Feeding Responses of Adult *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Eggs of Colorado Potato Beetle (Coleoptera: Chrysomelidae) and Green Peach Aphids (Homoptera: Aphididae)

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Environ. Entomol. 20(2): 644–651 (1991)

ABSTRACT Feeding responses that influence the effectiveness of a polyphagous endemic coccinellid, *Coleomegilla maculata* (DeGeer), for biological control of Colorado potato beetle, *Leptinotarsa decemlineata* (Say), in potato were examined in the laboratory. Consumption rate, functional response, prey preference, and the effect of alternate prey were studied for *C. maculata* adult females feeding upon eggs of Colorado potato beetle; *Myzus persicae* (Sulzer) and corn pollen were alternate food sources. *C. maculata* females continuously supplied with eggs attacked an average of 20.8 eggs per 48 h, and introduction of *M. persicae* significantly reduced but did not eliminate egg feeding. Females starved for 24 h showed a Type II functional response to egg density when offered 10–70 eggs per 24 h in small cages at 26 ± 2°C. Data fit well to the Holling disk equation, which predicted maximum egg consumption of 31.5 eggs per 24 h. The functional response curve showed suppression of egg feeding at high egg densities when aphids were present as alternate prey, but no effect was evident at low egg densities. There was no change in functional response with corn pollen as the alternate food. When Colorado potato beetle eggs and aphids were available in equal numbers, females did not prefer either prey at low prey densities, but they preferred aphids over eggs at high densities. Eggs were an adequate (but not optimal) diet for larval development and adult oviposition relative to *M. persicae* or corn pollen. Some implications for ecology and effectiveness of *C. maculata* for control of Colorado potato beetle in potato are discussed.

KEY WORDS Insecta, *Coleomegilla maculata, Leptinotarsa decemlineata,* functional responses

COLORADO POTATO BEETLE, *Leptinotarsa decemlineata* (Say), is a major pest of potato in the northeastern United States. Resistance of the beetle to virtually all available chemical controls (Forgash 1985) and environmental contamination caused by insecticides used for its control (Zaki et al. 1982) have resulted in a search for effective biological control agents.

The coccinellid *Coleomegilla maculata* (DeGeer) is a native predator of Colorado potato beetle eggs and is common in potato fields in western Massachusetts. Previous studies of *C. maculata* in potato have focused on its predation on green peach aphid, *Myzus persicae* (Sulzer) (Mack & Smilowitz 1982a,b; Obrycki & Tauber 1985). In corn, *C. maculata* adults and larvae feed upon corn leaf aphid, *Rhopalosiphum maidis* (Fitch), corn pollen (Wright & Laing 1980), and eggs of European corn borer, *Ostrinia nubilalis* (Hübner) (Conrad 1959). Although *C. maculata* has been recognized as an important predator of both aphids and insect eggs in other crops, it has yet to be evaluated for effectiveness against Colorado potato beetle eggs in potato.

Coleomegilla maculata is a mobile, polyphagous predator (Conrad 1959, Wright & Laing 1980) which survives well on a variety of food sources. Aphids alone, either alive or dried, are a sufficient diet for larval development and egg production by adults (Smith 1965a,b; Atallah & Newsom 1966). Corn pollen alone was sufficient to maintain a population of *C. maculata* for five generations when reared in the laboratory (Hodek et al. 1978). Warren & Tadic (1967) successfully reared *C. maculata* larvae on *Hyphantria cunea* (Drury) eggs. Assessment of larval development rates and rate of egg production by females on a diet of Colorado potato beetle eggs is needed, because the effectiveness of a predator population depends in part on its ability to increase its numbers through reproduction. This study compared these rates for Colorado potato beetle eggs, *M. persicae,* and corn pollen.

A second component of predator effectiveness is the change in rate of attack by individual predators as prey density changes, the functional response. Colorado potato beetle eggs undergo rapid fluctuations in density in potato fields, with peak densities occurring in the latter half of June and the

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end of July (Voss & Ferro 1989). The individual functional response of *C. maculata* to these changes in prey density needs to be understood. Mack & Smilowitz (1982a) described a temperature-mediated functional response of *C. maculata* to *M. persicae*.

