Distribution and Abundance of Carabidae (Coleoptera) Associated with Soybean Aphid (Hemiptera: Aphididae) Populations in Central New York

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ABSTRACT Carabid beetles were pitfall-trapped in soybean, *Glycine max* (L.) Merr., fields hosting populations of soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), in central New York state in July and August 2004 and 2006. Carabids were collected from five fields located in three counties in 2004 and from two fields both located at the same farm in 2006. In total, adults of 60 carabid species were collected, 10 of which represent introductions from Europe. *Agonum muelleri* (Herbst), a Palearctic native, was the dominant carabid species both years, a role not previously reported in U.S. carabid assemblages. Both years, *A. muelleri* was the most abundantly trapped species, and it was collected in more than half of the pitfall traps. The majority of carabid individuals trapped, including *A. muelleri*, belonged to species overwintering as adults. The most common larval overwinterer, the European native *Pterostichus melanarius* (Illiger), made up only 6.0% (2004) and 5.5% (2006) of the total carabids species caught, yet this species was relatively broadly distributed (in 40.1% of traps in 2004 and 26.0% of traps in 2006). In three no-tillage fields with canopy closure, densities of the seven most common carabid species were high at the beginning of the season, but they decreased in early August as aphid densities began increasing. A significant negative exponential relationship described this relationship between activity density of carabids and aphid density. A no-choice feeding assay confirmed that the dominant species *A. muelleri* readily eats soybean aphids, which is consistent with carabid predation on soybean aphid populations. Pitfall traps were arrayed to allow comparisons of carabid beetle distributions among field edges, and distances 10 and 20 m into fields. Among the seven most common species, significantly more adults of *A. muelleri*, *Poecilus chalcites* (Say), *Poecilus lucublandus* (Say), and *Pt. melanarius* were trapped within fields compared with at field edges.

KEY WORDS predator communities, biological control, invasive species, pitfall trapping, field crop

Ground beetles (Carabidae) are an extremely abundant and diverse component of the epigeal field-crop arthropod community. The contribution of these commonly found predators toward control of pests has been investigated in multitudes of studies. Symondson et al. (2002) reviewed the dynamics of the interactions between generalist predators and their many pest and nonpest prey. They concluded that generalist predators, either alone or in assemblages, significantly reduced prey numbers in ≈75% of manipulative field experiments. Carabid predation of pests in crops has been suggested as slowing early season population increase and thereby facilitating control by later-arriving specific predators and parasitoids (Scheller 1984). For example, polyphagous predators, including carabid assemblages, are considered important agents in control of aphid populations in cereals in England (see Lövei and Sunderland 1996). In the English ce-

real system, the effects of predators were most notable early in the seasons when aphid population densities were low, although relative importance of different predator groups differed by year and site.

An invasive aphid pest in North American soybean, *Glycine max* (L.) Merr., *Aphis glycines* Matsumura, was first discovered in Wisconsin in 2000 (Ragsdale et al. 2004) and then in New York state in 2001 (Losey et al. 2002). *A. glycines* can impact plants directly by causing a reduction in soybean growth and seed yield and indirectly by vectoring at least six plant viruses. The aphids also produce honeydew that facilitates growth of sooty mold that covers leaves and thus decreases photosynthesis (see Fox et al. 2004). Since *A. glycines* was discovered in the Midwest and Northeast region, in numerous instances localized or more widespread populations of soybean aphid have reached outbreak levels requiring insecticide applications to prevent yield loss (Myers et al. 2005; J. K. Waldron, personal communication).

Several studies have been conducted in North America to investigate mortality in soybean aphid

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populations due to resident natural enemies. In the midwestern states, a diverse fauna of generalist foliar and ground predators has been documented in soybean fields hosting *A. glycines* populations (Rutledge et al. 2004, Fox et al. 2005). Fox (2002) and Rutledge et al. (2004) each reported 29 species of carabids in soybean fields hosting soybean aphids in Michigan in 2001–2002. Among the generalist foliar predators *Orius insidiosus* (Say) and coccinellids, particularly *Harmonia axyridis* (Pallas), were identified as key foliar predators of *A. glycines* in the Midwest, based on sampling and caged predator exclusion trials (Rutledge et al. 2004, Fox et al. 2004, Mignault et al. 2006). Several species of parasitoids have been reared from soybean aphids in the Midwest and Northeast region, but levels of parasitism have been very low (Nielsen and Hajek 2005, Kaiser et al. 2007; T. Noma, personal communication). Eight species of entomopathogenic fungi have been identified infecting soybean aphids in the northeast, and at times infection levels have been extremely high (84%), leading to prevention of outbreak populations of soybean aphids (Nielsen and Hajek 2005; unpublished data). To date, the carabid fauna associated with soybean aphid populations in the northeast has not been investigated.

Carabid biology and behavior influence the ability of these predators to help control aphid populations. The phenology of individual carabid species can influence their ability to colonize fields and contribute to the control of aphid populations. Whereas carabids are best known as ground-dwelling predators, some are known to climb or fly onto plants, and this behavior is especially associated with carabids eating aphids (e.g., Chiverton 1988, Snyder and Ives 2001). Carabids on the ground are also known to consume aphids that jump or fall from plants, e.g., *Acyrthosiphon pisum* (Harris) (Losey and Denno 1998). Among all carabid species in a landscape, some readily disperse into or onto crops whereas others remain in adjacent natural environments (Den Boer 1977, Den Boer and Den Boer-Daanje 1990). Studies in corn-soybean cropping systems in the Midwest have demonstrated diverse assemblages of carabid species along environmental gradients within soybean fields (French et al. 2004).

In this study, we investigated the ground beetle fauna associated with soybean fields hosting soybean aphid populations in central New York state in 2004 and 2006. Our objectives were to investigate carabid species diversity and abundance in soybean fields. The abundance of invasive carabid species in soybean fields, in contrast to native species, was evaluated as well as carabid phenology and the association of carabid abundance with aphid density. Feeding of the dominant carabid species *Agonum muelleri* (Herbst) on soybean aphids was quantified in the laboratory. Soybean fields in central New York state are frequently adjacent to woodlots, which we hypothesized could provide a permanent refuge for ground beetle populations that could move into soybean fields. Therefore, we also evaluated whether activity densities of carabids along field edges differed from activity densities within fields.

