

Reproductive Response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Colorado Potato Beetle (Coleoptera: Chrysomelidae) Eggs

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ABSTRACT A laboratory study was conducted to quantify the preoviposition period, duration and frequency of oviposition, and the fecundity of *Coleomegilla maculata* DeGeer feeding on a range of Colorado potato beetle, *Leptinotarsa decemlineata* (Say), egg densities. *L. decemlineata* eggs are suitable prey for *C. maculata* egg production. A water and honey-Wheat mixture diet was not sufficient for *C. maculata* reproduction, but 28–48% of adults remained alive on this diet for up to 98 d. The preoviposition period was significantly shorter for *C. maculata* females feeding on pea aphids, *Acyrtosiphon pisum* (Harris), (5.8–6.8 d) than for females feeding on *L. decemlineata* eggs (11.3–23 d). At the lowest *L. decemlineata* egg density (2 eggs per day), females had significantly longer preoviposition periods than at the higher prey densities (5, 10, and >15 eggs per day). Interoviposition periods and the numbers of days on which females laid eggs were not different among diets. Fecundity among females feeding on the different diets averaged from 33.2 to 102.7 eggs and was not significantly different on the preimaginal diet of either *A. pisum* or *L. decemlineata* eggs. Results of this study indicate that *C. maculata* could reproduce and maintain its populations in potato fields when *L. decemlineata* eggs are scarce.

KEY WORDS *Coleomegilla maculata*, *Leptinotarsa decemlineata*, reproductive response

THE COLORADO POTATO BEETLE, *Leptinotarsa decemlineata* (Say), is the most destructive insect pest of potatoes, *Solanum tuberosum* L., in the United States (Lashomb and Casagrande 1981, Ferro 1985, Hare 1990). Development of widespread resistance by the beetle to most insecticides and environmental contamination caused by insecticides used for its control (Ferro 1985, Forgash 1985, Hare 1990, Radcliffe et al. 1991) have resulted in increased efforts in biological control, including manipulation of naturally occurring predators (e.g., Ferro 1985; Hough-Goldstein and Keil 1991; Biever and Chauvin 1992a, b; Olkowski et al. 1992; Hough-Goldstein et al. 1993).

Coleomegilla maculata DeGeer is a predatory coccinellid species that is widely distributed east of the Rocky Mountains in North America (Obrycki and Tauber 1978, Gordon 1985). It is a common predator in potato fields throughout the eastern United States (Obrycki and Tauber 1985, Groden et al. 1990, Hazzard and Ferro 1991, Hazzard et al. 1991). This coccinellid preys upon 50% of 1st-generation *L. decemlineata* eggs in Massachusetts (Hazzard et al. 1991). It was also found to be the most abundant coccinellid species in potato fields in Rhode Island, Michigan (Groden et al. 1990), and North Carolina (Hilbeck and Kennedy 1996).

C. maculata reproduces on various artificial diets, pollen, aphids, *L. decemlineata* eggs, and fall webworm (Smith 1961, 1965a, b; Atallah and Newsom

1966; Warren and Tadic 1967; Hodek et al. 1978; Hazzard and Ferro 1991). Hazzard and Ferro (1991) measured the rate of *C. maculata* oviposition when maintained on an excess of *L. decemlineata* eggs for 7 d but did not address the reproductive response of *C. maculata* to lower egg densities that may occur in the field. Because prey populations change over time, predators in crops are continually faced with shifting prey populations that can result in periods of low prey availability. Predators that persist under varied prey levels survive periods of scarcity and respond to increase in prey density. In contrast, predators that cannot survive periods of starvation may find the crop habitat unsuitable and thus would not be consistently found there (O'Neil and Wiedenmann 1987).

As part of an assessment of *C. maculata* predation of the Colorado potato beetle (Munyaneza 1996), the objective of this study was to quantify the reproductive response of *C. maculata* to a range of *L. decemlineata* egg densities.

