Within-plant Distribution of Predators on Cotton: Comments on Sampling and Predator Efficiencies

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Within-plant Distribution of the Immatures of *Heliothis zea* (Boddie) on Cotton

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Fruit Predation Submodel: *Heliothis* Larvae Feeding Upon Cotton Fruiting Structures

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Within-plant Distribution of Predators on Cotton: Comments on Sampling and Predator Efficiencies (Wilson and Gutierrez)

Within-plant distribution of four predators found in California cotton fields is described. Adult stages of all predators were found in greatest frequency in the terminal portions of the plant, and, within that region, adults tended to be more common on fruiting parts than the same species of larvae. In general, the smaller predators, *Geocoris* and *Orius*, were found higher on the plant than the larger predators *Chrysopa* (larvae) and *Nabis*. Their respective areas of activity corresponded to the location of suitably sized (stages) prey. Those predators closest to the plant terminal were more effectively sampled with the standard University of California sweepnet.

Within-plant Distribution of the Immatures of *Heliothis zea* (Boddie) on Cotton (Wilson, Gutierrez, and Leigh)

A detailed study of the within-plant distribution of cotton bollworm (*Heliothis zea* (Boddie)), its eggs and larvae, was conducted in the field, and sampling schemes for them were developed.

The average location of bollworm eggs was approximately one-third of the distance in nodes from the terminal, while older larvae were found lower on the plant than younger larvae. The sampling scheme for bollworm eggs relies on the finding that the mainstem leaves are the preferred oviposition site. Field observations indicate that early first instar larvae can be detected in squares by the presence of frass and the flaring of the bracts. These criteria are used in a suggested sampling scheme for first-through-third instar larvae.

Fruit Predation Submodel: *Heliothis* Larvae Feeding Upon Cotton Fruiting Structures (Wilson and Gutierrez)

Field and laboratory data on the numbers and age distribution of two varieties of cotton fruits, the association of various-age bollworm larvae (*Heliothis zea* (Boddie)) and various age fruit, as well as the attack rates of the larvae on the fruits were used to develop a submodel describing predation of bollworm larvae on cotton fruits. The submodel will be used in the coupling of bollworm- and cotton-plant population models. This model is an important step in the development of dynamic economic threshold levels for bollworm in cotton.

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Fruit Predation Submodel:
Heliothis Larvae Feeding Upon
Cotton Fruiting Structures[1,2]

INTRODUCTION

THERE IS AN INCREASED AWARENESS in pest management that the interactions of pests and crops are poorly understood and that the static concept of the economic injury level (Stern *et al.* 1959) fails to consider adequately the changing susceptibility to damage as plants develop, the multiplicity of biological interactions as modified by weather, and other physical factors. Only recently has the technology for handling these complexities become available (Gutierrez *et al.* 1975, 1976, 1977; Fick and Liu 1976; Brown, Jones, and Harris 1976; and Wang *et al.* 1977).

In this study a submodel is developed to link a population model for cotton *(Gossypium hirsutum* L.) (Gutierrez *et al.* 1975 and Wang *et al.* 1977) and a population model for bollworm *(Heliothis zea* (Boddie)) (Wang and Gutierrez, in progress; Wilson, in progress). An attempt is made to incorporate and mathematically represent the dominant factors that determine the numbers and ages of cotton fruits attacked by bollworm larvae at any stage of the crop's growth and development.

METHODS

All data required to develop the bollworm predation submodel were collected in the field and numerically categorized as follows:
1. Numbers and ages of fruit that occur through the season.
2. Feeding patterns of different-age larvae through the season.
3. Duration of feeding times of different-age larvae on different ages of fruit.
4. Percent of larvae (by age class) that feed on the same fruit following a molt.
5. Percent damaged shed fruit at their different ages.
6. Percent lint loss in damaged bolls of different ages.

Studies of data categories 1 and 2 were conducted in 1974 at Shafter, California; data categories 1 through 6 were conducted at both Corcoran, California, in 1975, and at Costa de Hermosillo, Sonora, Mexico, in 1976.

Acala SJ-1 was grown during 1974, Acala SJ-2 during 1975, and Deltapine Smooth Leaf during 1976. The numbers and sizes of fruits on the plants were recorded by mainstem and branch node throughout the season to provide detailed information on

the growth patterns of the plant. Branches were identified as being either primary (sympodial) or vegetative (monopodial). During 1974, four sets of six one meter-row samples (all plants of 1 meter) of cotton were examined on each of six sampling dates during the season, but only five plants were taken three times per week during the 1975 and 1976 seasons. In addition, dry matter accumulation estimates were obtained for the various plant parts during 1975-76 (c.f. Gutierrez *et al.* 1975).

