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ESTIMATING PARASITISM OF COLORADO POTATO BEETLE EGGS, *LEPTINOTARSA DECEMLINEATA* (COLEOPTERA: CHRYSOMELIDAE), BY *EDOVUM PUTTLERI* (HYMENOPTERA: EULOPHIDAE)[1]

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ABSTRACT

A computer simulation was used to evaluate methods for estimating parasitism of Colorado potato beetle egg mass populations by *Edovum puttleri*. The algorithm incorporated the specific attack behavior of *E. puttleri*, and a development time for parasitized egg masses of ca. 2.9 times that of healthy egg masses. Of the methods compared, a modification of Southwood's graphical technique was found to be most accurate in relation to the true parasitism derived from the algorithm. A regression equation is presented to correct the error in this method at high levels of parasitism. A second simulation was used to test the accuracy of this correcter where in a jacknife procedure was used to generate a mean and variance for estimates of parasitism.

An exotic hymenopteran egg parasitoid, *Edovum puttleri* Grissell, is currently being reared by several state and federal laboratories for experimental releases against the Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say), on potatoes, tomatoes, and eggplant. This parasitoid has not been found to overwinter in the Northeast (Obrycki et al. 1985) and its use is presently restricted to inundative releases throughout the growing season. Evaluation of the percent parasitism is complicated by the difference in developmental time between parasitized and nonparasitized eggs. *E. puttleri* requires ca. 2.9 times as long to develop as healthy CPB eggs (Obrycki et al. 1985), hence parasitized eggs are in the field three times as long and are more likely to be encountered in sampling than unparasitized eggs. This development time differential must be considered in constructing sampling programs to avoid inflating percent parasitism estimates.

A technique for estimating percent parasitism described by Groden (1982) accounts for the difference in host and parasitoid development times by estimating parasitized and nonparasitized densities independently using a modification of Southwood's graphical technique (Southwood 1978). With repeated frequent sampling, where the sampling interval is less than the development or residence times of parasitized and nonparasitized hosts, incidence curves (time [x-axis] vs. density [y-axis]) for the two populations can be constructed. Total densities are calculated by determining the area under these curves and dividing by their respective development times. Percent parasitism is calculated by dividing the parasitized host density by the sum of the parasitized and nonparasitized densities and multiplying by 100. Estimating the parasitized and nonparasitized popula-

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Table 1. Methods used for estimating percent *E. puttleri* parasitism of CPB egg masses from simulated field samples. ($PDENS_j$ = parasitized egg density at time j, $TDENS_j$ = total egg density at time j, p = peak host density, DD_j = degree-days at time j, TPDENS = total parasitized egg density, NPDENS = total nonparasitized egg density, N = number of samples.)

1	$\%PAR1 = (PDENS_p/TDENS_p)*100$
2	$\%PAR2 = ((\sum_{1}^{N}(PDENS_j/TDENS_j))/N)*100$
3	$\%PAR3 = ((\sum_{1}^{t}(PDENS_j)/(\sum_{1}^{t}TDENS_j))/N)*100$
4	$\%PAR4 = \left(\frac{\sum_{2}^{t}(PDENS_j + PDENS_{j-1})/2*(DD_j - DD_{j-1})}{\sum_{2}^{t}(TDENS_j + TDENS_{j-1})/2*(DD_j - DD_{j-1})}\right)*100$
5	$\%PAR5 = (TPDENS/(TPDENS + NPDENS))*100$, where
	$TPDENS = \sum_{2}^{t}((PDENS_j + PDENS_{j-1})/2*(DD_j - DD_{j-1}))/217$
	$NPDENS = \sum_{2}^{t}((NPDENS_j + NPDENS_{j-1})/2*(DD_j - DD_{j-1}))/75$

tions independently does not take into account that individuals are moving from the nonparasitized to the parasitized population as one is sampling. This error is dependent upon the parasitoid attack pattern (age-dependence of parasitoid susceptibility, Groden 1982), but can be corrected if the pattern of attack for a given species of parasitoid has been described and quantified.

The purpose of this study is to show how the difference in development times between healthy CPB eggs and those parasitized by *E. puttleri* influence estimates of percent parasitism derived from commonly used methods. The accuracy of the method described by Groden (1982) is examined for this host-parasitoid system.

MATERIALS AND METHODS

We used a computer program to simulate field populations of unparasitized and parasitized CPB egg masses in potatoes following a release of *Edovum puttleri*. Recruitment and loss of individuals, both parasitized and unparasitized, are a function of degree-day accumulation. Recruitment into the egg stage was based upon field data collected in Rhode Island from 1980 to 1985.