Presence of alternate food sources within or near potato fields may influence *C. maculata* feeding rates on Colorado potato beetle eggs. Aphids, primarily *M. persicae* and potato aphid, *Macrosiphum euphorbiae* (Thomas), colonize potato by early July (Obrycki et al. 1983; D.N.F., unpublished data) at the end of oviposition by overwintered Colorado potato beetle adults. Frequently, aphids are present throughout the second Colorado potato beetle oviposition period. If *C. maculata* prefers aphids to eggs, its predation upon Colorado potato beetle eggs deposited late in the first and throughout the second oviposition period could be reduced.

Cornfields planted near potato are alternate sites of *C. maculata* feeding and reproduction, particularly after tasseling when pollen is available (Wright & Laing 1980, Benton & Crump 1981). Feeding responses of *C. maculata* to corn pollen as an alternate food may influence its persistence in potato and the rate of predation on Colorado potato beetle eggs.

The objective of this research was to determine the rate of attack on eggs by adult *C. maculata* under two regimes: (1) eggs supplied continuously to *C. maculata*, with predation measured over a succession of 48-h intervals; and (2) eggs supplied to starved individuals, with predation measured after 24 h. The number of eggs attacked per predator in 24 h was studied over a range of prey densities to determine whether the functional response adheres to the common nonlinear Type II model, the "disk equation" (Holling 1959). We examined the effect of the presence of *M. persicae* on *C. maculata* rate of attack on eggs under each regime and the effect of aphids or corn pollen on the functional response to eggs. A further objective was to assess preference for green peach aphids versus Colorado potato beetle eggs.

Materials and Methods

Effect of *M. persicae* on Rate of Attack on Colorado Potato Beetle Eggs. Experiments were conducted on F_2 offspring of *C. maculata* adults collected on 30 September 1986 at a winter aggregation site near a potato field in Great Barrington, Mass. Larvae were reared singly in Petri dishes on a diet of corn pollen, Colorado potato beetle eggs, and *M. persicae* at 25 ± 3°C, 80% RH, and a photoperiod of 16:8 (L:D). Adults received only Colorado potato beetle eggs before experiments were begun.

Individual females >1 wk old (n = 19) were placed into vented plastic boxes (5 by 6 by 12 cm) with one mature potato leaf on which Colorado potato beetle eggs had been laid within the previous 36 h. All individuals were fed until satiation with eggs before the experiment. Eggs were moved without injury with a brush so that each egg mass contained 30 eggs. Potato leaves were kept fresh by placing stems in one-quarter strength Hoagland's solution (Hoagland & Arnon 1950) in a floral water pic. Water was provided to beetles with moistened dental wicking.

Every 48 h thereafter, eggs and leaves were removed and replaced with fresh eggs (<36 h old) on a new potato leaf. Any eggs laid by *C. maculata* were removed. This pretreatment period continued for three 48-h intervals.

Colorado potato beetle eggs that were removed from experimental boxes were examined under a dissecting microscope to determine rate of attack. An egg was considered attacked if the chorion was punctured. An attacked egg was considered "partially eaten" if more than one-third of the yolk remained and "all eaten" if less than one-third remained.

At the beginning of the fourth 48-h interval, two treatment groups were established: (1) those receiving 40 *M. persicae* in addition to 30 eggs (n = 9); (2) those receiving only 30 eggs as before (n = 10). The aphids used were late instars or apterous adults reared on potato. Eggs and aphids were replenished every 48 h for three posttreatment intervals. Only the number of eggs attacked was counted.

The mean number of eggs attacked in treatment (aphids and eggs) and control (eggs alone) groups were compared for each 48-h interval using a t test. Because repeated measures were made of the same individuals, the effect of aphids was assessed by computing the average attack rate per individual over the pretreatment and posttreatment periods and taking the difference ("post-pre"). This difference was compared for treatment and control groups using a t test of the difference.

