The Parasitoids of the Asparagus Miner (Diptera: Agromyzidae): Field Parasitism and the Influence of Food Resources on Life History

The Parasitoids of the Asparagus Miner (Diptera: Agromyzidae): Field Parasitism and the Influence of Food Resources on Life History

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ABSTRACT The goals of this study were to identify pupal parasitoids of the asparagus miner, *Ophiomyia simplex* Loew (Diptera: Agromyzidae), and examine the effect of different diets and floral resources on the lifespan of adult asparagus miners and their parasitoids. We also measured the effect of parasitism on stem damage caused by the asparagus miner. The identity and abundance of the parasitoids of the asparagus miner were determined in asparagus fields in Michigan from weekly asparagus miner pupal collections during the 2010–2013 seasons. Twelve species of hymenopterous parasitoids were reared from asparagus miner pupae, including *Chorebus rondanii* (Giard) (Ichneumonoidea: Braconidae), 10 species in three families of Chalcidoidea, and one species of Bethylidae (Chrysidoidea), that represent new host records for the asparagus miner. *C. rondanii* and *Thinodytes cephalon* (Walker) (Pteromalidae) were the most common parasitoids. The effects of different diets and flowers on the lifespan of the pest and parasitoid adults were also evaluated. Buckwheat resulted in the shortest life span for the asparagus miner, whereas Riddell's goldenrod significantly increased its lifespan relative to the control. Parasitoid lifespan was doubled when individuals were fed sugar-rich diets. In the field, parasitoids preferred stems that contained more pupae and damage. The two most commonly reared parasitoids should be considered as targets for future conservation biological control efforts of the asparagus miner.

KEY WORDS conservation biological control, integrated pest management, *Asparagus officinalis*, parasitoid

Natural enemies are a vital part of agroecosystems, providing important services such as biological control (Gurr et al. 2003). The goal of conservation biological control programs is to maximize the abundance or efficacy of the endemic natural enemy population to increase suppression of pest populations in a field or greenhouse setting (Landis et al. 2000, Barbosa 2003). The prerequisite for this is to understand the identity and basic biology of the natural enemies present in the system so that their biocontrol impact can be maximized through specific techniques, such as the provisioning of required resources. Previous work in perennial agroecosystems has examined plant species or combination of species whose flowers attract and maintain a vibrant natural enemy community (Fiedler 2007; Isaacs et al. 2009; Walton and Isaacs 2011a, b). Among the various criteria for plants supporting ecosystem services, some to consider when selecting flowering plants for resource provisioning of biological control agents are (Fiedler et al. 2008)—1) flowers should attract the most effective natural enemy species of the pests (Maingay et al. 1991, Patt et al. 1997), 2) flowers should be accessible to the natural enemies (Baggen et al. 1999), 3) the plant should not attract other pests into the field (Kehrli and Wratten 2011), 4) the plant should be commercially available (Hickman and Wratten 1996), and 5) resources for the natural enemies should be provided throughout the entire growing season (Rebek et al. 2005, Stephens et al. 1998). As a result, plant selection is often a multifactorial process.

The asparagus miner, *Ophiomyia simplex* Loew (Diptera: Agromyzidae), is a pest of asparagus, *Asparagus officinalis* (L.) (Asparagaceae), and has the potential to spread pathogenic fungi such as *Fusarium* spp. (Gilbertson et al. 1985, Tuell 2003, Morrison et al. 2011), making it a major concern to the asparagus industry (J. Bakker, personal communication). Gilbertson et al. (1985) indicated the association between *Fusarium* spp. and the asparagus miner may be a primary constraint on asparagus production in Massachusetts. Damicone and Manning (1987) showed that decreasing the abundance of asparagus miner also decreases the incidence of *Fusarium* crown and root rot in fields. The insect is bivoltine, and its larvae bore through cortical tissue in the plant (Eichmann 1943), creating undulating mines along the asparagus stem. It has the potential to decrease the vigor of asparagus

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fields during the postharvest period and can cause early decline of fields due to the introduction of diseases, which may reduce the economic lifespan of a field by 5–8 yr.

The asparagus miner overwinters as pupae (Barnes 1937). In Michigan, the first-generation adults usually emerge in mid-May, with first peak adult abundance occurring around mid-June and the second generation peaking in late July or August (Lampert et al. 1984, Morrison et al. 2014). Adequate control measures are difficult to develop because the adult flight is prolonged and the larvae are impervious to foliar insecticide sprays because they remain protected within the asparagus stems. Systemic insecticides are being evaluated (Z. S., unpublished data), but none are currently available to asparagus growers to control asparagus miner larvae in stems.

The natural enemies of the asparagus miner remain poorly studied, especially in continental North America where the only recorded parasitoids are two species of Hymenoptera originally described from Europe, *Chorebus rondanii* (Giard) (Braconidae) and *Pediobius epigonus* (Walker) (Eulophidae) (Supp Table 1 [online only]). Mailloux et al. (2004) provided an illustrated identification guide to the parasitoids and predators found in asparagus fields in Canada, but this is not specific to the asparagus miner and, except for one pest and parasitoid species, no information is given for abundance, behavioral, or ecological data of the natural enemies. Further, the photograph in Mailloux et al. (2004) that illustrates *Pediobius* (=*Pleurotropis*) *epigonus* (Fig. 6) is a female pteromalid and not a eulophid based on the number of antennal segments, wing venation, and other habitus features. In Europe, in addition to *C. rondanii* and *P. epigonus*, *Neochrysocharis moczari* Szelényi (Eulophidae) was described as a parasitoid of the asparagus miner in Hungary (Szelényi 1973). Barnes and Walton (1934) also reared *P. epigonus*, *Dacnusa bathyzona* Marsh (Braconidae), and *Sphegigaster* sp. (Pteromalidae) from asparagus miner pupae in the United Kingdom. Finally, *Centrodora xiphidii* Perkins (Aphelinidae) is recorded as a parasitoid of the asparagus miner in Hawaii (Bianchi 1941).

