Effect of Pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) Population Density, Predation, and Cannibalism in Sweet Corn

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ABSTRACT   *Coleomegilla maculata* (DeGeer) is an abundant, polyphagous predator in corn fields; it can develop and reproduce on a diet of only corn pollen. We used sweet corn (*Zea mays* L.) in field experiments to investigate the effect of pollen abundance on *C. maculata* population densities, predation by *C. maculata* on *Helicoverpa zea* (Boddie) eggs, and egg cannibalism by *C. maculata*. Plots designated as "no-pollen plots" were detasseled immediately before anthesis, whereas tassels were left intact in "pollen plots." In both years, when pollen was absent in all plots (i.e., before and after anthesis) there were no significant differences in *C. maculata* population density, *H. zea* egg predation, or *C. maculata* egg cannibalism between pollen and no-pollen plots. During anthesis in 1996, *C. maculata* egg and larval densities were significantly higher in pollen plots compared with no-pollen plots, but not in 1995. Predation on *H. zea* eggs was significantly lower in pollen plots than in no-pollen plots in 1995, but not in 1996. During anthesis in both years, egg cannibalism was lower in pollen plots compared with no-pollen plots and significantly so in 1996. Even when abundant pollen led to increased *C. maculata* larval populations in pollen plots (i.e., in 1996), predation on *H. zea* eggs and cannibalism of *C. maculata* eggs was not higher in the pollen plots, suggesting that abundant pollen diverts *C. maculata* from carnivory. Thus, even though *C. maculata* populations may increase during anthesis in corn, this increased abundance is not likely to translate into increased predation on *H. zea* eggs.

KEY WORDS   *Coleomegilla maculata*, *Helicoverpa zea*, *Zea mays*, cannibalism, predation

THE LADY BEETLE *Coleomegilla maculata* (DeGeer) is abundant in corn (Smith 1971, Coll and Bottrell 1995, Hodek and Honěk 1996), often being one of the predominant coccinellid species found in this crop (Harris 1969, Foott 1973, Colunga-Garcia et al. 1997). In Kentucky, *C. maculata* is the most abundant coccinellid species in sweet corn (Pfannenstiel 1995).

The polyphagous habits of *C. maculata* are well documented. It feeds on the mobile life stages, as well as the eggs, of many pest species. *C. maculata* is an important predator on eggs of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Groden et al. 1990, Hazzard and Ferro 1991), corn earworm, *Helicoverpa zea* (Boddie) (Whitcomb and Bell 1964, Bryson 1974), tobacco budworm, *Heliothis virescens* (F.) (Bryson 1974), and European corn borer, *Ostrinia nubilalis* (Hübner) (Conrad 1959, Coll and Bottrell 1991, Andow 1992). Clearly, *C. maculata* is less aphidophagous than many coccinellid species. In contrast, little is known about the predators that feed on *C. maculata* eggs in the field.

Predation upon eggs of various coccinellid species is most often reported as egg cannibalism. Adult and larval coccinellids are reported to frequently cannibalize eggs in laboratory colonies and in field populations (Balduf 1935, Stevens 1992, Osawa 1993, Hodek and Honěk 1996). Generally, egg cannibalism by larvae is reported as sibling egg cannibalism, with 1st instars eating unhatched eggs (fertile or sterile)

within their own cluster (Banks 1955, Kaddou 1960, Pienkowski 1965, Warren and Tadic 1967, Rogers et al. 1972). Wright and Laing (1982) investigated predation upon *C. maculata* egg clusters in corn during 1976 and 1977 and found that 44.4 and 77.1% of the egg clusters examined were attacked during the 2 yr, respectively, but reported no direct observation of predators attacking the eggs. Osawa (1993) reported that egg cannibalism in the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), sometimes exceeded 50% and was the 2nd most important mortality agent in a key factor analysis of a *H. axyridis* population. Based on field observations of *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae), Mills (1982) suggested that there is no predation on coccinellid eggs other than egg cannibalism, and survival of coccinellid eggs from oviposition to hatching is dependent on egg cannibalism by adults and larvae. Although we did observe predators other than *C. maculata* feeding on *C. maculata* eggs, our preliminary investigation revealed that *C. maculata* adults and larvae were the predominant predators of *C. maculata* egg clusters on sweet corn in Kentucky.

Besides feeding on a variety of prey, *C. maculata* uses other food sources such as plant pollen and fungal spores (Smith 1961, Putman 1964, Forbes 1880). Pollen from various plants has been tested as food for *C. maculata* (Smith 1961, Ewert and Chiang 1966, Harris 1969, Pfannenstiel 1995) and a diet of only corn pollen

is sufficient for this species' growth and development. Anthesis in corn generally occurs over a 10- to 14-d period during which corn pollen is shed from tassels daily and collects on corn plant surfaces. Sweet corn produces ≈3 times more pollen per anther than does field corn (Goss 1968) and may provide an abundant, alternative food source for *C. maculata*. Abundant pollen might lead to higher *C. maculata* densities (e.g., aggregation of adults), increased oviposition by *C. maculata*, increased predation on pests, and increased egg cannibalism by *C. maculata*. Conversely, if abundant pollen diverts *C. maculata* from carnivory, its presence might lead to decreased predation and cannibalism.