Functional Response of *C. maculata* to Colorado Potato Beetle Eggs. Adult *C. maculata* used in these experiments were the F_1 offspring of late-diapause adults collected at a winter aggregation site in Amherst, Mass., on 11 April 1988.

Egg clusters collected from male-female parent pairs were hatched and reared in sibling groups on a diet of Colorado potato beetle eggs, green peach aphids, and corn pollen. Total losses from cannibalism and other causes of mortality from the second instar to the pupal stage were 20.2%. Adults were removed from group boxes and placed individually in Petri dishes within 48 h after emergence. No mating was observed among adults <48 h old. Females used were 8–28 d old. Adult diet consisted of Colorado potato beetle eggs and *M. persicae*. Rearing and experiments were conducted at 25 ± 3°C, 80% RH, and a photoperiod of 16:8 (L:D).

For the functional response and preference experiments, a randomized complete block design was used. Each experiment was repeated twice with five or six replicates in each experiment except that with corn pollen, which was conducted once with nine replicates. Sibling groups (reared from the egg batches of one male–female pair) formed the blocks with one sibling in each block receiving each treatment.

Coleomegilla maculata females had no food for 24 h before experiments were begun. Egg masses (<36 h old) of the desired density were provided to individual females, as described in previous experiments. Females were observed feeding within minutes of placing the leaflet (eggs) in the box, indicating that search time within this arena was very short relative to the time period measured. After 24 h, the leaflet was removed and the number of eggs attacked was determined.

Functional Response to Eggs Alone. Egg attack rate was tested over a range of egg densities. Individual beetles were provided with egg densities of 10, 16, 22, 28, 34, 42, 50, 60, or 70 per cage. Two separate masses on one leaf were used for densities 50 and 60; two masses on two separate leaves for density 70; and a single mass on a single leaf for all other densities.

Functional Response to Eggs with Aphids Present. Forty *M. persicae* nymphs (half third or fourth instars, half first or second instars) were placed upon the same leaflet as the egg mass. Egg densities tested were 10, 16, 22, 28, 34, 42, 50, and 60 per beetle. Leaves were trimmed so that any curled or nonexpanded leaflets that could provide refuge for aphids were removed. Aphids distributed themselves about the leaflets over the course of 24 h. The number of aphids eaten was calculated as the number available minus the number remaining after 24 h. Preliminary tests showed that aphids did not become reproductive during this period.

Functional Response to Eggs with Pollen Present. Corn pollen was presented as an alternate food source at egg densities of 16, 22, 28, 34, 42, 50, and 60 per beetle to test its effect on functional response. Sifted pollen (4.8 ml) that had been collected in September 1987 from sweet corn and frozen until 1 July 1988 was placed in a Petri dish next to the leaflet with eggs. Thus, both food sources were in a "patch"; the patches were 2–4 cm apart. Egg attack rate was measured after 24 h; pollen consumption was not measured.

Analysis of Functional Response Data. Data were fit to a modified Holling disk equation (Williams & Juliano 1985):

$$N_a/TP = aN/(1 + aT_hN),$$

where N_a is the number of prey attacked, T is the total time prey was exposed, P is the number of predators, N is the initial prey density, a is the rate of attack, and T_h is the handling time. In these experiments, $T = P = 1$. Handling time, T_h, is defined as the time that elapses from discovery of prey until search is resumed.

Conceptually, the Rogers linearization of the disk equation (the "random predator equation") (Rogers 1972) is more appropriate than the model used for experimental conditions in which prey is depleted over time. However, the statistical validity of this equation for regression analysis is questionable (Livdahl & Stiven 1983, Williams & Juliano 1985). Furthermore, it has been shown to give highly biased parameter estimates in simulations where true parameter values were known (Williams & Juliano 1985, Juliano & Williams 1987). Unbiased estimates are achieved using nonlinear least-squares regression of the disk equation (Juliano & Williams 1987), which in this analysis was done using the NLIN procedure in SAS (SAS Institute 1987). Confidence limits and asymptotic standard errors for these parameters were used as indicators of differences between the functional response curves with and without alternate prey, as suggested by Livdahl & Stiven (1983). A reciprocal linearization of the disk equation, $P/N_a = (1/aTN) + T_h/T$ (Livdahl & Stiven 1983), provided initial estimates of a and T_h, which are required for the NLIN method.

