Optimal Oviposition by the Corn Earworm (Lepidoptera: Noctuidae) on Whorl-Stage Sweet Corn

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ABSTRACT Commercial fields of sweet corn in coastal southern California were sampled for corn earworm, *Heliothis zea* (Boddie), eggs in 1986 and 1987. Staggered planting schedules within each study site produced fields of varying maturity that overlapped in occurrence. Using stepwise regression, we quantified the dependence of egg density on field size, adult population level as estimated with pheromone traps, and field maturity as estimated by plastochron index. Also included were three variables associated with the probability of female moths finding a more suitable host: the hectares of older corn available, distance to the closest older cornfield, and the mean distance to all older cornfields. We found egg density to be significantly related to field maturity and the distance to the closest older cornfield. In 1987, when the average distance between fields was less than in 1986, egg density was more closely associated with field maturity and, therefore, host suitability. These results are discussed in relation to optimal oviposition theory.

KEY WORDS Insecta, *Heliothis zea*, optimal oviposition theory

OPTIMAL FORAGING THEORY states that animals, whose behavior is the result of natural selection, forage such that energy intake is maximized (Pyke et al. 1977). Optimal oviposition theory, an offshoot of optimal foraging theory, states that as a result of evolution, ovipositing insects select hosts such that offspring fitness is maximized (Jaenike 1978). Host selection by phytophagous insects has been described behaviorally as acceptance or rejection of a possible host because of the insect's physiological drive and stimuli from the plant (Miller & Strickler 1984). As the time since last oviposition increases (i.e., the insect's physiological drive increases), the threshold for host acceptance lowers and less suitable hosts become acceptable. Therefore, the probability of an insect accepting a host is dependent upon the suitability of that host for offspring survival and the probability of its finding a more suitable host in the time available (Jaenike 1978).

The objective of our study was to determine if oviposition by *Heliothis zea* (Boddie) in commercial fields of whorl-stage sweet corn agrees with the predictions of optimal oviposition theory (Jaenike 1978). Do adult females oviposit in relation to host suitability for the offspring? Is oviposition behavior related to the probability of finding a more suitable host? If so, is this probability more closely associated with the total area of more suitable hosts, the mean distance to all fields of more suitable hosts, or the distance to the closest field of more suitable hosts?

Materials and Methods

The study site during 1986 was on the Irvine Ranch in Orange County, Calif. (Fig. 1). During that year, 177.8 ha of 'Jubilee' sweet corn were planted from February through May (Table 1) and harvested in June and July. This staggered planting schedule resulted in cornfields of different ages that overlapped in occurrence. Interspersed among these fields were fields of other vegetables, strawberries, and citrus orchards. Corn was the only highly suitable host for *H. zea* grown within the study site. The study site was surrounded by citrus orchards and residential development. The Irvine Ranch applied methomyl and fenvalerate every 3 d following the onset of silking in each cornfield to control *H. zea*.

The study site during 1987 was at Osumi Farms (Fig. 1), located near the southwest corner of the Irvine Ranch site. At this site, 64.8 ha of 'Jubilee' sweet corn were planted from February through April (Table 1) and harvested in June and July. Corn was not grown by the Irvine Ranch during 1987. As with the Irvine Ranch plantings the previous year, cornfields of different ages overlapped in occurrence along with other fields of vegetables. Corn was the only highly suitable host available to *H. zea* within the study site. The study site was surrounded by residential development. Osumi Farms sporadically applied permethrin to each cornfield following the onset of silking to control *H. zea*.

Cornfields were sampled twice weekly for *H. zea* eggs from the time when plants were approximately 30 cm tall until tasseling (Table 1). Systematic samples of each field were taken by examining every 50th plant in a randomly-chosen row, at least 50 rows from the edge, until 20 plants were sampled. All leaves of each plant were examined for eggs. Oatman (1966) examined the natural enemies of *H. zea* eggs and larvae in the same

