

Soybean Aphid Predators and Their Use in Integrated Pest Management

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ABSTRACT The discovery of the soybean aphid, *Aphis glycines* Matsumura, in U.S. soybean production systems in 2000 has provided a unique opportunity to study the interaction of a new invader with existing natural enemy communities. One research thrust has been examining the role of predators in soybean aphid dynamics in the Midwest. We discuss the roles of predatory arthropods in field crops and set forth a conceptual model that we have followed to identify key predators in the soybean aphid system. We identify *Orius insidiosus* (Say) and *Harmonia axyridis* (Pallas) as potentially key predators and show our findings on their phenology in soybean fields and their impact on soybean aphid population dynamics. Finally, we discuss how this information can be used in integrated pest management programs for soybean aphid and point to gaps in our knowledge where future studies are needed.

KEY WORDS biological control, predators, invasive species, *Orius insidiosus*, *Harmonia axyridis*

THE INVASION OF THE SOYBEAN aphid, *Aphis glycines* Matsumura, into U.S. soybean production systems has stimulated research on its ecology, impact, and management. Among the initial research thrusts has been a focus on the aphid's natural enemies and their potential use in biological control (Heimpel et al. 2004). In Asia, the soybean aphid is attacked by a number of natural enemies, including >30 species of predators, eight species of aphidiine and aphelinid parasitoids, and several species of fungal pathogens (Quimio and Calilung 1993, van den Berg et al. 1997, Chang et al. 1994, Wang and Ba 1998, Wu et al. 2004). In Indonesia, naturally occurring populations of the coccinellid *Harmonia arcuata* (F.) and the staphylinid *Paederus fuscipes* Curtis play an important role in suppressing the soybean aphid (van den Berg et al. 1997). In Japan, the soybean aphid is rarely a pest and is thought to be under the control of a complex of natural enemies (K. Honda, personal communication). The importance of predators in control of soybean aphid in Asia provides insight into their potential importance as a part of pest management programs for this invasive pest in North America.

Although previous studies have identified many natural enemies found in soybean systems (Deitz et al. 1976, Elvin 1983, Pitre 1983, Ferguson et al. 1984), the potential negative impact of soybean aphid on midwestern U.S. soybean production necessitated rapid identification of those that may be key biocontrol

agents. In this article, we review recent findings that illuminate the range of natural enemies present in north central U.S. soybean systems and their potential use in soybean aphid management. We focus on predators, because to date few parasitoids and pathogens have been found attacking the aphid in North America. (During 2001 and 2002, extensive sampling and observations in soybean failed to discover significant numbers of parasitoids attacking soybean aphid. Only three parasitized soybean aphid mummies [aphelinid] were found in Indiana in 2001 and none in 2002. A greenhouse colony of soybean aphids was infested by *Lysiphlebus testaceipes* (Cresson) in spring 2002, but no wasps were seen in the field. Entomopathogenic fungi were found in the field in some areas. In Minnesota, 3% of apparently healthy aphids that were held in the laboratory on excised soybean leaves showed signs of fungal infection. Four species of entomopathogenic fungi were identified, the most predominant one was *Pandora neoaphidis* (Remaudière & Hennebert) [D. Ragsdale, personal communication]). No aphids with signs of fungal infection were seen in Indiana. Although future studies may reveal the importance of pathogens and parasites, predators will continue to be an important part of soybean aphid population dynamics in most systems. We present an overview of past studies of predation that illustrate key adaptations of predators to soybean habitats and discuss an approach to identify those predators whose impact on soybean aphid warrants further study. Finally, we discuss the potential roles of predators in aphid dynamics and present some pest management

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options suggested by our current understanding of soybean aphid–predator dynamics.

Arthropod Predators in Soybean. Predatory arthropods abound in many field crops. Pimentel and Wheeler (1973) reported >200 predator species that occur in alfalfa fields, whereas Deitz et al. (1976) list >150 predators among the nearly 500 arthropods identified from North Carolina soybean fields. Closer examination of sampling data shows that although many species of predators can be found in field crops, relatively few sustain populations there (O’Neil 1984). Interestingly, a similar group of these “resident” predators is commonly found in field crops, suggesting that predators that sustain populations in field crops share a critical set of adaptations to ephemeral crop environments (O’Neil and Wiedenmann 1987, Wiedenmann and Smith 1997). This is not to say predators evolved these strategies in the crop environment, but rather that predators found in crops can consistently find sufficient prey in the crop to maintain their population growth (Gutierrez et al. 1990, Wiedenmann et al. 1996, Legaspi and Legaspi 1997). Understanding these critical adaptations may advance our ability to integrate predators into integrated pest management (IPM).