Our objectives were to determine the effect of sweet corn pollen abundance on the population densities of all life stages of *C. maculata*, predation on the eggs of an important corn pest (*H. zea*), and egg cannibalism by *C. maculata*. In addition, we report the diel patterns of *C. maculata* adults and larvae feeding on *H. zea* eggs and cannibalizing *C. maculata* eggs.

Materials and Methods

'Golden Queen' sweet corn plots (10 by 10 m) were planted near Lexington, KY, on 23 May and 25 May in 1995 and 1996, respectively, in a completely randomized block design with 2 treatments and 4 replications. The 2 treatments consisted of plots in which tassels remained intact (=pollen plots) and plots in which all tassels were removed manually just before anthesis (=no-pollen plots). Plots were separated by bare alleys 3 m wide in 1995 and 10 m wide in 1996. Weed management in all plots and alleys was done by treating with alachlor (2.5 kg [AI]/ha) + atrazine (1.5 kg [AI]/ha) immediately after planting and supplemental mechanical removal.

Pollen abundance, in both pollen and no-pollen plots, was quantified during anthesis in 1995 and 1996 to document the differences between the 2 types of plots. Pollen traps were made from squares (12 by 12 cm) of transparency film, sprayed on 1 side with adhesive (Tangle-Trap, The Tangle-Foot Company, Grand Rapids, MI) and placed, sticky side up, on a platform (12 by 12 cm) mounted horizontally on a wooden stake. The outside 1-cm edge of the transparency film was used to attach the film to the platform with binder clips. Only the inner area 10 by 10 cm of the film was used for pollen quantification. Two pollen traps were placed near the center of each plot at 1 m above ground between different pairs of corn rows. Pollen traps within a plot were from 2 to 4 m apart and all traps remained in the plots for 24 h. Two randomly chosen 1-cm² areas per pollen trap were examined under a light microscope and the numbers of pollen grains were recorded. Pollen was quantified on 1 date during anthesis in 1995 and on 4 dates during anthesis in 1996.

Population densities of all life stages of *C. maculata* per square meter were measured in pollen and no-pollen plots twice during and once after anthesis in 1995, and once before, twice during, and once after

anthesis in 1996. Density samples taken during anthesis in 1995 were done at 4 and 9 d after beginning of anthesis and in 1996 at 4 and 14 d after start of anthesis. Densities generally were sampled between 1200 and 1600 hours EST and all were completed by 1800 hours. Two randomly selected 1-m² sites per plot were sampled on each date. Sweet corn plants and the soil surface were examined visually for eggs, larvae, pupae, and adults. Larvae and adults were aspirated and retained in a vial until both sites within a plot were sampled, and then the insects were released back into that plot. Measured population density of each life stage was compared between pollen and no-pollen plots with respect to anthesis (i.e., before, during, and after anthesis) using nested analysis of variance (ANOVA) (SAS Institute 1995).

A *H. zea* colony was maintained at room temperature and a photoperiod of 15:9 (L:D) h by modified methods of Ignoffo (1965). Adults were provided 5% honey-water solution in 3.8-liter paper cartons lined with green floral paper for an oviposition substrate. We devised a system that permitted the moths to feed through a screen without contaminating their legs, bodies, or wings with the honey-water solution; therefore, the moths did not contaminate the ovipositional substrate with sugars. *H. zea* eggs used in predation studies were collected by removing and replacing the green floral paper from the large cartons daily. Eggs were stored at 10 ± 1°C and used in predation studies ≤5 d after oviposition. Although *H. zea* moths lay eggs singly, for our research purposes we cut groups of singly laid eggs (on ≈6 cm² of green floral paper) from the larger sheets of floral paper and used them in the field predation studies. The average number of *H. zea* eggs per group (±SE) was 10.9 ± 0.1. This kept the number of eggs in the *H. zea* egg groups similar to the number of eggs in the *C. maculata* egg clusters, as explained below.

A laboratory colony of *C. maculata*, which originated from adults collected near Lexington, KY, was maintained for collection of egg clusters used in field studies of egg cannibalism. Egg clusters used in field studies were from mated, laboratory-reared *C. maculata*. The colony was kept in an environmental chamber at 27 ± 1°C and a photoperiod of 15:9 (L:D) h. Beetles were reared in 9-cm-diameter petri dishes and fed a meat diet (100 g beef liver, 100 g ground beef, and 12 ml of 5% sucrose [wt:vol]) (Cohen 1985) wrapped in laboratory film (Parafilm "M", American Can, Greenwich, CT). Water was provided by a moistened, cotton dental wick. Green floral paper was cut into 10-cm-diameter circles and used to line lids of petri dishes containing *C. maculata* females. This allowed females to oviposit on a substrate that was easily removed and replaced. Egg clusters were collected daily and stored at 10 ± 1°C. The quantity of egg clusters needed for a single run of this experiment usually required collection of eggs for 2–3 d, and all *C. maculata* eggs used in field studies were ≤5 d old. *C. maculata* egg clusters, attached to ≈6 cm² of green floral paper, were cut from the larger circle of paper. Because *C. maculata* typically lays an inconsistent num-

ber of eggs per cluster in the field, a predetermined and consistent number of eggs per cluster was not used. Laboratory-collected *C. maculata* egg clusters used in our experiments averaged (±SE) 9.6 ± 0.1 eggs per cluster, whereas field data revealed 10.6 ± 0.4 eggs per cluster (*n* = 173) in naturally oviposited *C. maculata* egg clusters (T.E.C., unpublished data).

