Carabidae Population Dynamics and Temporal Partitioning: Response to Coupled Neonicotinoid-transgenic Technologies in Maize

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ABSTRACT Insecticidal *Bt* crops and seed treatments represent additional pest management tools for growers, prompting ecological studies comparing their impact on farm system inputs and effects to nontarget organisms compared with conventional practices. Using high taxonomic and temporal resolution, we contrast the dominance structure of carabids and dynamics of the most abundant species in maize (both sweet and field corn) agroecosystems using pest management tactics determined by the purchase of seed and application of pyrethroid insecticides. In the seed-based treatments, sweet corn contained Cry1Ab/c proteins, whereas field corn contained the coupled technology of Cry3Bb1 proteins for control of corn rootworm and neonicotinoid seed treatments aimed at secondary soil-borne pests. The insecticide treatments involved foliar pyrethroids in sweet corn and at-planting pyrethroids in field corn. The carabid community, comprised of 49 species, was dominated by four species, *Scarites quadriceps* Chaudoir, *Poecilus chalcites* Say, *Pterostichus melanarius* Illiger, and *Harpalus pensylvanicus* DeGeer, that each occupied a distinct temporal niche during the growing season. Two species, *Pt. melanarius* and *H. pensylvanicus*, exhibited differences between treatments over time. Only *H. pensylvanicus* had consistent results in both years, in which activity densities in field corn were significantly higher in the control in July and/or August. These results, along with laboratory bioassays, led us to hypothesize that lower adult captures resulted from decrease in prey availability or exposure of *H. pensylvanicus* larvae to soil-directed insecticides—either the neonicotinoid seed treatment in the transgenic field corn or an at-planting soil insecticide in the conventional field corn.

KEY WORDS *Bt*, Carabidae, Cry3Bb, *Harpalus pensylvanicus*, neonicotinoids

The use of genetically engineered (GE) crops has risen steadily over the past decade, and adoption has been highest in U.S. agriculture, where over 145 million acres of GE crops were planted in 2008 (NASS 2008). Although most of the GE crop acreage consists of herbicide-tolerant crops, insect-resistant (*Bt*) varieties of cotton and maize have established a firm foothold in U.S. agriculture. In 2008, *Bt* maize represented 57% of total U.S. maize acreage and consisted of cultivars expressing Cry1- or Cry3-based endotoxins used to control European corn borer and corn rootworm, respectively (NASS 2008). The introduction of *Bt* crops has been accompanied with concern for negative effects to nontarget insects (Hails 2000, Wolfenbarger and Phifer 2000, Groot and Dicke 2002), especially those in the same insect order at which the Cry proteins are directed and important biological control agents found in agricultural fields. Numerous studies in both the field and the laboratory have examined such effects for a variety of invertebrates, including (among others) butterflies (Losey et al. 1999, Wraight et al. 2000), lacewings (Hilbeck et al. 1998, Guo et al. 2008), ladybird beetles (Lundgren and Wiedenmann 2002, Al-Deeb and Wilde 2003, Bai et al. 2006, Hoheisel and Fleischer 2007), and ground-dwelling beetles (Duan et al. 2004, Ahmad et al. 2005, Mullin et al. 2005, Leslie et al. 2007).

Comparing population dynamics of nontarget organisms between farm systems using transgenic versus conventional pest management practices may elucidate underlying interactions between the transgenes and the ecology of the surrounding habitat. Groot and Dicke (2002) noted that nontarget species could come in contact with *Bt* toxins by feeding directly on *Bt* plants, feeding on target or nontarget herbivorous insects, or through the environment (e.g., accumulation of toxins in the soil). Introduced transgenes can also alter pest management inputs, thereby indirectly affecting nontarget organisms and farmland biodiversity (Hails 2000, Leslie et al. 2007). For example, lepidopteran-specific (Cry1-based) transgenic maize and cotton can eliminate or reduce pyrethroid applications directed at European corn borer and pink bollworm, respectively (Hutchison et al. 2004). Similarly, coleopteran-specific (Cry3-based) transgenic maize may shift insecticide use patterns from at-planting applications of soil insecticides toward seed treat-

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ments (Smith et al. 2004). The efficient control of target pests by *Bt* crops can alter trophic relationships as well: Riddick et al. (1998) found lower abundances of the carabid, *Lebia grandis* Hentz, a specialist predator of *Leptinotarsa decemlineata* (Say), in transgenic potato fields designed to control *L. decemlineata*, whereas the abundance of the generalist predator, *Coleomegilla maculata* DeGeer, was not affected because of its ability to feed on alternate prey.

