



University of  
Massachusetts  
Amherst

## **Coleomegilla maculata (DeGeer) predation on eggs of Colorado potato beetle, Leptinotarsa decemlineata (Say).**

Item Type	thesis
Authors	Hazzard, Ruth V.
DOI	<a href="https://doi.org/10.7275/18860396">10.7275/18860396</a>
Download date	2025-05-13 13:56:55
Link to Item	<a href="https://hdl.handle.net/20.500.14394/46699">https://hdl.handle.net/20.500.14394/46699</a>

UMASS/AMHERST



312066007687755

COLEOMEGILLA MACULATA (DEGEER) PREDATION

ON EGGS OF COLORADO POTATO BEETLE,

LEPTINOTARSA DECEMLINEATA (SAY)

A Thesis Presented

by

RUTH V. HAZZARD

Submitted to the Graduate School of the  
University of Massachusetts in partial fulfillment  
of the requirements of the degree of

MASTER OF SCIENCE

May 1989

Department of Entomology

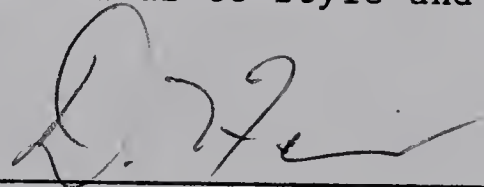
COLEOMEGILLA MACULATA (DEGEER) PREDATION  
ON EGGS OF COLORADO POTATO BEETLE,  
LEPTINOTARSA DECEMLINEATA (SAY)

A Thesis Presented

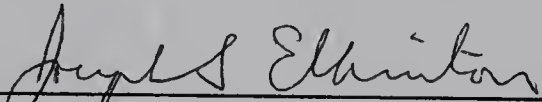
by

RUTH V. HAZZARD


Approved as to style and content by:



David N. Ferro, Chairperson of Committee



Joseph S. Elkinton, Member



Ring T. Carde, Member



John D. Edman, Department Head  
Department of Entomology

## ACKNOWLEDGMENTS

I am grateful to Dave Ferro for keeping the door to his office always open for me, and thereby opening the door to the profession of Entomology. Special thanks to Roy Van Driesche and Joe Elkinton for their assistance in this work, and to all of my professors for their generosity in teaching. I appreciate the help of Buddy, Tuan and Jennifer in counting eggs and feeding beetles, which made these experiments possible.

Jean and George Hazzard have given their loving support from beginning to end, both as parents and grandparents, and this could not have been accomplished without them. I thank my wonderful children Ethan and Jesse, who inspire me daily and keep me attuned to the delights of the present moment. To all those who have helped with their care, especially Allison who set us on our way, and Mary, Dawn, MaryAnn, and Timm, I extend great appreciation. Colleagues whose friendship has been invaluable are Arthur, Geni, Karen, Bob, Don, Kathy and Rolando. Loving thanks to my sister Anne, may our paths continue to weave together. And for wisdom and inspiration that is as important in the practice of science as in any other human endeavor, I offer thanks to the Ven. Dhyani Ywahoo and the circle of the Sunray Meditation Society.

TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGMENTS .....	iii
LIST OF TABLES .....	v
LIST OF FIGURES .....	vi
Chapter	
1. FEEDING RESPONSES OF ADULT <u>COLEOMEGILLA MACULATA</u> (DEGEER) TO EGGS OF COLORADO POTATO BEETLE AND TO GREEN PEACH APHIDS .....	1
Introduction .....	1
Materials and Methods .....	6
Results .....	13
Discussion .....	18
2. MORTALITY TO EGGS OF COLORADO POTATO BEETLE FROM PREDATION BY <u>COLEOMEGILLA MACULATA</u> (DEGEER) .....	33
Introduction .....	33
Materials and Methods .....	36
Results .....	41
Discussion .....	46
BIBLIOGRAPHY .....	59

LIST OF TABLES

- 1.1 The number of Colorado potato beetle (CPB) eggs attacked by individual C. maculata adult females before and after introduction of aphids. .... 25
- 1.2 Proportion of each prey type eaten by female C. maculata were offered equal numbers of M. persicae and Colorado potato beetle eggs. .... 26
- 2.1 Total recruitment of Colorado potato beetle eggs for 1986 and 1987 and generational mortality to the egg stage from predation. .... 51

## LIST OF FIGURES

- 1.1 Effect of the presence of aphids on rate at which Colorado potato beetle eggs were attacked by C. maculata adult females. ....27
- 1.2 Functional response of C. maculata adult females feeding on Colorado potato beetle eggs. ....28
- 1.3 Functional response of C. maculata feeding on Colorado potato beetle eggs with 40 aphids available/24 h in addition to eggs . ....29
- 1.4 Functional response of C. maculata feeding on Colorado potato beetle eggs with corn pollen available in addition to eggs .....30
- 1.5 Comparison of functional response of C. maculata adult females to Colorado potato beetle egg density with and without alternate prey .....31
- 1.6 C. maculata predation on Colorado potato beetle eggs and green peach aphids when offered both prey at equal density and equal encounter rate .....32
- 2.1 Number of Colorado potato beetle egg-consuming carabid beetles which were caught in ten pitfall traps in Plot D in a potato field in Gt. Barrington, Mass., during late July and August, 1987 .....52
- 2.2 Recruitment, density and mortality of second-generation Colorado potato beetle eggs, 1986  
53
- 2.3 Recruitment, density and mortality of first-generation Colorado potato beetle eggs, 1987  
55
- 2.4 Recruitment, density and mortality of second-generation Colorado potato beetle eggs, 1987  
57



## CHAPTER 1

# FEEDING RESPONSES OF ADULT COLEOMEGILLA MACULATA (DEGEER) TO EGGS OF COLORADO POTATO BEETLE AND TO GREEN PEACH APHIDS

### Introduction

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

A native predator of Colorado potato beetle eggs which is common in potato fields in western Massachusetts is the polyphagous coccinellid Coleomegilla maculata (DeGeer). Previous studies of C. maculata in potatoes have focused on its predation on green peach aphid, Myzus persicae (Sulzer) (Mack and Smilowitz 1982a,b; Obrycki and Tauber 1985). In corn C. maculata adults and larvae feed upon corn leaf aphid, Rhopalosiphum maidis (Fitch) and corn pollen (Wright and Laing 1980) as well as eggs of European corn borer,

Ostrinia nubilalis (Hübner) (Conrad 1959). Warren and Tadic (1967) found C. maculata to be an effective predator of the eggs of fall webworm, Hyphantria cunea (Drury) in elm trees. C. maculata adults rapidly reduced high densities of the eggs of cotton bollworm, Heliothis zea (Boddie), in field cages in Mississippi (Bryson and Schuster 1975). 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.

As a mobile and highly polyphagous predator (Conrad 1959, Wright and Laing 1980), C. maculata might be expected to survive well on a variety of food sources. Aphids alone, either live or dried, have been shown to be a sufficient diet for larval development and adult egg production (Smith 1965a,b; Atallah 1966). Larval survival and adult oviposition rates were higher on a diet of pea aphid, Acyrtosiphon pisum (Harr.) than of R. maidis (Smith 1965a,b). Hodek et. al. (1978) found that corn pollen alone was sufficient to maintain a population of C. maculata for five generations when reared in the laboratory. The adequacy of an egg diet for C. maculata survival has received relatively little attention. Warren and Tadic (1967) successfully reared C. maculata larvae on H. cunea eggs. Since the effectiveness of a predator population depends in part on its ability increase its numbers through reproduction, evaluation of larval development and female egg production on a diet of Colorado potato beetle eggs is needed. This study compared these rates for Colorado potato beetle eggs, M. persicae, and corn pollen.

A second important component of a predator's effectiveness in regulating a prey population which undergoes an extremely rapid rise in density, as the population of Colorado potato beetle eggs does, is the functional response of individual predators to increasing prey density. Mack and Smilowitz (1982a) evaluated the influence of temperature on C. maculata functional response to M. persicae. The nature of C. maculata functional response to Colorado potato beetle eggs and its rate of attack on eggs at a range of egg densities need to be determined to help in evaluating the capacity of this predator to regulate field populations of Colorado potato beetle.

Prey preference has not been examined for C. maculata, but this also needs to be understood for cropping systems with potato or potato and corn. More than one prey species of C. maculata is found in potatoes, either at once or in succession, over the growing season. In June, in areas where overwintering populations of Colorado potato beetle are high, adult Colorado potato beetles colonize potato fields as soon as plants emerge and begin oviposition within a week. The density of Colorado potato beetle eggs increases rapidly relative to other prey within potato fields. C. maculata adults frequently overwinter in aggregations near field borders and feed in uncultivated areas until food is available in cropping areas (Benton and Crump 1981). Although C. maculata has been shown to be less mobile than certain other Coccinellidae (Ewert and Chang, 1966), aggregation in sites of abundant food does occur (Gross et al. 1985, Nichols and Neel 1977, Smith 1971). When overwintering C. maculata adults are abundant in areas surrounding

potato fields, their arrival in potatoes is well synchronized with Colorado potato beetle oviposition (see Chapt. 2).

In potato fields in Massachusetts, Colorado potato beetle egg density typically declines in late June and early July as oviposition rate drops and eggs hatch. Aphids, primarily M. persicae and potato aphid, Macrosiphum euphorbiae (Thomas), colonize potatoes by early July (Obrycki et al. 1983, D.N. Ferro unpub. data), providing alternate prey within the field. Prey preference, relative numbers of eggs and aphids, and spatial distribution of prey influence C. maculata feeding rates on each prey type. If C. maculata prefers aphids to eggs, its impact upon Colorado potato beetle eggs deposited late in the ovipositional cycle of the first generation could be reduced.

Under certain conditions, there can be a period in July with few or no Colorado potato beetle eggs, before the first summer generation of adults begins oviposition. Presence of aphids may reduce C. maculata emigration from potato fields. In mid to late July egg densities rise again, often peaking in the first week of August (Obrycki et al. 1983; Voss and Ferro 1988). Once again there is co-occurrence of both prey types. By mid-August Colorado potato beetle oviposition has ceased (Voss and Ferro 1988) and eggs are no longer available as a food source for C. maculata.

Aggregation of C. maculata in corn after tasselling when pollen is available is common (Wright and Laing 1980, Benton and Crump 1981). While pollen and Colorado potato beetle eggs do not occur together in a single patch, some measure of the effect of pollen on

egg feeding rates will help assess the impact of this crop on C. maculata effectiveness for controlling Colorado potato beetle in potato.

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; 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 the functional response. 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.

Since adults are the most long-lived and mobile stage, and are the stage most abundant in potato fields (Hazzard, unpub. data), these studies focused on adult feeding responses. To provide a basis for estimating egg predation rates in populations consisting of both males and females, male and female attack rates were compared.

## Materials and Methods

### Number of Colorado potato beetle eggs attacked by C. maculata in the presence or absence of M. persicae

Experiments were conducted on F<sub>2</sub> offspring of field C. maculata adults collected on 30 September, 1986 at a winter aggregation site near a potato field in Great Barrington, Massachusetts. Larvae were reared singly at 25 ± 3 °C, 80% RH and L18:D6 in petri dishes on a mixed diet of corn pollen, eggs and M. persicae. Adults received only eggs prior to experiments.

Sources of variability in feeding rates in C. maculata adults include age (consumption is higher in the first week) and sex (females eat more than males) (Smith 1965b). These factors were controlled by using only females over one week old in experiments. Preliminary experiments found no difference between the rate of attack by females 7-17 and 23-28 days old.

Individual females (n=19) were placed into 5X6X12 cm vented plastic boxes (Nalge, Rochester, N.Y.) with one potato leaf on which Colorado potato beetle eggs had been laid within the previous 36 h. Because eggs can be moved gently with a brush without injury, egg masses could be manipulated so that each contained 30 eggs. Leaflets were kept fresh by placing stems in 1/4 strength Hoagland's solution (Hoagland and Arnon 1950) in a floral water pic. Water was provided by moistened dental wicking. Prior to the experiment all individuals were provided with more eggs than they could eat, so all were assumed equally well-fed.

After 48 h, eggs and leaflets were removed and replaced with fresh eggs <36 h old. Any eggs laid by C. maculata were removed each 48 h so they would not become a food source, since C. maculata females cannibalize their own eggs. This was continued for three 48 h intervals. This period prior to introduction of alternate prey is designated 'pre-treatment'.

Eggs were removed and examined under a dissecting microscope to determine feeding damage. Our interest was in the number of eggs attacked rather than the biomass consumed, as this corresponds to mortality in the field. An egg was considered attacked if the chorion was punctured. An attacked egg was considered 'half-eaten' if  $>1/3$  of the yolk remained and 'all eaten' if  $<1/3$  remained.

To test for the effect of aphid presence, half the group was given 40 M. persicae in addition to 30 eggs as before (n=9, eggs; n=10, eggs + aphids). The aphids used were late-instar nymphs or apterous adults reared on potato. Eggs and aphids were replenished after 48 h, for three 48 h intervals. Only the number of eggs attacked was counted. This period (three 48 h intervals after introduction of aphids to half the individuals) is designated "post-treatment".

Mean 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 pre-treatment and post-treatment

periods and taking the difference ('post-pre'). This difference was compared for treatment and control groups using a t-test of 'post-pre'.

