchards were sampled including 13 conventional and seven organic orchards. The orchards were located in the following counties: Okanogan (3), Douglas (2), Grant (5), Yakima (3) Franklin (5), and Chelan (2). Orchards were sampled weekly or biweekly from April through October. Up to fifty woolly apple aphid colonies were collected per visit using the methods described above. The adult predators were killed and pinned, and the larvae were reared to the adult stage by feeding them woolly apple aphids collected at unsprayed apple orchards located in the Tree Fruit Research & Extension Center in Wenatchee, WA. We also looked for eggs of predators (Syrphidae, Coccinellidae, and Neuroptera) on the shoots brought to the laboratory. All adult syrphid specimens were identified by Dr. F. Christian Thompson (USDA–ARS Systematic Entomology Lab, Washington, DC) or Peter Smytheman (Tree Fruit Research and Extension Center, Wenatchee, WA); and the adult Coccinellidae and Neuroptera were identified by Dr. James Johnson (Department of Plant, Soil and Entomological Sciences, University of Idaho). In addition, percentage parasitism by *A. mali* was estimated on a subsample of up to 15 colonies per orchard by counting the number of mummies (intact and exited) and the total number of aphids per colony, and thereafter averaging the percentage parasitism across all colonies. We also calculated the percentage of colonies parasitized (i.e., with one or more mummies). Aphids with no visible external signs of parasitism were not included in these estimates.

Results and Discussion

Predators. Averages of 0.02, 0.06, and 0.05 predators per aphid colony were observed in 2006, 2007 and 2008, respectively. In addition, an average of 0.10 predator eggs (syrphid, coccinellid, and lacewing) was recorded in 2008. Syrphidae, Neuroptera, and Coccinellidae were the most common predator groups encountered in woolly apple aphid colonies; with Syrphidae being the most abundant (62–81%) in all 3 yr with Coccinellidae and Neuroptera ranging from 6 to 24% of totals (Fig. 1). Syrphids were most abundant during the summer months (Fig. 2), which coincides with the mid-season peak of woolly apple aphid activity (Beers et al. 2010).

The species complex of Syrphidae found as larvae in woolly apple aphid colonies consisted of three species of *Syrphus*, two species of *Eupeodes*, and one species of *Heringia* (Table 1). Only the two *Eupeodes* spp., *Syrphus opinator* Osten Sacken and *Heringia calcarata* Loew, previously had been reported to feed on woolly apple aphid in the United States (Carroll and Hoyt 1984, Walker 1985, Short and Bergh 2004). The two most common species found were the generalists *Eupeodes americanus* Wiedemann and *Eupeodes fumipennis* Thomson; however, their occurrence alternated between years (Table 1). The only specialist syrphid species of woolly apple aphid encountered was *H. calcarata* (Short and Bergh 2004). Up to now *H. calcarata* only had been reported in the eastern United States (Short and Bergh 2004, Bergh and Short 2008). To our knowledge, this is the first documented occurrence of *H. calcarata* in Washington, or for that matter, the western United States, although the taxonomy of this group needs further study. Subsequent trapping studies using herbivore-induced plant volatiles indicate that *Heringia* sp. (tentatively identified as *H. calcarata*) may be the most common syrphid in woolly apple aphid-infested orchards (E.H.B., unpublished data).

Heringia calcarata is one of the few natural enemies, besides the nematode *Steinernema carpocapsae* Weiser (Brown et al. 1992), known to attack the root colonies of woolly apple aphid below the soil surface (Short and Bergh 2004), thereby, making it an interesting biological control agent for this pest. Nonetheless, the fact that both generalist and specialist predatory syrphids occur in the orchards may be advantageous in the control of woolly apple aphid. Predators with different diet breadths occurring at different time periods may provide better and continuous prey control. For instance, generalist predators such as *E. americanus* can provide early season woolly apple aphid control, before the aphid density increases and *H. calcarata* comes into the system (Bergh and Short 2008).

