

Influence of a Native Weed, *Acalypha ostryaefolia* (Euphorbiaceae), on *Coleomegilla maculata* (Coleoptera: Coccinellidae) Population Density, Predation, and Cannibalism in Sweet Corn

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ABSTRACT We investigated the density of *Coleomegilla maculata* (DeGeer), predation by *C. maculata* on *Helicoverpa zea* (Boddie) eggs, and egg cannibalism by *C. maculata* when the weed *Acalypha ostryaefolia* Riddell was grown in stands of sweet corn (*Zea mays* L.). Densities of *C. maculata* eggs and larvae were significantly higher in weedy plots than in weed-free plots during each of the 3 yr the study was done. Pupal density was significantly higher in weedy plots in 1995 and 1996, but not in 1997. Adult *C. maculata* density was significantly higher in weedy plots in 1995, but not in 1996 or 1997. Egg cannibalism by adult and larval *C. maculata* is common on sweet corn plants in Kentucky. *C. maculata* frequently oviposits on *A. ostryaefolia* in and around sweet corn plots, and our preliminary observations suggested egg cannibalism was less frequent on *A. ostryaefolia* than on sweet corn plants. There was a trend for higher abundance of *C. maculata* eggs on corn plants in weed-free plots than on corn plants in weedy plots; in weedy plots, >85% of eggs were on *A. ostryaefolia* plants rather than on corn plants. However, larvae were always more abundant on corn plants in weedy plots than on corn plants in weed-free plots and significantly so in 1995 and 1997. Predation of *H. zea* eggs was significantly higher on corn plants in weedy plots than on corn plants in weed-free plots, whereas cannibalism of *C. maculata* eggs was significantly higher on corn plants in weedy plots only during 1 of the 3 yr. Thus, presence of *A. ostryaefolia* in sweet corn plots increased *C. maculata* egg and larval population densities and predation of *H. zea* eggs. Direct observations of *H. zea* egg predation and egg cannibalism by *C. maculata* revealed that adults predominantly were diurnal but larvae fed day and night.

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

WHEN WE EXAMINED various weed species growing in and around sweet corn (*Zea mays* L.) plots, it appeared that *Coleomegilla maculata* (DeGeer) egg clusters occurred more frequently on a native weed species, hophornbeam copperleaf (*Acalypha ostryaefolia* Riddell [Euphorbiaceae]), than on other nearby weed species (e.g., lambsquarter [*Chenopodium album* L.], prickly sida [*Sida spinosa* L.], and pigweed [*Amaranthus* spp.]). A preliminary examination of egg cannibalism on hophornbeam copperleaf and on nearby sweet corn plants revealed that *C. maculata* egg clusters on *A. ostryaefolia* suffered less cannibalism than those on sweet corn. This suggested that hophornbeam copperleaf might provide refuge from egg cannibalism for *C. maculata* and lead to higher *C. maculata* larval population densities on sweet corn.

However, when interspersed within a crop, the presence of an alternate plant for oviposition might result in significant numbers of the mobile, predatory stages (i.e., adults and larvae) of *C. maculata* on the alternate plant and decrease the natural enemy's abundance on the crop. If that occurred, one would expect lower predation by *C. maculata* of pests on the crop. Andow and Risch (1985) found that corn monocultures had a higher abundance of *C. maculata*

adults and higher predation rates of European corn borer egg masses than did polycultures of corn, beans, and squash. However, Shelton and Edwards (1983) found that *C. maculata* (stages not reported) abundance was significantly higher in weedy than weed-free soybean plots.

Cannibalism of coccinellid eggs is common, and many reported cases are incidences of sibling egg cannibalism by 1st instars soon after they hatch (Banks 1956, Pienkowski 1965, Warren and Tadic 1967, Rogers et al. 1972, Kawai 1978, Osawa 1989). Nonsibling egg cannibalism also has been reported. For example, Mills (1982) found that most cannibalism of *Adalia bipunctata* (Coleoptera: Coccinellidae) eggs was nonsibling cannibalism. Cottrell and Yeargan (1998) showed that *C. maculata* adults and larvae were the predominant 'predators' of *C. maculata* eggs on sweet corn, accounting for >90% of observed predation events. They also found that cannibalism, plus a small percentage of predation, of *C. maculata* egg clusters on corn led to partial or total destruction of 15-30% of the egg clusters every 3 h.

It has been suggested that oviposition by coccinellids near aphid infestations may increase the chance of egg cannibalism by nearby foraging adults and larvae

(Osawa 1989, Agarwala and Dixon 1993). However, Boldyrev et al. (1969) stated that some species of Coccinellidae may seek oviposition sites that are characteristically different from foraging sites. Osawa (1989) found that natural oviposition by the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas), at a distance >10 cm from aphid clumps significantly reduced nonsibling egg cannibalism. In addition, Banks (1956) found that coccinellids do not always oviposit near aphids on bean stems, and Cottrell and Yeargan (1998) reported that *C. maculata* eggs on sweet corn generally were not associated with any apparent nearby food source (e.g., clumps of aphids).

Our objectives were to examine the influence of *A. ostryaefolia*, when grown with sweet corn, on population densities of all life stages of *C. maculata*, predation of *H. zea* eggs, and egg cannibalism by *C. maculata* adults and larvae. Based on direct observations of feeding events on corn and *A. ostryaefolia*, we also report diel patterns of egg predation and egg cannibalism by *C. maculata* adults and larvae, as well as predation by other species.

Materials and Methods

Field Plots and Sampling *C. maculata* Populations. 'Golden Queen' sweet corn plots (10 by 10 m) were planted near Lexington, KY, on 19 June, 20 June, and 4 June in 1995, 1996, and 1997, respectively, in a randomized complete block design with 4 replicates. All plots were separated by 3-m-wide bare alleys. Weeds were managed in weed-free plots and alleys by treatment with alachlor + atrazine (2.5 kg [AI] + 1.5 kg [AI]/ha) immediately after planting combined with season-long manual removal of all weeds. Weed management in weedy plots was done by treating with alachlor (2.5 kg [AI]/ha) immediately after planting combined with selective mechanical removal of all weed species other than *A. ostryaefolia* throughout the season. *A. ostryaefolia* was allowed to grow in weedy sweet corn plots; its densities were not controlled in 1995 or 1996 and were higher than corn density per square meter. In 1997, we reduced and controlled the densities of *A. ostryaefolia* to $\approx 1/2$ the density of corn per square meter to determine if a low density of *A. ostryaefolia* would affect *C. maculata* similarly. When sweet corn plants were ≈ 0.5 m tall, greenhouse-grown *A. ostryaefolia* seedlings were transplanted into weedy plots midway between rows of corn at an evenly spaced density of 2 *A. ostryaefolia* seedlings per meter. Season-long mechanical removal of all naturally germinated *A. ostryaefolia* plants, as well as all other weed species, was done in all plots in 1997.