Materials and Methods

2004 Study Sites. Five fields planted with soybean were sampled weekly from 28–29 June to 23–24 August 2004, for a total of eight sample dates. Studies were conducted to investigate carabid and aphid populations during the time interval when soybean plants are sensitive to aphid feeding (Ragsdale et al. 2006): early flowering (R1) through full pod (R4) (Fehr et al. 1971). Soybean planting and development were not synchronous in all fields and planting dates differed. Studies began when fields were at V1/R1 (first node/beginning flowering) and ended when fields were at R6/R7 (full seed/beginning maturity). All fields were in New York state: one field was in Cayuga Co. (field 1), and two fields each were in Tompkins Co. (fields 3 and 4) and Wayne Co. (fields 5 and 6). Fields were representative of common soybean-growing practices in the region, with fields 1 and 4–6 cultivated as no-till. Further details on cultivars planted and cropping practices are provided in Nielsen and Hajek (2005). All fields were sprayed with glyphosate by the second sample date, and fields 3 and 4 were sprayed again on 4 July. The only insecticide use occurred in field 5; this field was sprayed with λ-cyhalothrin (Warrior) for control of soybean aphid on 22 July, but not within 10 m of our study plot. Each week, the soybean growth stage and heights of plants were recorded. Field 3 (Tompkins Co.) differed because it was planted with 76.2-cm spacing between rows, whereas all other fields were planted with either 19.1- or 38.1-cm row spacing. As a result, field 3 differed markedly as a habitat for carabids, because the canopy never closed between rows, in contrast to the other fields where canopies closed ≈1–3 wk after sample collection began. Thus, in field 3 large areas of soil remained exposed to the sun between rows until the end of sampling.

At least one side of each field was bordered by *Rhamnus cathartica* L., the primary host of soybean aphid, growing within woodlots behind a small area of herbaceous plants (<1–2 m) at the field margin. Sampling areas for all fields were established along one margin of the field bordered by the woody vegetation. However, our plot in field 3 was an exception, because the sample plot was not directly adjacent to natural vegetation; in this field pitfall traps were separated by a 5.6-m grass-covered track from the edge of the woodlot.

2006 Study Sites. Two fields (A and B) were sampled on the same farm as field 1 from the 2004 studies. The three fields (field 1 from 2004 and field A and B from 2006) ranged from ≈150 to 350 m from each other. Once again, fields were representative of common soybean-growing practices in the region. Both fields were planted on 8 May with Hyland Razor with 19.1-cm row spacing. Both fields were no-till, had been planted with corn, *Zea mays* L., for the previous 2 yr, and both were sprayed with glyphosate on 13 June. These two fields (A and B) were separated by ≈150 m

containing cornfields and a grassy road. Fields were sampled every 3–7 d from 11 July to 21 August, for a total of 10 sample dates. Studies began when fields were at R2 (full flower) and ended when plants were at R6/R7 (full seed/beginning maturity).

Estimation of Aphid Density. Aphid populations were estimated by counting all aphids on the top trifoliate (a three-part compound leaf) (Chung et al. 1980, Su et al. 1996). In 2004, soybean aphids were counted weekly on the top trifoliate of each of 30 randomly chosen plants along a diagonal transect from one edge of the field to 20 m into the field (20- by 30-m plot). In 2006, two 20- by 100-m subplots were established within each field, with the outer longer edge of each subplot 10 m from the field edge. In each of these plots, all aphids on the top trifoliates of 20 randomly chosen plants were counted on each sampling date.

Carabid Sampling. In each field, the same areas used for aphid sampling were also used for placement of pitfall traps to collect carabids. Each pitfall trap was composed of two 1,000-ml stackable plastic containers (11.5 cm in diameter by 14.5 cm in height). One container was set inside the other so that the outer container remained in the ground and the inner container could easily be removed and emptied without disturbing the surrounding soil. The top of the outer container was flush with the soil, whereas the inner container was 2.5 cm shorter. A cover made of hardware cloth (mesh, 12.5 by 12.5 mm) encased in duct tape (15 by 15 cm) was placed 10 cm above the pitfall trap. The covers were included to both help shield the trap from rain and to protect it from birds and raccoons.

Approximately 100 ml of antifreeze, composed predominantly of ethylene glycol (Keuka Packaging Inc., Hall, NY), was mixed with 100 ml of water and poured into the inner container of each pitfall trap. In 2004, nine pitfall traps were placed in a 3 by 3 grid in each field. Three pitfall traps, separated by 10 m, were placed along the edge of the soybean planting. A second set of three pitfall traps were placed 10 m into the field, with another three 20 m into the field. In 2006, three pitfall traps were placed 10 m from each other along a transect 20 m from the field edge in each subplot in each field. On each sampling date (weekly in 2004 and every 3–7 d in 2006) traps were emptied into individual 0.47-liter plastic deli cups and then refilled with the antifreeze mixture. In the laboratory, the contents of the traps were filtered through a 0.8-mm mesh to remove any silt accumulated in the traps. All carabids were carefully removed from the remaining debris with a pair of forceps and transferred to 70% ethanol.

Taxonomy. Carabid beetles were reported following the classification of Bousquet and Larochelle (1993). *Trechus quadristriatus* (Schrank) was determined using diagnostic criteria of Bousquet et al. (1984). Representative specimens of all species from all fields have been deposited in the Cornell University Insect Collection (CUIC) as voucher lot no. 1255.

Feeding Trials. To evaluate whether the dominant invasive *A. muelleri* feeds on *A. glycines,* no-choice feeding trials were conducted in the laboratory. In early August 2006, *A. muelleri* individuals were collected from Musgrave Research Farm, Cayuga Co. Studies were conducted at 25°C, 50% RH, and a photoperiod of 14:10 (L:D) h. Six adult beetles were maintained individually in 90-mm petri dishes lined with moistened filter paper for a 19-h acclimation/starvation period before the trial. One soybean leaflet with 10 *A. glycines* adult apterae from a laboratory colony was placed in each dish. As controls, a leaflet with 10 adult apterae was placed in each of six additional petri dishes lined with moist filter paper. Aphids and carabids remained in experimental and control petri dishes for 24 h, after which time carabids were removed. Aphid apterae that remained and nymphs that had been produced over the previous 24 h were counted in each dish. The experiment was repeated once more with seven beetles.