Preference for Eggs Versus Aphids. To test the preference of *C. maculata* for alternate prey under varying prey densities, equal numbers of *M. persicae* and eggs were presented at five densities: 10:10, 20:20, 30:30, 40:40, and 50:50. Any difference between the numbers of eggs eaten (n_e) and numbers of aphids eaten (n_a) can be considered an indication of preference for one prey type relative to the other, if random movement of the predator about the leaf is assumed and rate of encounter with eggs and aphids is equal. The null hypothesis for absence of preference is that $n_e - n_a$ equals 0. This is equivalent to the hypothesis that the ratio n_e/n_a equals 1, as used by Murdoch (1969) to measure preference. To equalize rate of encounter of prey types, single eggs were distributed evenly across the underside of the leaf, which was then placed with the underside facing up. A 1:1 proportion of small and large aphid nymphs was also distributed evenly, and their refugia were removed. Aphids did not aggregate as they moved about the leaf; however, since some movement to the reverse side of the leaf was unavoidable, and eggs could only be placed on one side, the assumption of equal encounter rate was not fully upheld. In controls without predators, all aphids were found after 24 h.

The experiment was repeated twice with five replicates per treatment in each experiment. The sign test (Sokal & Rohlf 1981) was used for statistical analysis because the assumption of normality was violated in one treatment.

Larval Development on Alternate Diets. First-instar *C. maculata* (<24 h old) were reared on one of three diets: (1) Colorado potato beetle eggs, (2) corn pollen, or (3) green peach aphids. A randomized complete block design consisting of 14 replicates for each of three treatments was used. Each block had three siblings from a single *C. maculata* egg mass. Larvae received excess food, which was renewed every other day. Water was provided by

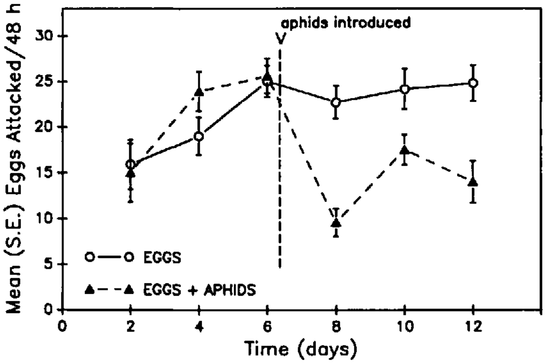

Fig. 1. Mean number of Colorado beetle eggs attacked, alone (O) or in the presence of *M. persicae* (▲), by *C. maculata* adult females.

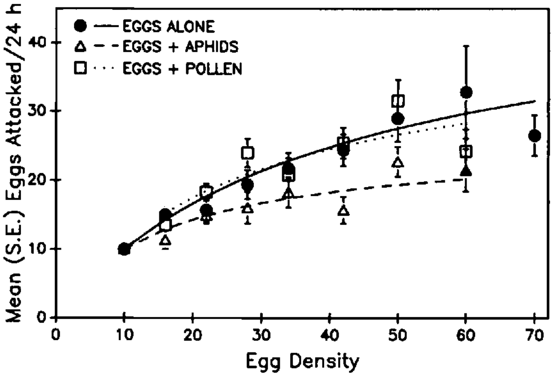

Fig. 2. Comparison of functional response of *C. maculata* adult females to Colorado potato beetle eggs with and without *M. persicae* or corn pollen as alternate food.

moistened dental wicking. Death, pupation, or adult emergence were recorded daily. Effect of diet on development time was tested using the GLM procedure (SAS Institute 1987) and Tukey's studentized range test.