Changes in pest management tactics are rarely introduced independently or in isolation. For example, all commercially available Cry3-based field corn contains neonicotinoid seed treatments for control of secondary pests (Smith et al. 2004). Although the majority of studies have found little or no direct nontarget effects after exposure to Cry toxins (summarized by Romeis et al. 2006, Marvier et al. 2007, Wolfenbarger et al. 2008), other technology associated with transgenics, such as seed treatments, could affect nontarget organisms. As part of a tiered approach (Dutton et al. 2003) to determine the impact of *Bt* maize (and associated seed treatments) on nontarget epigeal Carabidae, our current field study was preceded by laboratory bioassays that identified neonicotinoid seed treatments found on transgenic maize as a major mortality factor for carabids, and alternatively, found no negative effects of Cry1Ab/c or Cry3Bb1 toxins delivered to carabids in transgenic corn pollen (Mullin et al. 2005).

Ground beetles, or Carabidae, have been used as bioindicators for agricultural practices because of their sensitivity to changes in the environment, abundance in agricultural settings, diversity of functional roles, relative ease of identification to species level, and ease of sampling using pitfall traps (Duelli et al. 1999). Many carabids are voracious feeders and can be loosely grouped as generalist predators, granivores, or specialist predators, although a wide range of more narrowly defined feeding guilds have been described (Toft and Bilde 2002). Therefore it is highly likely that carabids will directly or indirectly come into contact with *Bt* toxins in *Bt* crop fields. Indeed, Zwahlen and Andow (2005) were able to detect Cry1Ab in carabids collected from fields with *Bt* crops or crop residues. However, based on our bioassay results, it is unlikely that carabid population dynamics in the field would be directly affected by exposure to *Bt* toxins present in transgenic maize systems, even Cry3-based coleopteran-specific toxins. Rather, neonicotinoid seed treatments, conventional insecticide applications, or indirect trophic effects will likely have greater impacts on carabids than *Bt* corn.

Northeastern U.S. agroecosystems, where this study was conducted, are characterized by a complex mix of numerous small farms nested in heterogenous landscapes, of which maize is often a component of dairy and vegetable production. Therefore, maize for animal feed and sweet corn are prominent features of these landscapes and are often in close proximity, resulting in mosaics of varying types of maize. Currently, insect management inputs are determined by two primary factors: purchase of the seed (i.e., transgenes and seed treatments) and application of conventional insecticides during the growing season. Adding complexity to these agroecosystems, the management inputs can vary dramatically between both types of maize. At-planting soil insecticides, primarily directed against corn rootworm, dominate inputs in maize grown for animal feed. Foliar insecticide use later in the season is highest in sweet corn, where several ear-damaging insects can severely limit production as described in Crop Profiles and Pest Management Strategic Plans of states throughout the sweet corn growing region of the United States (www.northeasternipm.org). These maize pest management inputs can be replaced or altered by the use of transgenic technologies and seed treatments.

Here, we characterized the carabid community in central Pennsylvania maize fields over 2 yr and identified feasible candidates to test nontarget pest management effects in maize. Candidates were chosen based on their level of activity density (high numbers needed for statistical analysis purposes) and their seasonality to cover the range of times that pest management events occur. Carabids were sampled weekly to look for finer temporal partitioning than "spring" and "autumn" breeders and to identify species active during pest management events. We examined the population dynamics of the candidate species to compare differences between current pest management strategies appropriate for sweet corn and field corn, respectively. For each type of maize, we designed a 2 × 2 factorial experiment comparing systems with or without seed-based insect control tactics and with or without conventional insecticide applications during the growing season.

Materials and Methods

Experimental Design. A randomized complete block (RCB) factorial experiment was used to examine the effects of seed-based inputs and insecticide inputs on Carabidae in sweet corn and field corn (Table 1). Experiments were conducted on the Penn State research farms at the Russell E. Larson Agricultural Experimental Station in Pennsylvania, Furnace, PA, and spanned the 2003 and 2004 growing seasons. The study site contained Hagerstown silt loam soils with 0–3% slopes (HaA). In each year, we used 12 experimental units (each 57.7 by 19.2 m) of sweet corn and field corn, representing four treatments replicated three times. Each experimental unit underwent a minimal tillage regimen (mulch tiller) before planting. Snap beans were planted adjacent to experimental units to provide a rotational crop for sweet corn in the second year, whereas field corn was not rotated, as is common practice in this growing region. All experimental units included a 3-m alfalfa border.

The four treatments (Table 1) were a 2 × 2 factorial defined by presence/absence of seed technologies and presence/absence of conventional pyrethroid insecticides. In sweet corn, the seed technology consisted of a transgene expressing Cry1Ab/c toxins (Tra) versus its isoline (Iso), and the conventional insecti-

Table 1. Pest management inputs defining the 2 × 2 factorial experiment for both sweet corn and field corn farm systems

Type of maize	Seed management (factor A)	Pyrethroid applications (factor B)	Treatment label
Sweet corn	Isoline	None	Iso
		Four foliar applications during silking stage[a]	Iso/PyrSilk
	Transgene (Cry1Ab/c)[b]	None	Tra
		Four foliar applications during silking stage[a]	Tra/PyrSilk
Field corn	Isoline	None	Iso
		At planting soil application[c]	Iso/PyrSoil
	Transgene (Cry3Bb1)[d] and neonicotinoid seed treatment[e]	None	TraNeo
		At planting soil application[c]	TraNeo/PyrSoil

Factor A refers to pest management inputs determined by the purchase of the seed and these seed treatments. Factor B refers to application of pyrethroids by growers and these insecticide treatments.

