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Field Abundance and Performance of Hoverflies (Diptera: Syrphidae) on Soybean Aphid

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Abstract

The management of the soybean aphid *Aphis glycines* Matsumura is a major challenge to soybean production in the north-central United States. The identification and characterization of the insect predator community has informed integrated pest management strategies by providing insight on predators that can suppress soybean aphid populations. Hoverflies (Diptera: Syrphidae) are known predators of *A. glycines*, but more information is needed on their diversity, abundance, and performance to evaluate their importance as biological control agents of *A. glycines*. In this study, syrphid abundance was evaluated across two growing seasons in four soybean fields in east-central Minnesota. Six methods were used to quantify syrphid abundance at the larval, pupal, and adult life stages; describe species composition and richness for adults; and directly compare larval abundance to aphid abundance. The syrphid community comprised eight species, dominated by *Toxomerus marginatus* (Say) and *Toxomerus geminatus* (Say). Syrphid abundance was relatively low in soybean fields. Feeding trials were conducted to compare the performance of the most common syrphid (*T. marginatus*) on a diet of *A. glycines* with two native aphids, *Aphis nerii* Boyer de Fonscolombe and *Aphis monardae* Oestlund. Despite their low abundance in soybeans, *T. marginatus* larvae perform well on *A. glycines*, *A. nerii*, and *A. monardae* in laboratory feeding trials, implying that factors other than host suitability are limiting their potential to exert biological control on soybean aphids.

Keywords: *Syrphinae*, *Glycine max*, aphidophagy

Introduction

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is a major pest of soybeans in most of the soybean-growing regions of North America, causing up to a 40% reduction in yield (Ragsdale et al. 2007, 2011). Since its detection in 2000 and subsequent outbreaks in North America, there has been a concerted effort to describe the soybean aphid predator community, quantify the extent to which it exerts biological control, and understand the role of habitat in mediating those interactions (Fox et al. 2004; Rutledge et al. 2004; Costamagna and Landis 2006, 2007; Mignault et al. 2006; Costamagna et al. 2007, 2008; Gardiner et al. 2009; Gagnon et al. 2011; Koh et al. 2013). There are several significant predators of soybean aphid, including ladybird beetles (Coleoptera: Coccinellidae), the insidious flower bug *Orius insidiosus* Say (Hemiptera: Anthocoridae), predatory midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae), and lacewing species (Neuroptera: Chrysopidae and Hemerobiidae) (Desneux et al. 2006, Costamagna and Landis 2007, Donaldson et al.

2007, Costamagna et al. 2008, Gardiner et al. 2009). Predation from these and other arthropods can exert strong biological control, often providing adequate population suppression to keep soybean aphids below the economic threshold and thus protecting soybean yield and reducing insecticide use (Costamagna et al. 2007, Landis et al. 2008, Gardiner et al. 2009, Heimpel et al. 2013).

Another potentially important predator group of soybean aphids include aphidophagous hoverflies (Diptera: Syrphidae: Syrphinae) (Vockeroth 1992, Kaiser et al. 2007, Noma and Brewer 2008). Adult syrphids were among the most common aerially dispersing predators collected by sticky cards in soybean fields sampled across four states in the upper Midwest (Schmidt et al. 2008, Gardiner et al. 2009). However, syrphid larvae (the predatory stage) are much less abundant than other predators, such as coccinellids and anthocorids, on soybean plants, comprising an estimated 0.1–8% of the predator community (Rutledge et al. 2004, Costamagna and Landis 2006, Donaldson et al. 2007, Gardiner et al. 2009, Noma et al. 2010). Few studies have quantified syrphid species composition

throughout the soybean-growing season. Among those, two studies conducted in southern Michigan shortly after soybean aphid was first detected (2003–2006) showed that seven syrphid species oviposit and develop to adult stage on out-planted soybean aphid colonies (~1,000 aphids per plant); *Allograpta obliqua* (Say) was the most common (Kaiser et al. 2007, Noma and Brewer 2008). However, parallel observations at the same sites showed that larvae were not nearly as abundant in soybeans stands (<0.1 larva per plant) as compared with those in out-planted soybeans (up to six larvae per out-planted soybean), and *Toxomerus marginatus* (Say) was more common than other syrphid species in stands than in out-planted soybeans (Noma and Brewer 2008). Beyond these experiments, little is known about the species composition, abundance, or performance of syrphids in soybeans, despite their significance as aphid predators in other crops (Smith et al. 2008). More information on species composition from other parts of the soybean-growing region will strengthen our ability to make inferences on their potential role in the biological control of soybean aphids.

Performance of syrphids feeding on aphids is fundamental to syrphid population growth and biological control, yet this information is lacking for soybean aphids. Although there are at least seven syrphid species that can develop on soybean aphid (Kaiser et al. 2007, Noma and Brewer 2008), the rate of syrphid development on soybean aphid remains unknown. The relatively low abundance of syrphids in soybeans implies that syrphids may perform poorly on soybean aphid. Although poor syrphid larval performance can result from secondary defense compounds (Vanhaelen et al. 2002), soybean aphids are considered to have low resistance and are suitable for several predator and parasitoid species (Mignault et al. 2006, Desneux et al. 2009, Hopper et al. 2013). Thus, a better understanding of syrphid larval development on soybean aphids would enhance our knowledge of syrphid performance on soybeans aphids.

