

Hymenopteran Parasitoids and Dipteran Predators Found Using Soybean Aphid After Its Midwestern United States Invasion

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Ann. Entomol. Soc. Am. 100(2): 196–205 (2007)

ABSTRACT Parasitoids and predatory flies that can attack soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), in soybean, *Glycine max* (L.) Merr., fields were identified 3 to 4 yr after the aphid was first sighted in the north central United States. We detected 15 species by exposing soybean aphid to ovipositing parasitoids and predatory flies at two locations in southern Michigan. The species detected were (in order of the number of specimens recovered from high to low) *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae), *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae), *Allograpta obliqua* Say (Diptera: Syrphidae), *Aphidius colemani* Viereck (Hymenoptera: Braconidae), *Eupeodes americanus* Wiedemann (Diptera: Syrphidae), *Leucopis glyphivora* Tanasijtshuk (Diptera: Chamaemyiidae), *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae), *Sphaerophoria contigua* Macquart (Diptera: Syrphidae), *Binodoxys kelloggensis* Pike, Starý & Brewer (Hymenoptera: Braconidae), *Eupeodes volucris* Osten Sacken (Diptera: Syrphidae), *Paragus hemorrhous* Meigen (Diptera: Syrphidae), *Toxomerus marginatus* Say (Diptera: Syrphidae), *Aphelinus albipodus* Hayat & Fatima (Hymenoptera: Aphelinidae), *Syrphus rectus* Osten Sacken (Diptera: Syrphidae), and *Praon* sp. (Hymenoptera: Braconidae). These species were capable of finding, attacking, and completing development on soybean aphid in soybean fields. Based on a literature review, host aphid ranges of the species detected varied widely, with a tendency toward broader host ranges. These data add to the existing information on the predatory complex currently known to attack soybean aphid in the north central United States. Implications for biological control of soybean aphid are discussed.

KEY WORDS *Aphis glycines*, biological control, natural enemies

Soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), was first sighted in the United States in July 2000 in Wisconsin (Venette and Ragsdale 2004, Ragsdale et al. 2004). It is currently distributed in 20 U.S. states and parts of Canada from Mississippi to Ontario and Delaware to Nebraska. Lower Michigan is in the approximate center of the aphid's current distribution (Venette and Ragsdale 2004). Heavy infestation by soybean aphid can cause severe damage to soybean plants. Up to 40% yield loss has been attributed to this aphid in Michigan and surrounding states (DiFonzo and Hines 2002). The North Central Research Program (2004) reported an economic threshold of 250 aphids per plant at the early reproductive (R1–R3) plant growth stages. Because the tolerable infestation levels are relatively high, biological control is a reasonable pest management option,

assuming biological control agents are available naturally or through introduction.

Before the invasion of the soybean aphid, few aphid species have been found on soybean. Irwin (1994) reported that several aphids [*Rhopalosiphum maidis* (Fitch), *Aphis spiraeicola* Patch, *Myzus persicae* (Sulzer), *Rhopalosiphum padi* (L.), *Aphis craccivora* Koch, and *Aphis gossypii* Glover] are potential vectors of soybean viruses, but he noted that these aphids do not colonize soybean. Voegtlin et al. (2004) added that although *A. gossypii* has been known to colonize soybean in North America, it rarely does so in the north central United States. Despite the previous low occurrence of aphids on soybean, a complex of 22 predator species that potentially attack soybean aphid was documented in 2001 and 2002, the first 2 yr after the aphids' first detection (Rutledge et al. 2004). Of these, the coccinellids *Harmonia axyridis* (Pallas), *Coccinella septempunctata* L., and the anthocorid *Orius insidiosus* (Say), were numerically dominant and were capable of suppressing soybean aphid (Fox et al. 2004, Rutledge and O'Neil 2005). To date, few incidences of parasitism of soybean aphid have been documented in the United States (DiFonzo and Hines 2002, Rutledge et al. 2004, Nielsen and Hajek 2005). Rutledge et al. (2004) found only three individual parasitoid mum-

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mies of soybean aphid. This lack of parasitism in the United States contrasts with China, where 15 parasitoid species are important in limiting soybean aphid population growth, with *Lysiphlebus* sp. being the most significant (Liu et al. 2004, Wu et al. 2004a). In Japan, *Aphelinus albipodus* Hayat & Fatima (Hymenoptera: Aphelinidae) is an important parasitoid of soybean aphid (Wu et al. 2004b). Ten predatory fly species have been recorded attacking soybean aphid in China, and a few species have been reported in the United States (Fox et al. 2004, Liu et al. 2004, Rutledge et al. 2004, Wu et al. 2004a).

The objectives of this study were to identify resident parasitoids and predatory flies attacking soybean aphid in lower Michigan and to compare potential host aphid ranges of the natural enemies detected based on a literature review. These data add to the existing information on the predatory complex currently known to attack soybean aphid and contribute to the discussion of approaches for biological control of this aphid in the north central United States.

Materials and Methods

Sampling Sites. Our work was conducted at the Michigan State University (MSU) Kellogg Biological Station's Long Term Ecological Research site (KBS LTER) in Hickory Corners, MI (42° 24' N, 85° 24' W) and the Michigan State University Entomology Farm in East Lansing, MI (42° 69' N, 84° 50' W) in 2003 and 2004. At the KBS LTER site, we sampled 10 1-ha soybean plots in 2003, and four 9.1- by 27.4-m soybean plots in 2004. The Entomology farm location consisted of one soybean field (100 by 50 m) in 2003 and eight 18.3- by 6.1-m soybean plots in 2004. The Entomology farm is ≈80 km from the KBS LTER site.

Sampling Procedures. Natural enemy surveys were done in three collection periods in 2003 and four collection periods in 2004 during the soybean growing season. The 2003 samples were taken on 27–30 June, 1–5 August, and 12–15 September at the KBS LTER, and 9–12 July, 8–11 August, and 19–23 September at the Entomology Farm. The 2004 samples were taken on 14–17 June, 16–19 July, 16–19 August, and 7–10 September at the KBS LTER, and 21–24 June, 19–22 July, 23–26 August, and 13–16 September at the Entomology Farm. At each sampling site pots of soybean plants infested with soybean aphid were set in the soybean fields where they were exposed to parasitism and predation. This method has been previously shown to be effective in detecting hymenopteran parasitoids and dipteran predators (Noma et al. 2005). In 2003, 60 pots in total were placed in the field at the KBS LTER and 15 pots in total at the Entomology farm during each of three sampling periods. In 2004, 20 pots in total were placed in the field at the KBS LTER and 40 pots in total at the Entomology farm during each of four sampling periods. At the KBS LTER, one pot was set at each of four sampling stations scattered within each of the soybean plots. At the Entomology farm in 2003, the four quadrants of the field sampled were considered separately to calculate means.