Predators may live and reproduce directly within the crop habitat, or they may use the crop only to find food. In many annual crops, prey populations are temporally unpredictable, with prey being scarce at some times and plentiful at others. Because available prey species also change over time, predators in crops are continually faced with a shifting prey base that can result in periods of food shortages. Predators that persist in the face of such varied food are typically generalist feeders that take advantage of whatever prey are plentiful and have adaptations to survive periods of food scarcity (Symondson et al. 2002). Additionally, the ability to use nonprey food items, such as plant sap, pollen, and fungal spores, enables predators to maintain their presence in the crop environment longer than predators that require constant prey resources. In contrast, predators that are closely linked to a particular prey or incapable of surviving periods of starvation may find crop habitats unsuitable (Symondson et al. 2002). Such predators would not be consistently found in crop fields, although they may be important even as transient visitors.

In a series of studies, we examined the search and life history strategies of *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), a generalist predator in many crops, including soybean. Although not a confirmed predator of soybean aphid, the adaptations of this predator to soybean, and other annual crops, illuminate the relative contribution of prey number and crop growth to the predator’s success in finding prey, its life history characteristics, and its control potential. In field studies, when offered Mexican bean beetle larvae, *Epilachna varivestis* Mulsant, in numbers reflecting realistic field densities, *P. maculiventris* attacked relatively few prey per day (O’Neil 1988, Wiedenmann and O’Neil 1992, O’Neil 1997). By relating the predator’s search efficiency to plant size, we

found that this predator used a search strategy to increase the area searched as prey density (number of prey/leaf area) decreased (O’Neil 1988, 1997). Measurement of the predator’s longevity and reproduction showed that, under realistic levels of prey availability, *P. maculiventris* maintained longevity and reduced reproductive output as the number of prey attacked declined (Wiedenmann and O’Neil 1990, Legaspi and O’Neil 1993). Other life history responses to low prey inputs included developmental delays in nymphs, decreased body weights, and reduced clutch sizes (op. cite, Legaspi 1991).

These studies of *P. maculiventris* suggest several approaches for the study of predation of the soybean aphid. If predators are to consistently attack soybean aphid over time, they must accommodate plant growth by adjusting the amount of the plant searched to find prey. We can test this hypothesis by measuring attack rates over a range of prey densities to determine whether attack rates change as the plant changes in size. Furthermore, we expect that predators in soybean should possess the capacity to use nonprey food items and/or show trade-offs in life history characteristics under low prey availability. We can measure these characteristics as well as the breadth of a predator’s diet through laboratory study and field observations. Finally, the low level of attack by *P. maculiventris* indicates that its contribution to prey dynamics would be greatest at low prey densities, thus suggesting that predators of soybean aphid would be most important early in the invasion when aphid densities are low. Testing this hypothesis would require measurement of predation over a range of prey densities and developing models of predator–prey dynamics that incorporate predator impacts at low prey densities.

Identifying Key Predators. A predator’s contribution to prey dynamics can often be subtle (Losey and Denno 1998a), and the collective impact of a number of species is often what determines prey density (Winder 1990, Holland et al. 1996, Landis and van der Werf 1997, Sunderland et al. 1997). However, there is a need to focus initial research on those predators that have the greatest impact on aphid dynamics. Such key predators occur in the crop in sufficient numbers and at critical times to impact aphid population dynamics. Thus, a predator that seems to be at very low densities and attacks few prey late in the season may be viewed as less important than a predator that attacks many prey early in the season and delays or prevents pest outbreaks. In making this distinction, we hope to focus limited resources on critical predator–pest interactions and help prioritize research on potentially important natural enemies.

With this goal in mind, we have followed an integrated approach to identify predators of soybean aphid and their potential contribution to aphid dynamics. The initial stage of the process has included sampling to detect the presence of potential predators and comparison of their phenology to that of the aphid and soybean crop. Direct observations and laboratory feeding assays were used to verify which of these

potential predators attack aphids in the laboratory and field. Laboratory and field experiments were used to assess the potential of predators to impact soybean aphid population dynamics. Finally, we used sampling and direct observation to identify alternative prey of important predators.

Potential Soybean Aphid Predators. In a series of studies over 2 years, we identified the predatory arthropods that occur in soybean fields in Michigan and Indiana and that may contribute to soybean aphid suppression (Table 1). A variety of species of carabid beetles were present throughout the season occurring in both early and mid-season trials. Coccinellids were most abundant in mid-season trials with the seven-spotted lady beetle, *Coccinella septempunctata* L., and *Harmonia axyridis* (Pallas) occurring in the early season as well. *Orius insidiosus* Say was present in both early and mid-season reaching highest numbers in the latter trials. Although not an exhaustive list, these species represent the arthropod fauna most likely to attack soybean aphid. A notable exception is the lack of information on spiders, which were not effectively sampled by our techniques. From this list of potential predators, we selected a subset to determine whether they would consume soybean aphids in laboratory no-choice trials. Of the 22 species/life stages we tested, 20 killed or consumed significant numbers of soybean aphid adults, and 18 were significant predators of immature aphids (Table 2). Species varied greatly in the number of aphids killed/consumed and in their relative impact on adult and immature stages. A mortality ratio, dividing number of adult aphids consumed by number of immature aphids consumed, is a simple means to examine a predator's relative impact on different life stages (Landis and van der Werf 1997). Several predators such as the carabid *Elaphropus aniceps* (Le Conte) and the staphylinid *Philonotus thoracicus* (Gravenhorst) have low mortality ratios, indicating that these relatively small predators consume more immature than adult aphids. Such selective predation has the potential to shift aphid population age structures and may impact population dynamics. The seasonal occurrence of the predators in soybean fields (Table 3) is a further indication of which species may have the greatest potential for impacts on soybean aphid. Those predators that occur early and in high numbers, such as the coccinellids and *O. insidiosus*, are more likely to contribute to preventing outbreaks than those that only occur late in the season, such as the chrysopids.

