Population Responses and Food Consumption by Predators *Coleomegilla maculata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) During Anthesis in an Illinois Cornfield

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ABSTRACT We monitored numbers of *Coleomegilla maculata* DeGeer and *Harmonia axyridis* (Pallas) eggs, larvae, and adults in an Illinois cornfield during anthesis. Larvae and adults were collected from the field and their gut contents were examined. Also, daily pollen deposition was recorded over the sample period, and prey biomass per plant was calculated for each of four replicate plots of field corn. The numbers of egg clutches and adults per plant were compared with daily pollen deposition, and pre- and postanthesis daily pollen deposition, densities of egg clutches, and adult densities were compared. Also, we compared the numbers of larvae and adults collected per plot and pollen and prey densities in the plots. Finally, the proportions of larvae and adults that had fed on corn pollen or prey were compared between predator species. We found that the number of coccinellid egg clutches increased significantly after anthesis and that the densities of adults of both species were not significantly different pre- and postanthesis. Larval and adult populations of *H. axyridis* were significantly correlated with prey densities, but *C. maculata* were not. All instars of *C. maculata* and *H. axyridis* occurred in corn during anthesis, and corn pollen was found in the guts of all four instars and in adults of both species. Dissections revealed that the majority of *C. maculata* larvae and adults had pollen in their guts, and a minority of *H. axyridis* larvae and a single adult had pollen in their guts. Conversely, the majority of *H. axyridis* larvae and adults had insect prey in their guts, and <40% of *C. maculata* larvae and adults had prey in their guts. Potential mechanisms for the numerical increases of coccinellids observed during anthesis and the implications of pollen feeding for risk assessment of transgenic insecticidal corn to *C. maculata* are discussed.

KEY WORDS biological control, pollinivory, risk assessment, transgenic crops, *Zea mays*

SEVERAL INSECT NATURAL ENEMIES feed on corn, *Zea mays* L., pollen in midwestern cornfields (Ostrom et al. 1997, Corey et al. 1998). Pollinivory by entomophagous insects may allow them to survive periods of low prey densities (Benton and Crump 1981, Hagen 1986, Hemptinne and Desprets 1986, Alomar and Wiedenmann 1996, Hodek and Honěk 1996) or provide them with critical or extra nutrients necessary for egg production or overwintering (Schneider 1969, Jervis and Kidd 1986, Hodek and Honěk 1996). Coccinellid beetles commonly feed on pollen (Hodek and Honek 1996), and two prevalent coccinellids in midwestern cornfields are *Harmonia axyridis* (Pallas) and *Coleomegilla maculata* DeGeer (Cottrell and Yeargan 1998a,b; Wright and DeVries 2000, Hoogendoorn and Heimpel 2002, Pfannenstiel and Yeargan 2002).

H. axyridis is an exotic coccinellid that has invaded much of North America after repeated intentional introductions from Asia (Koch 2003). Originally established as a biological control agent of tree and ornamental pests, this insect now can be found in several habitats (Colunga-Garcia and Gage 1998, Koch 2003). *H. axyridis* is primarily aphidophagous, although this species also feeds on mites, psyllids, and other soft-bodied insects (Hodek and Honek 1996, Koch 2003). Also, *H. axyridis* has been observed to feed on pollen and nectar of *Spirea douglasii* Hook in Oregon (LaMana and Miller 1996). Concern over the impact of *H. axyridis* on native coccinellids through direct and indirect competition (Brown and Miller 1998, Colunga-Garcia and Gage 1998, Cottrell and Yeargan 1998b, Hoogendoorn and Heimpel 2002) makes it important that we gather population data on and understand the feeding behavior of this species in several North American habitats. The ecology of *H. axyridis* in the corn habitat has not been well studied, and more information is needed to understand the ecology of this predator, its interactions with native predators, and the implications of this species' estab-

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lishment for biological control in the corn agroecosystem.

