ESTIMATING ADULT COCCINELLID POPULATIONS IN WHEAT FIELDS BY REMOVAL, SWEEPNET, AND VISUAL COUNT SAMPLING[1]

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Abstract

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Removal sampling, sweepnet sampling, and visual count sampling conducted while walking at constant velocity through a field were used to sample populations of adults of five coccinellid species in plots established in spring wheat fields, *Triticum aestivum* L. Estimates of absolute population density obtained from two 20-min removal samples taken from each of six 5- by 5-m sub-plots per plot proved reliable and were used to convert estimates obtained from sweepnet sampling (180 sweeps per plot) and visual counts (36 min per plot walking at 10 m/min) into absolute estimates of population density. Population density estimates obtained by removal sampling were quite precise except for species with low capture efficiencies and low population densities.

Crop plant growth stage influenced the numbers of beetles caught in sweepnet samples and was incorporated in regression models for converting sweepnet catch to absolute density. Values of R^2 of regressions ranged from 0.51 to 0.90, depending on species. Visual counts were influenced by temperature and aphid density, and these variables were incorporated in regression models. Values of R^2 for regressions relating visual counts to population densities ranged from 0.63 to 0.94, depending on species.

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Résumé

L'échantillonnage d'enlèvement, de filet de balayage et de comptage visuel, faits en marchant d'une vélocité constante à travers d'un champ, ont été utilisés pour échantillonner les populations d'adultes de cinq espèces de coccinelles aux lotissements établis dans les champs de blé de printemps, *Triticum aestivum* L. Les évaluations de la densité absolue des populations obtenues à partir de deux échantillons d'enlèvement de 20 min, pris dans chacun de six sous-lotissements de 5 m par 5 m par lotissement ont prouvé digne de confiance et ont été utilisées pour convertir les évaluations obtenues à partir d'échantillonnage de filet de balayage (180 balayages par lotissement) et de comptage visuel (36 min par lotissement, en marchant à 10 m/min) en évaluations absolues de la densité de la population. Les évaluations de la densité de la population obtenues par l'échantillonnage par enlèvement ont été assez précises, sauf dans le cas des espèces ayant une efficacité de prise et une densité de population basses.

L'étape de croissance de la plante a eu une influence sur le nombre de coccinelles pris aux échantillons de balayage et a été incorporée aux modèles de régression pour convertir les valeurs de prises par le filet de balayage en densité absolue. Les valeurs de R^2 des régressions ont varié de 0,51 à 0,90, selon l'espèce. Les comptages visuels ont été influés par la température et la densité des pucerons, et ces facteurs variables ont été incorporés aux modèles de régression. Les valeurs de R^2 dans les cas de régressions reliant les comptages visuels aux densités de populations ont varié de 0,63 à 0,94, selon l'espèce.

Introduction

Coccinellids are conspicuous aphidophagous predators in wheat, *Triticum aestivum* L., fields in the Northern Great Plains of the United States. Their generalist feeding habits

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and high mobility permit them to exploit prey in a wide variety of habitats (Hodek 1973). Perhaps due to their mobility amid constantly changing agricultural landscapes, coccinellid beetle populations in small grain fields in the Northern Great Plains vary widely and unpredictably in time and space (Elliott and Kieckhefer 1990). Because of this unpredictability, precise, yet time-efficient sampling methods for coccinellids are needed for use in ecological research on cereal aphids and integrated pest management programs.

Two previous studies describe sampling methods for coccinellids that provide satisfactory estimates of absolute population densities. Frazer and Raworth (1985) developed a method for sampling adult coccinellids in strawberry fields in Canada by comparing visual count samples made while walking along rows of strawberry plants with samples taken by complete enumeration of beetles within field cages placed in the field. Count samples were adjusted for the influence of abiotic and biotic variables on the visibility of beetles to observers. Lapchin et al. (1987) compared removal sampling and visual count sampling for estimating coccinellid population densities in cereal crops in Europe. They found that De Lury's method (Seber and Le Cren 1967) could be used to calculate reliable estimates of absolute population densities of three coccinellid species using results of removal sampling. In particular, they showed that sampling efficiency remained constant among successive samples from a plot, and that a large proportion of the total population contained within a 25-m^2 plot was removed in collections made during two 20- to 25-min inspections of the plot. Lapchin et al. (1987) also found that visual counts of three coccinellid species made while walking through plots for a constant amount of time were linearly related to population density.