Development period of unparasitized egg masses was 75 DD, base 10°C (Logan 1981). Development period of parasitized egg masses was 217 DD, base 10°C (Obrycki et al. 1985). The flow of egg masses from an unparasitized to a parasitized state was determined by applying an exponential decay attack rate to the unparasitized egg mass population

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Table 2. Sample output of simulated field samples generated from the CPB-*E. puttleri* model using parasitoid release times of 40 and 80 DD. True percentage of the population parasitized = 37.83.

DD	Egg Masses per Plant	Parasitized Egg Masses per Plant	% Parasitized Egg Masses
1	0.00	0.00	0.00
51	0.17	0.01	6.90
101	1.33	0.36	27.13
151	0.96	0.57	59.00
201	0.70	0.59	84.30
251	0.62	0.60	97.07
301	0.41	0.41	100.00
351	0.06	0.06	100.00
401	0.01	0.01	100.00

Table 3. Comparison of different methods for estimating total (%) *E. puttleri* parasitism of CPB egg masses over a range of true parasitism. Parasitoid release times = 40 and 80 DD.

True % Parasitism	Estimates of Total Parasitism (%)				
	Method 1	Method 2	Method 3	Method 4	Method 5
5	4	60	14	14	5
20	14	70	42	42	20
40	29	76	63	63	37
60	45	81	76	76	53
80	65	86	86	86	69
95	98	91	94	94	83

following a parasitoid release. This attack rate was derived from data collected by Lashomb (unpublished) and is a function of degree-days from release time (t): rate = $e^{(4.23-0.0102*t)}$, $r^2 = 0.93$. This attack rate was not applied equally across all age classes of unparasitized egg masses. Krainacker et al. (1986) found that susceptibility of egg masses to parasitoid attack was greatest between 0 and 20 DD age, declined linearly from 20 DD to 50 DD age, and egg masses 50 DD and older were no longer parasitized. Egg mass mortality independent of parasitism was not considered in the model.

In modeling egg mass susceptibility we used a discrete boxcar approach by keeping track of 1 DD age intervals of egg masses. All the masses in the age classes from 1–20 DD were susceptible to parasite attack (the attack rate was multiplied by the numbers of egg masses in each age class). A linearly decreasing proportion of individuals (100% to 0%) were susceptible to parasitism in the age classes 20 to 50 DD and no egg masses were allowed to be parasitized that were older than 50 DD. Only unparasitized egg masses were attacked since *E. puttleri* discriminates between parasitized and unparasitized egg masses (Obrycki et al. 1985).

We used this program to evaluate various methods for estimating field-level parasitism by incorporating a sampling subroutine summed the number of healthy and parasitized egg masses in the program at 50 DD intervals. This provided a minimum of 7 data points to describe the host incidence curve as suggested by Ruesink (1975). These simulated samples represent sample means through time and were used to estimate generational percent parasitism of the egg mass population using the following five methods (Table 1):

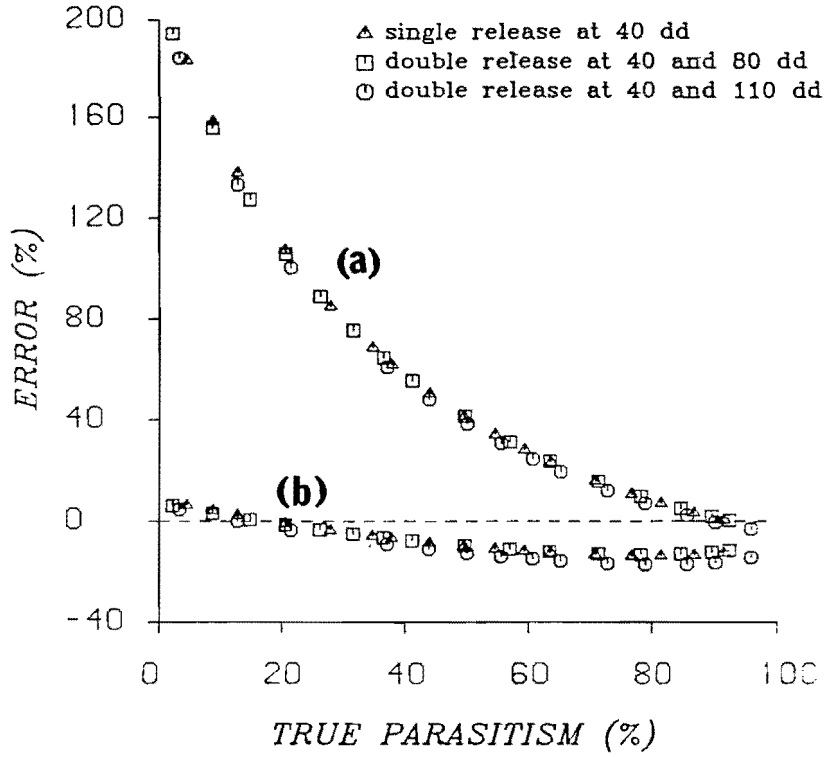

Figure 1. Predicted errors in estimates of percent *E. puttleri* parasitism of CPB egg masses with different parasitoid release patterns using modifications of Southwood's technique where (a) differences in parasitoid and host development times are not taken into account, and (b) difference in parasitoid and host development times are taken into account.