The current study 1) used four adult sampling techniques (vacuum-suction, sweep nets, yellow sticky cards, and timed observations) to quantify and describe seasonal abundance and species composition of adult syrphid flies; 2) counted syrphid larvae and pupae on soybean plants during two years; and 3) conducted aphid feeding trials in the laboratory to estimate larval performance of the most dominant syrphid on soybean aphid from objective 1. Performance on soybean aphid was compared with that of two native aphid–plant associations: *Aphis nerii* Boyer de Fonscolombe reared on *Asclepias incarnata* L. and *Aphis monardae* Oestlund reared on *Monarda fistulosa* L. The *A. nerii*–*As. incarnata* association could be mildly toxic and thereby unsuitable for syrphids; however, cardenolides were shown to be virtually absent in *A. nerii* feeding on *As. incarnata* (Martel and Malcolm 2004), and parasitoids are able to complete development on this aphid–plant association (Desneux et al. 2009). Taken together, information on larval performance and field abundance provides timely information on the potential importance of syrphids as biological control agents.

Materials and Methods

Abundance and Composition of Hover flies. *Research Site.* Field sampling was conducted at the University of Minnesota Rosemount Research and Outreach Center in east-central Minnesota, from four 4-ha (10-acre) soybean *Glycine max* (L.) fields: Field A (Center of field: 44° 44'16.64" N, 93° 05'33.06" W), Field B (44° 44'02.34" N, 93° 03'55.71" W), Field C (44° 42'24.46" N, 93° 04'26.04" W), and Field D (44° 41'04.07" N, 93° 03'24.65" W). Average distance between all plots was 3.4 km (minimum = 1.7 km, maximum = 5.5 km). All sampling was conducted within a 45 by 50m or smaller area in the center of each 4-ha field. Sampling near the middle of relatively large soybean fields was intended to minimize effects from surrounding habitats and provide a better representation of the syrphid community in soybeans. Fields were planted with the soybean cultivar "Pioneer 91M51" (susceptible to soybean aphid) on 30 May to 31 May 2012 and 13 June to 14 June 2013 and maintained under standard agronomic practices, including applications of the herbicide glyphosate, sethoxydim, quizalofop p-ethyl, and fluthiacet-methyl. There were no insecticide or fungicide applications to the field or in a pretreatment to seeds.

Timed Observations—2012. Timed observations were performed in 2012 to directly observe adult syrphid abundance. The timed observations involved 5min of visual searching along a diagonal transect through a 300 m² area at the center of each field. Every 30 s the observer advanced along the transect to a new stationary position where they searched a 1-m radius. Syrphid adults were identified to genus using characters from Vockeroth (1992). From 19 July to 5 September seven and eight weekly timed observations were conducted for fields A, B and C, D, respectively (two samples were not collected).

Sticky Cards. In 2012, the abundance and composition of adult syrphids was sampled with unbaited yellow sticky cards, PHEROCON AM No-Bait Traps (Trécé, Inc., Adair, OK), placed approximately 5 cm above the mean soybean canopy height on a 2.74-m-tall fiberglass post. Protruding wires were attached to the top of the post to minimize bird perching activity. At each plot, four sampling locations were established within a 75-m² area at the center of the field. Sticky cards were placed on the posts for 7-d intervals from 8 June (8 d after planting) to 21 September (11 d before harvest). Syrphids were identified to genus and species by J.C.L. using keys from Vockeroth (1992). Identifications were further confirmed by referencing identified specimens in the University of Minnesota Insect Collection, UMSP (Saint Paul, MN). All syrphids were identified to species and counted on traps collected every other week (four fields × four posts per field × eight sampling periods; *N* = 127; one trap was lost).

Vacuum-Suction Sampling. In 2012, arthropods were collected using a vacuum-suction sampling device created by modifying a Toro PowerVac T25 gasoline-powered handheld leaf blower/vac with the addition of a layer of fine-mesh

no-see-um netting (openings of 0.65 by 0.17 mm; Quest Outfitters, Sarasota, FL) secured over the vacuum opening with a rubber band. A 56-cm-long piece of flexible plastic tubing with an 81-cm² circular opening was attached to the vacuum to collect arthropods. Sampling was conducted by running the leaf blower at full throttle (maximum air speed, 257 kmph) while placing the flexible tubing over soybean plants to vacuum for 2 min, approximately a 20-m-length row, for each sample. After each sample was collected, the no-see-um mesh pouch and its entire contents were placed in a plastic bag and immediately frozen in a portable Engel MT15 freezer (Engel, Jupiter, FL) before adult syrphids were identified to species and counted. Every other week, from 26 June to 18 September 2012, three samples were collected along transects at each field within a 500-m² area near the center of the field, for a total of seven sampling periods (four fields \times three samples per field \times seven sampling periods; $N = 84$).

Sweep Net Sampling. Sweep net sampling was conducted during the 2012 and 2013 growing seasons. Each sample consisted of 20 figure-eight sweeps conducted over approximately a 20-m-long transect of soybeans with a 38-cm-diameter sweep net. All sweep net contents were placed directly into Whirl-Pak bags (Fisher Scientific, Pittsburgh, PA) containing >95% ethanol, and all syrphids were identified to species and counted. Every other week, from 28 June to 20 September 2012 and 19 June to 25 September 2013, three samples were collected at each field within a 500-m² area near the center of the field, for a total of seven sampling periods in 2012 (four fields \times three samples per field \times seven sampling periods; $N = 84$) and eight sampling periods in 2013 (four fields \times three samples per field \times eight sampling periods; $N = 96$).