[a] Lambda-cyhalothrin (Warrior; Syngenta, Greensboro, NC) 11.4% AI, 222 ml/ha.

[b] Rogers Attribute WSS 0984 (Syngenta Seeds, Boise, ID).

[c] Tefluthrin (Force 3G; Syngenta), 3% AI, 3.7 kg/ha.

[d] DeKalb DKC60–12 YGRW (Monsanto, St. Louis, MO).

[e] Imidacloprid (160 μg/seed) or clothianidin (250 μg/seed) (Bayer CropScience, Research Triangle Park, NC).

cide management consisted of four pyrethroid applications during the silking stage (PyrSilk). The four treatments therefore consisted of combinations of the presence or absence of the transgene and PyrSilk and were labeled as (1) Iso (i.e., control), (2) Tra, (3) Iso/PyrSilk, and (4) Tra/PyrSilk. The conceptual framework of the field corn study was identical, except that the seed technology consisted of a neonicotinoid seed treatment and a transgene expressing Cry3Bb1 toxins (i.e., TraNeo) versus its isoline (Iso), and the conventional insecticide management consisted of a soil-directed at-planting application of a pyrethroid (i.e., PyrSoil). Therefore, the four treatments in field corn consisted of the combination of the presence or absence of TraNeo and PyrSoil and were labeled as (1) Iso, (2) TraNeo, (3) Iso/PyrSoil, and (4) TraNeo/PyrSoil.

In the conventional insecticide management treatments, sweet corn received four late-season foliar applications of the pyrethroid lambda-cyhalothrin (11.4% [AI], 222 ml/ha, Warrior 1 EC; Syngenta, Greensboro, NC), for control of lepidopteran ear-feeding pests. Conventionally managed field corn received an at-planting soil application of the pyrethroid tefluthrin (3% [AI], 3.7 kg/ha, Force 3G; Syngenta, Greensboro, NC), for control of corn rootworm and other seed- and root- feeding insects. These predetermined insecticide use patterns were consistent with northeastern maize pest management.

Our choice of transgenes focused on those that were commercially available and most likely to influence insecticide use patterns in the United States. In the sweet corn, we used cultivars expressing Cry1Ab/c toxins, aimed primarily at European corn borer, which is expected to reduce broad-spectrum foliar insecticides. Syngenta Seeds (Boise, ID) WSS 0984 sweet corn expressing Cry1Ab/c endotoxins for control of European corn borer was used for the transgenic treatment, whereas Boreal F1 sweet corn was the near isoline. For field corn, we used transgenic cultivars (DeKalb DKC60–12 YGRW; Monsanto, St. Louis, MO) expressing Cry3Bb1 endotoxins, aimed at root-feeding stages of *Diabrotica* spp. These Cry3 cultivars are expected to reduce broad-spectrum soil insecticides, but as mentioned above, these cultivars are coupled with neonicotinoid seed treatments (160 μg imidacloprid/seed or 250 μg clothianidin/seed; Bayer CropScience, Research Triangle Park, NC) to control additional damage to seeds, seedlings, and roots. All commercially available rootworm-directed *Bt* field corn varieties contain neonicotinoid seed treatments; thus, this systems-based study contains a realistic evaluation of this coupled technology on Carabidae dynamics. In the field corn experimental units that did not use seed-based insecticidal technology, we planted the near isoline, DKC60–17, which does not contain neonicotinoid seed treatment. Additionally, all corn seed used was treated with a fungicide blend shown previously not to be directly toxic to Carabidae in the laboratory (Mullin et al. 2005).

Insect Collection and Identification. Pitfall traps were used to capture all epigeal coleopteran specimens. The pitfall traps were made from plastic deli containers, 14.1 cm deep with 10.9 cm ID, and were inserted flush with the ground. Another small collection cup (5.5 cm deep, 8.2 cm ID) filled with ethylene glycol was placed inside for removal of specimens. An inverted top of a 2-liter soda bottle was put in each deli container to act as a funnel, limiting escape by beetles and access of the ethylene glycol to small mammals. Ten traps, arranged in two transects of five, were placed at 9, 18, 27, 36, and 45 m from the margins within the rows of all field corn and sweet corn plots for a total of 240 traps. Each plot of field corn and sweet corn had 22 rows, and the traps were placed in rows 8 and 14 from the south side of the plot. In 2003, trapping consisted of 10 sampling dates between 12 June and 15 September. In 2004, there were 11 trapping dates extending from 5 June to 27 September. Trapping occurred every 7–14 d depending on weather conditions. For each sampling period, one row of five traps was opened in each field corn and sweet corn plot for a total of 120 open traps. The open rows were alternated each week to avoid oversampling a portion of the field. All traps were open for 72 h, after which all beetles were transferred to 70% ethanol. Beetles were later