(1) percent parasitism at peak host abundance, (2) mean percent parasitism over all sample dates, (3) percentage of the pooled samples (over the entire generation) parasitized. (4) a modification of Southwood's method that does not take into account differences in development time between parasitoid and host (Gage 1974, Lampert and Haynes 1985), and (5) a modification of Southwood's method described by Groden (1982) that does account for differences in development time. The accuracy of these estimates was compared over a range of parasitism levels by varying the number of parasitoids released.

The influence of the parasitoid release pattern on the accuracy of these methods was examined. Three different release patterns were simulated and compared: a single release at 40 DD after initial CPB oviposition, a double release at 40 and 80 DD, and a double release at 40 and 110 DD. True parasitism was regressed as a function of the estimated parasitism to yield an equation that corrects for the error in method five.

The final stage of this study tested the accuracy of estimating *E. puttleri* parasitism with method 5 over a range of parasitism levels, sample sizes, and seasonal densities. Again this was done with simulation. The spatial distribution of CPB egg masses in the field was examined over a range of densities (using field-collected data from two CPB egg mass generations in Rhode Island), and was best described as a Poisson frequency distribution

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Table 4. Percentage of time jackknife estimtes fell within set % error of the true parasitism. Based on 10 simulations per seasonal density, sample size and parasitism level.

			Seasonal Density (egg masses/plant)								
			0.5 Jackknife Sample Size			1.5 Jackknife Sample Size			5.0 Jackknife Sample Size		
True % Parasitism	% Error	Percentage Point Range	50	100	200	50	100	200	50	100	200
4.13	10	± 0.41	10	0	0	10	0	0	0	0	0
	15	± 0.62	10	0	0	10	0	0	0	0	0
	25	± 1.03	10	0	20	20	0	0	0	0	0
	50	± 2.06	70	40	40	60	40	20	60	40	30
23.14	10	± 2.31	30	60	50	10	40	70	70	80	90
	15	± 3.47	50	80	80	80	80	70	90	100	100
	25	± 5.79	80	80	100	100	100	100	100	100	100
	50	± 11.52	100	100	100	100	100	100	100	100	100
52.49	10	± 5.25	40	50	70	30	80	80	90	90	100
	15	± 7.87	60	90	90	80	90	100	90	100	100
	25	± 13.12	100	100	100	100	100	100	100	100	100
	50	± 26.25	100	100	100	100	100	100	100	100	100
83.49	10	± 8.35	90	90	90	70	70	90	80	100	100
	15	± 12.52	100	90	100	80	100	100	100	100	100
	25	± 20.87	100	100	100	100	100	100	100	100	100
	50	± 41.75	100	100	100	100	100	100	100	100	100

(Groden unpublished data). Therefore, the generated sample means from the computer program were input into a random number generating subroutine (Davies 1971) to generate random samples of various sizes from a Poisson distribution for each of 13 sample dates. Sample means of parasitized and nonparasitized densities per sample date were calculated from these data, and estimates of percent *E. puttleri* parasitism were calculated using method 5 and the regression corrector. The jackknife technique (Mosteller and Tukey 1972, Zahl 1977) was used to generate a mean and variance for estimates of percent parasitism for each set of samples. Ten samples per sample date were omitted sequentially for each estimate calculated, thus 5, 10, and 20 estimates were used to calculate the jackknife mean and variance with sample sizes of 50, 100, and 200, respectively. For each sample size, 10 simulations were run for each of four levels of true percent parasitism and the three levels of seasonal egg mass density. The error in the jackknife means was calculated as a percentage of the true percent parasitism.

RESULTS AND DISCUSSION

An example of the simulated samples generated by the program is presented in Table 2. Estimates of percent parasitism increase through time, eventually reaching 100%. In this case, peak parasitoid attack occurred at the time of second release (80 DD), yet percent parasitism increased as the healthy egg masses hatched and the parasitized eggs remained in the population. This is the same trend that has been found to occur in potato fields in Michigan (Drummond and Miller 1987). The comparison of the different methods for estimating percent *E. puttleri* parasitism over a range of true parasitism levels is presented in Table 3. The first method (estimating parasitism at peak host abundance)