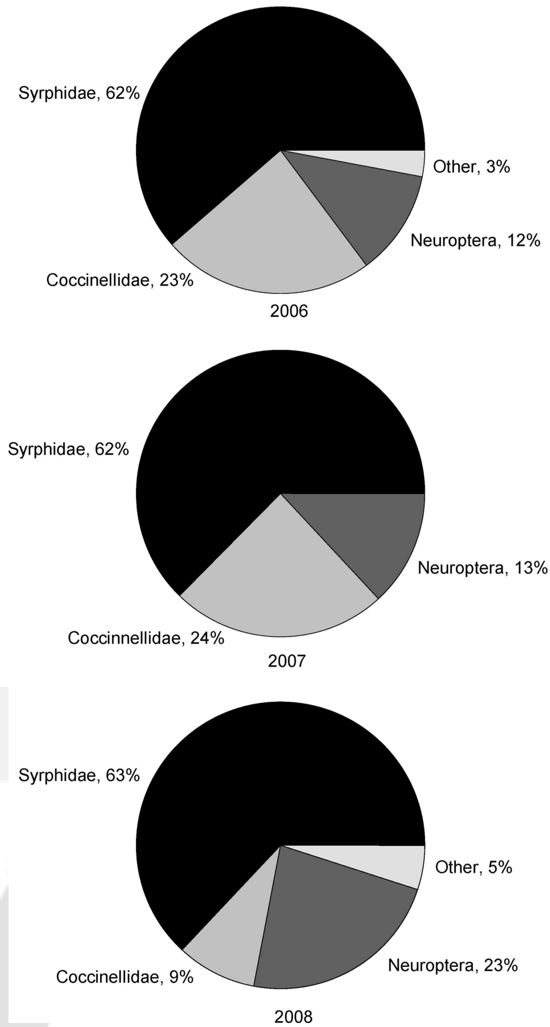

Fig. 1. Taxonomic composition of predator groups found in woolly apple aphid colonies, 2006 (n = 34), 2007 (n = 47), and 2008 (n = 271). Other predators included spiders, nabids, earwigs, and *D. brevis*.

The adult syrphid species captured while hovering by the trees in the 2007 specific targeted search were *Syrphus opinator* Osten Sacken (n = 6), *Eupeodes fumipennis* (Thomson) (n = 3), *Syritta pipiens* (L.) (n = 1), *Eumerus stigatus* (Fallen) (n = 1), and *Melangyna umbellatarum* (F.) (n = 2). Only the first two species (*E. fumipennis* and *S. opinator*) were found in the colony samples as larvae (Table 1), emphasizing the importance of larval rearing; of the remaining three species, only *Melangyna* is aphidophagous.

The Coccinellidae tended to be more numerous in July and August (Fig. 2). The most common Coccinel-

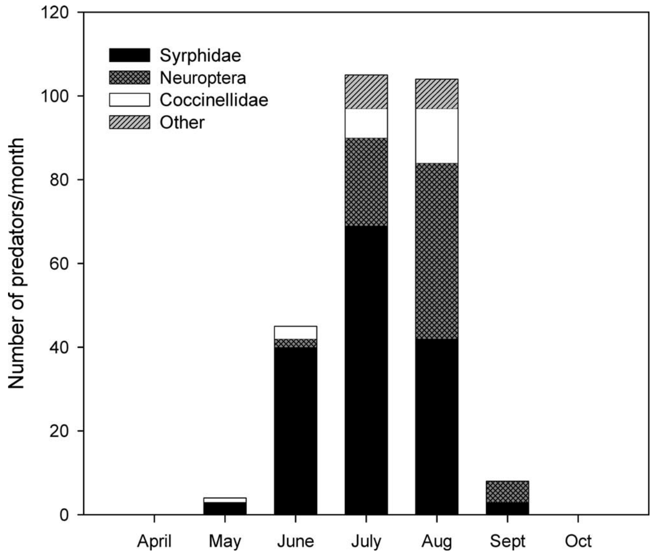

Fig. 2. Woolly apple aphid predator composition and abundance at different times of the year, 2008 (number of predators collected monthly in all orchards).

lidae species found were *Coccinella transversoguttata* Brown and *Hippodamia convergens* Guérin-Méneville, with other species found less frequently (Table 1). All Coccinellidae species found are generalist predators that feed on aphids and other soft-bodied arthropods; however, only *C. transversoguttata*, *H. convergens*, and *A. bipunctata* had been reported before to feed on woolly apple aphid (Walker 1985, Aslan and Karaca 2005). *Harmonia axyridis* (Pallas) and *Coccinella septempunctata* L. are exotic species, and are known to have the potential to displace native species (Burgio et al. 2002, Alyokhin and Gary 2004, Evans 2004, Snyder and Evans 2006). Their introduction into the United States dates back as early as 1916 for *H. axyridis* (Koch and Galvan 2008) and early in the 1970s for *C. septempunctata* (Angalet et al. 1979). Although they may contribute to biological control of woolly apple aphid, a careful assessment of their overall impact on this agroecosystem is necessary.

