Estimating Populations of Aphidophagous Coccinellidae (Coleoptera) in Winter Wheat

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Environ. Entomol. 26(1): 4–11 (1997)

ABSTRACT Coccinellids are important natural enemies of aphid pests in wheat, *Triticum aestivum* em Thell, in the Great Plains of the United States. Coccinellid community development in wheat fields is unpredictable; therefore, precise, efficient sampling methods for coccinellids are needed for use in integrated pest management research and decision making. Our objectives were to compare removal sampling with quadrat sampling for estimating population density of adult and larval coccinellids in winter wheat, and to determine if timed count sampling and sweepnet sampling were useful for estimating adult and larval coccinellid densities. Removal sampling accurately estimated population density for adults of most species but consistently underestimated larval density. Timed count samples and sweepnet samples were significantly correlated with absolute density of both larval and adult coccinellids. Regression models were developed to convert estimates of relative to estimates of absolute population density. Depending on sampling method and life stage, models included the number of tillers per 0.3 m, wheat plant growth stage, plant height, and the number of aphids per tiller as variables; R^2 values ranged from 0.89 to 0.93. Sweepnet sampling was more precise per unit of effort than timed count, quadrat, or removal sampling for estimating adult coccinellid density. Removal sampling (removing all coccinellids seen during 2 successive 15-min searches from each of 9 plots (25 m^2) was the least efficient method.

KEY WORDS Aphidophagous, coccinellidae, sampling, wheat

NATURAL ENEMIES PLAY a fundamental role in integrated pest management programs, yet natural enemies are underutilized in integrated pest management programs developed for ephemeral crops because quantitative information on the role of natural enemies in biological control is lacking or information on the effect of natural enemies on pest populations is unavailable to pest managers, or for both reasons.

Aphidophagous coccinellids are a ubiquitous group of predators in most regions of the United States and are often the dominant natural enemies in ephemeral crops (Elliott and Kieckhefer 1990a, b; Kieckhefer and Elliott 1990). Coccinellids are important predators of aphid pests in several field crops (Neuenschwander et al. 1976, Kring et al. 1985, Rice and Wilde 1988), and their generalist feeding habits and high mobility permit them to exploit prey in a wide variety of habitats (Hodek 1973). Perhaps because of their mobility amid constantly changing agricultural landscapes, coccinellid community development in ephemeral agroecosystems is unpredictable in time and space (Elliott and Kieckhefer 1990b). Consequently, their effect on pests is unpredictable. Because of this unpredictability, precise, efficient sampling methods for coccinellids are needed for use in integrated pest management research and decision making.

To incorporate the impact of aphidophagous coccinellids in the integrated pest management decision-making process, one must be able to estimate their population density, determine their effect on pest aphid populations, and relate pest numbers to economic thresholds. An adequate sampling procedure for coccinellids must estimate absolute population numbers accurately or be transformable to absolute population density (Morris 1955). Numerous procedures are available for estimating population densities of arthropods in crops (see for example Pruess et al. 1977, Byerly et al. 1978, Ellington et al. 1984, Fleischer et al. 1985) but are generally inadequate for use in integrated pest management research and decision making because sampling time is excessive, specialized sampling equipment is required, the methods are not precise or consistent, or a combination of these factors.

A few studies specifically addressed the problems of estimating coccinellid populations in field

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0046-225X/97/0004–0011$02.00/0