Daily observations were made on the feeding habits of bollworm larvae at different ages feeding on various ages of cotton fruits. The duration of feeding times and the numbers and ages of fruits attacked were also recorded. Total number of fruit in the different age (size) classes consumed by different groups of 100 same-age larvae during their instar period in the set of m experiments can be described by [1].

$$T_{j1} = b_{1j}F_{11} + b_{2j}F_{21} + \cdots + b_{nj}F_{n1}$$

$$T_{j2} = b_{1j}F_{12} + b_{2j}F_{22} + \cdots + b_{nj}F_{n2} \qquad [1]$$

$$\vdots \qquad\qquad\qquad\qquad \vdots$$

$$T_{jm} = b_{1j}F_{1m} + b_{2j}F_{2m} + \cdots + b_{nj}F_{nm}$$

, where T_{jk} is the average instar period in degree days (D°) of the jth age larvae in each kth of m experiments, F_{ik} is the number fruit of age i attacked by the 100 larvae of age j, and the various b_{ij} are the feeding times of jth age larvae of ith age fruit. T_{jk} and F_{ij} were estimated from field observations, but the b_{ij} were estimated by solving the set of equations [1]. The resultant matrix [2] need not be square.

$$\vec{T} = B \cdot \vec{F} \qquad [2]$$

Calendar time was converted to D°. (Campbell *et al.* and Frazer and Gilbert 1976). The thermal threshold of 11.6 °C was estimated from laboratory experiments, wherein groups of 20 larvae were reared individually on artificial diet in each of four constant-temperature cabinets (Wilson, unpublished data).

For the 1974 and 1975 studies, larvae collected on corn near Bakersfield and Corcoran, California, respectively, were allowed to complete development on artificial diet and later used in the field tests. During 1974 adult females were confined in field cages on meter-row sections of field cotton for oviposition, and their eggs were allowed to hatch. In the 1975 studies larvae were reared on artificial diet, and at various ages larvae were placed on the terminals of cotton plants. During the 1976 season, natural infestations of bollworm were observed. Data from the 1974 and 1975 experiments (artificial infestations) and the 1976 experiments (natural infestations) were similar.

Meteorological data for each site were provided by the USDA Cotton Research Station, Shafter, California, 1974; J.G. Boswell Ranch, Corcoran, California, 1975; and CIANO, Costa de Hermosillo, Sonora, Mexico, 1976. The CIANO station was approximately 17 miles northeast of the research plot.

RESULTS

The first part of this section provides supporting field evidence for the assumptions in the submodel, while the second part formulates it.

Field results

Fruit-age preference.—Figure 1 shows the relationship between fruit mass and age for individual Acala SJ-2 and Deltapine Smooth Leaf fruit. Each point represents a sample of twenty fruits that were tagged when first visible and of estimated 50 degree days (D°) of age, or as yellow flowers of age 520 D°. The Acala bolls were 1.44 times larger than Deltapine bolls, a fact that should be kept in mind in the following discussion.
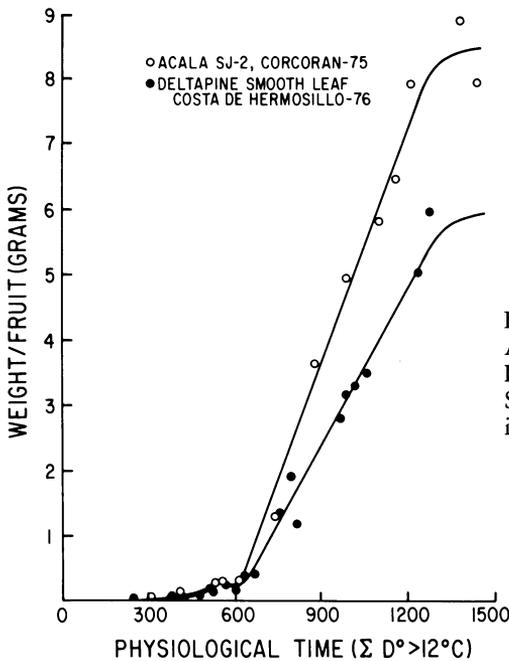

Fig. 1. Comparison of the growth patterns Acala SJ-2 (Corcoran, California, 1975) and Deltapine Smooth Leaf (Costa de Hermosillo, Sonora, Mexico, 1976) fruits. The time scale is in degree days (D° above 12 °C).

