SAMPLING FOR ADULT COCCINELLIDS AND THEIR NUMERICAL RESPONSE TO STRAWBERRY APHIDS (COLEOPTERA:COCCINELLIDAE: HOMOPTERA:APHIDIDAE)

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Abstract

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Searching for adult coccinellids in large cages placed over sections of strawberry fields produced an average of 10 times as many coccinellids per metre of row as a relative method of sampling. Methods of converting relative indices to absolute indices of abundance were found. Results suggest that the frequently observed slow increase in abundance of aphid predators in response to increasing aphid abundance may be an artifact resulting from using relative indices of abundance that make no correction for the effects of hunger on predator activity. Calibrating the samples shows that numbers of adult coccinellids follow the trend of aphid abundance closely enough that coccinellid numbers may be predictable.

Résumé

La recherche de coccinelles adultes dans de grandes cages placées dans des champs de fraisiers a montré en moyenne dix fois plus de coccinelles par mètre de rang qu'une méthode relative d'échantillonage. On a trouvé le moyen de transformer les indices d'abondance relative en indices absolu. Les résultats suggèrent que la lente recrudescence observée fréquemment chez les prédateurs de pucerons en reponse à l'accroissement d'abondance des pucerons peut être un artefact dû à l'usage d'indices de la faim sur l'activité des prédateurs. La calibration des échantillons montre que le nombre de coccinelles adultes fluctue avec l'abondance des pucerons suffisament pour que le nombre de coccinelles puissent être prédit.

Introduction

Strawberries are an important commercial crop in southwestern British Columbia. Despite the predominant use of the virus-tolerant cultivar, Totem, plant viruses transmitted by aphids pose a continually increasing threat to the industry. Evaluating the role of natural enemies of the aphids on strawberry is one facet of the research at this station aimed at developing an integrated control program of the pests and virus diseases of strawberries. Before the impact of a predator population can be appraised an efficient and accurate sampling method for them is required.

A functional response of coccinellids attacking pea aphids was formulated into a model that accounted for the mortality of the aphids in the field (Frazer and Gilbert 1976). The approach and model were also found useful in describing similar predator and prey systems in California (Baumgaertner *et al.* 1981). In the development of these models, it was as difficult to determine the numbers of predators in a field as it was to determine their impact once their numbers were known. Frazer and Gill (1981) evaluated the interaction of predator hunger, circadian rhythm, and aphid density on numbers of adult coccinellids observed in alfalfa fields. Calibrating relative indices of abundance was hampered by the effects of temperature on coccinellid activity which affected accuracy in sampling for them. The methods used were too expensive and time consuming to be used routinely in research and certainly so in monitoring for pest management purposes. If an accurate relationship between numbers of coccinellids and aphid numbers can be described, it could be used to predict the coccinellid numbers from aphid densities, thereby eliminating the need to sample for coccinellids. Wright and Laing (1980) found a linear numerical response in adult coccinellids and their eggs when preying on corn. However, Mills (1981) found an asymptotic relationship between the number of adult coccinellids and lime aphid numbers, and the level of the asymptote varied between years.

We designed the experiment reported here to determine the relationship between observed and actual numbers of coccinellids, taking into account those environmental factors that we knew would affect our observations. We hoped to circumvent many of the laborious steps used for earlier models in determining absolute numbers from calibrated census data. The use of absolute numbers is only the first step in developing a predictive numerical response.

Materials and Methods

The plots. The foliage of strawberry cultivars differs slightly in ways that combined, may affect the probability of observing coccinellids. Cultivar nutritional differences may also affect the aphids and coccinellids in ways that affect their number. Two varieties were included to test for such differences. Plots of Hood and Totem strawberries consisted of 20 rows of plants each row 10 m long. The plants were transplanted at 70-cm intervals within rows spaced 1 m apart on 5 May 1981. The experiments reported here were done in these plots during 1982 when the rows had filled out to a solid mat of plants rotovated to a 50-cm-wide row.