Coleomegilla maculata population densities were sampled on 3 dates during each year. Two randomly selected 1-m² sites per plot were sampled on each date. In both weedy and weed-free plots, sweet corn plants and the soil surface were examined visually for all life stages of *C. maculata*. In weedy plots, all *A. ostryaefolia* plants in each of the randomly selected 1-m² sites were examined (for mobile adults and older larvae), and *A. ostryaefolia* plants were cut, placed in

plastic bags, and further examined for all life stages of *C. maculata* in the laboratory. Plant densities were recorded on all dates when *C. maculata* was sampled. On 2 of 3 dates in 1996, leaf area (per square meter) of the *A. ostryaefolia* was measured (LI-COR, model LI-3000, Lambda Instrument, Lincoln, NE). Leaf area of mature corn (per square meter) in weedy plots was also measured, but only on the 3rd sampling date of 1996. Repeated measures analysis of variance (ANOVA) (Analytical Software 1992) was used to compare the population density of each *C. maculata* stage (egg, larva, pupa, and adult) in weedy plots versus weed-free plots and to compare the density of each life stage on corn plants in weedy versus weed-free plots.

Production of *H. zea* and *C. maculata* Eggs for Field Experiments. A *Helicoverpa zea* (Boddie) 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 to prevent ovipositing moths from contaminating their ovipositional substrate with honey water. This was done by placing 50-ml honey-water containers with protruding tissue wicks into 460-ml paper cartons covered with a screened lid. The smaller carton was placed into the large carton and moths inserted their probosci through the screen to reach the honey-water solution on the tissue wick. *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 $10 \pm 1^\circ\text{C}$ and used in predation studies ≤ 5 d after oviposition. Although *H. zea* moths lay eggs singly, we cut groups of singly laid eggs (on ≈ 6 cm² of green floral paper) from the larger sheets of floral paper and used these groups in field predation studies. The mean number (\pm SE) of *H. zea* eggs per group was 9.4 ± 0.1 ($n = 2,517$ groups) and was similar to the mean number of *C. maculata* eggs per cluster collected in the laboratory for the cannibalism studies, as explained below.

A laboratory colony of *C. maculata* was started from adults collected near Lexington, KY, and maintained for collection of egg clusters used in field studies of egg cannibalism. The colony was maintained at $27 \pm 1^\circ\text{C}$ and a photoperiod of 15:9 (L:D) h in an environmental chamber. Beetles were reared in 9-cm-diameter petri dishes and provided a blended beef diet (100 g beef liver, 100 g ground beef, and 12 ml of 5% sucrose [wt:vol]) wrapped in laboratory film (Parafilm "M," American Can Company, Greenwich, CT) (Cohen 1985). Water was provided by placing a moistened, cotton dental wick into the petri dish. Green floral paper was cut into 10-cm-diameter circles and used to line lids of petri dishes containing *C. maculata* females. This paper provided females an ovipositional substrate that could be removed easily and replaced. Egg clusters used in field studies were from mated, laboratory-reared *C. maculata*. Egg clusters were collected daily and stored at $10 \pm 1^\circ\text{C}$. The quantity of *C. maculata* 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. Egg clusters were on ≈ 6 cm² of green floral paper. Because naturally oviposited *C. maculata* egg clusters in the field contain an inconsistent number of eggs per cluster, a predetermined and consistent number of eggs per cluster was not used in our field studies. The mean number of eggs per cluster (\pm SE) laid by *C. maculata* in the field was 12.1 ± 0.3 ($n = 401$ clusters) and in the laboratory was 9.5 ± 0.1 ($n = 1,633$ clusters).

Field Studies of Egg Predation and Cannibalism. Predation of *H. zea* eggs and cannibalism of *C. maculata* eggs were examined independently, although not concurrently (usually within 24 h [range, 24–72 h]), on 3 dates in 1995 and on 4 dates in 1996. Egg predation and cannibalism were examined on corn in weedy plots, on *A. ostryaefolia* in weedy plots, and on corn in weed-free plots. However, in 1997, predation of *H. zea* eggs was not studied and *C. maculata* egg cannibalism was examined on 3 dates on corn in weedy plots (but not on *A. ostryaefolia* plants) and on corn in weed-free plots. Four egg stations per row were marked along 2 rows (3rd and 9th) in each 12-row plot in 1995 and 1996 and along 3 rows (3rd, 6th, and 10th) in 1997. Egg stations within a row were separated by 2-m intervals, with the 1st and last stations in a row 2 m from the row ends. Thus, in 1995 and 1996, each plot contained either 8 groups of *H. zea* eggs or 8 clusters of *C. maculata* eggs. In 1997, each plot contained 12 clusters of *C. maculata* eggs. The 6-cm² pieces of green floral paper (with attached eggs) were pinned to sweet corn stalks 15–45 cm above ground, a range of heights where most *C. maculata* egg clusters were found to be naturally oviposited on sweet corn (Cottrell and Yeargan 1998). For predation and cannibalism of eggs on *A. ostryaefolia*, the pieces of green floral paper (with eggs attached) were stapled to the upper surface of an *A. ostryaefolia* leaf at a height similar to which the floral paper was pinned on sweet corn. Each year, eggs were placed 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; predators observed in the act of feeding on either type of egg were collected and recorded. All attacked *H. zea* egg groups and *C. maculata* egg clusters were replaced every 3 h. Percent predation of *H. zea* egg groups and percent cannibalism of *C. maculata* egg clusters were adjusted for statistical analysis using an arcsine transformation (Zar 1996). Predation and cannibalism of eggs on corn in weedy plots, on *A. ostryaefolia* in weedy plots, and on corn in weed-free plots were compared using repeated measures ANOVA (Analytical Software 1992). Least significant difference (LSD) was used to separate means when significant differences were detected ($P < 0.05$) by ANOVA. Data are presented as untransformed means \pm SE.

