Development of Three Populations of *Coleomegilla maculata* (Coleoptera: Coccinellidae) Feeding on Eggs of Colorado Potato Beetle (Coleoptera: Chrysomelidae)

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ABSTRACT Laboratory experiments were conducted to compare the preimaginal survival, development rate, adult weight, and sex ratio of 3 *Coleomegilla maculata* DeGeer populations feeding on *Leptinotarsa decemlineata* (Say) eggs and pea aphids, *Acyrthosiphon pisum* (Harris). Preimaginal survival of *C. maculata* from Iowa, Rhode Island, and Honduras reared on *L. decemlineata* eggs alone ranged from 1.7 to 30%. The highest mortality of *C. maculata* immature stages occurred during the early (1st and 2nd) stadia. Higher preimaginal survival for Rhode Island population (30%) than for Iowa (5%) and Honduras (1.7%) populations suggests that *C. maculata* in Rhode Island may be better adapted to feeding on *L. decemlineata* eggs as early instars. Development of *C. maculata* at 26°C was slowest (18 d) on *L. decemlineata* eggs alone and fastest (13 days) on pea aphids alone. However, when 1st and 2nd instars of *C. maculata* were provided with aphids, followed by *L. decemlineata* eggs, there was no observed delay in larval development. Older *C. maculata* larvae readily feed on *L. decemlineata* eggs, and in the presence of additional prey such as aphids for early instars, *L. decemlineata* eggs alone are an adequate diet for subsequent *C. maculata* development and survival.

KEY WORDS *Coleomegilla maculata, Leptinotarsa decemlineata,* preimaginal development, predation, predator-prey interactions

PREDATORY ARTHROPODS USE ingested prey for survival, development, and reproduction (Slansky and Rodriguez 1987, Crawley 1992). When prey is suitable and consumption of prey is high, a greater proportion of predators will survive, complete their development faster, and more fecund females will be produced (Holling 1961, Slansky and Rodriguez 1987, Crawley 1992).

Coleomegilla maculata DeGeer, a predatory coccinellid widely distributed east of the Rocky Mountains in North America (Obrycki and Tauber 1978, Gordon 1985), is one of the common insect predators in potato agroecosystems in northeastern United States (Obrycki and Tauber 1985, Groden et al. 1990, Hazzard and Ferro 1991, Hazzard et al. 1991, Hilbeck and Kennedy 1996). This polyphagous coccinellid feeds on many items, such as pollen, aphids, insect eggs, and other soft-bodied insects (e.g., Conrad 1959, Hodek 1973, Mack and Smilowitz 1982, Gordon 1985, Obrycki and Tauber 1985, Giles et al. 1994, Pilcher et al. 1997). *C. maculata* also preys upon the eggs and larvae of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), (Groden et al. 1990, Hazzard and Ferro 1991, Hazzard et al. 1991, Olkowski et al. 1992), the most destructive insect pest of potatoes, *Solanum tuberosum* L., in the United States. *C. maculata* is the most important natural enemy attacking 1st generation *L. decemlineata* eggs in Massachusetts, preying upon 50% of eggs (Hazzard et al. 1991).

Studies have shown that factors such as temperature and the quality or quantity of prey influence *C. maculata* development (Putman 1957; Smith 1961; Smith 1965a, b; Atallah and Newsom 1966; Obrycki and Tauber 1978; Pilcher et al. 1997). However, with the exception of the study by Hazzard and Ferro (1991), little attention has focused on the development of *C. maculata* when feeding on eggs and larvae of *L. decemlineata.* Hazzard and Ferro (1991) found that 79% of *C. maculata* survived to adults when reared on *L. decemlineata* eggs alone. However, in preliminary developmental studies conducted in Iowa (Munyaneza 1996, unpublished data), survival of *C. maculata* larvae on *L. decemlineata* eggs was typically <10%.

Coleomegilla maculata is widely distributed in North, Central, and South America (Gordon 1985, Castro 1993). This polyphagous coccinellid may have adapted to feeding and developing on *L. decemlineata,* depending on its exposure to this prey. Also, crossing studies conducted by L. E. Gomez and J.J.O. (unpublished data) between *C. maculata* from Iowa and Honduras indicated that these coccinellids may belong to different subspecies or species rather than different populations.