The goals of the current study were to determine for commercial asparagus fields in Michigan: 1) the identity of the pupal parasitoids of the asparagus miner, 2) the effect of different diets and floral resources on the lifespan of adult asparagus miners and their pupal parasitoids to determine the potential of using floral resources to enhance the efficacy of the parasitoid community, and 3) how damage affects parasitism on asparagus stems.

Materials and Methods

Study Site. Three commercial farms were used in 2010, 2011, and 2012, and two farms in 2013. Multiple fields were used at some of the farms, resulting in a total of five field sites in the first two years, three in 2012, and four in 2013. Fields were located 1.21–16.14 km apart in Oceana County, MI (Supp Table 2 [online only]), which is the major asparagus-producing region of Michigan. The asparagus fields were bordered by habitats characteristic of Michigan, and have been described in detail elsewhere (see Morrison and Szendrei 2013).

Insect Collections. Immature asparagus miner stages were collected according to the methods in Morrison and Szendrei (2013). Specifically, 8–53 stems were collected from each field (mean ± SEM: 33.8 ± 11 stems) every 6–10 d throughout the growing season from 1 to 5 fields per sampling date for a total of 3,647 stems from 2010 to 2013. The dates of collection ranged from 22 July to 17 September in 2010, 31 May to 3 October in 2011, 14 June to 7 October in 2012, and 18 June to 5 September in 2013. Asparagus stems were collected 30 m into the field by cutting them 5 cm below the soil surface, and then again at the height of the longest mine (defined as the mine terminating highest on the stem). Stems were sealed in plastic bags and placed in a cooler with ice packs until transported to the laboratory. Samples were stored at 5°C in the laboratory, and the stems were processed within 1–14 d. A razor blade was used to carefully peel the epidermis from the asparagus stem to reveal the immature stages. The following were recorded for each stem: the number of larvae, pupae, and castings (puparia). Pupae were placed individually in cups (3 by 5.5 cm H:D) in 2010, 2011, and 2013 or petri dishes in 2012 (1.5 by 6 cm H:D) and stored at 5°C until subsets were used in the diet assay or floral assay (described below under the Diet Assay and Floral Assay subsections). Sets of 60 pupae were placed in an environmental chamber at a constant 26°C (a photoperiod of 16:8 [L:D] h and 75% relative humidity) or on a lab bench (a photoperiod of 16:8 [L:D] h and 23.7 ± 0.2°C) every week during the course of the experiments to allow adults to emerge. Emergence of adult asparagus miners or parasitoids was checked daily, asparagus miners were sexed (only from pupae collected in 2013), and the family of parasitoid was recorded.

Parasitoid Identification. All parasitoids from all years and experiments were identified to family using an authoritative key to the Nearctic Chalcidoidea (Gibson et al. 1997), and for Hymenoptera (Marshall 2006; Evans 1964, 1978). Parasitoids not used in experiments in 2010–2012 were sent for species identification to the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC) in Ottawa, ON. As a result, species identifications were not made for a subset of the 2010–2012 individuals that were damaged in the diet and floral assays (see below). However, identifications were made for all individuals reared in 2013. Voucher specimens are deposited in the CNC and at the Michigan State University A.J. Cook Arthropod Research Collection (voucher number 2014–01) in East Lansing, MI.

Diet Assay. Upon emergence from pupae, adult asparagus miners or parasitoids were fed one of five different diets in random order, as they emerged on different days. Bioassays were conducted from 2010 to 2013 with pupae collected from the field. Adults were fed only one kind of diet ad libitum over their lifespan.

The diets included no food ($n = 41$ individuals), water only ($n = 89$), sugar solution (20.4% m/v; $n = 91$), honey solution (10% vol:vol; $n = 120$), or asparagus spears (fresh, snapped at the tip; $n = 17$). The water, sugar, and honey solutions were added to a piece of cotton ball and presented to the adults in their containers. Adults were kept either on a lab bench at 24 ± 0.40°C or in an environmental chamber at a constant 26 ± 0.07°C, and the temperature was monitored with a digital thermometer daily. Adults were checked daily, and the adult lifespan was calculated as the duration from emergence to death.

Floral Resource Assay. A portion of the newly emerged adult asparagus miners or parasitoids from the pupal collections were used in this experiment from 27 July 2012 to 10 October 2013. Each adult was placed in a mesh cage (47.5 by 47.5 by 93 cm L:W:H from Megaview Science Co., Ltd., Taichung, Taiwan) with one of four different plants in flower and provided with supplemental water. The assays also included a negative control of an adult insect with water only. The water was provided by filling a screw cap vial (2 dram from Bioquip Products, Rancho Dominguez, CA) with water, folding a wipe (11 by 21 cm W:L from Kimberly-Clark Professional, Roswell, GA), inserting it into the vial as a wick, and sealing it with Parafilm (Parafilm "M," Pechiney Plastic Packaging, Menasha, WI) to prevent evaporation and drowning of the adult. Adults were kept in the laboratory on a photoperiod of 16:8 (L:D) h, with full spectrum lights suspended above the cages, at 24 ± 0.4°C. Though there were not always enough adults emerging on a given day to run the full set of treatments, whenever two or more adults emerged, one control treatment was concurrently included. The total adult lifespan and sex of the adult was recorded in 2013.