crops. Ives (1981) used Jolly's (1965) method to estimate densities of adult coccinellids in fields of alfalfa, *Medicago sativa* L., based on mark–recapture data. Mack and Smilowitz (1980) compared sweepnet and drop cloth sampling for estimating populations of coccinellids in fields of potato, *Solanum* sp. These authors did not compare their sampling procedures with simultaneous absolute population estimates to determine their accuracy. Frazer and Raworth (1985) developed a sampling procedure for adult coccinellids in fields of strawberry, *Fragaria* sp., in Canada by comparing samples taken by counting coccinellids while walking along rows of strawberry plants with samples taken by complete enumeration of beetles within large screened cages placed in the field. Absolute population estimates were obtainable by adjusting timed counts for abiotic and biotic variables that influenced the visibility of beetles to observers. Lapchin et al. (1987) compared removal sampling and timed counts for estimating coccinellid population densities in fields of wheat, *Triticum aestivum* em Thell, in Europe. They found that De Lury's method (Seber and Le Cren 1967) could reliably estimate absolute population densities of adults of 3 coccinellid species based on results of removal sampling. Specifically, they demonstrated 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 2 inspections (20–25 min) of the plot. Lapchin et al. (1987) also found that counts of coccinellids made while walking through plots for a constant amount of time were linearly related to population density. Michels and Behle (1992) found that sweepnet, drop cloth, pitfall trap, and timed count estimates of adult coccinellid populations in sorghum, *Sorghum bicolor* Moench, were strongly correlated. However, estimates based on pitfall trapping were unacceptable. Elliott et al. (1990) sampled adult coccinellids in spring wheat fields using removal, sweepnet, and visual count sampling. Their results confirm the findings of Lapchin et al. (1987) for adult *Coccinella septempunctata* L.—that reliable estimates of population density can be obtained from removal sampling. They also demonstrated that removal sampling could reliably estimate absolute densities of 4 additional species. Elliott et al. (1990) found counting and sweepnet estimates of adults of 5 coccinellid species could be converted to absolute population estimates; however, it was necessary to incorporate several biotic and abiotic variables that influenced the efficiency of the relative sampling methods into models to convert relative to absolute density (Elliott et al. 1990).

Results of previous studies are insufficient to provide general methods for sampling coccinellids. Although they describe a variety of sampling procedures, and in some cases demonstrate a functional relationship between relative and absolute population estimates, there is no information on comparative studies of several procedures to determine those best suited for both larval and adult coccinellids. The purpose of this study was to provide such information for coccinellids in winter wheat. Our 2 specific objectives were as follows: (1) to compare removal with quadrat sampling to determine if removal sampling provided reliable estimates of the absolute population of adult and larval coccinellids, and (2) to use timed count search and sweepnet sampling methods to sample adult and larval coccinellids and to determine relationships between estimates obtained with these relative sampling methods and those obtained by absolute population sampling methods.

Materials and Methods

Sampling Techniques. The research was conducted during the spring and summer of 1991 and 1992 in irrigated winter wheat fields near Bushland, TX, and Stillwater, OK. All fields were either production fields or experiment station fields that were managed using typical agronomic practices, except that no insecticides were applied. Study plots were established in fields and sampled several times throughout the growing season. In February of each year, 16 plots were established at Bushland and 18 plots were established at Stillwater, giving a total of 34 plots. Each plot was divided into 36 subplots (5 by 5 m). The plots were sampled during each of 5 phenological stages of wheat development: tillering, stem elongation, boot, head emergence–flowering, and the soft dough stage of grain-filling.

Relative sampling methods (removal sampling, sweepnet sampling, and timed counts while walking at a constant velocity) and an absolute method (complete enumeration in enclosed quadrats) were used to sample coccinellids. All sampling methods were used simultaneously to sample coccinellids in a plot. Because practical limitations of identifying coccinellid larvae to species in a field environment, larvae were recorded as a group. Adult coccinellids were always recorded by species.

Each time a plot was sampled, a row (5 m wide), encompassing 6 of the 36 subplots, was chosen at random. An observer walked through each of the 6 subplots within that row at a velocity of 10 m/min (total of 1 min per subplot, 6 min total per row). All adult coccinellids seen in a path ≈1 m wide 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 2 additional rows of 6 subplots chosen so that no 2 adjacent rows were used for visual count sampling. This gave a total of 18 subplots sampled per plot.