Figure 2a presents the proportion of fruit in each age category that was attacked by each larval instar during 1976 at Hermosillo, Mexico. Two general points can be made: 1) older larvae attack older fruits (Fig. 2a), and 2) all larval stages attack progressively older fruits late in the season (see Fig. 2b for first and fifth instar results). The shift in age preference late in the season reflects to some degree the shift in age structure of the fruit population. Note that the oldest bolls were rarely attacked (Fig. 2c). The results shown in Figures 2a-c are not general; rather they summarize counted observations. Interactions of bollworm and fruit populations, both in various densities, result in a wide variety of outcomes—thus aptly demonstrating the need for a general predation submodel to predict their interactions.

Larval feeding times.—As larvae grow, their consumption rates increase. The influence of fruit size on the feeding times of fourth and fifth instar larvae on Acala and Deltapine varieties are compared in Figure 3. The reciprocal of the slope of the forced regression is 1.59 (Fig. 3) and is the ratio of the average feeding time by the same age

larvae on equal-age Acala and Deltapine fruit (t_A/t_D). This ratio compares favorably with the ratio of their mass (1.44). As expected, a longer time was spent feeding on the large Acala fruits, which may explain why bollworm larvae damaged more Deltapine fruits than Acala fruits during equivalent time periods (see Table 1). Larvae occasionally fed on the same structure for more than one instar, especially when the damage inflicted was slight (e.g., first and second instar larvae feeding on medium and large squares or fouth instar larvae feeding on medium and large bolls).
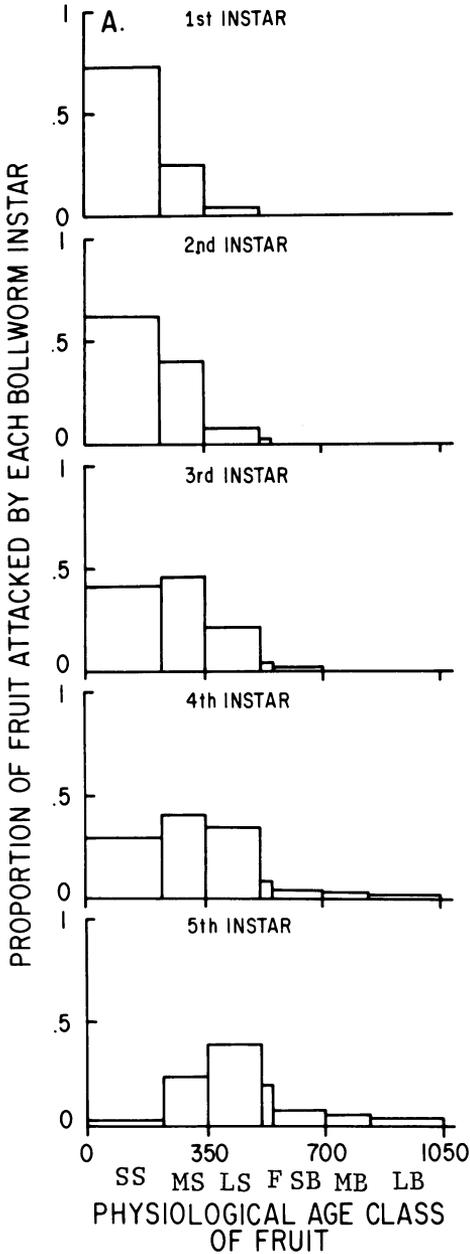
Fig. 2A to C. (B and C follow on page 28.) A (left). Proportion of attacks by each instar (seasonal average) on each age class of cotton fruit.
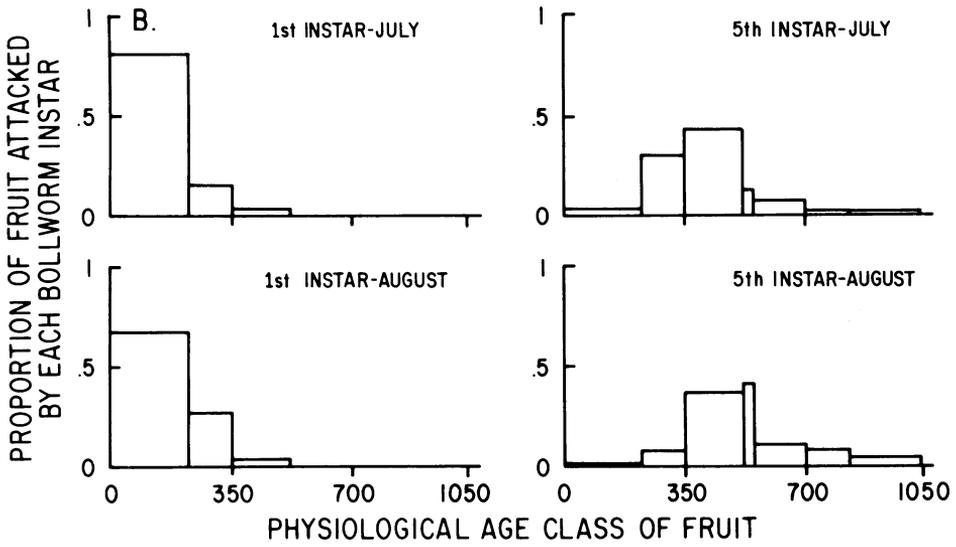
B. Proportion of 1st and 5th instar larvae attacks on each fruit age class for July and August. C. The proportion of fruit in the various age categories for July and August. (Deltapine cotton, Costa de Hermosillo, Sonora, Mexico, 1976). The SS, MS, LS and SB, MB, LB are small, medium and large squares and bolls respectively, and F is the flower stage.
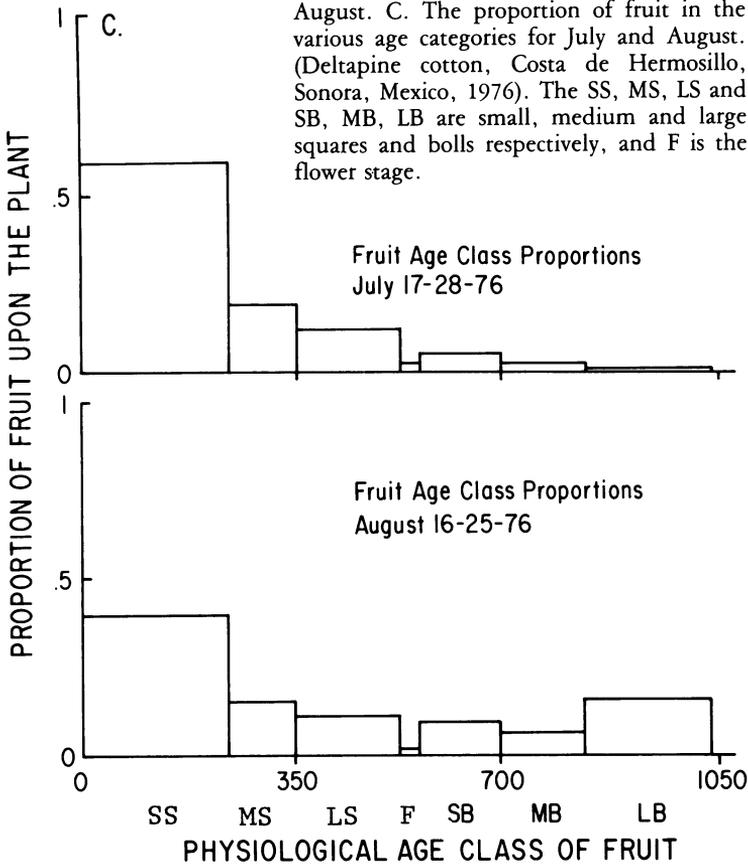
Table 1.