We used removal sampling, sweepnet sampling, and visual count sampling conducted during a timed walk at constant velocity through a field for sampling adult coccinellid populations in wheat fields in eastern South Dakota. Absolute estimates of beetle population densities obtained from removal samples using De Lury's method were used to convert relative estimates obtained from sweepnet and visual count samples to absolute density estimates.

Materials and Methods

During 1988 and 1989, the following five species of coccinellid beetles were sampled from ten 30- by 30-m plots established in 1-ha spring wheat (var. Guard) fields planted on a research farm adjacent to the USDA, ARS, Northern Grain Insects Research Laboratory near Brookings, SD: *Hippodamia convergens* Guerin-Meneville, *H. tredecimpunctata tibialis* (Say), *H. parenthesis* (Say), *Coleomegilla maculata* (DeGeer), and *Coccinella septempunctata* L. Wheat was planted (76 kg/ha) in 15.2-cm rows using a 14-row John Deere drill. Two plantings were made each year, one at mid-April and a second at mid-May.

Plots were divided into thirty-six 5- by 5-m sub-plots, the corners of which were marked by flags. To minimize disturbance to foliage and coccinellids within plots, all observation and sampling were conducted while walking parallel to the rows of wheat and stepping only in the areas between rows. Each time a plot was sampled, a row of sub-plots, each of which comprised six sub-plots extending across the plot, was chosen at random. An observer walked through each of the six sub-plots within that row at a velocity of 10 m/min (total of 2 min per sub-plot). All adult coccinellids seen in an approximately 1-m-wide path immediately in front and along the direction of movement of the observer were counted and recorded. The same path was traversed only once by the observer. The observer repeated the same procedure in two additional rows of sub-plots chosen so that no two adjacent rows were used for counting, e.g. so that count samples were taken in every other row of sub-plots (total of 18 sub-plots per plot).

Immediately after the observer finished counting within a row, another observer began removal sampling within it. The removal sampler entered a sub-plot chosen at random from among the six sub-plots within the row and collected in an aspirator all coccinellids seen in a 20-min search of the entire area within the sub-plot; both the soil surface and plants were inspected for coccinellids. A second 20-min collection was made within the sub-plot immediately after the first. As soon as removal sampling was completed in the sub-plot, a second sub-plot within the row was chosen from among the five remaining sub-plots and two 20-min removal samples were taken from it. Thus, on each sampling occasion, removal samples were taken from a total of six sub-plots per plot. A third 20-min collection was made in one of the six sub-plots on 10 occasions.

Sweepnet samples were taken concurrent with visual counts and removal sampling from the three rows of sub-plots not otherwise sampled. Two samples, each consisting of 30 pendular sweeps with a 38-cm-diameter sweepnet, were taken from each row of sub-plots (total of six sweep samples and 180 sweeps per plot).

In conducting removal sampling, sub-plots were not enclosed to prevent beetles from entering or leaving them. However, in preliminary studies conducted in fields with dense beetle populations, we enclosed 25-m^2 sub-plots with 1.2-m-high barriers made of black plastic screening prior to conducting removal sampling within them.

In total, eight 30- by 30-m plots were established in wheat fields, and all plots were sampled on more than one occasion; at least 4 days passed between successive samples from the same plot.