Table 2. Species list of Carabidae collected from sweet corn and field corn farm systems in Rock Springs, PA, during 2003 and 2004

Agonum cupripenne Say
A. muelleri Herbst
A. placidum Say
A. punctiforme (Say)
Amara aenea DeGeer
A. exarata Dejean
A. familiaris Duftschmidt
A. impuncticollis Say
Anisodactylus harrisi LeConte
A. rusticus Say
A. sanctaecrucis (F.)
Bembidion affine Say
B. mimus Hayward
B. quadrimaculatum oppositum Say
B. rapidum LeConte
Bradycellus rupestris Say
Calathus gregarius Say
Chlaenius tricolor tricolor Dejean
Cicindela punctulata Olivier
C. sexguttata F.
C. tranquebarica Herbst
Clivinia bipustulata F.
C. impressefrons LeConte
Colliuris pensylvanica L.
Cyclotrachelus furtivus LeConte
Diplocheila obtusa LeConte
Dyschirius globulosus Say
Elaphropus anceps (LeConte)
Harpalus affinis Shrank
H. caliginosus F.
H. compar LeConte
H. erythropus Dejean
H. faunus Say
H. herbivagus Say
H. longicollis LeConte
H. pensylvanicus DeGeer
H. rubripes Duftschmidt
Microlestes linearis LeConte
M. pusio LeConte
Patrobus longicornis Say
Poecilus chalcites Say
P. lucublandus Say
Pterostichus melanarius Illiger
P. mutus Illiger
P. stygicus Say
Scarites quadriceps Chaudoir
Stenolophus comma F.
S. ochropezus (Say)
Trechus quadristriatus (Shr.)

sorted, pinned, and identified to species. Identifications were performed by Robert Davidson (Carnegie Museum of Natural History, Pittsburgh, PA), David Biddinger (Pennsylvania State University), and Tim Leslie (Pennsylvania State University), using several taxonomic keys (Downie and Arnett 1996, Ciegler 2000, Marshall 2006) and voucher specimens from previous studies (Hoheisel 2002, Leslie et al. 2007). Voucher specimens are housed in the laboratory of S. J. Fleischer, Department of Entomology, Pennsylvania State University.

Data Analysis. Data were recorded as average activity density (no. of beetles/trap/72 h) for each species at the plot level. A complete species list was compiled, and species were ranked in order of highest to lowest activity densities. Species with the highest activity density (>200 individuals in each of the 2 yr) were chosen to examine year-to-year temporal patterns and treatment effects on population dynamics. All analyses of treatment effects were performed separately for each crop and year to avoid confounding effects of crop rotation and pest management inputs that differed between sweet corn and field corn. A mixed model repeated-measures procedure (SAS v.9.1.3) was conducted on each species to examine the effect of date, seed technology, conventional insecticide applications, and their interactions. An autoregressive covariance structure was used in the analysis, because of the use of evenly spaced serial measurements, resulting in higher correlation between activity densities measured closer in time. Block was included in the analysis as a random variable. Post hoc Tukey means separation tests were used to identify the direction of the treatment effects on activity densities.

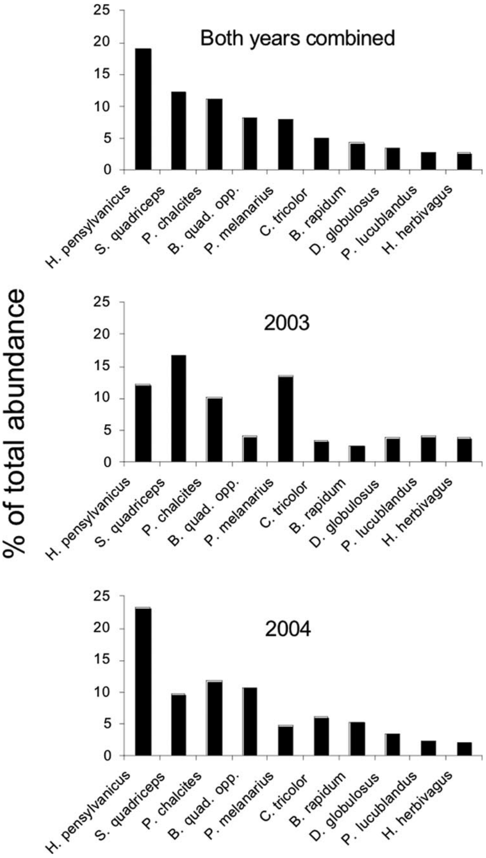

Fig. 1. Dominance distribution of the Carabidae with highest activities densities collected in sweet corn and field corn farm systems in Rock Springs, PA, during 2003 (n = 2,748 carabids) and 2004 (n = 4,518 carabids). Refer to species list (Table 2) for full genus names.