The objectives of this study were to compare preimaginal survival and developmental time and

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Table 1. Percentage preimaginal survival (mean of replicate means ± SEM) for *C. maculata* populations from Iowa, Rhode Island, and Honduras reared on pea aphids, *L. decemlineata* eggs, and pea aphids plus *L. decemlineata* eggs

Diet	Population			F^a	P
	Iowa	Rhode Island	Honduras		
Aphids only	80.00 ± 2.89a	85.00 ± 4.00a	78.33 ± 4.41a	0.81	0.4898
Aphids (1st instars) + eggs	45.00 ± 2.88b	55.0 ± 2.66ab	48.33 ± 4.41b	6.03	0.5069
Aphids (1st and 2nd instars) + eggs	70.33 ± 2.88a	75.00 ± 2.64a	68.33 ± 4.41a	0.76	0.5069
Eggs only	5.00 ± 5.00c,B	30.00 ± 14.41b,A	1.66 ± 1.66c,B	0.50	0.0367
F	36.56	8.78	65.22	—	—
P	0.0001	0.0065	0.0001	—	—

Means (population) followed by the same lower case letter within columns are not statistically different at $P < 0.05$.
Means (diet) followed by the same capital letter within rows are not statistically different at $P < 0.05$.
[a] ANOVA: df = 3, 11 for each population; df = 2, 8 for each diet.

selected adult characteristics (weight, sex ratio) of 3 populations of *C. maculata* feeding on *L. decemlineata* eggs and pea aphids, *Acyrthosiphon pisum* (Harris).

Materials and Methods

Adult *C. maculata* were field-collected from Story County, Iowa; Washington County, Rhode Island; and El Paraiso (Honduras) in July 1995. Mating pairs were maintained at 26 ± 1°C and a photoperiod of 16:8 (L:D) h. They were provided with water, a 1:1 mixture of honey and Wheast (Qualcepts, Minneapolis, MN), pea aphids, and green peach aphids, *Myzus persicae* (Sulzer). Each mating pair was held in a 0.24-liter (0.5-pint) cage covered with a piece of white organdy cloth. Oviposition was checked daily, and egg clusters were collected and incubated at 26 ± 1°C. On the day of hatching, each 1st instar was transferred to a separate glass vial (≈10 ml). *L. decemlineata* eggs used in the experiment were from colonies maintained at 26 ± 1°C and a photoperiod of 16:8 (L:D) h on greenhouse-grown potato ('Red Pontiac') plants.

First-instar *C. maculata* from each population were assigned to 4 diet treatments: pea aphids, *L. decemlineata* eggs, and 2 mixtures of pea aphids and eggs. In one aphids–eggs treatment, pea aphids were provided only to 1st instars and *L. decemlineata* eggs alone to older instars; in the other treatment, 1st and 2nd instars received pea aphids, followed by *L. decemlineata* eggs only.

Larvae were individually reared to adults, at 26 ± 1°C and a photoperiod of 16:8 (L:D) h. They were provided with an excess of prey daily and checked for molting. The developmental time was recorded for each preimaginal stadium. The 4th instar included the prepupa, an immobile stage preceding the pupal stage. Approximately 24 h after adult eclosion, sex and weight were recorded. Each diet treatment was replicated 3 times for each population; there were 20 individuals in each replicate.

Results were analyzed by using SAS general linear models procedure (SAS Institute 1985). Two-way analysis of variance (ANOVA) was used to test for differences in adult survival, developmental time, adult weight, and sex ratio of *C. maculata* feeding on the different diets and among populations. Adult survival and sex ratio data were transformed to arcsine of the square root of the proportions before ANOVA. The Student-Newman-Keuls sequential procedure was used for pairwise comparisons among means. The level of significance for all tests was set at $P < 0.05$.

Voucher specimens are deposited in the Iowa State Insect Collection, Department of Entomology, Iowa State University, Ames.