Attack Rate of Male and Female *C. maculata* on Eggs. The number of Colorado potato beetle eggs attacked over 24 h was measured for individual unmated male and female adults. All had been reared as larvae on eggs, corn pollen, and green peach aphids, received eggs and aphids after adult emergence, were starved for 24 h before the experiment, and were provided 45 eggs for 24 h. Twenty male–female sibling pairs with emergence dates no more than 3 d apart were compared for number of eggs attacked and number half-eaten. Age of adults ranged from 11 to 27 d. A paired *t* test was used to compare differences in the number of eggs attacked by males and females.

Rate of *C. maculata* Oviposition on Alternate Diets. A diet sufficient for maintenance of *C. maculata* adult females may not be adequate for production of eggs (Smith 1965b). Unrelated adult pairs were confined with a diet of either eggs or aphids ($n = 20$ pairs per treatment). Daily oviposition was measured for 7 d after a 1-wk preconditioning period. Males and females were 29–40 d old when oviposition was first measured. Pairs were fed every other day; each received food in excess. *C. maculata* eggs were removed so that they would not serve as a source of food. A *t* test was used to assess the difference in daily oviposition on the two diets.

Table 1. Standard errors and 95% confidence intervals for estimates of parameters *a* and T_h in the Holling disk equation for *C. maculata* feeding on Colorado potato beetle eggs with and without alternate prey

Prey	Parameter	Estimate	Asymptotic SE	95% CL	
				Lower	Upper
Eggs	a	1.2659	0.082	1.1030	1.4289
	T_h	0.0205	0.000	0.0205	0.0205
Eggs + aphids	a	1.6435	0.825	0.0045	3.2826
	T_h	0.0393	0.009	0.0213	0.0573
Eggs + pollen	a	1.1540	0.415	0.7089	2.3701
	T_h	0.0245	0.005	0.0112	0.3379

Results

Effect of *M. persicae* on Rate of Attack on Colorado Potato Beetle Eggs. Adult females provided with a continuous supply of eggs attacked 20.84 ± 1.11 ($\bar{x} \pm$ SE) eggs per 48 h ($n = 19$) (Fig. 1). The number of eggs attacked was reduced in the treatment group after aphids were introduced, with the greatest decrease occurring in the first 48 h after aphid introduction. Group means were not different for the time interval immediately preceding introduction of aphids (*t* test, $t = -0.2274$; df = 17; $P = 0.8228$) but were different for the time interval immediately after ($t = 5.5622$, df = 17, $P < 0.0001$) and continued to be significantly different through day 12.

Individuals fed both aphids and eggs during the posttreatment period continued to attack Colorado potato beetle eggs, but the rate of attack was reduced an average of 7.93 ± 1.52 eggs per 48 h, or 36.7%. This change in attack rate of individuals (post–pre) was significantly different from that of *C. maculata* which continued to feed on eggs alone (*t* test, $t = 7.0431$; df = 12.7; $P = 0.0001$).

Functional Response of *C. maculata* to Eggs Alone. The data were fit to the Holling disk equation using weighted variance because variability in the rate of attack increased with prey density, as is common with functional response data (Williams & Juliano 1985). Parameters were first estimated with the Livdahl-Stiven (1983) reciprocal linearization method, which gave $a = 1.47$, $T_h = 0.033$ d with $R^2 = 0.237$. These were entered into the NLIN procedure, which gave more precise estimates of $a = 1.27$, $T_h = 0.021$ d (Table 1) with $R^2 = 0.990$; the resulting curve is plotted in Fig. 2.

Attack rates were higher for starved beetles than with continuously fed *C. maculata*. At the lowest density ($n = 10$), all eggs were eaten by all indi-

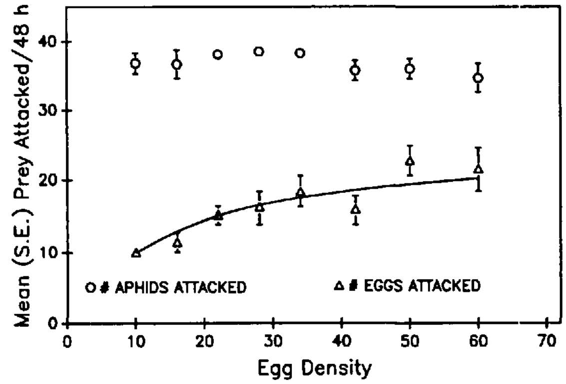

Fig. 3. Functional response of *C. maculata* to Colorado potato beetle eggs in the presence of aphids (*M. persicae*).