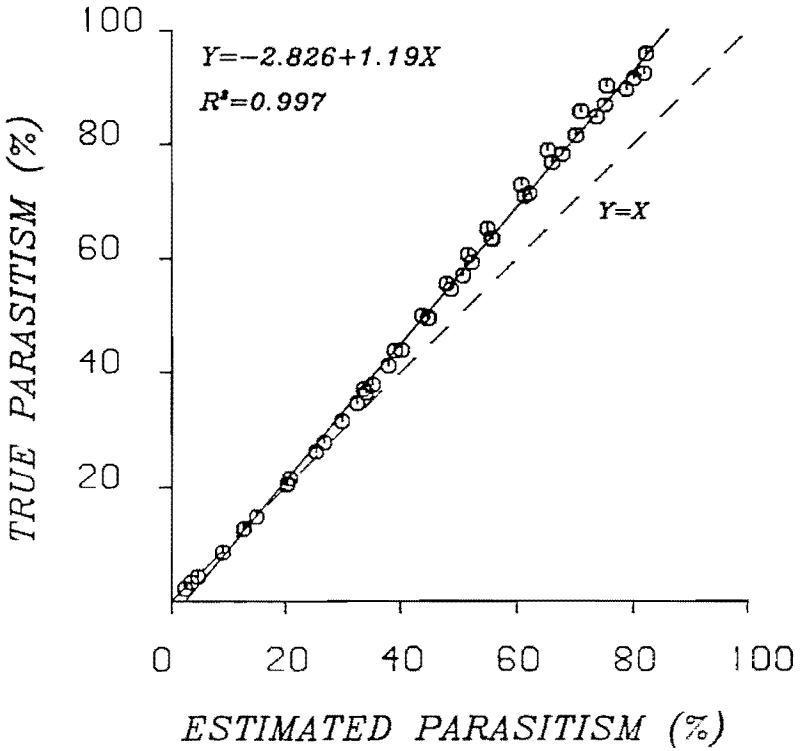

Figure 2. True percent *E. puttleri* parasitism of CPB egg masses as a function of estimated percent parasitism when parasitized and nonparasitized egg mass densities are estimated independently.

severely underestimated parasitism except at extremely high levels of attack. The second method (mean percent parasitism of all samples) severely over estimated the true parasitism except at the highest rates of true parasitism. Methods 3 and 4 also severely overestimated the true impact of *E. puttleri* except at high levels of parasitism.[5] The modification of Southwood's method which estimates parasitized and nonparasitized densities independently (method 5) was accurate at low levels of parasitism, but underestimated percent parasitism as true parasitism increased. Among the release patterns compared, the magnitude of this error in method 5 did not vary significantly (Fig. 1). Regressing true parasitism as a function of the estimated parasitism (Fig. 2), yielded

[5]Because the model sampled the population at exact regular degree day intervals, and we used a step-wise integration to solve for the area under the incidence curve with the modification of Southwood's method, these estimates are exactly equal. Given differences in DD accumulation from one day to the next in a real field situation, this would not be the case, but the trend in the errors would be the same.

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the following equation for correcting the estimate of percent *E. puttleri* parasitism calculated by method 5:

$$y = 1.20x - 2.83, r^2 = 0.99,$$

where y = true parasitism (%) and x = estimated parasitism (%).

The results of simulation runs to determine the accuracy of method 5 with the regression corrector for estimating *E. puttleri* parasitism are presented in Table 4. At low levels of parasitism, even with a large sample size, the estimate did not even fall within 50% of the true percent parasistism in half the runs. Hence, the estimates of percent parasitism at low levels of parasitism are more accurate without the regression corrector. As parasitism increases, this error in nonparasitized egg mass density becomes more significant, as was evident in Fig. 1. The usefulness of the corrector increased with increasing parasitism, and also with increasing seasonal density and sample size. At high levels of parasitism and high CPB egg mass densisities, 100% of the estimates of parasitism fell within 10% of the true parasitism with sample sizes of 100 or greater. At moderate levels of parasitism and low CPB egg mass densities, the sample size must be increased to maintain the same level of accuracy. Though with a true parasitism of 23%, and a sample size of 200, one can only be assured of the estimate falling within 25% of the true parasitism but this is till within an absolute value of six percentage points.

Estimating parasitized egg mass an nonparasitized egg mass densities independently with Southwood's graphical technique and using the regression equation to correct estimates of percent parasitism calculated from these densities, is one way of accounting for the differences in *E. puttleri* and CPB egg masss development times and evaluating releases of this parasitoid. Other investigators have marked individual egg masses as they are laid and followed the fate of those egg masses through time. This can be extremely labor intensive as new cohorts must be identified and followed continuously through the egg generation for accurate estimates. However, if the difference in developmental times of this parasitoid and its host are not taken into account when sampling, erroneous conclusions regarding *E. puttleri's* potential for biological control of the CPB could results. Using the technique described above, one may be able to estimate percent *E. puttleri* with an acceptable level of precision over a range of CPB infestation levels by adjusting the sample size.

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