Sampling coccinellids. Adult coccinellids were sampled 1–7 times during each day by doing ''walking counts''. An observer walked between the rows of strawberries at an even pace recording with a hand-held talley counter the adult coccinellids seen. The observer walked continuously, scanning one row of plants at a time. Number of coccinellids seen, name of the observer, time of day, duration of the walk, total length of row scanned, temperature, and average solar radiation per minute during the walk were recorded for each walking count. Almost all adult coccinellids seen were *C. californica* (Mannerheim). Larval coccinellids were not sampled. Temperature recorded was that of a precision mercury thermometer in a Stevenson screen placed 1 m above the plants. Solar radiation was estimated as photosynthetically active radiation (PAR) in $\mu E/m^2/sec$. PAR is linearly related to total solar radiation and is therefore an index of radiant heat (Howell *et al.* 1983). In all, 134 walking counts were made from 17 May to 17 June 1982. An average of 4 walking counts were made each day.

Observer differences. To estimate the effect of observer differences, three observers walked a few metres behind each other over the same lengths of row. This was done 7 times between 1325 and 1550 h on 7 June 1982, a warm (15.9°), cloudless, calm day. Temperatures and solar radiation remained almost constant during this time. On each of the 7 occasions, two walking counts were made over the same lengths of rows by each of the three observers to provide replication. Different parts of the plots were walked to provide a range of coccinellid numbers that were observed.

Aphid density. An index of aphid, *Chaetosiphon fragaefolii* (Cockerell), density on the plants was determined at no longer than weekly intervals throughout the study period. Samples of 40 to 60 immature, unexpanded leaves were collected and the aphids on them were counted. Weights of adult aphids to ± 1 μg and average numbers of aphids per leaf were determined.

Calibration. Wooden cages covered with insect-proof screen (11 × 11 mesh/cm) were placed over a previously sampled section of a field immediately after a walking count on 13 occasions. Caging was not replicated. The cages covered 7.2 m of row. Soil was banked around the bottom of the cage to prevent escape of insects. The cages were thoroughly searched for coccinellids several times a day for up to 7 days until no further coccinellids were found. The total number found and removed from the cages was recorded. The number of coccinellids per metre of row in the cages was used as an estimate of the absolute number present. When personnel and shortages of cages prevented placement of a cage, absolute numbers used in analyses were derived by linear interpolation and degrees of freedom reduced accordingly. Cage placement was determined by moving them down rows of strawberries two cage lengths and across rows one cage width each time.

Results

Observer differences. There were considerable and significant ($P \leq 0.05$) differences between the number of coccinellids recorded and the number of coccinellids seen per minute by each observer (Table 1), but not between the times to walk the same length of row. Linear regression was used to convert values of the two less efficient observers to values that would have been observed by observer 1. In all cases, the correlation coefficient between pairs of observers' scores was 0.94 (40 df) or better.

Table 1. Average number of adult coccinellids seen per walk, time taken to walk, and average number seen per minute of walking. Numbers within a column followed by the same letter are not different (Duncan's multiple-range test at $P \leq 0.05$)

Observer	Number	Time (min)	C/min
1	28.1 a	3.8 a	7.5 a
2	14.9 b	3.2 a	4.46 b
3	25.6 c	3.2 a	7.6 c

Aphids. Strawberry aphid density increased and then decreased on Totem but less sharply on Hood during the study. Density varied over an order of magnitude during the study (Fig. 1A). Average weights of adult aphids varied sixfold (Fig. 1B), but did not differ significantly between cultivars.

Walking and cage counts. Coccinellid numbers in walking counts in both cultivars decreased (Fig. 2A) during the study but there was no trend relative to aphid density (Fig. 2B) or to aphid weight (Fig. 3). There was, however, a positive relationship between numbers of adult coccinellids found in the cages and average weight of adult aphids present