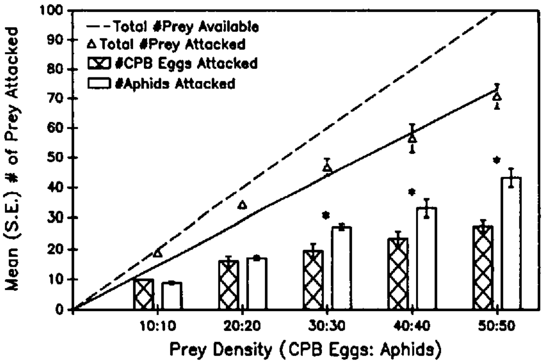

Fig. 4. *C. maculata* predation on Colorado potato beetle (CPB) eggs and aphids (*M. persicae*) when offered both prey at equal densities and equal probability of encounter. Means (*) are significantly different ($P < 0.05$) using the sign test (Sokal & Rolf 1981).

viduals. The highest recorded mean attack rate was 32.8 ± 6.7 eggs/d at $n = 60$. Maximum predation rate predicted by the disk equation model, within the density range tested, is 31.5 eggs/d at $n = 70$. Of all eggs attacked over all densities ($n = 100$), 8.4% were left half-eaten.

Functional Response to Eggs with Aphids Present. Aphids reduced the number of eggs attacked at all egg densities above $n = 10$. Parameters of the disk equation estimated by NLIN were $a = 1.64$ and $T_h = 0.039$ with $R^2 = 0.98$ (Fig. 3). Handling time, T_h, was significantly higher than with eggs alone, but search rate, a, was not (Table 1). The rate of predation on aphids did not change with egg density (SAS GLM; $F = 0.85$; df = 7, 36; $P = 0.5512$) (Fig. 3). Total number of prey items attacked was higher when aphids were present than when absent at all densities. Of all eggs attacked over all densities ($n = 90$), 20.0% were left half-eaten.

The blocking groups used in the randomized block design of functional response experiments consisted of siblings reared from the eggs of one male–female pair. A linear model testing for treatment, block, and experiment effects (SAS GLM) found block effects to be significant in experiments with eggs alone ($F = 6.31$; df = 5, 75; $P = 0.0001$) and with eggs plus aphids ($F = 2.18$; df = 10, 70; $P = 0.0293$), suggesting that genetic influences on feeding responses may be important.

Functional Response to Eggs with Pollen Present. The presence of pollen did not have any effect on the rate of attack on Colorado potato beetle eggs. The parameter estimates for the disk equation were $a = 1.54$, $T_h = 0.024$ with $R^2 = 0.90$ (Fig. 2), which are not significantly different from those with eggs alone (Table 1). Because pollen consumption was not measured, it is not known whether feeding on pollen took place in a contemporary fashion or not at all.

Preference for Eggs Versus Aphids. Preference was measured by the difference between the number of eggs attacked (n_e) and aphids attacked (n_a) when both were offered at equal densities. The mean difference was 1.0 ± 0.54 at density 10:10 and −1.0 ± 1.50 at density 20:20. Neither value was significantly different from that expected if no preference existed, according to the sign test ($P = 0.984$ and $P = 0.773$, respectively). At the three higher densities, the differences were significant, indicating a preference for aphids. The difference ($n_e - n_a$) was −7.8 ± 1.71 ($P = 0.002$) at prey density 30:30, −9.5 ± 2.28 at 40:40 ($P = 0.001$), and −15.7 ± 2.59 at 50:50 ($P = 0.011$).