Results

Over the 2-yr study, 7,256 Carabidae representing 49 species (Table 2) were collected, a higher number than is generally recorded (≈ 30 species) for temperate cropping regions (Luff 2002). In 2003, we collected 2,748 carabids (1,403 in field corn, 1,345 in sweet corn), and in 2004, we collected 4,518 carabids (2,426 in field corn, 2,092 in sweet corn). Dominance distribution was strongly skewed with 10 species accounting for >75% of the total abundance (Fig. 1). *Scarites quadriceps* Chaudoir and *Pterostichus melanarius* Illiger were the most abundant species in 2003 and *Harpalus pensylvanicus* DeGeer, *Poecilus chalcites* Say, and *Bembidion quadrimaculatum oppositum* Say were the most abundant species in 2004 (Fig. 1).

Of the species with the highest activity densities, *H. pensylvanicus*, *S. quadriceps*, *Po. Chalcites*, and *Pt. melanarius* were the only species with >200 individuals collected in each of the 2 yr. Date was significant (repeated-measures analysis of variance [ANOVA], $\alpha = 0.05$) for all four species in both years as depicted by the shaded areas in Fig. 2. The four species exhibited peak activity density during different times of the

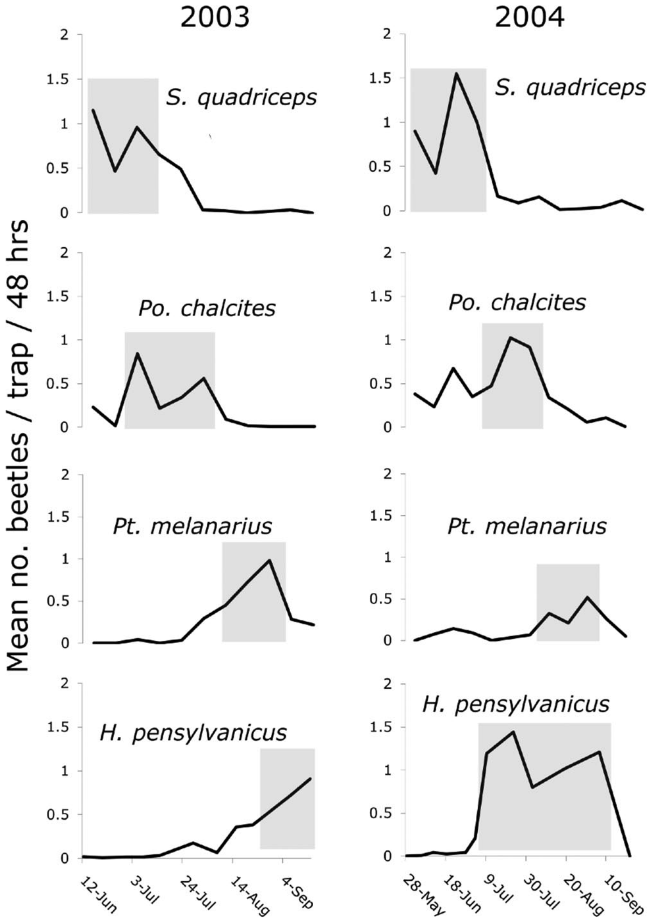

Fig. 2. Population dynamics of the four carabid species with highest activity densities collected in sweet corn and field corn farm systems at Rock Springs, PA (2003 and 2004). Shaded areas depict time of peak activity densities.

season; *S. quadriceps* emerged first, followed by *Po. chalcites*, *Pt. melanarius*, and *H. pensylvanicus* (Fig. 2). This pattern held true in both years except that *H. pensylvanicus* emerged earlier and remained active for the remainder of the growing season in 2004 (Fig. 2). The significant treatment and interaction effects for these carabids with the highest activity densities in each type of maize and year are summarized below.

Scarites quadriceps. *Scarites quadriceps*, a spring breeder, was consistently the first species to emerge with activity densities highest in June and early July and very few individuals trapped after mid-July (Fig. 2). *S. quadriceps* did not respond to insecticide treatments across dates, although mean activity density was higher in *Bt* sweet corn (0.36 beetles/trap ± 0.05 SE) than in isoline sweet corn (0.21 ± 0.04) in 2003 ($F_{1,78} = 4.15$, $P = 0.045$).