Immediately after the observer finished counting within a row, 3 of the 6 subplots within the row were selected randomly for removal sampling. The

removal sampler entered a subplot within the row and collected in a standard mouth aspirator all coccinellids seen in a 15-min search of the entire 5-m area within the subplot; both the soil surface and plants were inspected for coccinellids. A 2nd 15-min collection was made within the subplot immediately after the first. This 2nd 15-min collection was taken to show that emigration and immigration during the time interval for removal sampling was low and nearly equal. Two 15-min removal samples were then taken from the 2 other subplots within the row. In total, removal samples were taken from 9 subplots per plot on each sampling.

Quadrat sampling was conducted in the 3 subplots within the row not used for removal sampling. Quadrat sampling was accomplished within plywood enclosures (1.0 by 1.0 m, 0.4 m high). The enclosure was placed at 2 random locations within each subplot sampled, and all coccinellids trapped inside it were counted through aspiration as in the removal samples.

The 3 sampling techniques previously described used 18 of the 36 total subplots available in a full 30-by 30-m plot. The remaining 18 subplots, 3 rows of 6 subplots, were used for sweepnet samples. These samples consisted of 25 pendular sweeps through each of the remaining 3 rows of 6 subplots (3 of 25 samples each per plot) with a standard beating net (38 cm diameter). After each 25-sweep sample, the insects were shaken to the bottom of the sweepnet, then all coccinellids were counted. Adults were recorded by species and larvae were recorded as 1 group.

De Lury's method (Seber and Le Cren 1967) was used to estimate the number of beetles per square meter in each plot on each sampling occasion. Using De Lury's method, a maximum likelihood estimate of the total population within a subplot is given by

$$n = c_1^2/(c_1 - c_2),$$

where c_1 and c_2 are the numbers of coccinellids collected in the 1st and 2nd sample, respectively. Then the number of coccinellids per square meter in the plot is given by $n \div 25$ (the total area of a subplot was 25 m^2). The variance of n is given by

$$s^2 = c_1^2 c_2^2 (c_1 + c_2)/(c_1 - c_2)^4,$$

and it follows that the variance of the number of coccinellids per square meter is given by $(1/25)^2 s^2$.

Several abiotic and biotic environmental variables were measured concomitant with sampling. The following meteorological variables were measured at 1-min intervals using Campbell CR-10 microloggers: wind velocity (m/sec), air temperature (°C), percentage relative humidity, and solar irradiance (kw/m^2). The mean of each variable for the hour nearest the mid-point of the time during which timed count and sweepnet sampling were conducted was calculated. The following biotic variables were measured immediately after the coccinellid sampling: wheat plant height (cm), wheat plant phenological stage (Zadoks et al. 1974), canopy coverage, the number of tillers per 0.3-m of row, and the number of aphids (greenbug, *Schizaphis graminum* (Rondani); bird cherry-oat aphid, *Rhopalosiphum padi* (L.); and corn leaf aphid, *Rhopalosiphum maidis* (Fitch)) per tiller. Canopy coverage is a useful surrogate for leaf area index (Daubenmire 1959). Wheat plant height, plant growth stage, canopy coverage, and the number of tillers per 0.3-m of row were measured at randomly selected points in each of 2 subplots per row (total of 12 measurements for each variable). One of the first 3 subplots within a row in which measurements were taken was selected randomly, the 2nd subplot in the row was chosen by skipping 2 intervening subplots. The number of aphids per tiller was estimated by counting aphids on 3 tillers selected randomly from within each of the 2 subplots per row (total of 36 tillers).

Models for Converting Sweepnet and Count Sampling. Relationships between absolute (m_d) and relative (m_r) population density were modeled using the general formula of Ruesink and Haynes (1973):

$$m_d = f(x_1, x_2, \ldots, x_n)m_r, \quad (1)$$

where f is a function of the x_is, and the x_is are measured biotic and abiotic variables that influence catch using the relative sampling procedure. The function, f, in equation 1 was estimated for each life stage (adult and larval) and for each relative sampling procedure. Partial correlation coefficients (after adjusting relative sampling data for absolute population density) were calculated to determine the degree of association between population estimates obtained from each relative method and each of the variables mentioned above. Partial correlations were used to determine variables to include in f. Because of their simplicity and general suitability for describing both linear and nonlinear phenomena, we used polynomial functions of the x_is to model f. Stepwise regression using the maximum R^2 method (SAS Institute 1988) was used to determine appropriate models for f. Variables were entered in a regression model until the incremental increase in R^2 failed to exceed 0.04. Only variables with significant partial correlations with sampling efficiency for a particular relative sampling method were included in regressions.