Results

***Coleomegilla maculata* Population Density.** During 1995, 1996, and 1997, more eggs were found per square meter in weedy plots than in weed-free plots ($F = 8.41$; $df = 1, 19$; $P = 0.0092$; $F = 10.60$; $df = 1, 19$; $P = 0.0042$; $F = 5.22$; $df = 1, 19$; $P = 0.0341$, respectively) (Fig. 1) as were larvae ($F = 170.37$; $df = 1, 19$; $P = 0.0000$; $F = 9.36$; $df = 1, 19$; $P = 0.0064$; $F = 17.99$; $df = 1, 19$; $P = 0.0004$, respectively). In addition, more pupae were found in weedy plots than in weed-free plots during 1995 and 1996 ($F = 7.11$; $df = 1, 19$; $P = 0.0152$; $F = 6.51$; $df = 1, 19$; $P = 0.0195$; respectively), but not in 1997 ($F < 0.01$; $df = 1, 19$; $P = 1.0000$) (Fig. 1). Adult densities differed in 1995, when more were found in weedy plots than weed-free plots ($F = 10.43$; $df = 1, 19$; $P = 0.0044$) but not in 1996 or 1997 ($F = 0.32$; $df = 1, 19$; $P = 0.5789$; $F < 0.01$; $df = 1, 19$; $P = 0.9477$; respectively) (Fig. 1). These egg, larval, pupal, and adult densities represent all *C. maculata* found per square meter, including any found on corn plants, on *A. ostryaefolia* plants, or on the ground.

Larval *C. maculata* densities on corn plants in weedy plots were higher than those on corn plants in weed-free plots during 1995 and 1997, but not in 1996 ($F = 16.89$; $df = 1, 19$; $P = 0.0006$; $F = 6.04$; $df = 1, 19$; $P = 0.0237$; $F = 0.12$; $df = 1, 19$; $P = 0.7313$, respectively) (Fig. 2). Densities of *C. maculata* eggs ($F = 2.05$; $df = 1, 19$; $P = 0.1685$; $F = 3.74$; $df = 1, 19$; $P = 0.0683$; $F = 2.07$; $df = 1, 19$; $P = 0.1661$), pupae ($F = 1.00$; $df = 1, 19$; $P = 0.3299$; $F = 0.52$; $df = 1, 19$; $P = 0.4810$; $F < 0.01$; $df = 1, 19$; $P = 1.0000$) or adults ($F = 0.34$; $df = 1, 19$; $P = 0.5660$; $F = 1.14$; $df = 1, 19$; $P = 0.2489$; $F = 0.04$; $df = 1, 19$; $P = 0.8359$) on corn plants did not differ between weedy and weed-free plots during 1995, 1996, or 1997, respectively (Fig. 2). Although, there was a trend of more eggs occurring on corn plants in weed-free plots than on corn plants in weedy plots.

Larval densities on the ground were higher in weedy plots than in weed-free plots in 1995 and 1996, but not in 1997 ($F = 54.91$; $df = 1, 19$; $P = 0.0000$; $F = 14.37$; $df = 1, 19$; $P = 0.0012$; $F = 2.28$; $df = 1, 19$; $P = 0.1475$, respectively) (Fig. 3). Adult densities on the ground were higher in weedy plots during 1995 ($F = 7.12$; $df = 1, 19$; $P = 0.0152$) but not in 1996 or 1997 ($F = 1.00$; $df = 1, 19$; $P = 0.3299$; $F = 1.16$; $df = 1, 19$; $P = 0.2958$; respectively) (Fig. 3). Eggs and pupae were never found on the ground.

Densities of *A. ostryaefolia* per square meter (in weedy plots) were 4.7 and 3.3 times greater than the density of sweet corn plants in 1995 and 1996, respectively. Nonetheless, average leaf area of mature corn plants per square meter was ≈ 3 times greater than the average leaf area of weeds per square meter in 1996 (17,130 and 5,460 cm², respectively; the only year that leaf area was measured). *A. ostryaefolia* density was reduced in 1997 to $\approx 1/2$ the density of sweet corn plants (i.e., a 6- to 8-fold reduction compared with *A. ostryaefolia* densities of the 2 previous years). Even though *A. ostryaefolia* density exceeded the density of corn plants during 2 of the 3 yr, more leaf area was present on corn plants.

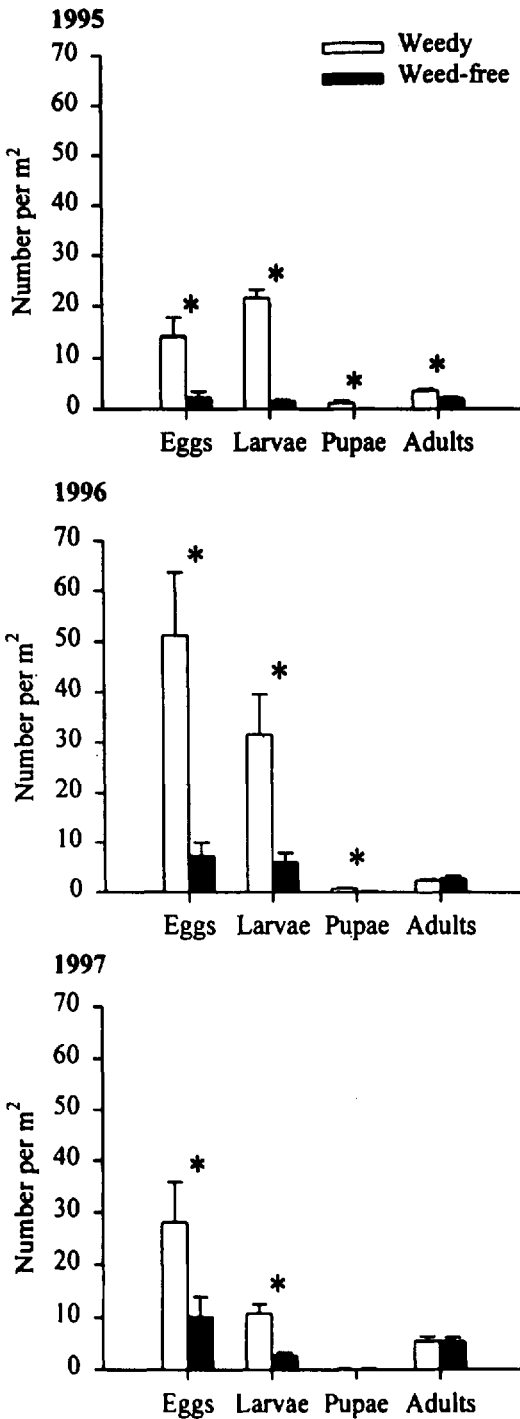


Fig. 1. Population density per square meter (\pm SE) of *C. maculata* in weedy versus weed-free sweet corn plots: 1995, 1996, and 1997. *, Significant difference between pairs of vertical bars ($P < 0.05$).

