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NUMERICAL RESPONSE OF COCCINELLIDS TO APHIDS IN CORN IN SOUTHERN ONTARIO¹

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Abstract

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Populations of two abundant coccinellid species, *Coleomegilla maculata lengi* Timberlake and *Hippodamia tredecimpunctata tibialis* Say, responded rapidly to corn leaf aphid populations [*Rhopalosiphum maidis* (Fitch)] once the aphids became exposed to predation when the plants tasselled. *Coleomegilla m. lengi* oviposited at lower densities of aphids than did *H. t. tibialis* but *H. t. tibialis* was shown to have a greater numerical response than C_* *m. lengi* at high densities of aphids due to its greater fecundity. The numerical response of the coccinellids by oviposition was linear with a lag of $\frac{1}{2}$ week behind the aphid population.

Résumé

Les populations de deux espèces abondantes de coccinelles, Coleomegilla maculata lengi Timberlake et Hippodamai tredecimpunctata tibialis Say, ont répondu rapidement aux populations du puceron du mais [Rhopalosiphum maidis (Fitch)] une fois que les pucerons devinrent exposés à la prédation lors de la sortie de la panicule. $C_* m_*$ lengi a pondu à des densités de pucerons plus faibles que $H. t_*$ tibialis, cependant $H. t_*$ tibialis a montré une réponse numérique plus forte que $C_* m_*$ lengi aux densités élevées de pucerons, dû à sa fécondité plus élevée. La réponse numérique de ponte des coccinelles s'est révélée linéaire avec un retard d'une demi-semaine sur la population de pucerons.

Introduction

Corn is an important field crop in southern Ontario that is very rarely, if ever, treated to control aphids. Yet aphids have been shown to reduce yields of corn significantly in some years (Foott and Timmins 1973; Foott 1975). This study was undertaken to determine the relationship between the populations of coccinellids and the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), in field corn and to determine some of the factors that affect the ability of coccinellids to check the growth of aphid populations.

Foott (1973) studied coccinellid populations in corn in Essex County, Ontario and concluded that they were unable to prevent damage by the corn leaf aphid because large coccinellid populations were not present until after the density of aphids had peaked and most of the injury to the plant had occurred. He found no relationship between the number of coccinellid eggs deposited on a plant and the plant's aphid population. The three predominant coccinellids were *Hippodamia convergens* Guerin-Meneville, *H. tredecimpunctata tibialis* (Say), and *Coleomegilla maculata lengi* Timberlake.

Most investigations of field populations of coccinellids have dealt solely with adults (Foott 1973; Frazer and Gilbert 1976). However, coccinellid larvae are

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voracious predators with the potential to have a major impact on prey populations. Therefore, we studied adult and immature stages of the coccinellids.

Traps have been used to monitor populations in previous field studies (Ewert and Chiang 1966) and adults seen per unit of time have been counted (Foott 1973) but both indices were influenced by weather. Coccinellids are more active on warm, sunny days with little wind and counts of adult beetles flying per unit of time are biased. Such counts cannot be translated into absolute population densities which are important when considering predator-prey interactions. Therefore, we chose a sampling scheme based on inspection of entire corn plants.

"A numerical response is a change in predator density brought about by a change in prey abundance" (Crawley 1975). Numerical responses are influenced by birth and survival rates and by dispersal of mobile stages of a predator from an area of low prey density to an area of high prey density. Attraction to areas of high prey density could be due to aggregations of prey or to features of a typical prey environment.

The corn leaf aphid colonizes the corn field when the plants are approximately 1 month old (Foott 1977). As populations of aphids increase, adult coccinellids that are randomly searching the environment will contact prey at more frequent intervals. These adults begin to oviposit once a hypothetical, minimum threshold of prey density is exceeded. We examined the numerical responses of the two coccinellid species to determine why they did not control R. maidis.