Materials and Methods

Adult *C. maculata* were collected from alfalfa fields in Story County, Iowa, in June 1995. All studies were conducted in the laboratory at $26 \pm 1^\circ\text{C}$ and a photoperiod of 16:8 (L:D) h. Pairs were fed pea aphids, *Acyrtosiphon pisum* (Harris) and eggs were collected. *C. maculata* larvae were reared singly in

Table 1. Percentage of *C. maculata* females ovipositing at least once during the experiment and percentage survival for 98 d

Imaginal diet	% females ^a ovipositing		% survival for 98 d	
	Aphids as preimaginal diet	Eggs as preimaginal diet ^b	Aphids as preimaginal diet	Eggs as preimaginal diet
Water and honey-Wheat	0	0	28 ^c	48
Pea aphids	96	88	68	64
Eggs (>15)	88	92	76	72
10 eggs	92	52	56	28
5 eggs	88	80	60	32
2 eggs	84	84	60	56

^a 25 females were started in each treatment.

^b First instars were reared on pea aphids, in addition to *L. decemlineata* eggs.

^c 24% of the total number of females died, stuck in the honey-Wheat mixture.

glass vials (10 ml) on either *A. pisum* or a mixture of *L. decemlineata* eggs and *A. pisum*. In the aphid/egg diet, aphids were provided only to 1st instars because 1st-instar survival on *L. decemlineata* eggs is usually very low (Munyaneza 1996; unpublished data). Sex was determined on the day of adult eclosion. All mating pairs, in 0.24-liter cages (1/2 pint), were provided with water and a 1:1 mixture of honey and Wheat (Qualcepts, Minneapolis, MN). This artificial food was provided to adults because *C. maculata* typically feed on >1 type of food or prey in the field, including pollen and honeydew. From each larval diet, 25 pairs were assigned to each of the following 6 adult diets: (1) water and the honey-Wheat mixture only, (2) daily excess of pea aphids, (3) daily excess of *L. decemlineata* eggs (>15), (4) 10 eggs, (5) 5 eggs, and (6) 2 eggs. For the 2-egg per day diet, 10 additional mating pairs without the honey-Wheat mixture were observed to determine if this supplementary food had an effect on *C. maculata* egg production. Mating was observed during the first 7 d of adult life. *C. maculata* males were removed from the cages 10 d after the pairs were established. During the 10 d before the removal of the males, the number of eggs and aphids provided as prey was doubled.

Oviposition was checked each day during a 98-d experimental period; all eggs were counted from each female, including the remains of cannibalized eggs. The preoviposition period was determined by recording the number of days from eclosion to the initiation of egg laying. The number of days on which eggs were laid and days between successive ovipositions (the interoviposition period) were recorded for each female. The oviposition period is defined as the interoviposition periods plus the number of days on which there was oviposition. Fecundity, defined as the total number of eggs laid per female, was calculated for the 98-d experimental period. The percentages of females that oviposited at least once during the experiment and those that survived for 98 d were recorded.

Data were analyzed by using SAS general linear models procedure (SAS Institute 1985). Analysis of variance (ANOVA) was used to test for differences in preoviposition and interoviposition periods, num-

ber of days on which eggs were laid, daily oviposition, and fecundity among diets. The Student-Newman-Keuls sequential procedure was used for pairwise comparisons among means. To determine if there was an interaction between preimaginal and imaginal diets, a 2-way ANOVA was performed comparing females reared on each larval diet and then maintained on an excess of either *A. pisum* or *L. decemlineata* eggs as adults. The level of significance for all the tests was set at $P < 0.05$.

Voucher specimens are deposited in the Iowa State University Insect Collection, Department of Entomology, Iowa State University, Ames, IA 50011.