The following environmental variables were measured near the midpoint of the time period during which count and sweepnet sampling were being conducted within a plot: average wind speed (metres per minute), temperature (°C), relative humidity, light intensity (watts per square metre), and time of day. The numbers of aphids per tiller, crop height, and crop growth stage [using an integer scale with values from 0 to 10 (Zadoks et al. 1974)] were measured in each plot at least once each week. The number of aphids per tiller was estimated by counting all aphids on four randomly selected tillers from each sub-plot (total of 144 tillers). When aphid density and crop growth variables were not determined on the same day a plot was sampled, these variables were estimated for that day by linear interpolation between appropriate measured estimates for the plot.

Partial correlation coefficients (data adjusted for beetle absolute population density) were calculated to determine the degree of association between beetle population estimates obtained from sweepnet samples and visual counts and each of the eight variables.

De Lury's method (Seber and Le Cren 1967) was used to estimate population densities of beetles within a plot on each sampling occasion from combined data from the six sub-plots from which removal samples were taken. Using De Lury's method, a maximum likelihood estimate of the total population within the six sub-plots is given by

$$n = c_1^2/(c_1 - c_2) \quad [1]$$

where c_1 and c_2 are the number of individuals collected in the first and second samples from sub-plots, respectively. Seber and Le Cren (1967) give an approximation of the variance (s^2) of n:

$$s^2 = c_1^2 c_2^2 (c_1 + c_2) / (c_1 - c_2)^4. \quad [2]$$

The efficiency of removal sampling, defined as the proportion of the total population within the six sub-plots caught in two 20-min searches, was estimated by the following equation:

$$E = (c_1 + c_2) / n. \quad [3]$$

Constancy of capture probability was investigated using data from sub-plots from which three removal samples were taken. Goodness-of-fit tests (Seber and Le Cren 1967) were employed to test for non-constancy of capture probabilities among successive removal samples. Non-constant probability of capture was indicated by a significant ($P<0.05$) chi-square statistic.

Table 1. Average number of adult coccinellids per 125 m^2 [estimated using De Lury's method (Seber and Le Cren 1967)], mean coefficient of variation (CV), and mean capture efficiency (*E*) based on removal samples from six 25-m^2 sub-plots from a 30- by 30-m plot (n = 33 plots)

Species	Mean (range)	CV (range)	*E* (range)
H. convergens	298.3 (22.6–2136.0)	0.20 (0.04–0.92)	78.4 (31.2–93.8)
H. tredecimpunctata	24.3 (0.00–408.6)	0.19 (0.00–0.87)	91.3 (49.0–100.0)
C. septempunctata	54.6 (1.20–144.0)	0.28 (0.00–2.40)	82.2 (36.0–95.5)
C. maculata	46.1 (0.00–336.0)	0.52 (0.00–2.08)	71.3 (38.4–100.0)
H. parenthesis	10.8 (0.00–65.2)	0.45 (0.00–1.29)	81.0 (49.0–100.0)
Combined species	417.7 (50.0–3000.6)	0.14 (0.04–0.57)	78.8 (44.4–90.0)

We used the general model proposed by Ruesink and Haynes (1973) for converting relative estimates of insect populations obtained by sweepnet sampling to estimates of absolute population density to convert estimates obtained by both sweepnet sampling and visual count sampling to absolute density estimates. Their model relates absolute and relative density by

$$D = MR \quad [4]$$

where D is absolute density, R is relative density, and M is a multiplication factor. M is a function of all variables other than population density that influence estimates obtained using the relative sampling method.

Results

Estimating Populations from Removal Samples. In preliminary removal samples taken from within 5- by 5-m sub-plots enclosed with black plastic screening, the number of beetles landing on the screen during two consecutive 20-min samples was always very low (<10 beetles), and similar numbers were found on the inner and outer sides of the screen.

Plots were sampled on 21 different days (6 in 1988 and 15 in 1989), and a total of 33 samples were taken using the procedures described in the previous section.