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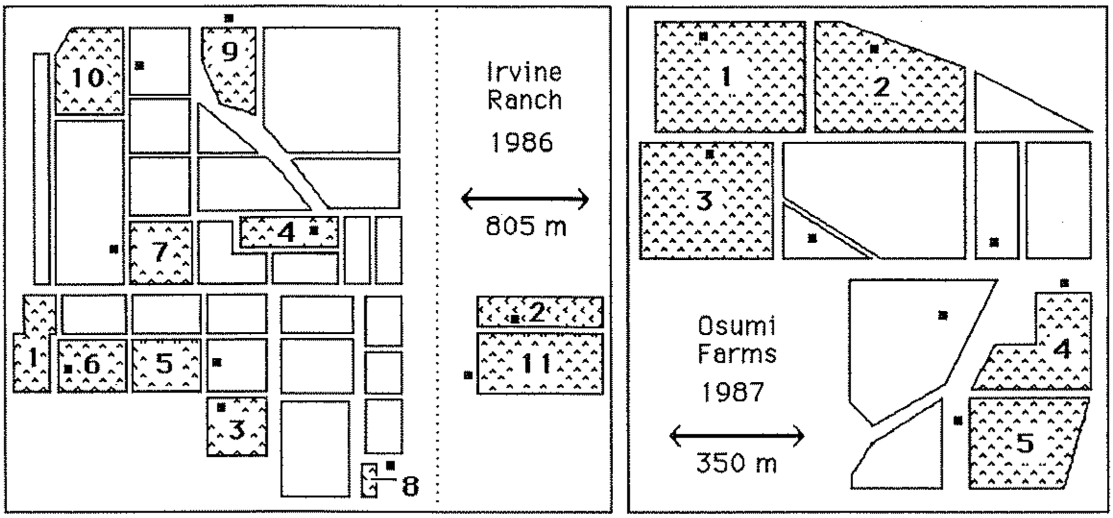

Fig. 1. Field layout of the study sites. Sampled fields of sweet corn are numbered according to planting order. Unnumbered fields were planted to other crops. Small black squares represent pheromone traps. The map of the Irvine Ranch in 1986 (left) is discontinuous along the vertical dotted line.

region as this study and found that predators on tasseling sweet corn occurred in low density, especially during the spring. Therefore, because whorl-stage corn most likely would support even fewer predators, estimates of egg density were assumed to reflect oviposition behavior.

The plastochron index (Erickson 1976) of every other plant sampled for eggs was measured. This index provided an estimate of plant age that was continuous and linear with physiological time. Higher plastochron index values indicated greater plant maturity. The decimal portion of the index was dependent upon the length of the first leaf >20 cm and the length of the first leaf <20 cm, and the value to the left of the decimal point was the number of leaves >20 cm. The mean plastochron index of the 10 sampled plants on each date was used to estimate the plastochron index of the field (see Table 1).

Double-cone, nylon-mesh *Heliothis* pheromone traps (Scentry, Chandler, Ariz.) were placed within the study sites to estimate *H. zea* population levels during the study. Ten traps were monitored in 1986, and eight were used in 1987 (Fig. 1). The openings of the traps were placed 1 m above bare ground, and traps next to corn were raised periodically to keep their openings above the plant canopy. Micro-capillary *H. zea* lures (Scentry) were

Table 1. Sampling information, egg counts, plastochron index values, field size, and availability of older corn for *H. zea* on whorl-stage sweet corn

Year and field	Planting date	No. samples	Interval sampled	Eggs/20 plants		Plast. index		Ha	Ha of older corn	$\bar{x}$ m to older corn	m to closest older corn
				$\bar{Y}$	Range	$\bar{X}$	Range				
1986											
1	17 Feb.	7	11 Apr.–5 May	3.7	0–8	7.9	3.6–10.4	14.6	0.0	—	—
2	22 Feb.	7	11 Apr.–6 May	4.0	0–9	7.6	3.3–10.5	15.0	14.6	4,981	4,981
3	27 Feb.	8	21 Apr.–17 May	2.1	0–5	6.3	1.5–9.9	17.0	29.6	4,444	1,463
4	16 Mar.	8	30 Apr.–22 May	2.5	1–6	6.6	3.6–10.4	8.9	46.6	3,517	1,621
5	19 Mar.	8	3 May–26 May	1.9	0–5	6.5	2.4–10.3	18.2	55.5	2,681	593
6	25 Mar.	7	9 May–30 May	0.9	0–2	6.2	2.1–10.5	18.6	73.7	1,415	435
7	31 Mar.	6	17 May–2 June	0.5	0–1	5.6	1.9–9.2	15.0	92.3	2,121	751
8	15 Apr.	5	19 May–2 June	1.2	0–3	7.9	4.6–10.7	4.5	107.3	2,509	1,186
9	3 May	5	31 May–14 June	3.0	2–5	7.4	5.1–9.1	18.6	111.8	2,669	1,146
10	6 May	5	31 May–14 June	2.2	1–4	6.4	4.4–9.5	17.0	130.4	2,582	949
11	12 May	5	3 June–17 June	0.4	0–1	5.2	3.0–6.7	30.4	147.4	5,381	316
1987											
1	10 Feb.	5	8 Apr.–22 Apr.	2.0	0–4	6.6	4.3–9.6	16.2	0.0	—	—
2	9 Mar.	6	12 Apr.–29 Apr.	2.0	1–5	6.0	3.2–8.9	14.2	16.2	460	460
3	18 Mar.	7	16 Apr.–6 May	2.7	0–6	5.8	3.0–9.2	16.2	30.4	433	368
4	21 Mar.	6	26 Apr.–13 May	2.8	1–6	4.2	1.6–6.2	8.1	46.6	945	814
5	8 Apr.	5	6 May–24 May	0.6	0–1	4.7	2.0–9.2	10.1	54.7	853	276