Predation of *H. zea* egg groups and cannibalism of *C. maculata* egg clusters were examined concurrently but in separate pollen and no-pollen sweet corn plots. Predation and cannibalism in pollen and no-pollen plots were examined on 1 date before, 1 date during, and 1 date after anthesis in 1995, and on 1 date before, 3 dates during, and 1 date after anthesis in 1996. Four egg stations per row were marked along 2 rows (4th and 9th) in each 12-row plot. Egg stations within a row were separated by 2-m intervals, with the 1st and last stations in a row being 2 m from the rows' ends. Thus, each plot contained either 8 sentinel groups of *H. zea* eggs or 8 sentinel clusters of *C. maculata* eggs (both egg types were on sections of green floral paper). Eggs on green floral paper were pinned to sweet corn stalks 15–45 cm above ground, a range of heights where most *C. maculata* egg clusters are naturally oviposited on sweet corn (T.E.C., unpublished data). Eggs were pinned on corn in the field at 1200 hours EDT and examined every 3 h through 1200 hours the following day. During each examination interval, data were recorded for any *H. zea* egg group or *C. maculata* egg cluster that had been preyed upon (either partially or completely), predators observed in the act of feeding on either type of egg were collected and recorded, and attacked *H. zea* egg groups and *C. maculata* egg clusters were replaced. For each egg type in each treatment, the average percent predation of egg groups or clusters over the eight 3-h intervals was calculated. Measured percent predation of *H. zea* egg groups and percent cannibalism of *C. maculata* egg clusters (including the small percentage of predation on *C. maculata* eggs by other predators) were compared with corresponding predation and cannibalism of eggs placed in no-pollen plots with respect to anthesis (i.e., before, during, and after anthesis). Percent predation was adjusted using an arcsine transformation (Zar 1996) and subjected to a 1-way ANOVA (Analytical Software 1992). Data are presented as untransformed means ± SE.

Results

Detasseling sweet corn plants in no-pollen plots caused a drastic reduction in pollen abundance compared with pollen plots. In 1995, pollen abundance was quantified on 1 date during anthesis and found to be 57 times greater in pollen plots than in no-pollen plots (Fig. 1). On average, 1,332 pollen grains per square centimeter were found in pollen plots during the 24-h sampling period, compared with 23 pollen grains per square centimeter in no-pollen plots. The presence of small amounts of pollen in no-pollen plots presumably was due to air-borne drift from pollen plots. For this reason, alley widths between plots were increased
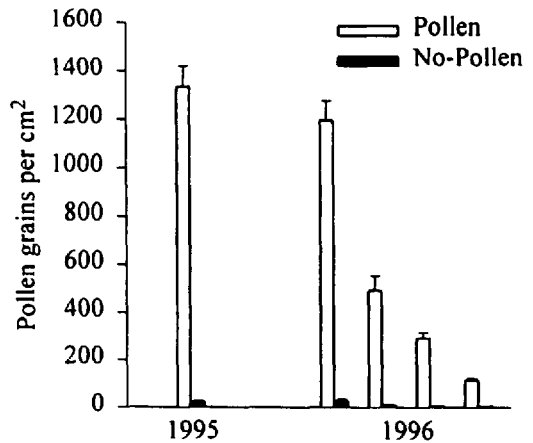

Fig. 1. Quantification of sweet corn pollen (mean ± SE) in pollen and no-pollen plots during anthesis on 1 date in 1995 and on 4 dates in 1996.

from 3 m in 1995 to 10 m in 1996. Across 4 sample dates during anthesis in 1996, pollen was on average 51 times more abundant in pollen plots than in no-pollen plots (Fig. 1) and ranged from 30 to 68 times greater on the 4 sample dates.

Population densities of all *C. maculata* life stages were measured in both pollen and no-pollen plots when pollen was not being released by corn (before and after anthesis) and when pollen was being released by corn (during anthesis). Before anthesis in 1996, no significant differences in population densities of any life stage (egg, larva, pupa, or adult) were found between pollen and no-pollen plots (Fig. 2a). *C. maculata* densities were not determined before anthesis in 1995. After anthesis, there also were no significant differences in densities between pollen and no-pollen plots in any life stage during 1995 or 1996 (Fig. 2c). However, during anthesis, egg and larval densities were significantly higher in pollen plots compared with no-pollen plots in 1996 (*F* = 5.13; df = 1, 28; *P* < 0.05 and *F* = 4.97; df = 1, 28; *P* < 0.05, respectively), but not in 1995 (Fig. 2b).

