

Mortality of Coccinellid (Coleoptera: Coccinellidae) Larvae and Pupae When Prey Become Scarce

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ABSTRACT Coccinellid larvae are known to prey upon conspecific and heterospecific eggs, larvae, prepupae, and pupae. This behavior may depend on both the aggregation and intensive search of potential cannibals and predators near aphid colonies and the disappearance of aphids before coccinellid larvae have completed their development. We examined how coccinellid density and prey availability influence cannibalism and interspecific predation of larvae and pupae of 4 species of coccinellids. We determined whether coccinellid mortality and dispersal were density-dependent when prey become scarce, and estimated the leaving rates of *Coleomegilla maculata* (DeGeer), *Adalia bipunctata* (L.), and *Hippodamia convergens* (Guerin) larvae from plants with aphids and plants without aphids. Our results show that larval and pupal cannibalism and interspecific predation occur more frequently when aphid populations crash, but we found no evidence of coccinellid density-dependent mortality or density-dependent larval dispersal among species. However, *A. bipunctata* and *H. convergens* were significantly more aggressive and more likely to leave a plant without aphids than was *C. maculata*. These results suggest that the decision to stay on a plant is not strongly aphid- or pollen-mediated for *C. maculata*, but the decision to stay or leave does appear to be aphid-mediated for *H. convergens* and to some extent *A. bipunctata*. Whether a coccinellid larva stays or leaves and its tendency to cannibalize can affect larval and pupal survival and the population dynamics of each species.

KEY WORDS coccinellids, cannibalism, interspecific and intraguild predation, dispersal, prey scarcity

LADYBIRD BEETLE LARVAE are frequently observed to prey on conspecific and heterospecific eggs, larvae, prepupae, and pupae. Older instars are known to kill younger instars (Sengonca and Frings 1985, Agarwala and Dixon 1992), and late instars are known to prey on prepupae and pupae (Takahasi 1989, Hodek and Honěk 1996). Cannibalism and interspecific predation are two of the most important mortality factors in coccinellid populations (Wright and Laing 1982; Osawa 1989, 1992; Schellhorn 1998). A recent field study showed that coccinellid egg cannibalism and interspecific predation kill 13–45% of the eggs of *Coleomegilla maculata* (DeGeer) in 48 h (depending on their distance from aphid aggregations) when prey are abundant, and 83% of the eggs in 24 h when prey are scarce (Schellhorn 1998, Schellhorn and Andow 1999). Pupae and molting larvae may experience 14–35% mortality from cannibalism and interspecific predation (Osawa 1992). Numerous studies have examined coccinellid egg predation by coccinellid adults and larvae (Banks 1955, Pienkowski 1965, Mills 1982, Wright and Laing 1982, Osawa 1993, Cottrell and Yeargan 1998) or coccinellid egg and larval predation by

other aphidophagous predators, commonly called intraguild predation (Polis et al. 1989, Lucas et al. 1998, Phoofolo and Obrycki 1998). However, few studies experimentally investigate the interaction among coccinellid larvae and pupae in relation to prey availability in the field.

Cannibalism and interspecific predation of coccinellids larvae and pupae have been attributed to both the disappearance of prey before larvae complete their development (Bode 1980, Takahasi 1989), and to the presence of prey when larvae aggregate (Osawa 1992). Takahasi (1989) documented that older coccinellid larvae of *Harmonia axyridis* (Pallas) preyed on pupae and prepupae of *Coccinella septempunctata* (L.) because of the delayed development of the latter species, and because aphids were scarce. Osawa (1992) suggested that pupal cannibalism of *H. axyridis* was high in the presence of aphids. He noted that *H. axyridis* larvae searched intensively near large aggregations of aphids and subsequently encountered and preyed upon pupae. Aggregation of *H. axyridis* and *Adalia bipunctata* (L.) larvae to large aphid colonies also was shown by Kawai (1976) and Banks (1956), respectively. However, prey populations often are diminished before all larvae complete their development (Schellhorn 1998). The propensity of larvae to aggregate to prey colonies and a diminishing prey population may make the molting larvae and pupae

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susceptible to cannibalism and predation. Yet no study has examined the relationship between coccinellid larval density and prey scarcity and the subsequent larval and pupal mortality from cannibalism and interspecific predation.

In this study, we examined how coccinellid density and prey availability influence cannibalism and interspecific predation of larvae and pupae of 4 species of coccinellids. Our first objective was to describe how cannibalism and interspecific predation rates change with prey availability, and determine larval tendencies toward cannibalism and predation. We predicted that as prey become scarce, cannibalism and predation rates would increase (Dong and Polis 1992, Lucas et al. 1998); and that each species would have similar tendencies toward cannibalism and predation (Hodek and Honěk 1996). The second objective was to determine how coccinellid density affects mortality and dispersal rates. We predicted that both cannibalism and dispersal rates would be higher at high coccinellid densities than at low coccinellid densities because the increase in coccinellid densities when prey is scarce would increase the rate of density-dependent behaviors (Dong and Polis 1992). Based on results from objective number two that showed that some species remained on plants without aphids while others dispersed, last objective was to determine the importance of aphids and corn pollen for coccinellid dispersal. We predicted that in the absence of both aphids and corn pollen, each species would leave plants at a similar rate. We conclude with a discussion on the costs for larvae of leaving versus staying on a plant when prey become scarce.