Table 2. Regression analysis of *H. zea* egg density (transformed $[Y + 0.5]^{1/2}$) on whorl-stage sweet corn

Year	Variable	Regression coefficient	SE	df[a]	F	P	Partial R^2	Total R^2
1986	Y intercept	0.266	—	—	—	—	—	
	Plastochron index	0.091	0.027	57	11.33	0.0014	0.125	
	Field distance[b]	0.017	0.005	57	12.89	0.0007	0.249	0.373
1987	Y intercept	−0.677	—	—	—	—	—	
	Plastochron index	0.173	0.036	21	23.58	0.001	0.377	
	Field distance[b]	0.060	0.019	21	10.49	0.004	0.207	0.585

[a] Mean square error: 0.250 in 1986, 0.152 in 1987.

[b] Distance (m) to the closest older cornfield (transformed $X^{1/2}$).

used in 1986, and they were replaced every 2 wk. A significant difference (Friedman test) in moth catch between lure ages ($F = 19.23$; df = 11; $P = 0.0001$) (probably caused by a burst of pheromone from new lures) was eliminated by discarding the first trapping period following lure replacement ($F = 1.02$; df = 10; $P = 0.42$). Polyvinyl-chloride *H. zea* lures (Scentry) were used in 1987, and they were replaced weekly after being aged for 2 d at 27 ± 1°C. The moth catch in 1987 did not decline as lures became older.

The sampling period in both years was divided into 3-d intervals, and the moths per day in all of the traps combined was calculated for each interval. Pheromone traps were monitored at least once during each 3-d interval. In 1986, egg density lagged behind pheromone trap catch. To adjust for this lag, moth catch was shifted in 3-d increments until, after a 9-d shift, maximal correlation between egg density and moth catch occurred.

The density of *H. zea* eggs in a particular cornfield on a given day was considered to be dependent upon several factors. These were the population level of *H. zea* adults within the study site, the field size, the suitability of the field for offspring survival, and the probability of a female moth within the field finding a more suitable host. To test these factors, stepwise regression (PROC STEPWISE; SAS Institute 1985, 763–774) was performed with egg density (eggs per 20 plants) transformed $(Y + 0.5)^{1/2}$ as the dependent variable. Pheromone trap catch, field size (ha), and plastochron index were tested for significant relationship with egg density, as were three factors associated with the probability of finding a more suitable host—the hectares of available older corn, the distance (m) to the closest older cornfield (transformed $X^{1/2}$), and the mean distance (m) to all older cornfields (transformed $X^{1/2 1}$) (see Table 1). The distance between fields was measured from the center of each field. Independent variables entered the regression model if $P \leq 0.05$, but were dropped if $P > 0.05$ when an additional variable was added. This prevented less-significant, collinear variables from being retained. The cornfield planted first in each year was excluded from the regression analysis, because the last two independent variables listed above could not be calculated. In addition, the discarded pheromone trap data during 1986 prevented three observations from being included in the analysis.

The survival data of Gross et al. (1976) were analyzed to compare the relationship between egg density and plant age with the relationship between larval survival and plant age. For our analysis, their data on percentage of larval survival were first transformed using arcsine $Y^{1/2}$. These transformed values, and the midpoint of each of their "number of leaves" age class, then were standardized by subtracting the mean and dividing by the standard deviation to eliminate the influence of each variable's scale (Sokal & Rohlf 1981). Standardized percentage of survival then was regressed on standardized plant age. Similarly, the transformed egg densities and plastochron index values in the present study also were standardized. Multiple regression (PROC REG; SAS Institute 1985, 655–709) of standardized egg density on standardized plastochron index and the distance to the closest older cornfield then was performed. The standard partial regression coefficient of egg density on plastochron index was compared with the standard regression coefficient of percent survival on plant age.

Results

Densities of *H. zea* eggs in whorl-stage corn (Table 1) increased with increasing plastochron index during 1986 and 1987 (Table 2). Because the suitability of whorl-stage sweet corn for larval development also increases with plant maturity (Gross et al. 1976), our finding of a positive correlation between egg density and plant maturity conforms to our expectation of how optimally ovipositing *H. zea* females ought to behave (Jaenike 1978).