Visual Observations of Larvae and Pupae. Some life stages of syrphids can be difficult to sample using the above described methods because of their habit of taking refuge in protected areas of the plant. Therefore, hoverfly larvae and pupae were quantified in 2012 and 2013 by a thorough visual inspection of the entire soybean plant within a 0.25-m² sample quadrat. Once every week, from 1 June to 21 September 2012 and 6 June to 26 September 2013, four quadrats were sampled at each field within a 500-m² area near the center of the field, for a total of 17 sampling periods in both 2012 and 2013 (four fields \times four samples per field \times 17 sampling periods; $N = 272$ per yr).

Visual Observations of Larvae in Relation to Aphid Density. Syrphid larvae and soybean aphids (total number of alates and apterae) were quantified in 2012 and 2013 by visually inspecting randomly selected soybean plants along two concentric grids within a 45- by 50-m area in the center of each 4-ha soybean field. Observations were made weekly from 26 July to 13 September 2012 and from 1 July to 2 October 2013. Plant size was estimated by counting the number of trifoliates per plant.

***T. marginatus* Performance on *A. glycines*, *A. monardae*, and *A. nerii*.** A sweep net was used to collect adult *T. marginatus* from a 0.21-ha restored tallgrass prairie at the University of Minnesota, Saint Paul, MN (44.98° N, 93.23° W). Adult *T. marginatus* were identified and introduced into plexiglass-mesh cages (approximately 30 by 30 by 46 cm) with *A. glycines* (on *G. max*), *A. monardae* (on *M. fistulosa*), or *A. nerii* (on *As. incarnata*) and a mixture of fresh-cut native and nonnative forbs from the restored prairie [e.g. crown vetch *Securigera varia* (L.), early sunflower *Heliopsis helianthoides* (L.), tickseed *Coreopsis* sp., white clover *Trifolium repens* L., and spiderwort *Tradescantia* sp.]. Caged flies were monitored for mating and ovipositions, and leaves with eggs were cut from the plant and isolated in a Petri dish. Eggs were collected from the same aphid-plant associations as used in the feeding trials, except eggs from *A. monardae* cages that were used for feeding trials of *A. nerii* (larvae were not available from *A. nerii* cages at the start of the trials, although adults oviposited in the *A. nerii* cage).

Syrphid eggs were observed for larval emergence. Newly hatched larvae were fragile and therefore left undisturbed on leaves for 24 h (day one). Leaves and larvae were kept in a growth chamber at 25°C with a photoperiod of 16:8 (L:D) h for the entire experiment, except during examination and feeding. On day two, larvae were each transferred to a separate host plant leaf (the petiole cut was placed into a 0.6-ml microcentrifuge tube, containing deionized water, covered by a parafilm layer) with 30–50 aphid nymphs measuring 0.5–1.0 mm in length. Every 24 h until pupation, larvae were transferred to a fresh leaf with typically 30–100 aphid nymphs so that live aphids were available in excess (*ad libitum*). More aphids were generally provided to larvae in later stages of growth when there were higher feeding rates. Upon pupation of syrphid larvae, excess aphids were removed, and the pupae were monitored daily until eclosion of the adults. Three replications were consecutively performed: 10 larvae fed *A. glycines* (28 June to 21 July 2012); three larvae fed on each of *A. glycines*, *A. monardae*, and *A. nerii* (22 July to 5 August 2012); and two larvae fed *A. glycines* and five fed on each of *A. monardae* and *A. nerii* (19 August to 4 September 2012). Total sample size therefore included 15 larvae fed *A. glycines*, eight larvae fed *A. nerii*, and eight larvae fed *A. monardae*.

The following metrics of *T. marginatus* performance were measured: number of individuals that successfully pupated and the time (d) from egg hatch to successful pupation. Among the successfully pupated individuals, the number that subsequently emerged as adults and time (d) to emergence was recorded.

Analysis. Generalized linear mixed models (glmmPQL) from the open-source statistical software R (R Core Development Team 2005) were used to model seasonal change in abundance, detected by sticky cards, timed observations, sweep nets, and larval surveys. Underlying Poisson and binomial distributions were assumed for count and binary data, respectively. The generalized linear mixed model underestimated the

raw mean larval and pupal abundance in 0.25-m² quadrats. We, therefore, analyzed abundance with a linear mixed model (lme in the statistical software R) when syrphids were present (11 July–7 September; $N = 288$) and present those P -values which were similar to the P -values from the generalized linear mixed model. The linear mixed model was also used to analyze syrphid to aphid ratio. Differences in abundance among the two most common species, pupae versus larvae, and years, as well as year-dependent differences in life stage or species abundance (two-way interaction), were treated as fixed effects and tested using the t -statistic. Polynomial terms (i.e. linear, quadratic, and cubic) were tested for significance ($P < 0.05$) and fit to approximate change in abundance over time. Variation between plots, repeated samples within plots, and subsampling was treated as random effects.