To prepare the pots, 15 soybean seeds (variety RT2985, Cropland Genetics, St. Paul, MN) were planted in round plastic pots (17 cm in height and 15.2 cm in diameter) filled with 2 liters of soil (Baccto high-porosity professional planting mix, Michigan Peat Company, Houston, TX). When the soybean plants had reached the third trifoliate vegetative stage (V2) (Fehr and Caviness 1977), plants were infested with aphids by using plant clippings from a cultured soybean aphid colony. The colony was obtained from the former USDA-APHIS Plant Protection Laboratory in Niles, MI, and maintained on soybean plants at 22°C and a photoperiod of 16:8 (L:D) h. The infested plant clippings from the colony were distributed evenly by mass among the pots (Ahern and Brewer 2002). Infestation averaged ≈1,300 aphids per pot. The potted soybean plants infested with aphids were taken to the field within 4 d of infestation. An additional five pots of infested soybean plants were kept in the laboratory to check for possible parasitoid or predatory fly contamination in the laboratory.

In the field, the pots were buried halfway to the rim in the ground, and aphids were exposed to ovipositing parasitoids and predatory flies for 3–4 d at each sampling period. A square plate of clear Plexiglas (18 by 18 cm) was suspended over each pot to deter rain from washing away the aphids. After field exposure, the pots were collected, returned to the laboratory, and covered with cloth mesh fastened over the pot with an elastic band. The pots were incubated at 21°C and a photoperiod of 16:8 (L:D) h in the laboratory for 1 wk to allow natural enemies to develop. After this incubation period, the plants were clipped at the base and were placed in emergence canisters with an attached collection vial to capture emerging adult parasitoids and predatory flies (Noma et al. 2005). The canisters were maintained at room temperature (21°C) under constant light for 2 wk. We supplied an abundant resource of aphids in the pots (average infestation of 1,300 per pot when placed in the field) to reduce complications of intraguild predation (i.e., reduce the chances of predators consuming aphids that have been parasitized) (Mayhöfer and Klug 2002). Ladybugs and lacewings also were removed as the pots were brought back from the field.

The specimens collected in the emergence canister vials were examined under a dissecting microscope. The inner contents of the emergence canister also were checked to maximize likelihood of detecting predatory flies and parasitoids. Species were identified using keys and other materials found in Vockeroth (1992), Pike et al. (1997), Gagné (1981), and Heiss (1938).

Soybean aphids were sampled from every plot at both locations during each collection period. In each plot, 20 randomly selected soybean plants were inspected for aphid infestation. The number of aphids on each plant was estimated using the count ranges 0, 1–5, 6–10, 11–25, 26–50, 51–100, 101–500, and 501–10,000 aphids. The last category was based on our field observations and past studies (DiFonzo and Hines 2002), which indicated wide variation of aphid densities once

Table 1. Relative abundance (mean number of specimens per pot \pm SEM) of soybean aphid parasitoids and predatory flies detected at the Kellogg Biological Station LTER (KBS LTER), Hickory Corners, and the Entomology farm (Ent. Farm), Michigan State University, East Lansing, MI

Species	2003		2004	
	KBS LTER	Ent. Farm	KBS LTER	Ent. Farm
Parasitoids ^a				
B: <i>Lysiphlebus testaceipes</i>	0.22 \pm 0.10bc	1.38 \pm 0.66b	2.63 \pm 1.19bc	1.26 \pm 0.39b
B: <i>Aphidius colemani</i>	0.23 \pm 0.11bc	0.04 \pm 0.04b		0.25 \pm 0.22c
A: <i>Aphelinus asychis</i>	0.01 \pm 0.01c	0.23 \pm 0.12b		0.02 \pm 0.01c
B: <i>Binodoxys kelloggensis</i> ^b		0.02 \pm 0.02b	0.16 \pm 0.10c	0.02 \pm 0.01c
A: <i>Aphelinus albipodus</i>	0.01 \pm 0.01c	0.02 \pm 0.02b		
B: <i>Praon</i> sp. ^c	0.01 \pm 0.01c	0.02 \pm 0.02b		0.01 \pm 0.01c
Predatory flies ^a				
Ce: <i>Aphidoletes aphidimyza</i>	2.57 \pm 0.74a	10.72 \pm 2.35a	18.80 \pm 2.02a	29.35 \pm 2.48a
S: <i>Allograpta obliqua</i>	0.24 \pm 0.05b	0.28 \pm 0.12b	0.91 \pm 0.18b	1.08 \pm 0.20b
S: <i>Eupeodes americanus</i>	0.18 \pm 0.06bc		0.04 \pm 0.03c	0.17 \pm 0.06c
Ch: <i>Leucopis glyphinivora</i>	0.01 \pm 0.01c		0.04 \pm 0.04c	0.26 \pm 0.08c
S: <i>Sphaerophoria contigua</i>	0.01 \pm 0.01c		0.20 \pm 0.09bc	0.03 \pm 0.02c
S: <i>Eupeodes volucris</i>	0.01 \pm 0.01c	0.13 \pm 0.13b		
S: <i>Paragus haemorrhous</i>	0.04 \pm 0.02bc			0.01 \pm 0.01c
S: <i>Toxomerus marginatus</i>	0.01 \pm 0.01c	0.02 \pm 0.02b		
S: <i>Syrphus rectus</i>				0.03 \pm 0.02c

Numbers represent the mean number of specimens detected per pot \pm SEM. Different letters within a column indicate a significant difference by Tukey's multiple comparisons at $\alpha = 0.05$.
^a Parasitoid (Hymenoptera) families: B, Braconidae; A, Aphelinidae. Predatory fly (Diptera) families: Ce, Cecidomyiidae; S, Syrphidae; Ch, Chamaemyiidae.
^b Described as a new species (Pike et al. 2007).
^c We were unable to identify the species because the key relied on female characteristics to identify the species and only male specimens were found.

populations surpassed several hundred per plant. All aphid mummies were recorded individually.

Host Aphid Range of Natural Enemies Detected. Known aphid hosts and their plant habitats associated with soybean aphid enemies detected in this study were summarized through a literature review by using Agricola, covering the period 1916–2005 (Agricola 2005).

Voucher Specimens. *Leucopis glyphinivora* Tanasijtshuk (Diptera: Chamaemyiidae) was deposited as SDG dissection 1258-1270 in the United States National Museum collection, Washington, D.C. Paratypes of the newly described species found in this study, *Binodoxys kelloggensis* Pike, Starý & Brewer (Hymenoptera: Braconidae) (Pike et al. 2007) were deposited in the A. J. Cook Arthropod Research Collection of the Entomology Department, Michigan State University (8 ♀, 8 ♂). All other species were deposited in the A. J. Cook Arthropod Research Collection (VC 2006-01).