The four different plants used were *Fagopyrum esculentum* Moench (Polygonaceae) (buckwheat, exotic, annual), *Lobularia maritima* (L.) (Brassicaceae) (sweet alyssum, variety Carpet of Snow, exotic, annual), *Vicia faba* L. (Fabaceae) (faba bean, variety broad Windsor, exotic, annual), and *Solidago riddellii* Frank ex Riddell (Asteraceae) (Riddell's goldenrod, native, perennial). The negative control consisted of adults with water only without any potted plants. Plants were selected based on previously published literature concerning attraction of natural enemies to each plant species (e.g., Fiedler and Landis, 2007a, b), ability of parasitoids and asparagus miner adults to use flowers, and commercial availability. The annual plants were raised in the greenhouse from seed (Eden Brothers, Asheville, NC), with a single seed planted in a pot (10.5 by 10.5 by 12.5 cm L:W:H) into potting soil (SureMix Perlite, MI Grower Products, Inc., Galesburg, MI). Riddell's goldenrod was obtained from WildType Nursery (Mason, MI) from seed planted in 2011, with no insecticides applied to the plants in the year that they were used for the current experiments. Experiments were carried out in a laboratory at Michigan State University's campus (East Lansing, MI). At least seven individuals of each annual species were planted weekly, and all plants were watered daily during the cool season and twice daily during the summer. Plants were kept on a photoperiod of 16:8 (L:D) h throughout the year, except Riddell's goldenrod (a perennial), which was allowed to senesce outside in ambient temperature and light conditions during the winter. Fertilizer (20-20-20 N:P:K with micronutrients, J. R. Peters, Allentown, PA) was delivered to plants in liquid form (1% m/v).

Asparagus Miner Damage and Parasitism. In addition to recording the number of pupae and larvae per stem collected from the field, the length of the longest mine, and the percent mining damage within the bottom 5 cm of the stem's circumference were also recorded as measures of damage. The percent mining was assessed visually by examining the proportion of surface exhibiting mining damage on the lower part of the stem. Parasitism rates by different parasitoid families of asparagus miner pupae were calculated per stem.

Statistical Analysis. To analyze the data from the diet assay, a 2-way factorial ANOVA with unequal sample sizes was performed. The response variable was the lifespan (days) of adult parasitoids or asparagus miners, while the two explanatory factors were diet type and insect taxonomic (family) identity. The residuals did not conform to the assumption of normality that is required by the parametric test, so the data were log-transformed. Pairwise tests were performed using Tukey's HSD test. The cutoff for significance for this test and for the floral assay was $\alpha = 0.05$. This analysis and all subsequent statistical tests were performed with the R Statistical Computing Software (R Core Development Team 2013).

The data from the floral assay were analyzed with a 2-way ANOVA with unequal sample sizes using an incomplete block design. The response variable was lifespan of asparagus miner adults, with flower type as the explanatory variable and date as the random blocking variable. The residuals from the data were inspected and conformed to a normal distribution, so no transformation was required. Pairwise post hoc comparisons were performed with Tukey's HSD.

To evaluate if parasitism of asparagus miner pupae affects damage in the field, Welch t-tests were performed on damage data recorded from collected stems that were linked with whether they had parasitized pupae. Specifically, three t-tests were performed that examined whether the average percent stem mined (within 5 cm of the base of the stem), the average longest mine, or average asparagus miner pressure (composite measure including asparagus miner pupae, larvae, and puparia) were significantly different between stems that either had or had not experienced parasitism. The average percentage stem mined was arcsine-transformed to theoretically give the variable more freedom to vary so that it can fulfill the requirements of a t-test, namely that the variable is not bounded by limits. The residuals from the other t-tests were inspected to confirm assumptions of normality, but variances

Table 1. Number of parasitoids and percent parasitism of asparagus miner pupae collected between 2010 and 2013 in six commercial asparagus fields in Oceana County, MI

	2010[a]		2011[b]		2012[c]		2013[d]		Total[e]	
	Abund	% parasitism	Abund	% parasitism	Abund	% parasitism	Abund	% parasitism	Abund	% parasitism
Braconidae										
Chorebus rondanii	3	1.6	22	5.5	20	15.7	16	5.2	61	6.0
Pteromalidae										
Pteromalidae morph[f]	40	21.5	27	6.8	7	5.5	0	0.0	74	7.2
Cyrtogaster vulgaris	2	1.1	7	1.8	3	2.4	5	1.6	17	1.7
Halticoptera sp.	0	0.0	0	0.0	0	0.0	1	0.3	1	0.1
Merismus megapterus	0	0.0	1	0.3	0	0.0	1	0.3	2	0.2
Spaniopus dissimilis	0	0.0	0	0.0	0	0.0	1	0.3	1	0.1
Sphegegaster cracentis	0	0.0	2	0.5	0	0.0	0	0.0	2	0.2
Thinodytes cephalon	26	14.0	28	7.0	7	5.5	13	4.2	74	7.2
Trichomalopsis viridascens	0	0.0	1	0.3	0	0.0	1	0.3	2	0.2
Overall Pteromalidae[f,g]	68	36.6	66	16.5	17	13.4	22	7.1	173	16.9
Eupelmidae										
Brasema ?allynii	0	0.0	0	0.0	1	0.8	1	0.3	2	0.2
Eupelmus vesicularis	0	0.0	2	0.5	2	1.6	2	0.6	6	0.6
Overall Eupelmidae[f]	0	0.0	2	0.5	3	2.4	3	1.0	8	0.8
Eulophidae										
Neochrysocharis sp.[h]	2	1.1	6	1.5	0	0.0	6	1.9	14	1.4
Bethylidae										
Laelius utilis	0	0.0	0	0.0	0	0.0	1	0.3	1	0.1
Total parasitism	73	39.2	96	24.0	40	31.5	48	15.5	257	25.1