Larval performance in the laboratory was also analyzed using mixed models in the statistical software R. Time (d) of development from egg hatch to pupation and that from pupation to emergence was analyzed with linear mixed-effect models (lme) that included replication as a random effect. Proportion of individuals that pupated and the proportion of pupae that emerged as adults were analyzed with a generalized linear mixed-effects model (glmer) including replication as a random effect. Results of ANOVA are presented in Table 1 for proportion pupated or emerged (likelihood ratio test based on chi-square distribution) and time to pupation or emergence (F -test). Table 1 presents the average (\pm SE) performance and statistical comparisons among aphids for all three replications. A second analysis was performed for replications two and three when all aphid species were concurrently tested, but the results did not qualitatively differ from the tests involving all three replicates.

Results

Abundance and Species Composition of Adult Syrphids.

Timed Observations. In 2012, a total of 11 adult syrphids were observed equivalent to an average 0.37 adult syrphids (± 0.11 SE) per 5 min or one syrphid every 13.6 min ($N = 30$ timed observations; Figure 1a). *Toxomerus* was the dominant genus observed, comprising 91% of all observed adult syrphids (Figure 1a). The observation of one *Eristalis* sp. adult comprised the remaining 9%.

Sticky Cards. In 2012, a total of 124 adult syrphids were collected, an average 0.98 syrphids (± 0.17) per sticky card (average abundance by plot: $A = 1.00$, $B = 0.72$, $C = 0.97$, and $D = 1.22$; $N = 127$ sticky cards; Figure 1b). There were significantly more *T. marginatus* than *Toxomerus geminatus* (Say) ($t_{126} = 2.36$, $P = 0.020$), and together these species comprised 83.1% of all syrphids (Figure 1b). In total, eight hoverfly species were collected and identified from the four soybean fields with the following relative abundances: *T. marginatus* (56.5%), *T. geminatus* (26.6%), *Eristalis stipator* Osten Sacken (5.6%), *Eupeodes americanus* (Wiedemann) (5.6%), *Eristalis tenax* (L.) (2.4%), *Sphaerophoria philanthus* (Meigen) (1.6%), *Sphaerophoria contigua* Macquart (0.8%), and *Helophilus latifrons* Loew (0.8%).

Sweep Net Sampling. In 2012, a total of 12 syrphid adults were collected, an average of 0.14 syrphids (± 0.05) per sweep net sample (average abundances by plot: $A = 0.10$, $B = 0.19$, $C = 0.10$, and $D = 0.19$; $N = 84$ sweep net samples; Figure 1c). In 2013, a total of six syrphid adults were captured, an average of 0.06 syrphids (± 0.02) per sweep net sample (average abundances by plot: $A = 0.00$, $B = 0.04$, $C = 0.17$, and $D = 0.04$; $N = 96$ sweep net samples; Figure 1d). There were significantly more *T. marginatus* than *T. geminatus* in sweep nets ($t_{179} = 7.88$, $P < 0.001$; Figure 1c-d) but no detectable differences in abundance among years ($t_{165} = -1.19$, $P = 0.23$) or species by year interaction ($t_{178} = 0.96$, $P = 0.34$).

Vacuum-Suction Sampling. In 2012, vacuum-suction sampling captured zero adult syrphids ($N = 84$ samples).

Abundance of Syrphid Larvae and Pupae. **Sweep Net and Vacuum-Suction Sampling.** In 2012, sweep netting captured zero syrphid larvae and pupae ($N = 84$). In 2013, three syrphid larvae and one pupa were collected, an average 0.031 larvae (± 0.018) and 0.010 pupae (± 0.010) per sweep net sample ($N = 96$). Vacuum-suction sampling captured one larvae and zero pupae in 2012, an average of 0.012 larvae (± 0.012) per vacuum-suction sample ($N = 84$).

Visual Observation of Larvae and Pupae. There were more larvae than pupae ($t_{287} = -3.26$, $P = 0.0012$), and there was marginal statistical support ($t_{286} = -1.97$, $P = 0.0502$) that this difference was larger in 2013 versus 2012. In 2012, 17 syrphid larvae and 10 pupae were observed, an average density of 0.063 larvae (± 0.018) (average densities by plot: $A = 0.074$, $B = 0.029$, $C = 0.074$, and $D = 0.074$) and 0.037 pupae (± 0.011) (average densities by plot: $A = 0.029$, $B =$

Table 1. *T. marginatus* average (\pm SE) larval performance on *A. glycines*, *A. nerii*, and *A. monardae*

Life stage development	<i>A. glycines</i>	<i>A. nerii</i>	<i>A. monardae</i>	Sample sizes ^a	Test statistic	P -value
Proportion larvae that pupated	0.80 (± 0.10)	0.88 (± 0.12)	0.75 (± 0.15)	15, 8, 8	$\chi^2=0.42$	0.81
Proportion pupae that emerged	0.75 (± 0.13)	0.57 (± 0.19)	0.83 (± 0.15)	12, 7, 6	$\chi^2=1.21$	0.55
Proportion larvae that pupated and emerged	0.60 (± 0.13)	0.50 (± 0.18)	0.63 (± 0.17)	15, 8, 8	$\chi^2=0.299$	0.86
Days from egg hatch to pupation	12.33 (± 1.13)	10.71 (± 0.47)	11.00 (± 0.73)	12, 7, 6	$F_{2,20}=0.069$	0.93
Days from pupation to adult emergence	4.78 (± 0.15)	5.00 (± 0.00)	4.60 (± 0.40)	9, 4, 5	$F_{2,13}=0.995$	0.40

Test statistics and corresponding P -values are presented for χ^2 tests (Likelihood Ratio test performed via glmer in R) and F -tests (ANOVA performed using lme in R).

a. Samples sizes are shown in order for *A. glycines*, *A. nerii*, and *A. monardae*.