In general, the ground-dwelling predators tested consumed fewer aphids than foliar-foraging predators, and although several of the ground-dwelling predators are very abundant, they may have less opportunity to encounter soybean aphid in the field. The soybean aphid does not readily drop in response to disturbance (T.B.F., unpublished data) as do other aphid species (Losey and Denno 1998b). Furthermore, we did not observe any carabid species to climb plants in search of aphids, although this could have occurred at night. Only a few of the foliar-foraging predators constituted >15% of the total abundance in any sample period

(Table 1). These included the damsel bugs (*Nabis* spp.), chamymaemyiid larvae (*Leucopus* spp.), and the coccinellids *C. septempunctata* and the convergent lady beetle, *Hippodamia convergens* Guérin-Ménéville, which were occasionally abundant. By far, the most numerous predators were the minute pirate bug, *O. insidiosus*, and the multicolored Asian lady beetle, *H. axyridis*.

In Indiana, sampling indicated that *O. insidiosus* and *H. axyridis* combined accounted for >85% of all predators found in the field. Adults and immatures of both species were observed consuming soybean aphids in the field. In Kentucky, another coccinellid, *Scymnus louisianae* J. Chapin, was found attacking soybean aphids (Brown et al. 2003). Although this species has not been seen further to the north, *Scymnus* spp. are well adapted to surviving periods of low prey density (Naranjo et al. 1990) and may be important predators in the southern range of soybean aphid. Therefore, although soybean contains a rich assemblage of natural enemies, our sampling data and observations have narrowed the list of potentially key natural enemies to a relatively small number of species, including *O. insidiosus* and *H. axyridis*, and to a lesser extent *C. septempunctata* and *H. convergens*.

Our next step has been to determine the impact of predators on soybean aphid dynamics. In Michigan, the impact of early season predation on *A. glycines* establishment was studied in 2001 and 2002 by using clip cages that allowed distinguishing aphid losses due to predation and emigration. We found evidence that predation reduced adult *A. glycines* survival over and above emigration in four of six trials over both years (Fox 2002). In these trials, survival of adults at 24 h averaged 44% in open cages in contrast to 73% survival in predator exclusion treatments. Predation losses increased from early June to July and were greater in 2002 than 2001. We concluded that predators can significantly reduce *A. glycines* adult establishment and are more likely to cause important reductions the later *A. glycines* immigration to soybean occurs. Observations during these trials showed that *O. insidiosus*, *H. axyridis*, *C. septempunctata*, and *H. convergens* were the most common foliar-foraging predators (Fox 2002).

Predator exclusion or open sham cages (1 m²) were also used to assess predation impacts on *A. glycines* density in 2002 (Fox 2002). Cages were initially infested with 110–130 aphids/m², and populations were assessed every 3–4 d for 5 wk. We found evidence that foliar-foraging predators, particularly *H. axyridis*, *Coleomegilla maculata* De Geer, *C. septempunctata*, and *O. insidiosus*, dramatically impacted *A. glycines* populations. Within 2 wk of cage establishment, aphid density averaged 76 adults per plant in exclusion cages but only 3.4 adults per plant in open cage treatments. The abundance and species richness of predators in the open cage treatments were greater than in the exclusion cage treatments. Subsequent reversal of the cage treatments (i.e., switching exclusion and open cages) resulted in a reversal in predator and aphid numbers. After 2 wk, aphid density in the former

Table 1. Potential *A. glycines* predators sampled in soybean in two separate experiments during early (7 June–3 July) and mid-season (26 June–12 August), East Lansing, MI, 2001–2002