[a] n = 186 pupae collected in 2010, and the total number of asparagus miners that emerged was 113 adults.
[b] n = 400 pupae collected in 2011, and the total number of asparagus miners that emerged was 304 adults.
[c] n = 127 pupae collected in 2012, and the total number of asparagus miners that emerged was 87 adults.
[d] n = 309 pupae collected in 2013, and the total number of asparagus miners that emerged was 261 adults.
[e] n = 1,022 pupae collected over 4 yr, and the total number of asparagus miners that emerged was 765 adults.
[f] Morph designation indicates that the individual was only taken to the family level because species-level identification was not possible at time of emergence and specimen was since used for the diet and floral assays.
[g] Combined abundance and parasitism rates for all the morphs or species within a family.
[h] Identified to either *N. formosus* or *N. diastatae*.

were unequal. As a result, the Welch degrees-of-freedom correction was applied.

To determine if there was greater parasitism on stems with more asparagus miner pupae, a regression was performed with the number of parasitized pupae per stem as the response variable and the number of asparagus miner pupae on the stem as the explanatory variable. A Kruskal–Wallis test was performed to determine whether certain parasitoid families were more efficient at parasitizing asparagus miner pupae. Parasitoid family was the explanatory, categorical variable, while the response variable was the average percent parasitism of the total number of asparagus miner pupae per stem over the n = 3–65 stems that were parasitized by a given individual belonging to one of four parasitoid families. A Kruskal–Wallis test was used because parametric assumptions were not fulfilled, even after transformation. Multiple comparisons between the parasitoid families were performed using the Steel–Dwass algorithm after a significant result from the Kruskal–Wallis test. For these multiple comparisons, a Bonferonni correction was used (α = 0.01).

Results

Parasitoid Identity and Abundance. A total of 12 species of parasitoids from Hymenoptera were reared from asparagus miner pupae, including *C. rondanii* (Braconidae), 10 species in three families of Chalcidoidea (Eulophidae, Eupelmidae, and Pteromalidae), and one species of Bethylidae (Chrysidoidea) (Table 1, Supp. Table 3 [online only]). The pteromalids were *Cyrtogaster vulgaris* Walker, *Halticoptera* sp., *Merismus megapterus* Walker, *Sphegigaster cracentis* Heydon & LaBerge, *Spaniopus dissimilis* Walker, *Thinodytes cephalon* (Walker), and *Trichomalopsis viridascens* (Walsh). The eupelmids were *Eupelmus vesicularis* (Retzius) and a species in an unrevised genus questionably identified as *Brasema allynii*. There was also a single eulophid that was identified as either *Neochrysocharis formosus* (Westwood) or *Neochrysocharis diastatae* (Howard). The bethylid was *Laelius utilis* Cockerell (Table 1, Supp Table 3 [online only], Supp Fig. 1 [online only]). All of the chalcids and the bethylid represent new parasitoid records for the asparagus miner.

All of the parasitoids were solitary except for the eulophid, which had an average of 9.3 ± 1 individuals per pupa. Most of the reared parasitoids belong to Pteromalidae, which parasitized ≈17% of the asparagus miner pupae collected (Table 1). Pteromalidae had a 3-fold greater abundance than the next most common family, Braconidae. Eulophidae had one of the lowest rates of parasitism, accounting for <1.4% of total parasitism. Parasitism by Eupelmidae and Bethylidae was the lowest at 0.8 and 0.1% of all the pupae, respectively. Overall, the single most abundant species was *T. cephalon*, parasitizing 7.2% of the total asparagus miner pupae, while the second most abundant parasitoid was *C. rondanii*, which parasitized 6.0%

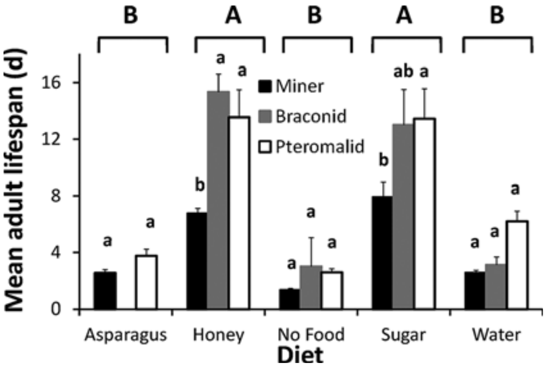

Fig. 1. Mean + SEM (d) longevity of asparagus miner adults and two groups of parasitoids (Braconidae and Pteromalidae) on various diets in a bioassay. Adults were fed ad libitum during their lifespan. Diets (across species) with shared and capitalized letters are not significantly different from one another (Tukey's HSD, α = 0.05). Lower case letters represent comparisons within a diet, between species (Tukey's HSD).