C. maculata is widely distributed in North and Central America and is frequently encountered in agroecosystems (Colunga-Garcia et al. 1997; Krafsur and Obrycki 2000; Wright and DeVries 2000, and references therein). *C. maculata* is consistently one of the most prevalent coccinellid predators in midwestern corn and is considered an important source of mortality to several pests of corn, including the corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (Homoptera: Aphidae); European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae); and corn earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) (Wright and Laing 1980, Cottrell and Yeargan 1998a, Phoofolo et al. 2001).

Although considered an important predator, *C. maculata* also consumes pollen as part of its diet in the field (Forbes 1880). Laboratory studies have revealed that a high proportion of *C. maculata* can complete larval development and can produce mature eggs on a diet consisting solely of corn pollen (Lundgren and Wiedenmann 2004). There is some evidence that corn pollen is a preferred food source to prey (Smith 1965), and it is believed that the abundance of corn pollen during anthesis may detract from predation of pests (Cottrell and Yeargan 1998a, Pfannenstiel and Yeargan 2002). Several studies have revealed increases in preimaginal populations of *C. maculata* during anthesis relative to other periods of the growing season (Andow and Risch 1985, Cottrell and Yeargan 1998a, Pfannenstiel and Yeargan 2002). Although these studies provide a snapshot of *C. maculata* populations during anthesis, food consumption of *C. maculata* during anthesis has not been well studied, and potential reasons for population increases are largely correlative and speculative.

Because some predators are facultatively phytophagous on corn pollen, transgenic insecticidal corn that expresses the δ-endotoxins of *Bacillus thuringiensis* (Bt) could pose a risk to predators in cornfields. Several attempts have been made to assess the toxicity of transgenic insecticidal corn pollen to *C. maculata.* Pilcher et al. (1997) found that feeding on pollen from transgenic corn (event MON810) that expresses the Cry1Ab protein toxin to resist lepidopteran pests did not affect the fitness of *C. maculata* larvae in the laboratory or of *C. maculata* populations in the field. Similarly, studies on the impacts of coleopteran-specific transgenic corn pollen (event MON863 that expresses Cry3Bb1) showed no effects on *C. maculata* fitness in the laboratory (Duan et al. 2002, Lundgren and Wiedenmann 2002). An important step in assessing the risk of transgenic corn pollen to natural enemies is determining which predators are present in cornfields and feed on corn pollen during anthesis. We investigated which life stages of *C. maculata* and *H. axyridis* occurred in corn during anthesis and what proportion of these populations fed on corn pollen. The results of this research can be used to begin addressing the risk of transgenic corn events to *C. maculata* and *H. axyridis.*

Materials and Methods

Field Site. Research was conducted between 16 July and 31 July 2003 in Champaign, IL (N 40.062° and W 88.190°), in a 3.6-ha (187 by 192 m, N to S × E to W) cornfield. The corn hybrid planted was Pioneer 34B24, and it expressed the Yieldgard gene for resistance to lepidopteran pests. Rows were 0.71 m apart, with 0.20 m between plants within each row. Four 10 by 10-m plots were established near the corners of the field, western plots were two rows from the western edge of the field, and eastern plots were eight rows from the eastern edge of the field. Sampling began 5–6 d before anthesis, which commenced either on 21 or 22 July in the different plots.

Prey density can affect the population sizes of coccinellids (Hodek and Honěk 1996), so we developed an index of prey densities in our experimental plots. On 25 July, we severed seven plants in each plot at the soil line and removed the severed plants from the field. Within 20 min of their removal, we transferred all insects and insect eggs small enough to be consumed by coccinellids from the plants using a fine paintbrush and placed them in 70% ethanol. Sealed samples were held at 4°C until processing. Prey from all of the plants in each plot were combined. In the laboratory, we dried the samples at 105°C for 24 h. The prey sample per seven plants was weighed on an electronic balance to the nearest 0.01 mg.