Results

Influence of Adult Diet on Oviposition and Survival. Females provided with only water and a honey-Wheat mixture did not lay eggs (Table 1). However, 28% of females reared on aphids and 48% of females reared on the aphid/egg diet survived for 98 d (Table 1). The average life span for these females was 68.5 ± 17.5 d (mean \pm SD) for those reared on aphids and 71 ± 21.3 d for those reared on the aphid/egg diet. In contrast, 88–96% of females maintained on aphids and 52–92% of those maintained on *L. decemlineata* eggs, as adults, oviposited at least once during the experiment, and their survival ranged from 28 to 76% (Table 1). In the absence of the honey-Wheat mixture, 60% of females provided with 2 *L. decemlineata* eggs daily initiated oviposition after 4 wk.

Influence of Preimaginal Diet of *A. pisum* on Oviposition. Preoviposition periods ranged from 4 to 21 d for females feeding on aphids, and 5–44, 5–42, 6–44, and 8–49 d for those feeding on >15, 10, 5, and 2 eggs, respectively. The majority of females on each diet (except those getting 2 eggs per day) had preoviposition periods ranging from 4 to 15 d. Less than 5% of females on each diet had preoviposition periods >35 d. These females were considered to be in reproductive diapause. Therefore, to examine the influence of preimaginal diet on preoviposition period, an ANOVA was performed on those females with a preoviposition period ≤ 35 d. There were significant differences in the preovi-

Table 2. Mean \pm SEM preoviposition period and interoviposition periods, number of days on which eggs were laid, daily oviposition, and fecundity of *C. maculata* females reared on *A. pisum*

Imaginal diet	Preoviposition period	Interoviposition period	No. ovipositions	Daily oviposition	Fecundity ^a (eggs/female)
Aphids	6.77 \pm 0.91a	3.18 \pm 0.72	5.41 \pm 0.78	12.23 \pm 1.11	73.45 \pm 14.41
Eggs (>15)	13.04 \pm 2.22b	3.99 \pm 0.70	7.68 \pm 1.00	13.86 \pm 1.01	109.36 \pm 16.73
10 eggs	12.41 \pm 1.86b	4.00 \pm 0.66	7.91 \pm 1.05	13.85 \pm 0.93	111.82 \pm 19.16
5 eggs	14.95 \pm 2.35b	4.55 \pm 0.99	7.75 \pm 0.89	12.61 \pm 1.16	106.47 \pm 13.21
2 eggs	23.05 \pm 2.28c	4.05 \pm 0.67	8.52 \pm 1.29	11.90 \pm 0.94	102.66 \pm 17.05

Means followed by the same letter within columns are not different at 0.05 level of significance.

^a Fecundity was calculated for the 98-d experimental period.

position periods among females on the 5 diets (ANOVA, $F = 8.05$; $df = 4, 105$; $P < 0.0001$) (Table 2). Females feeding on aphids had a shorter preoviposition period (6.8 \pm 0.9 d) than those feeding on *L. decemlineata* eggs. Females feeding on 2 *L. decemlineata* eggs had the longest preoviposition period (23.1 \pm 2.3 d) (Table 2).

Interoviposition periods ranged from 0 (for continuously ovipositing females) to 41 d. Between 83 and 90% of females feeding on aphids, >15, 10, 5, and 2 eggs had interoviposition periods ranging from 0 to 7 d. Less than 23% of females had interoviposition periods of >13 d and ranged from 22 to 53 d. Thus, ANOVA was performed on females with interoviposition periods ≤ 13 d. Interoviposition periods did not differ significantly among females feeding on the 5 different diets (ANOVA, $F = 0.38$; $df = 4, 96$; $P < 0.8239$) (Table 2).

The number of days on which eggs were laid did not differ significantly among the females on the different diets (ANOVA, $F = 1.39$; $df = 4, 106$; $P < 0.2410$) (Table 2). The majority of females (95.5, 86.7, 81.8, 85.0, and 76.2% of females feeding on aphids, >15, 10, 5, and 2 eggs per day, respectively) laid eggs for 1–12 d during the 98-d experimental period.