Within weedy plots in each year, a higher proportion of *C. maculata* eggs was found on *A. ostryaefolia* than on corn (Fig. 4). The mean numbers (\pm SE) of naturally oviposited *C. maculata* eggs per cluster on

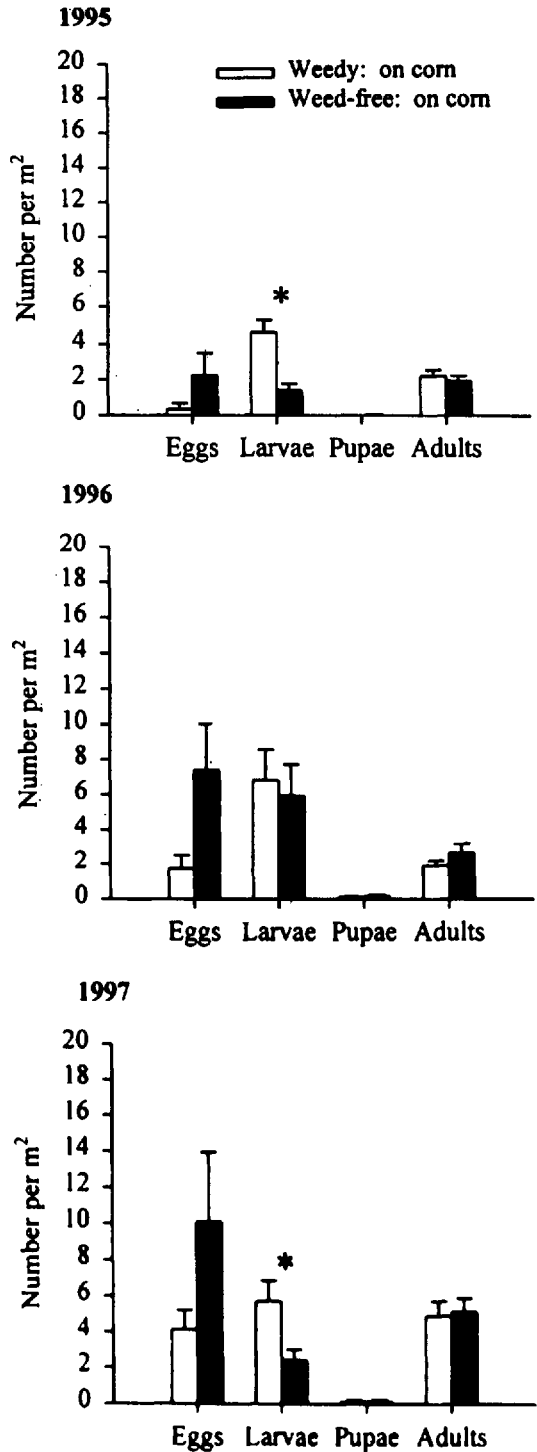


Fig. 2. Population density per square meter (\pm SE) of *C. maculata* on sweet corn only in weedy and weed-free plots: 1995, 1996, and 1997. *, Significant difference between pairs of vertical bars ($P < 0.05$).

corn plants and *A. ostryaefolia* plants in weedy plots were similar (11.6 ± 1.2 [$n = 25$] and 12.0 ± 0.3 [$n = 340$], respectively); the mean number of eggs per

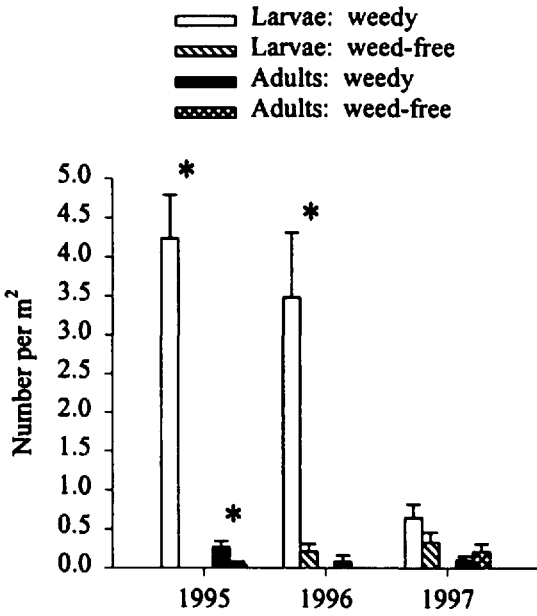


Fig. 3. Density per square meter (\pm SE) of *C. maculata* adults and larvae on the ground in weedy and weed-free plots in 1995, 1996, and 1997. *, Significant difference between pairs of vertical bars ($P < 0.05$).

cluster on corn in weed-free plots was 13.2 ± 1.1 ($n = 36$). In 1995 and 1996, more of the larval population occurred on *A. ostryaefolia* than on corn or on the ground, whereas more larvae were found on corn in 1997 (Fig. 4). In 1996 and 1997, we separately recorded newly hatched larvae (which remain clustered near the eggs from which they hatched for ≈ 1 d) and older larvae. In these years, 73.5 and 67.0%, respectively, of *C. maculata* larvae found on *A. ostryaefolia* were newly hatched, whereas virtually all larvae found on corn were older (Fig. 5). More pupae were found on *A. ostryaefolia* than on corn in 1995 and 1996, but more were found on corn in 1997 (Fig. 4). The proportion of adults on corn was higher than the proportion on *A. ostryaefolia* or on the ground during all 3 yr (Fig. 4).

Predation of *H. zea* Eggs. In 1995 and 1996, predation of *H. zea* egg groups was significantly higher when placed on corn in weedy plots than either on *A. ostryaefolia* in weedy plots or on corn in weed-free plots ($F = 76.52$; $df = 2, 30$; $P < 0.05$ and $F = 74.84$; $df = 2, 42$; $P < 0.05$, respectively) (Fig. 6a). Predation of *H. zea* eggs was not examined in 1997. Direct observations of predators feeding on *H. zea* eggs revealed that *C. maculata* adults and larvae were predominant, accounting for 56% of those events (Table 1). Adults and larvae were responsible for 19 and 81%, respectively, of observed predation events by *C. maculata*. *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) was frequently observed feeding on *H. zea* eggs, accounting for 19% of observed predation events. Adult *O. insidiosus* accounted for 19% of the cases involving this species, whereas nymphs accounted for 81%. In all treatments during 1995 and 1996, *C. maculata* was