Statistical Analysis. To obtain a field aphid density estimate, we used the midpoint of each aphid count range per plant and calculated the average density among the 20 plants sampled per plot during each sampling period. Aphid parasitism rates in the field were estimated by dividing the average number of mummies per plant by the average number of aphids detected per plant for each sampling date. As a relative indicator of species prevalence, number of recoveries per potted plant was compared among species using data summed across all sampling periods within each year, site, and plot. The counts (x) were transformed into a logarithmic scale ($\log [100x + 1/6]$) to satisfy the assumption of normality for analysis of variance

(ANOVA) (Mosteller and Tukey 1977). An ANOVA (PROC GLM, SAS Institute 2000) was used in which insect count per pot was the dependent variable, and the listing of natural enemies collected was the independent variable. The analysis was performed separately for each sampling site and year. When significant differences among species were detected in the analysis, Tukey's multiple comparisons procedure was used for mean separation of species abundance.

Results

Parasitoids and Predatory Flies Detected. We detected a total of 15 parasitoid and predatory fly species attacking soybean aphid at the two locations across all sampling periods. There were six species of parasitoids (Hymenoptera: four Braconidae and two Aphelinidae) and nine species of predatory flies (Diptera: seven Syrphidae, one Cecidomyiidae, and one Chamaemyiidae) (Table 1). Fourteen species were identified to species (five parasitoids and nine predatory flies). All *Praon* sp. (Hymenoptera: Braconidae) detected were males, not allowing species identification. In 2003, *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) was the most abundant natural enemy detected from both field sites (KBS LTER, $F = 13.31$; $df = 12, 52$; $P < 0.0001$; Ent Farm, $F = 17.30$; $df = 9, 30$; $P < 0.0001$). *Allograpta obliqua* Say (Diptera: Syrphidae) was also significantly more abundant than the other natural enemies except *A. aphidimyza* at the KBS LTER site in 2003. Although six parasitic wasps in total were detected, season-long differences in relative abundance were not detected in

2003. Field aphid infestation peaked at an average density of $1,950 \pm 170$ (SEM) aphids per plant.

In 2004, *A. aphidimyza* was once again the most abundant species detected at both field sites (KBS LTER, $F = 49.55$; $df = 6, 21$; $P < 0.0001$; Ent Farm, $F = 327.45$; $df = 11, 36$; $P < 0.0001$). *A. obliqua* was also more abundant than most of the other species detected. *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae) was the most abundant parasitoid among five detected at the Entomology farm in 2004. Only two parasitoid species (*L. testaceipes* and *B. kelloggensis*) were detected at the KBS LTER. Field aphid densities were lower than the previous year, with average infestation levels peaking at a density of 62 ± 10 (SEM) aphids per plant.

Aphid Host Range of Species Detected. The four parasitoids identified to species were known to use 18–147 other aphid species as hosts (Table 2). Of these species, *L. testaceipes* had the greatest number of documented aphid hosts (147 species) and associated plant habitats (42 plant families). The three other parasitoids (*Aphidius colemani* Viereck [Hymenoptera: Braconidae], *Aphelinus asychis* Walker [Hymenoptera: Aphelinidae], and *A. albipodus*) were each known to parasitize 18 aphid species feeding on plants from five to eight different plant families (Table 2).

The nine species of flies that attacked soybean aphid were previously documented to prey on two to 70 aphid species (Table 2). Of these, *L. glyphivora* and *A. aphidimyza* had the greatest number of known aphid prey species (70 and 63, respectively), although for the former, this represents the first published record on soybean aphid. *Toxomerus marginatus* Say (Diptera: Syrphidae) had the least number of known aphid prey species (two) (Table 2). The other flies detected (*A. obliqua*, *Eupeodes americanus* Wiedemann (Diptera: Syrphidae), *Eupeodes volucris* Osten Sacken [Diptera: Syrphidae], *Paragus hemorrhous* Meigen [Diptera: Syrphidae], *Sphaerophoria contigua* Macquart [Diptera: Syrphidae], and *Syrphus rectus* Osten Sacken [Diptera: Syrphidae]) had documented aphid hosts ranging from 10 to 25 species (Table 2). The known plant groups in which these predatory flies preyed on aphids ranged from one (*T. marginatus*) to 10 (*E. volucris* and *S. contigua*) plant families (Table 2). All 13 of the above-mentioned parasitoid and predatory fly species were documented to attack a number of aphid species in the genus *Aphis*, of which soybean aphid is a member. *Aphis* species made up the greatest proportion of the aphid host ranges of the natural enemies (21–53%) compared with aphid species in other genera (Table 2).

Discussion

Within 3 yr of soybean aphid's invasion of the north central United States, we detected a diverse group of hymenopteran parasitoids (six species) and dipteran predators (nine species) attacking soybean aphid, even though few of these species had been previously detected (Rutledge et al. 2004, Nielsen and Hajek 2005). In comparison, 15 parasitoid and 10 predatory

fly species have been detected in China and are reported as significant natural enemies of soybean aphid (Liu et al. 2004, Wu et al. 2004a). We note that *P. hemorrhous* is closely related to but apparently distinct from *Paragus tibialis* Fallen (Vockeroth 1992), which is recorded attacking soybean aphid in China (Liu et al. 2004).

There are more species of parasitoids and predatory flies in China than detected in our study, but the taxonomic diversity is about the same. Our detection of field parasitism was low (up to 0.6% parasitism), but it did exceed the previous trace detections (Rutledge et al. 2004). Aphid predation by the flies was also commonly observed in the field (M.E.K. and T.N., unpublished data). Our parasitoid and predatory fly detections in soybean, both from the aphid-infested plants and field observations, support more work on the ecological associations of these species, particularly some of the relatively more abundant predatory fly species detected in this study. For the parasitoids, the low detection levels were disappointing, supporting consideration of introducing additional parasitoids if such low detections continue. However, taxonomic diversity of the species detected reflected that found in China (Wu et al. 2004).