Functional response of *C. maculata* to Colorado potato beetle eggs

Adult *C. maculata* used in these experiments were the F<sub>1</sub> offspring of late-diapause adults collected at a winter aggregation site in Amherst, Massachusetts on 11 April, 1988. Rearing methods differed from those described above in several ways. Egg clusters collected from male-female parent pairs were hatched and reared in sibling groups in 5X6X12 cm boxes. Larval cannibalism under these conditions was low relative to more crowded rearing conditions. Total losses from cannibalism and other causes of mortality, from the 2nd instar to the pupal stage, were 20.2%. Within 48 h after emergence adults were removed from group boxes and placed individually in petri dishes. No mating was observed among adults <48 h old and it was assumed that females were unmated. Since mated females vary greatly in oviposition rates (pers. observation), it was assumed that by using unmated females an additional source of feeding variability unrelated to treatment effects could be eliminated. Females used were 8-28 days old. Adult diet consisted of Colorado potato beetle eggs and *M. persicae*.

For the functional response and preference experiments a randomized complete block design was used. Sibling groups (reared from the egg batches of one male-female pair) formed the replicates with one sibling per replicate receiving each treatment. *C. maculata* females had no food for 24 h prior to the experiment. Egg



masses (<36 h old) of the desired density were provided to individual females, as described above. Females were observed feeding on masses within minutes of placing the leaf in their box, indicating that search time within this arena was very small relative to the time period measured.

After 24 h, the leaflet was removed and the number of eggs attacked was determined. Each experiment was repeated twice with 5 or 6 blocks in each experiment. The experiment with corn pollen had nine replicates. When experimental animals were used in successive experiments, they were fed aphids and eggs for 48 h prior to the 24 h fast.

Functional Response to Eggs Alone. Egg attack rate was tested over a range of egg densities to determine the nature of the functional response. 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. Changes in the shape of the functional response curve in the presence of alternate prey may indicate switching among prey or changes in prey preference. Forty M. persicae, half large nymphs (third and fourth instars) and half small nymphs (first and second instars), were placed upon the same leaflet as the egg mass. This number was chosen based on the estimated feeding rate of 48 green peach aphids/day when aphids were the sole food source (Mack and Smilowitz 1982a). Egg densities tested were 10, 16, 22, 28, 34, 42, 50, and

60 per beetle. Leaves were trimmed so that any curled or non-expanded leaflets which 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 number available minus number remaining after 24h.

Functional Response to Eggs with Pollen Present. At egg densities of 16, 22, 28, 34, 42, 50, and 60 per beetle, corn pollen was presented as alternate food source, 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" and these 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 the Holling disc equation (Holling 1959) for a Type II functional response, which is commonly used to describe the relationship between predation rate and prey density (Williams and Juliano 1985). The equation is as follows:

$$\frac{N_a}{T P} = \frac{a N}{1 + a T_h N}$$

where  $N_a$ =number of prey attacked,  $T$ =total time prey was exposed,  $P$ =number of predators,  $N$ =initial prey density,  $a$ =rate of attack, and  $T_h$ =handling time. In these experiments  $T$  was one day and  $P$  was one predator per cage, therefore these terms were dropped from the equation. Handling time,  $T_h$ , is defined as the time that elapses from discovery of prey until search is resumed.

The disc equation was fit to the data using the NLIN procedure in SAS (SAS Institute 1987, p.675). This method was determined by Williams and Juliano (1985) to give the best estimates of the parameters  $T_h$  and  $a$ . A reciprocal linearization of the disc equation (Livdahl and Stiven 1983) was also tried, using the equation

$$\frac{P}{N_a} = \frac{1}{a T N} + \frac{T_h}{T}$$

This gave a poorer fit, but provided initial estimates of  $a$  and  $T_h$  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. If random movement of the predator about the leaf is assumed, and rate of encounter with eggs and aphids is equal, then 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. The null hypothesis for absence of preference is that  $n_e - n_a$  equals zero. This is essentially equivalent to the hypothesis that the ratio  $n_e/n_a$  equals one, as used by Murdoch (1969) to measure preference. In order 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. Aphids, half large nymphs and half small nymphs, were also distributed evenly and refugia removed. Aphids did

not tend to 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 5 replicates per treatment in each experiment. Because the assumption of normality was violated in one treatment, the sign test (Sokal and Rohlf 1981) was used for statistical analysis.

#### Larval Development on Alternate Diets

First-instar C. maculata larvae <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 x 3 treatments was used. Each block had 3 siblings from a single C. maculata egg mass. All larvae received an excess of food which was renewed every other day; water was provided by moistened dental wicking. Observations were made daily to record death, pupation or adult emergence.

#### Rate of Attack on Colorado Potato Beetle Eggs by Male and Female C. maculata

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 prior to the experiment and were provided 45 eggs for 24 h. Twenty male-female sibling pairs with emergence dates no more than

three days apart were compared for number of eggs attacked and number half-eaten. Age of adults ranged from 11 to 27 days.

#### Rate of Oviposition on Alternate Diets

The diet of C. maculata adult females can affect the rate of oviposition; a diet sufficient for maintenance 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 seven days after a one week pre-conditioning period. 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.

#### Results

##### Number of Colorado potato beetle eggs attacked by C. maculata in the presence or absence of M. persicae

Mean eggs attacked by adult females provided with a continuous supply of eggs was  $20.84 \pm 1.11$  eggs/48 h (n=19) (Table 1.1, p.25). 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 (Fig. 1.1, p.27). 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 highly significantly different for the time interval immediately after ( $T=5.5622$ ,  $df=17$ ,  $p<0.0001$ ) and continued to be significantly different during intervals five and six (Fig. 1.1, p.27).

However, complete switching to aphids did not occur. The mean change in attack rate from pre- to post-treatment periods was  $7.93 \pm 1.52$  eggs/48 h for those individuals having both aphids and eggs, a reduction of 36.7%. Mean change in attack rate (post versus pre) was significantly different for the two diets (t-test,  $T=7.0431$ ,  $df=12.7$ ,  $p=0.0001$ ) (Table 1.1, p.25).

Functional response of *C. maculata* to Colorado potato beetle eggs

Functional Response to Eggs Alone. The data were fit to the Holling disc 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  $a=1.47$ ,  $T_h=0.033$  with  $R^2=0.237$ . These were entered into the NLIN procedure, which gave more precise estimates of  $a=1.27$ ,  $T_h=.021$ , with  $R^2=0.990$ , and the resulting curve is plotted in Figure 1.2 (p.28).

Attack rates were higher for starved beetles than with continuously-fed *C. maculata*. At the lowest density, all eggs were eaten by all individuals. The highest recorded mean attack rate was  $32.8 \pm 6.7$  eggs/day. Maximum predation rate predicted by the disc equation model, within the density range tested, is 31.5 eggs/day at  $N=70$ . Of all eggs attacked over all densities ( $n=100$ ), 8.4% were left half-eaten ( $>1/3$  of the yolk remaining).

Functional Response to Eggs with Aphids Present. Aphids reduced the number of eggs attacked at all egg densities above  $N=10$ . Parameters of the disc equation estimated by NLIN were  $a=1.64$  and

$T_h=0.039$  with  $R^2=0.985$  (Fig. 1.3, 1.5, pp.29, 31). Handling time, as defined by the Holling disc equation, was higher than with eggs alone, as would be expected with a lower rate of predation. The mean number of aphids attacked, out of 40 available, ranged from a minimum of  $34.7 \pm 2.1$ , when egg density was 60, to a maximum of  $38.5 \pm 0.7$ , when egg density was 28 (Fig. 1.3, p.29). There was no relationship between aphid predation rate and egg density (GLM procedure, SAS;  $F=0.85$ ,  $df=7$ ,  $p=0.5512$ ). There was a suppression of egg predation but not a complete switch to aphids, nor was there a one-for-one replacement of aphids for eggs. Total prey items attacked was higher at all densities when aphids were present than when absent. Of all eggs attacked over all densities ( $n=90$ ), 20.0% were left half-eaten.

Functional Response to Eggs with Pollen Present. The presence of pollen did not have any effect on the rate of attack of Colorado potato beetle eggs. The parameter estimates for the disc equation were  $a=1.54$ ,  $T_h=0.024$ , with  $R^2=0.904$  (Fig. 1.4 and 1.5, pp.30, 31). Since pollen consumption was not measured, it is not known whether feeding on pollen took place in a complementary fashion or not at all.

The blocking groups used in the randomized block design of each experiment consisted of siblings reared from the eggs of one male-female pair. A linear model testing for treatment, replicate and experiment effects (GLM procedure, SAS) found replicate effects to be significant in experiments without ( $F=6.31$ ,  $df=5$ ,  $p=0.0001$ ) and with aphids ( $F= 2.18$ ,  $df=10$ ,  $p=0.0293$ ), suggesting a genetic

influence on feeding. Because mothers were field-collected and of unknown history, maternal effects could explain this as well.

#### 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  $1.0 \pm 0.54$  at density 10:10 and  $-1.0 \pm 1.50$  at density 20:20. Neither value was significantly different from that which would be expected if no preference exists, according to the sign test ( $p=0.9844$  and  $p=0.7734$ , respectively). At the three higher densities the difference was significant, indicating a preference for aphids.  $n_e - n_a$  was  $-7.8 \pm 1.71$  ( $p=0.0020$ ) at prey density 30:30,  $-9.5 \pm 2.28$  at 40:40 ( $p=0.0010$ ) and  $-15.7 \pm 2.59$  at 50:50 ( $p=0.0107$ ). These results were corroborated by a t-test of the hypothesis that  $n_e - n_a$  is zero, although normality was violated in the data for density 10:10.

The actual number of eggs and aphids attacked increased for both prey types as density rose (Fig. 1.3, p.29). At prey density 10:10 nearly all of both types of prey was eaten. Total prey attacked was fit to a linear model with total available prey as the independent variable (SAS REG procedure;  $y=0.731x$ ,  $F=1090.44$ ,  $df=49$ ,  $p=0.0001$ ,  $R^2=0.958$ ). There was no significant improvement at the 0.05 level from the addition of a 2nd-order term, suggesting that, within this density range, the rate of attack on prey was not yet leveling off. The proportion of eggs attacked/eggs available dropped with rising density from 0.99 at the lowest density to 0.55



at the highest. The proportion of aphids attacked/aphids available showed no trend in relation to density and varied between 0.83 and 0.91 (Table 1.2, p.26).

#### 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 ( $n=14$ ,  $F=40.73$ ,  $df=2$ ,  $p=0.0001$ ; GLM procedure, SAS) with development fastest on a diet of aphids and slowest on eggs. There was a difference of 5.0 days between mean development time on the aphid diet ( $x = 14.86 \pm 0.27$ ) and the egg diet ( $x = 19.82 \pm 0.59$ ) with pollen being intermediate ( $16.21 \pm 0.271$ ) at  $26 \pm 1$  °C. All three means were significantly different at the 0.05 level using a Tukey's Studentized Range Test (GLM procedure, SAS). Survival rate was lower on eggs (79%) than either of the other diets (100%, aphids, 100%, pollen) and variability in development time was also higher.

#### Rate of Attack on Colorado Potato Beetle Eggs by Male and Female *C. maculata*

A paired t-test of the difference in eggs attacked by males and females of 20 age-matched sibling pairs showed a highly significant difference ( $n=20$ ,  $T=5.989$ ,  $p=0.0001$ ). Females attacked an average of  $24.5 \pm 1.6$  eggs/24 h while males attacked  $16.2 \pm 1.4$  eggs. Males left half-eaten a higher proportion of eggs that they attacked than did females (23.3%, males and 16.3%, females).

### Rate of Oviposition on Alternate Diets

Average daily oviposition was  $0.865 \pm 0.468$  on the egg diet and  $3.885 \pm 0.675$  on the aphid diet. This difference was highly significant (t-test,  $n=20$ ,  $T=3.675$ ,  $p=0.0007$ ). Eighty percent of the females fed aphids were gravid while only 25% of those fed eggs produced 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/day) as in the aphid group (10.9 eggs/day).

### Discussion

The multitude of factors which influence the rate at which an insect predator attacks its prey makes it difficult to obtain estimates of a predator's capacity. While important influences must be controlled in the laboratory in order to isolate the effects of one factor, these interact in a natural setting in complex ways. However, by examining the effects of each factor independently or in simple interactions, one provides the framework for a more comprehensive understanding of that predator's activity. Previous research on the predatory capacity of C. maculata has considered the effects of temperature (Mack and Smilowitz 1982a,b), food concentration (Gross et al. 1985, Wright and Laing 1980) and plant characteristics (Obrycki and Tauber 1983). In these experiments we 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 available continuously provides an estimate of the upper limit of feeding capacity of a resident population in a patch of abundant prey. With 30 eggs provided every 48 h over six days, average rate of attack was 10.4 eggs/day. Conditions which might cause this to be higher include greater abundance of prey and slightly higher temperature. As subsequent tests of functional response showed, even when less than the total available prey is attacked at a given prey density, this does not necessarily represent the upper limit of feeding capacity. Temperatures of 24-26 °C are optimal for C. maculata growth and development (Obrycki and Tauber 1978). However, Mack and 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 ca. 29 °C. Conditions which 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 over 28 days. Because male attack rate was significantly lower than that of females, any estimate of the predation capacity of a population of C. maculata should include consideration of the sex ratio.