Neuroptera was the third most abundant predator group in the in the 2006–2007 surveys, but the second most abundant in the 2008 survey (Fig. 1) The wider geographic distribution and higher number of orchards sampled indicates that the latter survey was a more reliable indicator, although seasonal variation may also play a role. Neuroptera were found slightly later in the season than the Syrphidae (July–September) (Fig. 2). The most common Neuroptera species found was *Chrysopa nigricornis* Burmeister, with *Chrysoperla plorabunda* Fitch and *Hemerobius* spp. encountered only occasionally. Because of their commercial availability and resistance to some insecticides, green lacewings are among one of the most commonly released predators for augmentative biological control in orchards and other agroecosystems (Aldrich 1999). *Chrysopa nigricornis* is a large lacewing species that occurs throughout the United States, especially on the Pacific Northwest (Agnew et al. 1981). This species is an important generalist predator that feeds on aphids and other soft-bodied arthropods (Tauber et al. 2000). Many lacewings, *C. nigricornis* in particular, have been a target of experiments testing their attractiveness to pheromone and other semiochemical-based attractants. For instance, Zhang et al. (2006) observed the pheromone iridodial (male-produced pheromone) to be attractive to all the lacewing species we described here, especially *C. nigricornis.* Likewise, recent work by Jones et al. (2011) has shown that the semiochemical squalene is highly attractive to

Table 1. Species composition of the three primary predator groups found in woolly apple aphid colonies, 2006–2008

Group or species[a]	2006	2007	2008	Total (3 yr)
Syrphidae				
Syrphus ribesii (L.)		1		1
Syrphus torvus Osten Sacken	2	4		6
S. opinator	5	8		13
E. fumipennis		59		59
E. americanus	5		13	18
H. calcarata			1	1
Coccinellidae				
C. tranversoguttata	3		8	11
C. septempunctata	1		2	3
H. convergens	6		8	14
Hippodamia tredecempunctata (L.)			1	1
A. bipunctata			2	2
H. axyridis			2	2
Neuroptera				
C. nigricornis	2		24	26
C. plorabunda			2	2
Hemerobius spp.			1	1
Totals		72	64	160

[a] Only adult specimens (reared from larvae or captured as adults) were identified to the species level (larvae that died during the rearing process are not included).

C. nigricornis, but only to males. Lacewings also have been reported to be attracted to methyl salicylate (James 2003 and 2006). These materials are proposed for attracting beneficial species in orchards to enhance biological control.

Other predator groups encountered attacking woolly apple aphid, although in lower numbers, were damselbugs (Hemiptera: Nabidae), *Deraeocoris brevis* (Uhler) (Hemiptera: Miridae), spiders (Araneae), and earwigs (Dermaptera).

The higher numbers of predators in June, July, and August (Fig. 2) coincides with high densities of woolly apple aphid in central Washington. However, the second peak of aphids in September and October appears to be less subject to predation (Beers et al. 2010). Optimum temperatures for woolly apple aphid development of 13–25°C (Asante et al. 1991) prevail during this period, and this combination of circumstances may lead to the second peak during the fall (Walker 1985).

In most respects, the predator composition during this 3-yr study was similar to the predator complex encountered elsewhere (Asante 1997). One exception was the Neuroptera, which have not been mentioned as potential predators of woolly apple aphid in the United States. In a previous study conducted in Wenatchee, WA by Walker (1985), the main predator groups observed were Coccinellidae (*C. transversoguttata, H. convergens, Coccinella novemnotata* Herbst); Chrysopidae (*C. nigricornis* and *Chrysopa coloradensis* Banks); and predatory bugs (*Deraeocoris brevis*). Walker's findings generally agree with the results of our study, with the exception that only one syrphid species *Eupeodes* (*Metasyrphus*) *fumipennis* Thompson was observed in the study of Walker (1985), and was not considered as important as *C. transversoguttata, C. nigricornis*, and *D. brevis. Deraeocoris brevis*, although important in the 1985 study, occurred in very low frequencies in our studies. The difference may be ascribed to the limited nature of Walker's observations (single unsprayed research orchard, 2 yr) versus the regional survey we conducted; however, it is also possible that there might have been a genuine shift in the predator complex in response to changing pesticide programs over time.

Many of the predators encountered attacking woolly apple aphid in our survey also overlap the predator composition of *Aphis pomi* DeGeer (Carroll and Hoyt 1984). Some of these predators include *C. transversoguttata* and *H. convergens* (Coccinellidae), *C. nigricornis* (Chrysopidae), *Deraeocoris brevis* (Miridae), *M. fumipennis* (Syrphidae), and Forficulidae. Carroll and Hoyt (1984) also observed peach orchards, riparian trees, and shrubs to be important sources of some of these aphid predators. Likewise, Rathman and Brunner (1988) monitoring arthropod colonization of potted apple trees placed in riparian or sagebrush steppe habitats, observed that riparian habitats were better sources of aphid natural enemies.