Efficiency of Sampling Methods. We defined the relative net efficiency, *rne*, of estimates of population density using a particular sampling technique, t, as

$$rne_t = (s_t/m_t)c_t,$$

where c_t is the cost per sample unit using a particular technique (in the current study measured as the time required to obtain a single sample unit); s_t is the standard deviation, calculated in the usual way; and m_t is the estimate of the number of coc-

Table 1. Comparison of number of coccinellids in removal and quadrat samples

Stage Species	Removal sampling		Quadrat sampling		Paired t-test[a]	
	Mean[b] ± SE	n[c]	Mean[b] ± SE	n[c]	t	P
Adult						
H. convergens	1.62 ± 0.35	33	1.71 ± 0.36	33	0.68	0.50
H. sinuata	0.19 ± 0.0015	16	0.30 ± 0.053	15	2.07	0.08
C. septempunctata	0.30 ± 0.13	28	0.35 ± 0.13	25	1.15	0.26
C. maculata	0.054 ± 0.004	10	0.091 ± 0.014	11	2.27	0.04
Combined species	1.89 ± 0.36	34	2.06 ± 0.39	34	1.26	0.22
Larva						
Combined species	0.51 ± 0.092	18	1.65 ± 0.29	19	4.26	0.001

[a] Paired t-tests comparing mean numbers of coccinellids estimated using the 2 sampling methods.
[b] Mean number of coccinellids per square meter.
[c] Number of the 34 plots sampled in which each coccinellid occurred.

cinellids per square meter. Sample units consisted of 25 pendular sweeps with a sweepnet, a 6-min count while walking, complete enumeration of coccinellids in a quadrat (1.0 by 1.0 m), and 2 consecutive 15-min removal samples. Analysis of variance (ANOVA) was used to compare *rne* for estimating the number of coccinellids per square meter of the various sampling techniques. Note that the smaller the value of rne_t, the greater the precision per unit cost for a particular technique.

The sample variance for timed count and sweepnet sampling consists of 2 components. One component, s_t^2, is caused by sampling error and is calculated in the usual way. The 2nd component results from estimating the number of coccinellids per square meter using a regression model (i.e., equation 1). The variance for this component depends on the value of m_t and is

$$sr^2 = mse_t ,$$

where X·X is the matrix sums of squares and cross products of the independent variables, X_h is a vector of values of the independent variables for which the value of the dependent variable is to be estimated, and mse_t is the error mean square of the regression (Neter et al. 1990). Then, rne_t for timed count and sweepnet methods is

$$rne_t = \{(S_t + mse_t^{1/4})/m_t\}c_t.$$

Analysis of variance was used to compare rne_t among sampling techniques.

Results

Removal and Quadrat Sampling. Removal sampling and quadrat sampling were used to estimate population densities (number of coccinellids per square meter) for adults of those species that were present in enough of the 34 plots (Bushland and Stillwater combined) sampled to make useful comparison of the 2 sampling methods possible. The average across all plots of the number of adult coccinellids per square meter based on quadrat sampling varied from a high of 1.71 for *Hippodamia convergens* Guérin-Méneville to a low of 0.091 for *Coleomegilla maculata lengi* Timberlake (Table 1). Corresponding averages based on removal sampling ranged from 0.054 for *C. maculata lengi* to 1.62 for *H. convergens*. Overall, population density estimates from removal and quadrat sampling were numerically similar and not significantly different for all adults. However, the estimate of *C. maculata lengi* obtained from removal sampling was significantly lower than that obtained from quadrat sampling ($P = 0.04$; Table 1). For larvae, the mean based on quadrat sampling (1.65) was significantly greater than that based on removal sampling (0.51) ($P = 0.001$).