Data Analysis and Interpretation. During 2004, pitfall traps in field 5 were increasingly disturbed by vertebrates as the field season progressed so that after the third sample date (20 July), virtually all traps were being dug up each week, spilling much of the contents. Therefore, data from field 5 are only included to subjectively record species diversity. Fields 3 and 6 each lost samples from one date due to flooding (19 July and 28 July, respectively; all nine traps each time). These lost samples are included in statistical analyses as missing data.

As many studies have discussed, pitfall traps reflect the activity and density of carabid species, but catches also are influenced by numerous biotic and abiotic factors (see Spence and Niemelä 1994). In particular, temperature, moisture, surrounding vegetation, and trap design and placement can influence pitfall trapping. However, other methods that have been used for sampling carabids also are biased (see Spence and Niemelä 1994). Spence and Niemelä (1994) state that pitfall traps are most useful as population indices for comparison of similar habitats or different years and our comparisons of carabid assemblages use data in this way.

To investigate relationships between aphid density and carabid density, further analyses were conducted with the seven most abundant species from 2004; these species each made up ≥4% of the total number of individuals collected. Aphid versus carabid densities were initially plotted separately by field but to alleviate problems due to the low densities of both aphids and carabids, data from fields with similar relationships were averaged to calculate an overall regression (PROC NLIN; SAS Institute 1999).

The effects of field, time (collection date), and distance from the field edge on the numbers of the seven most common carabid species collected from the pitfall traps were analyzed by multifactor analysis with random fields and numbers in pitfall traps as repeated measures on different dates. The PROC MIXED procedure in SAS version 8.2 (SAS Institute 1999) was used for the analysis. Counts of carabids were log-transformed [$\log_e$ (carabid per trap + 1)], and each species was analyzed separately. Counts

from traps were regarded as being more correlated, the fewer days there were between collections [type = AR(1) option in SAS]. Pairwise comparisons were conducted using least squares means (PROC MIXED). Comparisons of counts of log-transformed total carabids in 2004 versus 2006 were analyzed using a similar model with season and field as main effects and pitfall traps as autocorrelated repeated measures.

Results

Species Abundance and Diversity. Across all seven fields at five sites over 2 yr, representatives of 60 carabid species were trapped in pitfalls, totaling 7,935 individuals (Table 1). Among all species, 15 were found in only one of the fields and these each made up <1% of the total for that year. In 2004, each field that was sampled throughout the season hosted from 29 to 35 species. In 2004, the invasive European *A. muelleri* was by far the most common species, making up 46.9% of the individuals collected (Table 1). *Brachinus ovipennis* LeConte was the next most abundant species overall, with 11.2% of the total individuals, emphasizing the numerical dominance of *A. muelleri.* The native *Agonum cupripenne* (Say) constituted a significant element in pitfall trap catches, contributing 7.0% to the total number of carabids trapped but making up 14.3% of the total individuals in field 6. Other species totaling >4.0% of the total included *Chlaenius tricolor* Dejean, *Poecilus chalcites* (Say), *Poecilus lucublandus* (Say), and *Pterostichus melanarius* (Illiger). *A. muelleri* also was distributed throughout fields, being found in 66.3% of traps, whereas the next most widespread species, *Po. chalcites*, was captured in only 48.7% of traps. Interestingly, although several of these species were not collected in large numbers in individual traps, they were repeatedly found throughout the study, e.g., *Pt. melanarius* (40.1% of traps) and *Po. lucublandus* (42.3% of traps). *A. muelleri* was most abundant in fields 1, 4, and 6 (48.1–53.8%), but it was the third most abundant species in field 3 (15.0%), the one field where the canopy did not close due to wider row spacing. In field 3, both *Po. chalcites* (17.5%) and *Harpalus compar* LeConte (=*H. bicolor*) (15.9%) were slightly more abundant than *A. muelleri.* Field 3 also differed in the total number of carabids collected in pitfalls. Pitfall traps collected an average of 8.6 ± 1.0 carabids per trap per wk in field 3, whereas other fields yielded from 16.4 ± 7.2 to 44.2 ± 9.0 carabids per trap per wk.

In 2006, fewer carabids were collected in pitfall traps than in 2004, e.g., whereas 32.4 ± 4.8 *A. muelleri* (mean ± SE) were collected per pitfall trap per wk in pitfalls placed 10 and 20 m from the field edge in 2004 (maximum per trap per week, 183), in 2006 pitfalls placed 20 m from the field edge collected 3.1 ± 0.6 *A. muelleri* per pitfall trap per wk (maximum per trap per week, 49). The total number of species collected in 2006 also decreased compared with 2004, with 11–20 species collected per field. Even with the much lower trap catches in 2006, *A. muelleri* was again very abundant (24.2% of total collections), although *Po. chalcites*

was present at a similar level (23.7%) ($\chi^2 = 0.0376$, $P = 0.8463$). The top seven species in 2004 were once again the most abundant species in 2006, with the exception of *A. cupripenne*, which was third most abundant carabid species in 2004, and it was virtually not collected in 2006. *A. muelleri* (in 52.0% of traps) and *Po. chalcites* (in 53.0% of traps) were again the most widely dispersed species, whereas the next most broadly distributed species was *Po. lucublandus*, in 28.0% of traps.