When the equivalent number of eggs were presented to females who had fasted for 24 h, they ate approximately twice as much (ca. 20 eggs/day). Frazer and Gill (1981) developed a hunger curve by plotting aphids eaten versus starvation time for a different coccinellid, Coccinella californica (Mannerheim), feeding on pea aphids, Acyrtosiphon 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 one makes the assumption that at 24 h C. maculata had reached a maximum level of hunger, our results suggest what might be eaten by hungry C. maculata adults who 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. 1.3, p.29). Within the density range tested the maximum rate of attack was slightly over 30 eggs/day, although this may not represent the true upper limit because the curve did not reach a plateau even with 70 eggs available/day (Fig. 1.2, p.28). Changes in encounter rate with prey do not explain fully the continued rise in the rate of attack that occurred as density increased from 10 to 70 eggs. Because eggs were all in one (10-40 eggs) or two (50-70 eggs) dense masses that were encountered all at once, the rate of encounter with eggs did not change along with egg abundance. Predator hunger does not adequately explain the functional response, because the number eaten was below the number available for all densities above 10. Since hunger level was the same for all densities, one would have expected a response based solely on hunger to be constant after a certain threshold was reached. The behavioral mechanism that accounts for the higher attack rate when more eggs are present in the egg mass is a subject worthy of further study.

In field studies of mortality imparted by a predator population there is often evidence of variation in the mortality rate in the prey population over time. What we have confirmed here is that variation in predation rate per individual C. maculata, i.e., the

functional response, is one component of the total change in mortality imparted by this predator to Colorado potato beetle egg populations. Under conditions where predator age, sex, and previous feeding history were not controlled, the variability in functional response of individuals would be expected to be much higher.

Colorado potato beetle eggs are an adequate but not an optimal diet for larval development and female oviposition. Rate of larval development, larval survival rate, adult daily oviposition rate and proportion of females producing eggs were all higher on the aphid diet than on eggs. Corn pollen also produced faster larval development than eggs. However, individual ability to utilize eggs for growth and for egg development was variable; some individuals were able to use this source very well. Colorado potato beetle adults sequester alkaloids from potato foliage as it feeds, which may be transferred to their eggs. The toxicity of these secondary plant compounds to larval and adult C. maculata may be a partial explanation for slow development and low oviposition rates on Colorado potato beetle eggs.

What was not tested here, and is worthy of further exploration, is the effect of mixed foods on development and oviposition. Smith (1965c) determined that a mixture of corn pollen and R. maidis produced faster development and higher survival rate than either food alone. This may also be the case with mixed diets containing eggs.

Introduction of aphids to C. maculata that had been fed eggs since adult emergence (<sup>2</sup>14 days) caused an immediate drop in the rate of attack on eggs which moderated somewhat in subsequent

intervals but averaged out to a suppression of egg feeding by about one-third relative to pre-aphid levels. Thus, one would expect that aphid colonization of a field in which C. maculata had been feeding on Colorado potato beetle eggs would cause suppression, but not elimination, of egg predation.

This suppression also occurred where previous feeding exposure included aphids, but did not appear to be greater than when C. maculata had been fed eggs alone. The functional response of C. maculata to egg density was altered by the presence of aphids, with maximum suppression of about one-third relative to eggs alone. There was no indication of a sigmoid shape to the curve, which would have suggested switching from one prey to the other with increasing density. 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. Since most of the 40 aphids available were attacked (Fig. 1.3, p.29), it is possible that a 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. In both the preference and the functional response experiments we saw that when both aphids and eggs were present, but density was low, all of the eggs were attacked.

C. maculata showed no preference for aphids or eggs at the lower end of the range of densities tested here, 40 prey items (half aphids, half eggs) or less. At higher densities, a significant preference for aphids is exhibited. These results are consistent with some of the predictions of the optimal foraging model developed

by MacArthur and Pianka (1966) and the findings of Krebs et al. (1977). The model predicts that, given equal encounter rate and handling time but unequal net reward for two types of prey, preference for the more profitable prey will increase as total prey density increases. If one assumes that the net reward/prey is higher with aphids than with Colorado potato beetle eggs (based upon faster larval development and higher oviposition rates with an aphid diet), and that in the preference experiments handling time as well as encounter rate were equal for both types of prey, then the conditions of these experiments meet the assumptions of the MacArthur-Pianka model. At low prey density, no preference for aphids or eggs was observed, consistent with the prediction of the model. The partial preference observed at high densities, in which more aphids than eggs were attacked but eggs were not totally rejected, conforms with the observations of Krebs et al. (1977) on foraging in the great tit (Parus major). This differs from the model's prediction that prey of lesser value will be 100% rejected at high prey densities.

Aphid presence in potato fields where C. maculata are feeding on Colorado potato beetle eggs could be expected to have several effects: suppression of egg feeding due to increased encounters with aphids or preference for aphids over eggs, but 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; 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. The flexibility of predation rate, shown by the ability of individuals to eat more of single or multiple types of prey when more prey are available, may account in part for changes in mortality rate caused by populations of C. maculata feeding upon Colorado potato beetle eggs and aphids in potato fields.



TABLE 1.1 The number of Colorado potato beetle (CPB) eggs attacked by individual *C. maculata* adult females before and after introduction of aphids. Mean change ('post-pre') was significantly different in the two treatments (t-test,  $p=0.0001$ ).

	DIET			
	CPB Eggs (n=9)		CPB Eggs + Aphids (n=10)	
	$\bar{x}$	s.e.	$\bar{x}$	s.e.
Pre-treatment	19.96	1.54	21.63	1.69
Post-treatment	23.85	1.59	13.70	1.39
Post-Pre	3.89	0.71	-7.93	1.52

TABLE 1.2 Proportion of each prey type eaten by female C. maculata who were offered equal numbers of M. persicae and Colorado potato beetle eggs. Prey was offered at five densities.

---

PROPORTION EATEN

---

Prey Density	Eggs		Aphids	
	$\bar{x}$	s.e.	$\bar{x}$	s.e.
10:10	.99	1.010	.89	0.050
20:20	.81	0.082	.86	0.040
30:30	.65	0.071	.91	0.034
40:40	.59	0.058	.83	0.073
50:50	.55	0.036	.86	0.059

---

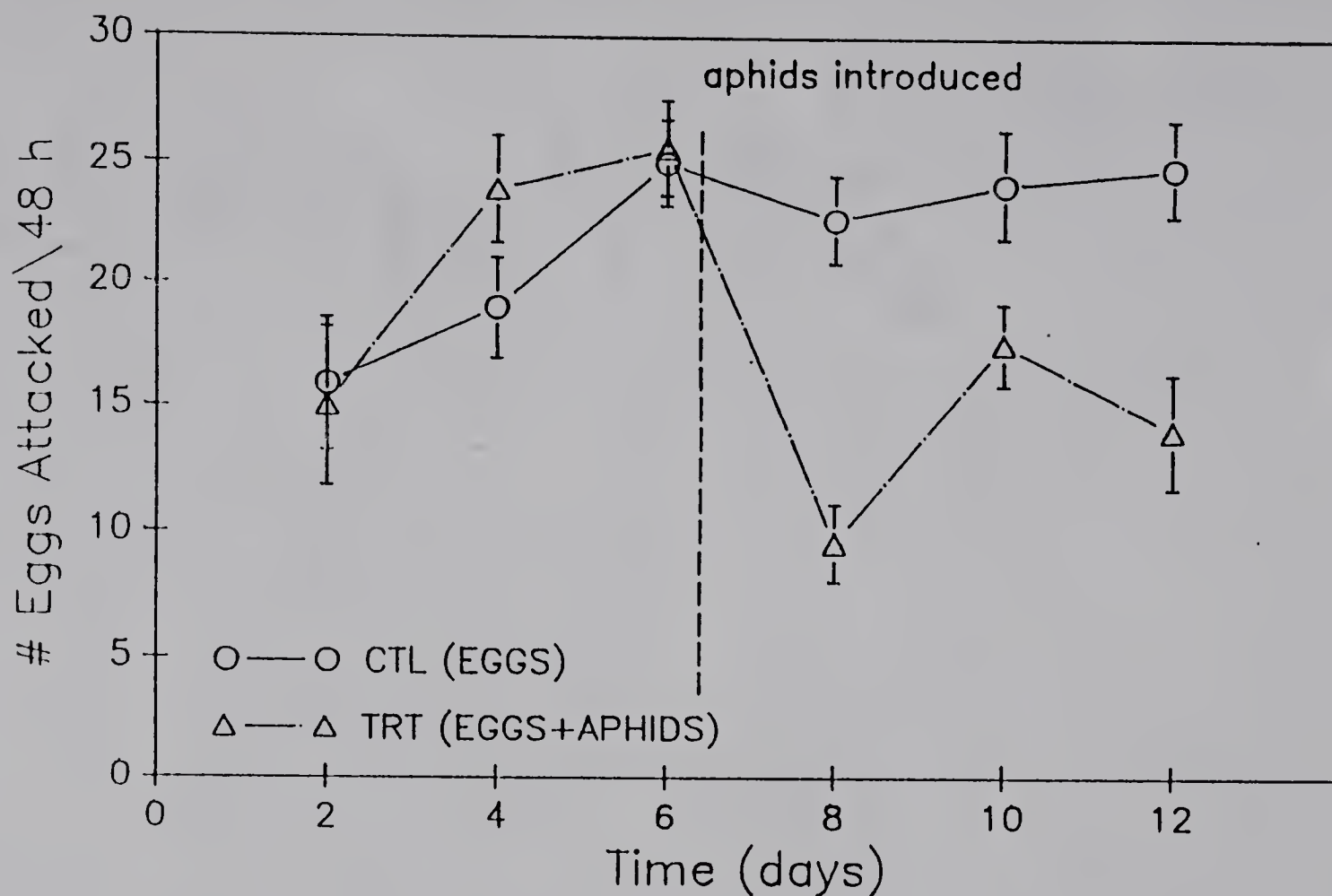


FIG.1.1 Effect of the presence of aphids on rate at which Colorado potato beetle eggs were attacked by *C. maculata* adult females. Each individual received 30 eggs/48 h for three 48 h intervals (6 days) ( $n=19$ ). At the beginning of interval 4, half ( $n=10$ ) received 40 aphids/48 h in addition to eggs. Means for each interval are significantly different ( $t$ -test,  $p < 0.05$ ) for intervals 4, 5, and 6, after aphids were introduced to the treatment group, but not for intervals 1-3. Bars indicate s.e. of the mean.

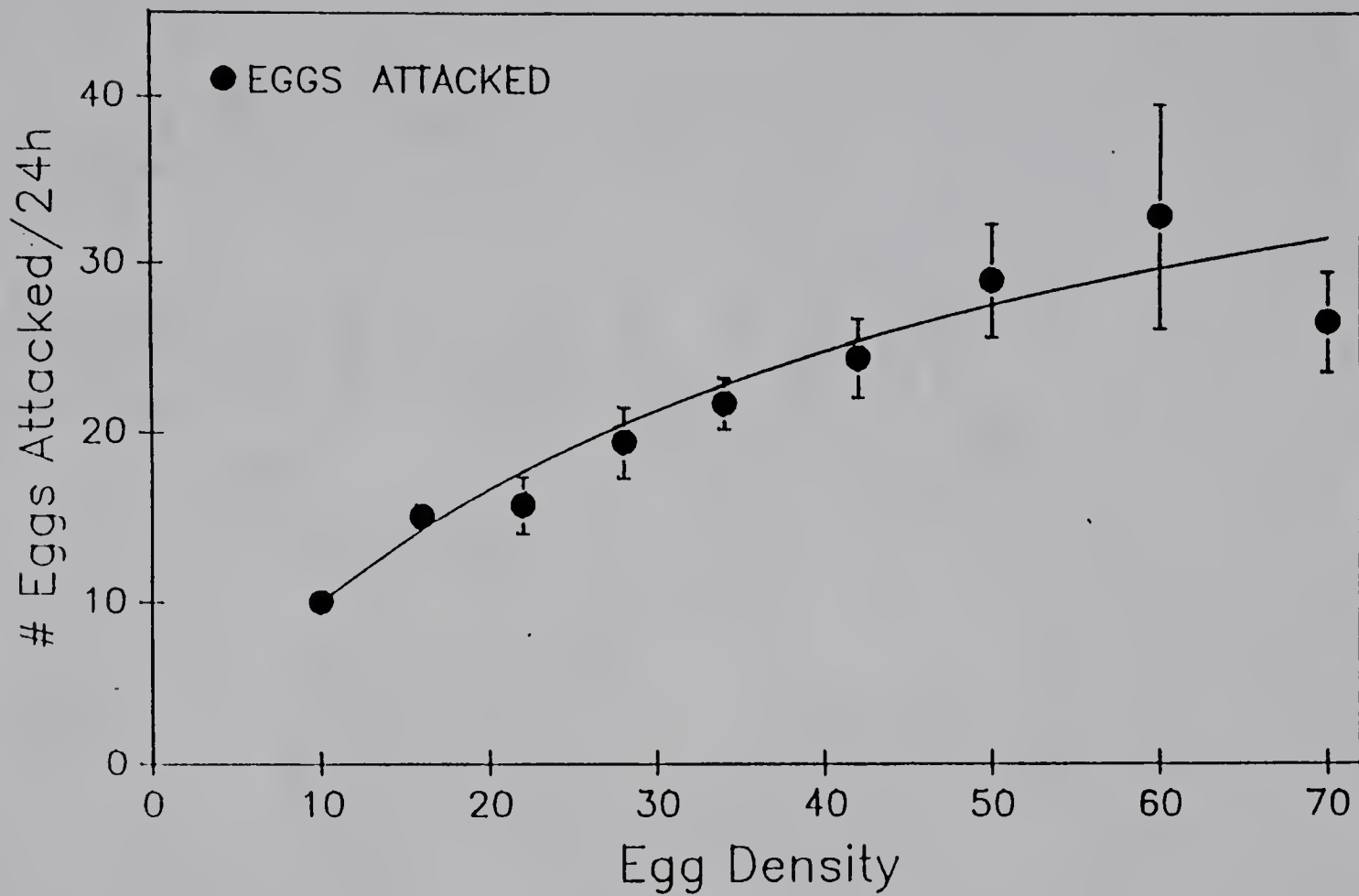


FIG.1.2 Functional response of *C. maculata* adult females feeding on Colorado potato beetle eggs. Means ( $n=12$ ) with s.e. are shown. The curve shows fit of the Holling disc equation, with parameters  $a=1.27$ ,  $T_h=0.020$  and  $R^2=0.9895$ .