Quadrat sampling provides accurate (unbiased) estimates of population density but is highly labor-intensive, a fact that motivated our search for an alternative method. If removal sampling accurately estimates population density, a linear regression of estimates derived from quadrat sampling versus that derived from removal sampling would have a slope of 1 and an intercept of 0. Furthermore, if both methods provide precise density estimates, sample data points should group tightly around the regression line (i.e., r^2 should be close to 1). Regression was not attempted for adult *C. maculata* because it occurred in only 11 of the plots, and densities were usually low.

Neither the slope nor intercept of regressions differed significantly from 1 or 0, respectively, for adult *H. convergens* or *C. septempunctata*, indicating that removal sampling provided accurate estimates of density (Table 2). However, the slope (2.17) differed significantly from 1 for adult *Hippodamia sinuata* Mulsant ($P = 0.001$). A slope exceeding 1 associated with an intercept near 0 (−0.07) indicates that quadrat sampling yielded larger estimates of density than removal sampling over most densities. For adult coccinellids pooled across species, the slope and intercept did not differ significantly from 1 or 0, respectively, indicating that the 2 methods provided similar estimates of density. For larval coccinellids, the slope of the regression was significantly greater than 1 ($P = 0.001$). Thus, removal sampling consistently underestimated larval population density. In regres-

Table 2. Parameter estimates and statistics for regressions relating the number of coccinellids per square meter estimated from quadrat sampling (dependent variable) to the number of coccinellids per square meter estimated from removal sampling

Stage Species	n	Intercept, a			Slope			r^2
		a	F	P	b	F	P	
Adult								
H. convergens	33	0.15	0.67	0.41	0.97	0.23	0.63	0.86
H. sinuata	16	−0.07	2.67	0.11	2.17	13.8	0.001	0.60
C. septempunctata	28	0.005	0.03	0.86	0.96	0.55	0.46	0.91
Combined species	34	0.19	0.88	0.36	0.98	0.07	0.79	0.85
Larva								
Combined species	19	0.15	1.47	0.23	2.06	17.0	0.001	0.42

sions for *H. convergens* and *C. septempunctata*, and combined adults, r^2 was ≥0.85, indicating that estimates of density from the same plot were similar; i.e., that sampling using both methods yielded relatively precise estimates.

Sweepnet and Timed Count Sampling. Because we were primarily interested in relative sampling methods for estimating total coccinellid density rather than species-specific estimates, we analyzed data for adults and larvae pooled across species to determine relationships between population estimates obtained from sweepnet and timed count samples and estimates obtained by absolute samples. Estimates of adult coccinellid density for each plot were constructed by taking the weighted averages of estimates obtained from removal and quadrat sampling, because both methods gave accurate estimates of population density. Estimates for each method were weighted by the inverse of their variance so that the more precise estimate contributed greater weight to the final density estimate. Pooling data in this manner permitted us to use the maximum amount of information at our disposal. For larval coccinellids, estimates derived from quadrat sampling were used because removal sampling provided biased estimates of larval density (see previous section).

Relative population estimates from timed count and sweepnet samples were significantly correlated with absolute density for both larval and adult coccinellids (Table 3). Timed counts were more highly correlated with absolute density for adults than sweepnet sampling. For larval coccinellids the opposite was true.