Family	Order	Species	Early season				Mid-season			
			2001		2002		2001		2002	
			Total	%	Total	%	Total	%	Total	%
Ground-dwelling ^a Coleoptera										
Carabidae										
		<i>Agonum cupripenne</i> Say ^{c,d}	1	0.5	—	—	2	0.3	6	4.4
		<i>Agonum placidum</i> (Say) ^c	—	—	—	—	136	22.4	—	—
		<i>Amara aenea</i> (De Geer) ^{c,e}	2	1.1	—	—	35	5.8	33	24.3
		<i>Amara apricaria</i> (Paykull) ^c	—	—	—	—	1	0.2	—	—
		<i>Amara familiaris</i> Duftschmid ^c	—	—	—	—	—	—	1	0.7
		<i>Amara rubrica</i> Haldman ^c	—	—	—	—	8	1.3	—	—
		<i>Anisodactylus rusticus</i> (Say) ^c	—	—	—	—	1	0.2	—	—
		<i>Anisodactylus sanctaecrucis</i> (F.) ^{c,d,e}	3	1.6	14	8.6	96	15.8	3	2.2
		<i>Bembidion quadrimaculatum</i> Say ^{c,d}	4	2.2	1	0.6	30	4.9	—	—
		<i>Bembidion rapidum</i> (LeC.) ^c	—	—	23	14.2	2	0.3	10	7.4
		<i>Bembidion</i> spp. ^c	5	2.7	2	1.2	—	—	9	6.6
		<i>Bradycellus rupestris</i> (Say) ^{c,d}	—	—	—	—	1	0.2	—	—
		<i>Chlaenius pusillus</i> Say ^c	—	—	—	—	3	0.5	—	—
		<i>Chlaenius tricolor</i> Dejean ^{c,d}	—	—	—	—	2	0.3	1	0.7
		<i>Clivina bipustulata</i> (F.) ^{c,d,e}	11	5.9	17	10.5	4	0.7	5	3.7
		<i>Clivina impressifrons</i> LeC. ^{c,d}	25	13.4	47	29.0	15	2.5	5	3.7
		<i>Colliuris pensylvanica</i> (L.) ^e	—	—	—	—	1	0.2	—	—
		<i>Cyclotrachelus sodalis</i> (LeC.) ^{c,d}	—	—	—	—	11	1.8	1	0.7
		<i>Elaphropus anceps</i> (LeC.)	63	33.9	—	—	63	10.4	—	—
		<i>Harpalus affinis</i> (Schrank) ^c	5	2.7	10	6.2	3	0.5	—	—
		<i>Harpalus herbivigus</i> Say ^{c,e}	1	0.5	—	—	—	—	1	0.7
		<i>Harpalus pensylvanicus</i> (DeG.) ^{c,d}	1	0.5	—	—	5	0.8	12	8.8
		<i>Poecilus chalcites</i> (Say) ^{c,d,e}	12	6.5	12	7.4	23	3.8	37	27.2
		<i>Poecilus lucublandus</i> (Say) ^{c,d}	4	2.2	10	6.2	11	1.8	4	2.9
		<i>Pterostichus commutabile</i> (Motschulsky) ^c	—	—	—	—	1	0.2	—	—
		<i>Pterostichus melanarius</i> (Illiger) ^c	6	3.2	2	1.2	41	6.8	—	—
		<i>Scarites quadriceps</i> Chaudoir ^c	34	18.3	9	5.6	25	4.1	—	—
		<i>Scarites subterraneus</i> F. ^{c,d,e}	4	2.2	1	0.6	—	—	6	4.4
		<i>Stenolophus comma</i> (F.) ^{c,d}	5	2.7	14	8.6	81	13.2	1	0.7
		<i>Stenolophus ochropezus</i> (Say) ^{c,d}	—	—	—	—	—	—	1	0.7
		<i>Photinus</i> spp. larvae	—	—	—	—	6	1.0	—	—
Lampyridae			186	100	162	100	606	100	136	100
Total no. and percent										
Foliar-foraging ^a Coleoptera										
Cantharidae										
		<i>Philonthus cognatus</i> Stephens adults	—	—	—	—	—	—	2	0.2
Coccinellidae										
		<i>Coccinella septempunctata</i> (L.) adults	5	13.2	4	66.7	5	1.2	28	2.7
		<i>Coccinella septempunctata</i> larvae	—	—	—	—	1	0.2	9	0.9
		<i>Coleomegila maculata</i> DeG. adults	—	—	—	—	6	1.5	41	4.0
		<i>Coleomegila maculata</i> larvae	—	—	—	—	5	1.2	9	0.9
		<i>Cycloneda munda</i> (Say) adults	—	—	—	—	—	—	1	0.1
		<i>Harmonia axyridis</i> (Pallas) adults	8	21.1	—	—	95	23.2	250	24.4
		<i>Harmonia axyridis</i> (Pallas) larvae	17	44.7	—	—	140	34.2	4	0.4
		<i>Hippodamia convergens</i> G.-Mén. adults	2	5.3	1	16.7	6	1.5	13	1.3
Diptera										
		Chamymaemyiidae							167	16.3
		Syrphidae							4	1.0
Heteroptera										
		Anthracoridae							62	15.2
		<i>Orius insidiosus</i> (Say) adults	6	15.8	—	—	34	8.3	139	13.6
		<i>Orius insidiosus</i> nymphs	—	—	—	—	—	—	—	—
		Nabidae							20	4.9
		<i>Nabis</i> spp. adults	—	—	1	16.7	7	1.7	31	3.0
		<i>Nabis</i> spp. nymphs	—	—	—	—	—	—	—	—
Neuroptera										
		Chrysopidae							9	2.2
		<i>Chrysoperla</i> spp. adults	—	—	—	—	14	3.4	11	1.1
		<i>Chrysoperla</i> spp. nymphs	—	—	—	—	—	—	—	—
		Hemerobiidae							1	0.2
		<i>Hemerobius</i> spp. larvae	—	—	—	—	—	—	—	—
Total number and percent			38	100	6	100	409	100	1025	100

^a Ground-dwelling predators were collected in 8.5-cm-wide by 13-cm-deep pitfall traps. Pitfall traps were left uncovered for 2 d during the early season study and 6 d during the mid-season study. After each respective time, the total number of predators collected was counted.