Predation of *H. zea* eggs and cannibalism of *C. maculata* eggs were examined at 3-h intervals, independently, in pollen and no-pollen plots when corn plants were not releasing pollen (before and after anthesis) and also when the corn plants in pollen plots were releasing pollen (during anthesis). Before anthesis, predation on *H. zea* eggs placed in pollen and no-pollen plots was not significantly different either in 1995 (*F* = 0.94; df = 1, 6; *P* > 0.05) or 1996 (*F* = 0.18; df = 1, 6; *P* > 0.05) (Fig. 3 a and b). Similarly, predation on *H. zea* eggs was not significantly different between pollen and no-pollen plots after anthesis in either 1995 (*F* = 0.11; df = 1, 6; *P* > 0.05) or 1996 (*F* = 5.27; df = 1, 6; *P* > 0.05) (Fig. 3 a and b). However, during anthesis, predation of *H. zea* eggs was significantly lower in pollen plots compared with no-pollen plots during 1995 (*F* = 6.99; df = 1, 6; *P* < 0.05). No significant difference in predation of

a) Before anthesis-1996
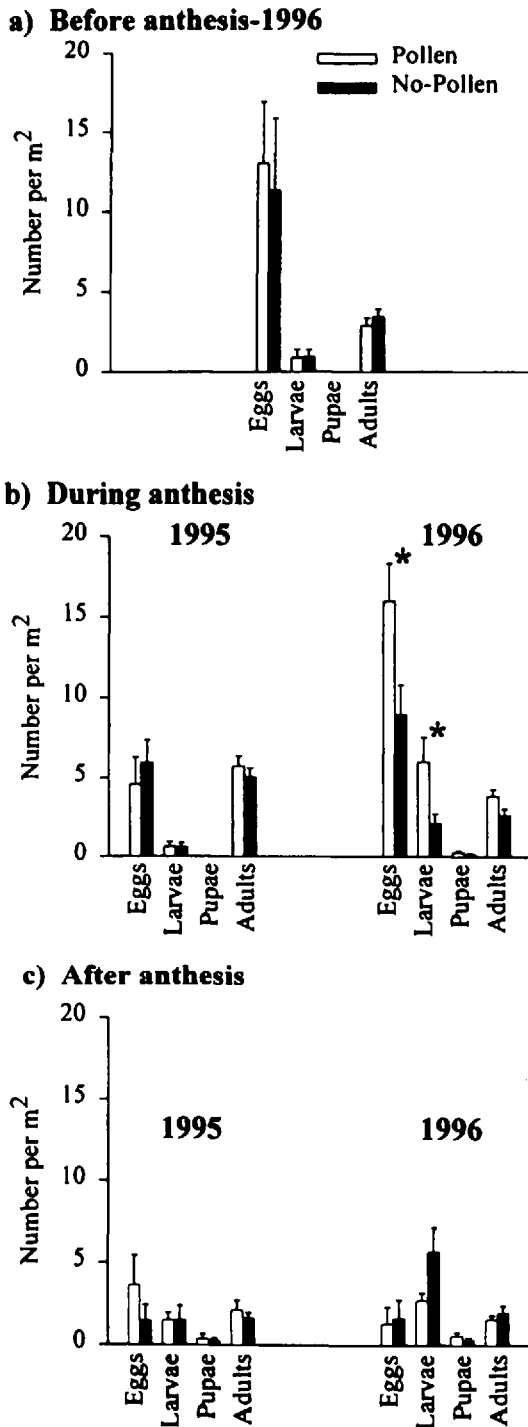

b) During anthesis

c) After anthesis

Fig. 2. Population density (±SE) of *C. maculata* in pollen and no-pollen plots (a) before, (b) during, and (c) after anthesis. * Indicates significant difference between the 2 adjacent bars (*P* < 0.05).

H. zea eggs was observed between pollen and no-pollen plots during anthesis in 1996 (*F* = 0.00; df = 1, 22; *P* > 0.05) (Fig. 3 a and b).
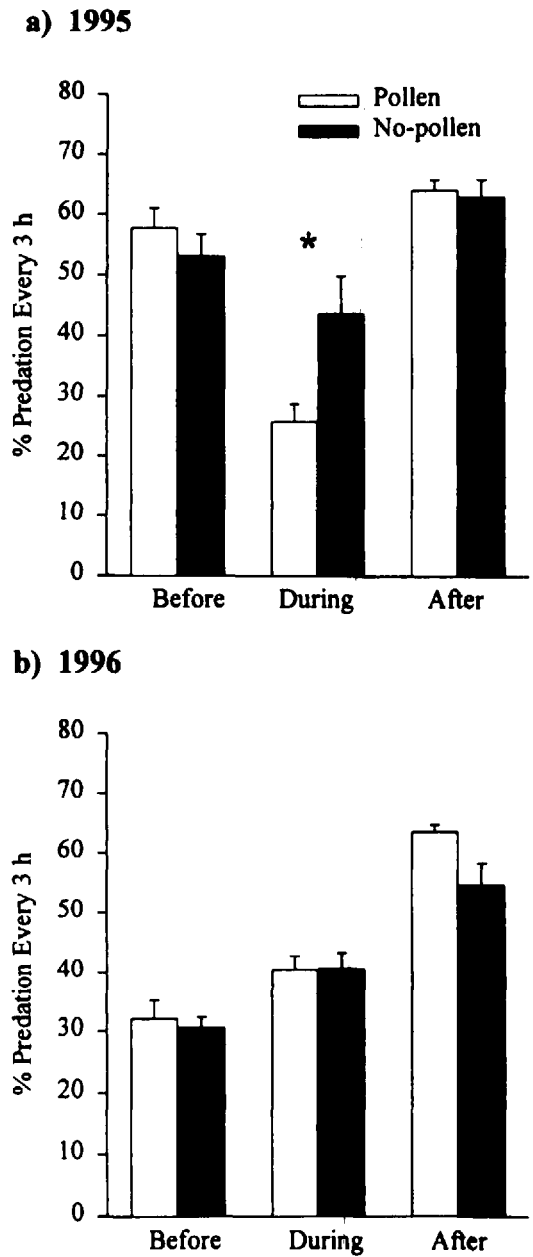
a) 1995