Natural History. The study was conducted in maize fields in southeastern Minnesota. Four species of coccinellids—*Coleomegilla maculata* (DeGeer), *Hippodamia tredecimpunctata* (Say), *Hippodamia convergens* (Guerin), and *Adalia bipunctata* (L.)—are consistently present and all use aphids as a main food source. The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), is the dominant aphid in maize, and forms large aggregations in the whorl before and during the initial period of tassel emergence. *Rhopalosiphum padi* (L.) and *Sitobion avenae* (F.) also are present in small aggregations scattered on the leaves and stalk of the plant.

Coleomegilla maculata, *H. tredecimpunctata*, and *H. convergens* can be found in wetlands, meadows, small grains, and alfalfa in early spring, and in maize from late spring until fall. They feed on aphids and lepidopteran eggs and larvae (Conrad 1959, Andow 1990). *C. maculata* also feeds on maize pollen (Forbes 1883) and perhaps maize rust spores, and is the most polyphagous of the 3 species (Hodek and Honěk 1996). *A. bipunctata* is found on shrubs, trees, and weeds from early spring until midsummer, and on maize from midsummer to early fall. It is primarily aphidophagous (Hodek 1973), but may also feed on pollen (Hemp-tinne and Desprets 1986).

The co-occurrence of all 4 coccinellid species in maize starts during peak aphid abundance (Wright and Laing 1980, Schellhorn 1998). Before this time, *C.*

maculata is rare, and *Hippodamia* spp. and *A. bipunctata* are absent (Schellhorn 1998). Many of the coccinellid offspring mature before the aphid populations crash (N.A.S., unpublished data). However, many late instars are still foraging for food, and pupae are abundant when aphid populations crash. This condition of starving, late instars larvae, and numerous prepupae and pupae may result in high larval and pupal cannibalism and interspecific predation.

Materials and Methods

Aphid and Coccinellid Population Densities. We conducted a series of observations and experiments during the summers of 1994, 1996, and 1997 on the St. Paul campus of the University of Minnesota, Ramsey County, MN. In 1994 and 1996, we conducted experiments to create conditions of varying aphid densities. By using a variety of maize that is susceptible to aphids ('Green Giant', Code 40) and a variety of maize that is resistant to aphids ('Green Giant', Code 39), we established high aphid density stands, and low aphid density stands. The 2 treatments were planted in plots (10 by 10 m), and were replicated 4 times in randomized complete blocks. In 1994, the resistant maize was planted 2 wk after the susceptible maize to ensure low aphid densities on the resistant maize. The seeds were planted in a plowed, harrowed, and herbicide (Lasso)-treated field on 21 May and 4 June. At the time of tasselling (17 July), corn development differed by 5 d between the 1st and 2nd plantings. In 1996, both treatments were planted at the same time. At weekly intervals throughout the entire growing season, we visually inspected 64 randomly selected plants per treatment (16 plants per replicate) and quantified aphid and coccinellid densities by species and developmental stage (including eggs), and cannibalism or predation events. During our visual sampling, we assessed cannibalism and predation events in the field by either directly observing the event or by examining the partial remains of cadavers. Most of this paper considers coccinellid species interactions after aphid populations have crashed.

We used Lloyd's index of mean crowding ($\text{mean} + [s^2/\text{mean} - 1]$) to estimate the degree of crowding experienced by an individual conspecific larva at peak predator densities, thus the potential conditions for cannibalism and predation (Lloyd 1967, Southwood 1978). To determine conspecific density-dependent pupal mortality, we examined the relationship between mean pupal density and mean larval density per plant on plants with conspecific pupae. The relationship between Lloyd's mean crowding index and mean density detects crowding or repulsion, and the ways that organisms use their habitat (Iwao 1968).

Cannibalism and Predation in the Laboratory. We conducted 2 laboratory studies on cannibalism and predation. For logistical reasons, we used only 3 of the 4 species (*C. maculata*, *A. bipunctata*, and *H. convergens*) in our laboratory and field experimental manipulations. In the 1st experiment, we used starved larvae to determine tendencies toward cannibalism and pre-

dition. Field-collected larvae were brought to the laboratory 30 h before the test and were fed *R. maidis* aphids ad libitum and given water. Next, the larvae were starved in petri dishes containing only moistened filter paper for 16 h before the experiments. Starving the larvae mimics their condition in the field when aphid populations have crashed. After starvation, 12 young 4th instars of a single species (cannibalism) or 6 individuals of 1 species with 6 individuals of another species (interspecific predation) were placed in a clear plastic dish (22 by 12 cm) with moistened filter paper. Mortality was monitored daily, and attacks every 2 or 4 h. There were 4 replications for each species; thus a total of 96 larvae of each species was tested.

In the 2nd experiment, we assessed whether predation on 2nd instars by 4th instars was independent of the hunger level of 4th instars. Six young 4th instars (either fed or starved) were confined with 6 young 2nd instars and mortality was recorded 1 and 3 h after beginning the test. The hunger levels of starved 4th instars were standardized as described above. However, fed 4th instars were allowed to feed ad libitum until 1 h before the test. For the starved condition, only *C. maculata* and *H. convergens* were tested because we had insufficient numbers of *A. bipunctata*, whereas all species were tested for the fed condition. There were 6 replicates of each species; thus, in total, 72 late-instar *C. maculata* and *H. convergens* and 36 *A. bipunctata* larvae were tested. All 2nd instars were *C. maculata*; thus, in total, 180 were tested.