Materials and Methods

Sampling design, 1977. Coccinellid and aphid populations were sampled in a 15 ha field of corn at the Guelph Research Station. The field was 93 m (111 rows) wide and 290 m long. A 16-row buffer zone was maintained around the field to reduce edge effects. Ten plots, each 20 rows wide and 90 plants long, were located randomly in the centre of the field and comprised 7.5% of the total area of the corn field.

The sample unit was three consecutive plants in a row. Early in the season, 25 units from each of the 10 plots were sampled randomly, but this was reduced to 20 for most of the summer, so at least 600 plants were examined on each sampling date. Sampling occurred twice a week from 21 June to 16 September and then once a week until 7 October, 1977; and on each date, the numbers of aphids, coccinellid eggs, late-instar larvae and pupae of all species were recorded.

Beginning 5 August, a few eggs from each cluster observed in four of the plots were taken to the laboratory and reared for species identification. Beginning 12 August the pupae from the same four plots were taken to the laboratory for emergence and identification.

Sampling design, 1978. In 1978 the sampling plan was altered to 20 plots, each 20 rows wide and 45 plants long, comprising the same proportion of the field as in 1977. The field was divided into four quarters and five plots were placed randomly within each quarter. Six hundred plants were sampled in units of three consecutive plants. Sampling began 27 June and continued twice a week until 19 September and then once a week until 2 October. All egg clusters were reared in the laboratory for species determination. Similarly, small coccinellid larvae and unknown coccinellid pupae were reared in the laboratory for identification. Beginning on 25 July, each plant was recorded as "closed whorl," "visible tassel," or "dropping pollen," to correlate development of the corn plants with the abundance of coccinellid food (aphids and corn pollen).

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Numerical response. The log densities of the coccinellids observed in both years were regressed against the log densities of aphids up to the peak density of aphids. Since there is, typically, a lag between the increase of populations of prey and their predators, the log densities of the coccinellids were also regressed against log densities of aphids sampled 1/2 week earlier. Differences in responses of the two major species of coccinellids and differences in responses of the coccinellids between the two years were examined by testing the quality of the regression lines (Chakravarti *et al.* 1967).

Results and Discussion

Field populations in 1977. The corn plants were ca. 10 cm high when sampling began. No aphids were present. The aphid population began to increase and reached a peak density of 85 aphids per plant on 12 July, during pollination of the corn (Fig. 1). The aphid population was composed almost entirely of the corn leaf aphid. The number of adult beetles at this time was very low (0.05 adult/plant). Increased oviposition was the most striking response of the beetle population to the increase in aphids. The density of coccinellid eggs closely followed the rise in aphid density, with a lag of a few days. The peak density of coccinellid eggs occurred 19 July, 1 week after peak aphid density. A rapid decrease in aphid density 19-22 July was followed by an equally rapid decrease in oviposition by the coccinellids.

The aphid population began to increase again 5 August and was followed by another increase in oviposition by the coccinellids. This second egg population was mainly H. t. tibialis (Table I). The numbers of aphids continued to increase even after the second peak in the density of coccinellid eggs but the aphids were clumped at this time into very large populations on a few plants.

On 19 July, the peak density of first-instar coccinellids occurred at the same time as did the peak density of their eggs. First-instar larvae were seen only when they were hatching from the eggs. Similarly, second-instar larvae were usually overlooked and the population density greatly underestimated. The numbers of late-instar larvae peaked on 29 July, and the pupal population peaked between 2 and 9 August.

The adult coccinellid population in corn increased initially by movement of adults from neighbouring grain fields where mature crops could no longer support aphid populations. By early August, however, adults were emerging from pupae in the corn field and contributing to the rise in the adult population. Numbers of $C.\ m.\ lengi$ adults peaked on 12 August, and remained relatively high and constant from 19 to 29 August. Numbers of $H.\ t.\ tibialis$ adults peaked on 19 August but were relatively constant 12 to 30 August. These populations gradually declined to almost zero by 7 October, when most beetles had migrated to their overwintering sites.

Although no coccinellid eggs were identified during the first egg-laying period (28 June to 5 August), it would appear that H. t. tibialis constituted a small proportion of all eggs, due to the appearance of the small number of later-instar larvae of this species between 22 July and 5 August (Fig. 2). Most coccinellid eggs seen during the second egg-laying period were H. t. tibialis (19 August to 22 September, Table I).