Like any sampling method, the one used in this study had both strengths and weaknesses. Because the predators we collected were in or near the aphid colonies, we have a reasonable degree of confidence that they were preying on woolly apple aphid. However, our samples were taken only during the day, so nocturnal predators such as earwigs and some spiders may have been underrepresented. The more mobile predators (e.g., Neuroptera and Coccinellidae) may also have been underrepresented in relation to the Syrphidae, which are relatively sessile once settled in a colony. The predatory bugs are highly mobile in both adult and nymphal stages, and even with the precaution of observing the colony before removing it, they may have escaped notice. The relatively low encounter rate of predators in association with the colonies may not, therefore, reflect the impact of predators; these samples constitute a "snapshot" in time, rather than the cumulative effect of predation. Lastly, there may be a bias in the species reported if there was differential survival in laboratory larval rearing; the overall survival of the various groups was 48% (Syrphidae), 42% (Neuroptera), and 66% (Coccinellidae).

A. mali. The characteristic black mummy formed by *A. mali* was the only one observed in woolly apple aphid colonies in the 3 yr of the study. *Aphelinus mali* generally is recognized as the most important, if not sole parasitoid of woolly apple aphid (Asante 1997) and the only endoparasitoid recorded from the western United States. We found no evidence of parasitism in the root colonies (n = 110 aphids) in samples of overwintering woolly apple aphids. All the mummies found were on the aerial parts of the trees (n = 1,077 aphids), with an average of 44% aphids parasitized in 2006 and 41% in 2007. *Aphelinus mali* never has been documented to attack edaphic colonies of woolly apple aphid and these data, although not exhaustive, confirm this. Hitherto, the only natural enemies known to attack woolly apple aphid in the roots are the Syrphidae *Heringia calcarata* (Short and Bergh 2004) and the nematode *Steinernema carpocapsae* Weiser (Brown et al. 1992).

The pattern of adult *A. mali* activity (sticky bands) was quite variable among orchards and years; this type of variability was also noted by Evenhuis (1958). In the AR orchard, captures were relatively low, and fluctuated throughout the season (Fig. 3). In the VA orchard F3 in 2006, there was a large peak of activity by adults early in the spring (about bloom), as the overwintering adults emerged from the mummies. When sampling was shifted to a nearby block in the same orchard in 2007, numbers were lower by an order of magnitude, although an early season peak was still apparent. The SK orchard in 2006 showed a similar early peak of activity around bloom, with relatively low numbers thereafter. The CR orchard (2007) had a small peak around bloom, and a much larger peak in the fall. The seasonal patterns seen in this study were more likely influenced by host availability and pesticide use, which mask the underlying phenology of this species. AQ: 5

The percentage parasitism fluctuated by month in the 3 yr of the study with little consistency, but did not exceed 35% when all orchards and samples were pooled (Table 2). This parasitism rate was relatively T2 low compared with the unqualified successes reported