Density-Dependent Dispersal and Mortality from Cannibalism. To determine if larval and pupal mortality from cannibalism and interspecific predation are density-dependent when prey are scarce, we conducted field experiments that measured coccinellid mortality rates at high and low coccinellid densities, and observed their dispersal and behavior. We placed a cage (2 by 2 by 2 m) over a single postanthesis plant, removed all predators and unwanted insects found, and surrounded the plant with a 120-cm ground barrier coated in Teflon. In each cage we pinned 2 coccinellid pupae (the average pupal density on a plant; Schellhorn 1998), 1 at the top (leaf 13, \approx 150 cm from the ground), and 1 at the bottom (leaf 6, \approx 35 cm from the ground). The introduced pinned pupae were collected in the field as late instars that were placed in laboratory containers lined with paper. Once larvae pupated, the paper with the attached pupae was cut out and the attached pupa was pinned to the corn stalk. In addition to the 2 pinned pupae, we then introduced 8 (high density) or 2 (low density) young 4th instars of 1 of the 3 ladybird species. Each cage was replicated either 6 (*C. maculata* and *H. convergens*) or 8 (*A. bipunctata*) times at each coccinellid density; thus a total of 40 cages. The larvae that were introduced into the cages were field-collected as 3rd instars and reared on 10–15 *R. maidis* aphids per day in the laboratory until young 4th instar (\approx 24–36 h after molting from 3rd instar). Twenty-four hours before being introduced into the cages, they were each fed 5 aphids and given water. In the field cages, the larvae were placed centrally on each maize plant. We ob-

served larval behavior and monitored pupal and larval mortality at 24- and 48-h intervals. After 48 h, the plants were dissected to locate any hiding larvae and the remaining larvae and pupae were recorded.

Leaving Rates. A field experiment was conducted to document coccinellid leaving rates when prey were abundant and scarce. Because results from the experiments mentioned above showed that some species remained on plants without aphids while others dispersed, we wanted to determine the importance of aphids and pollen for coccinellid dispersal. We established 2 treatments, 1 with aphids and 1 with no aphids, on young, 10-leaf-stage corn plants. Young corn plants in the preanthesis stage were chosen because they do not have any corn pollen on them; a food source for *C. maculata*. Plants in the aphid treatment were inoculated with 50 *R. maidis* aphids in the whorl. Plants in the no-aphid treatment were screened for aphids or other possible prey items and all found were removed. We then placed a single larva on a single plant and monitored leaving rates at 5-min intervals for 1 h and 40 min, and at 4, 6, and 24 h periods. All of the introduced larvae were handled in the same manner as above. The aphid treatment was replicated 24 times (8 replicates per species), and the no-aphid treatment was replicated 48 times (14 replicates for *C. maculata* and *A. bipunctata*, and 24 replicates for *H. convergens*).

Statistical Analysis. The relationship of mean crowding to mean density for a species was expressed over a range of densities by linear regression (Lloyd 1967). For each species, the predictor variable (mean number of larvae per plant) was calculated for each replicate and plotted against the response variable (mean crowding). An analysis of covariance (ANCOVA) was used to test the response variable for heterogeneity among species. Mean crowding was adjusted for species differences in density, also known as the covariate. The ANCOVA simulated the results that would have been obtained had a constant value been used for larval or pupal densities (Sokal and Rohlf 1981). A significant species effect indicated heterogeneous intercepts, and a significant species by mean density interaction indicated that differences in the slope among species vary with mean density. *G*-tests of independence was performed on data from the laboratory experiments on larval cannibalism and interspecific predation, and from the field experiments on the location on the plant that larvae were recovered. We tested whether the frequency of cannibalism or predation was independent of the species encountered, and whether the location on the plant was independent of the species. Log-linear contingency table analysis was performed on data from the field experiments on larval and pupal density-dependent mortality and larval density-dependent dispersal. The log-linear analysis is appropriate to test interactions among categorical variables (Sokal and Rohlf 1981). We tested the interaction among coccinellid density, species, and survival or coccinellid density, species and dispersal. A G^2 statistic to test the goodness-of-fit was computed for the log-linear analysis. A one-way analysis of variance was used to test for differences in

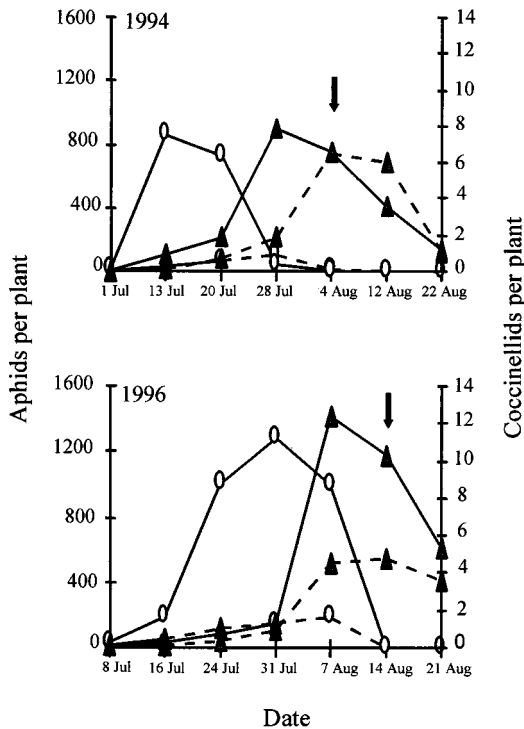


Fig. 1. Mean numbers of aphids (open circle) and coccinellids (adults and larvae) (black triangle) in high (solid line) and low (dotted line) aphid density maize in 1994 and 1996. Arrows indicate first observations of cannibalism and interspecific predation when aphid populations are diminished and coccinellid populations are at peak density.