AVERAGE NUMBER OF SQUARES AND BOLLS CONSUMED DURING INSTAR PERIOD

| Instar*	Acala SJ-2, 1975		Deltapine Smooth Leaf, 1976	
	Date of observation	Number damaged	Date of observation	Number damaged
1st	6/25–30	1.172	7/17–28	0.974
	7/1–2	1.143	8/16–25	1.054
2nd	6/25–7/2	1.252	7/17–28	1.337
	7/28	1.257	8/16–25	1.267
	9/2–8	1.176		
3rd	7/28–30	1.547	7/17–28	3.128
	8/7	1.534	8/16–25	2.674
	9/2–8	1.458		
4th	7/28–30	2.590	7/17–28	4.667
	8/7–13	2.319		
	9/2–8	1.957		
5th	7/28–30	4.629	7/17–28	8.661
	8/7–13	3.252		
	9/2–8	2.285		

*When larvae feed upon the same structure for more than one instar period, the feeding damage is attributed to the later instar.
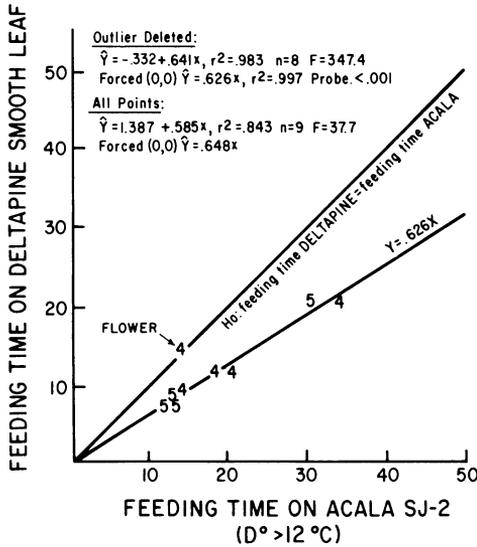
Fig. 3.   Regression of feeding time on Deltapine Smooth Leaf at Costa de Hermosillo, Sonora, Mexico, 1976, against feeding time on Acala SJ-2 at Corcoran, California, 1975. Time was recorded in minutes.

Table 2a-b summarizes the feeding times of the five bollworm instars on different sizes (ages) of Acala and Deltapine fruits, while Table 3a-b presents estimates for the probabilities that fruit of a particular age will shed when attacked by particular-age bollworm larvae.

To determine the proportion of fruit shed induced by larval feeding also required that we estimate shedding caused by plant carbohydrate stress, (i.e., when carbohydrate demand is greater than its supply). In early summer before plant stress occurs, first instar larvae were observed feeding upon squares, and the proportion of damaged fruit shed were determined. Estimates made later in the season for older lar-

vae were compounded by plant stress. But observations made in the field indicated that squares which will shed due to physiological stress can usually be identified two to three days in advance of shedding by their pale color and slight flaring of the bracts. Furthermore, bollworm larvae rarely fed on them. Hence, the two effects could be separated.

Table 2.

TWO STUDIES OF AVERAGE DURATION OF FEEDING IN DEGREE DAYS (D°)SPENT ON COTTON FRUIT BY DIFFERENT INSTARS OF BOLLWORM LARVAE

Instar	A. Feeding time (D°) on structure type* (Acala SJ-2, Corcoran, Calif., 1975)						
	SS	MS	LS	F	SB	MB	LB
1st	—	40.5	45.7	45.7	—	—	—
2nd	—	32.7	24.1	22.1	—	—	—
3rd	—	24.8	25.1	18.9	25.8	—	—
4th	—	13.3	19.3	13.2	17.6	32.8	28.7
5th	—	—	10.9	10.9	9.9	25.8	25.9

Instar	B. Feeding time (D°) on structure type* (Deltapine Smooth Leaf, Costa de Hermosillo, Sonora, Mexico, 1976)						
	SS	MS	SL	F	SB	MB	LB
1st	42.2	44.1	45.7	—	—	—	—
2nd	22.3	24.1	32.1	—	—	—	—
3rd	10.6	14.3	19.4	—	—	—	—
4th	6.3	8.6	11.6	13.9	11.3	19.8	—
5th	—	4.4	6.1	7.3	5.9	17.2	—

*The second letter (S, F, or B) denotes square, flower, and boll, respectively; the first letter (S, M. L) denotes small, medium and large, respectively—thus SS = small square.

Table 3.

TWO STUDIES OF PROPORTION OF FRUIT THAT SHED WHEN DAMAGED BY *HELIOTHIS ZEA (BODDIE)*

Instar	A. Structure type (Acala SJ-2, Corcoran, California, 1975)						
	SS	MS	LS	F	SB	MB	LB
1st	.75	0	0	0	—	0	0
2nd	1.00	0.50	0	0	—	0	0
3rd	1.00	0.89	0.68	0	0.67	0	0
4th	1.00	1.00	1.00	0.50	1.00	1.00	0.68†
5th	1.00	1.00	1.00	1.00	1.00	1.00	0.0 *

Instar	B. Structure type (Deltapine Smooth Leaf, Costa de Hermosillo, Sonora, Mexico, 1976)						
	SS	MB	LS	F	SB	MB	LB
1st	1.00	0.85	0.67	0	—	0	0
2nd	1.00	0.96	0.82	0	—	0	0
3rd	1.00	0.96	0.91	0	—	0	0
4th	1.00	1.00	0.99	0	1.00	1.00	1.00
5th	1.00	1.00	1.00	1.00	1.00	1.00	1.00

*Percent lint loss ≃ 2 × D°>12°C, overall lint loss average was 74 percent.
†Equals the overall lint loss average for all large bolls damaged by 4th instar larvae.