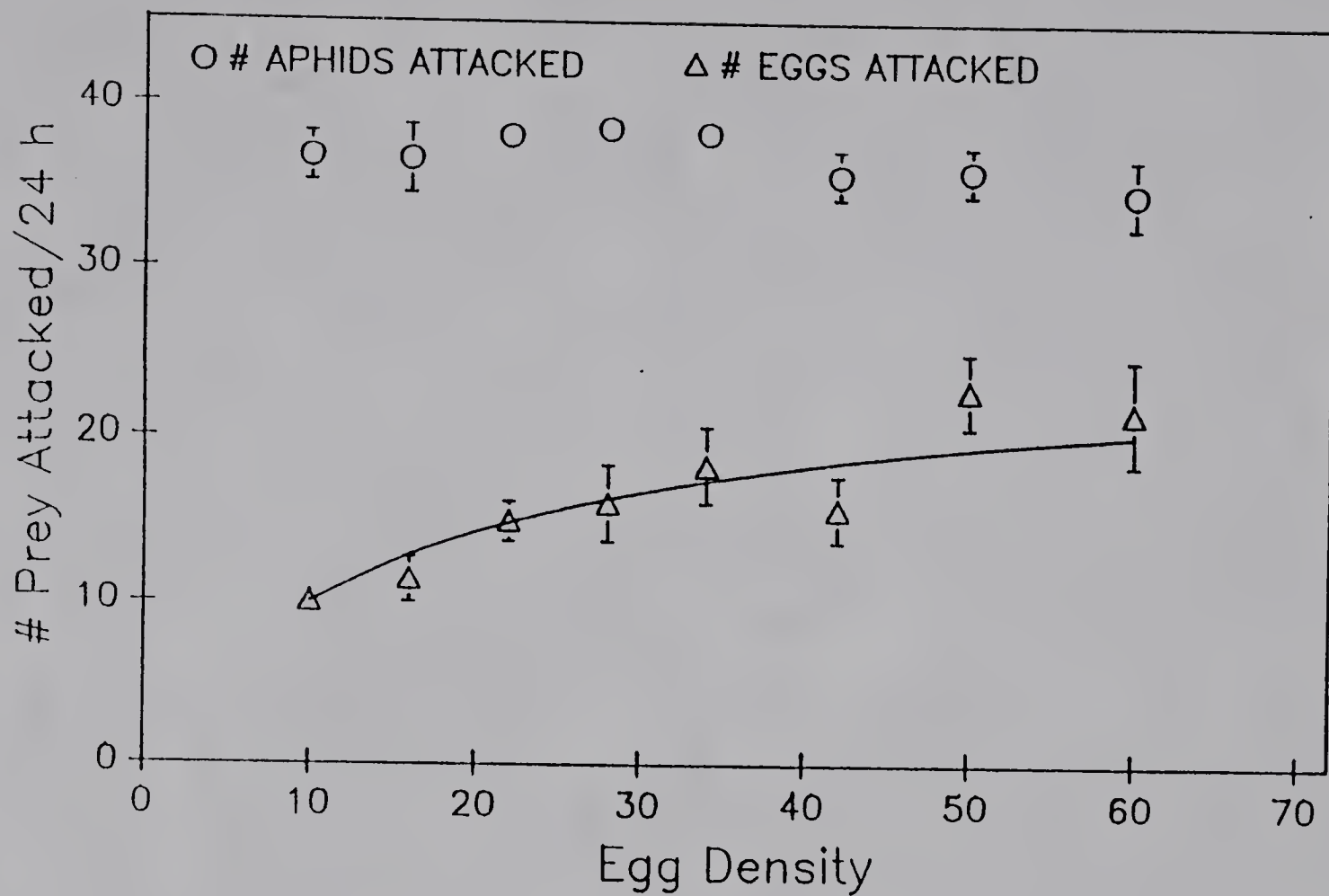


FIG.1.3 Functional response of *C. maculata* feeding on Colorado potato beetle eggs with 40 aphids available/24 h in addition to eggs. Mean number eggs and aphids attacked with s.e. are shown (n=12). Curve indicates fit of the data to Holling disc equation with  $a=1.64$ ,  $T_h=0.039$  and  $R^2=0.9853$ .

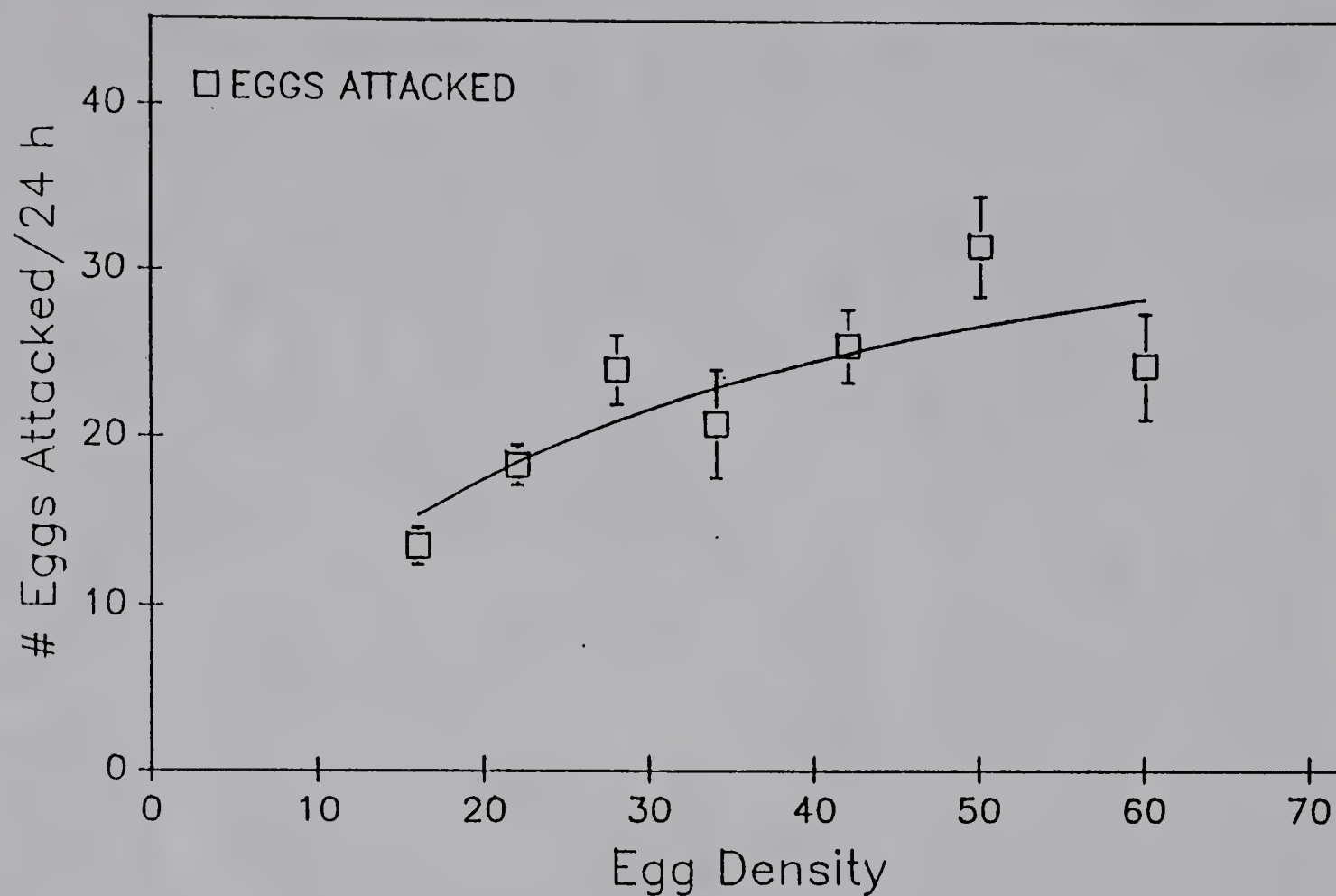


FIG.1.4 Functional response of C. maculata feeding on Colorado potato beetle eggs with corn pollen available in addition to eggs. Mean eggs attacked with s.e. are shown (n=9). Curve indicates fit of Holling disc equation with parameters  $a=1.54$ ,  $T_h=0.024$  and  $R^2=0.9037$ .

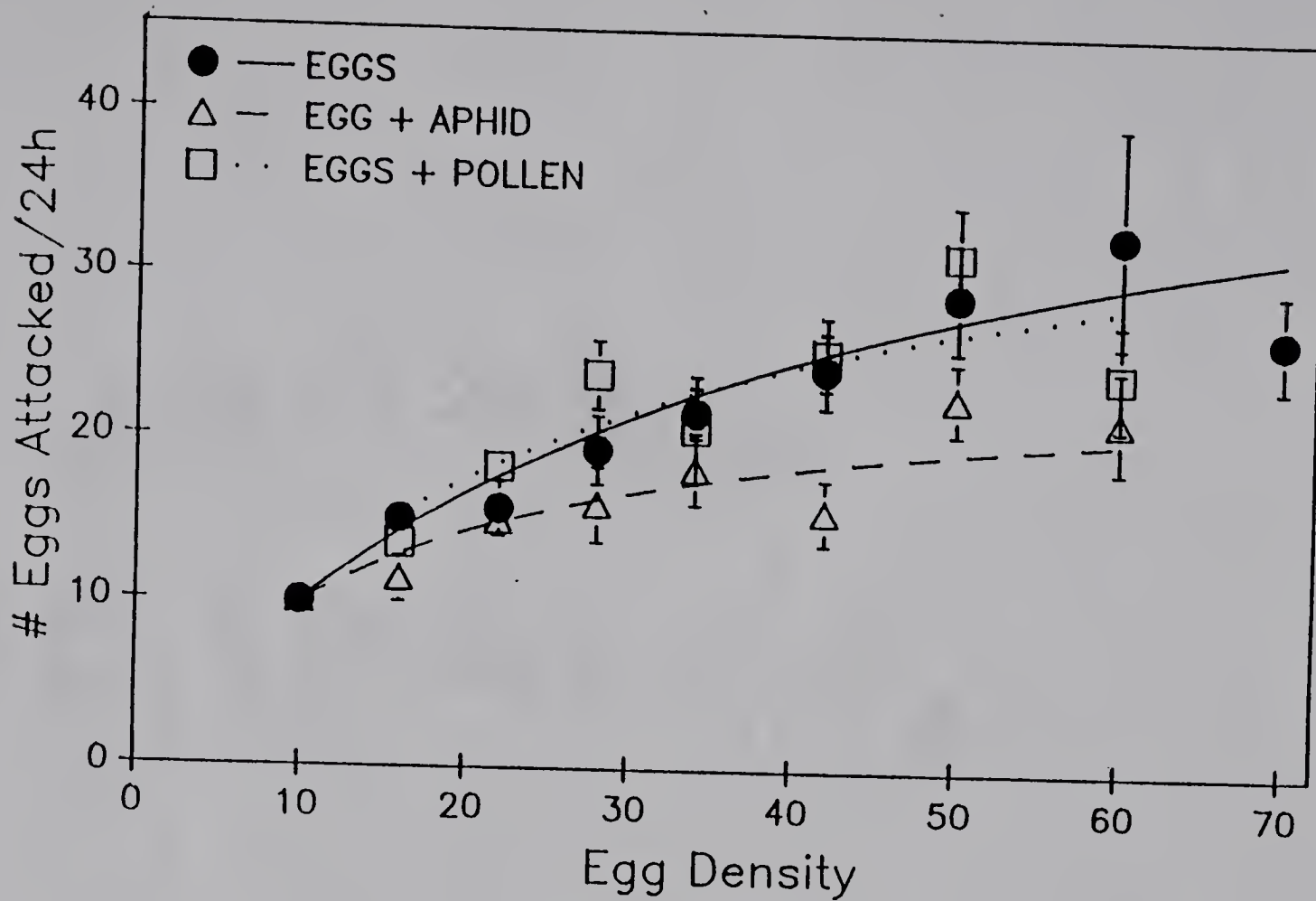


FIG.1.5 Comparison of functional response of *C. maculata* adult females to Colorado potato beetle egg density with and without alternate prey. Mean and s.e. are shown, with curves from Holling disc equation. See captions for Figures 1.2, 1.3, and 1.4 for parameters of disc equation.