Adults of Coccinella transversoguttata richardsoni Brown, C. trifasciata perplexa Mulsant, and Hippodamia glacialis glacialis (Fabricius) were first observed 15 July when there was already a significant aphid population. The numbers of these adults remained at less than 0.05 adult/plant throughout most of the season. Hip-

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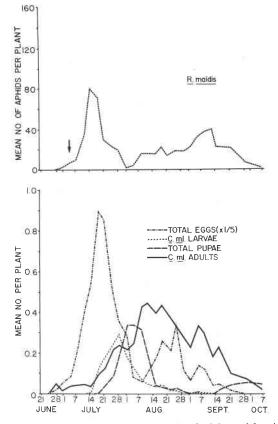


FIG. 1. Seasonal abundance of the corn leaf aphid, *R. maidis*, of adults and late-instar larvae of *C. m. lengi* and of eggs and pupae of all species of Coccinellidae in corn, Guelph, Ontario, 1977. Arrow indicates the beginning of tasselling period.

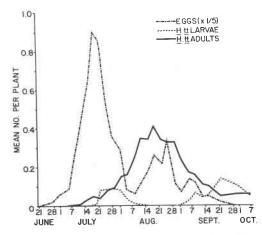


FIG. 2. Seasonal abundance of the adults and late-instar larvae of *H*. *t. tibialis*, and of the eggs of all species of Coccinellidae on corn, Guelph, Ontario, 1977.

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podamia parenthesis (Say), H. convergens Guerin, Adalia bipunctata (L.), and Coccinella novemnotata Herbst were found occasionally but were never numerous.

Populations in 1978. Prolonged drought in late June, and throughout most of July retarded development of the corn and plants did not begin to shed pollen until 1 August. The visible aphid population remained very low during July and increased only when the tassels emerged between 25 July and 8 August (Fig. 3). Aphids developed within the whorl of leaves surrounding the developing tassel and were protected from predation until exposed when the plant tasselled.

Populations of aphids are typically higher in dry years (Foott 1975) and this was confirmed when populations were compared for 1977 and 1978 which was relatively dry. A maximum density of 159 aphids per plant on 11 August was almost double the highest density of aphids seen in 1977. The plant development of 1978, retarded due to lack of rainfall, allowed a longer period for the populations of aphids to increase within the whorl. As in 1977, the density of aphids rapidly declined after the tassels had fully emerged. The population of aphids did not peak a second time as in 1977.

Oviposition by coccinellids followed the trend seen in 1977, increasing rapidly as the aphid population increased at tasselling and decreasing as the aphid population declined. *Coleomegilla m. lengi* oviposited between 7 July and 25 August, with a

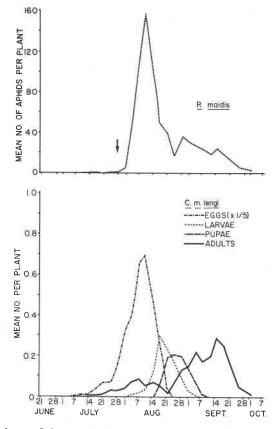


FIG. 3. Seasonal abundance of the corn leaf aphid, *R. maidis*, and of *C. m. lengi* in corn, Guelph, Ontario, 1978. Arrow indicates beginning of tasselling period. peak of 3.5 eggs/plant recorded on 11 August (Fig. 3). *Hippodamia t. tibialis* oviposited between 25 July and 22 August, with a peak density of 5.1 eggs/plant on 15 August (Fig. 4). Both species had one ovipositional period in corn in 1978.

Coleomegilla m. lengi reached a maximum of 0.31 mature larva/plant 18 August and pupae peaked at 0.21/plant on 25 August. Adults of C. m. lengi responded to the increasing density of aphids during early August by moving into the corn but moved out again once the density of aphids fell. Adults emerging from pupae in the field constituted the adult population present from 22 August to 2 October. Emigrant adults of C. m. lengi were seen in overwintering sites adjacent to the study area by 5 September.