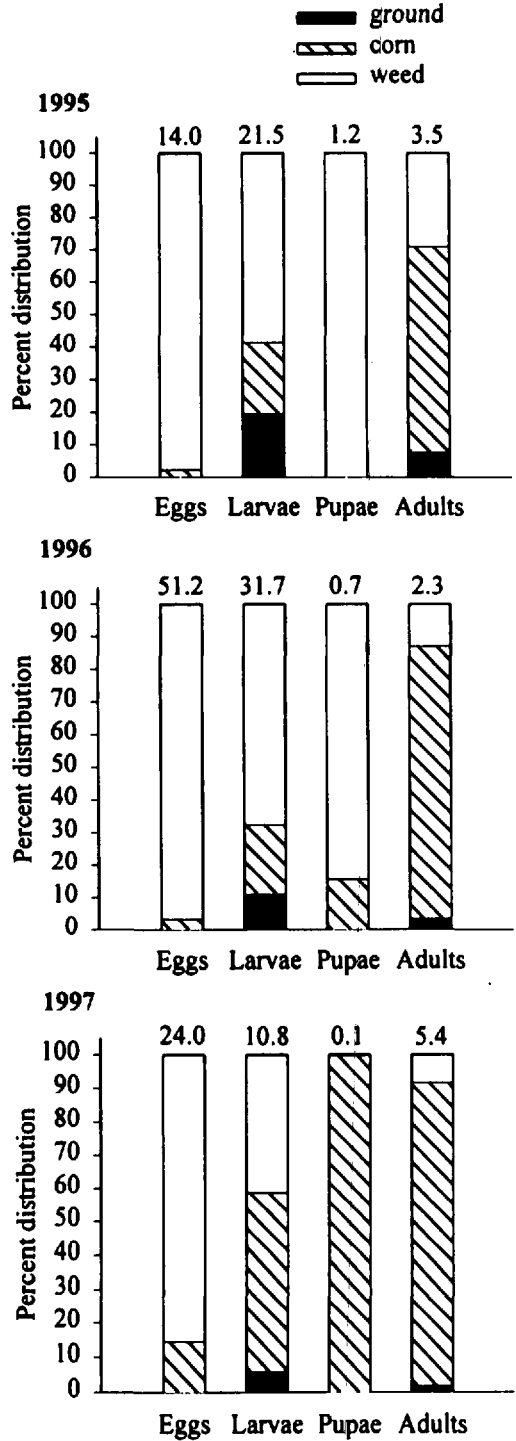


Fig. 4. Distribution of each *C. maculata* life stage on corn plants, on weeds, and on the ground in weedy plots during 1995, 1996, and 1997. Seasonal mean densities per square meter, for each life stage, are presented above each bar.

observed feeding on *H. zea* egg groups more than any other predator, except for *H. zea* eggs placed on corn plants in weed-free plots in 1995, where *O. insidiosus*

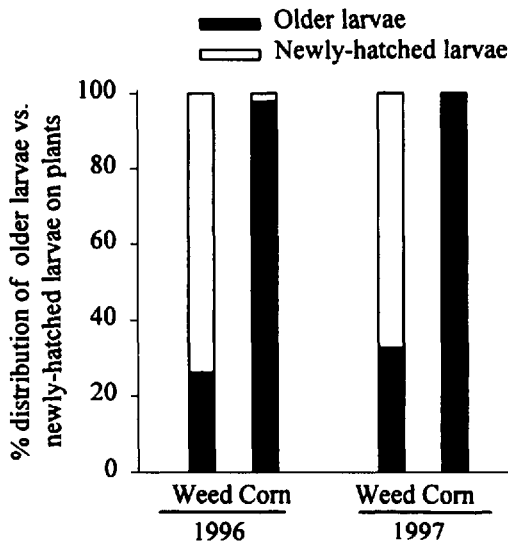


Fig. 5. Distribution of newly hatched (i.e., predispersal) *C. maculata* larvae and older *C. maculata* larvae on *A. ostryaefolia* and on corn in weedy plots during 1996 and 1997.

was the predator most frequently observed feeding on the eggs (Table 1). All other predators accounted for 25% of all observed predation events. Those predators included members of 5 insect orders and 2 arachnid orders (Table 1). Categories labeled "miscellaneous" in Table 1 consisted of Nitidulidae, other Coccinellidae, Chrysomelidae, and a few unidentified beetles, as well as Miridae, Berytidae, and unidentified hemipteran nymphs.

Observations of predators feeding on *H. zea* eggs revealed that *C. maculata* adults were most active during the day, but *C. maculata* larvae and other predators were active during the day and night (Fig 7). When *H. zea* eggs were placed on corn in weedy plots, more *C. maculata* larvae were observed feeding on the eggs than were *C. maculata* adults, and *C. maculata* larvae also were observed feeding more often than all other predators combined (including *O. insidiosus*) during all but 2 of the observation times (0300 and 0600 hours) (Fig. 7). Few predators were observed feeding on *H. zea* eggs on *A. ostryaefolia* in weedy plots (Fig. 7). On corn in weed-free plots, other predators combined (including *O. insidiosus*) always were observed feeding on *H. zea* eggs more frequently than were either *C. maculata* adults or larvae (Fig. 7).

Coleomegilla maculata Egg Cannibalism. Cannibalism of *C. maculata* egg clusters always was significantly lower when the egg clusters were placed on *A. ostryaefolia* plants than on corn plants in either type of plot during 1995 and 1996 ($F = 32.83$; $df = 2, 30$; $P < 0.05$, and $F = 37.39$; $df = 2, 42$; $P < 0.05$, respectively) (Fig. 6b). Egg clusters were not placed on *A. ostryaefolia* in 1997. Mean separation tests indicated that egg cannibalism on corn plants in weedy plots was significantly higher than on corn plants in weed-free plots in 1996, but not in 1995 (Fig. 6b). In addition, egg cannibalism on corn plants in weedy versus weed-free