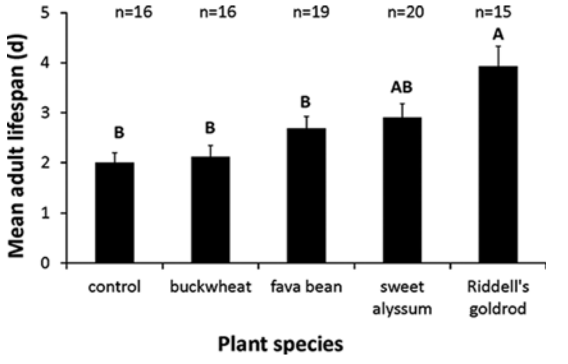

Fig. 2. Mean + SEM (d) longevity of asparagus miner adults that were allowed to feed on various flowers. Species with a shared capital letter are not significantly different from one another (Tukey's HSD, α = 0.05). The sample size of adults tested is above each bar.

of the total asparagus miner pupae (Table 1). Total parasitism by all species ranged from 39.2% in 2010 to 15.5% in 2013, with overall parasitism for all years and species reaching a total of 25.1%.

Diet Assay. The diet that asparagus miner or parasitoid adults were fed significantly affected their lifespan (ANOVA: $F = 86.74$; df = 4, 80; $P < 0.001$; Fig. 1), as did the family identity (including the families to which the pest and parasitoids belonged, ANOVA: $F = 18.63$; df = 2, 168; $P < 0.001$). Specifically, adults fed a sugar-rich diet (e.g., honey or sugar solution) had a significantly greater life span compared with adults fed water only, or snapped asparagus spears (Fig. 1). Adult parasitoids fed a sugar-rich diet lived about twice as long as asparagus miner adults fed on the same diet, with a lifespan of ≈13.8 d compared with 7.3 d for the asparagus miner. Relative to the control (water only), the life span of asparagus miner adults increased by a factor of 5.2, whereas the life span of parasitoid adults increased by a factor of 7.7 when fed sugar-rich diets.

Floral Resource Assay. Sex ratio of the adults was ≈1:1. The flower species that an asparagus miner adult had access to significantly influenced its longevity (ANOVA: $F = 38.06$; df = 4, 70; $P < 0.001$). Specifically, miners that were enclosed with Riddell's goldenrod lived about twice as long as those that had access to water only (Fig. 2). The asparagus miner life span on buckwheat and faba bean was similar to the control. Sweet alyssum resulted in intermediate life spans for the asparagus miner, with adults living ≈2.5 d on average.

Asparagus Miner Damage and Parasitism. Where asparagus miners were present, there was an average of 2.68 ± 0.1 pupae (mean ± SE; range 0–20) per stem between 2011–2013. There was a significant positive correlation between the number of pupae parasitized on a stem and the total number of asparagus miner pupae found on the stem (Adj. $R^2 = 0.883$; $P < 0.001$; Fig. 3). The highest number of pupae that were parasitized on a stem was four (Fig. 3), though stems with one or two parasitized pupae were much more common (W.R.M., unpublished data). There were significantly different parasitization rates of asparagus miner pupae per stem depending on parasitoid family (Kruskal–Wallis: $\chi^2 = 18.35$; df = 3; $P < 0.001$). When a stem was parasitized by braconids, 40 ± 0.1% (mean ± SE) of the asparagus miners in a given stem were parasitized. The average parasitization rate by pteromalids (46 ± 0.1%) was similar to braconids. Eupelmids attacked pupae when there was only a single asparagus miner individual located on a stem, resulting in a 100% parasitization rate. Eulophids parasitized twice as many pupae per stem (81 ± 0.2% on average) relative to braconids. Overall, stems that were parasitized had 1.4 times longer mines, 1.2 times greater proportion of the stem mined, and almost twice as many asparagus miner life stages than non-parasitized stems (Table 2).

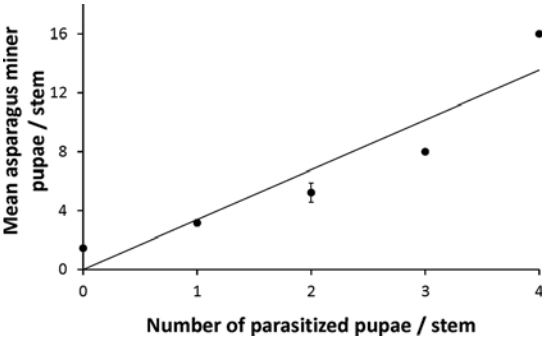

Fig. 3. Relationship between the number of parasitized asparagus miner pupae per stem and the mean number of asparagus miner pupae per stem (±SEM) for stems collected from Oceana Co., MI, between 2011 and 2013. There is a significant positive correlation between parasitism and the number of pupae per stem (R^2 = 0. 883, $P < 0.0001$; y = 3.39x−0.0068).

Table 2. Summary of damage measure and amount of asparagus miner pupal abundance on parasitized or nonparasitized asparagus stems

Measure	Parasitized		Nonparasitized		Between-group test		
	n	Mean ± SEM	n	Mean ± SEM	t	df[a]	P
Longest mine[b]	113	14.8 ± 0.61	3,534	10.8 ± 0.12	−6.34	118.1	<0.0001
% stem mined[c]	113	97.2 ± 0.09	3,534	81.4 ± 0.58	−13.57[d]	118.1	<0.0001
AM[e] pressure	113	6.06 ± 0.03	3,534	3.24 ± 0.05	−8.77	117.3	<0.0001

[a] Welch correction applied to degrees of freedom.
[b] In centimeters.
[c] Measure of the amount of the stem surface being girdled within the bottom 5 cm of the asparagus stem.
[d] Before testing, this variable was arcsine transformed to fulfill the requirements of a *t-test.*
[e] Asparagus miner (AM) pressure: a composite measure that additively combines the number of pupae, larvae, and castings (puparia) for a given stem.