b) 1996

Fig. 3. Predation of *H. zea* egg groups (±SE) on sweet corn in pollen and no-pollen plots before, during, and after anthesis in (a) 1995 and (b) 1996. * Indicates significant difference between the 2 adjacent bars (*P* < 0.05).

Many species of predators were observed feeding on *H. zea* eggs in sweet corn during 1995 and 1996 (Table 1). *C. maculata* and *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) were the 2 predominant predators. Together, *C. maculata* (adults and larvae) and *O. insidiosus* (adults and nymphs) accounted for 83.0% of all observed predation on *H. zea* eggs, and *C. maculata* alone accounted for 58.1% of observed predation events. Adults accounted for 43.2% of the ob-

Table 1. Number of direct observations of predators feeding on *H. zea* eggs on sweet corn before, during, and after anthesis in pollen and no-pollen plots, 1995 and 1996

		Before anthesis		During anthesis		After anthesis	
		Pollen	No-pollen	Pollen	No-pollen	Pollen	No-pollen
Coleoptera	*C. maculata* adults	28	20	13	24	7	13
	C. maculata larvae	7	11	25	35	32	28
	H. axyridis larvae	0	0	3	1	0	0
	Carabidae	4	5	0	1	1	0
	small Coccinellidae	0	0	0	1	1	0
	Elateridae	0	0	0	0	0	1
	Nitidulidae	1	0	0	1	0	0
	unidentified Coleoptera	0	1	1	0	1	0
Hemiptera	*O. insidiosus* adults	1	2	1	3	6	2
	O. insidiosus nymphs	8	6	31	25	12	7
	Miridae	1	1	1	0	0	0
	Nabidae	0	1	1	0	0	0
Neuroptera	*Chrysoperla carnea*	0	1	3	5	3	2
Hymenoptera	Formicidae	1	0	6	2	1	2
Orthoptera	Tettigoniidae	0	0	1	0	0	0
Collembola		0	0	0	0	1	0
Arachnida	Phalangiidae	1	0	2	1	1	3
	Clubionidae	1	2	1	1	0	1
	Acari	0	0	0	0	1	0

served predation by *C. maculata*, whereas larvae accounted for 56.8%. Before, during, and after anthesis, predation by *C. maculata* adults on *H. zea* eggs was predominantly diurnal, but larvae were both diurnal and nocturnal predators of *H. zea* eggs (Fig. 4 a–c). *O. insidiosus* accounted for 24.9% of all observed predation events on *H. zea* eggs. Adults and nymphs accounted for 14.4 and 85.6% of these events, respectively. The next 3 most frequently observed predators feeding on *H. zea* eggs were green lacewings (Neuroptera: Chrysopidae), ants (Hymenoptera: Formicidae), and ground beetles (Coleoptera: Carabidae). Together, they accounted for 8.9% of all observed predation events. All other predators accounted for 8.1% of observed predation events.

Before anthesis, cannibalism of *C. maculata* eggs placed in pollen and no-pollen plots was not significantly different in 1995 ($F = 0.00$; df = 1, 6; $P > 0.05$) or in 1996 ($F = 1.14$; df = 1, 6; $P > 0.05$) (Fig. 5 a and b). Similarly, after anthesis, egg cannibalism was not significantly different in pollen plots compared with no-pollen plots in 1995 ($F = 0.13$; df = 1, 6; $P > 0.05$) or in 1996 ($F = 0.62$; df = 1, 6; $P > 0.05$) (Fig. 5 a and b). When pollen was abundant (during anthesis) in pollen plots, there was a trend for lower egg cannibalism in pollen plots than in no-pollen plots, although, in 1995 the trend was not significant ($F = 1.34$; df = 1, 6; $P > 0.05$). However, egg cannibalism was significantly lower in pollen plots compared with no-pollen plots in 1996 ($F = 12.26$; df = 1, 22; $P < 0.05$) (Fig. 5 a and b).

Fewer species were observed feeding on *C. maculata* eggs than on *H. zea* eggs, and *C. maculata* accounted for 92.4% of these events (Table 2). Thus, most predation on *C. maculata* eggs on sweet corn was egg cannibalism. Adults and larvae accounted for 41.4 and 58.6% of those cannibalism events, respectively. As with predation by *C. maculata* on *H. zea* eggs, egg cannibalism (before, during, and after anthesis) by adults occurred primarily during daylight, but larvae

fed during both the day and night (Fig. 6 a–c). The next most frequently encountered predator of *C. maculata* eggs in sweet corn was the introduced multicolored Asian lady beetle, *H. axyridis*. Adults of this coccinellid were never observed feeding on *C. maculata* eggs, but *H. axyridis* larvae accounted for 3.2% of all observed predation events on *C. maculata* egg clusters. Combined predation by all other predators accounted for the remaining 4.5% of observed predation events. *O. insidiosus*, which frequently fed on *H. zea* eggs, was never observed to feed on *C. maculata* eggs.