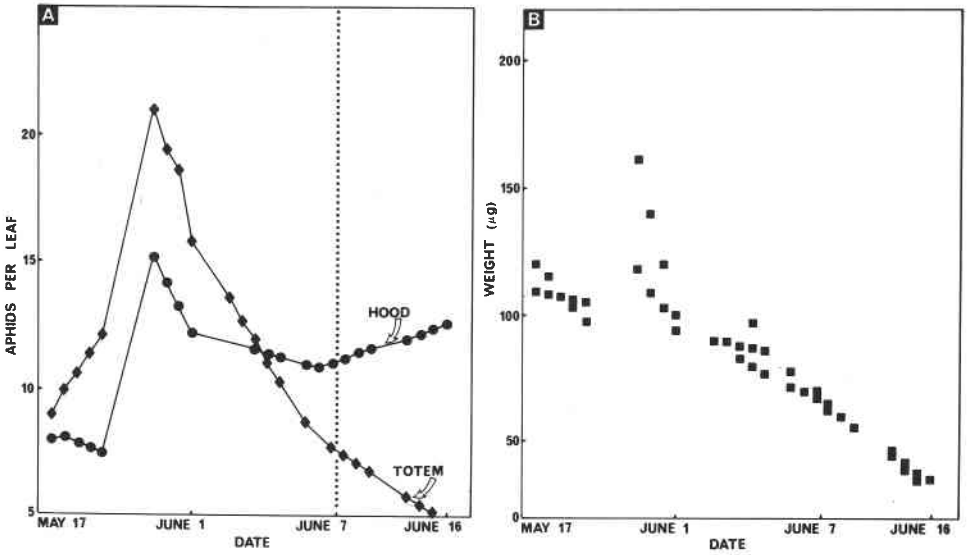

FIG. 1. (A), average numbers of strawberry aphids present in samples from two strawberry cultivars in 1982. (B), average weights of apterous adult strawberry aphids in 1982.

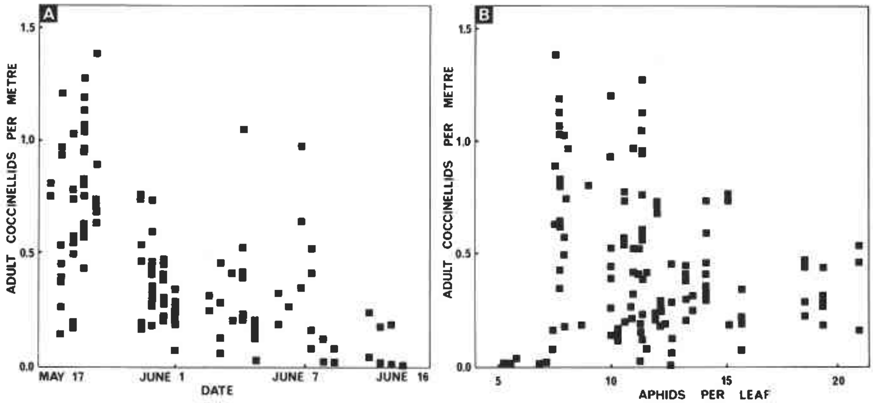

FIG. 2. (A), numbers of adult coccinellids observed in all walking counts during 1982. (B), numbers of adult coccinellids observed in all walking counts versus average number of strawberry aphids present.

(Fig. 4). Coccinellid numbers observed in walking counts increased with increased numbers from the cages but to an asymptote (Fig. 5). Numbers from cages (Fig. 6) followed the major trends in aphid density (Fig. 1A) more closely than those from walking counts (Fig. 2A).

Analysis

No significant differences in observability of coccinellids (number seen/number estimated to be present) were found between cultivars. Data from both cultivars were therefore pooled. Data were subdivided into two sets. One set (between-days) consisted of one walking count from each day that produced the largest number of coccinellids that day and the number of coccinellids estimated from the cages for that day. This data set was used to determine if there was a relationship between the numbers of beetles actually present (cages), and the estimates of aphid numbers and weight. The relationships between numbers observed in walking counts, time of day, and weather variables were derived from all walking counts within each day. SPSS^{x}® was used for analyses.

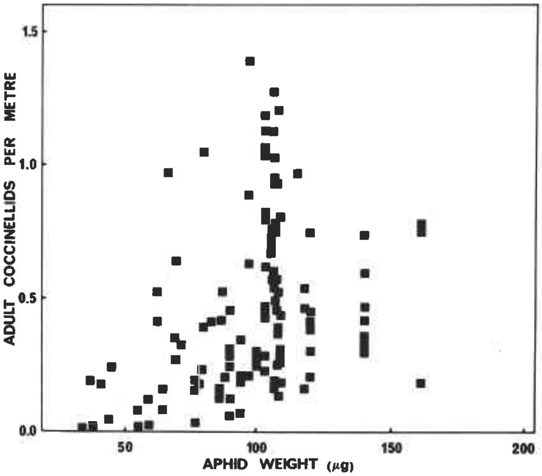

FIG. 3. Numbers of adult coccinellids observed in all walking counts versus weight of apterous adult strawberry aphids present.