The total number of eggs and aphids attacked increased linearly as density increased (SAS REG, $y = 0.731x$, $P = 0.0001$, $r^2 = 0.96$) (Fig. 4). At prey density 10:10, nearly all of both types of prey was eaten. The proportion of eggs attacked decreased linearly with density, from 0.99 at the lowest density to 0.55 at the highest ($y = 1.047 - 0.011x$, $P = 0.0001$ for both parameters, $r^2 = 0.44$) (Table 2). The proportion of aphids attacked showed no trend in relation to density and varied between 0.83 and 0.91 ($P = 0.6620$).

Larval Development on Alternate Diets. Larvae were able to complete their development on each of the three food sources tested (green peach aphid, corn pollen, or Colorado potato beetle eggs). Diet had a significant effect on larval development time

Table 2. Proportion of each prey type eaten by female *C. maculata* offered equal numbers of *M. persicae* and Colorado potato beetle eggs

Prey density	Proportion eaten			
	Eggs		Aphids	
	$\bar{x}$	SE	$\bar{x}$	SE
10:10	0.99	1.01	0.89	0.05
20:20	0.81	0.08	0.86	0.04
30:30	0.65^a	0.07	0.91^a	0.03
40:40	0.59^a	0.06	0.83^a	0.07
50:50	0.55^a	0.04	0.86^a	0.06

[a] Mean proportions for eggs and aphids consumed are significantly different ($P < 0.05$) using the sign test (Sokal & Rohlf 1981).

($n = 14$; $F = 40.73$; df = 2, 36; $P = 0.0001$; SAS GLM). Development was fastest on a diet of aphids ($\bar{x} = 14.86 \pm 0.27$) and slowest on eggs ($\bar{x} = 19.82 \pm 0.59$), with pollen being intermediate ($\bar{x} = 16.21 \pm 0.27$) ($P < 0.05$, Tukey's test). Survival was lowest on eggs (79%) compared with the other diets (100%, aphids; 100%, pollen), and variability in development time was also higher.

Attack Rate by Male and Female *C. maculata* on Eggs. Females attacked significantly more eggs than males ($n = 20$, $t = 5.989$, $P = 0.0001$), averaging 24.5 ± 1.6 eggs/24 h compared with 16.2 ± 1.4 eggs/24 h for males. Males left a higher proportion of half-eaten eggs than did females (23.3%, males; 16.3%, females).

Rate of *C. maculata* Oviposition on Alternate Diets. Females laid more eggs per day on the aphid diet (3.89 ± 0.69) than on the egg diet (0.87 ± 0.47). This difference was significant (t test, $n = 20$, $t = 3.675$, $P = 0.001$). Eighty percent of the females fed aphids produced eggs compared with 25% of those fed eggs. However, individual ability to utilize the egg diet was variable. The maximum daily oviposition by one individual was almost as high in the egg group (8.7 eggs/d) as in the aphid group (10.9 eggs/d).

Discussion

Previous research on the predatory capacity of *C. maculata* has considered the effects of temperature (Mack & Smilowitz 1982a,b), food concentration (Wright & Laing 1980, Gross et al. 1985), and plant characteristics (Obrycki et al. 1983). Our experiments have considered the effects of satiation and hunger, prey density, presence of alternate prey, and sex on the rate of attack of prey.

The rate at which *C. maculata* attacked eggs of Colorado potato beetle when prey was continuously available in excess provides an estimate of the upper limit of average daily feeding capacity. Average rate of attack was 10.4 eggs/d when 30 eggs were provided every 48 h over 6 d. Conditions that might increase this include greater abundance of prey and slightly higher temperature. Subsequent tests of functional response showed that even when less than the total available prey was attacked at a given prey density, the upper limit of feeding capacity may not necessarily have been reached. Temperatures of 24–26°C are optimal for *C. maculata* growth and development (Obrycki & Tauber 1978). However, Mack & Smilowitz (1982a) found that predation rate (as indicated by $1/T_h$) and attack rate (a) continued to rise with an increase in temperature, up to ≈29°C. Conditions that would reduce the rate of feeding on continuously available prey include lower temperatures, inclusion of males, a large arena in which to search for prey, and possibly predator ages >28 d. Any estimate of the predation capacity of a population of *C. maculata* should include consideration of the sex ratio, because male attack rate was significantly lower than that of females.