Poecilus chalcites. *Poecilus chalcites*, another spring breeder, reached peak activity density after *S. quadriceps* with highest records from late June through the end of July (Fig. 2). No significant treatment effects were detected in 2003; however, in 2004, *Po. chalcites* mean activity density differed between treatments in both field and sweet corn. In 2004, mean activity densities were significantly higher in Iso field corn (0.96 ± 0.14) than in the Iso/PyrSoil (0.44 ± 0.08), TraNeo (0.12 ± 0.03), and TraNeo/PyrSoil (0.42 ± 0.09) treatments ($F_{1,86} = 9.36$, P = 0.003). *Po. chalicites* mean activity density also varied between insecticide management regimens in sweet corn in 2004 ($F_{1,86} = 4.95$, $P = 0.0287$), with a higher mean activity density recorded in the Tra/PyrSilk sweet corn (0.8 ± 0.19) than in the Iso (0.14 ± 0.01), Iso/PyrSilk (0.19 ± 0.06), and Tra (0.1 ± 0.03) treatments.

Pterostichus melanarius. *Pterostichus melanarius*, an autumn breeder, peaked in activity density during August (Fig. 2). Treatment effects were only detected in 2003. *Pt. melanarius* exhibited a significant date by treatment interaction in sweet corn ($F_{9,78} = 2.92$, $P = 0.0049$), with higher activity densities found in the Iso control treatment for three dates in August and September 2003 (Fig. 3, indicated with asterisks) based on Tukey mean comparisons ($\alpha = 0.05$). No date by treatment interactions were significant in field corn; however, in 2003, mean activity density varied between treatments ($F_{1,78} = 6.89$, $P = 0.0104$), with highest activity densities in the Iso (0.49 ± 0.1) and in the TraNeo/PyrSoil (0.75 ± 0.13) field corn and low-

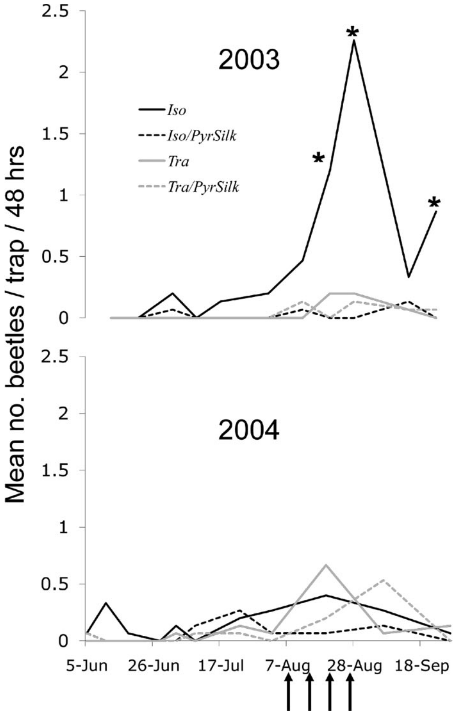

Fig. 3. 2003 and 2004 population dynamics of *Pt. melanarius* in sweet corn for each of four treatments: (1) isoline, i.e., control (Iso), (2) isoline with foliar pyrethroid applications (Iso/PyrSilk), (3) Cry1Ab/c transgenes (Tra), and (4) Cry1Ab/c transgenes with foliar pyrethroid applications (Tra/PyrSilk). *Date where activity density of *Pt. melanarius* was significantly higher in Iso treatment than in the other three treatments based on Tukey means separation test ($\alpha = 0.05$). Arrows indicate when foliar pyrethroid applications were applied in Iso/PyrSilk and Tra/PyrSilk treatments.

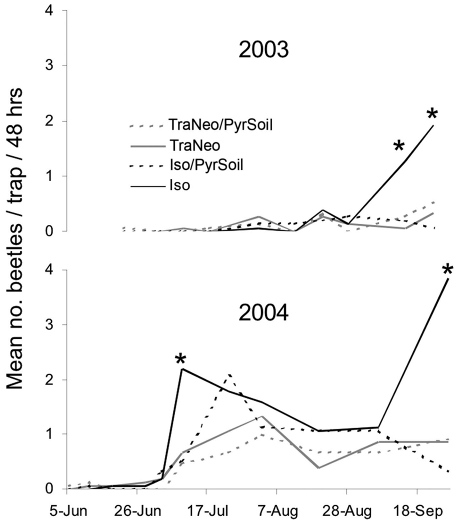

Fig. 4. 2003 and 2004 population dynamics of *H. pensylvanicus* in field corn for each of four treatments: (1) isoline, i.e., control (Iso), (2) isoline with at-planting soil pyrethroid application (Iso/PyrSoil), (3) Cry3Bb1 transgenes with neonicotinoid seed treatment (TraNeo), and (4) Cry3Bb1 transgenes with neonicotinoid seed treatment and at-planting soil pyrethroid application (TraNeo/PyrSoil). *Dates where activity density of *H. pensylvanicus* was significantly higher in the Iso treatment than in other three treatments based on Tukey means separation test ($\alpha = 0.05$). The soil pyrethroid was applied in Iso/PyrSoil and TraNeo/PyrSoil treatments during planting in mid-May.

est activity densities in TraNeo (0.22 ± 0.05) and Iso/PyrSoil (0.13 ± 0.03) field corn.