Mean efficiencies (E) of removal samples ranged from 71.3% for *C. maculata* to 91.3% for *H. tredecimpunctata* (Table 1). Minimum values of E ranged from 31.2 to 49.0%, depending on species. Mean coefficients of variation, calculated using Eqs. [1] and [2] [$(s^2)^{1/2}/n$], of population estimates for *H. convergens, H. tredecimpunctata*, and *C. septempunctata* ranged from 0.19 to 0.28 (Table 1), indicating that estimates were usually reasonably precise. However, for *C. maculata* and *H. parenthesis*, average coefficients of variation were large, 0.52 and 0.45, respectively, due to a combination of low sampling efficiency and low population density.

The efficiency of removal sampling was inversely related to population density for all species except *C. septempunctata* and *C. maculata* (Table 2). For *C. septempunctata* and *C. maculata* correlations between E and population density were negative, though not significantly different from zero. Most partial correlations (adjusted for absolute population density) between E and crop, aphid, and environmental variables were not statistically significantly different from zero (Table 3).

For uncommon species, numbers of beetles collected in sub-plots from which three removal samples were taken were often inadequate to facilitate chi-square tests to assess the constancy of capture probabilities among successive removal samples. No chi-square tests could be conducted using data on *H. tredecimpunctata*, and numbers of chi-square tests for other species ranged from one for *H. parenthesis* to eight for *H. convergens*. Only 27 of a total possible of 60 tests (five species plus combined species times 10 sub-plots) could be conducted, and none were statistically significant. Thus, the data, though limited, yielded no evidence of variation in capture probabilities among successive removal samples from sub-plots.

Table 2. Pearson correlation coefficients between the number of adult coccinellids per square metre and the efficiency (*E*) of removal sampling, the number of adult coccinellids captured per 180-sweep sample, and the number counted during 2-min visual counts ($n = 33$)

Species	Capture efficiency (*E*)	Sweepnet sampling	Visual counting
H. convergens	−0.58*	0.69*	0.74*
H. tredecimpunctata	−0.74*	0.40	0.53*
C. septempunctata	−0.35	0.69*	0.73*
C. maculata	−0.30	0.41	0.69*
H. parenthesis	−0.49*	0.80*	0.68*
Combined species	−0.44*	0.87*	0.81*

*$P<0.05$.

Relationships among Sampling Methods. Species relative abundances calculated from estimates obtained by each sampling method were averaged across all samples. Average relative abundances of most species were similar regardless of sampling method (Table 4). However, based on single factor analysis of variance and Tukey's multiple comparison tests (Neter and Wasserman 1974), mean relative abundance of *H. parenthesis* calculated from visual counts was significantly lower ($P<0.05$) than that calculated from sweepnet and removal samples.

Population estimates obtained by removal sampling from plots were significantly correlated with estimates obtained from 180-sweep samples and 36-min visual count samples (Table 2) except for sweep samples of *H. tredecimpunctata* and *C. maculata*. Partial correlations (data adjusted for population density) of population estimates from sweepnet samples and visual counts with measurements of abiotic, crop, and aphid variables are listed in Tables 5 and 6. Temperature and aphid density were most consistently correlated with the numbers of beetles observed in visual counts (Table 5); partial correlations between temperature and visual counts ranged from 0.20 to −0.64 and differed significantly from zero for three of five species and for combined species (Table 5). Partial correlations between numbers of beetles in visual count samples and aphid densities ranged from −0.03 to 0.47 and were significant for two species and combined species. Significant partial correlations between temperature and numbers of beetles observed in visual count samples were negative indicating that the number of beetles observed decreased as temperature increased, whereas significant partial correlations between visual counts and aphid density were positive, indicating that beetles were more easily observed at high aphid densities. Partial correlations of other abiotic and crop variables with numbers of beetles counted were, with few exceptions, non-significant.

After accounting for relationship between sweepnet catch and absolute density, partial correlations between sweepnet catch and abiotic and biotic variables indicated that crop growth stage, plant height, and temperature most strongly influenced the numbers of beetles caught in sweepnet samples (Table 6). The capture of species with significant partial correlations increased with increasing temperature, crop growth stage, and crop height.