Invasive Species. Of the 60 carabid species collected in pitfall traps in New York soybean fields, 10 have been introduced to North America from Europe. All 10 species were collected in 2004, whereas in 2006 only four of these species were collected. For nine of the species among these invasives, we also collected congeneric native species, often in the same fields. Based on total captures of individual beetles, 53.5% of the overall carabid individuals trapped by pitfalls in 2004 were of European origin. In 2006, 30.1% of the total carabids in pitfalls were invasives from Europe. In both years, the invasive *A. muelleri* was numerically the most abundant carabid. The invasive *Pt. melanarius* was the fifth and sixth most common species in 2004 and 2006, respectively (Table 1). Within the carabids collected in the genera *Agonum* and *Pterostichus*, the numerical dominance of the alien species was overwhelming. In 2004, *A. muelleri* represented 87% of the *Agonum* individuals, although among the seven species of *Agonum* collected, *A. muelleri* was the only non-native. In 2006, although two other species of *Agonum* were trapped, they were uncommon, and *A. muelleri* was again the most abundant species in this genus. In 2004, *Pt. melanarius* accounted for 76% of all *Pterostichus;* among the five species of *Pterostichus* collected, *Pt. melanarius* was the only non-native. In 2006, *Pt. melanarius* was once again the most abundant species in this genus. The other eight non-native species were never abundant (all <1% of total).

In 2004, two of the European natives collected had not been reported previously in the literature from New York state: *Trechus quadristriatus* (Schrank) and *Harpalus rufipes* (DeGeer). However, specimens in the CUIC document that *T. quadristriatus* was present in Ithaca, NY, in 1984 (J.K.L., unpublished data). Neither of these species constituted even 1% of the total collection from any field in 2004, and they were not collected in 2006. *T. quadristriatus* was found in two fields, in both Tompkins and Cayuga counties, whereas *H. rufipes* was found in one field in Wayne Co.

Carabid Phenology. The majority of carabid species collected could be classified as overwintering as an adult or as a larva (Table 1). The exception was an uncommon species *Trechus apicalis* Motschulsky, which overwinters as either an adult or larva (Lindroth 1963b). Among those species overwintering as adults or larvae (total, 7,934), 88.0% of the individuals overwinter as adults (78.3% of the species). Among the seven most common carabid species collected in 2004 (Fig. 1), all overwinter as adults. This is in agreement with the abundance of adults of these species earlier in the season. Although *Pt. melanarius* can overwinter as an adult, it primarily overwinters as a larva

Table 1. Relative percentages of carabid species collected from pitfall traps in central New York, from 28–29 June to 23–24 August 2004 and 11 July–21 August 2006[a,b,c]

Species	2004						2006		
	Field 1 N = 3180	Field 3 N = 559	Field 4 N = 1827	Field 5 N = 569	Field 6 N = 1143	Total N = 7278	Field A N = 415	Field B N = 242	Total N = 657
Agonum cupripenne (Say) (A)	5		5	17	14	7	<1		<1
Agonum harrisii LeConte (A)	<1		<1		<1	<1			
Agonum melanarium Dejean (A)	<1		<1			<1			
Agonum muelleri (Herbst)* (A)	53	15	54	18	48	47	27	20	24
Agonum octopunctatum (F.) (A)			<1		<1	<1			
Agonum palustre Goulet (A)	<1					<1			
Agonum placidum (Say) (A)	<1	<1				<1	<1		<1
Amara cupreolata Putzeys (A?)[d]			<1		<1	<1			
Amara familiaris (Duftschmid)* (A)			<1			<1	<1		<1
Amara littoralis Mannerheim (A)		<1				<1			
Anisodactylus sanctaecrucis (F.) (A)		1	<1	<1	<1	<1	2		2
Bembidion americanum Dejean (A)				<1	<1	<1			
Bembidion inaequale Say (A)				4	2	<1			
Bembidion obtusum Audinet-Serville* (A)			<1		<1	<1			
Bembidion patruele Dejean (A)				<1		<1			
Bembidion quadrimaculatum L. (A)	<1	6	<1	13	<1	2	<1		<1
Bembidion rapidum (LeConte) (A)	<1	<1			<1	<1			
Bembidion versicolor (LeConte) (A)	<1	<1	<1		<1	<1			
Brachinus ovipennis LeConte (A)	16	14	11	<1	3	11	11	3	8
Bradycellus rupestris (Say) (L)		<1			<1	<1			
Calathus opaculus LeConte (L)				<1		<1			
Carabus nemoralis Müller* (A)			<1			<1			
Chlaenius impunctifrons Say (A)	<1				<1	<1		<1	<1
Chlaenius nemoralis Say (A)			<1	<1		<1			
Chlaenius sericeus (Forster) (A)	<1	<1	2		5	1			
Chlaenius tricolor Dejean (A)	2	4	2	24	13	5	5	21	11
Cicindela punctulata Olivier (A)		<1			<1	<1			
Cicindela sexguttata F. (A)	<1			<1	<1	<1			
Clivina bipustulata (F.) (A)	<1	<1		<1		<1			
Clivina fossor (L.)* (A)	<1	2	<1		<1	<1	<1		<1
Colliuris pensylvanica (L.) (A)	<1		1	<1	1	<1	<1		<1
Cyclotrachelus sodalis (LeConte) (L)	3					1	2	10	5
Diplocheila obtusa (LeConte) (A)	<1					<1			
Dyschirius globulosus (Say) (A)				<1	<1	<1			
Dyschirius politus (Dejean)* (A)				<1	<1	<1			
Elaphropus anceps (LeConte) (A)	<1	<1	<1	5	<1	<1	4		2
Galerita janus (F.) (A)		<1				<1			
Harpalus affinis (Schrank)* (A)	<1	<1	<1			<1			
Harpalus compar LeConte (L)		16	<1		<1	1	2	3	2
Harpalus eraticus Say (A)					<1	<1			
Harpalus pensylvanicus (DeGeer) (L)	<1	<1	<1	<1	1	<1	6	5	5
Harpalus puncticeps (Stephens)* (L)		<1			<1	<1			
Harpalus rufipes (DeGeer)* (L)					<1	<1			
Loricera pilicornis (F.) (A)		<1				<1			
Microlestes linearis (LeConte) (A)		<1				<1			
Patrobus longicornis (Say) (L)	<1	<1	<1	<1	<1	<1			
Platynus hypolithos (Say) (A)	<1	<1	<1			<1			
Poecilus chalcites (Say) (A)	8	18	6		<1	7	32	9	24
Poecilus lucublandus (Say) (A)	5	9	3	2	2	4	6	6	6
Polyderis laevis (Say) (A)					<1	<1			
Pterostichus commutabilis (Motschulsky) (A)	<1					<1			
Pterostichus luctuosus (Dejean) (A)			<1			<1			
Pterostichus melanarius (Illiger)* (L)	5	1	10	12	3	6	<1	14	5
Pterostichus permundus (Say) (L)	<1	5	3			2	<1	9	3
Pterostichus stygicus (Say) (L)			<1	<1		<1			
Scarites subterraneus F. (A)				<1	<1	<1			
Stenolophus comma (F.) (A)	<1	<1				<1	<1		<1
Stenolophus ochropezus (Say) (A)		<1			<1	<1	<1		<1
Trechus apicalis Motschulsky (A, L)		<1				<1			
Trechus quadristriatus (Schrank)* (L)	<1	<1				<1			