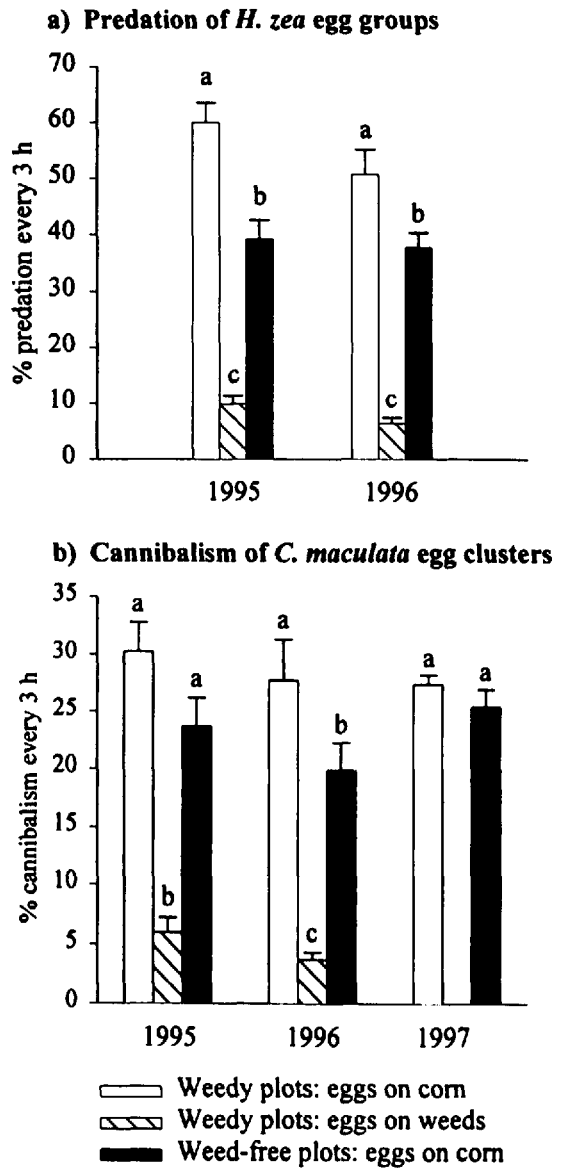


Fig. 6. Predation of *H. zea* egg groups (\pm SE) and cannibalism of *C. maculata* egg clusters (\pm SE) placed on corn plants and weeds in weedy plots and on corn in weed-free plots. Cannibalism of *C. maculata* eggs on *A. ostryaefolia* was not examined in 1997. Significant differences within groups of bars ($P < 0.05$) are indicated by different letters above individual bars.

plots was not different in 1997 ($F = 1.38$; $df = 1, 19$; $P > 0.05$).

Fewer species were observed feeding on *C. maculata* eggs than on *H. zea* eggs, and *C. maculata* adults and larvae were by far the predominant 'predators' observed (Table 2). Direct observations indicated that cannibalism accounted for 89% of all observed egg predation over the 3 yr. Larval and adult *C. maculata* were responsible for 87 and 13% of cannibalism events, respectively. *Harmonia axyridis* and an elaterid beetle (Coleoptera: Elateridae) accounted for 5 and 3% of

Table 1. Number of direct observations of predators feeding on *H. zea* eggs placed on sweet corn and on *A. ostryaefolia* in weedy plots and placed on sweet corn in weed-free plots

		Weedy: eggs on corn		Weedy: eggs on weed		Weed-free: eggs on corn	
		1995	1996	1995	1996	1995	1996
Coleoptera	<i>C. maculata</i> adults	12	13	2	3	8	6
	<i>C. maculata</i> larvae	33	94	1	2	5	55
	<i>H. axyridis</i> larvae	1	0	0	0	0	2
	Carabidae	4	11	0	0	2	6
	Elateridae	2	0	0	0	5	0
	miscellaneous	1	5	0	0	1	8
Hemiptera	<i>O. insidiosus</i> adults	0	5	0	2	1	7
	<i>O. insidiosus</i> nymphs	2	13	1	1	19	28
	Nabidae	0	1	0	0	2	0
	miscellaneous	1	2	2	3	1	5
Hymenoptera	Formicidae	2	4	0	1	3	8
Orthoptera	Tettigoniidae	1	0	0	0	0	0
	Gryllidae	0	1	0	0	0	0
Collembola		0	3	0	0	1	0
Opiliones	Phalangidae	0	1	0	0	1	0
Araneae	Clubionidae	2	4	0	0	4	5

observed predation events, respectively. All other predators accounted for the remaining 4% of observed predation events (Table 2).

Egg cannibalism by larval *C. maculata* was observed during the day and night, whereas egg cannibalism by adults was observed infrequently and occurred most often during the day (Fig. 8). On corn in weedy and weed-free plots, egg predation events by other predators also were infrequently observed and most occurred at night (Fig. 8). Only *C. maculata* adults and larvae were observed to feed on *C. maculata* eggs placed on *A. ostryaefolia* (Fig. 8).

Discussion

Coleomegilla maculata is abundant in corn fields in eastern North America (Foott 1973, Coll and Bottrell 1995, Hodek and Honěk 1996, Colunga-García et al. 1997). Pfannenstiel (1995), Hoffmann et al. (1997), and Cottrell and Yeargan (1998) have shown it to be the single-most abundant coccinellid species in sweet corn. In this study, we have shown that the population density of larval *C. maculata* on sweet corn can be even further increased by the presence of *A. ostryaefolia*, which apparently provides a refuge from cannibalism for *C. maculata* eggs.

Most *C. maculata* eggs in weedy plots were found on *A. ostryaefolia*. The total leaf area of corn was ≈ 3 times greater than total leaf area of *A. ostryaefolia*, and even if one considered only the leaf area of the lower $\frac{1}{3}$ of the corn plants (where most *C. maculata* eggs on sweet corn are oviposited) that area would still be comparable with the total leaf area of *A. ostryaefolia*. In 1997, *A. ostryaefolia* density was reduced to $\approx \frac{1}{6}$ of that in 1996, which resulted in an even greater difference in leaf area between the plants (i.e., corn \gg *A. ostryaefolia*). Again, however, most *C. maculata* eggs were found on *A. ostryaefolia*.

Overall, *C. maculata* accounted for $\approx 91\%$ of adult Coccinellidae sampled in this study. Even though the recently established *H. axyridis* was 1st documented on field crops (i.e., sweet corn and tobacco) in Ken-

tucky during 1993 (Pfannenstiel 1995), it was the 2nd most abundant coccinellid in sweet corn throughout our study. However, *H. axyridis* only accounted for $\approx 7\%$ of adult Coccinellidae. *Coccinella septempunctata* (Coleoptera: Coccinellidae) accounted for 1% and *Cycloneda munda* (Coleoptera: Coccinellidae) accounted for $< 1\%$ of adult Coccinellidae. In fact, of the 4 coccinellid species found during this study, only *C. maculata* and *H. axyridis* larvae were found in sweet corn during this study, and the latter accounted for $< 6\%$. With *C. maculata* comprising the vast majority of both adult and larval Coccinellidae in sweet corn, it is likely that eggs of other coccinellid species present during our study would have been negligible and most would have been *H. axyridis* eggs.

Alternate host plants in crop systems can provide food resources and refuge for natural enemies (Altieri and Whitcomb 1979). In some cases, the alternate plant(s) may have a negative impact on the crop by decreasing density of a specific natural enemy and thus reduce pest mortality caused by that natural enemy (Andow and Risch 1985). In our study, we found consistently more *C. maculata* eggs on corn plants in weed-free plots than on corn plants in weedy plots during each year, suggesting that, within weedy plots, *C. maculata* moved to *A. ostryaefolia* to oviposit. However, oviposition on *A. ostryaefolia* did not reduce the density of predatory *C. maculata* larvae on corn plants in weedy plots. In fact, larval densities were higher on corn plants in weedy plots than on corn plants in weed-free plots and significantly so in 1995 and 1997; total densities of *C. maculata* larvae were higher in weedy plots every year. Larvae on corn plants in weedy plots apparently moved to the corn plants from *A. ostryaefolia*. Evidence for movement between plant species is provided, in part, by the presence of larvae on the ground. In addition, during 1996 and 1997, $\approx 70\%$ of larvae found on *A. ostryaefolia* were newly hatched and not yet dispersed from oviposition sites, whereas 99% of larvae found on corn were older larvae (1st through 4th instars that had dispersed from oviposition sites).