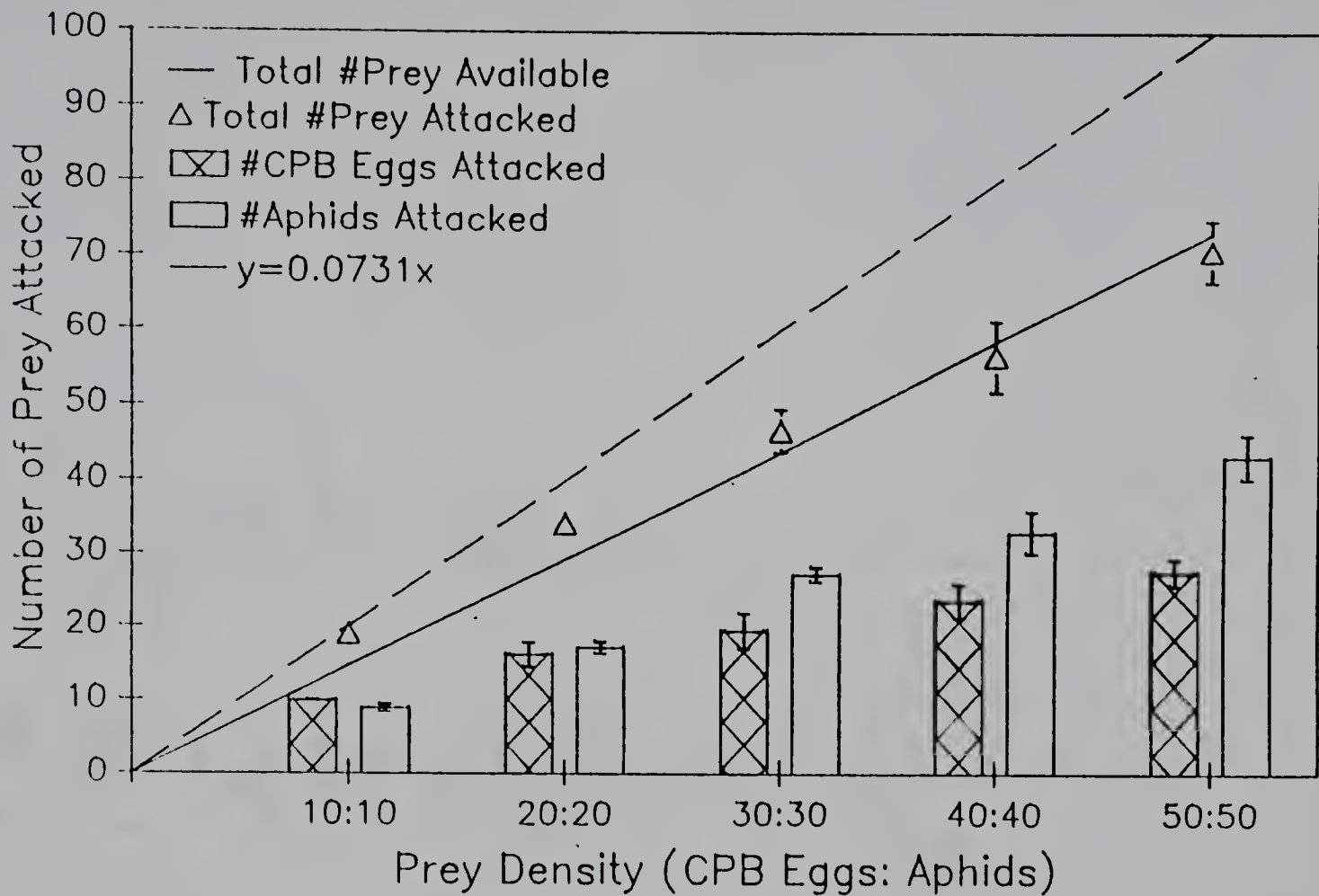


FIG.1.6 *C. maculata* predation on Colorado potato beetle eggs and green peach aphids when offered both prey at equal density and equal encounter rate. Preference is measured by  $n_e - n_a$ , the difference between number of eggs eaten and number of aphids eaten.  $N_e - n_a$  is significantly different from zero at density 30:30 and above (sign test,  $p < 0.05$ ) but not at lower densities. Total prey attacked increased linearly with density ( $y = 0.7308x$  with  $R^2 = 0.9578$  and  $p = 0.0001$ ). Bars indicate s.e. of the mean ( $n = 10$ ).



## CHAPTER 2

### MORTALITY TO EGGS OF COLORADO POTATO BEETLE FROM PREDATION BY COLEOMEGILLA MACULATA (DEGEER)

#### Introduction

In commercial potato fields in Massachusetts, management of the Colorado potato beetle, Leptinotarsa decemlineata (Say) has depended almost exclusively on repeated applications of insecticides. Consequently, natural enemy populations have remained low and their contribution to pest control has been negligible. In the absence of insecticides, or with use of compatible insecticides, predators and parasites of the Colorado potato beetle may reach densities capable of suppressing Colorado potato beetle populations below economically damaging levels (Ferro 1985).

Quantifying the mortality caused by field populations of predators or parasites is an essential step in the development of management strategies which include the action of natural enemies. Larval predation by Podisus maculiventris (Say) and Perillus bioculatus (F.) and parasitism by Myiopharus doryphorae (Riley) have received attention (Drummond et al. 1984, Tamaki and Butt 1978, Horton and Capinera 1987, Tamaki et al. 1983). However, the impact

of endemic predators upon the egg stage of Colorado potato beetle has not yet received quantitative evaluation.

In western Massachusetts, Coleomegilla maculata (DeGeer) migrates into potato fields shortly after plant emergence in June and is visible on plants throughout the season. This polyphagous coccinellid readily feeds upon Colorado potato beetle eggs as well as on aphids and pollen and has been shown to aggregate in patches where food is plentiful (Coderre et al. 1987; Wright and Laing 1980). If C. maculata colonizes potato fields in sufficient numbers, its impact on the survival of Colorado potato beetle eggs may be significant. Other predators which may contribute to egg mortality include Podisus spp., Lebia grandis Hentz, other Carabidae, Phalangida, and spiders.

Measuring the total mortality occurring in a life stage during one generation of a field population of insects requires estimates of 1) total numbers entering the stage in the generation and 2) numbers lost to the mortality factor over the entire generation. Because the period of Colorado potato beetle oviposition is long relative to the developmental time of the egg, eggs begin to hatch before egg laying as a whole has ended. Therefore no single sample of egg density reflects the total numbers entering the egg stage (Van Driesche 1983). Similarly, measures of mortality which depend upon the evidence present in density samples cannot in any simple way be converted to a mortality rate for the generation.

Total numbers entering a stage, and subsequently dying in the stage, can be determined through direct measurement of these quantities, as was done by Van Driesche and Bellows (1988) for

evaluation of losses to parasitism in field populations of Pieris rapae L. attacked by the parasitoid Cotesia glomerata L.. Two rates must be measured: the rate of recruitment of the insect into the stage of interest and the rate of deaths from the mortality factor being evaluated. Values of these measures are obtained for each interval between successive sample dates. When these are summed, they estimate total numbers entering the stage in the generation and total numbers dying in the stage due to the mortality agent.

In the present study, the approach of Van Driesche and Bellows (1988) was modified for a predator-prey system. Since Colorado potato beetle eggs are an immobile prey, they can be marked as they enter the population in the field and their survival can be determined by repeated observation. Application of the recruitment method of sampling enables measurement of the numbers of eggs laid in each inter-sample interval and the predation on these cohorts of eggs. Total eggs laid and numbers eaten by predators are found by summing all cohorts in the generation. This method also provides a measure of the rate of predation on the total prey available (of all ages) during any given time interval, which may be expressed as a daily predation rate.

This study was conducted on a commercial-scale potato farm practicing annual rotation of potato with other crops and with a history of relatively low insecticide use. Cropped fields were surrounded by weedy uncultivated areas which provided alternate food sources and refugia for C. maculata and other mobile predators.

Aggregations of C. maculata adults overwintered close to potato fields and C. maculata was relatively abundant throughout the farm.

The objectives of this study were: 1) to assess the abundance of C. maculata and other endemic predators; 2) to measure the daily predation rates on Colorado potato beetle eggs; and 3) to determine mortality of successive egg cohorts and of each full generation of Colorado potato beetle eggs from native predators.

### Materials and Methods

#### Egg Recruitment and Mortality

This study was conducted at Taft Farm in Great Barrington, Massachusetts, a diversified vegetable farm where potatoes were grown in rotation with sweet corn, bush beans, and other vegetables. 1986 study plots were on the edge of a 14 ha commercial potato field (var. Russett Burbank) planted on 4 June. The first generation density of Colorado potato beetle eggs were so low that it was not possible to collect enough samples to estimate the research parameters. A 20x100 m (0.2 ha) plot with higher Colorado potato beetle densities (B) was selected for the second generation. Conventional commercial practices were used for weed and disease control, fertilization, and tillage. No insecticide treatments were made to the study plots or to the surrounding field. Sampling began after plant emergence in the first generation and in Plot B started when eggs of newly-emerged first-generation Colorado potato beetle adults were first observed (4 August). One hundred randomly

selected plants (first generation) or stalks (second generation) were marked with stakes and searched twice each week for new egg masses. All newly recruited egg masses were labeled with a date-specific code of colored paint on the upper side of the leaflet and the eggs in each new mass were counted. All masses were re-examined on each successive sampling date to determine the number of eggs damaged or intact. Missing eggs were assumed to have been removed by predation, except during the interval when hatch occurred.

In 1987 a 20x80 m study plot (C) was established in the center of the one edge of a 10.2 ha potato field (var. Russett Burbank, planted 13 May) and was left free of all insecticide use. Sections of the surrounding field were treated with one or more insecticides (M-One, fenvalerate, azinphos-methyl, carbaryl, oxydemeton-methyl, and rotenone) for control of Colorado potato beetle and other insect pests, except for a 10-row border around the study area to minimize drift into the plot. The entire planting was subject to conventional commercial weed and disease control and hilling, as in 1986. Egg predation was measured in the same manner as in 1986 except that observations were made three times per week and masses were marked with colored surveyor's tape tied to the nearest leaf petiole. One hundred plants were marked on 5 June at plant emergence but this was reduced to 50 plants on 22 June because egg density was too high to allow all eggs on 100 plants to be observed on every sample date.

In both 1986 and 1987, no attempt was made to quantify predation which occurred during the interval when eggs hatched. Egg damage from chorion-feeding or cannibalism by Colorado potato beetle

larvae, which commonly occurs during hatch, cannot be reliably distinguished from that caused by chewing predators. Therefore, if first-instar larvae were found on the mass or the adjacent leaflets or stalk, then changes in the egg mass during that interval were not attributed to predation. The number of eggs surviving up to the time of hatch was assumed to be the same number that were present on the previous observation date. Thus, mortality from larval cannibalism during and just after hatch was not measured in this study, and predation was underestimated to the extent that it occurred during the interval when hatch took place. Cannibalism has been estimated in the field (Harcourt 1971) and in the laboratory (Van Driesche et al. 1989) to kill approximately 15% of Colorado potato beetle eggs during hatch.

Due to heavy defoliation by Colorado potato beetle larvae and adults in Plot C, the study was moved at the beginning of the second generation (24 July) to an area (D) previously protected by insecticides. This 10x40 m (0.08 ha) plot was located ca. 100 m away, in the same potato field as Plot C. Fifty complete stalks were permanently staked, egg masses were marked and their fate recorded, as above.

Plant densities were as follows: Plot B, 7.8 stalks/m<sup>2</sup>; Plot C, 2.54 plants/m<sup>2</sup>; Plot D, 7.8 stalks/m<sup>2</sup>. All samples were converted to numbers/m<sup>2</sup>.

#### Natural Enemies

Abundance of C. maculata and other diurnal predators was monitored by recording the number observed on marked plants or

stalks during examination of Colorado potato beetle eggs. Sampling took place between 1100 and 1400 h. In 1986 Podisus spp. were also monitored by traps baited with three species-specific pheromones provided by J. Aldrich (USDA, Beltsville, Md.). In 1987, on three occasions, staked plants were searched four times during the night (1900-2100, 2230-2400, 0130-0300 and 0530-0700 h) for nocturnal predators, with the aid of a flashlight. On 15 June, 56 plants (with 101 egg masses) and on 30 June 90 plants (99 masses) were searched in Plot C. Fifty stalks (57 masses) were observed on 27 July in Plot D.

The presence of carabids in Plot C was also assessed using burlap "traps" which consisted of 50 X 150 cm pieces of burlap wrapped around potato plants, placed on the ground, or wrapped around wire hoops touching potato foliage. This design was developed by E. Groden (pers. comm.) especially for sampling L. grandis. These were checked every 2-5 days from 5 - 22 June. Carabid species and abundance were monitored in Plot D by placing ten pitfall traps at random from 27 July to 24 August and checking them every 2-5 days.

Specimens of all species captured in pitfall traps were tested for consumption of Colorado potato beetle eggs. They were returned to laboratory and held in screened 7 X 7 X 8 cm plastic boxes (25°C, 75%RH) with 2-3 cm of pasteurized soil mix (1:1 loam:sand). All were given fresh Colorado potato beetle eggs and moistened dental wicking and eggs were checked daily for signs of predation. Species that consumed eggs were further tested in large screened cages (36 X 36 X 48 cm) to determine their foraging range on a potato plant.

Each cage contained a potted potato plant and sterilized potting soil covering the floor of the cage to a depth of approximately 4 cm. On each plant, one egg mass was pinned to a leaf near the top of the plant, one half-way up the plant, and one to a leaf that touched the ground. Egg masses were checked daily for predation.

### Analytical Methods

For each observation date, information was obtained on the fate of all remaining previously marked egg masses and on the number of new eggs laid since the last sample date. The daily egg recruitment rate was calculated by dividing number of eggs recruited per interval by the number of days ( $n$ ) in that interval ( $n = 3$  or  $4$  in 1986;  $n = 2$  or  $3$  in 1987). The sum of eggs recruited over all intervals of each egg generation is the total generational egg recruitment. All the eggs laid in a given interval constitute, for analysis purposes, an even-aged cohort whose mortality rate is  $1-S$ , where  $S$  equals the proportion of cohort eggs surviving to hatch.