[a] Pitfall traps in field 5 were increasingly raided by vertebrates as the field season progressed, so numbers for this site are only representative of three of eight sample dates. Due to flooding, fields 3 and 6 each lost one sample date (dates 3 and 4, respectively; all nine traps for each instance).

[b] *, species is not native to North America and has been introduced from the Palaearctic (Bousquet and Larochelle 1993).

[c] Overwintering stages are indicated parenthetically after species names: A, adults overwinter; L, larvae overwinter; AL, both life stages recorded overwintering. Seasonality of larval and adult life stages was determined using Lindroth (1961 et seq., 1992), Bousquet (1999), and Turin (2000), interpreted in light of field data obtained in this study.

[d] The overwintering stage for *A. cupreolata* is not recorded in the literature but, based on the overwintering stage for the rest of this genus and that adults of *A. cupreolata* emerge in early August (Lindroth 1968), we hypothesize that *A. cupreolata* overwinters as an adult.
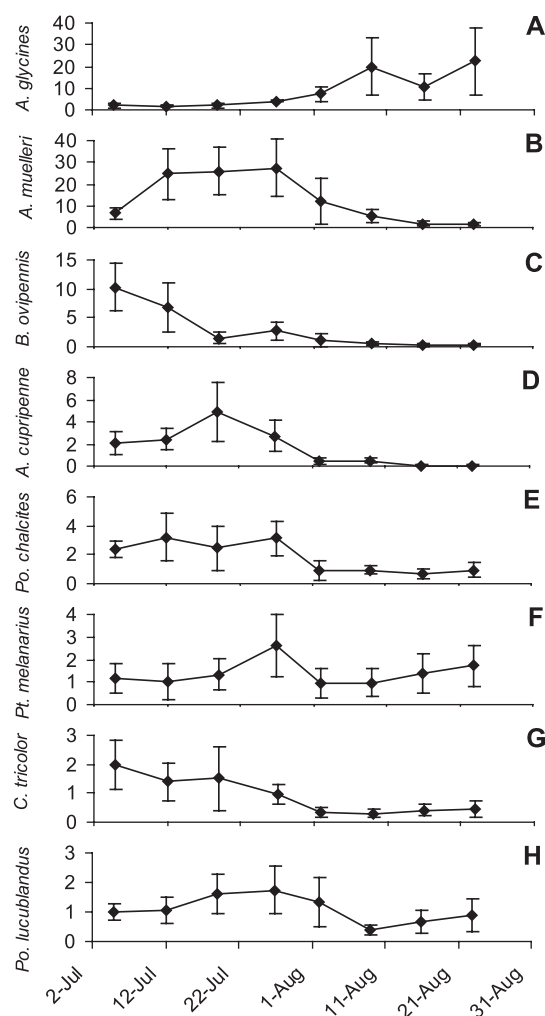
Fig. 1. Mean ± SE number of *A. glycines* per top trifolium (A), *A. muelleri* (B), *B. ovipennis* (C), *A. cupripenne* (D), *Po. chalcites* (E), *Pt. melanarius* (F), *C. tricolor* (G), and *Po. lucublandus* (H) captured per pitfall trap across four New York state soybean fields from 5 July to 24 August 2004 (fields 1, 3, 4, and 6). Due to pitfall flooding, on 19 July in one Tompkins Co. field (field 3) and 28 July in one Wayne Co. field (field 6), only three fields were included for those dates. Graphs for carabid species are arranged vertically from the most abundant to least abundant for the top seven carabid species.

Fig. 2. Numbers (mean ± SE) of adult apterae and nymphal *A. glycines* remaining after 24 h in a no-choice feeding trial with adult *A. muelleri*. For each aphid life stage, different letters indicate differences at a 5% significance level.

Carabid Activity Density and Aphid Density. We compared carabid activity density and density of aphid populations between 2004 and 2006 by using data from the only farm used in both 2004 and 2006 studies (Musgrave Research Farm, Cayuga Co.). Aphid densities differed significantly between the 2 yr of this study (Kruskal–Wallis test: $\chi^2 = 9.0163$, $P = 0.027$). In 2004, aphid numbers averaged 16.6 ± 4.1 on the top trifoliate, whereas in 2006 aphids on the top trifoliate averaged 1.5 ± 0.5. Whereas aphid densities increased late in the season in 2004 (Fig. 1A), the aphid population remained at low density throughout the 2006 sampling period. We did not analyze further any relationship between aphid and carabid densities for 2006 because of the sparse aphid populations that year.

Comparing carabid captures 20 m into soybean fields (field 1, A and B), in 2004 and 2006 carabid activity densities differed significantly among fields for the first three sample dates, with higher populations in 2004 compared with either field in 2006 ($P < 0.05$; least squared means tests) (Fig. 3). For the second three dates, the 2004 carabid populations were once again more abundant than both 2006 fields ($P < 0.05$; least squared means tests). Total carabid activity densities in these fields averaged 41.9 ± 12.7 carabids per wk per trap in 2004, whereas in 2006 activity densities averaged 12.2 ± 0.9.

In 2004, when carabid activity densities were high early in the season, soybean aphid populations were low (Fig. 1) and when soybean aphid populations increased later in the season, most carabids were scarce. For the seven most common carabid species in 2004, plotting aphid density versus carabid activity density for individual fields separately, field 3 displayed a very different relationship compared with

(Lindroth 1992, Bousquet 1999), which would be consistent with the increasing numbers of this species in late August as our sampling ended.