Discussion

Before and after anthesis, pollen and no-pollen plots were equivalent with regard to pollen abundance (i.e., no corn pollen present in either type of plot). Thus, we expected similar results in pollen and no-pollen plots before anthesis, and that is what we found. After anthesis, pollen was similarly scarce in the 2 types of plots due to its short viability, rapid decomposition (Anderson and Kulp 1922, Goss 1968), and rains that washed residual pollen from plant surfaces. Again, we observed no differences in *C. maculata* densities, *H. zea* egg predation, or *C. maculata* egg cannibalism when pollen was absent.

During anthesis, pollen was abundant in pollen plots and only traces of wind-blown pollen were found in no-pollen plots. Separating the plots by alleys 3 m wide in 1995 and 10 m wide in 1996 was intended to further decrease the occurrence of pollen in no-pollen plots, but this appeared to have little effect on interception of drifting pollen. The increased distance between plots, however, may have affected relative densities of *C. maculata* in pollen and no-pollen plots as seen in 1996, but not in 1995.

Coleomegilla maculata, like many other coccinellid species, lays eggs in clusters that are exposed (Hagen 1962) and relatively conspicuous on corn. Egg clusters generally are oviposited on the lower one-third of the
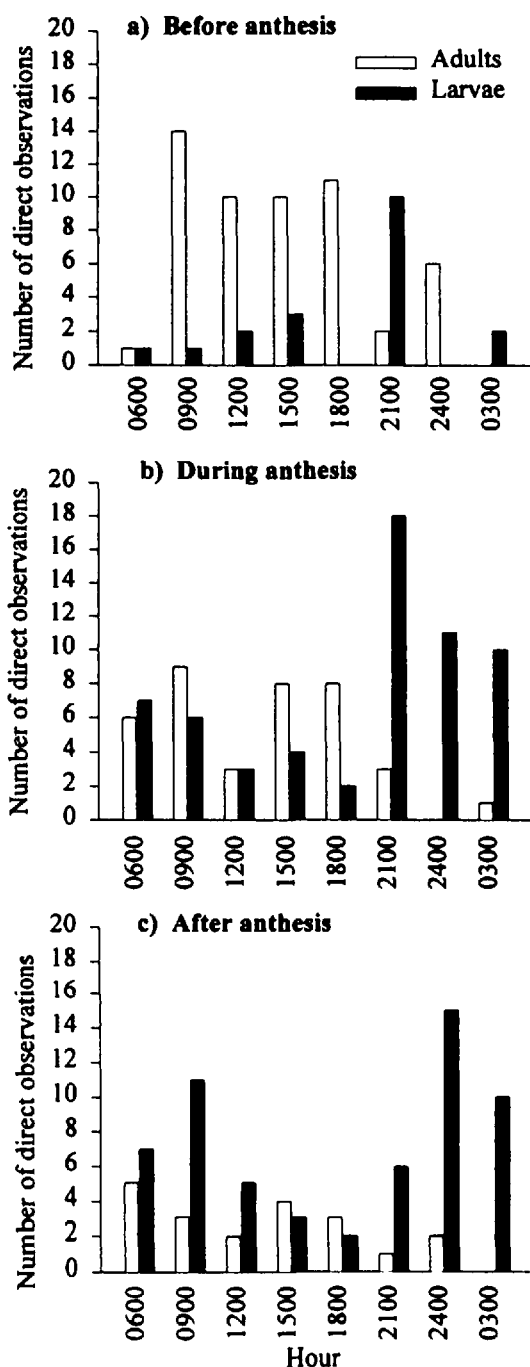
Fig. 4. Diel periodicity of *C. maculata* adults and larvae feeding on *H. zea* eggs on sweet corn (a) before anthesis, (b) during anthesis, and (c) after anthesis (combined data from pollen and no-pollen plots in 1995 and 1996).

Fig. 5. Cannibalism of *C. maculata* egg clusters ($\pm$SE) on sweet corn in pollen and no-pollen plots before, during, and after anthesis in (a) 1995 and (b) 1996. * Indicates significant difference between the 2 adjacent bars ($P < 0.05$).