Working on the invasive Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), in the west central Great Plains of the United States, Brewer et al. (2005) found good parasitoid diversity but low parasitoid occurrence during the first 3 to 5 yr of the aphid's invasion. During the following 5 yr, shifts in parasitoid prevalence and abundance occurred with a few species that were most likely long-term residents of the region contributing substantially to aphid mortality when conditions were conducive to aphid outbreaks (Brewer et al. 2005). This longitudinal study was complicated by releases of introduced parasitoids, and taxonomic difficulties in separating some resident and introduced strains and species (Brewer et al. 2005). Cornell and Hawkins (1993), based on a literature review, also found parasitoid–host association shifts through decades-long time periods after establishment of an introduced herbivore. Our findings are certainly consistent with the view that resident predatory flies and parasitoids have the potential to contribute to suppression of soybean aphid, along with the better understood aphid suppression by *H. axyridis* and *O. insidiosus* (Fox et al. 2004, Rutledge and O'Neil 2005). We caution against speculating on these parasitoids and predatory flies contributing to soybean aphid biological control for the reasons discussed above and because the aphid-infested plant material used were a different age and often contained a higher aphid density than the soybean plants in the surrounding fields. Additional experimentation would be beneficial to estimate the potential of the more prevalent species detected in contributing to soybean aphid biological control.

Soybean aphid parasitoids and predatory flies detected in this study mostly have broad host aphid records of at least nine aphid species within seven aphid genera (with the exception of *T. marginatus*,

Table 2. Aphid host records and associated plant families documented for parasitoids and predatory flies detected utilizing soybean aphid in two locations in Michigan, 2003 and 2004

Parasitoids/predatory flies ^a	Aphid genera: no. host species ^b	Plant family association ^c	References ^d
<i>Lysiphlebus testaceipes</i>	<i>Acyrtosiphon</i> : 3 sp.	8, 24, 26	C
	<i>Anoecia</i> : 1 sp.	19	C
	<i>Aphis</i> : 63 sp.	3, 4, 5, 7, 8, 10, 11, 12, 14, 16, 17, 18, 19, 21, 22, 24, 26, 28, 29, 32, 34, 36, 39, 41, 42, 43, 44, 45, 46, 48, 49, 50, 52, 55	C, L, P, Q, R
	<i>Aphthargelia</i> : 1 sp.	14	C
	<i>Boernerina</i> : 1 sp.	9	C
	<i>Brachycaudus</i> : 3 sp.	8, 11	C, R
	<i>Braggia</i> : 2 sp.	39	C, Q
	<i>Brachycorynella</i> : 1 sp.	7	C
	<i>Brevicoryne</i> : 1 sp.	12	C, L, Q
	<i>Capitophorus</i> : 2 sp.	8	CL
	<i>Cavariella</i> : 2 sp.	3	C
	<i>Ceruraphis</i> : 1 sp.	14	C
	<i>Chaetosiphon</i> : 1 sp.	44	C
	<i>Chaitophorus</i> : 2 sp.	47	C
	<i>Cinara</i> : 2 sp.	35	C
	<i>Cryptomyzus</i> : 1 sp.	Unknown	Q
	<i>Dactynotus</i> : 2 sp.	Unknown	Q
	<i>Diuraphis</i> : 1 sp.	37	C, I
	<i>Dysaphis</i> : 2 sp.	44	C, Q
	<i>Ericaphis</i> : 1 sp.	44	C
	<i>Eriosoma</i> : 2 sp.	44, 53	C
	<i>Hyadaphis</i> : 2 sp.	3	C, R
	<i>Hyperomyzus</i> : 1 sp.	8, 26	C
	<i>Hysteroneura</i> : 1 sp.	Unknown	L, Q
	<i>Illinoia</i> : 1 sp.	44	C
	<i>Kakimia</i> : 1 sp.	Unknown	Q
	<i>Lipaphis</i> : 1 sp.	Unknown	Q
	<i>Macrosiphum</i> : 10 sp.	8, 24, 34, 44, 50	C, L, Q, R
	<i>Melanaphis</i> : 3 sp.	Unknown	Q, R
	<i>Myzus</i> : 5 sp.	4, 8, 43, 44, 50	C, L, Q, R
	<i>Nasonovia</i> : 1 sp.	26	C
	<i>Nearctaphis</i> : 4 sp.	24, 44, 49	C
	<i>Phorodon</i> : 1 sp.	13	C, Q
	<i>Pseudoepameibaphis</i> : 1 sp.	8	C
	<i>Pterocomma</i> : 1 sp.	47	C
	<i>Rhopalosiphum</i> : 7 sp.	12, 37, 44, 52	B, C, I, L, Q, R
	<i>Roepkea</i> : 1 sp.	Unknown	Q
	<i>Schizaphis</i> : 1 sp.	37	C, Q, S
	<i>Sipha</i> : 1 sp.	Unknown	Q
	<i>Sitobion</i> : 3 sp.	37, 43, 44	C, Q
	<i>Toxoptera</i> : 3 sp.	46	L, P, Q, R
	<i>Tuberculatus</i> : 1 sp.	25, 47	C
	<i>Uroleucon</i> : 2 sp.	8	C
<i>Aphidius colemani</i>	<i>Acyrtosiphon</i> : 1sp.	Unknown	S
	<i>Aphis</i> : 6sp.	6, 20, 24, 50	A, C, P, S
	<i>Brachycaudus</i> : 2 sp.	8	C, S
	<i>Ephedraphis</i> : 1sp.	Unknown	S
	<i>Hyadaphis</i> : 1 sp.	31	C
	<i>Hyalopterus</i> : 1 sp.	37, 44	P, S
	<i>Lipaphis</i> : 1 sp.	Unknown	C
	<i>Macrosiphum</i> : 1 sp.	Unknown	C
	<i>Melanaphis</i> : 1 sp.	Unknown	P
	<i>Myzus</i> : 2 sp.	24, 50	C
	<i>Toxoptera</i> : 1 sp.	Unknown	P
<i>Aphelinus asychis</i>	<i>Aphis</i> : 4 sp.	8, 24, 32	A, C, D, W
	<i>Acyrtosiphon</i> : 1 sp.	24	G
	<i>Brevicoryne</i> : 1 sp.	12	G, V
	<i>Dactynotus</i> : 1 sp.	8	G
	<i>Diuraphis</i> : 2 sp.	37	G
	<i>Lipaphis</i> : 1 sp.	12	G, V
	<i>Myzus</i> : 2 sp.	12	G, W
	<i>Rhopalosiphum</i> : 2 sp.	37	G
	<i>Sitobion</i> : 1 sp.	37	G
	<i>Schizaphis</i> : 1 sp.	37	G
	<i>Therioaphis</i> : 2 sp.	24	O
<i>Aphelinus albipodus</i>	<i>Aphis</i> : 7 sp.	3, 8, 20, 32, 50	A, G, V, W, X, Y
	<i>Acyrtosiphon</i> : 1 sp.	24	G
	<i>Brevicoryne</i> : 1 sp.	12	G
	<i>Diuraphis</i> : 2 sp.	37	G