Pollen Deposition. Pollen traps, two in the center of each experimental plot, were used to measure the relative pollen deposition over the duration of anthesis. Pollen traps consisted of a 100-mm diameter plastic petri dish (BD Biosciences, Franklin Lakes, NJ) that was sprayed on one face with aerosol Tangletrap (The Tanglefoot Company, Grand Rapids, MI). The petri dish, with the Tangletrap surface facing up, was placed in a test tube clamp that was attached to a metal pole 1 m above the soil surface. Thus, the petri dishes were parallel to the soil surface at a uniform height for all traps. Each petri dish was changed daily, brought into the laboratory, and frozen at −10°C until processing.

In the laboratory, the number of pollen grains within a randomly selected 1-cm^2 area of each pollen trap was counted under 50× magnification. Anthesis occurred on different dates in the different plots, and we considered the first day of anthesis to be when >100 grains per cm^2 were deposited on the pollen traps of each plot; we considered anthesis to be over when <70 grains per cm^2 were deposited. Trap catches in each plot were consolidated, and a mean density of pollen grains was determined for each day of anthesis. The mean daily pollen densities that were deposited on the traps before and after anthesis were compared with a *t*-test (JMP 3.2.6; SAS Institute, Cary, NC). Also, the cumulative amount of pollen deposited per square centimeter over anthesis in each plot was calculated as a relative index of pollen abundance in the different plots.

Population Responses of Coccinellids to Corn Pollen. Between 16 July and 21 July, we estimated the densities of the different life stages of *C. maculata* and

H. axyridis in the experimental plots. For each sample day, 15–30 randomly selected plants were examined in each of the plots, but the same number was sampled for all plots each day. Sampled plants were left intact within the plots. Larvae, pupae, and adults of *C. maculata* and *H. axyridis* were collected from sampled plants and placed in 1.5-ml microcentrifuge tubes on dry ice until we returned them to the laboratory. At the laboratory, insects were stored at −80°C until they were processed. Also, on each plant the number of coccinellid egg clutches was recorded and left on the plant; the number of eggs in each clutch was not counted. We frequently encountered recently hatched clutches of *H. axyridis* and *C. maculata* before they could disperse from their chorions; these newly hatched clutches were considered separately from other first instars because they had not had a chance to forage for food or disperse to realistic densities.

In the laboratory, each field-collected specimen was identified and instars of *C. maculata* larvae were staged based on head capsule width (J.G.L., unpublished data). For *H. axyridis*, we determined the first, second, third, and fourth instars are likely represented by mean ± SEM head capsule widths measuring 0.43 ± 0.002, 0.59 ± 0.002, 0.83 ± 0.006, and 1.14 ± 0.024 mm, respectively. Larvae and adults of the two species were easily distinguished based on coloration. Egg clutches were not identified to species.

Mean numbers of egg clutches, newly hatched clutches and larvae of each species and instar, and adults of each species per plant were calculated for each sample date. We conducted two analyses to determine whether adult migration or oviposition was related to anthesis. The mean daily egg clutch densities and adult densities found before and after anthesis were compared with *t*-tests. Also, the daily densities of egg clutches and adults were correlated with the daily densities of pollen grains by using regression analysis (JMP 3.2.6). Large variations in larval densities were observed in the different plots. To understand whether these densities were correlated with pollen or prey densities, the total number of *H. axyridis* larvae and *C. maculata* larvae were compared with the amount of prey biomass per plant (as measured on 25 July), and the sum of the pollen deposited per square centimeter each day by using separate regression analyses. Also, we compared the amount of prey biomass per plant with the cumulative amount of pollen deposited per plot with a regression analysis, to evaluate whether prey populations respond to pollen densities. The numbers of *H. axyridis* and *C. maculata* adults collected in each plot were also related to prey biomass by using separate regression analyses.