Damaged squares (age 221 to 520 °D), 50 shed, and 48 retained for at least 4 days after termination of feeding, were dissected to determine the cause of shedding. Damaged squares which will shed normally do so before 4 days under dry desert conditions. The only readily observable difference between shed and retained squares was that the carpel wall of 48 out of 50 shed squares had been penetrated. Two shed squares without carpel damage were otherwise extensively damaged by multiple entry points.

Of 1,390 fruit which were attacked by first through third instar larvae, only four were bolls. Of 4,541 fruit attacked by all instars during 1975 and 1976, only 475 were bolls ($<$10%). All larval stages prefer to attack squares and flowers (Quaintance and Brues 1905; Kincade, Laster, and Brazzel 1967; Tanskiy 1969; and Baldwin *et al.* 1974); hence, the common name bollworm is a misnomer.

While bolls are not preferred, damage to bolls by large larvae is very obvious and can be of considerable economic importance. This damage can be put into perspective by comparing the maximum 0.25 gram dry matter and 520 °D investment lost when a large square is destroyed, compared to 8.5 grams and 1040 °D (i.e., Acala variety) lost when a large boll is completely destroyed.

The percent lint loss (ϕ) caused to Acala bolls by fifth instar larval feeding for varying feeding period (t) may be summarized in Equation 3.

$$\phi = \begin{cases} 10.44 + 2.96t^* & 0 < t \leqslant 30.3 \ D° \\ \\ 100 & 30.3 \ D° < t \end{cases} \quad [3]$$

The relevant regression statistics are $r^2 = .564$, $n = 10$ and $.01 < P < .05$.

Saprophytic fungi which enter bolls at the wound cause additional damage. This loss may be particularly severe under conditions of high relative humidity as was observed during the 1976 season.

A frequency-dependent predation equation

Bollworms exhibit changing preferences for various-age fruits as the age distributions (of the larvae and fruits) and strata within the plant change. Preferences are measured as changes in the proportion of fruits attacked in each age class by the various-age larvae.

At any stage of the crop's growth, we can sample the fruit population and estimate the proportion of fruits in each age class (A_i, where $i = 1,7$). Because the fruits and the larvae are more likely found in some strata than in others, the A_i do not represent the actual availability of the fruits to the various age larvae. The actual availability of fruits (F_{ij}) of age i to the jth stage larvae were also estimated in the field by counting the fruits by age on fruiting branches containing j^{th} age larvae. We must assume that all of the fruit on the branch are equally exposed to the larvae (usually 1) on the branch. We further assume that there is a relationship between F_{ij} and A_i for each larval stage. Because we know F_{ij} and A_i from field samples, and $\Sigma F_{ij} = 1$ for each jth age larvae and $\Sigma A_i = 1$, we estimated the coefficients C_{ij} of that relationship by $F_{ij}/A_i = C_{ij}$. All within-instar-across fruit values (C_{ij}) (seven of them) were adjusted as a fraction of the maximum one (i.e., $0 < C_{ij}^* = C_{ij}/C(max) < 1$, where C_{max} is the largest of the set of C_{ij}, $i = 1$, $2 \cdots 7$). Similar computations were performed for the other j^{th} age larvae. The C_{ij} in

this case equal a composite fruit availability by larval age and plant strata. Thus we see that the relationship between F_{ij} and A_i is described by equation 4.

$$F_{ij} = C^*_{ij}A_i / \sum_{i=1}^{7} C^*_{ij}A_i \qquad [4]$$

If the jth instar larvae were randomly stratified over the plant, equation 4 would collapse to $F_{ij} = A_i$ with all of the C_{ij} values equal to 1 for that instar.

Of course, the larvae in each age class prefer some age fruits more than others, and this preference must be included in equation 3. Equation 4 shows the relationship between the proportion of attacks by the jth instar larvae against the ith fruit age class (P^{ij}), and the actual fruit age class availability (F_{ij}). Preference (S_{ij}) is estimated in a manner similar to the computations for C^*_{ij} (equation 4). Estimates of P_{ij} are taken from field data.

$$\hat{P}_{ij} = S_{ij}F_{ij} / \sum_{i=1}^{7} (S_{ij}F_{ij}) \qquad [5]$$

The maximum S value is determined by the same method used in Equation 4, except in this case the maximum P_{ij}/F_{ij} value is used. A little algebra shows that the fully expanded form of [5] is [6]

$$\hat{P}_{ij} = S_{ij}C^*_{ij}A_i / \sum_{i=1}^{7} (S_{ij}C^*_{ij}A_i) \qquad [6]$$