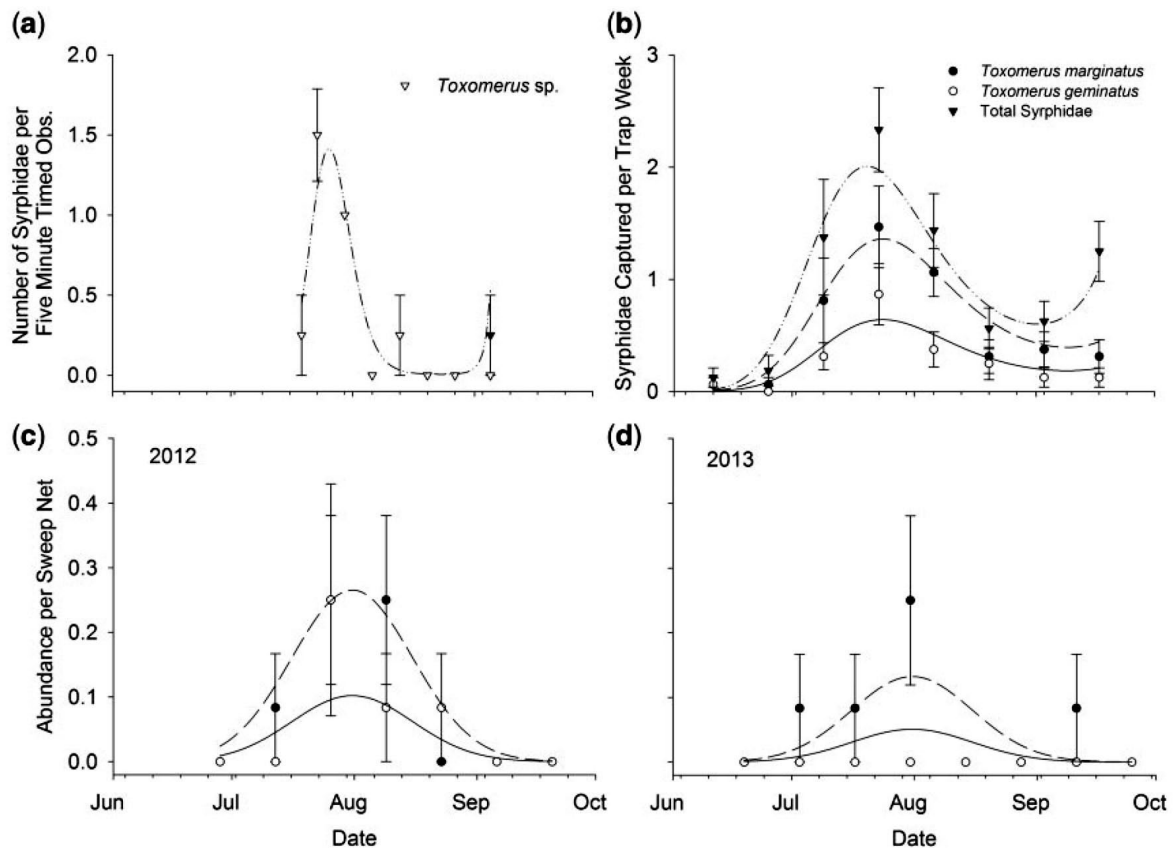


Figure 1. Syrphid average (\pm SE) adult abundance across four soybean fields (4 ha per field) based on (a) 5-min timed observations in 2012, (b) yellow sticky cards in 2012, and (c) sweep nets in 2012 and (d) 2013 in Rosemount, MN. Based on a generalized linear mixed model, the curves represent best fit polynomial terms for a single continuous variable (total syrphidae across time) or two continuous variables (*T. marginatus* versus *T. geminatus* across time). Dashed curves with double-dots, dashed curves, and solid curves represent total syrphids, *T. marginatus*, and *T. geminatus*, respectively.