Gut Contents of Coccinellids. The digestive tract of each collected larva and adult was removed under 50× magnification. The contents of the guts were gently extracted at room temperature in water by using fine forceps, and the contents were described for each individual. The proportions of larvae and adults of each species that had fed on corn pollen or insect prey were calculated for each plot. Mean proportions of *C. maculata* and *H. axyridis* larvae and adults that had fed on pollen and prey were then compared within and between the species with *t*-tests.

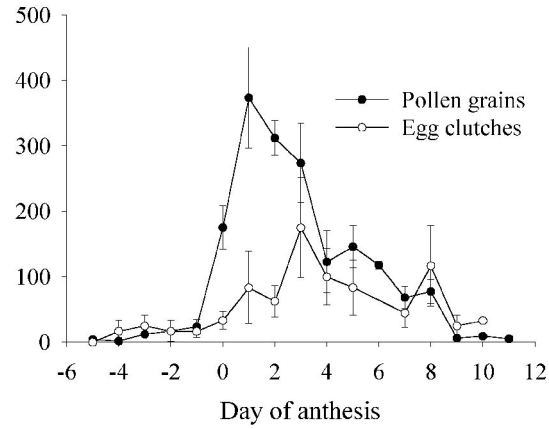

Fig. 1. Density of pollen (grains per square centimeter) and the density of coccinellid egg clutches (clutches per 1000 plants) over the sample period. Day 0 indicates the onset of anthesis. Error bars represent SEMs.

Results

Pollen was deposited for ≈8 d, with a mean ± SEM maximum of 373.63 ± 76.93 grains per cm^2 per day (Fig. 1). Significantly more pollen was deposited on the pollen traps per day after the onset of anthesis than before anthesis ($F_{1, 15} = 5.78$; $P = 0.04$) (Table 1). In total, 69 coccinellid egg clutches were observed over the sample period. Daily egg clutch densities were significantly correlated with daily pollen deposition ($F_{1, 14} = 8.74$; $P = 0.01$) (Fig. 1), and the mean daily number of egg clutches was significantly higher after anthesis than before anthesis ($F_{1, 15} = 4.62$; $P = 0.05$) (Fig. 1). Totals of 31 *C. maculata* and 28 *H. axyridis* adults were collected during the sample period. Adults were only discovered in the samples from three of the four plots. Numbers of *C. maculata* and *H. axyridis* adults were not correlated with daily pollen deposition (*C. maculata:* $F_{1, 14} = 0.075$, $P = 0.79$; *H. axyridis:* $F_{1, 13} = 1.44$; $P = 0.25$). Although the number of adults was generally larger postanthesis, these differences were not significant (*C. maculata:* $t = 1.43$, df = 14, $P = 0.18$; *H. axyridis:* $t = 1.12$, df = 13, $P = 0.28$) (Table 1). In general, densities of adult coccinellids remained

Table 1. Mean ± SEM pre- and postanthesis densities of pollen, coccinellid egg clutches per plant, and *C. maculata* and *H. axyridis* adults per plant for each sample date

	Pollen deposition (grains per cm^2 per day)	Egg clutches per plant per day	Adults per plant
Preanthesis	11.69 ± 4.02a	0.017 ± 0.0049a	0.017 ± 0.0058a
Postanthesis	140.63 ± 35.51b	0.068 ± 0.015b	0.052 ± 0.015a

Sample sizes for preanthesis and postanthesis comparisons were 5 and 11 d, respectively. Values within columns followed by different letters are significantly different (*t*-test, $\alpha = 0.05$).