leaving rates among species on plants with aphids or no aphids. When the test statistic was significant, a Tukey's honestly significant difference (HSD) test was used to identify the differences among the 3 species. The description of the statistical model and statistical test results are presented elsewhere to show that the aphid treatments were quantitatively distinct before the crash in aphid populations (Schellhorn 1998).

Results

Aphid and Coccinellid Population Densities. Cannibalism and interspecific predation events occurred after aphid populations crashed in both 1994 and 1996 (Fig. 1) (Table 1). There was not a single observation of larval or pupal cannibalism or predation (either as victims or perpetrators) while aphids were still present. Previous aphid densities did not influence cannibalism and predation events (Table 1). In 1994, the victims were more often pupae than larvae, but in 1996 the reverse was true (Table 1). The cannibalism and predation events represented a very small percentage of the total population density of each coccinellid species ($\approx 0-5.0\%$, depending on species, date, and previous aphid density). The total number of events recorded was highest for *C. maculata* ($n = 49$) compared with all other species combined ($n = 28$)

Table 1. Percentage of plants sampled with a cannibalism or predation event

		% of plants		
		1994		
Aphid density	Date	28 July	4 August	12 August
High		0	23 (7, 8)	8 (1, 4)
Low		0	22 (6, 8)	16 (3, 7)
		1996		
Aphid density	Date	7 August	14 August	21 August
High		0	27 (13, 4)	11 (7, 0)
Low		0	14 (9, 0)	0

Numbers in parentheses are numbers of larvae and pupae, respectively, that were victims in high and low aphid density maize stands on 3 dates; 64 plants were sampled on each date for each aphid density.

for both years at each aphid density. However, *C. maculata* also was the most abundant species, *Hippodamia* spp. were intermediate, and *A. bipunctata* was least abundant at each aphid density and throughout the season for both years (Fig. 2; Schellhorn 1998).

In 1996, larval crowding was observed (Fig. 2). In the treatments that previously had either high (Fig. 2c) or low (Fig. 2d) aphid densities, as larval density increased, individual larvae became more crowded by conspecifics. In 1994, a similar result was observed for *C. maculata* and *H. tredecimpunctata* at high aphid densities (Fig. 2a), but the result was not consistent for the other species or at low aphid densities (Fig. 2b). The slope of mean density and crowding was significantly different among species in 1994 at high aphid densities, and in 1996 at low aphid densities (Table 2). For *H. convergens* in the high-aphid treatment in 1994, small increases in the larval mean density resulted in greater crowding of conspecifics compared with the other species (Table 2). This indicated that in a treatment that previously had high aphid densities, individuals of *H. convergens* aggregated to conspecifics more than other species aggregated to conspecifics (Fig. 2a). In 1996 in the low aphid treatment, a similar pattern was observed for *A. bipunctata* (Table 2; Fig. 2d).

The crowding index for *C. maculata* pupae showed that the mean number of conspecific larvae on a plant with conspecific pupae was inversely density-dependent (Fig. 3a and b). As *C. maculata* pupal density increased, fewer *C. maculata* larvae were on a plant with a pupa (Fig. 3a and b). This indicates that either cannibalism rates were higher on plants with high densities of conspecifics than on plants with low densities of conspecifics, or a slight difference in coccinellid development rates among plots. However, neither of these hypotheses has been pursued. There was no consistent relationship of conspecific larval crowding and pupal density for the other species.

Cannibalism and Predation in the Laboratory. Although results from the field showed that *C. maculata* was the most frequently observed victim of cannibalism or interspecific predation, in laboratory experiments, *C. maculata* had a significantly lower daily cannibalism rate (0.08) than either *A. bipunctata* (0.40) or *H. convergens* (0.27) ($n = 144, G = 14.07, df =$