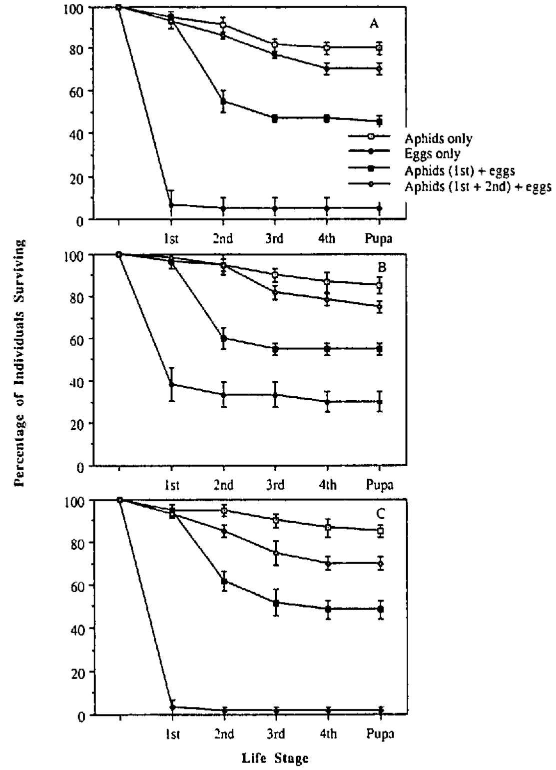

Fig. 1. Survivorship curves of *C. maculata* populations reared on different diets at 26°C and a photoperiod of 16:8 (L:D) h. (A) Iowa, (B) Rhode Island, and (C) Honduras. Each diet treatment was replicated 3 times for each population and 20 first instars were started in each replicate.

Table 2. Preimaginal developmental time (days; mean of replicate means ± SEM) for 3 populations of *C. maculata* feeding on pea aphids, *L. decemlineata* eggs, and pea aphids plus *L. decemlineata* eggs

Life stage	Aphids only	Aphids (1st instars) + eggs	Aphids (1st and 2nd instars) + eggs	Eggs only[a]	*F*; df	*P*
			Iowa			
1st instar	2.26 ± 0.23a	1.97 ± 0.12a	2.31 ± 0.33a	3.00 ± 1.00b	14.15; 3, 10	0.00039
2nd instar	2.16 ± 0.08a	2.40 ± 0.17ab	2.52 ± 0.13ab	3.00 ± 1.00b	10.97; 3, 9	0.0045
3rd instar	2.47 ± 0.13	3.55 ± 0.35	2.59 ± 0.13	3.66 ± 1.53	0.39; 3, 9	0.8031
4th instar	3.93 ± 0.36	4.38 ± 0.06	3.65 ± 0.03	5.33 ± 1.53	0.42; 3, 9	0.7614
Pupa	3.28 ± 0.06	4.78 ± 0.16	3.72 ± 0.17	3.34 ± 0.58	1.47; 3, 9	0.2962
			Rhode Island			
1st instar	2.25 ± 0.17a	2.17 ± 0.01a	2.34 ± 0.04a	4.24 ± 0.26b	19.45; 3, 11	0.0019
2nd instar	2.21 ± 0.30	2.49 ± 0.04	2.10 ± 0.15	2.79 ± 0.29	0.25; 3, 11	0.8640
3rd instar	2.07 ± 0.10	2.99 ± 0.26	3.09 ± 0.05	2.47 ± 0.29	0.36; 3, 11	0.8034
4th instar	3.83 ± 0.16	4.99 ± 0.12	3.83 ± 0.25	4.41 ± 0.26	0.42; 3, 11	0.7112
Pupa	3.10 ± 0.19	3.20 ± 0.16	3.33 ± 0.01	2.98 ± 0.21	0.81; 3, 11	0.5002
			Honduras			
1st instar	2.30 ± 0.22a	2.17 ± 0.02a	2.43 ± 0.30a	4.60 ± 0.78b	17.73; 3, 10	0.0021
2nd instar	2.35 ± 0.05	2.54 ± 0.09	2.40 ± 0.01	2.36 ± 0.94	0.53; 3, 9	0.6700
3rd instar	2.39 ± 0.13	3.24 ± 0.07	2.77 ± 0.25	2.94 ± 0.83	0.57; 3, 9	0.6683
4th instar	4.04 ± 0.32	4.90 ± 0.24	3.85 ± 0.18	4.60 ± 1.12	0.45; 3, 9	0.7212
Pupa	3.28 ± 0.06	3.90 ± 0.55	3.56 ± 0.13	3.62 ± 0.41	2.03; 3, 9	0.2817

Means followed by the same letter within rows are not statistically different at $P < 0.05$.

[a] Mean ± SD for Iowa and Honduras populations. There was complete development in only 1 replicate for this diet.