Partial correlations (data adjusted for population density) between relative population estimates (from timed counts and sweepnet sampling), and meteorologic, crop, and aphid variables give the degree of association between the efficiency of sampling using the relative method and the particular variable (after accounting for the effect of population density on catch). Several partial correlations were significant (Table 4). Significant partial correlations were observed between timed counts of larvae and plant variables such as canopy coverage and the number of tillers per 0.3 m of row. Among meteorological variables, relative humidity and wind velocity also were correlated with timed counts of larvae. Timed counts of adults were significantly correlated only with plant phenological stage. Crop plant variables were strongly correlated with the sweepnet catch for adults, and relatively large correlations with crop variables were observed for larvae, although only the number of tillers per 0.3 m of row was significant (Table 4). Sweepnet catch of coccinellid larvae was significantly correlated with all meteorological variables and the number of aphids per tiller.

Models for Converting Sweepnet and Count Sampling. Regression models were developed us-

Table 3. Pearson correlation coefficients between the estimated number of coccinellids per square meter (absolute density) and the number captured per sweep and the number seen per minute of counting (relative population estimates)

Sampling method	Life stage (n)	
	Adult (34)	Larva (18)
Sweepnet[a]	0.65*	0.81*
Timed count[b]	0.94*	0.65*

*, Differs significantly from zero ($\alpha = 0.05$).

[a] Number of coccinellids captured per sweep with a sweepnet 38-cm in diameter.

[b] Number of coccinellids seen per minute of counting while walking at a constant velocity.

Table 4. Partial correlation coefficients between the number of coccinellids in samples using 2 sampling methods (sweepnet and timed count) and several biotic and abiotic variables

Variable	Timed count		Sweepnet	
	Adult (32)	Larva (18)	Adult (32)	Larvae (18)
Plant height	0.31	0.36	0.57*	0.41
Growth stage	0.46*	0.27	0.80*	0.22
Canopy coverage	0.27	0.66*	0.41*	0.38
Tillers/0.3-m row	0.23	0.56*	0.43*	0.61*
Air temp	0.01	0.24	0.19	0.67*
Relative humidity	0.23	−0.65*	0.26	−0.87*
Solar irradiance	−0.18	0.41	0.03	0.68*
Wind velocity	0.05	0.54*	−0.16	0.68*
No. aphids/tiller	−0.33	0.03	−0.45*	0.73*

*, Differs significantly from zero ($\alpha = 0.05$). Population density (based on removal or quadrat sampling or both) was held at expected values. Sample sizes are in parentheses.

Table 5. Least square regression models relating the number of coccinellids counted and the number of coccinellids per sweep to the number of coccinellids per square meter

Sampling method stage (n)	Model[a]	R^2
Timed counting		
Adult (32)	$D = 1.14C$	0.93
Larva (18)	$D = (15.2 - 0.458T + 0.003907^2)C$	0.89
Sweepnet sampling		
Adult (32)	$D = (28.3 - 2.98G)S$	0.93
Larva (18)	$D = 0.437HS$	0.91

[a] C, number of coccinellids counted per minute of counting; S, number of coccinellids per sweep; D, number of coccinellids per square meter; G, plant growth stage; H, wheat plant height; T, number of tillers per 0.3 m of row.

Table 6. Relative net efficiency (mean ± SE) of 4 sampling methods for estimating population density (number per square meter) of adult and larval coccinellids

Sample unit	Adult[a]	Larvae[b]
Square meter quadrat	18.9 ± 2.86b	19.9 ± 3.26b
Two 12-min removal samples	16.4 ± 1.05b	21.6 ± 1.49b
25 sweeps	6.19 ± 0.83a	6.11 ± 1.33a
6-min count while walking	15.0 ± 3.89b	6.84 ± 1.80a

Means within a column followed by the same letter do not differ significantly based on the *LSD* test ($\alpha = 0.05$).
[a] ANOVA statistics were $F = 3.69$; df = 3, 90; $P = 0.0148$.
[b] ANOVA statistics were $F = 16.83$; df = 3, 47; $P = 0.0001$.

ing equation 1. Note that the x_i s in equation 1 are assumed to operate independently in their effects on relative sampling methods. Among crop variables, plant phenological stage ranged from 2.0 (tillering) to 8.0 (soft dough), plant height ranged from 6.0 to 61.3 cm, the number of tillers per 0.3 m of row ranged from 18.5 to 84.7, and canopy coverage ranged from 2.56 to 5.56. The number of aphids per tiller ranged from 0 to 3.33. Among meteorological variables, temperature varied from 5.7 to 29.2°C, windspeed varied from 1.24 to 7.11 m/s, relative humidity varied from 14.3 to 92.1%, and solar irradiance varied from 0.20 to 0.95 kw/m^2.