Discussion

Of the parasitoids we reared from the asparagus miner, only *C. rondanii* was reported previously as a parasitoid of the asparagus miner, once in Massachusetts (Krombein et al. 1979) and in Europe (Giard 1904). It is a host-specific parasitoid of the asparagus miner (Griffiths 1968) and was the second-most common parasitoid reared in the current study. The most common parasitoid reared was *T. cephalon*, and its parasitism rate probably is underestimated because most of the "Pteromalidae morphs" (Table 1) were likely also this species. Prior host records of *T. cephalon* include Cecidomyiidae and Chloropidae (Diptera) (Supp Table 3 [online only]). This species, along with *C. rondanii,* may be effective natural enemies of the asparagus miner and good candidates for conservation biological control of this pest in Michigan. The species assemblages of parasitoids for the asparagus miner in other regions of the United States should be assessed to evaluate whether these two species are also good candidates for biological control elsewhere, as the dominant parasitoids for a particular host can vary depending on region especially in large countries like the United States or Canada (Mason et al. 2011).

Most of the other chalcid parasitoid species identified in our study are omnivorous or polyphagous and parasitize a variety of hosts. Agromyzids are among the hosts of these polyphagous species (for example *C. vulgaris, M. megapterus* and species of *Halticoptera*). *T. cephalon, S. dissimilis* and *Tr. viridascens* are known to parasitize Chloropidae and Cecidomyiidae (Supp Table 3 [online only]), and previous literature suggests that they are parasitoids of leaf or stem miners. Thus, it may be likely that these species switched from native hosts to the asparagus miner when it was introduced to North America. The host of *Sp. cracentis* is unknown. An unidentified species of *Sphegigaster* Spinola was reported as a parasitoid of the asparagus miner in Europe (Barnes 1937, Barnes and Walton 1934), but it is likely different from the species we reared.

Based on known biology, at least two of the parasitoids, *E. vesicularis* and *B. ?allynii,* could be either primary parasitoids of the asparagus miner or hyperparasitoids through one of the other parasitoid species. Hyperparasitism may constrain biological control in simplified environments, such as monocultures (Rosenheim et al. 1995), especially if primary hyperparasitoids are abundant, though the outcome of intraguild predation often depends on crop-specific conditions (Müller and Brodeur 2002). Regardless, the impact of these two species on biological control services in the field is likely minimal because of their low abundance (Table 1).

We reared only a single specimen of the bethylid *L. utilis.* This rearing is anomalous because *L. utilis* has never been recorded as using any hosts other than beetles of the family Dermestidae. However, with only a single rearing during 4 yr of data collection, asparagus miners are at least not typical hosts for this species.

Sugar-rich diets increased the lifespan of the pteromalid and braconid parasitoids, indicating that the addition of nectar and floral resources could benefit biological control in this system. Of concern, however, is the observation that the provisioning of sugar-rich diets also increased the life span of the asparagus miner. This suggests that it is important to provide flowers in the field that the natural enemy community can exploit without inadvertently benefiting the pest species (Kehrli and Wratten 2011). During asparagus bloom, the abundantly available flowers may provide resources to both the asparagus miner (Ferro and Gilbertson 1982) and the parasitoids. At other times of the year, the majority of flowers are on the field margins, with the asparagus field being relatively depauperate of floral resources. It may be most important to supply the parasitoid community with floral resources during these periods.

The asparagus miner had the shortest lifespan when individuals were allowed access to buckwheat, while they had the longest lifespan on Riddell's goldenrod. Despite the fact that goldenrod has been shown to attract chalcidoids and braconids (Fiedler and Landis 2007a, Landis et al. 2013), we would not recommend it for use in floral plantings or conservation strips for asparagus because of its beneficial impact on the asparagus miner lifespan. Buckwheat is an exotic plant from central Asia, and it has also been shown to attract chalcidoids and braconids in Michigan (Fiedler and Landis 2007a), the groups to which *T. cephalon* and *C.*

rondanii belong. However, the same study showed that buckwheat also attracts insects such as *Lygus* spp. (Hemiptera) and the Japanese beetle, *Popillia japonica* Newman (Scarabaeidae) (Landis et al. 2013), which are pests in asparagus fields. Attracting *Lygus* spp. may not cause problems for asparagus production because asparagus plants can recover, even at a young age, from infestations by this pest (Grafius and Morrow 1982), though long-term potential for damage may still exist.

This study showed that there is a positive correlation between the number of pupae parasitized on the stem, the amount of damage on the asparagus stem, and the total number of asparagus miner pupae. This means that pupal parasitoids may have a preference for stems that are already damaged by asparagus miner pupae. This could be due to the amount of cues emanating from damaged stems—usually the higher the concentration of host kairomone cues, the greater the attractiveness of a patch to the parasitoid (van Alphen et al. 2003). Among other signals, possible kairomones that may be used by parasitoids of the asparagus miner are presence of mining damage, exposure of pupae where the skin of the plant has been broken, and alteration of the volatiles bouquet emitted by the plant or flowers (see Geervliet et al. 1996, Dannon et al. 2010). The chemical ecology of the asparagus miner, the crop and its parasitoids deserve special attention in follow-up studies to develop alternative control approaches for this pest. Additionally, we found some support for models of optimal searching behavior, which indicate that when prey distribution is variable (as in the case of the asparagus miner, as some stems had one nonparasitized miner pupa, whereas others had up to 15), then parasitoids are expected to incrementally increase their time at a patch with each oviposition (Iwasa et al. 1981).