The rate of predation on all eggs present in an interval, regardless of when they were laid, was also calculated from the data recorded for each interval. This rate was expressed as the absolute numbers eaten per  $m^2$  per interval or as the proportion of available prey that were eaten, per day, during the interval.

The estimate of available prey must take into account the dynamic interaction of eggs entering the population via oviposition and those leaving it via hatch or predation. The density of eggs present on each sampling date reflects the sum of these processes for a given moment in time. The number of eggs available to



predators during the interval between two sampling dates was taken to be the average of the number present at the beginning and the end of the interval. The proportion of eggs surviving the interval (S), is the ratio of numbers surviving the interval over total number available. The daily mortality rate for an interval with n days is then given by  $1 - \sqrt[n]{pS}$ .

For statistical analyses, a linear regression model (Proc Reg, SAS Institute, 1987, p773) was used to test for a relationship between egg density (number of eggs available) as the independent variable and the daily mortality rate. Similarly, the consumption rate of each predator (eggs eaten/predator/day) was regressed against egg density.

## Results

### Natural Enemies

In nocturnal observations, no carabids were seen in the potato foliage. Total predators observed on plants on the three sample dates were as follows: adult Coleomegilla maculata (13), Phalangida spp.(5), spiders (3), Chrysopa spp. (2), Podisus spp.(1), and other hemipteran predators (6). The reason for the absence of Lebia grandis is unknown but may be due to the use of herbicides in these fields. L. grandis, especially the soil-dwelling immature stages, is readily killed by certain herbicides (E. Grodon, pers. comm.).

In burlap and board traps placed in Plot C, only 14 carabids were caught in all, mostly Agonum placidum Say. No L. grandis were

captured. During this period potato plants were small and most of the soil bare and exposed.

Pitfall trap catches in Plot D included four species which subsequently were found to consume eggs: L. grandis, Pterostichus lucublandus Say, P. melanarius Illeger, and Anisodactylus sanctaecrucis Fabricius (Fig 2.1, p.52). One other species captured, Harpalus pensylvanicus DeGeer, consumed leaf tissue but not eggs in the laboratory. Both L. grandis and P. lucublandus consumed all or most of the eggs provided in small cages, whereas P. melanarius, A. sanctaecrucis, and A. placidum ate eggs sporadically. In large cages where egg masses were placed at three levels in the potato foliage, only L. grandis foraged in the foliage off the ground. A. sanctaecrucis and P. melanarius ate eggs on the leaf that touched the ground but not on leaves in the canopy. In this group of carabids, only L. grandis possesses adhesive setae on the tarsomeres which permit adhesion to plant stems (G.Ball, pers. comm.). Thus in this plot the egg-consuming carabids that were present in significant numbers could only have fed upon eggs on leaves touching the ground.

Pheromone traps used in 1986 failed to capture any Podisus spp., although identical traps used at another potato field in western Massachusetts did capture Podisus spp.

The most abundant predator observed on plants during both day and nighttime sampling was C. maculata. Other predators found in the foliage during daytime observations were nymphs and adults of Podisus spp., Phalangida, and spiders. Podisus and Phalangid! were seen more frequently later in the season in both 1986 and 1987.

Only C. maculata was consistently observed on all sample dates when Colorado potato beetle eggs were present in the field.

C. maculata was more abundant during the second generations of 1986 and 1987 than during the first generation of 1987, reaching a maximum mean density of 1.56 individuals/m<sup>2</sup> in both years (Fig.2.2e, 2.3e, 2.4e, pp.53, 55, 57). In the second generation in 1986 these samples included larvae, but in 1987 larvae were seen only in the first generation. The number of C. maculata larvae did not exceed the number of adults except on one occasion. In the first generation of 1987, C. maculata density peaked when Colorado potato beetle egg abundance was increasing, while in the second generation density of C. maculata was highest after peak egg abundance, when egg density was declining (Fig.2.2e, 2.3e, pp.53, 55). Between the sampling dates of 3 and 5 August, 1987 the density of C. maculata increased fivefold just after maximum egg availability and remained high for about a week, then declined to zero (Fig.2.3e, p.55).

#### Egg Recruitment and Mortality

In 1986, colonization of the early season study plot by overwintering Colorado potato beetle adults was both delayed and reduced by rotation of potato fields from one side of the Housatonic River to the other. First generation egg densities were too low to conduct the planned study. Because of the delay in colonization by overwintering adults, emergence of first-generation adults was delayed, causing the oviposition of second-generation eggs to begin on approximately 1 August (Fig 2.2a, p.53). The oviposition period lasted 17 days and the rate of recruitment peaked at  $69.8 \pm 8.6$

eggs/m<sup>2</sup>/day in the 7-11 August interval and then ended one week later. Total recruitment for the generation was 625 eggs/m<sup>2</sup> of which 39.9% (249 eggs/m<sup>2</sup>) were eaten by predators before hatch (Table 2.1, p.51). A total of five egg cohorts, which originated during successive 3 or 4-day intervals, were evaluated for predation. Mortality of cohorts (proportion killed by predation) was relatively uniform, with rates being perhaps higher in the first two cohorts as compared to the last three (Fig.2.2b, 54)

Recruitment declined rapidly after 11 August and the date of maximum egg recruitment coincided with maximum egg density (Fig. 2.2c, p.53). Egg density peaked at  $417.8 \pm 49.5$  eggs/m<sup>2</sup> on 11 August. Some eggs remained in the field for about one week after the last new oviposition, and were observed for damage from predation until 24 August. The daily mortality rate (eggs eaten/eggs available/day) was highest during the three periods of highest density (0.077, 0.061 and 0.065 for intervals preceding 7, 11 and 14 August, respectively) (Fig 2.2d, p.53).

In 1987, because of proximity of the study field to the previous year's potatoes and to overwintering sites of Colorado potato beetle, colonization by beetle adults began immediately after plant emergence. The first oviposition was recorded on 5 June. The egg-laying period lasted 28 days, with the last new eggs marked on 3 July. Peak recruitment rate was  $70.4 \pm 9.2$  eggs/m<sup>2</sup>/day, during the interval of 17-19 June (Fig 2.3a, p.55). Total recruitment for the first generation averaged 749 eggs/m<sup>2</sup> of which 37.8% (280 eggs/m<sup>2</sup>) were eaten by predators (Table 2.1, p.51). Thirteen egg cohorts were marked and traced to hatch. For the cohorts which originated

from 12-17 June, mortality rose from 25.2% to 46.6%. Mortality fell to 33.7% for the 19 June cohort and remained relatively constant for succeeding groups (Fig 2.3b, p.55).

Peak egg density was  $296.0 \pm 28.9$  eggs/m<sup>2</sup> and occurred three days after maximum recruitment (Fig 2.3c, p.55). The daily mortality rate exhibited a gradual increase over the course of the generation. While the number of prey rose tenfold (from  $26.9 \pm 6.3$  on 8 June to  $286.0 \pm 34.7$  eggs/m<sup>2</sup> on 22 June) the proportion of available prey eaten did not fall (Fig 2.3d, p.55).

Recruitment of second generation eggs began earlier than in 1986, on about 21 July, and lasted 17 days. High rates of egg deposition from 27 to 31 July produced higher egg densities in a shorter period of time than in the first generation (Fig 2.4a, p.57). Total recruitment was 988 eggs/m<sup>2</sup> of which 58.1% (574 eggs/m<sup>2</sup>) were eaten by predators. Unlike the two previous generations described, cohort mortality rate declined steadily from initial levels of 69.2% and 71.6% for the first two cohorts to 29.6% for the seventh and final cohort (Fig.2.4b, p.57).

Egg density reached a maximum of  $458.5 \pm 68.2$  eggs/m<sup>2</sup> two days after peak egg recruitment (Fig 2.4c, p.57). While the number of eggs eaten was highest when the availability of eggs was greatest (intervals ending on 29 and 31 July and 3 August) the only periods during which the proportion eaten increased in correspondence with a density increase were the first two intervals, during the initial increase in egg density (Fig 2.4d, p.57).

The daily rate of mortality showed no relationship to egg density in the first generation ( $n=13$ ,  $R^2=0.002$ ,  $p=0.8962$ ) or second

generation in 1987 ( $n=8$ ,  $R^2=0.142$ ,  $p=0.3577$ ) and showed a positive though not significant relationship to egg density in 1986 ( $n=5$ ,  $R^2=0.758$ ,  $p=0.0546$ ). With a prey such as Colorado potato beetle eggs that undergoes large and rapid fluctuations in density, maintenance of a relatively stable mortality rate represents a significant positive relationship between predator foraging behavior and prey density.

The predator rate of attack on eggs (eggs eaten/predator/day) showed a positive linear relationship with prey density in both the first ( $R^2=0.582$ ,  $F=15.3$ ,  $df=1$ ,  $p=0.0024$ ,  $y=0.473x$ ) and second ( $R^2=.526$ ,  $p=0.0416$ ,  $y=0.665x$ ) generations. This suggests that the functional response to prey density which has been demonstrated for C. maculata under laboratory conditions is also operating in the field.

### Discussion

The predominance of Coleomegilla maculata in samples of foliage-dwelling predators suggests that this is the most important predator of Colorado potato beetle eggs in the fields studied. C. maculata was both the most abundant predator and the only one consistently present when Colorado potato beetle eggs were available as prey. Colonization of early-season potatoes by adult C. maculata occurred shortly after plant emergence in 1987 and was well synchronized with the first occurrence of Colorado potato beetle eggs. Subsequent losses to egg predation were significant. In potato fields in Rhode Island and Michigan, E. Groden (pers.comm.)

also found the numbers of C. maculata to be well synchronized with first-generation Colorado potato beetle egg populations. No other endemic predator or parasite of egg and larval stages has been shown to cause significant early-season mortality to Colorado potato beetle eggs or larvae with the exception of L. grandis (E. Groden., pers. comm.). However, L. grandis was not a significant predator in these fields. Mortality to early life stages of the first generation of Colorado potato beetle is especially significant because it prevents feeding damage during the plant growth stage when potato yield is most affected.

Estimates of total mortality occurring prior to the larval stage should include the influence of cannibalism during hatch. If the estimate of mortality rate from cannibalism of 15% made by Harcourt (1971) and Van Driesche et al. (1989) is added to mortality from predation, total mortality in these fields is estimated to be 54.9% for 1986 and 52.8% and 63.1%, respectively, for first and second generations of 1987. It has been noted by E. Groden (pers. comm.) that C. maculata readily consumes first-instar larvae of Colorado potato beetle in laboratory cages at the average rate of 11.2 larvae/day and may be equally preferred as eggs. If this occurs in the field as well, then mortality from C. maculata predation on the early larvae supplements the egg mortality which has been documented in this study.

Fluctuations in the numbers of C. maculata observed in foliage may be due to adult immigration and emigration from the plot, reproduction, or variation in foraging activity in the plant canopy. Movement of adults between potato, other crops, and field borders

probably occurs constantly throughout the growing season in response to changing prey populations. E. Groden (pers. comm.) found that C. maculata was present in plots of sweet corn, alfalfa, green beans, cole crops, and cucurbits that were adjacent to potato plots in Rhode Island and Michigan, with highest densities occurring in sweet corn after tasselling (pollen shed). Numerical response of C. maculata via immigration of adults into a patch of abundant food can occur rapidly. Gross et al. (1985) found that adult C. maculata density increased significantly within one hour and peaked by eight hours after application of lepidopteran larval homogenate as a food source to corn plots. Wright and Laing (1980) saw a numerical response of C. maculata to corn leaf aphid density. In the latter two cases, adult arrival was associated with deposition of eggs. Reproduction occurs in potato fields as well, as evidenced by presence of larvae in samples (Fig 2.2e, 2.3e, pp.53,55). However, its contribution to fluctuation in total C. maculata numbers may be small relative to adult movement, as larvae comprised no more than half of any sample and frequently were absent from samples altogether. This may be explained in part by the fact that Colorado potato beetle eggs are not the optimal food for oviposition or larval development (see Chapt.1).

Ambient temperature, time of day, and predator hunger influence foraging activity and therefore numbers observed in samples. Benton and Crump (1981) found that in sweet corn in New York State, locomotor activity of C. maculata was greatest in early morning and that beetles foraged in the upper levels of corn only in the early morning hours and descended to lower levels before noon. Mack and



Smilowitz (1980) studied sampling methods for C. maculata in potatoes and found 0900-1115 hours to be the least variable period of daylight hours, although the 1115-1535 hours period gave the highest means. The numbers of coccinellids observed foraging may be severalfold fewer than the absolute numbers present because satiated individuals rest at the base of plants in cracks in the soil (Frazer and Gill 1981). Thus, samples derived from foliage observations may significantly underestimate the absolute density of C. maculata present, and attempts to correlate those sample numbers with other phenomena must recognize the degree of error associated with the patterns of foraging behavior in this coccinellid.

The combined records of egg recruitment and egg survival provide insight into the relationship between the rate of mortality occurring in the egg stage and the number of prey entering and leaving the stage. In 1986 egg recruitment was relatively low (625 eggs/m<sup>2</sup>) while generational mortality to eggs was 39.9%, resulting in survival of 376 eggs/m<sup>2</sup>. In 1987, total egg recruitment was greater in the second generation (988 eggs/m<sup>2</sup>) than in the first (740 eggs/m<sup>2</sup>) and stage-specific mortality of eggs was also higher (59.1% as compared to 37.8% in the first generation). The net outcome was that the number of eggs surviving to hatch was lower (414 eggs/m<sup>2</sup>) in the second generation than in the first (460 eggs/m<sup>2</sup>) (Table 2.1, p.51). The eggs that survived in the first generation of 1987 resulted in more severe defoliation by subsequent life stages than those of the second generation, in part because potato foliage biomass was less at the time of the first generation than at the time of the second. Because it is the interaction of

pest numbers, stage-specific mortality rate and plant susceptibility that determines whether economic thresholds are exceeded, a rate of predation which is adequate for economic control at a certain pest density and plant growth stage may not be adequate under other conditions.