Starved females ate approximately twice as much as satiated females (≈20 eggs in 24 h) when presented with 30 eggs. Frazer & Gill (1981) developed a hunger curve by plotting aphids eaten versus starvation time for *Coccinella californica* (Mannerheim) feeding on pea aphids, *Acyrthosiphon pisum* (Harris). For *C. californica*, maximum hunger was reached by 20 h and further starvation up to 48 h did not appreciably increase consumption. If *C. maculata* had reached a maximum level of hunger at 24 h, our results suggest what might be eaten by hungry *C. maculata* adults that arrived at a patch of food and stayed there for 24 h.

The functional response of *C. maculata* to egg density conforms well to that described by Holling (1959) as Type II, a convex curve with decreasing slope at high prey densities (Fig. 2). The maximum attack rate of slightly >30 eggs/d may not represent the true upper limit of predation capacity because the curve did not reach a plateau within the density range tested (Fig. 2).

Colorado potato beetle eggs are an adequate but not an optimal diet for larval development and female oviposition. Rates of larval development and survival, oviposition rate, and the proportion of females producing eggs were all higher on the aphid diet than on the egg diet. Larval development was faster on corn pollen than on eggs.

Introduction of aphids to *C. maculata* that had been fed eggs since adult emergence (≥14 d) caused an immediate drop in the rate of attack on eggs. This moderated somewhat in subsequent intervals but averaged to a suppression of egg feeding by about one-third after introduction of aphids. Thus, one would expect that aphid colonization of a field in which *C. maculata* had been feeding on Colorado potato beetle eggs would reduce, but not eliminate, egg predation.

This reduction also occurred where previous feeding exposure included aphids but did not appear to be greater than when *C. maculata* had been conditioned to eggs alone. The functional response of *C. maculata* to egg density was altered by the presence of aphids, with a maximum suppression of about one-third relative to eggs alone. There was no indication of a sigmoid shape in the curve, which would have suggested switching from one prey to the other with increasing density (Akre & Johnson 1979). We did not see a complete switch to aphids but rather an increase in total numbers of prey eaten when the prey consisted of both eggs and aphids. Because most of the 40 aphids available were attacked (Fig. 3), it is possible that greater suppression would have occurred if the density of aphids were higher.

Suppression of egg feeding occurred only when densities of prey exceeded a threshold level. When both aphids and eggs were present but density was low, all of the eggs were attacked in both preference and functional response experiments. *C. mac-*

ulata showed no preference for aphids or eggs at 40 prey items/d (half aphids, half eggs) or less. At higher densities, a significant preference for aphids was exhibited.

In potato fields where *C. maculata* are feeding on Colorado potato beetle eggs, colonization of the field by *M. persicae* could be expected to cause suppression of egg feeding due to increased encounters with aphids and preference for aphids over eggs. However, this is likely to occur only at prey densities above a certain threshold; below such a threshold, one might expect complementary feeding on the two prey types and no suppression of egg feeding. Other likely effects are enhanced reproduction of *C. maculata* because of greater egg deposition and faster larval development with aphids included in the diet, and maintenance of a resident population of *C. maculata* through periods when Colorado potato beetle eggs are scarce. Individual functional response may account in part for changes in the mortality rate caused by populations of *C. maculata* feeding upon Colorado potato beetle eggs in potato fields.

Acknowledgment

We thank Arthur Tuttle, Craig Stevens, Tuan Nguen, and Jennifer Grant for assisting in the research. We are indebted to Joe Elkinton, Ring Cardé, and Roy Van Driesche for critically reviewing this manuscript, and to Julie Gould for assistance in statistical analysis. This research was supported by Massachusetts Agricultural Experiment Station NE-154 and Massachusetts Department of Agriculture, publication 3008.

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Received for publication 10 October 1989; accepted 15 November 1990.