^b Foliar-foraging predator counts during the early season study were taken as the number of predators observed per 5 min in 2001 and per 3 min during 2002 by direct observation in a 1 by 0.3-m area. During the mid-season study, predators were counted during a 3-min nonintrusive visual examination and then a hand examination of foliage to account for predators that might be missed by initial observation.

^c The same genus was present in southern Indiana soybean in summer 1985 or 1986 (Wiedenmann et al. 1992).

^d The same species was present in southern Indiana soybean in summer 1985 or 1986 (Wiedenmann et al. 1992).

^e The same species was captured in pitfall traps in a Tippecanoe County, Indiana, soybean field in summer 2001 (C.E.R., unpublished data).

Table 2. Number of *A. glycines* surviving, percentage of mortality, and mortality ratio of *A. glycines* in 24 h no-choice feeding trials with potential predators from soybean, 8 June–10 August 2001, East Lansing, MI

Family	Order	Species	n	<i>A. glycines</i> Adults		<i>A. glycines</i> Nymphs		Mortality Ratio
				Mean (\pm SEM) no. remaining	% Mortality	Mean (\pm SEM) no. remaining	% Mortality	
Coleoptera								
Carabidae		<i>Anisodactylus santaecrusis</i> (F.) adults	6	6.7 \pm 0.3*	33	4.3 \pm 0.6*	42	1.3
		<i>Bembidion quadrimaculatum</i> Say adults	6	5.2 \pm 1.3*	49	2.7 \pm 1.1*	60	1.2
		<i>Clivina impressifrons</i> LeC. adults	18	7.6 \pm 0.7*	25	5.3 \pm 1.0 NS	32	1.3
		<i>Elaphropus anceps</i> (LeC.) adults	46	7.7 \pm 0.3*	24	3.7 \pm 0.5*	53	2.2
		<i>Harpalus herbivigus</i> Say adults	5	8.2 \pm 1.1 NS	19	4.6 \pm 1.6 NS	43	2.3
		<i>Poecilus chalcites</i> (Say) adults	12	4.9 \pm 0.8*	50	1.5 \pm 0.5*	78	1.6
		<i>Poecilus lucublandus</i> (Say) adults	25	3.8 \pm 0.5*	62	2.2 \pm 0.5*	64	1.0
		<i>Pterostichus melanarius</i> (III.) adults	43	7.4 \pm 0.4*	26	4.3 \pm 0.5*	44	1.7
Coccinellidae		<i>Coccinella septempunctata</i> (L.) adults	51	2.1 \pm 0.3*	78	1.7 \pm 0.2*	69	0.9
		<i>Coccinella septempunctata</i> larvae	14	1.1 \pm 0.3*	89	0.1 \pm 0.1*	98	1.1
		<i>Coleomegilla maculata</i> DeG. adults	24	6.4 \pm 0.7*	37	2.2 \pm 0.5*	70	1.8
		<i>Harmonia axyridis</i> (Pallas) adults	60	1.4 \pm 0.2*	86	0.6 \pm 0.2*	88	1.0
		<i>Harmonia axyridis</i> larvae	50	1.4 \pm 0.2*	86	0.3 \pm 0.1*	94	1.1
		<i>Hippodamia convergens</i> G.-Mén. adults	17	1.3 \pm 0.2*	87	0.7 \pm 0.5*	86	0.9
		<i>Philonthus thoracicus</i> (Grav.)	5	8.3 \pm 0.5 NS	17	4.4 \pm 1.7 NS	46	2.7
Staphylinidae								
Dermoptera								
Forficulidae		<i>Forficula auricularia</i> L. adults	5	1.0 \pm 0.4*	90	0.6 \pm 0.6*	88	0.9
Heteroptera								
Anthracoridae		<i>Orius insidiosus</i> (Say) adults	24	6.2 \pm 0.3*	37	6.6 \pm 0.9 NS	19	0.2
		<i>Orius insidiosus</i> nymphs	22	5.7 \pm 0.4*	42	5.0 \pm 0.8*	29	0.7
Nabidae		<i>Nabis</i> spp. adults	46	1.5 \pm 0.2*	85	1.2 \pm 0.3*	77	0.9
		<i>Nabis</i> spp. nymphs	27	2.2 \pm 0.4*	78	1.8 \pm 0.5*	66	0.8
Neuroptera								
Chrysopidae		<i>Chrysopa</i> spp. adults	37	5.7 \pm 0.6*	44	5.1 \pm 0.8*	27	0.6
		<i>Chrysopa</i> spp. larvae	17	1.7 \pm 0.3*	82	0.7 \pm 0.4*	87	1.0
Control			84	9.4 \pm 0.1	6	8.7 \pm 0.6	—	—

NS, not significant; *, significant at $P \leq 0.05$. Nymph percentage of mortality was calculated based on expected nymph production as determined in control dishes. Mortality ratio was determined as the ratio of nymph mortality to adult mortality.