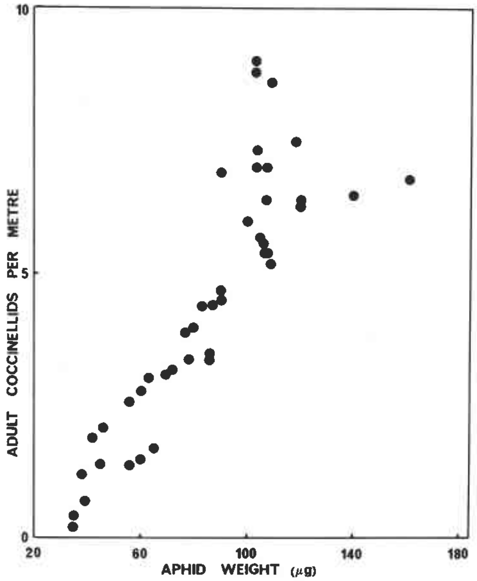

FIG. 4. Numbers of adult coccinellids trapped by caging versus the average weight of apterous adult strawberry aphids present.

Between days. Numbers of beetles observed in walking counts were poorly related to aphid density (Fig. 2B) and were only slightly better related to average aphid weight (Fig. 7A). Variation in numbers of beetles present per metre of row estimated by field caging (C) each day was accurately ($R^2 = 0.93$; 9 df) described by a curvilinear combination of aphid density (A) per leaf and aphid weight (W = μg/aphid).

$$C = 0.160W - 0.424A - 0.056A^2 - 0.00869AW - 3.60 \qquad [1]$$

Within-days. Number of beetles observed in walking counts was poorly related to temperature (Fig. 7B) and solar radiation (Fig. 8A) but was curvilinearly related to time of day (Fig. 8B), although with much variation. Peak numbers of beetles were observed when the walking count was made between about 1100 and 1300 PDT each day. The best

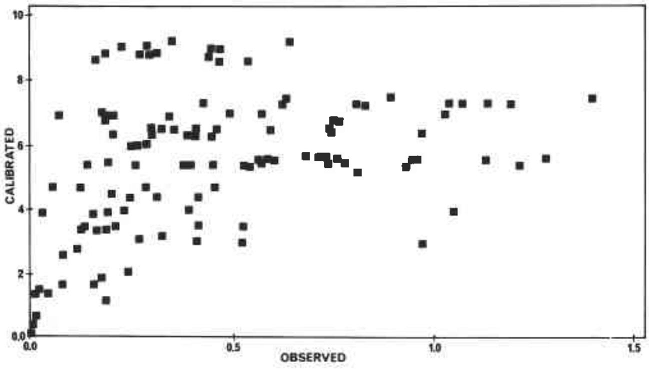

FIG. 5. Numbers of adult coccinellids per metre of row by caging (calibrated) versus the numbers in walking counts.

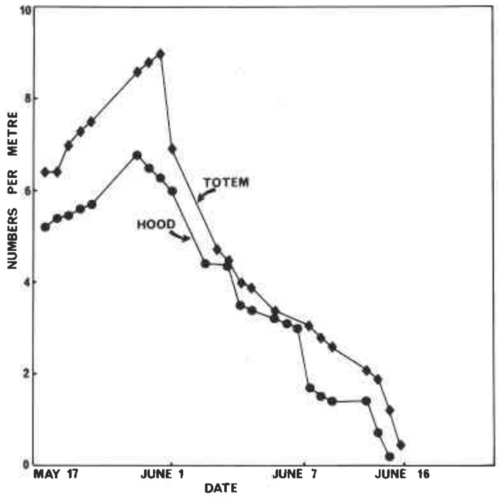

FIG. 6. Numbers of adult coccinellids per metre of row trapped by caging 2 cultivars of strawberries during 1982.

fitting equation, using only meteorological variables and polynomials composed of them explained 25% of the variation in the number of beetles observed.

Hunger as well as time of day affects activity (Frazer and Gill 1981). Assuming that availability of aphids would affect activity and therefore observability, aphid variables were added to the analysis. The best fitting equation explained 64% of the variation in beetles observed in walking counts. Dependent variables in this equation (Table 2) included radiation, temperature, time, aphid density, aphid weight, aphid availability (density times weight), and the squares of radiation and temperature. The two equations are not presented here because of their size. Also their parameters would be relevant only to this study because plant size, vigor, plant density, and leaf size would affect the ability to see coccinellids.