Results

There were no significant differences between diet treatments and *C. maculata* populations on preimaginal survival (ANOVA, $F = 2.56$; df = 6, 30; $P < 0.0721$), total preimaginal developmental time (ANOVA, $F = 0.97$; df = 6, 30; $P < 0.4818$), adult weight (ANOVA, $F = 1.12$; df = 4, 23; $P < 0.8852$), and sex ratio (ANOVA, $F = 1.08$; df = 4, 23; $P < 0.9547$).

There were significant differences in preimaginal survival on *A. pisum*, *L. decemlineata* eggs, and the combination of *A. pisum* and eggs for each *C. maculata* population (Table 1). However, there were no significant differences in survival to adult on the different diets among the three populations, except for *C. maculata* reared on *L. decemlineata* eggs only (Table 1). The lowest percentage survival was observed for individuals reared on *L. decemlineata* eggs (1.7, 5, and 30% for Honduras, Iowa, and Rhode Island populations, respectively), whereas those reared on *A. pisum* alone had the highest adult survival (78.3, 80, and 85% for Honduras, Iowa, and Rhode Island populations, respectively) (Table 1). Within populations, preimaginal survival was higher for *C. maculata* fed *A. pisum* as 1st and 2nd instars than for those provided *A. pisum* to 1st instars only (Table 1).

The highest mortality of *C. maculata* immature stages reared on the different diets occurred during the early (1st and 2nd) instars in all the populations (Fig. 1). Observations with a light microscope indicated that very young 1st instars did not feed on *L. decemlineata* eggs. Late 2nd instars, however, were observed feeding on *L. decemlineata* eggs.

Comparisons of the preimaginal stage and total developmental times among diets within each population showed significant differences (Tables 2 and 3), but there were no significant differences in the total developmental time on each diet among the 3 populations (Table 3). Total developmental time was the longest (18.3, 18.1, and 16.9 d for Iowa, Honduras, and Rhode Island populations, respectively) for *C. maculata* reared on *L. decemlineata* eggs. Individuals reared on *A. pisum* had the shortest total developmental time (13.5, 14.1, and 14.4 d for Rhode Island, Iowa, and Honduras populations, re-

Table 3. Total preimaginal developmental time (days; mean of replicate means ± SEM) of *C. maculata* feeding on the different diets for Iowa, Rhode Island, and Honduras populations

Diet	Population			*F*[a]	*P*
	Iowa	Rhode Island	Honduras		
Aphids only	14.10 ± 0.43b	13.46 ± 0.060c	14.36 ± 0.46b	0.81	0.4878
Aphids (1st instars) + eggs	17.08 ± 0.42a	15.84 ± 0.47ab	16.75 ± 0.36a	2.41	0.1708
Aphids (1st and 2nd instars) + eggs	14.79 ± 0.33b	14.69 ± 0.29bc	15.01 ± 0.14b	0.37	0.7070
Eggs only[b]	18.33 ± 1.53a	16.89 ± 0.22a	18.12 ± 1.09a	7.26	0.1210
F	16.54	11.97	14.74	—	—
P	0.0026	0.0025	0.0036	—	—

Means followed by the same letter within columns are not statistically different at $P < 0.05$.

[a] ANOVA: df = 3, 9 for each population; df = 2, 8 for each diet except df = 2, 4 for eggs only.

[b] Mean ± SD for Iowa and Honduras populations.

Table 4. Adult weight (mg; mean of replicate means ± SEM) of *C. maculata* feeding on the different diets for Iowa, Rhode Island, and Honduras populations