A. muelleri **Feeding Assays.** The no-choice feeding assay demonstrated that *A. muelleri* readily fed on *A. glycines* in petri dishes. Counts of aphids in control dishes were higher than those in dishes with *A. muelleri* adults (adult apterae: $\chi^2 = 9.6194$, $P = 0.0019$; nymphs: $\chi^2 = 8.3958$, $P = 0.0038$) (Fig. 2). This feeding assay was replicated with another seven beetles with similar results.
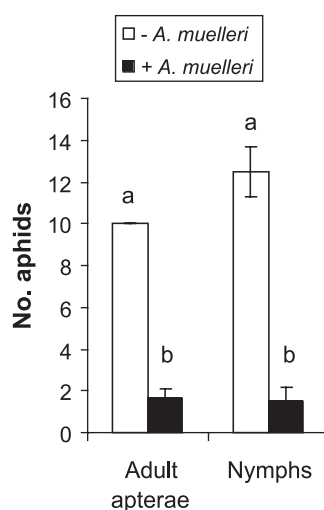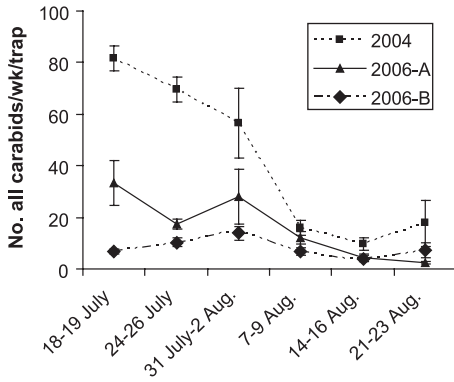
Fig. 3. Numbers (mean ± SE) of individuals of the total carabid assemblage captured in pitfall traps 20 m from margins of soybean fields at Musgrave Research Farm, Cayuga Co., NY, in 2004 and 2006. Dates indicate the date that a pitfall trap was emptied.

other fields. In field 3, where densities of both carabids and aphids were lower, there was a slight downward trend, but the linear relationship was not significant (r^2 = 0.0036, P = 0.8995). For fields 1, 4, and 6, exponential transformations provided the best fit, with r^2 values ranging from 0.24 to 0.68. To alleviate the problems due to low densities, data were averaged across fields to describe a significant exponential relationship (mean activity density of the seven most common carabids per pitfall trap per wk in 2004 = 59.8001 × $e^{(-0.1225 \times \text{mean aphids per top trifoliate})}$; $F_{2,6}$ = 49.99; r^2 = 0.9434) modeling a negative relationship between aphid and carabid densities (Fig. 4).

Locations of Species within Fields. For the seven major species of carabids in 2004, numbers of individuals varied significantly among fields (P = 0.0027) and among sampling dates (P = 0.0070). Numbers of carabids were numerically higher for traps located 10–20 m into the fields compared with the field edge for the numerically dominant *A. muelleri* (P = 0.0005) as well as *Po. chalcites* (P < 0.0001) and *Po. lucublandus* (P = 0.0124) (Fig. 5). Differences in *Pt. melanarius* by dis-
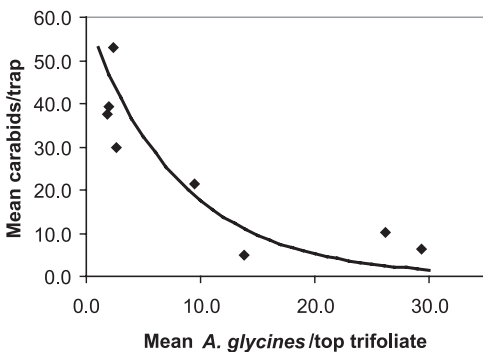

Fig. 4. Exponential relationship between aphid densities per top trifoliate and activity densities of the seven most abundant carabids per pitfall trap in the mean counts from fields 1, 4, and 6.

tance into the field were marginally significant (P = 0.0545), and post hoc tests showed more individuals at 10 m than at the field margin. For *B. ovipennis* (P = 0.1514), *A. cupripenne* (P = 0.7160), and *C. tricolor* (P = 0.8504), no significant effects of distance from the field edge were found (Fig. 5). Interactions between date and distance from the field edge were only significant for *Po. lucublandus* (P = 0.0035), *Po. chalcites* (P = 0.0373), and *Pt. melanarius* (P = 0.0294). *Pt. melanarius* and *Po. lucublandus* had very patchy distributions of activity through time relative to their locations in fields, with no clear trend in location within fields by date. More *Po. chalcites* were trapped within the field compared with the edge of the field in the beginning of the season, but this patchiness disappeared later in the season when collections were infrequent throughout the fields.

We tested field and location further, to specifically investigate potential differences in field 3, which differed from other fields because it was tilled and soybean was planted in wider rows so that the canopy never closed. This interaction was only significant for two species, *Po. chalcites* and *A. cupripenne*, and no clear pattern in distribution within field 3 compared with other fields was seen.