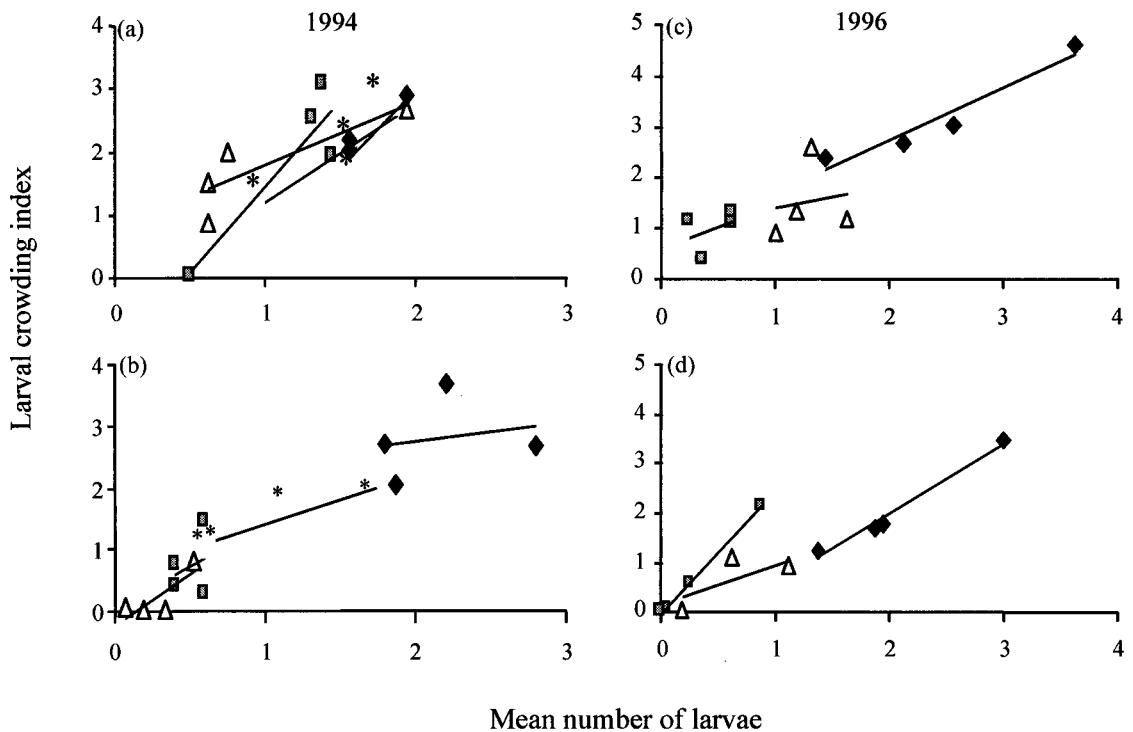


Fig. 2. Relationship between the larval crowding index (mean + [$s^2/\text{mean} - 1$]) and mean larval density per plant for *C. maculata* (black diamonds), *H. tredecimpunctata* (stars), *A. bipunctata* (open triangles) and *H. convergens* (gray boxes) in 1994 and 1996, respectively, in high (a, c) and low (b, d) aphid densities. *H. tredecimpunctata* was absent in 1996. Each point for a symbol is the value of a replicate. In 1994 the values are from 4 August. In 1996 the values are from 14 August.

2, $P = 0.0008$). Furthermore, mortality rates caused by cannibalism or interspecific predation were not significantly different for *C. maculata* ($G = 2.754$, $df = 2$, $P = 0.252$) or *H. convergens* ($G = 2.00$, $df = 2$, $P = 0.367$) (Table 3). However, *A. bipunctata* experienced significantly higher mortality when combined with *H. convergens* than when combined with *C. maculata* or conspecifics ($G = 7.328$, $df = 2$, $P = 0.025$) (Table 3). We observed that *A. bipunctata* was attacked by *H. convergens*, but when combined with *C. maculata*, most attacks on *A. bipunctata* were by conspecifics.

Coleomegilla maculata 2nd instars that encountered fed 4th instars were at least twice as likely to escape being eaten than when they encountered starved 4th instars of *C. maculata* ($G = 8.24$, $df = 1$, $P = 0.004$) or *H. convergens* ($G = 120.73$, $df = 2$, $P < 0.0001$; Table 4). However, there was no difference in attack rate among species that were fed ($G = 0.576$, $df = 2$, $P = 0.749$) or starved ($G = 0.736$, $df = 1$, $P = 0.390$). Small larvae would therefore have a chance of escaping predation if the predator had recently fed.

Density-Dependent Dispersal and Mortality from Cannibalism. In the density-dependent field experiments, cannibalism was rarely observed, and there was no significant interaction among coccinellid density, species, and mortality ($G^2 = 0.233$, $df = 2$, $P = 0.1022$) (Table 5). However, the nonsignificant trend was similar to the laboratory results where *A. bipunctata* had

Table 2. ANCOVA of relationship between mean larval crowding (Y) and mean larval density (X) among coccinellid species

Source of variation	MS	F	df	P
1994 High Aphid Density				
Species	0.4424	1.60	3	0.2638
Density \times species	1.7917	6.49	4	0.0120
Error	0.2761	—	8	—
Low Aphid Density				
Species	0.2554	0.92	3	0.4753
Density \times species	0.2248	0.81	4	0.5543
Error	0.2787	—	8	—
1996 High Aphid Density				
Species	0.0047	0.01	2	0.9873
Density \times species	0.9552	2.55	3	0.1522
Error	0.3752	—	6	—
Low aphid density				
Species	0.1112	2.06	2	0.2089
Density \times Species	2.060	38.07	3	0.0003
Error	0.0541	—	6	—
Parameter estimates				
1994 high aphid density				
<i>C. maculata</i> : $Y = 2.4409 (\pm 1.6901)X - 1.9089 (\pm 2.8379)$				
<i>H. tredecimpunctata</i> : $Y = 1.5599 (\pm 0.8128)X - 0.3799 (\pm 1.2721)$				
<i>A. bipunctata</i> : $Y = 1.0154 (\pm 0.4754)X - 0.7651 (\pm 0.5367)$				
<i>H. convergens</i> : $Y = 2.7225 (\pm 0.6888)X - 1.2607 (\pm 0.8387)$				
1996 low aphid density				
<i>C. maculata</i> : $Y = 1.4144 (\pm 0.1965)X - 0.8407 (\pm 0.4187)$				
<i>A. bipunctata</i> : $Y = 0.8013 (\pm 0.2973)X - 0.1428 (\pm 0.2556)$				
<i>H. convergens</i> : $Y = 2.494 (\pm 0.3359)X - 0.0437 (\pm 0.1532)$				

A significant interaction ($P < 0.05$) indicates that differences in the slope among species vary with mean density, also known as the covariate.