Diet	Sex	Population			*F*; df	*P*
		Iowa	Rhode Island	Honduras		
Aphids only	Male	6.20 ± 0.25	6.11 ± 0.61	6.00 ± 0.06	0.07; 2, 8	0.9351
	Female	8.13 ± 0.55	7.72 ± 0.36	8.40 ± 0.36	0.62; 2, 8	0.5692
	F; df	10.07; 1, 5	5.11; 1, 5	43.20; 1, 5	—	—
	P	0.0337	0.0866	0.0028	—	—
Aphids (1st instars) + eggs	Male	6.67 ± 0.30	6.45 ± 0.53	6.40 ± 0.36	0.13; 2, 8	0.8837
	Female	8.55 ± 0.32	7.83 ± 0.82	8.83 ± 0.18	0.99; 2, 8	0.4240
	F; df	18.58; 1, 5	2.00; 1, 5	36.75; 1, 5	—	—
	P	0.0125	0.2298	0.0037	—	—
Aphids (1st and 2nd instars) + eggs	Male	6.30 ± 0.38	6.02 ± 0.61	6.47 ± 0.35	0.23; 2, 8	0.8006
	Female	8.94 ± 0.28	7.98 ± 0.66	8.53 ± 0.40	1.01; 2, 8	0.4202
	F; df	31.08; 1, 5	4.65; 1, 5	14.96; 1, 5	—	—
	P	0.0051	0.0973	0.0180	—	—
Eggs only[a]	Male	6.20 ± 1.42	5.82 ± 0.35	5.70 ± 0.97	—	—
	Female	7.80 ± 1.58	7.50 ± 0.55	—	—	—
	F; df	—	6.58; 1, 5	—	—	—
	P	—	0.0623	—	—	—
	Male[b]	F = 0.46; df = 3, 9	*F* = 0.24; df = 3, 11	*F* = 0.91; df = 3, 9	—	—
		P < 0.7212	*P* < 0.8640	*P* < 0.4901	—	—
	Female[b]	*F* = 1.52; df = 3, 9	*F* = 0.11; df = 3, 11	*F* = 0.45; df = 3, 9	—	—
		P < 0.3024	*P* < 0.9535	*P* < 0.6553	—	—

[a] Data for this diet were not included in statistical analyses for Iowa and Honduras populations because of very low or no survival on *L. decemlineata* eggs only.

[b] ANOVA: *F*, df, and *P* values are for either males or females within columns.

spectively) (Tables 2 and 3). *C. maculata* fed *L. decemlineata* eggs after *A. pisum* for 1st and 2nd instars had a shorter total developmental time than those provided with *A. pisum* as 1st instars only (Tables 2 and 3). This pattern was consistent for the 3 populations (Tables 2 and 3). The developmental times of 1st and 2nd instars feeding on *L. decemlineata* eggs only were generally longer than the times for those feeding on aphids (Table 2).

Iowa and Honduras *C. maculata* females developing on the different diets, as larvae, weighed more than males (Table 4). In contrast, differences in weight between *C. maculata* females and males, when reared on same diets, were not statistically different for the Rhode Island population (Table 4). There were no significant differences in weight among either males or females within each population when fed the different diets (Table 4). Similarly, there were no significant differences in weight between males or females reared on the same diets across the different populations (Table 4).

Sex ratio within and among the different populations did not vary significantly when fed on the different diets (Table 5).

Discussion

Preimaginal survival of *C. maculata* reared on *L. decemlineata* eggs was 1.7, 5.0, and 30.0% for Honduras, Iowa, and Rhode Island populations, respectively. Previously, 79% of *C. maculata* in Massachusetts survived to the adult stage when reared on *L. decemlineata* eggs (Hazzard and Ferro 1991). In the current study, the greatest mortality of *C. maculata* immature stages occurred during the early (1st and 2nd) instars for all the populations. Observations with a light microscope indicated that young 1st instars (<24 h old) of *C. maculata* were not able to feed on *L. decemlineata* eggs. However, late 2nd instars were observed feeding on *L. decemlineata* eggs. One possible explanation for these observations is that the *L. decemlineata* egg chorion is too hard for the soft mouthparts of young 1st instars, but

Table 5. Percentage of females (mean of replicate means ± SEM) for *C. maculata* populations from Iowa, Rhode Island, and Honduras

Diet	Population			*F*[a]	*P*
	Iowa	Rhode Island	Honduras		
Aphids only	51.6 ± 1.17	59.3 ± 4.90	55.4 ± 10.13	0.24	0.7926
Aphids (1st instars) + eggs	47.3 ± 12.19	40.7 ± 4.66	43.0 ± 9.94	0.11	0.8934
Aphids (1st and 2nd instars) + eggs	57.7 ± 3.85	47.5 ± 7.15	60.7 ± 2.99	1.92	0.2265
Eggs only	66.7 ± 6.71(SD)	60.0 ± 23.09	No survival	—	—
F[a]	0.54	0.55	1.17	—	—
P	0.6700	0.6607	0.3717	—	—

[a] ANOVA: df = 2, 8 for diets; df = 3, 9 for Iowa; df = 3, 11 for Rhode Island; and df = 2, 8 for Iowa, Rhode Island, and Honduras populations.