corn plant and may be found on the undersides of leaves, as reported by Coderre et al. (1987), and also on the stalk, as we found during this study. Unlike some of the more aphidophagous species of lady beetles, *C. maculata* egg clusters on corn are not consis-
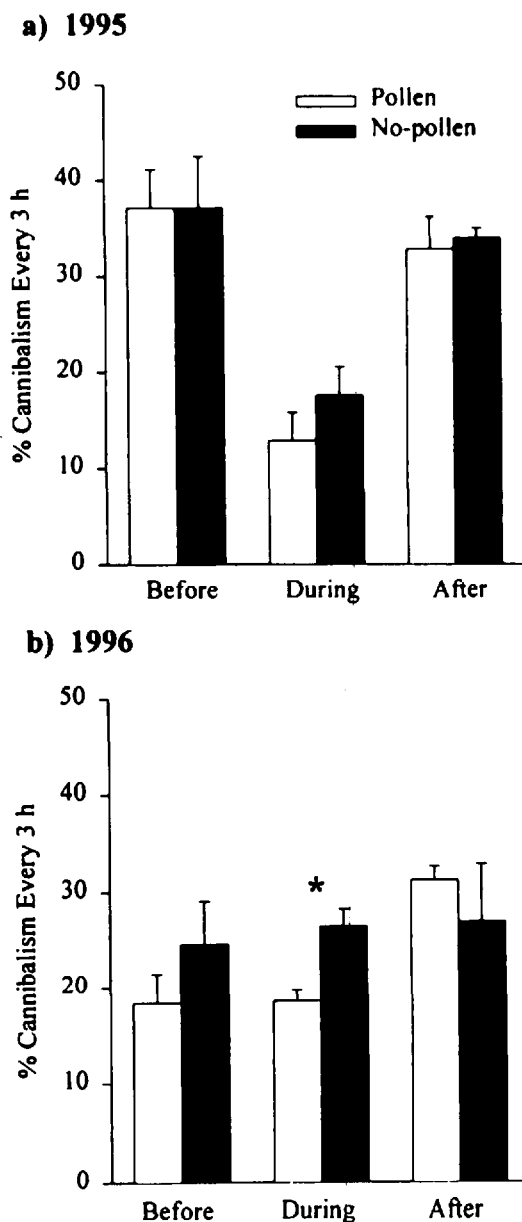
tently associated with a nearby food source (i.e., clumps of aphids) (T.E.C., unpublished data). Even though adult females readily feed on pollen, increased oviposition on corn in pollen plots may not have been a direct result. In 1995, the 3-m-wide alleys between plots may have presented adults with a nearly contiguous habitat, providing little hindrance to movement between pollen and no-pollen plots by ovipositing females. Smith (1971) found that *C. maculata* maintains seasonally steady adult densities in corn even

Table 2. Number of direct observations of predators feeding on *C. maculata* eggs on sweet corn before, during, and after anthesis in pollen and no-pollen plots, 1995 and 1996

		Before anthesis		During anthesis		After anthesis	
		Pollen	No-pollen	Pollen	No-pollen	Pollen	No-pollen
Coleoptera	*C. maculata* adults	14	18	6	10	6	6
	C. maculata larvae	14	5	22	17	18	9
	H. axyridis larvae	0	0	1	3	1	0
	Carabidae	0	0	0	0	0	1
Neuroptera	*Chrysoperla carnea*	0	0	1	0	0	1
Hymenoptera	Formicidae	0	0	0	0	0	1
Orthoptera	Gryllidae	0	0	0	0	1	0
Diplopoda		0	0	0	0	1	1

when pollen is abundant. He commented that corn pollen is a preferred food of *C. maculata* in the laboratory but pollen availability in the field does not determine local distribution of adult *C. maculata*. Smith's (1971) findings, in which he used contiguous corn plots, are consistent with our findings when plots were nearly contiguous. However, in 1996, when alley widths were increased to 10 m (with the intention of further reducing pollen drift into no-pollen plots), females may have been less likely to move from food-rich pollen plots to the no-pollen plots for oviposition. The 10-m-wide alleys between plots presented *C. maculata* females with a more patchily distributed food source and may have reduced their departure from the pollen plots, thus increasing the probability that a female would oviposit in a pollen plot. This is supported, in part, by the fact that during anthesis in 1996, significantly more eggs and larvae were found in pollen than in no-pollen plots. Similarly, Banks (1955) found that aphid-infested bean stems had more coccinellid eggs laid on heavily infested stems and attributed this to female coccinellids spending more time foraging on these stems. In our study, *C. maculata* females entering no-pollen plots (with virtually no pollen available) during anthesis would be apt to disperse from no-pollen plots into pollen plots. Also, in 1996 during anthesis, adults were more abundant in pollen plots compared with no-pollen plots ($F = 4.08$, df = 1, 28; $P = 0.0531$). This was the only time when differences in adult densities between the 2 types of plots approached statistical significance. When pollen was absent (before and after anthesis) movement by adults between pollen and no-pollen plots may have been more random, as suggested by the similar population densities found in both types of plots.

As with *C. maculata* densities when pollen was absent, predation of *H. zea* eggs and cannibalism of *C. maculata* eggs were not significantly different between pollen and no-pollen plots in either year. However, when pollen was abundant in pollen plots, *H. zea* egg predation and *C. maculata* egg cannibalism in pollen plots were never higher than in no-pollen plots. In fact, predation on *H. zea* eggs in 1995 was significantly lower in pollen plots than in no-pollen plots when both *C. maculata* adult and larval densities were equivalent in both plot types. Even in 1996 when densities of *C. maculata* larvae were significantly higher in pollen plots, *H. zea* egg predation was equiv-

alent between the 2 types of plots and *C. maculata* egg cannibalism was significantly higher in no-pollen plots. These results suggest that abundant pollen reduced the per capita rate of carnivory by *C. maculata* on *H. zea* eggs and *C. maculata* eggs.