Of the three independent variables associated with the probability of finding a more suitable host, the distance to the closest older cornfield explained the greatest amount of variation in egg density and was significant in 1986 and 1987 (Table 2). Therefore, in this insect–host system, the probability of the insect finding a more suitable host was more closely associated with the distance to the closest older cornfield rather than with the mean distance to (or the total area of) all older cornfields.

Egg density was not significantly related in either year to pheromone trap catch or field size when the plastochron index and the distance to the closest older cornfield were included in the model. The wide range of field sizes in 1986 (Table 1) should have permitted the detection of an association between field size and egg density if one existed. Although the size of the host patch has been reported to affect the density of phytophagous insects variously, most studies (see Kareiva 1983) have dealt with patch sizes much smaller than those encountered in this study. The large monocultures of commercial agriculture may diminish any possible influence of patch size on *H. zea* oviposition behavior.

Differences in oviposition behavior between the two study sites were evident. As a result of the partial R^2 values (Table 2), the distance to the closest older cornfield explained more variation in egg density than did the plastochron index during 1986. The opposite was true in 1987, although the difference was not as great. With the average distance between cornfields greater at the Irvine Ranch in 1986 than at Osumi Farms in 1987, the probability of female moths finding more suitable hosts may have been a greater factor influencing oviposition behavior than field maturity.

The relationship between oviposition and host suitability also was different between the two study sites. The standard partial regression coefficient of egg density versus plastochron index in 1986 (0.37 ± 0.11 [SE]) was much smaller than the standard regression coefficient of percentage of larval survival versus plant age (0.83 ± 0.18 [SE]; $F = 22.58$; df = 10; $P = 0.001$). Because egg density increased at a lower rate with increasing plant maturity than did larval survival, substantially more oviposition occurred on less suitable hosts during 1986. In contrast, the standard partial regression coefficient of egg density versus plastochron index in 1987 (0.69 ± 0.14 [SE]) was similar to the standard regression coefficient of percentage of larval survival versus plant age, indicating that oviposition was more closely related to host suitability during 1987.

Discussion

Kareiva (1982) reported that the flea beetles, *Phyllotreta cruciferae* (Goeze) and *P. striolata* (F.), have greater foraging discrimination between crucifer patches of varying quality as the distance between patches decreases. In addition, the more mobile *P. cruciferae* was better able to discriminate patch quality than *P. striolata*. Our results with *H. zea* are similar to Kareiva's; in particular, the high degree of mobility of *H. zea* permitted discrimination between host patches (fields) of varying quality (maturity), and this discrimination decreased with increasing interfield distance. Kareiva also indicated that herbivore movement was greater in patches that were close together because the patches served as "stepping-stones," but that such intermediate crucifer patches would not be required by the strong flying *Pieris rapae* (L.). However, the strong flying *H. zea* also may move sequentially through host patches of increasing quality, because oviposition in this study decreased with decreasing distance to the closest more suitable host patch. Although *H. zea* that are ovipositing may not require intermediate patches for traversing large distances, movement into a more suitable field may place the insect closer to, and therefore increase the likelihood of movement into, a field of even greater suitability.

Dependence of oviposition by *H. zea* on host suitability and the probability of finding more suitable hosts have significance to pest management as well as to ecological theory. For example, sampling effort could be concentrated in fields that are isolated from more suitable hosts and therefore have a greater likelihood of containing pest densities above the economic threshold. However, the low R^2 values in this study (Table 2) preclude accurate prediction of egg density using these models.

Another implication of our results is that they may help explain the sporadic outbreaks of *H. zea* in crops that are normally not infested. In southern California, *H. zea* has been a sporadic pest of strawberries. During at least one of the outbreaks, unusually high spring temperatures may have caused emergence from overwintering pupae before more suitable hosts (corn and tomatoes) became available. This could have forced oviposition on strawberries, a crop not normally infested by *H. zea*.

An additional application involves the use of a trap crop, whereby the density of a highly mobile insect pest is decreased in a crop by the occurrence of a more suitable host nearby (Kennedy & Margolies 1985). In our study, nearby fields of older corn acted as a trap crop by reducing *H. zea* density in fields of whorl-stage corn, although this reduction was not of practical value. Similarly, corn has been observed to reduce *H. zea* density in nearby tomatoes (Roltsch & Mayse 1984). Using corn as a trap crop to protect strawberries from *H. zea* has received limited attention from growers in southern California.

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