Hippodamia t. tibialis reached maximums of 0.84 late-instar larva/plant 18 August and 0.69 pupa/plant 29 August (Fig. 4). Adults immigrated into the field in response to the high density of aphids from 25 July to 18 August and were later replaced by adults that had developed within the field. Adults emigrated during September and October.

Coleomegilla m. lengi and H. t. tibialis were the most abundant species of coccinellids in the study area in 1978. Coleomegilla t. richardsoni, C. t. perplexa, H. parenthesis, H. g. glacialis, and A. bipunctata were occasionally observed (< 0.03/plant on all sampling dates).

There was a direct linear relationship between the observed densities of aphids and eggs of coccinellids in both 1977 and 1978, with the population of the eggs of the predator lagging about 1/2 week behind the population of the prey (Figs. 1-4). When the density of coccinellid eggs is plotted against the density of aphids observed 1/2 week earlier, the curve increases rapidly at low densities of aphids then flattens out at high densities (Fig. 5), showing a typical numerical response (Holling 1959). When such a relationship can be shown to be constant between seasons, it is possible to predict the numerical response of the predator from the size of the population of the prey.

For each year and the two years combined, the regressions of the log of the density of the eggs of all species on the log of the density of the aphids for both immediate and lag responses showed no significant differences, but the lag response gave a better correlation. Therefore, Y = -0.45898 + 0.68133X is a general equation describing the response of oviposition of all coccinellid species to the aphid population in field corn (Fig. 6).

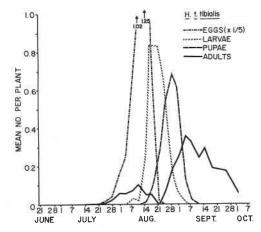


FIG. 4. Seasonal abundance of H. t. tibialis in corn, Guelph, Ontario, 1978.

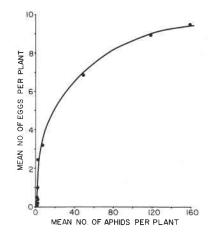


FIG. 5. The relationship between the density of eggs of all coccinellids and the density of aphids observed 1/2 week earlier during the period of increasing aphid abundance on corn, 4 July to 11 August, 1978, Guelph, Ontario.

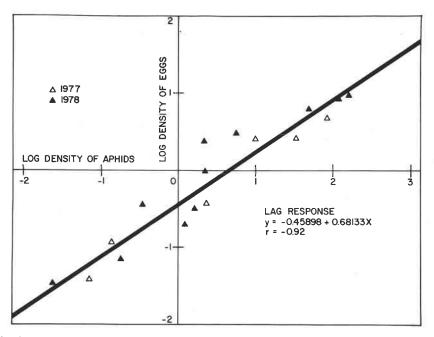
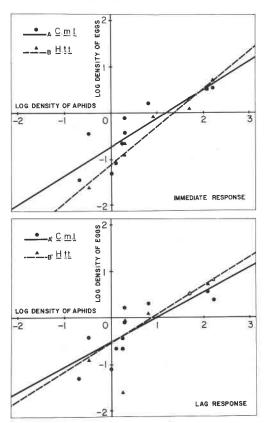


FIG. 6. The relationship between the log density of eggs of all species of coccinellids and the log density of aphids observed ¹/₂ week earlier (lag response) during the period of increasing aphid abundance on corn, Guelph, Ontario, 1977 and 1978.

Species of coccinellid eggs observed during the first ovipositional period of 1977 were not determined, so only the total ovipositional response could be studied. However, in 1978 populations, oviposition by C. m. lengi was synchronized better at low densities of aphids than was that of H. t. tibialis, since eggs of C. m. lengi were found a full 2 weeks earlier than those of H. t. tibialis (Figs. 3, 4). The relationships between the log of the densities of eggs and aphids for these two

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 $FIG_{\pm}7_{\pm}$ The relationship between the log density of eggs of C_{\pm} m. lengi and of H. t. tibialis and the log density of aphids observed on the same day (immediate response) and $\frac{1}{2}$ week earlier (lag response) during the period of increasing aphid abundance on corn, Guelph, Ontario, 1978.