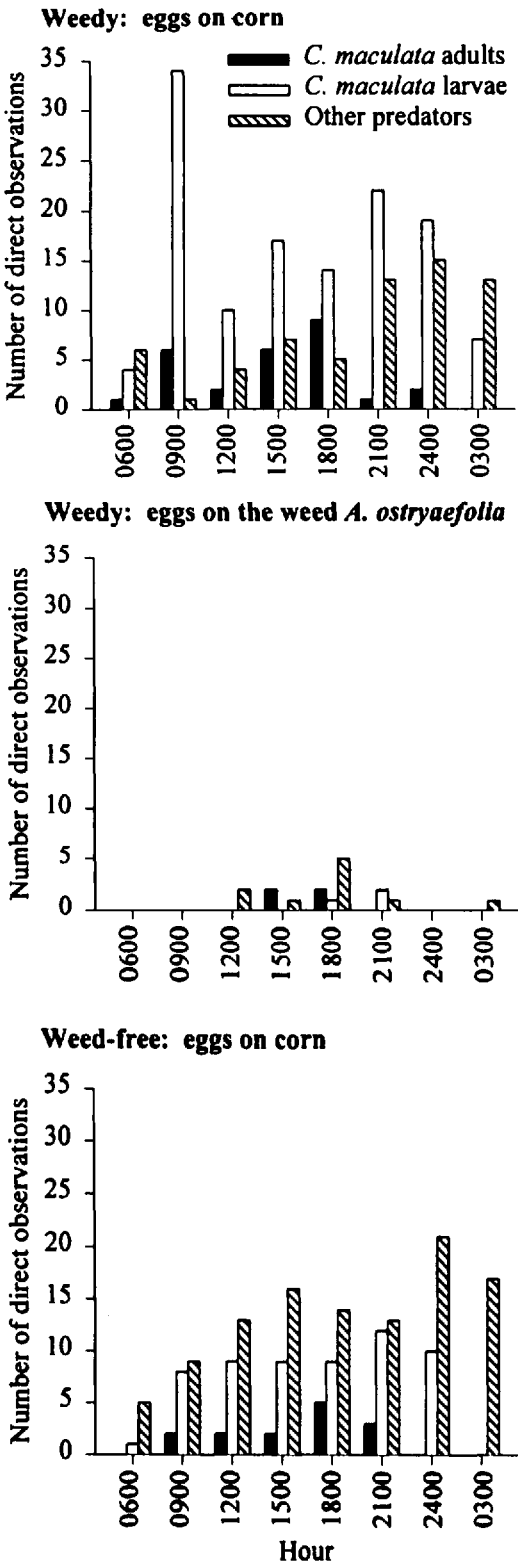


Fig. 7. Diel activity of *C. maculata* adults, larvae, and other predators feeding on *H. zea* eggs in weedy plots on corn, in weedy plots on *A. ostryaefolia*, and in weed-free plots on corn. Combined data from 1995 and 1996.

Pupal densities always were relatively low in both weedy and weed-free plots during each year. The highest seasonal average of pupae (per square meter) found in any year was 1.2 ± 0.4 and this was in weedy plots during 1995. When *A. ostryaefolia* density was higher than corn plant density, most pupae were found on *A. ostryaefolia*, but when *A. ostryaefolia* density was lower than corn plant density, all pupae were found on corn. When *A. ostryaefolia* densities were high, more larvae may have pupated on *A. ostryaefolia* or pupation may have occurred randomly on either plant species and those pupae on corn suffered higher predation and cannibalism.

Adult *C. maculata* densities apparently were not affected by the presence of *A. ostryaefolia* in sweet corn plots except in 1995, when significantly more adults were found in weedy plots. Nonetheless, *C. maculata* adult densities on corn plants in weedy plots and on corn plants in weed-free plots were not different in any year. Coll and Bottrell (1995) found that *C. maculata* densities (stages not reported) were always higher on corn than on beans (*Phaseolus vulgaris* L.) in monocultures of each crop, and *C. maculata* densities also were higher on corn than on bean in corn-bean dicultures. Additionally, Wetzler and Risch (1984) found higher *C. maculata* densities on corn in monocultures than on corn in corn-bean-squash polycultures. They commented that, given time, more *C. maculata* would accumulate in corn monocultures (a more attractive habitat) than in corn-bean-squash polycultures (a more repellent habitat). However, in our study, it appears that *C. maculata* adults were not attracted to, or arrested in, weed-free plots more than weedy plots, but when *A. ostryaefolia* was present, these plants served as relatively safe (from egg cannibalism) oviposition sites and adults foraged elsewhere (i.e., on nearby corn plants). Obrycki and Tauber (1985) found more coccinellid eggs on potato clones with high densities of glandular trichomes than on clones with low densities of trichomes. Those authors suggested that coccinellids might preferentially oviposit on clones with high densities of glandular trichomes but not remain on them or that eggs on potato clones without glandular trichomes might suffer higher mortality from predation, as did *C. maculata* eggs on corn plants in our study.

Predation of *H. zea* eggs on corn was significantly increased by the presence of *A. ostryaefolia* in weedy plots compared with weed-free plots. Risch et al. (1982) found that plant density, not diversity, affected predation on European corn borer egg masses (Lepidoptera: Pyralidae) by field-collected adult *C. maculata* when cage tests were done in a greenhouse. Those authors showed that predation in low density beans was significantly higher than predation in either high density beans or high density beans and squash. Our weedy plots, with higher overall plant densities, not only had higher densities of *C. maculata* per square meter, but also, higher rates of *H. zea* egg predation on corn.