Direct observations of diel foraging patterns by *C. maculata* adults and larvae have not been reported previously. Mack and Smilowitz (1979) did report on diel flight activity of *C. maculata* adults in potato fields as indexed by captured adults on sticky traps, and Hazzard et al. (1991) reported the presence (but not activity or foraging) of *C. maculata* adults on potato plants at night during their searches for nocturnal predators. During our predation and cannibalism studies, we observed predominantly diurnal foraging by *C. maculata* adults on both *H. zea* eggs and *C. maculata* eggs on sweet corn. In contrast, we observed that *C. maculata* larvae fed on both types of eggs during the day and also at night when adults rarely were active. Lower nighttime temperatures may have caused different feeding patterns between *C. maculata* adults and larvae. Giroux et al. (1995), however, reported that predation by adults or 4th instars of *C. maculata* on Colorado potato beetle eggs and early instars was comparable when tested at constant temperatures (from 7.5 to 30°C). However, they did not report nocturnal feeding behavior of the adults or larvae. Our observations suggest that total predation by *C. maculata* larvae may have been underestimated in earlier studies. In support of this, we observed more predation on *H. zea* eggs and cannibalism on *C. maculata* eggs by *C. maculata* larvae than by any other predator, including *C. maculata* adults.

In our studies, an abundant, alternative food source (i.e., corn pollen) apparently diverted predation by a polyphagous predator away from a pest species of corn, and an increase in predator density did not counteract the diversionary effect of pollen on predation. It is likely that other polyphagous predators could be affected similarly by an alternative, abundant food source. For example, *O. insidiosus* adults and nymphs (frequently observed feeding on *H. zea* eggs in our study) feed on corn pollen (Dicke and Jarvis 1962) and can complete nymphal development on only pollen (Kiman and Yeargan 1985). In fact, populations of *O. insidiosus* in corn peak during anthesis (Dicke and Jarvis 1962, Isenhour and Yeargan 1981, Coll and Bottrell 1991), and Dicke and Jarvis (1962)
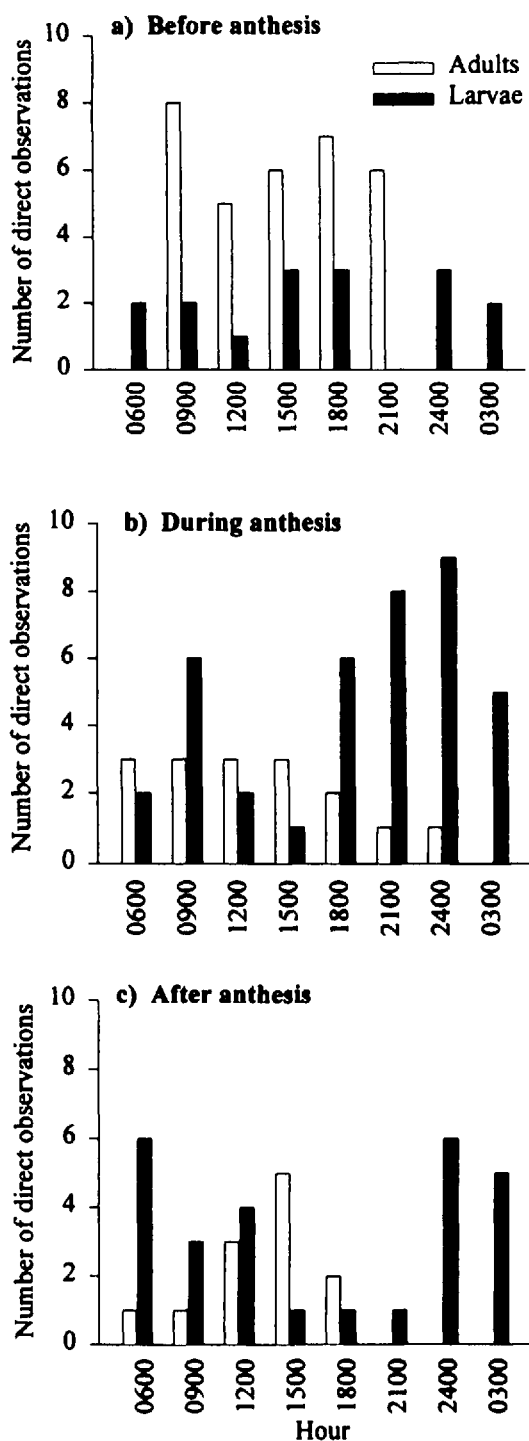
Fig. 6. Diel periodicity of *C. maculata* adults and larvae cannibalizing *C. maculata* eggs on sweet corn (a) before anthesis, (b) during anthesis, and (c) after anthesis (combined data from pollen and no-pollen plots in 1995 and 1996).

suggested lower predation of 2nd-generation European corn borer larvae in corn was due to pollen. Thus, predictions about biological control involving polyph-

agous predators in agroecosystems should not only consider the temporal and spatial distribution of pest species, but also, the temporal and spatial availability of suitable alternative food sources and the effects these have on specific polyphagous predators.

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