Immediate response:

Α	C. m. lengi	Y = -0.72509 + 0.6210X
		r = 0.86
В	H. t. tibialis	Y = -1.11324 + 0.82492X
		r = 0.97
Lag response:		
\mathbf{A}'	C. m. lengi	Y = -0.51399 + 0.54241X
		r = 0.83
\mathbf{B}'	H. t. tibialis	Y = -0.55206 + 0.62777X
		r = 0.96

species is shown in Fig. 7. Although eggs of C. m. lengi appeared earlier than eggs of H. t. tibialis, there is a stronger correlation between aphids and eggs of H. t. tibialis for the immediate and lag responses (r = 0.97; 0.96) than for aphids and eggs of C.m. lengi (r = 0.86; 0.83). At the highest densities of aphids, H. t. tibialis laid more eggs than did C. m. lengi although there is no statistical difference between the responses of the two species.

The relationship between the densities of aphids and adult coccinellids was examined by regression analysis for the increasing phase of the aphids. The correlation coefficients were greater for both species for an immediate rather than a lag response (C. m. lengi r = 0.91 vs. 0.82 and H. t. tibialis r = 0.83 vs. 0.68),



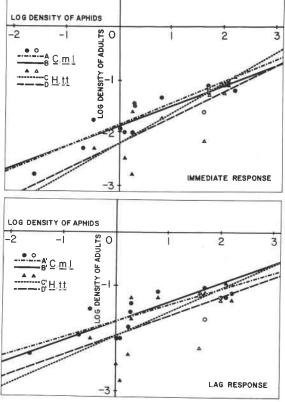


FIG. 8. The relationship between the log density of adults of *C. m. lengi* and of *H. t. tibialis* and the log density of aphids observed on the same day (immediate response) and ¹/₂ week earlier (lag response) during the period of increasing abundance (4 July to 11 August) and the period of increasing and decreasing abundance of aphids (4 July to 22 August) on corn, Guelph, Ontario, 1978. SYMBOLS: Closed symbols are pre-peak values (4 July to 11 August) and open symbols are post-peak values (15 August to 22 August).

Immediate response:

- A C. m. lengi, increasing aphid density Y = -1.87939 + 0.41906X, r = 0.91
- B C. m. lengi, increasing and decreasing aphid density Y = -1.87939 + 0.38817X, r = 0.90
- C H. t. tibialis, increasing aphid density Y = -2.21180 + 0.57471X, r = 0.83
- D H. t. tibialis, increasing and decreasing aphid density Y = -2.22770+0.49813X, r = 0.75

Lag response:

- A' C. m. lengi, increasing aphid density Y = -1.69337 + 0.30015X, r = 0.82
- B' C. m. lengi, increasing and decreasing aphid density Y = -1.70827 + 0.2680X, r = 0.79
- C' H. t. tibialis, increasing aphid density $Y = -1.97138 \pm 0.44214X$, r = 0.68
- D' H. t. tibialis, increasing and decreasing aphid density Y = -1.97544 + 0.36211X, r = 0.58

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indicating that the density of adults was determined by the density of aphids at that time. When the relationship between the densities of aphids and adults of these two species was examined for the full cycle of increasing and decreasing aphid density, the response for both species was similar to the response for increasing densities of aphids (Fig. 8). Therefore adult beetles responded to the populations of aphids in the same way throughout the entire aphid cycle and it continued to be an immediate response.

The correlation of adult c. m. lengi density to aphid density (r = 0.91) was closer than that of adult H. t. tibialis density to aphid density (r = 0.83) indicating that adult populations of C. m. lengi followed the aphid populations more closely. This could be associated, at least partly, with the relative mobilities of these two species. Ewert and Chiang (1966) showed that C. m. lengi adults were far less mobile than adults of H. t. tibialis in field corn. This could mean that, once in the field, C. m. lengi is more likely to remain when the density of an aphid population is low.