Discussion

We found great diversity in the carabid species present in the soybean fields sampled, although the number of species per field did not differ from normal expectations of between 10 and 40 carabid species per field (Lövei and Sunderland 1996), and they were similar to the numbers of carabid species found in Michigan soybean aphid-infested fields (Fox 2002, Rutledge et al. 2004). The aggregate carabid beetle species assemblage exhibited marked seasonality, and the midsummer decline in carabid adult abundance was due to the predominance of carabid species that overwinter as adults and spend the later summer as immature stages. Regression analysis demonstrated that when carabid numbers were high in 2004, soybean aphid numbers were low and soybean aphid numbers increased only after carabid numbers decreased in midsummer. Similarly, Winder (1990) found increased aphid density correlated with lower densities of polyphagous ground predators in European wheat. However, unlike our study, predator populations were manipulated by Winder and compared with a control so that seasonality could be eliminated as an explanation for the relationship. Lövei and Sunderland (1996) suggest that carabids are more important for extending the periods between pest outbreaks than for controlling outbreaks. Rutledge et al. (2004) also suggested that predators of soybean aphids occurring earlier and in high numbers are more likely to contribute to preventing outbreaks. Our data from 2004, when activity density of adult carabids was high early in the season would be consistent with these suggestions. In 2004, although soybean aphid density increased again in mid-late August, this was after the period from R1 to R4 (early flowering to full pod) when high popula-
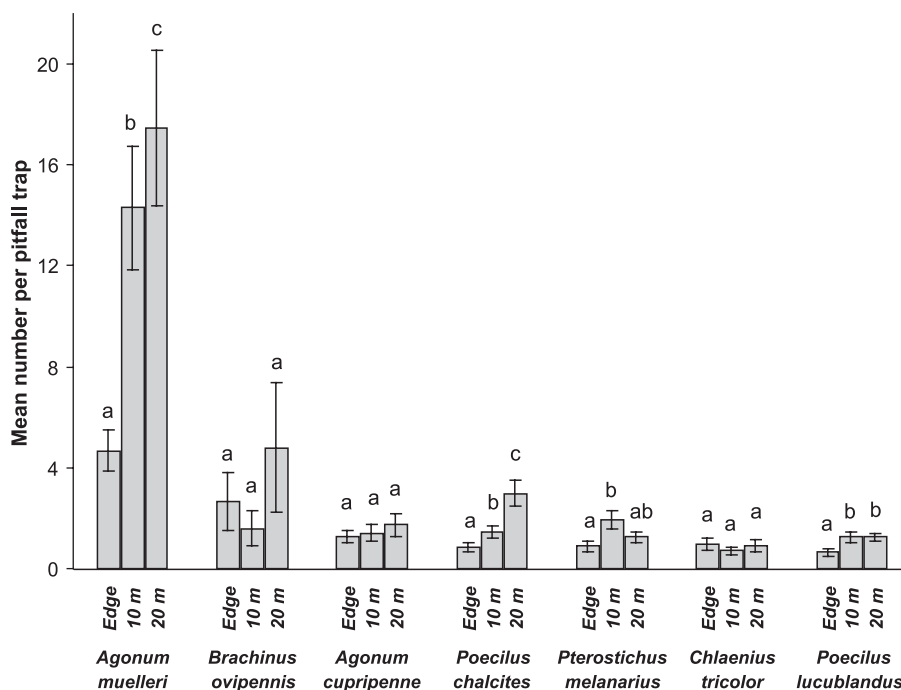
Fig. 5. Average activity densities of the seven most common carabid species accumulated over 8 wk from four fields (1, 3, 4, and 6) in 2004 (mean number captured per pitfall trap ± SE) as a function of distance from the edge of the field. The activity was measured by weekly counts of the number of carabids caught in three pit-fall traps placed at each distance from the edge per field. For each carabid species, different letters indicate differences in activity density at a 5% significance level.

tions of aphids can affect soybean yield (Ragsdale et al. 2006).

Carabids are generalist predators, consuming a variety of suitably sized prey that they encounter. A study in Switzerland demonstrated that *A. muelleri*, the most common carabid in our study, was the most voracious epigeal predator during the nighttime in winter wheat, *Triticum aestivum* L., fields (Lys 1995). For the seven most common carabid species in our study, we found a negative relationship between carabid density and aphid density (Fig. 4). It is highly likely that many carabids captured during our study will feed on soybean aphids given the opportunity. Our laboratory feeding assays showed that *A. muelleri* readily eats soybean aphids in a no-choice situation. *A. muelleri* ate similar numbers of *A. glycines* over 24-h as Rutledge et al. (2004) found for adults of two important species of Coccinellidae, *Coccinella septempunctata* (L.) and *H. axyridis.* In similarly designed assays, after 24 h, there were 1.7 ± 0.4 adult aphids remaining in trials with *A. muelleri* compared with 2.1 ± 0.3 and 1.4 ± 0.2 for *C. septempunctata* and *H. axyridis*, respectively. A study by Rutledge et al. (2004) also found that among eight carabids tested in no-choice tests, including *Po. chalcites, Po. lucublandus, Pt. melanarius,* and *A. sanctaecrucis,* all except one species (*Harpalus herbivigus* Say) fed on soybean aphids. However, because carabid beetles are known for mainly being active on the ground, their impact as predators of aphids on soybean foliage has been open

to question. Carabids have been shown to eat aphids dropping or falling to the ground (Losey and Denno 1998). Although soybean aphids can seem very sedentary (Fox et al. 2005), we have collected soybean aphids that are not alatae in pitfall traps, walking on soybean stems and on sticky traps placed below the canopy above the ground (J.J.H. and A.E.H., unpublished data). There is also the prospect of carabids climbing or flying onto soybean plants to eat soybean aphids, and this behavior has been reported in other systems (Lövei and Szentkirályi 1984). Laboratory studies have shown that *A. muelleri* will climb soybean plants (J.J.H. and A.E.H., unpublished data), and *Pt. melanarius* will climb alfalfa plants (Snyder and Ives 2001) to feed on aphids. Working in alfalfa with pea aphids, *A. pisum,* and *Pt. melanarius,* Snyder and Ives (2001) found that this predator had a much larger impact on aphid populations when plants were short, versus when plants were taller, supposedly because these carabids preferred not climbing as high to encounter aphids to eat.

The fields included in this study were predominantly no-tillage, and, for the carabid species most abundant in 2004, we found higher densities of three species within the fields compared with along the margins. None of the most abundant species had higher densities at field edges compared with field interiors. Our results for *A. muelleri* agree with findings of Afolina et al. (2001) from pitfall traps in winter wheat in Krasnodar, Russia. In contrast, a study in

Illinois reported that several carabid species were more abundant at the edge of a soybean field versus within the field (McCravy and Willand 2005). However, unlike most fields in our study, soybean in the McCravy and Willand (2005) study was planted at 76.2-cm row spacing; therefore, it had a much more open canopy. Even so, they found that *Po. chalcites*, the lone abundant species shared by their and our studies, was significantly more abundant within their fields. A pitfall study in European cornfields found no differences in the numbers of *A. muelleri* or *Pt. melanarius* near the edge of the field versus in the center (Alderweireldt and Desender 1990). We conclude that the most abundant carabids in our study were either habitat generalists (those species found at equal densities from field edge to field interior) or significantly preferred the microenvironment of soybean fields (those carabid species preferring field interiors). Our findings suggest that the majority of carabids trapped during our study probably overwintered within the fields or had no trouble moving from other overwintering sites into soybean fields in spring as aphid populations increased. Because carabids are able to disperse far into fields in just 1 wk (Welling 1990), the differences in carabid distribution are probably dictated more by microhabitat preferences than overwintering sites. In particular, in soybean both crop residue and topography are known to affect carabid distribution (Ellsbury et al. 2005).