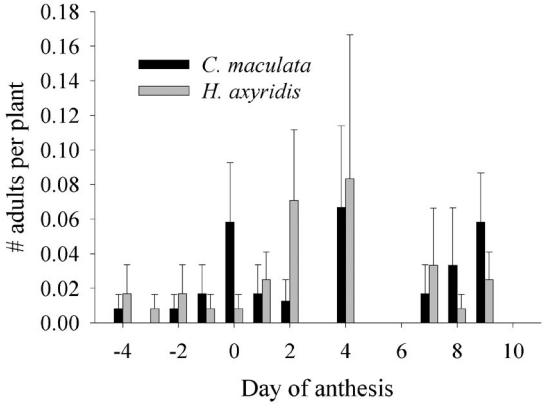

Fig. 2. Number of adult *C. maculata* and *H. axyridis* captured per plant each day of anthesis. No adults were captured on days 3, 5, and 6. Error bars represent SEMs.

below one per 10 plants over the sample period (Fig. 2).

In total, 26 larvae of *C. maculata* and 190 larvae of *H. axyridis* were collected over the sample period; five newly hatched *C. maculata* clutches and five newly hatched *H. axyridis* clutches were found during the sample period. More than 77% of *H. axyridis* larvae were captured on days 8 and 9 of anthesis (Fig. 3), all of which were collected in only two of the plots. We collected *C. maculata* in the samples from three of the four plots, and *H. axyridis* larvae in all four plots. The number of coccinellid larvae collected per plot was not well correlated with overall pollen deposition in the plots (*C. maculata:* $F_{1,2} = 0.045$; $P = 0.85$; *H. axyridis:* $F_{1,2} = 0.34$; $P = 0.62$). The cumulative number of *H. axyridis* larvae collected in each plot was significantly correlated with prey biomass in the plots ($F_{1,2} = 199.35$; $P = 0.005$), as was the cumulative number of adult *H. axyridis* that were captured per plot ($F_{1,2} = 19.36$; $P = 0.048$). In contrast, the numbers of *C. maculata* larvae and adults were not well correlated with this index of prey density (larva: $F_{1,2} = 3.54$; $P = 0.20$; adult: $F_{1,2} = 3.11$; $P = 0.22$). Prey density was not well correlated with pollen densities ($F_{1,2} = 0.50$; $P = 0.55$).

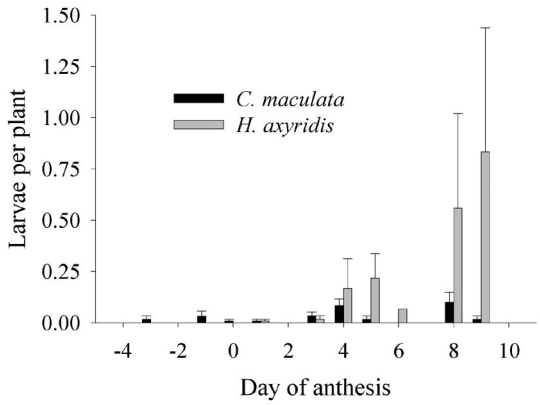

Fig. 3. Number of *C. maculata* and *H. axyridis* larvae per plant on each day of anthesis. No larvae were collected on days −5, −2, 2, and 7. Error bars represent SEMs.

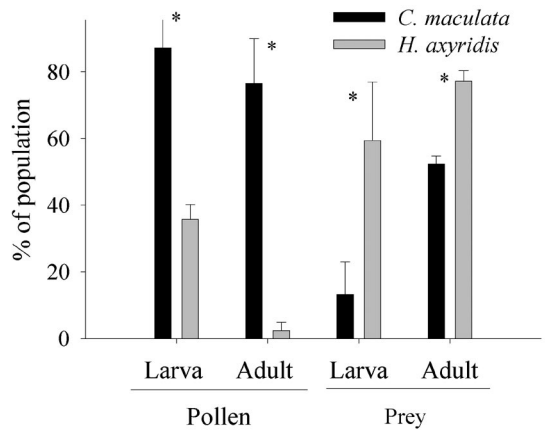

Fig. 4. Percentage of *H. axyridis* and *C. maculata* samples that had pollen and prey in their digestive tracts. Only the individuals collected during anthesis were used in the pollen comparisons. Statistical comparisons between species for each food type are displayed here; see text for intraspecific statistical comparisons. Error bars represent SEMs, and bars with * above them are significantly different (*t*-test, $\alpha = 0.05$).