Since adult populations of C. m. lengi follow the populations of aphids more closely than do those of H. t. tibialis, it seems contradictory to find a closer relationship between the densities of aphids and eggs of H. t. tibialis than those of C. m. lengi. Over the ovipositional period (14 July to 22 August) there were far more eggs laid by H. t. tibialis but there were 1.2 times as many adults of C. m. lengi as of H. t. tibialis, suggesting that fecundity of H. t. tibialis was greater than that of C. m. lengi. This could account for the better correlation between the densities of aphids and eggs of H. t. tibialis and eggs of H. t. tibialis and eggs of H. t. tibialis than for the densities of aphids and eggs of C. m. lengi.

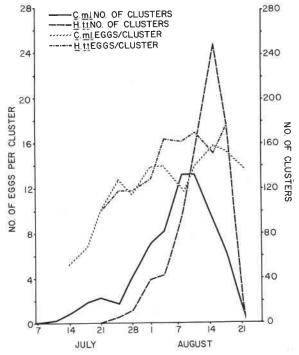


FIG. 9. The number of egg clusters observed on 600 corn plants and the number of eggs per cluster for C. m. lengi and H. t. tibialis on corn, Guelph, Ontario, 1978.

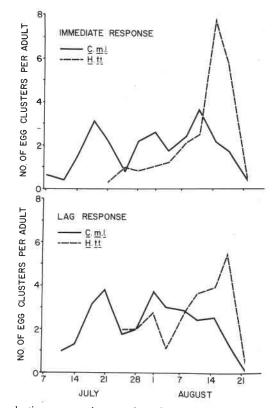


FIG. 10. Egg cluster production expressed as number of egg clusters produced, per adult beetle seen on the same day as their hosts (immediate response) and as number of egg clusters per adult beetle seen ¹/₂ week earlier than their hosts (lag response) for *C. m. lengi* and *H. t. tibialis* on corn, Guelph, Ontario, 1978.

The increasing populations of aphids had two major effects on oviposition by both dominant species of coccinellids on corn. The first was an increase in the mean number of eggs per cluster. Early in the ovipositional period, the number of eggs per cluster was low for both species (Fig. 9). This number increased rapidly to a nearly steady 14 eggs per cluster for C. m. lengi and 16.5 eggs per cluster for H. t. tibialis. The second effect was to stimulate egg production, especially in H. t. tibialis (Fig. 9). Figure 10 shows the number of clusters observed per adult beetle on the same day as counts of aphids and with a lag of 1/2 week behind the aphid densities. In both cases there is a relatively constant, or slightly declining, number of clusters per adult of C. m. lengi but an increasing number produced per adult of H. t. tibialis throughout the ovipositional period. It appears that, although the adult populations of C. m. lengi are quite sensitive to the population density of aphids, they have a smaller egg cluster than does H. t. tibialis and a relatively constant, maximum output of clusters per beetle which is reached at low aphid densities. Hippodamia t. tibialis colonizes more slowly but has a larger egg cluster and a much higher maximum output of clusters per beetle than does C. m. lengi. The number of clusters produced per H. t. tibialis increased steadily throughout the ovipositional period and did not level off as it did for C. m. lengi, indicating that the maximum potential output of clusters was not reached by this species even during the high densities of aphids observed in 1978.

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At low densities of aphids, C. m. lengi was the dominant species, due to greater sensitivity of the adults to the combination of pollen and the low aphid populations. At high densities of aphids, however, H. t. tibialis was the dominant species due to its greater fecundity.

Coccinellids do not provide economic control of the corn leaf aphid at the critical time of tasselling because the aphids increase to the damaging levels inside the whorl of leaves surrounding the tassel where they are protected from predation. However, once the tassels emerge and the aphids are exposed, the beetles respond rapidly by immigration and oviposition. The beneficial action of the coccinellids is the suppression of the aphid populations to tolerable levels for the rest of the growing season.

Acknowledgments

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