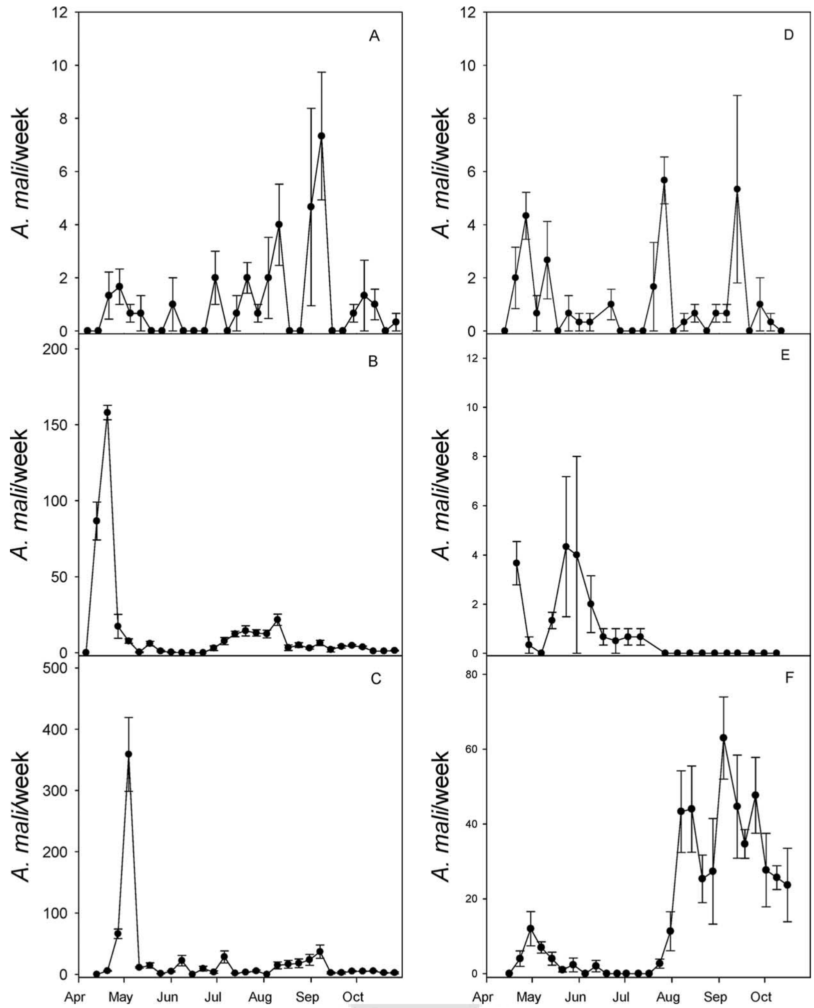

Fig. 3. Mean number of adult *A. mali* caught on sticky bands around the base of the tree trunk in four orchards (AH, VA, SK, and CR) in 2006 and 2007. A, 2006, AH; B, 2006, VA; C, 2006, SK; D, 2007, AH; E, 2007, VA; F, 2007, CR.

Table 2. Percentage parasitism of woolly apple aphid by *A. mali* in 2006–2008

Month	Mean % parasitism ± SEM	% parasitized colonies	No. colonies	No. orchards
2006				
June	16.80 ± 5.54	72.73	11	3
July	19.96 ± 7.46	81.82	11	3
Aug.	26.69 ± 5.20	100.00	11	3
Sept.	33.69 ± 10.37	100.00	6	3
Oct.	34.32 ± 7.40	100.00	3	3
2007				
April	1.95 ± 1.16	57.14	7	2
May	20.32 ± 9.91	87.50	8	2
June	13.06 ± 3.34	83.33	12	3
July	16.80 ± 4.03	100.00	11	3
Aug.	12.00 ± 8.06	62.50	8	3
Sept.	7.25 ± 3.00	50.00	10	1
Oct.	7.88 ± 6.56	50.00	4	1
2008				
July	34.15 ± 1.22	90.85	361	14
Aug.	32.15 ± 1.85	78.33	277	13
Sept.	30.47 ± 1.94	60.71	364	15
Oct.	10.83 ± 0.78	45.01	662	17

in many apple growing regions around the world (Howard 1929). One possibility is that there were relatively few insecticides before World War II, and the primary one used in orchards, lead arsenate, did not affect *A. mali* (Howard 1929); this changed with the widespread use of DDT in the mid-1940s (Newcomer et al. 1946). Many of the modern synthetic pesticides are likewise toxic to *A. mali* (Cohen et al. 1996, Bradley et al. 1997, Heunis and Pringle 2003), which may limit the impact of this parasitoid. Another reason for this difference may be because of regional climatic variation (Mols and Boers 2001). Low temperatures in many regions of the world have been reported as having a detrimental effect on the development of *A. mali* (Walker 1985, Asante and Danthanarayana 1993, Nicholas 2000). However, even moderate parasitism rates will contribute to biological control.

Our studies indicate that the overall diversity was low for predators, and nonexistent for parasitoids. Syrphids were proportionately more abundant in early summer (June); otherwise, seasonal abundance of the predators tended to echo the seasonal abundance of the host. The exception to this generalization occurs in September and October, when woolly apple aphid outbreaks frequently occur (Beers et al. 2010). The absence of predation during this period may explain in part the late-season outbreaks. Conversely, parasitoids remain active into the fall, and parasitism can reach high levels during that period, reducing the overwintering aerial aphid population.

Studies such as this provide a more quantitative basis on which to base future integrated control strategies. If conservation biological control strategies are to be implemented, then prioritizing which groups are most likely to contribute is an important first step. Our studies show that syrphids, especially the genus *Eupeodes*, are the most abundant predator group, and are thus the most likely targets for conservation biological control programs. These data also confirm previous observations that *A. mali* is the only parasitoid of importance in this system, and would also be a logical target for conservation. The next step will entail determining the relative impact of these groups on woolly apple aphids, as distinct from their relative frequencies in colony samples, to enhance their potential role in biological control.

Acknowledgments

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