All instars of *C. maculata* and *H. axyridis* occurred in corn during anthesis, and corn pollen was found in the guts of all four instars and in adults of both species. For *C. maculata*, the percentages of larvae that had pollen in their guts were 66.67, 100.00, 100.00, and 75.00% for first ($n = 12$), second ($n = 4$), third ($n = 5$), and fourth instars ($n = 4$), respectively (data were pooled over plots). For *H. axyridis*, the percentages of the larvae that had pollen in their guts were 45.58, 27.03, 37.93, and 66.67% for first ($n = 77$), second ($n = 74$), third ($n = 29$), and fourth instars ($n = 3$), respectively (data were pooled over plots). A significantly higher proportion of *H. axyridis* adults fed on prey than did *C. maculata* adults ($t = 6.35$, df = 4, $P = 0.0031$), and a significantly greater proportion of *H. axyridis* larvae fed on prey than did *C. maculata* larvae ($t = 2.58$, df = 5, $P = 0.049$) (Fig. 4). Conversely, a significantly greater proportion of *C. maculata* adults fed on pollen than did *H. axyridis* ($t = 5.43$, df = 4, $P = 0.0056$), and a significantly greater proportion of *C. maculata* larvae fed on pollen than did *H. axyridis* larvae ($t = 5.89$, df = 5, $P = 0.002$) (Fig. 4). A significantly greater proportion of *C. maculata* larvae fed on pollen than prey ($t = 9.14$, df = 4, $P < 0.001$), and the proportion of *C. maculata* adults feeding on pollen and prey was not significantly different ($t = 1.78$, df = 4, $P = 0.15$). The proportions of *H. axyridis* larvae that fed on pollen and prey did not differ significantly ($t = 1.30$, df = 6, $P = 0.24$), but a significantly higher proportion of *H. axyridis* adults fed on prey than pollen ($t = 19.18$, df = 4, $P < 0.001$). Other dietary items that were found during the gut dissections were cat-

egorized as fungal spores, and pollen from another species with reddish orange grains of 0.016–0.031-mm diameter. These other foods were found in both species, and the proportion of the populations that consumed these other foods was not calculated.

Discussion

The results of the current research and past published studies lead us to propose that the increases in coccinellid reproduction and the subsequent increases in larval populations that we observed directly after anthesis may be related to both increases in aphid availability and the abundance of corn pollen during this period. Furthermore, different mechanisms may be prompting the oviposition responses by different coccinellid species. For example, *C. maculata*, of which only 13% of larvae fed on prey during anthesis, may lay more eggs in response to pollen abundance; and *H. axyridis*, for which 36% of larvae and 2% of adults fed on pollen and 59% of larvae and 77% of adults fed on prey, likely responded to aphid densities. Whether they specialize on pollen or prey, anthesis seems to favor reproduction by predaceous coccinellids.

We observed that egg clutch densities increased during anthesis and that these densities were strongly correlated with rates of pollen shed (Fig. 1; Table 1). Anthesis did not result in a significant increase in the densities of *C. maculata* and *H. axyridis* adults in cornfields (Fig. 2), but the adults that occurred in cornfields during that time may have increased oviposition in response to changes in the habitat. Other studies have indicated similar increases in *C. maculata* eggs and larvae during anthesis (Wright and Laing 1980, Cottrell and Yeargan 1998a), although the motivating factors for those population increases were not clear.