Parasitoids/predatory flies ^a	Aphid genera: no. host species ^b	Plant family association ^c	References ^d
	<i>Lipaphis</i> : 1 sp.	12	G
	<i>Myzus</i> : 1 sp.	12, 37	G
	<i>Rhopalosiphum</i> : 2 sp.	37	G
	<i>Sitobion</i> : 1 sp.	37	G
	<i>Schizaphis</i> : 1 sp.	37	G
	<i>Therioaphis</i> : 1 sp.	24	G
Predatory flies			
<i>Aphidoletes aphidimyza</i>	<i>Acyrtosiphon</i> : 2 sp.	24	M
	<i>Aphis</i> : 14 sp.	8, 20, 37, 44, 54	A, J, M
	<i>Aulacorthum</i> : 1 sp.	Unknown	M
	<i>Brachycaudus</i> : 3 sp.	Unknown	M
	<i>Brevicoryne</i> : 1 sp.	12	M
	<i>Capitophorus</i> : 1 sp.	Unknown	M
	<i>Cavariella</i> : 1 sp.	Unknown	M
	<i>Chaetosiphon</i> : 1 sp.	Unknown	M
	<i>Chaitophorus</i> : 2 sp.	Unknown	M
	<i>Cryptomyzus</i> : 1 sp.	Unknown	M
	<i>Dysaphis</i> : 2 sp.	Unknown	M
	<i>Hyadaphis</i> : 2 sp.	Unknown	M
	<i>Hyalopterus</i> : 1 sp.	37	J, M
	<i>Hyperomyzus</i> : 1 sp.	Unknown	M
	<i>Hysteroneura</i> : 1 sp.	Unknown	M
	<i>Lipaphis</i> : 1 sp.	Unknown	M
	<i>Longicaudus</i> : 1 sp.	Unknown	M
	<i>Macrosiphoniella</i> : 2 sp.	Unknown	M
	<i>Macrosiphum</i> : 5 sp.	20, 44	F, J, M
	<i>Megoura</i> : 2 sp.	24	M
	<i>Metopeurum</i> : 1 sp.	Unknown	M
	<i>Microphium</i> : 1 sp.	Unknown	M
	<i>Myzocallis</i> : 1 sp.	Unknown	M
	<i>Myzus</i> : 3 sp.	12, 50	K, M
	<i>Nasonovia</i> : 2 sp.	Unknown	M
	<i>Periphyllus</i> : 2 sp.	Unknown	M
	<i>Phorodon</i> : 1 sp.	Unknown	M
	<i>Rhopalosiphum</i> : 2 sp.	Unknown	M
	<i>Schizaphis</i> : 1 sp.	Unknown	M
	<i>Schizoneura</i> : 1 sp.	Unknown	M
	<i>Sipha</i> : 1 sp.	Unknown	M
	<i>Uroleucon</i> : 2 sp.	Unknown	M
<i>Allograpta obliqua</i>	<i>Amphorophora</i> : 1 sp.	8	A
	<i>Aphis</i> : 8 sp.	20, 24, 39, 44	A, D, E
	<i>Brevicoryne</i> : 1 sp.	12	D
	<i>Macrosiphum</i> : 1 sp.	8	D
	<i>Myzocallis</i> : 1 sp.	Unknown	D
	<i>Myzus</i> : 2 sp.	12, 25	D
	<i>Rhopalosiphum</i> : 1 sp.	12	D
<i>Eupeodes americanus</i>	<i>Aphis</i> : 3 sp.	24, 44	A, N
	<i>Chaitophorus</i> : 1 sp.	Unknown	N
	<i>Dysaphis</i> : 1 sp.	Unknown	H
	<i>Eriosoma</i> : 1 sp.	Unknown	H
	<i>Microparsus</i> : 1 sp.	Unknown	N
	<i>Pterocomma</i> : 1 sp.	47	N
	<i>Schizoneura</i> : 1 sp.	44	N
	<i>Symdobius</i> : 1 sp.	9	N
<i>Leucopis glyphinivora</i>	<i>Acyrtosiphon</i> : 1 sp.	24	U
	<i>Amphorophora</i> : 1 sp.	44	U
	<i>Anuraphis</i> : 1 sp.	28	U
	<i>Aphidura</i> : 2 sp.	15, 44	U
	<i>Aphis</i> : 21 sp.	8, 20, 23, 24, 26, 27, 28, 30, 32, 39, 40, 44, 46, 47, 49, 50	A, U
	<i>Brachycaudus</i> : 7 sp.	8, 15, 44	U
	<i>Brachyunguis</i> : 2 sp.	51, 56	U
	<i>Brevicoryne</i> : 1 sp.	12	U
	<i>Cavariella</i> : 1 sp.	3	U
	<i>Chaitophorus</i> : 1 sp.	47	U
	<i>Cinara</i> : 1 sp.	38	U
	<i>Coloradoa</i> : 1 sp.	8	U
	<i>Cryptosiphum</i> : 1 sp.	8	U
	<i>Dactynotus</i> : 1 sp.	8	U
	<i>Diuraphis</i> : 1 sp.	37	U
	<i>Dysaphis</i> : 6 sp.	44	U
	<i>Eriosoma</i> : 1 sp.	44	U
	<i>Glyphina</i> : 2 sp.	9	U