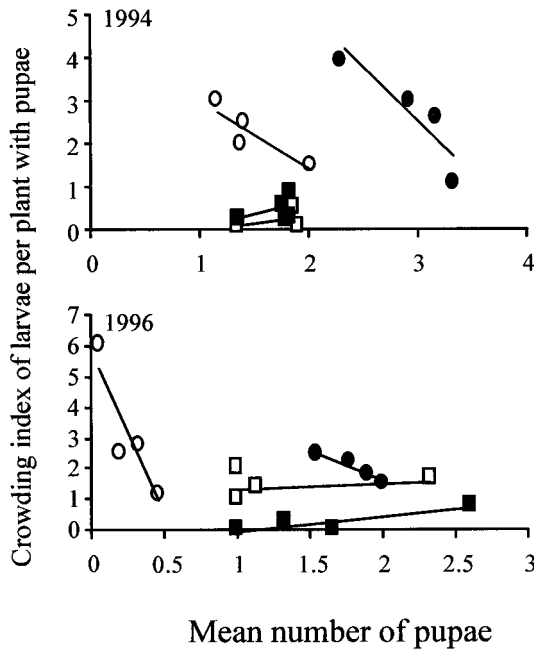


Fig. 3. Relationship between *C. maculata* larval crowding (mean + [s^2 /mean - 1]) on plants with conspecific pupae and mean *C. maculata* pupal density for 2 consecutive weekly samples in high and low aphid densities in 1994 and 1996. Open circles and squares indicate treatments that previously had low aphid densities and black circles and squares indicate treatments that previously had high aphid densities. Circles represent the first weekly sample (4 August 1994, 14 August 1996) and squares the following weeks sample (12 August 1994, 21 August 1996). Each point for a symbol is the value of a replicate.

the highest cannibalism rate, followed by *H. convergens*; neither species had rates above 6%. *C. maculata* was never observed in a cannibalism event (Table 5). The low cannibalism rates in the field compared with the laboratory experiments were most likely a result of reduced encounters on the corn plant compared with a dish. However, we observed that species behaved differently when food was not available. We found that *C. maculata* was hidden in the leaf sheaths whereas the other species were primarily foraging out in the open ($G = 47.110$, $df = 2$, $P < 0.0001$) (Fig. 4). More individuals of *H. convergens* were observed to

Table 3. Proportion of starved larvae cannibalized and preyed upon in 24 h in the laboratory

Victim	Cannibal and Predator			P
	<i>C. maculata</i>	<i>A. bipunctata</i>	<i>H. convergens</i>	
<i>C. maculata</i>	0.08	0.0	0.13	0.2523
<i>A. bipunctata</i>	0.38	0.40	0.71	0.0253*
<i>H. convergens</i>	0.13	0.21	0.27	0.3678

Daily mortality rates are for the species experiencing mortality (victim) when encountered by a cannibal or predator ($n = 96$).

*. $P < 0.05$ indicates that the frequency in victim mortality is not independent from the species encountered.

Table 4. Proportion of 2nd instars preyed upon by either starved or fed 4th instars in 1 h in the laboratory

Species	1-h mortality rates of 2nd instars	
	Starved	Fed
<i>A. bipunctata</i>	—	0.25
<i>C. maculata</i>	0.66***	0.33
<i>H. convergens</i>	0.75***	0.31

Statistical comparisons among species within each hunger condition were not significant. Mortality rates are for 2nd instars only; 4th instars were not attacked during the hour. There were 144 individuals for the comparison of *C. maculata* and *H. convergens* starved and fed larvae. There were 108 and 72 individuals for the among-species comparison of fed or starved larvae, respectively.

***. $P < 0.001$ indicates that the frequency of 2nd-instar mortality is not independent of the hunger level of 4th instars.

leave the plant, and were frequently found crawling on the ground in apparent attempts to escape the barriers (Fig. 5). However, dispersal was not density-dependent, and there was no significant interaction among coccinellid density, species, and dispersal from the plant ($C^2 = 0.04$, $df = 2$, $P = 0.980$) (Fig. 6). At both coccinellid densities, more *H. convergens* and *A. bipunctata* dispersed from the plant than *C. maculata* (Fig. 6).

Leaving Rates. All 3 species of coccinellid larvae rarely left a plant with aphids even after 24 h ($F = 2.46$, $df = 2$, $P = 0.675$; Fig. 7b). However, when there were no aphids, species left the plant at different rates ($F = 30.72$, $df = 2$, $P < 0.001$; Fig. 7a). More individuals of *H. convergens* left plants with no aphids at a significantly faster rate than the other species, where 50% left after searching for 30 min and 95% left after 1 h and 40 min. Individuals of *A. bipunctata* left and returned to the plant repeatedly, and *C. maculata* was very slow to leave plants with no aphids. After 24 h, 30% of *C. maculata* were still on the plants.