Analysis with Regression Models. Regression models were developed using Eq. [4] to relate *D* (number of beetles per square metre) and relative population estimates, *R* (number of beetles counted per 2 min or number caught per sweep). We assumed that relationships between absolute and relative population density were of the following general form:

$$D = f(x_1, x_2, \ldots, x_8)R \qquad [5]$$

where f is a polynomial function of the x_i's of at most third degree, and the x_i are measured variables (temperature, plant growth stage, etc.). Crop, aphid, and environmental variables

Table 3. Partial correlation coefficients between capture efficiency (*E*) of removal sampling of adult coccinellids and several abiotic and biotic variables

Species	Growth stage	Temperature	Wind	Light	Aphids per tiller	Humidity	Time	Plant height
H. convergens	0.32	−0.19	−0.05	−0.00	0.19	0.24	−0.21	0.26
H. tredecimpunctata	0.54*	0.19	−0.20	0.22	0.04	−0.40	0.36	0.57*
C. septempunctata	−0.10	0.32	−0.02	0.07	−0.20	−0.16	−0.22	−0.21
C. maculata	0.03	−0.27	−0.28	0.05	0.49*	0.05	−0.06	0.17
H. parenthesis	0.25	0.16	−0.02	0.56*	−0.07	−0.19	0.34	0.22
Combined species	0.28	−0.13	0.00	0.08	0.25	0.29	−0.27	0.21

*$P<0.05$.

Table 4. Average relative abundances (±standard error) of adult coccinellids sampled using three methods

Species	Sampling method*		
	Removal	Sweepnet	Visual count
H. convergens	0.69±0.026a	0.69±0.036a	0.70±0.029a
H. tredecimpunctata	0.02±0.005a	0.04±0.023a	0.03±0.004a
C. septempunctata	0.14±0.022a	0.11±0.024a	0.16±0.030a
C. maculata	0.11±0.022a	0.11±0.026a	0.10±0.016a
H. parenthesis	0.04±0.008a	0.05±0.011a	0.01±0.004b

*Means within rows followed by the same letter do not differ significantly ($P<0.05$) based on Tukey's multiple comparison test.

are assumed to operate independently in their effects on relative sampling methods. Equation [5] is a special case of Eq. [4]. In the absence of theory upon which to base decisions regarding appropriate functions to describe the effects of measured abiotic and biotic variables on relative sampling methods, polynomials were used because of their simplicity and general suitability for describing both linear and non-linear phenomena.

Among the crop variables, measurements of plant height ranged from 30 to 82 cm, and crop growth stage ranged from 2 (tillering) to 7 (milky ripe). The number of aphids per tiller ranged from 0.02 to 5.03. Among the environmental variables, relative humidity ranged from 30 to 87%, light intensity ranged from 700 to 1525 W/m^2, wind speed ranged from 0.67 to 6.50 m/s, temperature ranged from 18.3 to 35.6°C, and time of day ranged from 0930 to 1630 hours CST.

Stepwise regression was used to determine appropriate models for f. Variables were entered into regression models using the maximum R^2 improvement technique (SAS Institute 1985) until the incremental increase in R^2 due to inclusion of an additional variable failed to exceed 0.04. Use of a cut-off value of 0.04 for inclusion of additional variables was decided upon after examining results of stepwise regressions; the addition of a variable into a model usually accounted for more than a 4% increase in R^2, or a much smaller increase (1% or less). Based on examination of partial correlations between measured variables and sweepnet catch (Table 6), we considered temperature and crop growth stage for incorporation in f. Although crop height was correlated with sweepnet catch for several species, crop height and growth stage are obviously strongly correlated and inclusion of both variables would be largely redundant. For each species and for combined species, stepwise regression resulted in models for f that included crop growth stage; however, temperature did not enter into any models (Table 7). Coefficients of multiple determination ranged from a low of 0.51 for *H. tredecimpunctata* to a high of 0.90 for *H. parenthesis* (Table 7).