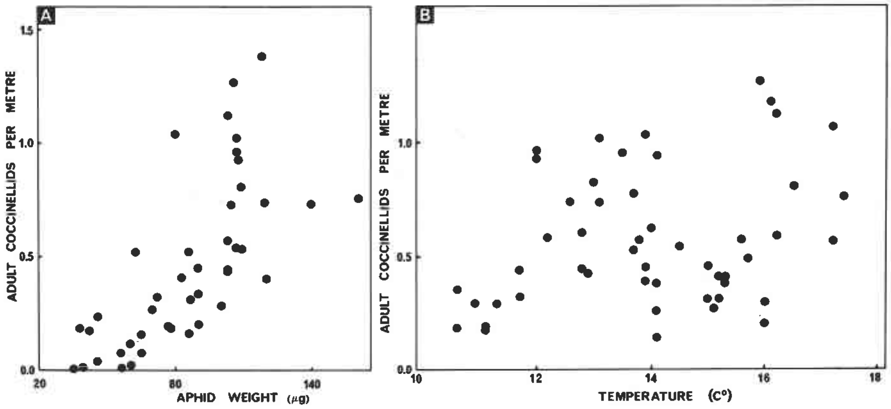

FIG. 7. Numbers of adult coccinellids observed in walking counts versus (A) average weights of apterous adult strawberry aphids present and (B) temperature at the time the count was made.

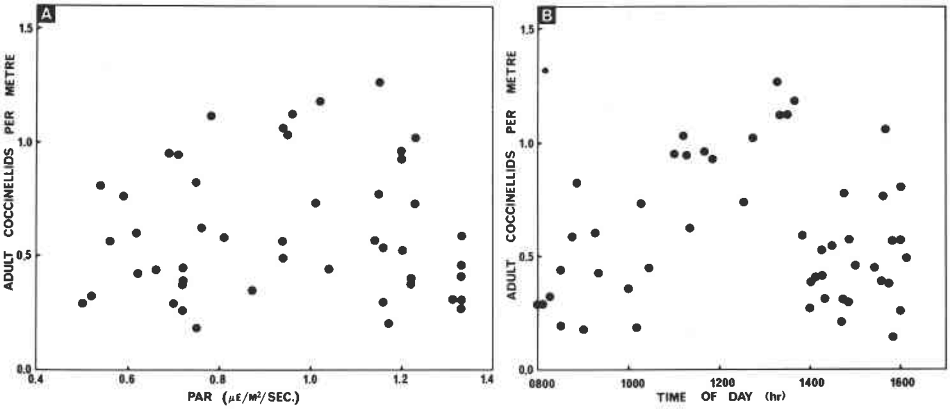

FIG. 8. Numbers of adult coccinellids observed in walking counts versus (A) incident solar radiation and (B) time of day when count was made.

Discussion

Variation in numbers of adult coccinellids present in the strawberry fields during this study was estimated accurately by the variations in strawberry aphid density and aphid biomass. The relationship (eq. [1]) between those variables quantifies a numerical response of coccinellids, but not in a manner consistent with the original numerical response definition (Solomon 1949) that was based solely on prey numbers. Aphid size is greatly affected by the nutritional status of their host plant and the effects of density-dependent competition of the aphids for the plant's nutrients. It is not surprising, therefore, that the attractiveness of an aphid population to predators is related to both number and size of aphids.

Hunger provides adult coccinellids with a very sensitive gauge of aphid density. Adult coccinellids rapidly accumulated in areas of alfalfa fields that had artificially high densities of aphids, and the average daily hunger level of coccinellids was dependent upon the aphid density (Frazer and Gill 1981). Adult coccinellids are induced to leave alfalfa fields whenever aphid density falls below a threshold level. That density is determined by the ability of the coccinellids to capture sufficient aphids to maintain their body weight (Frazer and Gilbert 1976). Six to 16% of adult coccinellids leave fields each day even when aphid densities greatly exceed the threshold density (Ives 1981).

That coccinellids leave even when aphid density is high reflects the stochastic nature of prey capture and the innate dispersal tendency of coccinellids. Many plants remain uncolonized even at high aphid densities and coccinellids landing on those plants could leave the field. Tendency to fly alternates with feeding bouts in *Hippodamia convergens* until their ovaries are mature (Davis and Kirkland 1982). Even when the ovaries are mature and egg production begins, many adult coccinellids continue to disperse. This dispersal

Table 2. Correlation matrix (119 df) of calibrated numbers of adult coccinellids per metre of strawberry row, coccinellids observed in walking counts, climatic and aphid factors