In no-choice feeding tests, *A. glycines* placed on an excised soybean leaf on moist filter paper in a petri dish and confined with or without a predator for 24 h. Pooled unpaired *t*-test with equal variance was used to evaluate *A. glycines* survival in predator or control treatments.

exclusion cages was reduced to an average of 12.2 adults per plant, whereas those in the former open cages reached 131.7 adults per plant. The entire experiment was repeated a second time with qualitatively similar results but lower aphid densities.

We also conducted laboratory assessments of *O. insidiosus* as a predator of soybean aphid. These studies were conducted in microcosms consisting of a potted soybean at the VI (unifoliate) stage in an acetate cage. Two assays were conducted. The first assay was a functional response experiment without prey replacement. In these trials, a known number of soybean aphids was placed on the plant and given an hour to settle. We then placed a single adult *O. insidiosus* female in the cage and allowed her to remain for 24 h. After that time, the predator was removed, and we counted the remaining aphids. The trials were conducted using 1, 2, 4, 8, 16, and 32 aphids. A maximum of 10.23 (\pm 3.5 SE) soybean aphids were killed by one *O. insidiosus* in 24 h (Fig. 1). A second assay was designed to evaluate the ability of *O. insidiosus* to control soybean aphid population growth over time. In these trial, adult females of *O. insidiosus* were placed in microcosms with one of three levels of soybean aphids (12, 24, or 48 aphids), and the system was allowed to run for 4 d. Control microcosms with the same densities of aphids, but without predators, were

also established. The numbers of aphids were counted at the end of the 4 d. At all densities of soybean aphids, the predators were able to prevent population growth and to reduce the initial population size (analysis of variance: $df = 5, 45$; $F = 7.59$; $P = 0.0001$). This was true even for the treatments with 48 aphids. When *O. insidiosus* were present, aphid numbers decreased to 38.7 (\pm 9.3 SE), but when no predator was present aphid numbers increased more than twofold to 104.1 (\pm 19.7 SE) (least significance difference: $P = 0.005$). Combined, these assays demonstrate that generalist predators have the potential to impact soybean aphid dynamics.

Predator Roles in Aphid Dynamics and Management. Broadly, we can categorize the roles of predators in prey dynamics as acting to suppress prey population growth, i.e., to prevent outbreaks, or to reduce prey densities after they have achieved outbreak levels (Murdoch et al. 1985). These distinctions, although somewhat artificial, do help in identifying relevant studies and in illuminating potential uses for predators in soybean aphid management. For a predator to be effective at suppressing aphid populations, it must 1) be present in the field in sufficient numbers during the time period that the aphids are invading the field (Ehler and Miller 1978) and remain in the field to exert pressure on the offspring of individuals that escape

Table 3. Seasonal occurrence of *A. glycines* predators in soybean, East Lansing, MI, 2001

Order		June	July	August	September
Family	Species				
Coleoptera					
Carabidae	<i>Anisodactylus santaecrusis</i> (F.)		_____		
	<i>Bembidion quadrimaculatum</i> Say	_____			
	<i>Clavina impressifrons</i> LeC.	_____			
	<i>Elaphropus anceps</i> (LeC.)	_____			
	<i>Harpalus herbivigius</i> Say		_____		
	<i>Poecilus chalcites</i> (Say)	_____			
	<i>Poecilus lucublandus</i> (Say)	_____			
	<i>Pterostichus melanarius</i> (Ill.)	_____			
Coccinellidae	<i>Coccinella septempunctata</i> (L.) adults	_____			
	<i>Coccinella septempunctata</i> larvae	_____			
	<i>Coleomegilla maculata</i> DeG. adults	_____			
	<i>Harmonia axyridis</i> (Pallas) adults	_____			
	<i>Harmonia axyridis</i> larvae	_____			
	<i>Hippodamia convergens</i> Guerin adults	_____			
	<i>Philonthus thoracicus</i> (Grav.)		_____		
Staphylinidae					
Dermoptera					
Forficulidae	<i>Forficula auricularia</i> Linnaeus	_____			
Heteroptera					
Anthocoridae	<i>Orius insidiosus</i> (Say) adults	_____			
	<i>Orius insidiosus</i> nymphs	_____			
Nabidae	<i>Nabis</i> spp. adults	_____			
	<i>Nabis</i> spp. nymphs	_____			
Neuroptera					
Chrysopidae	<i>Chrysopa</i> spp. adults		_____		
	<i>Chrysopa</i> spp. larvae		_____		

Seasonal occurrence was determined during the period of soybean aphid activity in soybean. Adult ground-dwelling predator data was gathered from pitfall trap counts. Seasonal occurrence of foliar-foraging predators was determined by direct observation of soybean foliage (7 June–4 September).

predation (Den Boer 1982); and 2) be able to locate widely dispersed prey. For a predator to be effective in reducing populations that have reached outbreak levels, it must 1) exhibit a strong numerical response, aggregating in areas of high aphid density; and 2) have attack rates that result in prey population reductions. Examining the two most commonly encountered predators of soybean aphid, *O. insidiosus* and *H. axyridis*, we can classify them into these two categories and point out areas of overlap in their roles over time.