Magnitudes of partial correlations (Table 5) suggested that visual counts were most strongly influenced by temperature and aphid density. These variables were used as independent variables in stepwise regressions. Either temperature or aphid density appeared in f for three species and combined species, and both variables were included in f for *H. tredecimpunctata* (Table 7). For *C. septempunctata*, neither temperature nor aphid density appeared in f. Coefficients of multiple determination of regressions relating visual counts to absolute density ranged from 0.63 to 0.94 (Table 7).

Discussion

In removal sampling, three conditions must be satisfied for De Lury's method to be appropriate for estimating the population size in a prescribed area (Seber and Le Cren 1967): (1) there is no net change in population size due to recruitment, mortality, immigration, or emigration during the time the two samples are taken; (2) the probability of capture remains constant among successive samples; and (3) the probability of capture is

Table 5. Partial correlation coefficients between the number of adult coccinellids observed in eighteen 2-min visual counts and several abiotic and biotic variables, holding population density (based on removal sampling) fixed

Species	Growth stage	Temperature	Wind	Light	Aphids per tiller	Humidity	Time	Plant height
H. convergens	0.47*	−0.64*	−0.28	−0.21	0.47*	0.36	−0.44*	0.50*
H. tredecimpunctata	0.14	−0.31	0.09	−0.46*	−0.03	0.26	−0.01	0.14
C. septempunctata	0.27	0.20	0.03	0.05	0.11	−0.03	−0.29	0.21
C. maculata	0.09	−0.43*	0.08	−0.51*	0.42*	0.01	−0.21	0.16
H. parenthesis	−0.10	−0.38*	−0.18	0.08	0.06	0.03	−0.19	−0.07
Combined species	0.34	−0.61*	−0.23	−0.25	0.38*	0.45*	−0.53*	0.36

*$P<0.05$.

Table 6. Partial correlation coefficients between the number of adult coccinellids in 180-sweep samples and several abiotic and biotic variables, holding population density (based on removal sampling) fixed

Species	Growth stage	Temperature	Wind	Light	Aphids per tiller	Humidity	Time	Plant height
H. convergens	0.54*	0.42*	−0.06	−0.07	−0.04	0.25	−0.15	0.38*
H. tredecimpunctata	−0.03	−0.07	−0.26	0.36	0.08	−0.26	0.02	0.01
C. septempunctata	0.72*	0.38*	−0.06	−0.10	−0.11	−0.23	0.27	0.66*
C. maculata	0.02	−0.24*	−0.25	−0.08	0.04	0.19	−0.37	0.09
H. parenthesis	0.54*	0.27	0.06	−0.14	−0.01	0.00	0.11	0.47*
Combined species	0.38*	0.44*	0.06	0.03	−0.19	−0.15	−0.08	0.22

*$P<0.05$.

Table 7. Regression equations for relating the number of adult coccinellids per square metre (D) to the number of adult coccinellids per sweep (S) in a 180-sweep sample, and to the number of adult coccinellids observed per 2 min in a sample consisting of eighteen 2-min visual counts made while walking at a velocity of 10 m/min (V)

Method/species	Equation*	R^2
Sweepnet sampling		
H. convergens	$D = (12.1 - 0.0294P^3)S$	0.83
H. tredecimpunctata	$D = (26.4 - 3.93P)S$	0.51
C. septempunctata	$D = (201.0 - 118.0P + 22.8P^2 - 1.42P^3)S$	0.83
C. maculata	$D = (72.7 - 44.5P + 9.06P^2 - 0.570P^3)S$	0.66
H. parenthesis	$D = (6.03 - 0.735P)S$	0.90
Combined species	$D = (10.8 - 0.0247P^3)S$	0.83
Visual count sampling		
H. convergens	$D = (0.0497 + 0.0000165T^3)V$	0.91
H. tredecimpunctata	$D = (-1.46 + 0.0731T - 0.00339A^3)V$	0.63
C. septempunctata	$D = 0.307V$	0.85
C. maculata	$D = (0.479 - 0.0425A)V$	0.78
H. parenthesis	$D = (0.745 - 0.196A)V$	0.72
Combined species	$D = (0.177 + 0.00000941T^3)V$	0.94