Table 2. Continued

Parasitoids/predatory flies ^a	Aphid genera: no. host species ^b	Plant family association ^c	References ^d
	<i>Hyadaphis</i> : 1 sp.	14	U
	<i>Hyalopterus</i> : 1 sp.	44	U
	<i>Lipaphis</i> : 1 sp.	Unknown	U
	<i>Laingia</i> : 1 sp.	37	U
	<i>Macrosiphoniella</i> : 2 sp.	8	U
	<i>Metopeurum</i> : 1 sp.	8	U
	<i>Microsiphum</i> : 1 sp.	8	U
	<i>Myzaphis</i> : 1 sp.	44	U
	<i>Myzus</i> : 2 sp.	44	U
	<i>Pterochloroides</i> : 1 sp.	44	U
	<i>Rhopalosiphum</i> : 2 sp.	37, 44	U
	<i>Roepkea</i> : 1 sp.	Unknown	U
	<i>Schizaphis</i> : 1 sp.	37	U
	<i>Semiaphis</i> : 1 sp.	Unknown	U
	<i>Sitobion</i> : 1 sp.	37	U
	<i>Thelaxes</i> : 1 sp.	25	U
	<i>Anuraphis</i> : 1 sp.	24	E
	<i>Aphis</i> : 7 sp.	19, 39, 52	A, E
	<i>Cinara</i> : 1 sp.	Unknown	D
	<i>Brevicoryne</i> : 2 sp.	Unknown	E
	<i>Capitophorus</i> : 1 sp.	26	E
	<i>Macrosiphum</i> : 2 sp.	24	E
	<i>Myzocallis</i> : 1 sp.	Unknown	E
<i>Eupeodes volucris</i>	<i>Myzus</i> : 3 sp.	44	E
	<i>Pemphigus</i> : 1 sp.	17	E
	<i>Periphyllus</i> : 1 sp.	1	E
	<i>Rhopalosiphum</i> : 1 sp.	Unknown	E
	<i>Aphis</i> : 7 sp.	8, 20, 24, 34, 39	A, E
	<i>Myzocallis</i> : 1 sp.	6	E
	<i>Myzus</i> : 1 sp.	12	E
<i>Paragus haemorrhous</i>	<i>Acyrtosiphon</i> : 1 sp.	24	T
	<i>Aphis</i> : 6 sp.	8, 19, 20, 34, 39	A, T
<i>Sphaerophoria contigua</i>	<i>Brachycaudus</i> : 1 sp.	Unknown	T
	<i>Brevicoryne</i> : 1 sp.	12	T
	<i>Chromaphis</i> : 1 sp.	New	T
	<i>Hyadaphis</i> : 1 sp.	12	T
	<i>Macrosiphoniella</i> : 1 sp.	8	T
	<i>Macrosiphum</i> : 2 sp.	8, 44	T
	<i>Myzaphis</i> : 2 sp.	8, 25, 33, 44	T
	<i>Myzus</i> : 2 sp.	12, 44	T
	<i>Nasonovia</i> : 1 sp.	8	T
	<i>Nearctaphis</i> : 1 sp.	Unknown	T
	<i>Neoceruraphis</i> : 1 sp.	14	T
	<i>Phorodon</i> : 1 sp.	44	T
	<i>Rhopalosiphum</i> : 1 sp.	44	T
	<i>Acyrtosiphon</i> : 1 sp.	24	D
	<i>Aphis</i> : 1 sp.	24	A
	<i>Aphis</i> : 5 sp.	14, 24, 34, 39, 44	A, E, Z
	<i>Cinara</i> : 1 sp.	35	E
	<i>Dysaphis</i> : 1 sp.	44	Z
	<i>Eriosoma</i> : 1 sp.	Unknown	Z
<i>Toxomerus marginatus</i>	<i>Macrosiphum</i> : 3 sp.	8, 24	E
	<i>Myzocallis</i> : 1 sp.	25	E
	<i>Myzus</i> : 1 sp.	12	E
	<i>Rhopalosiphum</i> : 1 sp.	2	E
<i>Syrphus rectus</i>			

^a Parasitoids and predatory flies identified to species were included in the table with the exception of *B. kelloggensis*. It is newly described, and its aphid hosts have not been determined, but probably they are in the genus *Aphis* (Pike et al. 2007).

^b Number of species in each aphid genus known to be attacked by the specified natural enemy. Species number is based only on those identified to species in the reference.

^c Plant families (by code) known to harbor the corresponding aphid species and on which the natural enemy species was observed. Codes: 1, Aceraceae; 2, Anacardiaceae; 3, Apiaceae; 4, Apocynaceae; 5, Araliaceae; 6, Asclepiadaceae; 7, Asparagaceae; 8, Asteraceae; 9, Betulaceae; 10, Bignoniaceae; 11, Boraginaceae; 12, Brassicaceae; 13, Cannabaceae; 14, Caprifoliaceae; 15, Caryophyllaceae; 16, Celastraceae; 17, Chenopodiaceae; 18, Clusiaceae; 19, Cornaceae; 20, Cucurbitaceae; 21, Dipsacaceae; 22, Ericaceae; 23, Euphorbiaceae; 24, Fabaceae; 25, Fagaceae; 26, Grossulariaceae; 27, Iridaceae; 28, Lamiaceae; 29, Liliaceae; 30, Loasaceae; 31, Loranaceae; 32, Malvaceae; 33, Oleaceae; 34, Onagraceae; 35, Pinaceae; 36, Pittosporaceae; 37, Poaceae; 38, Podocarpaceae; 39, Polygonaceae; 40, Portulacaceae; 41, Punicaceae; 42, Pyrolaceae; 43, Rhamnaceae; 44, Rosaceae; 45, Rubiaceae; 46, Rutaceae; 47, Salicaceae; 48, Saxifragaceae; 49, Scrophulariaceae; 50, Solanaceae; 51, Tamaricaceae; 52, Typhaceae; 53, Ulmaceae; 54, Urticaceae; 55, Valerianaceae; 56, Zygophyllaceae; Unknown, plant host not specified in the literature.

^d Literature sources by code: A, M.E.K. and T.N., personal observations; B, Pike et al. 1997; C, Pike et al. 2000; D, Vockerroth 1992; E, Heiss 1938; F, Lucas et al. 1998; G, Elliott et al. 1999; H, Short and Bergh 2004; I, Feng et al. 1992; J, Havelka and Zemek 1999; K, Choi et al. 2004; L, Schlenger and Hall 1960; M, Harris 1973; N, Metcalf 1916; O, van den Bosch et al. 1957; P, Star&yacut;e; 1976; Q, Mackauer and Star&yacut;e; 1967; R, Star&yacut;e; et al. 1988; S, Star&yacut;e; 1979; T, Knutson 1973; U, Tanasijtshuk 1986; V, Hayat 1998; W, Takada 2002; X, Heimpel et al. 2004; Y, Hayat and Fatima 2004; Z, Short and Bergh 2005.

which has only two aphid prey on record). The compiled records show that aphids in the genus *Aphis* were consistently the most common prey for the parasitoids and predatory flies compared with other aphid genera (Table 2). This trend at least partly reflects that the genus *Aphis* has the most species of all the aphid genera (Blackman and Eastop 2000). The majority of these parasitoids and predatory flies also have broad plant association records of at least five plant families. These records suggest that the parasitoids and predatory flies beginning to use soybean aphid are present in a variety of vegetation where other aphids are present (Table 2). With the narrow host plant range of soybean aphid in North America (Blackman and Eastop 2000), alternate aphid hosts on a variety of plants and the potential for these enemies to move into soybean may be particularly relevant in considering habitat manipulation strategies to encourage these parasitoids and predatory flies to use soybean aphid (Powell 1986). A potential challenge associated with parasitoids is that the physiological host range may not match the ecological host range (Powell 1986, van Emden 1965). Even those with very broad host ranges may have host and habitat preferences, possibly affecting the use of soybean aphid.