There are no established economic thresholds for the asparagus miner; however, Gilbertson et al. (1985) found similar numbers of pupae per stem (average 2.9 per stem) in western Massachusetts as in the current study. The same study found that 76% of the mines in stems collected from the field were infected with *Fusarium moniliforme* (=*proliferatum*), and 10% had *Fusarium oxysporum* f.sp. *asparagi*, the main agents responsible for the early decline of asparagus. These authors concluded that the asparagus miner is a significant pest in Massachusetts, and plays a role in increasing the frequency of crown and root rot in asparagus fields. Tuell (2003) isolated *Fusarium* sp. from different asparagus miner lifestages from Michigan. It is therefore likely that this pest plays a significant role in increasing the frequency of crown and root rot in asparagus fields in Michigan, and is a serious threat to the Michigan asparagus industry.

This study suggests that native chalcid generalist parasitoids of dipterous and other leaf or stem miners will include the asparagus miner as a host and assist in biological control of this pest. Of the parasitoids found, *C. rondanii*, a host-specific parasitoid, and *T. cephalon* may be the best candidates for conservation biological control of the asparagus miner based on observed parasitism rates. Buckwheat or faba bean were the best candidates for providing a flowering resource, though there may be other alternatives that were not examined. Further research is specifically needed into the following areas before a biological control program can be implemented in asparagus: 1) investigation of whether buckwheat or faba bean attracts and aids the natural enemy community of the asparagus miner in the field, 2) understanding the chemical ecology in interactions between the asparagus miner, its natural enemies, and the crop, and 3) ensuring that floral resources in the margins of asparagus fields do not benefit other nontarget pests in the field.

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References Cited

Baggen, L., G. Gurr, and A. Meats. 1999. Flowers in tritrophic systems: Mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. Entomol. Exp. Appl. 91: 155–161.

Barbosa, P. 2003. Conservation Biological Control. Academic, San Diego, CA.

Barnes, H. 1937. The asparagus miner (*Melanagromyza simplex* H. Loew) (Agromyzidae; Diptera). Ann. Appl. Biol. 24: 574–588.

Barnes, H., and C. Walton. 1934. The asparagus miner, Melanagromyza simplex Loew. Entomol. Mon. Mag. 120: 183–185.

Bianchi, F. 1941. Proceedings of the Hawaiian entomological society for the year 1940. Proc. Hawaii Entomol. Soc. 11: 14.

Damicone, J., and W. Manning. 1987. Influence of management practices on severity of stem and crown root, incidence of asparagus miner, and yield of asparagus grown from transplants. Plant Dis. 71: 81–84.

Dannon, E., M. Tamò, A. van Huis, and M. Dicke. 2010. Effects of volatiles from *Maruca vitrata* larvae and caterpillar-infested flowers of their host plant *Vigna unguiculata* on the foraging behavior of the parasitoid *Apanteles taragamae.* J. Chem. Ecol. 36: 1083–1091.

Eichmann, R. 1943. Asparagus miner really not a pest. J. Econ. Entomol. 36: 849–852.

Evans, H. 1964. A synopsis of the American Bethylidae (Hymenoptera, Aculeata). Bulletin 132, Museum of Comparative Zoology, Harvard University, Cambridge, Cambridge, MA.

Evans, H. 1978. The Bethylidae of America north of Mexico. Am. Entomol. Inst. 27: 1–332.

Ferro, D., and R. Gilbertson. 1982. Bionomics and population dynamics of the asparagus miner, Ophiomyia simplex (Loew), in Western Massachusetts. Environ. Entomol. 11: 639–644.

Fiedler, A. 2007. Evaluation of Michigan native plants to provide resources for natural enemy arthropods. Master of Science, Department of Entomology, Michigan State University, East Lansing, MI.

Fiedler, A., and D. Landis. 2007a. Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. Environ. Entomol. 36: 751–765.

Fiedler, A., and D. Landis. 2007b. Plant characteristics associated with natural enemy abundance at Michigan native plants. Environ. Entomol. 36: 878–886.

Fiedler, A., D. Landis, and S. Wratten. 2008. Maximizing ecosystem services from conservation biological control: the role of habitat management. Biol. Control 45: 254–271.

Geervliet, J., L. Vet, and M. Dicke. 1996. Innate responses of the parasitoids *Cotesia glomerata* and *C. rubecula* (Hymenoptera: Braconidae) to volatiles from different plant-herbivore complexes. J. Insect Behav. 9: 525–538.

Giard, A. 1904. Sur l'*Agromyza simplex* H. Loew parasite de l'asperge (Dipt.). Bull. Soc. Entomol. Fr. 176–178.

Gibson, G., J. Huber, and J. Woolley. 1997. Annotated Keys to the Genera of the *Nearctic Chalcidoidea* (Hymenoptera). NRC Research Press, Ottawa, Canada.

Gilbertson, R., W. Manning, and D. Ferro. 1985. Association of the asparagus miner with stem rot caused in asparagus by *Fusarium* species. Phytopathology 75: 1188–1191.

Grafius, E., and E. Morrow. 1982. Damage by the tarnished plant bug and alfalfa plant bug (Heteroptera: Miridae) to asparagus. J. Econ. Entomol. 75: 882–884.