Tables 4a-b and 5 a-b present computed values for S and $\overset{*}{C}$ for 1975–1976 for all ages of fruit and larvae. In general, older larvae are located lower on the plant (i.e., $\overset{*}{C} \rightarrow$ 1 for older fruit) and they prefer mature squares and flowers (i.e., S → 1). The differences observed between Acala and Deltapine varietes are partially due to differences in their growth characteristics (fruit size, internode lengths, and the like), but plant density appears to have some effect. This latter effect was examined in a qualitative manner but was not incorporated into the model. Table 6 compares the $S_{ij} \cdot \overset{*}{C}_{ij}$ values ($0 \leq$ SC ≤ 1) averaged for the total larval period for squares, flowers, and bolls at three planting densities (6.38, 11.95 and 3.83) during 1974-76, respectively. Note that as planting density decreased, the square stage was increasingly preferred (i.e., SC_s/SC_b ratio increases, where the subscript s is for squares, and b is for bolls). When cotton was grown at high planting densities, as with the 1975 Acala study, the number of branch nodes decreases, and fewer fruit are produced per plant (see also Gutierrez *et al.* 1975). Under these conditions, larvae travel further between successive feeding sites. Larvae older than the second instar normally move down the plant (Wilson, unpublished data); hence, at higher densities the probability of larvae feeding on older fruit is enhanced. (C values increase for older fruit at higher densities).

Comparison of model prediction and field results.—The applicability of the fruit-predation equation would be severely limited if new S_{ij} and C_{ij} values have to be calculated through the season. A series of Kolmogorov-Smirnov tests (Zar 1974), using Equation 6 to provide expected values for the proportion of fruit attacked by the different instars of bollworm, were performed on the 1975 and 1976 data (Table 7). For values of n greater than 160, Equation 7 presented by Smirnov 1939 (in Zar 1974), was used to estimate critical values for the test statistic.

$$D_\alpha = \sqrt{\frac{\ln 1/\alpha}{2n}}$$ [7]

Table 4.

TWO STUDIES OF COMPUTED LARVAL FOOD PREFERENCE VALUES (S_{ij}) FOR THE VARIOUS AGE FRUITS

Instar	A. Structure type (Acala SJ-2, Corcoran, California, 1975)						
	SS	MS	LS	F	SB	MB	LB
1st	0.5088	1.0	0.4564	0	0	0	0
2nd	0.2476	1.0	0.5032	–	0	0	0
3rd	0.2014	0.6421	0.8402	1.0	0.2170	–	–
4th	–	0.5207	0.9103	1.0	0.4685	0.3901	0.2439
5th	–	0.4620	0.7015	1.0	0.6642	0.6207	0.6501

Instar	B. Structure type (Deltapine Smooth Leaf, Costa de Hermosillo, Sonora, Mexico, 1976)						
	SS	MS	LS	F	SB	MB	LB
1st	0.6693	1.0	0.4124	0	0	0	0
2nd	0.5310	1.0	0.4071	0	0	0	0
3rd	0.3855	0.8733	0.7412	1.0	0.4119	0	0
4th	0.1050	0.5641	0.8409	1.0	0.3801	0.3783	–
5th	0.0172	0.3287	0.6701	1.0	0.6018	0.6987	0.5498

Table 5.

TWO STUDIES OF AGE SPECIFIC LARVAL STRATIFICATION COEFFICIENTS (C_{ij})

Instar	A. Structure type (Acala SJ-2, Corcoran, California, 1975)[*]						
	SS	MS	LS	FL	SB	MB	LB
1st	0.3990	0.8724	1.0	0	0	0	0
2nd	0.2403	0.7011	1.0	–	0	0	0
3rd	0.0693	0.7671	1.0	0.7555	0.3812	–	–
4th	–	0.2507	0.6414	0.8422	1.0	0.4101	0.1076
5th	–	0.0935	0.6153	0.7463	1.0	0.6072	0.2198

Instar	B. Structure type (Deltapine Smooth Leaf, Costa de Hermosillo, Sonora, Mexico[†]						
	SS	MS	LS	FL	SB	MB	LB
1st	1.0	0.6485	0.2876	0	0	0	0
2nd	1.0	0.9839	0.4894	0	0	0	0
3rd	0.7014	1.0	0.6132	0.2458	0.0884	0	0
4th	0.4790	1.0	0.9086	0.9659	0.2314	0.1004	–
5th	0.2068	0.5064	0.5719	1.0	0.1944	0.1400	0.0310

[*]Plant density equals 11.95 plants/meter-row.
[†]Plant density equals 3.83 plants/meter-row.