*P, plant growth stage; A, number of aphids per tiller; T, temperature.

large enough to cause a significant reduction in n. We found these conditions to be at least approximately satisfied for adult coccinellids sampled from 25-m^2 sub-plots in wheat fields. Removal sampling from enclosed sub-plots indicated that few beetles moved to and from sub-plots during sampling, and that immigration and emigration rates were similar. Therefore, effects of immigration or emigration occurring during the sampling period on population estimates constructed from sampling in unenclosed sub-plots were probably negligible. Furthermore, recruitment and mortality were assumed to be negligible during sampling (40 min). Data obtained from sub-plots from which removal samples were taken three times in succession yielded no evidence of unequal capture probabilities among successive samples from sub-plots. Finally, we estimated that we caught large proportions, 70% or more on average, of beetles in sub-plots during two 20-min collections. Our findings concur with those of Lapchin et al. (1987), that removal sampling can be used to obtain reliable estimates of absolute population densities of adult coccinellids.

Zippin (1956) determined that about 55% of individuals would need to be removed from a population of about 200 individuals during two collections to obtain population estimates with coefficients of variation of 0.30 using De Lury's method. For populations of fewer than 200 individuals, a greater percentage of the total population would need to be removed to obtain the same level of precision. On average, we caught from 71.3 to 91.3% of beetles (Table 1), depending on species, in six 25-m^2 sub-plots, and population estimates for most species were usually reasonably precise. However, for *C. maculata* and *H. parenthesis*, average precision was relatively low, 0.52 and 0.45, respectively, due to relatively low sampling efficiency combined with generally low population densities.

We found, as did Lapchin et al. (1987) for *C. septempunctata*, that capture efficiencies of most coccinellids were unaffected by variation in measured biotic and abiotic variables, and capture efficiencies decreased as population densities increased.

The lower relative abundance of *H. parenthesis* in visual counts compared with the other sampling techniques (Table 4) is probably accounted for by its small size and cryptic coloration and behavior, making it less likely to be seen by an observer walking through a wheat field. Absolute estimates of population density obtained from Eq. [5] are corrected for the consistent bias that accrues in visual counts. Therefore, if estimates of relative abundance are required, it may be advisable first to estimate population density using Eq. [5] and then to calculate relative abundances from the resulting estimates.

Iperti et al. (1988) found that visual counts of *C. septempunctata* populations in wheat fields were unaffected by crop growth stage, aphid density, or temperature. Our results with *C. septempunctata* agree with theirs, although we found that visual counts of several other coccinellid species were influenced by one or more of these variables. Frazer and Raworth (1985) found that visual counts of several coccinellid species in strawberry fields were influenced by aphid population density and biomass and by time of day. Among the variables we measured, aphid density and temperature were the most important variables influencing the efficiency of visual counts.

Capture efficiencies differed among species, and these differences were probably related to differences in size, coloration, and behavior that rendered species more-or-less vulnerable to capture. For species with low capture efficiency and low population densities, such as *H. parenthesis* and *C. maculata*, absolute density estimates obtained from removal samples using De Lury's method, although lacking desired precision, were adequate to develop useful equations for converting estimates obtained by sweepnet samples and visual counts to estimates of absolute density. For both species, large proportions of the variation in absolute density estimates were explained by appropriate polynomial functions of relative population density and one or more additional variables.

Ruesink and Haynes (1973) proposed Eq. [4] as a theoretical model for converting relative estimates of insect populations obtained by sweepnet sampling to estimates of absolute population density. Ruesink and Haynes's (1973) model sufficed for relating estimates of population obtained by both sweepnet and visual count sampling to absolute density by incorporating appropriate biotic and abiotic factors influencing estimates in M.

As with all sampling methods developed from limited data, the general applicability of equations presented in Table 7 across a range of environmental conditions should be questioned until verified experimentally.

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