Two potential explanations for the increases in egg densities that we observed during anthesis are 1) the increase in the abundance of corn pollen and 2) the increase in prey availability during anthesis. In 1 yr of their study, Cottrell and Yeargan (1998a) observed significantly more coccinellid eggs in sweet corn that was allowed to shed pollen relative to cornfields that were detasselled, suggesting that *C. maculata* responds to pollen abundance by increasing oviposition. Wright and Laing (1980) found that aphid populations increased during anthesis, and oviposition by coccinellids ensued. We also observed that large numbers of aphids resided within the top whorl of corn and were revealed to predators when the tassel became exposed. Interestingly, neither Cottrell and Yeargan (1998a) nor Wright and Laing (1980) addressed both prey abundance and pollen shed concurrently, and they came to different conclusions over which mechanism was causing the population increase of coccinellids during anthesis. Also, gut dissections were not conducted in either of these studies, and what the coccinellids were actually eating was not determined. Although gut dissections do not reveal what factors prompt reproduction by coccinellids during anthesis, gut contents are critical to understanding what *C. maculata* and *H. axyridis* are feeding on in the field.

Our research showed that a high proportion of *C. maculata* larvae and adults fed on corn pollen during anthesis and that relatively few *H. axyridis* larvae and adults fed on corn pollen (Fig. 4). Only one *H. axyridis* adult collected had pollen in its gut, and one-quarter of the 36% of *H. axyridis* larvae that fed on pollen had only a few grains in their guts. This research suggests that most *C. maculata* larvae and adults rely on corn pollen as food when it is available. Other research has shown that predation of lepidopteran eggs by *C. maculata* decreases during corn anthesis, and it is hypothesized that corn pollen may detract from predation during pollen shed (Cottrell and Yeargan 1998a, Pfannenstiel and Yeargan 2002). Our research supports the idea that *C. maculata* larvae are not very predaceous during anthesis (only ≈13% fed on prey), and a higher proportion of *C. maculata* larvae and adults consumed pollen than consume prey during anthesis (Fig. 4).

The known reputation of *H. axyridis* for predation on *C. maculata* in the laboratory (Cottrell and Yeargan 1998b) and the higher numbers of *H. axyridis* relative to *C. maculata* in midwestern corn give rise for concern. *H. axyridis* has quickly become the dominant aphidophagous species in many North American habitats, presumably at the expense of other coccinellid predators (LaMana and Miller 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998). Our study supports another recent published report that reveals the increasing abundance of *H. axyridis* populations relative to *C. maculata* populations in cornfields (Musser and Shelton 2003). A large proportion of *H. axyridis* adults and larvae fed on other insects during the sample period, and populations of *H. axyridis* larvae and adults were strongly correlated with prey densities. Although we did not attempt to identify prey species, we observed that a high number of larvae and adults were predaceous on coccinellid larvae. Cannibalism and intraguild predation on other coccinellids has been reported with *H. axyridis* in other research (Cottrell and Yeargan 1998b, Koch 2003). During the short sample period, we collected >7 times more *H. axyridis* larvae than *C. maculata* larvae in an Illinois cornfield. *H. axyridis* has a great ability to track aphid populations (Koch 2003, and references therein), and we observed that larval and adult densities of *H. axyridis* were strongly correlated with prey densities in our plots. It seems that, during anthesis, the niche overlap between these species is minimal, when *C. maculata* are largely pollinivorous and *H. axyridis* feed more on insects. A critical question pertaining to the interaction between these species is what happens to the feeding habits and populations of these coccinellids when alternative foods, such as corn pollen, are less abundant.

Finally, our research shows that the majority of *C. maculata* adults and larvae that occur in corn during anthesis ingest corn pollen. These data are a necessary step in determining the level of interaction that this species has with transgenic insecticidal pollen. A fur-

ther step that needs to be conducted to estimate the level of exposure of *C. maculata* to corn pollen is to quantify pollen consumption by these beetles under field conditions. Evaluating the toxicity of specific events to *C. maculata* and the exposure that this species has to corn pollen in the field will allow scientists and regulators to develop a relative risk index for transgenic insecticidal corn hybrids to *C. maculata.*

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