Fitted models for converting from timed count and sweepnet catch of adults (combined across species) and larvae to absolute population estimates are listed in Table 5. None of the ancillary variables improved R^2 enough to be included in the model for converting timed counts of adults to absolute density. Plant growth stage was incorporated in the model to convert sweepnet catch of adults to absolute density. This model underscores the often recounted caution that it is inappropriate to use regression models outside the range data used to develop the model. For example, at a Zadoks' plant growth measurement of $G = 10$, the model would yield negative estimates of density. For larvae, the number of tillers per 0.3 m of row was included in the model for converting timed counts to absolute density, whereas the model for converting sweepnet catch of larvae to density incorporated plant height. Coefficients of multiple determination of regression models ranged from 0.89 for the model for timed count samples of larvae, to 0.93 for the model for converting timed counts or sweepnet samples of adult coccinellids (Table 5); all the models were significant ($P \leq 0.05$).

Relative Efficiency of Sampling Techniques. For adult coccinellids, a 25-sweep sample was a significantly more efficient sample unit than the others studied (Table 6). This was true in spite of the additional variability incurred by estimating the number of coccinellids per square meter from the mean number of coccinellids per sweep using a regression model. The 6-min visual count was as efficient for sampling adults as the square meter quadrat and 12-min removal sample from within a 25-m^2 subplot.

For larval coccinellids, the 25-sweep and 6-min count sample units were significantly more efficient than the square meter quadrat or double 12-min removal sample units (Table 6). Double 12-min removal sample and the square meter quadrat sample units did not differ significantly, nor did the 25-sweep or 6-min count differ significantly.

Discussion

Three conditions must be satisfied in removal sampling for De Lury's method to be appropriate for estimating the population size in a prescribed area (Seber and Le Cren 1967). First, there must be no net change in the size of the population caused by recruitment, mortality, immigration, or emigration during the time the 2 samples are taken. Second, the probability of capture must not change among successive removal samples from the same area. Third, the probability of capture must be large enough that repeated removal samples result in a significant reduction in the size of the population. Lapchin et al. (1987) and Elliott et al. (1990) found that the 3 conditions for removal samples were satisfied by removal sampling performed by visual inspection and collection of all coccinellids observed in 25-m^2 plots in 2 successive samples. In that case, approximately unbiased estimates of the number of adult coccinellids in the prescribed area would result. Lapchin et al. (1987) and Elliott et al. (1990) used statistical tests based on the rate of decrease in capture among successive samples from plots to reach their conclusions. We used a direct method for comparing the suitability of removal sampling for both adult and larval coccinellids. We compared simultaneous estimates of density from removal sampling with those obtained from complete enumeration of coccinellids in enclosed quadrats. Complete enumeration of organisms in a defined area, although very time

consuming, provides estimates of absolute population. Our results are in general agreement with those of Lapchin et al. (1987) and Elliott et al. (1990) for adult coccinellids in that removal sampling yielded estimates consistent with those of quadrat sampling. Removal sampling was a poor method for sampling larval coccinellids, because the resulting density estimates generally underestimated true density. Furthermore, the very low r^2 for regression of larval density estimated from quadrat sampling versus density estimated from removal sampling suggests that the extent of bias in estimates from removal sampling varied from plot to plot. A possible explanation for our observations is that there is interspecific variation in the catchability of larvae within the plot. The criterion that each individual in the population be equally likely to be captured would not be satisfied in this case (Seber and Le Cren 1967). If there is interspecific variation in larval catchability, it could affect population estimates based on removal sampling because various portions of the larval population would be differentially susceptible to capture. Because we did not record the species of coccinellid larvae captured in the study, we cannot explore that possibility.