O. insidiosus has a number of traits that suggest it primarily acts to suppress growing aphid populations. It is a generalist predator and feeds on a variety of prey items found in soybean fields (e.g., whitefly nymphs, potato leafhopper, soybean thrips, and mites; Isenhour

and Yeargan 1981, Kampmeier 1984, McCaffrey and Horsburgh 1986, Coll and Ridgeway 1995, C.E.R., unpublished data]. It is present in soybean fields throughout the season where it reproduces and increases in density until the plants senesce (Table 3; Fig. 2). *O. insidiosus* feeds on soybean pollen and gain moisture and minerals from soybean xylem (Isenhour and Marston 1981, Cohen 1990, Armer et al. 1998), and our sampling data show that *O. insidiosus* exhibits a numerical response to the soybean aphid. The numbers of *O. insidiosus* in the field increases with the numbers of aphids at densities >10 aphids to a plant

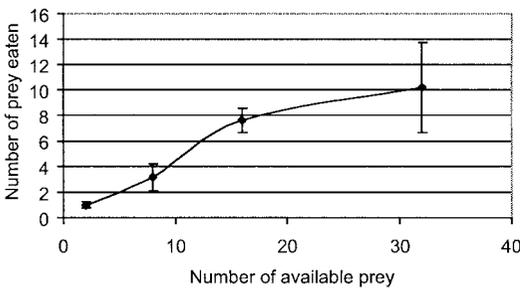


Fig. 1. Functional response of *O. insidiosus* to soybean aphid. Aphids were isolated with one female adult *O. insidiosus* on a unifoliolate plant for 24 h and the number of aphids remaining at the end of 24 h was counted.

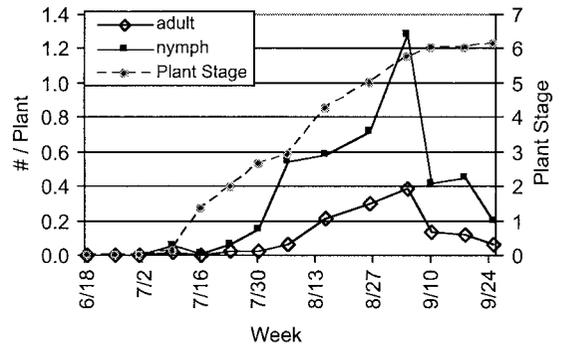


Fig. 2. Phenology of *O. insidiosus* and soybean plants in a soybean field in central Indiana in summer 2002. Plant stage is the reproductive stage. On this scale, 1 represents a plant with one flower, 6 is a plant with full pods, and 8 represents a plant ready to harvest.

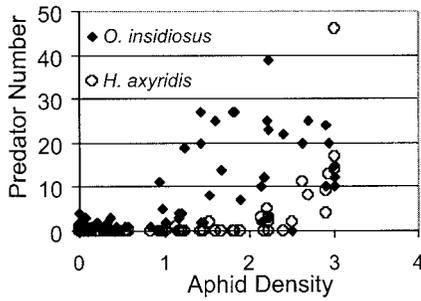


Fig. 3. Numerical response of *O. insidiosus* and *H. axyridis* to soybean aphid. Soybean aphid severity was rated on a scale of 0–3 per plant (0, 0 aphids; 1, 1–10 aphids; 2, 11–100 aphids; and 3, >100 aphids). Each point represents a sampling date during the summer of 2001 in one of 10 fields in Indiana.

(Fig. 3). Individual *O. insidiosus* were more likely to be on a plant with 10 or more aphids than on a plant with <10 aphids ($\chi^2 = 128.06$, $df = 3$, $P < 0.0001$). Finally, field data suggest that *O. insidiosus* is acting to prevent soybean aphid outbreaks. In 2001, we sampled 10 fields in central and northern Indiana weekly. In each field, we examined 30 randomly selected plants. Each plant was rated for soybean aphid abundance on a scale of 1–3, and individuals of other arthropod species, including *O. insidiosus*, were counted. These data showed a significant negative relationship between the length of time *O. insidiosus* were present in fields before the arrival of aphids and the peak aphid density of that field (Fig. 4). Fields that had established *O. insidiosus* populations when aphids arrived showed lower peak aphid densities than fields in which the aphid and *O. insidiosus* arrived simultaneously or fields in which *O. insidiosus* arrived after the aphids.