Harpalus pensylvanicus. The autumn-breeding *H. pensylvanicus* was the species collected most often (Fig. 1), exhibited the highest activity density in August and September (Fig. 2), and was rarely found before mid-July. *H. pensylvanicus* responded to insecticide management inputs in field corn in both 2003 ($F_{9,78} = 2.54$, $P = 0.0129$) and 2004 ($F_{10,86} = 2.01$, $P = 0.0419$). *H. pensylvanicus* activity densities were significantly higher in the Iso control treatment for dates in September 2003 and in July and September 2004 (Fig. 4, indicated with asterisks) based on Tukey mean comparisons ($\alpha = 0.05$).

Discussion

Little evidence to date exists that suggests transgenes conferring the expression of *Bt* Cry toxins directly affects nontarget organisms (Romeis et al. 2006, Wolfenbarger et al. 2008). Instead, it is more likely that dynamic shifts in insecticide use patterns and delivery systems caused, in part, by the deployment of transgenic crops may influence nontarget populations and communities through direct or indirect effects (Lövei 2001, Dutton et al. 2002, Marvier et al. 2007). This study identified prominent carabid species in Pennsylvania maize agroecosystems and provided field evaluations of transgenes, some of which are coupled with neonicotinoid seed treatments and conventional pest management practices (i.e., soil and foliar insecticide applications) on these populations. Working in conjunction with laboratory bioassay studies (Mullin et al. 2005) that identified neonicotinoid seed treatments present in Cry3-protected field corn, but not the Cry3 toxins directly (see also Duan et al. 2006), as a significant direct mortality factor for carabids, we used a range of insecticide management options relevant to current conditions.

Over the 2-yr study, four species (i.e., *S. quadriceps*, *Po. chalcites*, *Pt. melanarius*, and *H. pensylvanicus*) exhibited high activity densities in each of the 2 yr (>200 total individuals or 0.15 individuals/trap/72 h), and dominance distribution was highly skewed as the 10 carabid species (of the 49 total species) with highest activity densities accounted for >75% of all specimens captured. These results can be compared with other studies of carabids in different Pennsylvania agricultural systems. In a diversified vegetable farm setting, Leslie et al. (2007) found comparable species richness (i.e., 47 species), composition, and activity densities, except for far fewer *S. quadriceps.* It is likely that fewer *S. quadriceps* were found in this earlier study at a similar location because of the fact that pitfall trapping began shortly after the period of peak activity density for this species, highlighting the importance of temporal trapping considerations when studying carabid communities. A study examining carabid communities in Pennsylvania grazed dairy pastures also reported similar species richness (i.e., 44 species) but differed in community composition (Byers et al. 2000). Whereas species such as *Po. chalcites* and *Pt. melanarius* were frequently found in both systems, *H. pensylvanicus* had the highest activity density in maize and *Amara aenea* DeGeer was collected in high numbers in the grazed pasture (and was relatively scarce in maize). Both *H. pensylvanicus* and *A. aenea* are weed seed predators, and the local weed communities, which can vary greatly between agricultural systems (Davis et al. 2005), may have selected for or against each species based on their feeding preferences.

Activity densities were noticeably higher in 2004 (3.27 beetles/trap/72 h) than in 2003 (2.14 beetles/trap/72 h), primarily because of a three-fold increase in *H. pensylvanicus* activity densities as well a three- to four-fold increase in some smaller bodied carabids such as *B. quadrimaculatum oppositum* and *B. rapidum.* With the exception of *H. pensylvanicus,* more smaller-bodied carabids were found among the most abundant beetles in the second year. Büchs et al. (2003) suggested that smaller bodied insects may adapt better to disturbed environments, and our findings partially support this trend. *H. pensylvanicus* most likely increased in activity density because of higher weed densities, primarily giant foxtail (*Setaria faberi* Herrm.) and yellow foxtail (*Setaria glaucai* L.) in the experimental fields during the second year (unpublished data). The emergence of *H. pensylvanicus* adults is thought to coincide with the ripening of grass weed seeds, and feeding preference trials have shown that foxtail is a preferred seed for *H. pensylvanicus* (Kirk 1973, Best and Beegle 1977, Lund and Turpin 1977, Brust and House 1988, Lundgren and Rosentrater 2007).