Invasive Carabids in Soybean Fields. Soybean plants have been grown in China for 4,000–5,000 yr (Wu et al. 2004), and soybean aphids are native to eastern Asia (Ragsdale et al. 2004). Today, this co-evolved aphid–host plant system has been introduced to North American agriculture, where they encounter both native predatory carabid species as well as non-native carabid species accidentally introduced to North America (Lindroth 1957). The degree that non-native carabid species complement native taxa varies across ecosystems and geography in North America. In New York soybean fields, 10 among the total 60 carabid species (16.7%) were non-native, whereas in Michigan (2001–2002) soybean fields three of 29 carabid species (10.3%) were non-native (Fox 2002, Rutledge et al. 2004).

The invasive *A. muelleri* was clearly the dominant species in the carabid communities studied, particularly in the no-tillage fields with canopy closure where the largest percentage of individuals occurred at the furthest locations into the fields that were sampled (20 m). Because of its phenology, adults of this species were abundant only earlier in the season. After early August activity densities decreased. *A. muelleri* was first introduced to Newfoundland in the 1840s (Lindroth 1963a), and it was first recorded in New York state in 1921 (J.K.L., unpublished data). This species was collected in pitfall traps in cabbage fields in Ontario Co., NY, in 1979 and 1981, but it made up <1% of the total Carabidae captured (Shelton et al. 1983). Although *A. muelleri* was among the most common carabids collected in 1994–1997 in agricultural fields in southern Ontario (ranging from 0.1 to 25.13% abun-

dance) (Belaoussoff et al. 2003), our study provides the first record of *A. muelleri* being a dominant species (especially in 2004) in North America. Turin (2000) documented that *A. muelleri* is an ecological generalist but not dominant within any habitat types in The Netherlands. We hypothesize that *A. muelleri* could be a superior competitor against the native North American carabids and other non-native carabids in the soybean field habitats we sampled. However, it is also possible that the dominance of *A. muelleri* could be an example of the "enemy release hypothesis" (Keane and Crawley 2002), because this species is not known to be a dominant species in European carabid communities.

The other invasive carabid species that was relatively abundant in our study, *Pt. melanarius*, was first recorded in North America in 1926 in Nova Scotia (Lindroth 1966). *Pt. melanarius* was the dominant species in cabbage (*Brassica* spp.) fields in central New York in 1979 and 1981, accounting for >50% of the carabids captured (Shelton et al. 1983). In the current study, *Pt. melanarius* did not show the level of dominance seen during 1979 and 1981 in an area relatively near our study sites. However, in the 1979–1981 study, carabids were pitfall trapped in cabbage fields from late July to October; because *Pt. melanarius* is a larval overwinterer, this is the period when it would be more abundant. Perhaps our numbers for this species were lower because our sampling predominantly focused on a period earlier in the season. Likewise, we found that *A. muelleri* was more abundant before the beginning of August and therefore the Shelton et al. (1983) study in New York cabbage was not conducted when the majority of *A. muelleri* adults would have been active. Other studies in North America have documented *Pt. melanarius* as a dominant species in carabid assemblages (Niemelä et al. 2002, Pearce et al. 2002, Goulet et al. 2004) and a habitat generalist (Larsen et al. 2003).

Among the many studies of carabid assemblages in northern U.S. and Canada, we feel that our study adds to an invasion pattern. Spence and Spence (1988) demonstrated that invasive carabids were most abundant in anthropogenic habitats in British Columbia, and, where they occurred, invasives were often dominant members of carabid communities. Studies of carabid communities in anthropogenic habitats such as northeastern U.S. dairy pastures (Byers et al. 2000), Quebec, Canada, vineyards (Goulet et al. 2004), and parks in Ontario, Canada (Pearce et al. 2002), have similarly documented invasives ranging from 36 to 67% of the carabid individuals. Niemelä et al. (2002) also reported a strong positive association of non-native carabid species with urban versus natural environments in and near Edmonton, AB, Canada. Agricultural fields are disturbed habitats, and 53.5 and 30.1% of the total carabids captured in New York soybean fields were invasive species in 2004 and 2006, respectively; thus, in both years, carabid assemblages in soybean fields were dominated by invasive species.

However, this dominance by invasives in carabid assemblages does not seem to be characteristic across

the United States. Lindroth (1957) described a "Europeization" of the North American carabid fauna as invasive species moved westward from northeastern introductions and eastward from introductions in the Pacific Northwest. Although *Pt. melanarius* and *A. muelleri* were introduced to North America about the same time, and both are winged dispersers, the extent to which they have dispersed differs. *Pt. melanarius* has the larger distribution; it is present throughout the northern states and Canada (Bousquet and Larochelle 1993). *A. muelleri* has a more restricted distribution; in the west it occurs on the west coast in British Columbia plus Pacific coast states and in the Northeast region it occurs as far west as Minnesota and Wisconsin and as far south as Virginia and West Virginia (Bousquet and Larochelle 1993). Thus, regardless of the method of dispersal, it seems that *A. muelleri* has not spread as quickly as *Pt. melanarius.* Neither of these species were reported among carabids pitfall trapped in Iowa in 2001–2002 (Lopez et al. 2005), although *Pt. melanarius* was reported as a common species in six different Iowa habitats sampled from 1994 to 1998 (Larsen et al. 2003). *A. muelleri* was not found and *Pt. melanarius* occurred at <0.1% of the carabid assemblage in South Dakota corn in 2000–2001 (French et al. 2004). Because both of these invasive carabids can be dominant members of carabid assemblages, it seems highly probable that they will continue to disperse into the center of North America where they will potentially establish and build populations.

Acknowledgments

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