There were no significant differences in daily oviposition among females on the different diets (ANOVA, $F = 0.83$; $df = 4, 104$; $P < 0.5116$) (Table 2). The daily oviposition ranged from 5 to 24 eggs. The most frequent daily oviposition rates were between 6 and 15 eggs per day per female.

The total number of eggs per female (fecundity) did not differ significantly among females on different diets (ANOVA, $F = 0.94$; $df = 4, 103$; $P < 0.4466$) (Table 2). Fecundity ranged from 7 to 386 eggs. The majority of females (80.7, 71.3, 76.2, 80.4,

and 75.8% of females feeding on aphids, >15, 10, 5, and 2 eggs, respectively) laid 35–150 eggs.

During the 98-d oviposition period, rates of oviposition and the proportion of ovipositing females fluctuated. The proportion of females laying eggs increased during the first 5 wk, then it decreased. In contrast, the number of eggs laid per week per female increased during the first 3 wk, then it stayed almost steady until the end of the experimental period.

Influence of Preimaginal Diet of *A. pisum* and *L. decemlineata* Eggs on Oviposition. The preoviposition period ranged from 4 to 16 d for females feeding on aphids and 5–80, 6–23, 6–45, and 6–52 d for those feeding on >15, 10, 5, and 2 eggs, respectively. Less than 10% of females on each diet had preoviposition periods >35 d. Thus, only females with a preoviposition period ≤ 35 d were included in statistical analysis. The preoviposition periods of females feeding on the different diets were significantly different (ANOVA, $F = 14.20$; $df = 4, 91$; $P < 0.0001$) (Table 3). Similar to females reared on aphids, females feeding on aphids had a shorter preoviposition period than those feeding on *L. decemlineata* eggs. Furthermore, the longest preoviposition period was observed for females feeding on 2 *L. decemlineata* eggs per day (Table 3).

Interoviposition periods ranged from 0 to 53 d. Sixty-eight to 92% of females feeding on aphids, >15, 10, 5, and 2 eggs had interoviposition periods ranging from 0 to 10 d. The interoviposition periods of ≤ 13 d for females feeding on different diets were not statistically significant (ANOVA, $F = 0.16$; $df = 4, 74$; $P < 0.9601$) (Table 3).

There were significant differences in number of days on which eggs were laid by females on the different diets (ANOVA, $F = 2.39$; $df = 4, 94$; $P <$

Table 3. Mean \pm SEM preoviposition period and interoviposition periods, number of days on which eggs were laid, daily oviposition, and fecundity of *C. maculata* reared on *A. pisum* and *L. decemlineata* eggs and as preimaginal diet

Imaginal diet	Preoviposition period	Interoviposition period	No. ovipositions	Daily oviposition	Fecundity ^a (eggs/female)
Aphids	5.79 \pm 0.54a	3.91 \pm 0.88	6.08 \pm 0.86	9.07 \pm 0.67c	56.41 \pm 10.04ab
Eggs (>15)	14.10 \pm 2.23b	4.76 \pm 0.67	6.71 \pm 1.27	14.32 \pm 0.85a	95.48 \pm 19.87a
10 eggs	11.28 \pm 1.31b	4.60 \pm 1.46	2.57 \pm 0.50	12.17 \pm 1.13ab	33.21 \pm 8.37b
5 eggs	14.78 \pm 1.63b	4.43 \pm 0.80	6.35 \pm 0.85	12.62 \pm 0.90ab	76.06 \pm 11.03ab
2 eggs	22.94 \pm 2.47c	4.50 \pm 0.74	5.63 \pm 0.87	10.65 \pm 0.91bc	65.37 \pm 12.26ab

Means followed by the same letter within columns are not different at 0.05 level of significance.

^a Fecundity was calculated for the 98-d experimental period.