Discussion

We examined how the change in coccinellid density and prey availability influences cannibalism and interspecific predation of larvae and pupae of 4 species of coccinellids. Only in some cases are the results consistent with our initial predictions. Larval and pupal cannibalism and interspecific predation occur more frequently when aphid populations crash. However, neither previous initial aphid densities nor coccinellid densities appear to influence cannibalism and

Table 5. Proportion of larval and pupal cannibalism at high and low coccinellid densities in the field experiment

Species	Coccinellid density	
	High	Low
<i>A. bipunctata</i>	0.05 (4)	0.06 (2)
<i>C. maculata</i>	0.00	0.00
<i>H. convergens</i>	0.05 (3)	0.00

Number in parentheses is number of victims, both larvae and pupae, in 48 h. All statistical comparisons were not significant ($n = 280$).

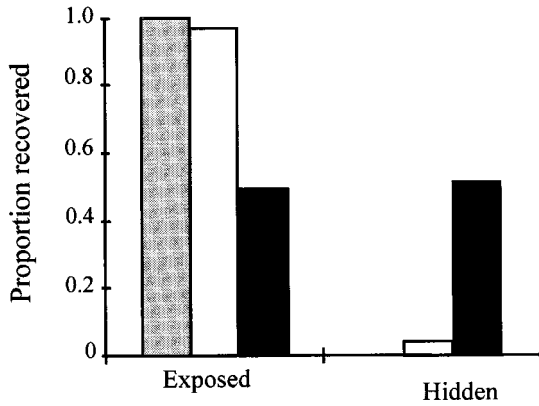


Fig. 4. Proportion of *H. convergens* (gray) ($n = 20$), *A. bipunctata* (white) ($n = 38$), and *C. maculata* (black) ($n = 43$) individuals recovered from the plant from either an exposed or hidden location after 48 h. Individuals that were recovered from hidden locations were found in the leaf sheath only after the plants were dissected.

interspecific predation frequency. Instead, species behave differently toward conspecifics and heterospecifics, and when prey is scarce. In the laboratory, *A. bipunctata* and *H. convergens* were significantly more cannibalistic than *C. maculata*, and *H. convergens* was particularly aggressive toward *A. bipunctata*. *C. maculata* was the least cannibalistic. This apparent contradiction between the field, where the per capita predation rate was similar among species, and the laboratory, where *C. maculata* was the least cannibalistic and predaceous, may be explained by their behavior when prey is scarce. *C. maculata* was very slow to leave a plant without aphids and pollen, and searched for >24 h. Furthermore, on postanthesis plants from the density-dependent experiment, 50% of

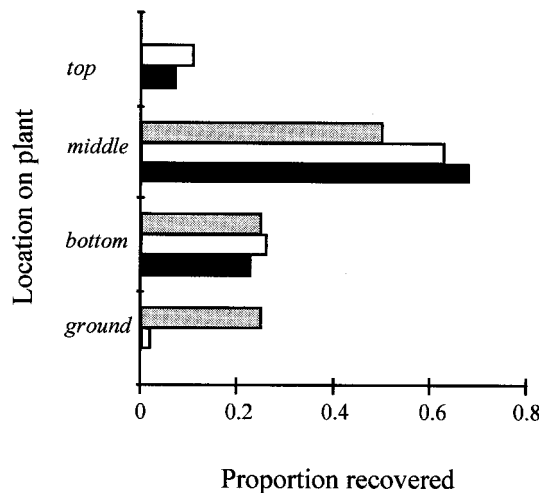


Fig. 5. The proportion of *H. convergens* (gray), *A. bipunctata* (white), and *C. maculata* (black) individuals recovered from different locations on the plant or ground after 48 h. Numbers of observations are as listed for Fig. 4.

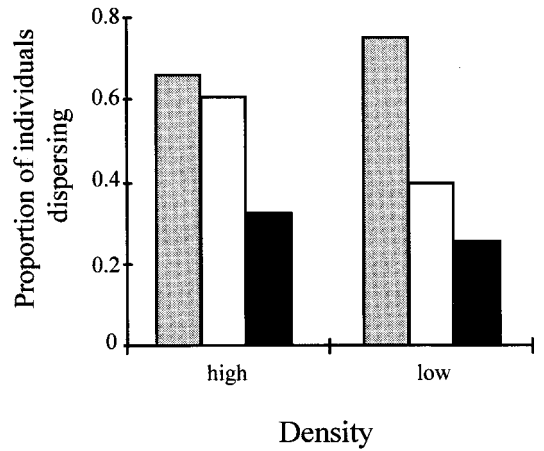


Fig. 6. Proportion of *H. convergens* (gray) ($n = 48$ high density, $n = 12$ low density), *A. bipunctata* (white) ($n = 64$, $n = 16$), and *C. maculata* (black) ($n = 48$, $n = 12$) individuals dispersing from corn plants at high and low coccinellid densities.

the *C. maculata* larvae were found in the leaf sheath, a location that frequently has small numbers of aphids and abundant water pools and pollen (N.A.S., unpublished data). However, *H. convergens* spent little time searching plants without aphids or pollen and was eager to leave, but they stayed on plants with aphids. *A. bipunctata* was more sporadic about leaving a plant, and frequently returned to plants that they previously left. Therefore, our prediction that in the absence of both aphids and corn pollen, species would disperse from plants at a similar rate was not supported. The leaving rate results indicate that for *C. maculata*, the decision to stay on a plant or to leave and search elsewhere is not strongly aphid- or pollen-mediated, but for *H. convergens* and to some extent *A. bipunctata*,