Despite these uncertainties, selected species we detected deserve special attention for further work, based on their relative prevalence early in the invasion front of soybean aphid found in this study (Table 1), their broad aphid and plant associations (Table 2), and their prior performance as biological control agents of aphids found in the literature. The fly *A. aphidimyza* was common at both field sites in both 2003 and 2004. The fly *A. obliqua* was the second most common predatory fly, particularly in 2004 (Table 1). Both have broad host aphid ranges and are found in many habitats (Table 2). Despite low field parasitism, continued observation of *L. testaceipes*, *A. colemani*, *A. asychis*, and *A. albipodus* is warranted based on past histories in North America (Pike et al. 2000, Brewer and Elliott 2004) and elsewhere (Wratten and Powell 1991, Stary 1999). More generally, as a foundation in considering biological control approaches to manage soybean aphid, we add parasitoids and predatory flies and known aphid-plant associations of these species to the information on the complex of predators previously detected attacking soybean aphid (Fox et al. 2004, Rutledge et al. 2004).

Acknowledgments

We thank A. Corbin (MSU) and the planning committee of Kellogg Biological Station LTER for permission to use plots. We thank D. Landis and A. Costamagna (MSU) for providing supplies. We thank A. Frasier (Kalamazoo College) for a review of an earlier version of this work. We also thank R. J. Gagné (USDA-ARS, Systematic Entomology Laboratory, Beltsville, MD) for confirming our cecidomyiid identification. We thank Alexandre Latchininsky (University of Wyoming) for assistance in translations from Russian. Support for this research was provided by the National Science Foundation Long-Term Ecological Research Program at the Kellogg Biological Station, the Project GREEN ini-

tiative of Michigan State University, and the North Central Region IPM Competitive Grants Program.

References Cited

- Agricola. 2005. AGRICOLA. National Agricultural Library, Beltsville, MD. (<http://agricola.nal.usda.gov>).
- Ahern, R. G., and M. J. Brewer. 2002. Effect of different wheat production systems on the presence of two parasitoids (Hymenoptera: Aphelinidae; Braconidae) of the Russian wheat aphid in the North American Great Plains. *Agric. Ecosyst. Environ.* 92: 201–210.
- Blackman, R. L., and V. F. Eastop. 2000. Aphids on the world's crops: an identification and information guide. Wiley, Chichester, NY.
- Brewer, M. J., and N. C. Elliott. 2004. Biological control of cereal aphids and mediating effects of host plant and habitat manipulations. *Annu. Rev. Entomol.* 49: 219–242.
- Brewer, M. J., T. Noma, and N. C. Elliott. 2005. Hymenopteran parasitoids and dipteran predators of the invasive aphid *Diuraphis noxia* after enemy introductions: temporal variation and implication for future aphid invasions. *Biol. Control* 33: 315–323.
- Choi, M., B. D. Roitberg, A. Shani, D. A. Raworth, and G. Lee. 2004. Olfactory response by the aphidophagous gall midge, *Aphidoletes aphidimyza*, to honeydew from green peach aphid, *Myzus persicae*. *Entomol. Exp. Appl.* 111: 37–45.
- Cornell, H. V., and B. A. Hawkins. 1993. Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. *Am. Nat.* 141: 847–865.
- DiFonzo, C., and R. Hines. 2002. Soybean aphid in Michigan: update from the 2001 season. Extension Bulletin E-2748, Michigan State University, East Lansing.
- Elliott, N. C., J. H. Lee, and S. D. Kindler. 1999. Parasitism of several aphid species by *Aphelinus asychis* Walker and *Aphelinus albipodus* Hayat and Fatima. *Southwest. Entomol.* 24: 5–12.
- Fehr, W. R., and C. E. Caviness. 1977. Stages of soybean development. SR80, Iowa State University, Ames, IA.
- Feng, M., J. B. Johnson, and S. E. Halbert. 1992. Parasitoids (Hymenoptera: Aphidiidae) and their effect on aphid (Homoptera: Aphididae) populations in irrigated grain in Southwest Idaho. *Environ. Entomol.* 21: 1433–1440.
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. DiFonzo. 2004. Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environ. Entomol.* 33: 608–618.
- Gagné, R. J. 1981. Cecidomyiidae, pp. 257–292. In J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. H. Teskey, J. R. Vockeroth, and D. M. Wood [eds.], *Manual of Nearctic Diptera*. Agricultural Canada, Ottawa, Canada.
- Harris, K. M. 1973. Aphidophagous Cecidomyiidae (Diptera): taxonomy, biology and assessments of field populations. *Bull. Entomol. Res.* 63: 305–325.
- Havelka, J., and R. Zemek. 1999. Life table parameters and oviposition dynamics of various populations of the predaceous gall-midge *Aphidoletes aphidimyza*. *Entomol. Exp. Appl.* 91: 481–484.
- Hayat, M. 1998. Aphelinidae of India (Hymenoptera: Chalcidoidea): a taxonomic revision. *Memoirs on Entomology, International* 13.
- Hayat, M., and K. Fatima. 1992. Taxonomic studies on *Aphelinus* (Hymenoptera: Aphelinidae). 5. Description of a new species and further records of *A. gossypii*, with a new synonymy. *Entomon.* 17: 103–107.