0.0563) (Table 3). Ninety-six, 86, 100, 100, and 100% of females feeding on aphids, >15, 10, 5, and 2 eggs per day, respectively, laid eggs for 1–13 d.

Daily oviposition among females on the different diets was significantly different (ANOVA, $F = 6.05$; $df = 4, 95$; $P < 0.0002$) (Table 3). The range of daily oviposition was 3–22 eggs. Similar to those of females reared on aphids, the most frequent daily oviposition rates were 6–15 eggs per day per female.

There were significant differences in fecundity among females on the different diets (ANOVA, $F = 2.62$; $df = 4, 94$; $P < 0.0400$) (Table 3). Fecundity ranged from 4 to 204 eggs with the majority of females (75, 76.2, 57, 88, and 77.8% of females feeding on aphids, >15, 10, 5, and 2 eggs, respectively) ovipositing 20 to 150 eggs.

There were fluctuations in rates of oviposition and the proportion of ovipositing females feeding on the different diets during the 98-d oviposition period. Similar to females reared on aphids, the proportion of ovipositing females increased in the first 5 wk, then decreased. Except for females feeding on 10 eggs per day that appeared to enter the diapause after the 5th wk, no oviposition was observed for the remaining 9 wk. A similar oviposition pattern to that of females reared on aphids was observed, except for females getting 10 eggs per day.

Interaction Between Preimaginal and Imaginal Diet. There was no significant interaction between preimaginal and imaginal diets on preoviposition period (ANOVA, $F = 0.91$; $df = 1, 86$; $P < 0.3420$), interoviposition period (ANOVA, $F = 0.74$; $df = 1, 79$; $P < 0.3922$), number of days on which eggs were laid (ANOVA, $F = 0.69$; $df = 1, 88$; $P < 0.4084$), and fecundity (ANOVA, $F = 0.01$; $df = 1, 88$; $P < 0.9187$) of females reared on each preimaginal diet and then maintained on aphids or more than 15 *L. decemlineata* eggs (Tables 2 and 3).

Discussion

C. maculata preys on several aphid species (Gordon 1985) and eggs and larvae of numerous insect species, including *L. decemlineata* (Gorden et al. 1990, Hazzard and Ferro 1991, Hazzard et al. 1991, Olkowski et al. 1992), *Ostrinia nubilalis* Hubner (Conrad 1959, Coll and Bottrel 1991, Phoofolo and Obrycki 1997), *Helicoverpa zea* (Boddie) (Whitcomb 1967), *Hypphantria cunea* (Durry) (Warren and Tadic 1967), and *Oulema melanopus* (L.) (Shade et al. 1970). *C. maculata* also feeds and develops on pollen and fungal spores (Smith 1961, 1965a, b; Warren and Tadic 1967; Hodek et al. 1978; Hazzard and Ferro 1991; Pilcher et al. 1997).

Similar to observations made by Hazzard and Ferro (1991), results of this study indicate that *L. decemlineata* eggs are suitable prey for *C. maculata* egg production. However, this study showed that reproduction can occur on as few as 2 eggs per day. A water and honey-Wheat mixture alone was not sufficient for *C. maculata* reproduction, but females remained alive on this diet for up to 98 d (Table 1).

Similarly, Smith (1965b) showed that some foods and artificial diets, although not adequate for egg production, increased longevity of *C. maculata*. Recently, Giles et al. (1994) observed that *C. maculata* survives on *Hypera postica* (Gyllenhal) larvae but does not reproduce on these larvae. In the alfalfa fields, *H. postica* may be used by *C. maculata* adults until food adequate for reproduction (e.g., pea aphids) is available.