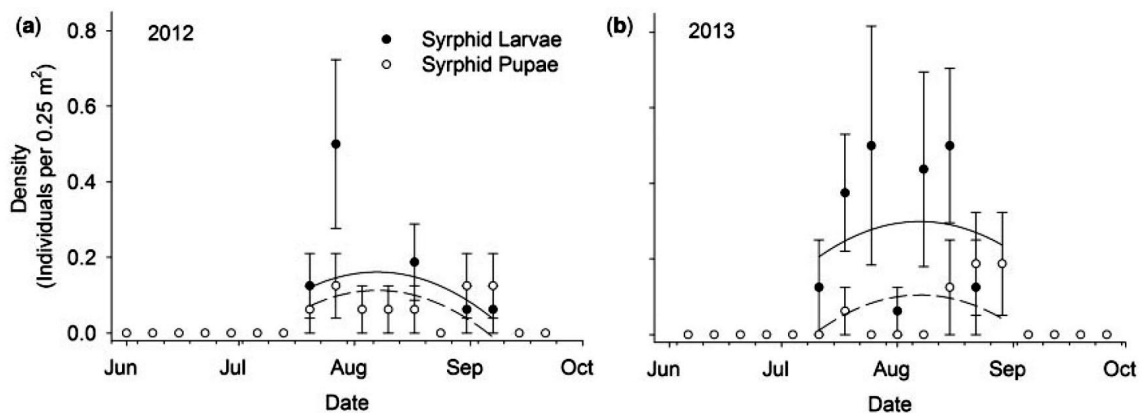


Figure 2. Syrphid average (\pm SE) larvae and pupae density across four soybean fields (4 ha per field) during (a) 2012 and (b) 2013 in Rosemount, MN. Curves represent best fit polynomial terms from a linear mixed model that compared syrphid pupae to larvae in 2012 and 2013. Dashed curves and solid curves represent pupae and larvae, respectively.

0.00, $C = 0.100$, and $D = 0.015$) per 0.25-m² quadrat ($N = 272$ quadrats; Fig 2a). In 2013, 37 larvae and nine pupae were observed, an average density of 0.136 larvae (± 0.033) (average densities by plot: $A = 0.382$, $B = 0.029$, $C = 0.088$, and $D = 0.044$) and 0.033 pupae (± 0.014) (average densities

by plot: $A = 0.132$, B, C , and $D = 0.000$) per 0.25-m² quadrat ($N = 272$ quadrats; Figure 2b).

Visual Observation of Syrphid Larvae and Aphids per Soybean Plant. In 2012, 424 plants were inspected and a total 15,315 soybean aphids were counted (total number

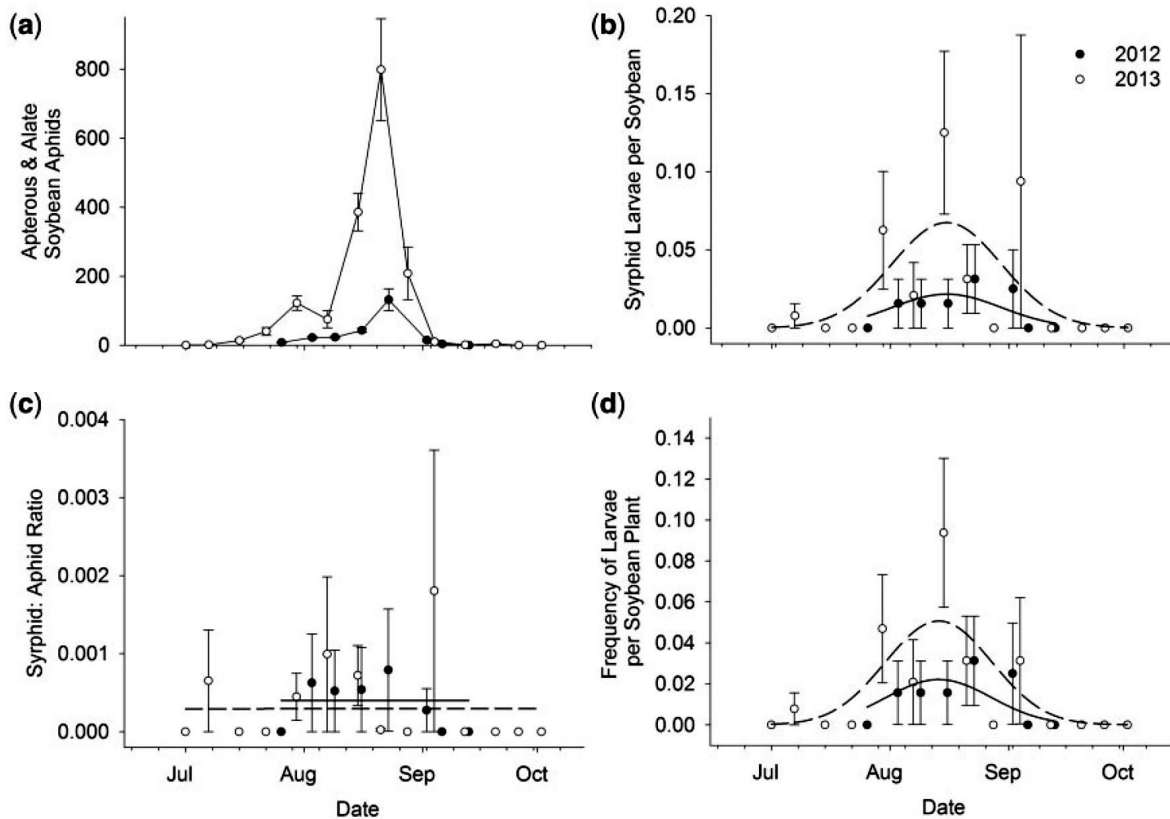


Figure 3. Soybean aphid (a) and syrphid larvae (b-d) average (\pm SE) abundance per soybean plant during 2012 and 2013 across four soybean fields (4 ha per field) in Rosemount, MN. Syrphid larvae abundance shown as (b) abundance per soybean plant, (c) ratio of syrphids to aphids, and (d) frequency of larvae per soybean plant (proportion of plants with one or more syrphids). Curves in b-d represent best fit polynomial terms for date based on a (generalized) linear mixed model that compared syrphid abundance, ratio of syrphids to aphids, and frequency of larvae in 2012 (solid line) versus 2013 (dashed line).