- Heimpel, G. E., D. W. Ragsdale, R. C. Venette, K. R. Hopper, R. J. O'Neil, C. E. Rutledge, and Z. Wu. 2004. Prospects for importation biological control of the soybean aphid: anticipating potential costs and benefits. *Ann. Entomol. Soc. Am.* 97: 249–258.
- Heiss, E. M. 1938. A classification of the larvae and puparia of the Syrphidae of Illinois exclusive of aquatic forms. *Illinois Biological Monographs* 16: 1–142.
- Irwin, M. E. 1994. Aphids, pp. 37–39. *In* L. G. Hingley and D. J. Boethel [eds.], *Handbook of soybean insects pests*. Entomological Society of America, Lanham, MD.
- Knutson, L. V. 1973. Taxonomic revision of the aphid-killing flies of the genus *Sphaerophoria* in the western hemisphere. *Misc. Publ. Entomol. Soc. Am.* 9: 1–50.
- Liu, J., K. Wu, K. R. Hooper, and K. Zhao. 2004. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in northern China. *Ann. Entomol. Soc. Am.* 97: 235–239.
- Lucas, E., D. Coderre, and J. Brodeur. 1998. Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* 79: 1084–1092.
- Mackauer, M., and P. Starý. 1967. *World Aphidiidae* (Hymenoptera: Ichneumonoidea). Dr. W. Junk, Publishers, Le François, Paris, France.
- Mayhöfer, R., and T. Klug. 2002. Intraguild predation on the aphid parasitoid *Lysiphlebus fabarum* (Marshall) (Hymenoptera: Aphididae): mortality risks and behavioral decisions made under the threats of predation. *Biol. Control* 25: 239–248.
- Metcalf, C. L. 1916. *Syrphidae of Maine*. Maine Agricultural Experiment Station, Ontario, ME.
- Mosteller F., and J. W. Tukey. 1977. *Data analysis and regression: a second course in statistics*. Addison-Wesley, Reading, MA.
- Nielsen, C., and A. E. Hajek. 2005. Control of invasive soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), populations by existing natural enemies in New York State, with emphasis on entomopathogenic fungi. *Environ. Entomol.* 34: 1036–1047.
- North Central Research Program. 2004. Soybean aphid research update. (http://www.planthealth.info/aphids_researchupdate.htm).
- Noma, T., M. J. Brewer, K. S. Pike, and S. D. Gaimari. 2005. Hymenopteran parasitoids and dipteran predators of *Diuraphis noxia* in the west-central Great Plains of North America: species records and geographic range. *Biocontrol* 50: 97–111.
- Pike, K. S., P. Starý, T. Miller, D. Allison, L. Boydston, G. Graf, and R. Gillespie. 1997. Small-grain aphid parasitoids (Hymenoptera: Aphelinidae and Aphidiidae) of Washington: distribution, relative abundance, seasonal occurrence, and key to known North American species. *Environ. Entomol.* 26: 1299–1311.
- Pike, K. S., P. Starý, T. Miller, G. Graf, D. Allison, L. Boydston, and R. Miller. 2000. Aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) of Northwest USA. *Proc. Entomol. Soc. Wash.* 102: 688–740.
- Pike, K. S., P. Starý, M. J. Brewer, T. Noma, S. Langley, and M. Kaiser. 2007. A new species of *Binodoxys* (Hymenoptera: Braconidae, Aphidiinae), parasitoid of the soybean aphid, *Aphis glycines* Matsumura, with comments on biocontrol. *Proc. Entomol. Soc. Wash.* (in press).
- Powell, W. 1986. Enhancing parasitoid activity in crops, pp. 319–340. *In* J. Waage and D. Greathead [eds.], *Insect parasitoids*. Academic, London, United Kingdom.
- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004. Soybean aphid biology in North America. *Ann. Entomol. Soc. Am.* 97: 204–208.
- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97: 240–248.
- SAS Institute. 2000. *SAS/STAT user's guide*, version 8. SAS Institute, Cary, NC.
- Schlinger, E. I., and J. C. Hall. 1960. Biological notes on pacific coast aphid parasites, and lists of California parasites (Aphidiinae) and their aphid hosts (Hymenoptera: Braconidae). *Ann. Entomol. Soc. Am.* 53: 404–415.
- Short, B. D., and J. C. Bergh. 2004. Feeding and egg distribution studies of *Heringia calcarata* (Diptera: Syrphidae), a specialized predator of woolly apple aphid (Homoptera: Eriosomatidae) in Virginia apple orchards. *J. Econ. Entomol.* 97: 813–819.
- Short, B. D., and J. C. Bergh. 2005. Separation of three common hover fly predators of woolly apple aphid based on the exochorionic sculpturing of eggs. *Can. Entomol.* 137: 67–70.
- Starý, P. 1976. *Aphid parasites (Hymenoptera, Aphidiidae) of the Mediterranean area*. Academia Publishing House, Czechoslovak Academies of Sciences, Prague, Czech Republic.
- Starý, P. 1979. *Aphid parasites (Hymenoptera, Aphidiidae) of the central Asian area*, 124 pp. Academia Publishing House, Czechoslovak Academies of Sciences, Prague, Czech Republic.
- Starý, P. 1999. Parasitoids and biocontrol of Russian wheat aphid, *Diuraphis noxia* (Kurdj.) expanding in central Europe. *J. Appl. Entomol.* 123: 273–279.
- Starý, P., J. P. Lyon, and F. Leclant. 1988. Biocontrol of aphids by the introduced *Lysiphlebus testaceipes* (Cress.) (Hym., Aphidiidae) in Mediterranean France. *J. Appl. Entomol.* 105: 74–78.
- Takada, H. 2002. Parasitoids (Hymenoptera: Braconidae, Aphidiinae: Aphelinidae) of four principal pest aphids (Homoptera: Aphididae) on greenhouse vegetable crops in Japan. *Appl. Zool.* 37: 237–249.
- Tanasijtshuk, V. N. 1986. Silver-flies (Chamaemyiidae). Fauna of the USSR, new series 134, Diptera 14 (7). Zoologicheskii Institut Akademii Nauk SSSR. Nauka, St. Petersburg, Russia.
- van den Bosch, R., E. I. Schlinger, and E. J. Dietrick. 1957. Imported parasites established: natural enemies of the spotted alfalfa aphid brought from the middle east in 1955–56 now established in California. *Calif. Agric.* 11: 11–12.
- van Emden, H. F. 1965. The role of uncultivated land in the biology of crop pests and beneficial insects. *Sci. Hortic.* 17: 121–36.
- Venette, R. C., and D. W. Ragsdale. 2004. Assessing the invasion by soybean aphid (Homoptera: Aphididae): where will it end? *Ann. Entomol. Soc. Am.* 97: 219–226.
- Vockeroth, J. R. 1992. The flower flies of the subfamily Syrphinae of Canada, Alaska, and Greenland. Canada Communication Group Publishing, Ontario, Canada.
- Voegtlin, D. J., S. E. Halbert, and G. Qiao. 2004. A guide to separating *Aphis glycines* Matsumura and morphologically similar species that share the same host. *Ann. Entomol. Soc. Am.* 97: 227–232.
- Wratten, S. D., and W. Powell. 1991. Cereal aphids and their natural enemies, pp. 233–258. *In* L. G. Firdbanks, L. G. Carter, J. F. Darbyshire, G. R. Potts [eds.], *The ecology of temperate cereal fields*. Blackwell Scientific, London, United Kingdom.
- Wu, Z., D. Schenk-Hamlin, W. Zhan, D. W. Ragsdale, and

G. E. Heimpel. 2004a. The soybean aphid in China: a historical review. *Ann. Entomol. Soc. Am.* 97: 227–232.

Wu, Z., K. R. Hopper, R. J. O'Neil, D. J. Voegtlin, D. R. Prokrym, and G. E. Heimpel. 2004b. Reproductive compatibility and genetic variation between two strains

of *Aphelinus albipodus* (Hymenoptera: Aphelinidae), a parasitoid of the soybean aphid, *Aphis glycines* (Homoptera: Aphididae). *Biol. Control* 31: 311–319.

Received 11 July 2006; accepted 28 October 2006.