C. maculata can contribute substantially to the control of both early and late generations of Colorado potato beetle in Massachusetts and that efforts to conserve this natural enemy will be help to reduce the need for chemical control. The synchrony of adult immigration into potato fields with the expansion of Colorado potato beetle egg populations represents a valuable mechanism for early-season control. However, native populations of C. maculata will not be sufficient to bring Colorado potato beetle population unless other practices such as field rotation and use of compatible pesticides are included in the management program.

Table 2.1 Total recruitment of Colorado potato beetle eggs for 1986 and 1987 and generational mortality to the egg stage from predation.

	Total Recruitment	Eggs Tracked	Eggs Eaten	Stage- Specific Mortality
	(eggs/m <sup>2</sup> )	(eggs)	(eggs/m <sup>2</sup> )	(% eaten)
1986				
Gener. 2	625	8011	249	39.9%
1987				
Gener. 1	740	17999	280	37.8%
Gener. 2	988	6097	574	58.1%

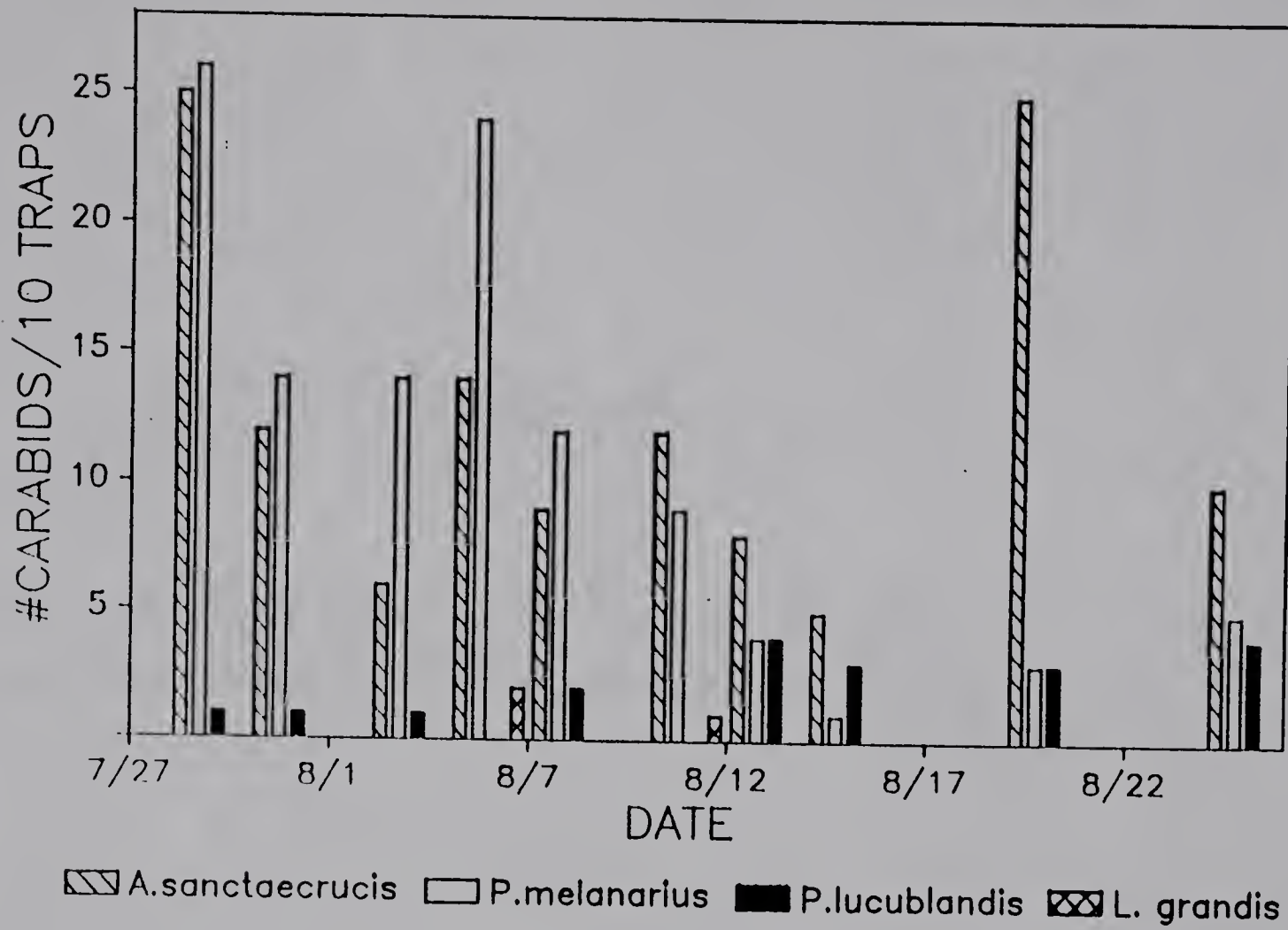


FIG 2.1 Number of Colorado potato beetle egg-consuming carabid beetles which were caught in ten pitfall traps in Plot D in a potato field in Gt. Barrington, Mass., during late July and August, 1987.

FIG.2.2 Recruitment, density and mortality of second-generation Colorado potato beetle eggs, 1986. Error bars for egg counts (Fig. 2.2a,c) indicate s.e. of the mean; those for proportions (Fig. 2.2b,d) indicate 95% confidence intervals. N=100 stalks. a) Daily recruitment of eggs/m<sup>2</sup>, the number of new eggs laid per day during the preceding time period, and the corresponding number of eggs in that cohort that were eaten by predators before hatch; b) Proportion of each egg cohort that was eaten by predators; c) Egg density, mean eggs/m<sup>2</sup>, of all ages, that were present on each observation date, and number eaten by predators during the period between successive observation dates; d) Daily mortality rate, the number of eggs eaten/number available/day (number of eggs available equals the average of the egg density at the beginning and end of the interval); e) C. maculata adult and larval density (number/m<sup>2</sup>), from visual observation of the 100 stalks on which eggs were traced.

GENERATION 2, 1986

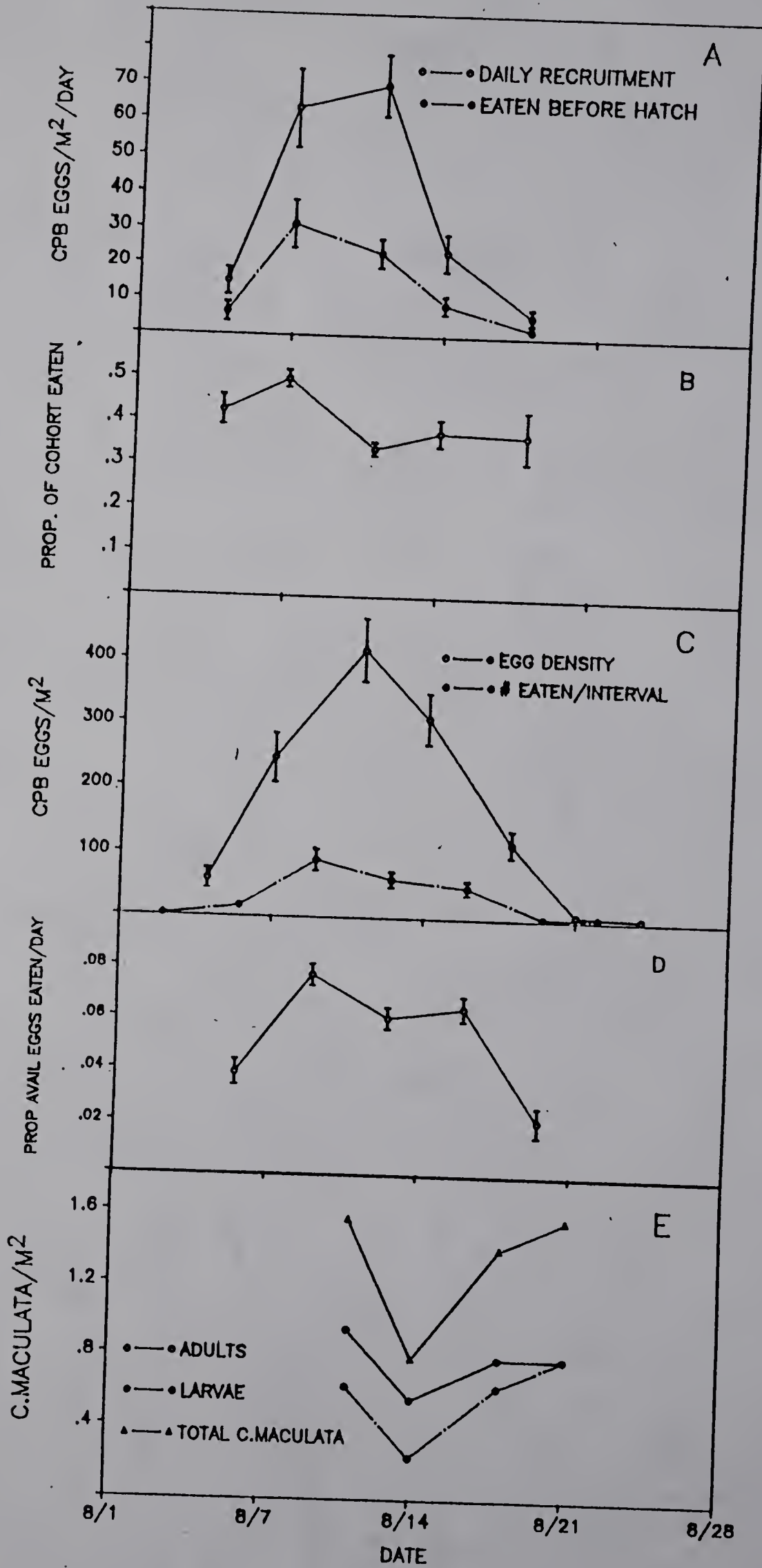


FIG.2.3 Recruitment, density and mortality of first-generation Colorado potato beetle eggs, 1987. N=100 plants, 5-22 June and 50 plants thereafter. See caption for Fig.2.1 for explanation of each graph.