In this study, the preoviposition period was significantly shorter for *C. maculata* females fed pea aphids than for those fed *L. decemlineata* eggs, regardless of the preimaginal diet. At the lowest egg density (2 eggs per day), females had longer preoviposition periods than at the higher prey densities. Similarly, Hodek et al. (1978) reported that the preoviposition period was almost 2 times shorter for *C. maculata* females fed pea aphids than for those fed corn pollen. Phoofolo and Obrycki (1997) found that preoviposition period of *C. maculata* fed *A. pisum*, as both larvae and adults, was almost 2 times (12.9 ± 3.06 d) that observed in our study (6.77 ± 0.91 d). This difference may have been caused by large variations in preoviposition period among females in the Phoofolo and Obrycki (1997) study.

The results of the current study differ from those of Hazzard and Ferro (1991) who reported that *C. maculata* females laid more eggs per day on a green peach aphid, *Myzus persicae* (Sulzer), diet (3.89 ± 0.69 eggs per female per day) than on *L. decemlineata* egg diet (0.87 ± 0.47 eggs per female per day). They also reported that 85% of females fed *M. persicae* produced eggs compared with 25% of those fed *L. decemlineata* eggs. In our study, 88–96% of females fed *A. pisum* and 84–92% of females fed *L. decemlineata* eggs (except those with *L. decemlineata* eggs as preimaginal diet and provided 10 eggs daily) produced eggs. The differences between the 2 studies may be the result of the relatively short experimental period (7 d) in the Ferro and Hazzard (1991) study. In our study, the preoviposition period for >50% of *C. maculata* females was between 6 and 15 d. Previously, several studies have shown that some diets may extend the preoviposition period in coccinellids. For example, Hodek et al. (1978) showed that corn pollen temporarily slowed oviposition in *C. maculata* females, but normal oviposition in these females resumed after 7 wk. Hodek et al. (1978) suggested that this oviposition inhibition was a diapause induced by food, similar to the one described by Hagen (1962) for *Hippodamia convergens* Guérin-Méneville.

Fecundity did not differ significantly among females feeding on the different diets with the exception of females reared 10 *L. decemlineata* eggs daily. This difference in fecundity was the result of 52% of females ovipositing and of all of the females in the 10 *L. decemlineata* eggs per day group presumably entering diapause by the 5th wk of the 14-wk experimental period. These results contrast with those of Phoofolo and Obrycki (1997) who reported that fecundity of female *C. maculata* was

influenced by both larval and adult diets of *A. pisum* and *O. nubilalis* eggs. They observed large variation in fecundity among females on each diet. In the current study, the fertility of *C. maculata* females was not quantified. However, observations of egg hatch indicated that eggs were fertile.

Groden et al. (1990), Hazzard and Ferro (1991), and Hazzard et al. (1991) pointed out that high densities of *M. persicae* in potatoes likely would decrease the effectiveness of *C. maculata* against *L. decemlineata*. However, the presence of aphids in potato fields would enhance the larval development of *C. maculata* (Hazzard and Ferro 1991, Munyaneza 1996). In a study of the development of *C. maculata* feeding on *L. decemlineata* eggs (Munyaneza 1996), results showed that alternate prey such as aphids were very important for the survival of early (1st and 2nd) instars of *C. maculata*, which have difficulties feeding on *L. decemlineata* eggs.

L. decemlineata eggs are suitable prey for *C. maculata* egg production, even at low prey densities. Studies of the hemipteran predator *Podisus maculiventris* (e.g., Legaspi 1991, Valicente and O'Neil 1995) showed that there is a trade-off between survival and reproduction when this predator receives low prey inputs. When fed 2 *L. decemlineata* eggs per day, *C. maculata* females did not show any difference in fecundity compared with females fed an excess of *A. pisum* but did show a significant delay in oviposition initiation. These results indicate that the reproductive threshold of *C. maculata* is <2 *L. decemlineata* eggs. In general, each female *L. decemlineata* produces ≈ 300 –500 eggs in egg masses of 10–40 eggs (Horton and Capinera 1987). As a result, once an *L. decemlineata* egg mass is found, it is likely that >2 eggs will be consumed by *C. maculata*.

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