Direct observations of predators feeding on *H. zea* eggs in weedy plots revealed that *C. maculata* larvae

Table 2. Number of direct observations of predators feeding on *C. maculata* eggs placed on sweet corn and on *A. ostryaefolia* in weedy plots and placed on sweet corn in weed-free plots

		Weedy: eggs on corn			Weedy: eggs on weed		Weed-free: eggs on corn		
		1995	1996	1997	1995	1996	1995	1996	1997
Coleoptera	<i>C. maculata</i> adults	3	2	12	1	6	0	4	6
	<i>C. maculata</i> larvae	30	70	60	3	6	5	49	13
	<i>H. axyridis</i>	0	1	8	0	0	0	2	5
	Elateridae	2	0	2	0	0	4	0	0
	Cantharidae	0	0	1	0	0	0	1	0
Hemiptera	<i>Podisus maculiventris</i>	0	0	0	0	0	0	0	1
Hymenoptera	Formicidae	0	0	0	0	0	2	0	0
Orthoptera	Gryllidae	0	0	0	0	0	2	0	0
Opiliones	Phalangidae	1	0	2	0	0	0	0	1

were the predominant predators, and they were observed to feed on *H. zea* eggs more frequently than all other predators combined, including *C. maculata* adults. In weed-free plots, without an ovipositional refuge, other predators (combined) were observed feeding on *H. zea* eggs more often than were *C. maculata* adults and larvae combined. Direct observations of predation on *H. zea* eggs by *C. maculata* showed that predation in sweet corn by *C. maculata* adults occurs diurnally whereas larvae feed both diurnally and nocturnally, as reported by Cottrell and Yeargan (1998). Nocturnal foraging by *C. maculata* larvae had not been reported before Cottrell and Yeargan (1998) and this study, but nocturnal predation by larvae is prevalent and may have been underestimated in past studies that focused only on diurnal events.

Growth of *A. ostryaefolia* with sweet corn resulted in an overall trend of more *C. maculata* egg cannibalism on corn plants in weedy plots than in weed-free plots, and in fact, the difference between plots was significant in 1996. However, *C. maculata* egg cannibalism on corn plants (with an ovipositional refuge) is less important in weedy plots than in weed-free plots, where all *C. maculata* eggs are oviposited on corn and, thus, subjected to much higher rates of cannibalism. Fewer predatory species were observed feeding on *C. maculata* eggs compared with *H. zea* eggs under comparable conditions. Direct observations of predation on *C. maculata* eggs revealed that most predation events (89%) were actually instances of egg cannibalism by adults and larvae. Combined data from 1995, 1996, and 1997 revealed that *H. axyridis* adults and larvae, combined, fed on *C. maculata* eggs about as often as all combined noncoccinellid predators. Some of the predators, most notably *O. insidiosus* and the clubionid spider *Clubiona abbotii* Koch, that fed on *H. zea* eggs were never observed feeding on *C. maculata* eggs.

Rates of predation on *H. zea* eggs and cannibalism on *C. maculata* eggs were both significantly lower on *A. ostryaefolia* than on corn in either type of plot during both years in which predation on *H. zea* eggs was studied. The low rate of predation on *H. zea* eggs on *A. ostryaefolia* compared with the rate of predation on corn may have been partially the result of the

dissimilar structures of the 2 plant species. Kareiva and Perry (1989) noted that extended straight-line searches by predators, as would be possible on corn plants because of their simple structure, enable predators to cover more surface area. Likewise, *C. maculata* eggs suffered significantly less cannibalism when placed on *A. ostryaefolia* compared with placement on corn. Thus, *A. ostryaefolia* not only served as an alternate oviposition site in weedy sweet corn plots, it decreased the risk of egg cannibalism and thereby enhanced the chance for *C. maculata* eggs to survive to hatch.

Even though *C. maculata* colonizes corn early in the season and their populations are generally higher in corn than in surrounding crops and habitats (Benton and Crump 1981), we showed that by providing an alternate oviposition site, densities of the predaceous larvae were markedly increased on sweet corn and predation of a pest species on this crop also increased. It seems likely that other weed species or cultivated plants would have similar effects on *C. maculata* populations in corn. Although weed species such as *A. ostryaefolia* would not be appropriate companion plants for a sweet corn production system, certain cultivated plants with desirable characteristics (e.g., nitrogen fixation) might have positive effects on *C. maculata* populations by acting as refuges from egg cannibalism. The selection of plant species to be used in intercropping or companion cropping systems should include consideration of how these plants may impact specific natural enemy populations and predation by those natural enemies.

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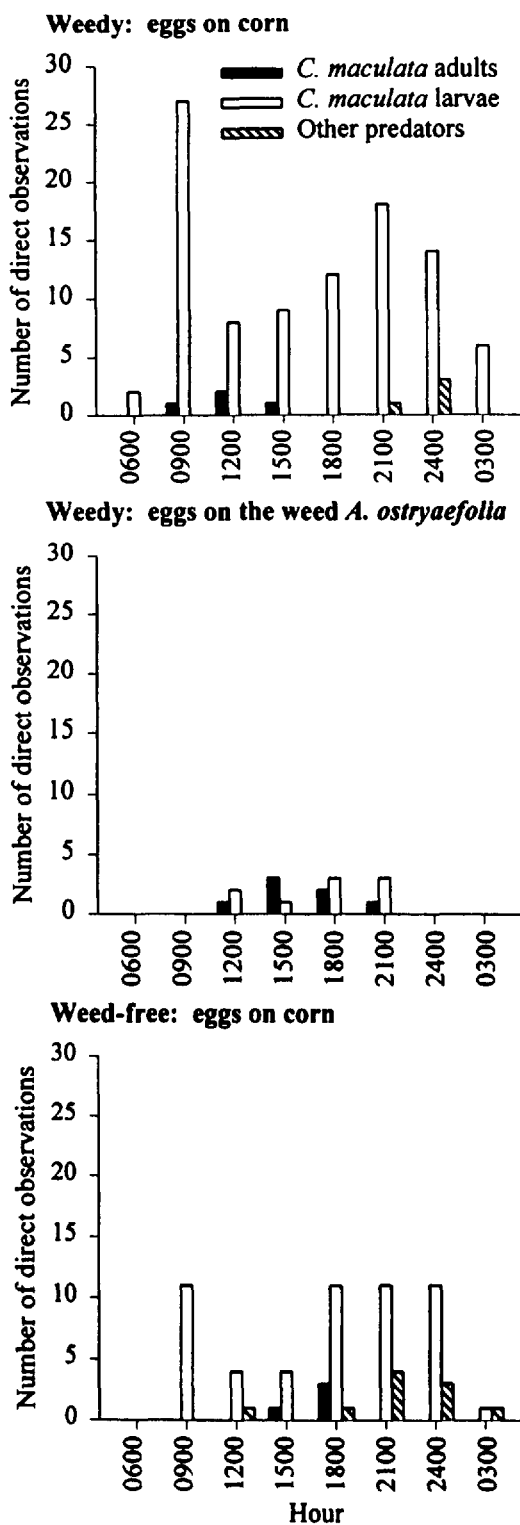


Fig. 8. Diel activity of *C. maculata* adults, larvae, and other predators feeding on *C. maculata* eggs: in weedy plots on corn, in weedy plots on *A. ostryaefolia*, and in weed-free plots on corn. Combined data from 1995 and 1996.

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