this does not explain the differences in survival observed between the Rhode Island population and the other 2 populations. *L. decemlineata* occurs in Iowa and Honduras but is not considered a pest there; its densities are generally low. In contrast, *L. decemlineata* is the major pest of potatoes in northeastern United States, including Rhode Island (e.g., Lashomb and Casagrande 1981, Hare 1990, Hazzard et al. 1991, Olkowski et al. 1992). This suggests that *C. maculata* are frequently exposed to *L. decemlineata* eggs in Rhode Island and has probably adapted to feeding on *L. decemlineata* eggs as young larvae. This type of intraspecific variation may explain the relatively high *C. maculata* survival observed in Massachusetts (Hazzard and Ferro 1991). Levels of intraspecific variation among *C. maculata* populations are being examined (J.J.O., unpublished data). Previous studies of allozyme variation of North American populations of *C. maculata* detected no significant differences among populations (Coll et al. 1994, Krafsur et al. 1995).

Another factor that may explain this high *C. maculata* survival observed in the Hazzard and Ferro (1991) study is the time of larval transfer to different diets after hatching. Cannibalism, especially by young larvae, is a common phenomenon in coccinellid species (Agarwala and Dixon 1992). After hatching, *C. maculata* larvae typically feed on *C. maculata* unhatched eggs and hatched egg chorions. Thus, if this feeding persists for several hours, the larvae increase in size and the probability of then successfully consuming *L. decemlineata* eggs may increase. Therefore, transfer of older 1st instars may result only in greater survival of subsequent stages and thereby in greater preimaginal survival. In our study, the larval transfer occurred immediately after eclosion.

Similar to results reported by Hazzard and Ferro (1991), developmental rate of the 3 populations of *C. maculata* was lowest on *L. decemlineata* eggs and highest on *A. pisum*. In the current study, aphids served as alternate prey for very young 1st instars that may not feed on *L. decemlineata* eggs. During this study, the preimaginal developmental times recorded for *C. maculata* reared on *A. pisum* (14.1, 13.5, and 14.4 d for Iowa, Rhode Island, and Honduras, respectively) are similar to those reported by Phoofolo and Obrycki (1997) on Iowa *C. maculata* reared, as larvae, on *A. pisum* (13.5 d), and on *Ostrinia nubilalis* (Hübner) eggs only and on alternated *A. pisum* and *O. nubilalis* eggs (13.4 d).

In most of the instances, females weighed more than males regardless of the diet on which they had been reared. These results were expected because *C. maculata* females typically are larger than males. Pilcher et al. (1997) observed similar results for *C. maculata* reared, as larvae, on *A. pisum*, transgenic *Bacillus thuringiensis* corn pollen, and corn pollen free of *B. thuringiensis*. In addition, similar results were found by Phoofolo and Obrycki (1997) for *C. maculata* reared on *A. pisum* and *O. nubilalis* eggs. Results of our study also indicated that there were no significant differences in weight between males or females among diets or across populations (Table 4). Thus, based on weight characteristics, we conclude that *L. decemlineata* eggs provide nutrients similar to those by aphids.

There was no indication of significant differences in sex ratio of adults reared on the different diets or among populations. Therefore, the sex ratio of *C. maculata* is not affected by *L. decemlineata* eggs as prey. Phoofolo and Obrycki (1997) observed similar results for Iowa *C. maculata* reared on *A. pisum* and *O. nubilalis* eggs.

Results of the current study indicate that *L. decemlineata* eggs are not suitable prey for early instars of *C. maculata* from Iowa and Honduras. However, late instars of *C. maculata* readily feed on *L. decemlineata* eggs, and in the presence of alternate prey such as aphids for early instars, *L. decemlineata* eggs may be an adequate diet for *C. maculata* development and survival. Aphids, especially *M. persicae*, are common in potato fields (e.g., Obrycki and Tauber 1985, Groden et al. 1990, Hazzard and Ferro 1991). Groden et al. 1990 and Hazzard and Ferro (1991) suggested that high densities of aphids in potatoes would decrease the *C. maculata* predation of *L. decemlineata* eggs. However, the presence of aphids in potato fields would increase *C. maculata* larval survival and development, especially for early instars, and thereby enhance the persistence of populations of *C. maculata* in potatoes.

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