	Abs.	Temp.	Time	Rad.	Obs.	a/l	wt
Absolute	1.0						
Temperature	−0.49	1.0					
Time	−0.22	0.67	1.0				
Radiation	−0.02	0.48	0.48	1.0			
Observed	0.36	−0.13	0.02	0.07	1.0		
Aphids/leaf	0.49	−0.28	−0.22	0.09	−0.20	1.0	
Aphid weight	0.69	−0.56	−0.22	−0.10	0.36	0.38	1.0

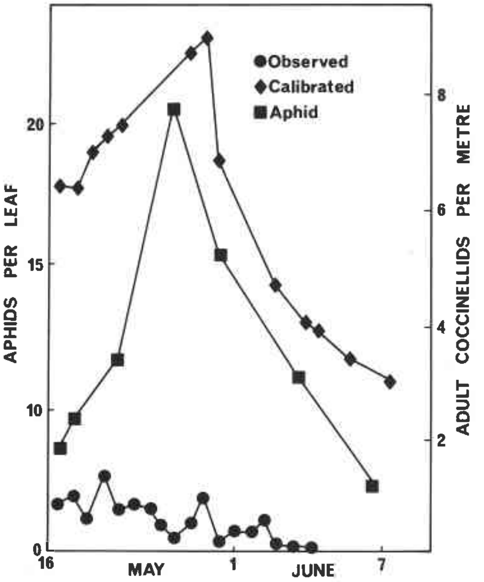

FIG. 9. Average numbers of aphids per leaf of Totem strawberry, numbers of adult coccinellids in walking counts (observed) and numbers from cages (calibrated).

was seen (Frazer *et al.* 1981) as a means to avoid competition between the adults and their progeny.

Despite these innate dispersive tendencies that are not directly related to prey capture by adult coccinellids, the goodness of fit of [1] implies that while fields are constantly losing and gaining individual coccinellids, the number of resident coccinellids is in a dynamic equilibrium with aphid availability. The net effect of dispersal and the equilibrium is to optimize the number of second generation coccinellids produced from a given pattern of aphid density over time (Frazer *et al.* 1981).

The numerical response was not evident from the walking count data. A circadian rhythm in searching behavior and hunger (Frazer and Gill 1981) and satiation effects (Mills 1982) on coccinellid behavior produce 10- to 100-fold differences in the proportion of resident coccinellid population likely to be found in sampling. Temperature and solar radiation further affect this proportion. The extent to which adult coccinellids can be underestimated was evident from sampling known numbers of coccinellids in large cages of alfalfa. No more than 10% of the coccinellids present were ever found in daily counts, even if the plants and debris around them were searched intensively (Frazer *et al.* 1981).

Using uncalibrated relative sampling methods that ignore the effects of coccinellid behavior and physiology on sampling efficiency will result in estimates of coccinellid abundance that seem unimportantly low and unresponsive to aphid density. Doing walking counts is surely a less efficient sampling method than by other methods (vacuum sampling, sweep nets). However, the difference between results from these methods would be trivial compared to the problem of not being able to sample satiated or inactive predators regardless of the method used. Any relative sampling method that demands that predators be active and on the upper plant canopy will likely be as inefficient as the walking counts.

Sampling without regard to the effects that weather, time of day, and visual acuity of samplers have on the sampling efficiency or sampling infrequently, would further bias estimates of predator abundance. Use of an absolute estimate, even without replication as in this study, shows a pattern of abundance that follows that of the aphids (Fig. 9).

The frequent observation that the increase in abundance of coccinellids is very slow in response to an aphid increase would have been seen here if the samples had not been calibrated (Fig. 9). The apparent poor synchrony of coccinellid numbers to aphid numbers is due to the effects of hunger and satiation on the activity of coccinellids and therefore on their likelihood of being sampled by relative methods. Satiated coccinellids are predominantly inactive (Frazer and Gill 1981; Mills 1982). Coccinellids become increasingly more active as they become hungrier. This effect of hunger would give the appearance that coccinellids are low in number when aphid populations are increasing and abundant only when aphid populations are declining. Frazer and Gilbert (1976) and Mack and Smilowitz (1982) reported the decisive effect that high temperatures have in inducing aphid "crashes". Equation [1] implies that as the aphids increase in numbers, so do the coccinellids but their abundance only becomes evident in the walking counts when they get hungry after having caused a significant reduction in aphid numbers. If the 10- to 100-fold difference in relative compared to absolute numbers of coccinellids is more general, coccinellids are having significantly more impact on aphid populations than is commonly recognized.

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