The four species abundant in both years exhibited unique temporal niches based on the period of their highest activity density. Carabids are often generalized as spring breeders and autumn breeders with recognition of annual variation or species-specific variation in life cycles (Thiele 1977, Loreau 1985, Holland 2002). For example, it would be known a priori that *S. quadriceps* and *Po. chalcites* are spring breeders and *Pt. melanarius* and *H. pensylvanicus* are autumn breeders before our study was conducted. However, we established that, not only are these four species found in high numbers in central Pennsylvania agroecosystems (see also Leslie et al. 2007), but that they seem to occupy temporal niches at a finer resolution than the generalized seasonal depictions, resulting in a temporal succession. In general, this succession consisted of *S. quadriceps, Po. chalcites, Pt. melanarius,* and *H. pensylvanicus* (Fig. 2). In one exception, *Pt. melanarius* and *H. pensylvanicus* overlap in abundant periods in 2004; however, these two species may occupy different functional niches as well: although both have omnivorous tendencies, *Pt. melanarius* is better know as a carnivore (Sunderland 2002), and the abundance of grass seeds—a preferred food source for *H. pensylvanicus*—likely reduced feeding competition between the two species. Therefore, the carabid species with the highest activity densities in this region seem to have transitioned toward segregating resources both temporally and possibly by feeding preferences. This temporal partitioning highlights the importance of full season sampling and species level identification. Detailed knowledge of temporal partitioning can also be useful in choosing appropriate species for examining external inputs that occur at distinct times in the field season (e.g., at-planting soil insecticide applications).

Treatment effects on the population dynamics of the most abundant carabids were only consistent for *H. pensylvanicus.* For several sampling periods in both years, *H. pensylvanicus* exhibited significantly higher activity densities in isoline field corn that had no insecticide inputs (Fig. 4). The other field corn treatments either contained an at-planting soil pyrethroid insecticide or the neonicotinoid seed treatments imidacloprid or clothianidin found on the transgenic cultivar. Some carabids are tolerant of even the most toxic of the pyrethroids such as deltamethrin (Basedow et al. 1985, Wiles and Barrett 1998), in contrast to their susceptibility to neonicotinoids (Mullin et al. 2005); thus, the soil tefluthrin or foliar lambda-cyhalothrin treatments may not have exerted as much population reduction impact as imidacloprid or clothianidin. However, deltamethrin sprays are known to cause reduction of other major epigeal insect groups (Basedow et al. 1985), which could affect carabids indirectly. All field corn insecticide management inputs occurred early in the season when the less-mobile *H. pensylvanicus* larvae would have been in close proximity to the corn seed in the soil. The possible presence of insecticide-induced mortality factors or a decrease in prey availability seems to be evident in the lower trap captures of *H. pensylvanicus* adults later in the season.

Pt. melanarius was the only other species exhibiting a date × treatment effect on its population dynamics, with activity densities higher in isoline sweet corn without insecticides for three sampling periods in 2003 (Fig. 3). As with *H. pensylvanicus,* early-season treatments may have affected *Pt. melanarius* larval abundance, or late season foliar sprays may have directly affected *Pt. melanarius* adults. This effect, however, was not evident in 2004 (Fig. 3) when *Pt. melanarius* activity densities were lower and the sweet corn had been rotated with snap beans.

Treatment effects were evident when comparing mean activity density between the different pest management regimens, but these results were not consistent and sometimes contradictory. For example, in 2004, *Po. chalcites* exhibited a higher mean activity density in isoline field corn unmanaged with insecticides but in sweet corn had the highest mean activity density in *Bt* sweet corn managed with insecticides. In another study examining Cry3-protected field corn under different insecticide use regimens, Bhatti et al.

(2005) found lower activity densities of carabids in maize treated with seed-, soil-, and foliar-applied insecticides (compared with no insecticide use), but analyses were performed at the family level and results were also not consistent across all years and trap types. Lopez et al. (2005) suggested that spatial and temporal variability can lead to such variability or lack of treatment effects in results and insecticide inputs can cause variation in behavior such as increased activity or dispersal (Wiles and Jepson 1994, Singh et al. 2001), which may affect trap captures. Additionally, *H. pensylvanicus* may have exhibited elevated numbers in the control treatment during the second year of our experiment, when corn rootworm caused damage in the nonrotated field corn creating open areas for weed invasion.

In conclusion, several carabid species exhibited high activity densities and occupied distinct temporal niches in Pennsylvania maize agroecosystems, making all candidates for studies addressing maize management in northeastern agroecosystems. Of these species, *H. pensylvanicus* exhibited the most consistent response to maize insect pest management inputs in the nonrotated field corn. *H. pensylvanicus* activity density was consistently higher in isoline field corn untreated with insecticides, whereas the lower population levels in the other treatments—conventional insecticide use, transgenes with neonicotinoid seed treatment, or a combination of both—were indistinguishable from one another. These results suggest that both conventional insecticide management and neonicotinoid seed treatments may represent a mortality factor detectable in a field setting for at least one carabid species, *H. pensylvanicus.*

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