In contrast, the multicolored Asian ladybeetle is one of several predators that can act to prevent or to reduce high aphid densities (Fox 2002, Fox et al. 2004). Adult *H. axyridis* effectively locate prey over large distances (Mondor and Warren 2000, Osawa 2000). Studies in Michigan in 2001 and 2002 show that *H.*

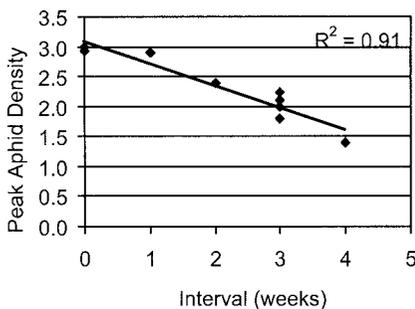


Fig. 4. Interval between *O. insidiosus* arrival in a field and subsequent soybean aphid arrival in that field versus the eventual peak severity of soybean aphids in that field. *O. insidiosus* never arrived after soybean aphids in any particular field. Each point represents a field. Data were collected in summer of 2001 in 10 fields in Indiana.

axyridis can be among the first coccinellids to arrive in soybean fields in the spring (Fox 2002). Early in the season when soybean aphids are scarce, *H. axyridis* adults occur in soybean where they search plants and consume aphids they encounter. At low aphid densities, oviposition is not induced, and adults may only be temporary residents in soybean fields. However, like many coccinellids, *H. axyridis* is capable of a distinct numerical response in the presence of abundant prey. Populations of *H. axyridis* frequently peak at or just after the population of aphid prey (Osawa 1993, 2000; Nakata 1995). *H. axyridis* is retained by concentrations of aphids, and these increased retention times have been shown to result in population level aggregations (Osawa 2000). Analysis of Indiana sampling data show that *H. axyridis* exhibit a strong numerical response to soybean aphids, becoming more common in fields once aphid numbers reach 100 or more a plant (Fig. 3). Within the field, individual *H. axyridis* are more likely to be found on a plant with 100 or more aphids than on plants with fewer aphids ($\chi^2 = 34.47$, $df = 3$, $P < 0.001$).

The functional response of *H. axyridis* to soybean aphid has not been reported. In a related species, *H. arcuata* (F.), adults and *Harmonia* spp. larvae (presumably *H. arcuata*) both show a type II functional response to *A. glycines* on soybean in Indonesian field studies (van den Berg et al. 1997). A key question is the ability of *H. axyridis* to regulate prey populations rather than simply respond to them. Osawa (2000) suggests that *H. axyridis* efficiently tracked aphid populations but did not regulate them in a botanical garden setting. In contrast, van den Berg et al. (1997) found that *H. arcuata* regulated *A. glycines* populations on soybean during the late but not the early season.

Pest Management Options. Further research is needed to better define the contribution of predators to soybean aphid dynamics. However, we have sufficient insight to advance a preliminary description of predator–aphid dynamics. Although many predaceous species occur in soybean fields, it is likely that a relatively small group of predators significantly impact aphid dynamics. What seems critical is the relative timing of the aphid's invasion into the soybean field, the density of predators early in the growth cycle of the aphid, and the response of predators to both low and high aphid densities. Aphids that arrive in fields with few predators will build to larger population sizes than fields that have many predators present when aphids arrive. The final peak density of aphids will depend, in part, upon the aphid/predator ratio and the suitability of the host plant for aphid reproduction. (There is also evidence that aphid population growth is dependent on the physiological age of the plant. van den Berg et al. (1997) showed a 50% decrease in soybean aphid reproduction as the plant mature past reproductive maturity. In contrast, studies from our laboratory [R.J.O. and C.E.R., unpublished data] have indicated a positive relationship between plant age and aphid reproduction. Further research is needed to address these conflicting findings.) Aphid growth will be further checked by the response of predators to

increasing aphid densities. The management implications for such a scenario include the need to sample predator populations in soybean, particularly early in the season before aphids arrive in the crop. The potential importance of plant phenology also suggests monitoring of plant growth and use of these data in predator-prey models to predict critical thresholds based on aphid numbers, plant size, and predator densities. If required, pesticide applications should be timed to minimize their impact on predators. This may be possible through choice of selective compounds, modification of application protocols, and spray timing. Other conservation techniques could include habitat management to attract or retain predators at crucial times (Landis et al. 2000) or perhaps the use of artificial attractants (e.g., sugar water) to attract predators (van der Werf et al. 2000). Finally, the current lack of parasitoids and pathogens in the system would suggest the potential for classical biological control. The addition of a natural enemy to the system may lead to higher levels of aphid mortality than provided by the indigenous predators alone (Gutierrez et al. 1988, Kindlmann and Ruzicka 1992). Alternatively, intraguild predation between introduced natural and indigenous enemies may cause a reduction in pest suppression (Ferguson and Stiling 1996, Brodeur and Rosenheim 2000, Michaud 2002). Study of the interactions between natural enemies would be warranted if a classical biological control program is implemented.

The soybean aphid has challenged pest managers to rapidly develop insights to protect a major commodity in an environmentally responsible manner. Understanding predator impact has proven critical to our appreciation of aphid dynamics and the identification of management options. The occurrence of soybean aphid as a key pest of soybean requires development of sampling programs, treatment options, and education programs to alert growers to the importance of natural enemies in crop protection. The challenge of these efforts requires coordinated efforts of management specialists, research scientists, and growers.

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