There were differences in the catchability of adult coccinellids. *H. sinuata* populations were poorly estimated by removal sampling, indicating that ≥1 of the assumptions on which removal sampling is based were violated. Considering that removal sampling is not universally applicable for coccinellids, and a similar *rne* was achieved using quadrat and removal methods, quadrat sampling is probably a more desirable method for use in ecological studies.

The sweepnet and 6-min-count units were more efficient (smaller *rne*) than either the square meter quadrat or double 12-min removal sample for estimating densities of adult and larval coccinellids, and estimates obtained by both methods were successfully converted to absolute density using Ruesink and Haynes (1973) model (equation 1). Lapchin et al. (1987) demonstrated a linear relationship between the density of coccinellids in wheat fields and the number observed in timed counts. However, the proportion of variance accounted for by their models was generally lower than we observed, suggesting that inclusion of ancillary variables may have resulted in improved fit to their data.

Although the time taken to collect and process a 25-sweep sample in the field depended on coccinellid density, it took only a few minutes on average to take and process the sample. Because the 6-min count was a fundamental sample unit, we could not evaluate *rne* for counts made for a shorter time. It is possible that counts made for a shorter period of time would result in estimates with *rne* comparable to that of the 25-sweep sample.

Elliott et al. (1990) found that plant phenological stage was important in South Dakota for converting sweepnet population estimates of coccinellid adults in wheat to absolute population estimates. Phenological stage was important in our model for converting sweepnet catch of coccinellids in Oklahoma and Texas. Although parameter estimates differ among the models from the 2 studies, they are remarkably identical in functional form. Thus, both studies indicate that a variable related to canopy height and thickness (e.g., plant phenology), which would be expected to affect the efficiency of sweepnet sampling, should be incorporated in models to improve the estimation of coccinellid density.

Elliott et al. (1990) included temperature in a model for estimating absolute population of adult coccinellids from timed counts. No variables measured in the current study (including temperature) improved estimation of absolute population of adults from timed counts. Species assemblages of coccinellids in South Dakota differ from those in Oklahoma and Texas. The discrepancy in variables included in models may be partly caused by differences in the response of various coccinellid species to different environmental factors. Differences in microhabitat use (thought to be related to micrometeorological factors) in agricultural crops by coccinellids has been reported (e.g., Ewart and Chaing 1966, Coderre and Tourneur 1986). The inclusion of temperature in the Elliott et al. (1990) model may reflect differences in species microhabitat use within wheat fields, perhaps related to temperature, that were manifested as differences in visibility of beetles to an observer walking through the field. It should be mentioned that there is no assurance that any of the variables included in our models are causal variables, only that their inclusion explains a larger proportion of the variability in the data than other variables measured.

Considering the differences observed in the Elliott et al. (1990) models for adult coccinellids in spring wheat in South Dakota, and those in this study in winter wheat in Oklahoma and Texas, it is not advisable to use either model in a new region or ecological situation without verifying their accuracy. However, the study does establish a foundation for developing efficient sampling methods for coccinellids in wheat by identifying variables that should be measured to estimate coccinellid density accurately with various relative sampling methods.

Acknowledgments

We extend our thanks to J. B. Bible (Texas Agricultural Experiment Station, Bushland, TX) and B. W. French, T. D. Johnson, P. L. Shelby, and M. Johnson (Plant Science Research Laboratory, USDA–ARS, SPA, Stillwater, OK) for technical assistance. We also thank T. L. Archer and M. D. Lazar (Texas Agricultural Experiment Station) and C. D. Patrick (Texas Agricultural Extension Service) for helpful comments on an early version of this article. This research was supported by a USDA–CSRS Southern Re-

gion Integrated Pest Management Program grant (Cooperative Agreement 91-34103-5839).

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Received for publication 30 January 1996; accepted 14 August 1996.