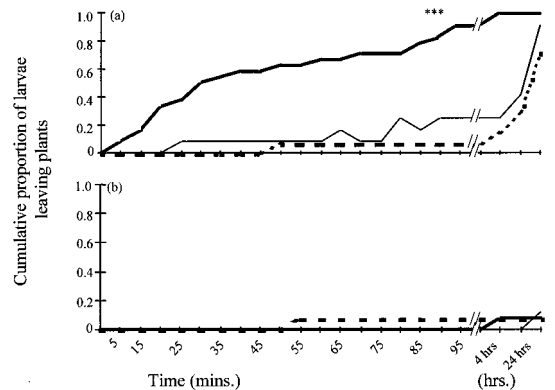


Fig. 7. Cumulative proportion of *H. convergens* (solid heavy line), *A. bipunctata* (solid fine line), and *C. maculata* (dotted line) larvae leaving (a) plants with no aphids, and (b) plants with aphids. The Tukey honestly significant difference (HSD) test was used to identify that *H. convergens* leaves at a significantly faster rate than either *A. bipunctata* or *C. maculata*. ***, $P < 0.001$.

the decision to stay or leave does appear to be aphid-mediated.

Others have examined the parameters that influence the magnitude and direction of cannibalism and intraguild predation in terrestrial invertebrates (see reviews by Polis 1981 and Polis et al. 1989). In a laboratory experiment, Lucas et al. (1998) demonstrated that in the absence of prey, predation occurred in the majority of the interactions among 3 aphid predators. They showed that larger sized individuals won confrontations and that sessile and slow moving individuals were extremely vulnerable to intraguild predation. In our experiment, we observed predation of sessile, molting larvae and pupae, but we standardized hunger levels, size, and development stage to focus on the behavioral response of each species. Our results indicate that aggressiveness and dispersal behavior when prey becomes scarce influences cannibalism and predation. Others also have found that vulnerability to attack is influenced by the relative aggressiveness of the interacting species. Phoofolo and Obryki (1992) and Lucas et al. (1998) found that lacewing larvae repeatedly preyed upon coccinellid larvae, *C. maculata*, and suggested that the lacewing's superiority could be attributed to its greater aggressiveness or shape of its mouth parts. The coccinellids in our study are closely related (from the same tribe) and morphologically similar (Rees et al. 1994), but differ in their aggressiveness. The less aggressive behavior of *C. maculata* toward con- and heterospecifics may be explained by their feeding breadth (Lucas et al. 1998). *C. maculata* is the most polyphagous and may be less likely to become prey when involved in predator-predator interactions, either by defending itself or avoiding the interaction.

Density-dependent behaviors, such as migration, interference, and mortality often increase as predator densities increase and prey becomes scarce (Dong and Polis 1992). In our density-dependent experiments, an increase in coccinellid density did not increase cannibalism or dispersal rates. This is most likely because of low encounter rates among searching individuals. Cannibalism rates may have been higher if some of the larvae were sessile and molting, therefore more vulnerable than individuals that are searching and able to defend themselves. Also, the dispersal pattern of *H. convergens* from plants with no prey may further reduce the probability of encountering con- and heterospecifics on the plant, but larvae leaving the plants also are vulnerable to predation by ground predators such as carabid beetles (Winder 1990).

The reason why each species stays or leaves a plant when prey is scarce is poorly understood. However, there are probably different risks associated with each species behaviors. *C. maculata* may stay on a plant without aphids because of the way that it searches and locates food between the leaf sheath and the stalk, including pollen. Furthermore, in a monospecific stand where there is little variation in plant or insect phenology, the probability of encountering prey elsewhere is not high. This suggests that *C. maculata* is adapted to low aphid conditions, and spends less en-

ergy by staying on the plant than would be required to leave. *H. convergens* may leave plants without aphids because they require a certain level of intensity of a feeding stimulus or because they have a short giving-up time, and will limit the amount of time that they search for an aphid before leaving the plant (e.g., Nakamura 1985). In addition, hunger levels have been shown to influence larval searching behavior (Carter and Dixon 1982), and although hunger levels were standardized across species, the differences in leaving rates among species may be caused by differences in physiological processes such as food metabolism.

If the risk of leaving is greater than the risk of staying, then individuals who leave should experience higher mortality and lower pupal recruitment than individuals who stay. In results presented elsewhere (Schellhorn 1998), we found that pupal recruitment was highest for *H. convergens* and lowest for *A. bipunctata*. Therefore, leaving plants without aphids is a behavior that results in high pupal recruitment for *H. convergens*. However, *A. bipunctata* makes efforts to disperse from plants without prey, but frequently returns to the plant, a behavior that creates the perfect opportunity for cannibalism; a behavior that may contribute to *A. bipunctata* rarity in maize (Schellhorn 1998).

Whether a coccinellid larva stays or leaves a plant without aphids and its willingness to cannibalize can affect larval and pupal survival and population dynamics. Larval behavior when prey is scarce may be similar to how larvae will behave in patches of plants without aphids. These results suggest that *H. convergens* (and to some extent *A. bipunctata*) will search for the large aggregations of aphids, whereas *C. maculata* will not, but is more likely to find small aggregations of aphids and pollen here and there. The searching behavior of *C. maculata* when prey is scarce in part explains why they are the most abundant coccinellid in corn.

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