of aphids per plot A = 4,061, B = 885, C = 8,479, and D = 2,402). In 2013, 903 plants were inspected, and a total 103,608 soybean aphids were counted (total number of aphids per plot A = 54,032, B = 24,423, C = 20,514, and D = 4,639). There were significantly more syrphid larvae in 2012 versus 2013 ($t_{1292} = 2.08$, $P = 0.038$). An average of 0.014 syrphid larvae (± 0.006) were observed per plant in 2012 (six syrphid larvae in total for 2012) versus 0.021 syrphid larvae (± 0.006) per plant in 2013 (19 total observed larvae; Figure 3b). Average abundance of syrphid larvae per plot in 2012 were: plot A = 0.018, B = 0.0096, C = 0.019, and D = 0.0096, and those in 2013 were: plot A = 0.038, B = 0.017, C = 0.013, and D = 0.017.

Peak soybean aphid density was observed on 23 August 2012 (131.9 aphids per plant) and 21 August 2013 (798.0 aphids per plant). Peak syrphid density was observed on 23 August 2012 (0.0312 larvae per plant) and 15 August 2013 (0.125 larvae per plant; Figure 3b). The ratio of syrphids to aphids varied from 0.0 to 0.0018, with the highest values per year occurring on 23 August 2012 and 4 September 2013 (Figure 3c). The frequency of syrphids per soybean plant varied from 0.00 to 0.094, with the highest values per year occurring on 23 August 2012 and 15 August 2013 (Figure 3d). There were no significant differences in the syrphid to aphid ratio ($t_{1293} = -0.45$, P

= 0.65) or the frequency of syrphids per soybean ($t_{1292} = 1.55$, $P = 0.12$) among the years.

T. marginatus Performance on *A. glycines*, *A. nerii*, and *A. monardae*. **Syrphid Performance.** Among the *T. marginatus* fed *A. glycines*, 80% pupated and, of those, 75% emerged as adults. Pupation and emergence to adult stage occurred in 12.3 and 4.8 d, respectively (Table 1). Proportion of larvae maturing to the adult stage and the time to maturation were similar for *T. marginatus* fed *A. glycines* versus *A. nerii* or *A. monardae*. No statistically significant differences were detected for any performance measures (Table 1).

Discussion

In this study, the syrphid community comprised eight species, dominated by *T. marginatus* and *T. geminatus*. However, syrphid abundance was relatively low in soybean fields. Laboratory feeding trials indicated that *T. marginatus* larvae perform equally on *A. glycines* as on native aphids. We first provide a discussion of syrphid community composition and abundance based on our collection methods. Then we consider the potential for syrphids to exert biological control on soybean aphids and discuss the factors potentially influencing syrphid populations in soybeans.

Sticky cards and sweep nets indicated that *T. marginatus* was the most common species followed by *T. geminatus*. Timed observations further confirmed that the genus *Toxomerus* was dominant in these soybean fields. Consistent with our study, Noma and Brewer (2008) reported for southern Michigan that *T. marginatus* larvae were relatively common compared with other syrphid species in soybean stands, but their larval density was low (Noma and Brewer 2008). Conversely, in those same fields, out-planted soybeans with elevated soybean aphid density suggested the syrphid community was dominated by *A. obliqua*, not *T. marginatus* (Noma and Brewer 2008). We contend that our sticky card, sweep net, and timed observation surveys, as well as the larval density surveys of Noma and Brewer (2008) on soybean stands, are likely to be more representative of the syrphid community occurring in soybean fields. Thus, while *T. marginatus* occurs at low density, they may be one of the more common species of syrphids to occur across the soybean-growing region.

Direct observations and counts showed that syrphid larval densities, and their ratio to aphids, are extremely low in soybeans. Averaged across years and plots there were 0.03 larvae per soybean plant when aphids were present and a ratio of 0.00021 larvae to aphids (equivalent to one larva per 4,762 aphids; Figure 3). Even when aphids reached their highest densities in 2012 (16 to 23 August) and 2013 (30 July to 28 August), the ratio of syrphids to aphids usually stayed well below 0.001, and syrphid larvae were present on no more than 10% of the soybean plants (Figure 3). Our estimates of larval density from searching 0.25-m² quadrats further confirmed the low density of syrphid larvae (Figure 2).

Our observations of syrphid larval density are consistent with the general finding that syrphids are less abundant compared with other predators of soybean aphids. In a related study by Rutledge et al. (2004), syrphids represented <1% of the total insect predator community and other predators, including *O. insidiosus* and *Harmonia axyridis* Pallas, were more abundant than syrphids. The highest larval density of syrphids observed in this study (0.13 syrphids per soybean plant on 15 August 2013) was less than one-tenth of the peak abundance of *O. insidiosus*, 1.7 adults and nymphs per plant (Rutledge et al. 2004). In southern Michigan, syrphid larval density was similarly low throughout the season in soybean stands across two sites (Noma and Brewer 2008, Brewer and Noma 2010).