Table 6

COLLAPSED SC*$_{ij}$VALUES (PREFERENCE AND STRATIFICATION ON PLANT NOT
SEPARATED AND ALL INSTARS CONSIDERED TOGETHER).

Variety	Year	Plants/meter-row	Squares	Flowers	Bolls	Sq./Bl.
Acala SJ-2	1974	6.38	0.3383	1.0	0.2543	1.3302
Acala SJ-4	1975	11.95	0.2900	1.0	0.3629	0.79911
Deltapine smooth leaf	1976	3.83	0.3629	1.0	0.0616	5.8936

Table 7.

KOLMOGOROV-SMIRNOV TEST STATISTIC (GOODNESS OF FIT)
(A) $H_0 : P_{ij} = A_i$, random food preference
(B) $H_0 : P_{ij} = S_{ij}C_{ij}A_i/\Sigma(S_{ij}C_{ij}A_i)$; for:

A. Acala SJ-2, Corcoran, California, 1975.

Instar	Date	(A) Observed K-G	(B) Observed K-G	n
1	6/25–30	.05417	.04114	48
	7/1–2	.35780**	.18470	41
2	6/25–7/2	.63000**	.39640	53
	7/28	.25800	.10212	16
3	7/28–30	.44196**	.09338	31
	8/7	.42217*	.07750	12
	9/2–8	.64844**	.04013	78
4	7/28–30	.42068**	.07838	167
	8/7–13	.41596**	.08699	113
	9/2–8	.48305**	.04496	141
5	7/28–30	.57113**	.06354	48
	8/7–13	.46825**	.03622	111
	9/2–8	.14204**	.04891	110

B. Deltapine Smooth Leaf, Costa de Hermosillo, Sonora, Mexico, 1976

Instar	Date	(A) Observed K-G	(B) Observed K-G	n
1	7/17–28	.19764**	.0658	246
	8/16–25	.41566**	.02354	378
2	7/17–28	.12669**	.02529	308
	8/16–25	.41713**	.02358	369
3	7/17–28	.28197**	.09745**	427
	8/16–25	.32654**	.11500**	396
4	7/17–28	.48994**	.01759	469
	8/16–25	.30211**	.06335	128
5	7/17–28	.55546**	.02611	789
	8/16–25	.42282**	.15419**	124

**Significance level ≤ 1%.

When the S_{ij} and C_{ij} values were made equal (HO: $P_{ij} = A_i$, random food selection), 21 of the 23 analyses were significantly different, which strongly supports the notion that bollworm feeding is not random. Using the average $(S_{ij}C_{ij})$ values to estimate attack patterns (HO: $P_{ij} = S_{ij}C_{ij}A_i/\Sigma(S_{ij}C_{ij}A_i)$), 20 of the 23 analyses were not significantly different. A word of caution is in order, because the model was tested against expected averages and not against totally independent data. Nonetheless, the model is more than a reasonable fit for this large series of data. Furthermore, the similarities between the data sets collected for each of the years lead us to believe that our assumptions are adequate. These results are extremely encouraging, because they allow us to compute larval attack patterns on fruits for any stage of growth of the cotton plant and for any variety if the appropriate variety and planting-density specific C_{ij} values are used. The stage of the crop's growth must, however, be computed (c.f. Gutierrez *et al.* 1975) or estimated from field data. Further, we expect that preference (S_{ij}) and stratification (C_{ij}) values may be somewhat different for other varieties of cotton with characters such as okra leaf and/or possibly frego bract.

Effects of hunger on larval food preference.—When food becomes limiting, such as early or late in the season or under extremely high levels of infestation, P_{ij} approaches A_i for each jth age larval class. Under these conditions, larvae appear less selective and feed upon any available food source $(S \rightarrow 1$ for all age larvae). During 1974, a few experimental plots had extremely high levels of bollworm infestation (greater than 200 eggs per meter-row). The resulting larval population consumed all the fruit and then fed upon leaves and stems. In another study, an infestation of bollworm occurred in the cotton in late May of 1976, before the plants had started fruit production. Hunger made the larvae less selective and they attacked vegetative parts and destroyed 50 percent of the terminals. Similar observations have been made in Australia on *H. punctigera* feeding on Deltapine-16 cotton early in the season and at the middle of the season, when larval numbers were observed to exceed 30 per meter (Wilson, unpublished).

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