Griffiths, G. 1968. V. The parasites of *Liriomyza* Mils and certain small genera of Phytomyzinae. Beitr. Entomol. 18: 63–152.

Gurr, G., S. Wratten, and J. Luna. 2003. Multi-function agricultural biodiversity: pest management and other benefits. Basic Appl. Ecol. 4: 107–116.

Hickman, J., and S. Wratten. 1996. Use of *Phacelia tanacetifolia* to enhance biological control of aphids by hoverfly larvae in cereal fields. J. Econ. Entomol. 89: 832–840.

Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. Front. Ecol. Environ. 7: 196–203.

Iwasa, Y., M. Higashi, and N. Yamamura. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. Am. Nat. 117: 710–723.

Kehrli, P., and S. Wratten. 2011. A perspective on the consequences for insect herbivores and their natural enemies when they share plant resources. ISRN Ecol. 2011: 1–6.

Krombein, K., P. Hurd Jr., D. Smith, and B. Burks. 1979. Catalog of Hymenoptera in America north of Mexico, vol. 1. Smithsonian Institution Press, Washington, DC.

Lampert, E., D. Cress, and D. Haynes. 1984. Temporal and spatial changes in abundance of the asparagus miner, Ophiomyia simplex (Loew) (Diptera: Agromyzidae), in Michigan. Environ. Entomol. 13: 733–736.

Landis, D., S. Wratten, and G. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. 45: 175–201.

Landis, D., A. Fiedler, and R. Isaacs. 2013. Michigan Plant Facts. Department of Entomology, Michigan State University, East Lansing, MI. (http://nativeplants.msu.edu/plant_facts) (accessed: 18 October 2013).

Mailloux, G., V. Vujanovic, and C. Hamel. 2004. Identification rapide des insects auxiliaires dans les aspergeraies du Quebec, pp. 1–27. Institut de Recherche et de Development en Agroenvironment, Saint-Bruno, Canada.

Maingay, H., R. Bugg, R. Carlson, and N. Davidson. 1991. Predatory and parasitic wasps (Hymenoptera) feeding at flowers of sweet fennel (*Foeniculum-Vulgare* Miller Var. Dulce Battandier and Trabut, Apiaceae) and spearmint (*Mentha-Spicata* L., Lamiaceae) in Massachusetts. Biol. Agric. Hortic. 7: 363–383.

Marshall, A. 2006. Insects: Their natural history and diversity. Firefly Books, Ltd., Richmond Hill, Canada.

Mason, P., J. Miall, P. Bouchard, D. Gillespie, A. Broadbent, and G. Gibson. 2011. The parasitoid communities associated with an invasive canola pest, Ceutorhynchus obstrictus (Coleoptera: Curculionidae), in Ontario and Quebec, Canada. Can. Entomol. 143: 524–537.

Morrison, III, W., and Z. Szendrei. 2013. Patterns of spatial and temporal distribution of the asparagus miner (Diptera: Agromyzidae): implications for management. J. Econ. Entomol. 106: 1218–1225.

Morrison, III, W., J. Tuell, M. Hausbeck, and Z. Szendrei. 2011. Constraints on asparagus production: the association of *Ophiomyia simplex* (Diptera: Agromyzidae) and *Fusarium* spp. Crop Sci. 51: 1414–1423.

Morrison, III, W., J. Andresen, and Z. Szendrei. 2014. The development of the asparagus miner (*Ophiomyia simplex* Loew; Diptera: Agromyzidae) in temperate zones: a degree-day model. Pest Manag. Sci. 70: 1105–1113.

Müller, C., and J. Brodeur. 2002. Intraguild predation in biological control and conservation biology. Biol. Control 25: 216–223.

Patt, J., G. Hamilton, and J. Lashomb. 1997. Impact of strip-insectary intercropping with flowers on conservation biological control of the Colorado potato beetle. Adv. Hortic. Sci. 11: 175–181.

R Core Development Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (http://www.R-project.org/) (accessed 17 October 2013).

Rebek, E., C. Sadof, and L. Hanks. 2005. Manipulating the abundance of natural enemies in ornamental landscapes with floral resource plants. Biol. Control 33: 203–216.

Rosenheim, J., H. Kaya, L. Ehler, J. Marois, and B. Jaffee. 1995. Intraguild predation among biological-control agents: theory and evidence. Biol. Control 5: 303–335.

Stephens, M., C. France, S. Wratten, and C. Frampton. 1998. Enhancing biological control of leafrollers (Lepidoptera: Tortricidae) by sowing buckwheat (*Fagopyrum esculentum*) in an orchard. Biocontrol Sci. Tech. 8: 547–588.

Szelényi, G. 1973. Three new chalcids with host records from Hungary (Hymenoptera, Eulophidae). Ann. Hist.-Nat. Mus. Natl. Hung. 65: 305–308.

Tuell, J. 2003. Fusarium and the asparagus miner (*Ophiomyia simplex*) in Michigan. Master of Science, Department of Plant Pathology, Michigan State University, East Lansing, MI.

van Alphen, J., C. Bernstein, and G. Driessen. 2003. Information acquisition and time allocation in insect parasitoids. Trends Ecol. Evol. 18: 81–87.

Walton, N., and R. Isaacs. 2011a. Survival of three commercially available natural enemies exposed to Michigan wildflowers. Environ. Entomol. 40: 1177–1182.

Walton, N., and R. Isaacs. 2011b. Influence of native flowering plant strips on natural enemies and herbivores in adjacent blueberry fields. Environ. Entomol. 40: 697–705.

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