Our study provides insight on the potential biological control of soybean aphids. Syrphid larvae were observed to be vastly outnumbered by aphids. Laboratory feeding studies show that one syrphid can kill 132–507 aphids during larval development depending on the syrphid species, environmental conditions, and aphid species (Soleyman-Nezhadiyan and Laughlin 1998, Hopper et al. 2011). Hopper et al. (2011) reported that individual *T. marginatus* killed 132 lettuce aphids (*Nasonovia ribisnigri* Mosley) over the larval stage. Predation rates can be 50% lower in field than under laboratory conditions (Tenhumberg 1995). Thus, the low syrphid density observed in the field combined with estimates of predation from

the literature suggests that there is limited potential for syrphids to exert biological control on soybean aphids.

Our results contrast other agricultural systems, in which syrphids are highly abundant in aphid colonies (Pineda and Marcos-García 2008, Gontijo et al. 2012), and larvae can be important predators exerting strong population-level control on aphids (Chambers and Adams 1986, Tenhumberg 1995, Tenhumberg and Poehling 1995). For example, the primary syrphid species in soybeans, *T. marginatus*, also complete their development on a major aphid pest of organic California lettuce, the nonnative *N. ribisnigri* (Hopper et al. 2011). *T. marginatus* is the dominant syrphid species feeding on *N. ribisnigri*, comprising 39% of the syrphid community followed by syrphids *A. obliqua*, *Sphaerophoria* sp., and *Eupeodes* sp. (Smith and Chaney 2007), which were also detected in our soybean fields. However, unlike in soybeans, syrphid larvae are highly abundant in field populations of *N. ribisnigri*, reaching average high densities of 2.75–9.08 larvae per lettuce plant, far greater than the peak 0.13 larvae observed per soybean plant in this study, and syrphids provide significant population suppression of *N. ribisnigri* (Smith et al. 2008).

A question that arises from this study is why are syrphids not as abundant in soybean aphids as they are in other agricultural systems (Gontijo et al. 2012)? In our study, *T. marginatus* performed well by feeding on soybean aphids in the laboratory, equally well as on two native species of aphids. However, some caution should be exercised in the comparison of *T. marginatus* performance among aphids, as our conclusions are based on a relatively small sample size ($N = 31$). Soybean aphids are suitable prey, unlike some aphids (e.g. *Ca variella theobaldi*) that can be toxic to syrphids (Ruzicka 1975). Further, syrphids occurred more commonly, often more than two syrphids per plant, on out-planted soybean plants when the larvae were allowed to develop in the laboratory (Kaiser et al. 2007, Noma and Brewer 2008, Brewer and Noma 2010). In out-planted soybeans surrounded by grassland, syrphids were >400% more abundant than coccinellids or *O. insidiosus* (Kosmala 2013). However, syrphids occurred at low density in the larger soybean stands (i.e., 4 ha) of the current study and in other large field studies (Gardiner et al. 2009). The potential importance of scale-dependent ecological effects is further implied by the observation that syrphid abundance was greater on out-planted soybeans in smaller (0.01–0.02 ha) versus larger (0.5–1.0 ha) soybean plots (Noma and Brewer 2008). Thus, syrphids can perform well on soybeans and soybean aphids, but their potential for population growth appears more limited in the context of larger soybean stands.

Multiple factors may limit syrphid populations in soybean stands. While pupation rates in the laboratory were 80%, the occurrence of only 35% as many pupae versus larvae in the field implies that successful pupation in the field is much lower. One potentially limiting factor to syrphids could be intraguild predation from coccinellids such as *H. axyridis* and *Coccinella septempunctata* and chrysopids, such as *Chrysopa* sp. (Hindayana et al. 2001, Alhmedi et al. 2010, Ingels and

De Clercq 2011), all of which often occur abundantly in soybeans (Gardiner et al. 2009) and are known intraguild predators of several other taxa in soybeans (Gardiner and Landis 2007, Chacon and Heimpel 2010, Gagnon et al. 2011). For example, *Coleomegilla maculata* have been observed feeding on syrphid pupae in alfalfa (Wheeler 1977). Further, dipteran protein, likely to include syrphids, has been detected in the guts of three coccinellid species (*C. septempunctata*, *C. maculata*, and *H. axyridis*) known to prey on soybean aphids (Moser et al. 2011). Finally, when coccinellid abundance was low, syrphids were much more common on outplanted soybeans than those observed in the current study (Kosmala 2013). Plant traits of soybeans such as pubescence (trichomes) may also limit syrphid performance. Pubescence was shown to reduce movement and performance of syrphids in other crops (Verheggen et al. 2009). It is perhaps no coincidence that syrphids are major predators of aphids in crops that lack dense pubescence (Chambers and Adams 1986, Nieto et al. 2006, Gontijo et al. 2012). Thus, although the ecological mechanisms limiting syrphid populations in soybeans remain unclear, the current body of literature suggests that syrphids can be added to the list of predators and parasitoids (e.g., *Binodoxys kellogensis*, *Lysiphlebus testaceipes*, and *C. maculata*), which can complete development on soybean aphids (Mignault et al. 2006, Brewer and Noma 2010), but have remained at low density in soybean stands (Schmidt et al. 2008, Brewer and Noma 2010, Noma et al. 2010).

In conclusion, the syrphid community dominated by *T. marginatus* showed a low abundance of larvae and pupae in four soybean fields across 2 yrs. The high developmental performance of *T. marginatus* on soybean aphid is consistent with the hypothesis that ecological factors (e.g. intraguild predation, syrphid–soybean interactions) limit populations of syrphids. A potential extension of this study would be to further characterize such factors and quantify their effects on syrphid abundance and predation in soybeans.

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