GENERATION 1, 1987

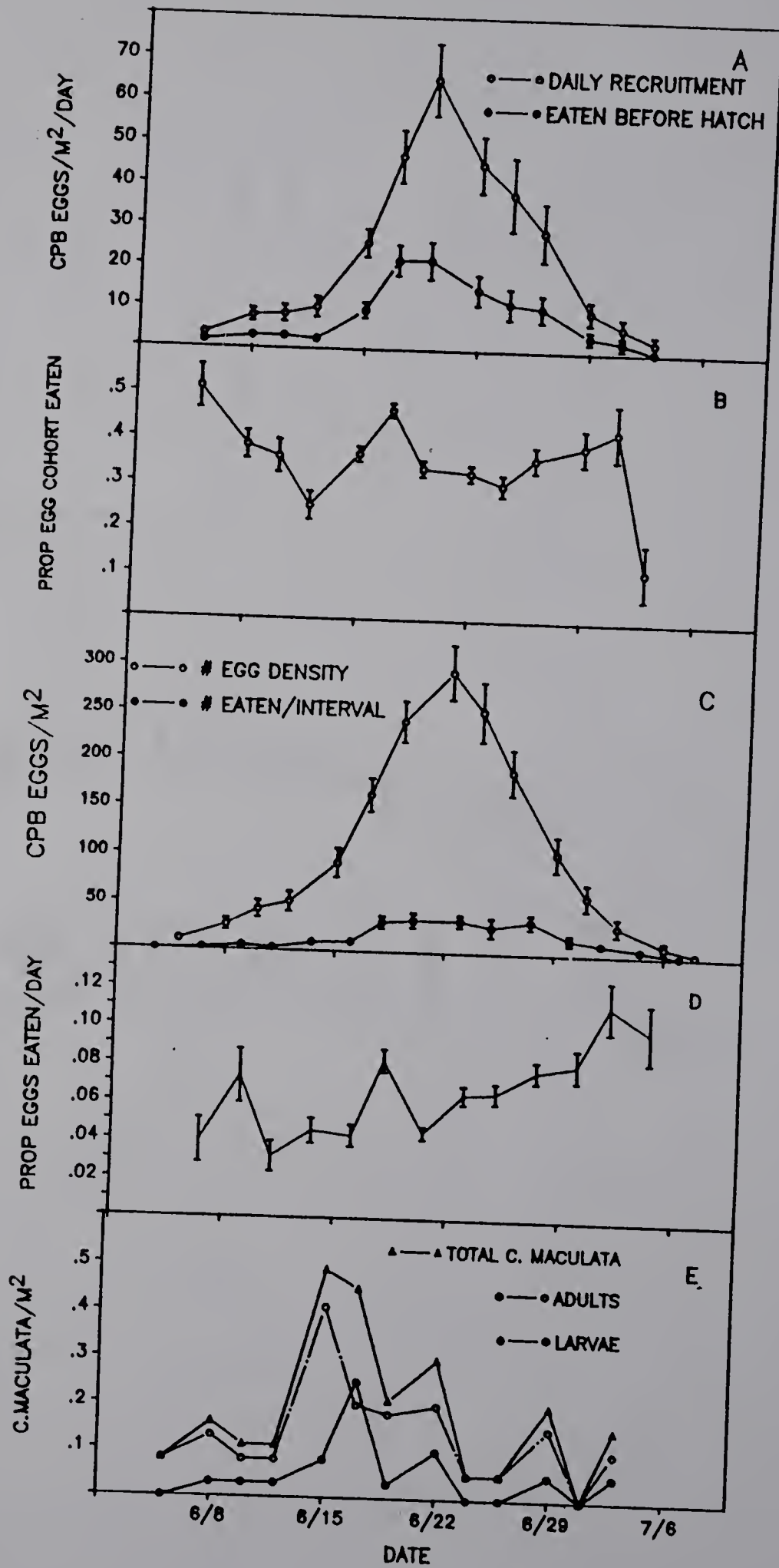
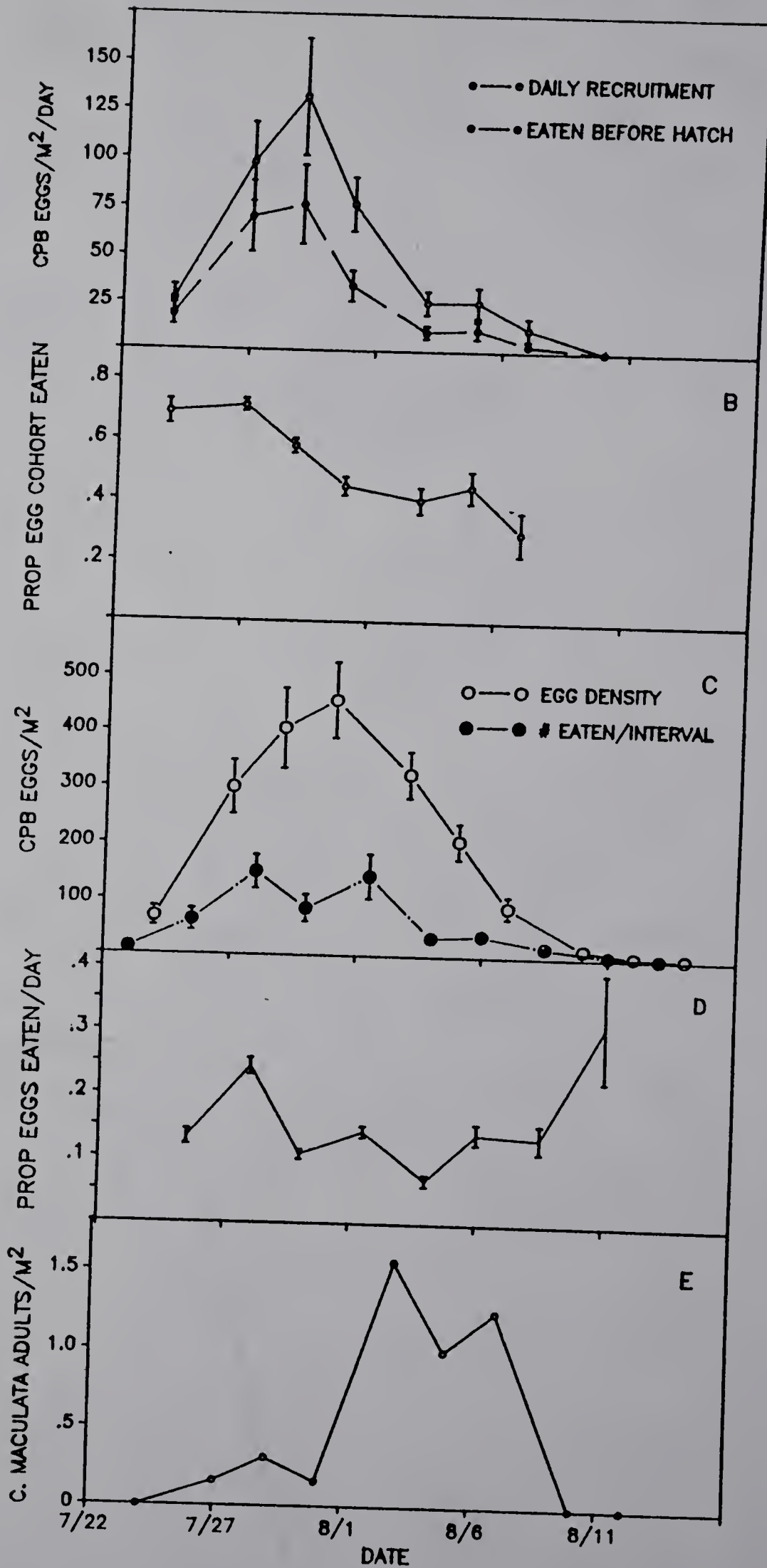




FIG.2.4 Recruitment, density and mortality of second-generation Colorado potato beetle eggs, 1987. See caption for Fig.2.1 for explanation of each graph.

GENERATION 2, 1987



## BIBLIOGRAPHY

- Atallah, Y. H., & L. D. Newsom. 1966. Ecological and nutritional studies on Coleomegilla maculata DeGeer (Coleoptera: Coccinellidae). I. The Development of an artificial diet and a laboratory rearing technique. J. Econ. Ent. 59: 1173-79.
- Benton, A. H., and A. J. Crump. 1981. Observations on the spring and summer behavior of the 12-spotted ladybird beetle, Coleomegilla maculata (DeGeer) (Coleoptera: Coccinellidae). N.Y. Entom. Soc. 89: 102-5.
- Bryson, C. T., and M. F. Schuster. 1975. Effectiveness of a spotted lady beetle as a predator of the bollworm on cotton. J. Econ. Ent. 68: 273.
- Coderre, D., L. Provencher, and J. Tourneur. 1987. Oviposition and niche partitioning in aphidophagous insects on maize. Can. Ent. 119: 195-203.
- Conrad, M. S. 1959. The Spotted lady beetle, Coleomegilla maculata (DeGeer) as a predator of European corn borer eggs. J. Econ. Ent. 52: 843-847.
- Drummond, F. A., R. L. James, R. A. Casagrande, and H. Faubert. 1984. Development and survival of Podisus maculiventris (Say) (Hemiptera: Pentatomidae), A predator of the Colorado potato beetle (Coleoptera: Chrysomelidae). Environ. Entomol. 13: 1283-1286.
- Ewert, M. A., and H. C. Chang. 1966. Dispersal of three species of Coccinellids in corn fields. Can. Ent. 98: 999-1003.
- Ferro, D. N. 1985. Pest status and control strategies of the Colorado potato beetle. pp. 1-8 in D. N. Ferro and R. H. Voss (eds.). Proceedings of the Symposium on the Colorado Potato Beetle, XVIIth International Congress of Entomology. Mass Agric. Expt. Stn. Bull. #704.

- Forgash, A. J. 1985. Insecticide resistance in the Colorado potato beetle. pp.33-53. In D.N. Ferro and R.H. Voss (eds.) Proceedings of the symposium on the Colorado potato beetle. XVIIth International Congress of Entomology Res. Bull. # 704. Mass. Agric. Expt. Sta.
- Frazer, B. D. and B. Gill. 1981. Hunger, movement, and predation of Coccinella californica on pea aphids in the laboratory and in the field. Can. Ent. 113: 1025-1033.
- Gross, H. R., Jr., S. D. Pair, and R. D. Jackson. 1985. Behavioral responses of primary entomophagous predators to larval homogenates of Heliothis zea and Spodoptera frugiperda (Lepidoptera: Noctuidae) in whorl-stage corn. Environ. Entomol. 14: 360-364.
- Harcourt, D. G. 1971. Population dynamics of Leptinotarsa decemlineata (Say) in eastern Ontario. III. Major population processes. Can. Ent. 103: 1049-1061.
- Hoagland, D. R., and D. I. Arnon. 1950. The water culture method for growing plants without soil. California Agricultural Experiment Station Circular #347
- Hodek, I., Z. Ruzika, and M. Hodkova. 1978. Feeding on pollen and aphids by Coleomegilla maculata Lengi. Annales de Zoologie. Ecologie Animale. 10: 453-459.
- Holling. C. S. 1959. Some characteristics of simple types of predation and parasitism. Can. Ent. 91: 385-398.
- Horton, D.R. and J. L. Capinera. 1987. Seasonal and host plant effects on parasitism of Colorado potato beetle by Myiopharus doryphorae (Riley) (Diptera: Tachinidae). Can. Ent. 119: 729-734.
- Kelleher, J. S. 1966. The parasite Doryphorophaga doryphorae (Diptera: Tachinidae) in relation to populations of the Colorado potato beetles in Manitoba. Annals Ent. Soc. Am. 59: 1059-1061.
- Krebs, J. R., Erichsen, J. T., Webber, M. I., and Charnov, E. L. 1977. Optimal prey selection in the great tit (Parus major). Anim. Behav. 25: 30-38.

- Livdahl, T. P., and A. E. Stiven. 1983. Statistical difficulties in the analysis of predator functional response data. *Can. Ent.* 115:1365-1370.
- MacArthur, R. H., and Pianka, E. R. 1966. On the optimal use of a patchy environment. *Amer. Natur.* 100: 603-609.
- Mack, T. P., and Z. Smilowitz. 1982a. Using temperature-mediated functional response models to predict the impact of Coleomegilla maculata (DeGeer) adults and 3rd-instar larvae on green peach aphids. *Environ Entomol.* 11: 46-52.
- Mack, T. P., and Z. Smilowitz. 1982b. CMACSISM, a temperature-dependent predator-prey model simulating the impact of Coleomegilla maculata (DeGeer) on green peach aphids on potato plants. *Environ. Entomol.* 11: 1193-1201.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs.* 39: 335-354.
- Nichols, P. R., and Neel, W. W. 1977. The use of Food Wheast as a supplemental food for Coleomegilla maculata (DeGeer) in the field. *Southwestern Entomol.* 2: 102-105.
- Obrycki, J. J., M. J. Tauber, and W. M. Tingey. 1983. Predator and parasitoid interaction with aphid-resistant potatoes to reduce aphid densities: a two-year field study. *J. Econ. Ent.* 76: 456-462.
- Obrycki, J.J., and M. J. Tauber. 1978. Thermal requirements for development of Coleomegilla maculata (Coleoptera: Coccinellidae) and its parasite Perilitus coccinellae (Hymenoptera: Braconidae). *Can. Ent.* 110: 407-412.
- Obrycki, J.J., and M. J. Tauber. 1985. Seasonal occurrence and relative abundance of aphid predators and parasitoids on pubescent potato plants. *Can. Ent.* 117: 1231-1237.
- Risch, S.J., R. Wrubel, and D. Andow. 1982. Foraging by a predaceous beetle, Coleomegilla maculata (Coleoptera: Coccinellidae), in a polyculture: effects of plant density and diversity. *Environ. Entomol.* 11: 949-950.

SAS Institute, Inc. 1987. SAS/STAT guide for personal computers, version 6 edition. Cary, NC.

Smith, B. C. 1965a. Differences in Anatis mali Auct. and Coleomegilla maculata lengi Timberlake to changes in the quality and quantity of the larval food (Coleoptera: Coccinellidae). Can. Ent. 97: 1159-1166.

Smith, B. C. 1965b. Effects of food on the longevity, fecundity, and development of adult coccinellids (Coleoptera: Coccinellidae). Can. Ent. 97: 910-919.

Smith, B. C. 1965c. Growth and development of coccinellid larvae on dry foods (Coleoptera: Coccinellidae). Can. Ent. 97: 760-768.

Smith, B. C. 1971. Effects of various factors on the local distribution and density of coccinellid adults on corn (Coleoptera: Coccinellidae). Can. Ent. 103: 1115-1120.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: The principles and practice of statistics in biological research. W. H. Freeman and Co., N.Y.

Tamaki, G. and B. A. Butt. 1978. Impact of Perillus bioculatus on the Colorado potato beetle and plant damage. USDA Technical Bulletin 1581.

Tamaki, G., R. L. Chauvin, and A. K. Burditt, Jr. 1983. Field evaluation of Doryphorophaga doryphorae (Diptera: Tachinidae), a parasite, and its host the Colorado potato beetle (Coleoptera: Chrysomelidae). Environ. Entomol. 12:386-389.

Van Driesche, R. G.. 1983. Meaning of "percent parasitism" in studies of insect parasitoids. Environ. Entomol. 12: 1611-1622.

Van Driesche, R. G., and T. S. Bellows, Jr. 1988. Host and parasitoid recruitment for quantifying losses from parasitism, with reference to Pieris rapae and Cotesia glomerata. Ecol. Entom. 13: 215-222.

- Van Driesche, R. G., T. S. Bellows, D. N. Ferro, R. V. Hazzard, and A. Maher. 1989. Estimating stage survival from recruitment and density data, with reference to egg mortality in the Colorado potato beetle, Leptinotarsa decemlineata (Say). Can. Ent. (in press).
- Voss, R. V., and D. N. Ferro. 1988. Role of reproductive diapause in the population dynamics of the Colorado potato beetle. Environ. Entomol. 17:863-871.
- Warren, L. O., and M. Tadic. 1967. Biological Observations on Coleomegilla maculata and Its Role as a Predator of the Fall Webworm. J. Econ. Ent. 60: 1492-1496.
- Williams, F. M., and S. A. Juliano. 1985. Further difficulties in the analysis of functional-response experiments and a resolution. Can. Ent. 117: 631-640.
- Wright E. J., and J. E. Laing. 1980. Numerical response of coccinellids to aphids in corn in southern Ontario. Can. Ent. 112: 977-988.
- Zaki, M., D. Moran, and D. Harris. 1982. Pesticides in groundwater: the aldicarb story in Suffolk Co., N.Y. Am. J. Publ. Health 72: 1391-1395.





