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AGE-SPECIFIC SURVIVORSHIP ANALYSIS OF *HELIOTHIS* SPP. POPULATIONS ON COTTON

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INTRODUCTION

Heliothis virescens (F.) and *Heliothis zea* (BODDIE) (Lepidoptera: Noctuidae) are important pests of cotton, *Gossypium hirsutum* (L.), and a number of other crops in the western hemisphere (KOGAN et al., 1978). In this paper we report the results of a detailed study of age-specific survivorship of eggs and larvae in naturally occurring *Heliothis* spp. populations on cotton. Our analysis includes characterization of survivorship curves, followed by the use of partial life tables to assess the influence of various factors on survivorship.

Biology of *Heliothis*

Aspects of the biology and life histories of *H. virescens* and *H. zea* have been reported in numerous articles, some of which date back more than a century (KOGAN et al., 1978). The immature stages of *H. virescens* and *H. zea* are quite similar morphologically; in fact, the eggs and small larvae are difficult to determine to species. The two species are also similar ecologically. The larvae of both species are polyphagous, with considerable overlap in host ranges. The adult moths, which are nocturnal in activity, are highly vagile. Eggs are laid singly on host plants, and a single female can lay up to 3,000 eggs during a brief adult lifespan (typically 7-10 days). The larvae prefer to feed on the fruiting parts rather than the foliage of host plants. On cotton, the larvae feed on squares (i.e. flower buds), flowers, and bolls. In the field, larvae usually pass through six instars prior to pupation (NEUNZIG, 1969), which occurs in the soil.

Details of the seasonal history of *Heliothis* spp. vary geographically; the brief description that follows will refer to Mississippi and neighboring states. Populations overwinter as diapausing pupae in the soil. There probably are four generations per year (NEUNZIG, 1969). The first generation larvae feed primarily on uncultivated hosts (SNOW and BRAZZEL, 1965); cotton is not available at this time. Larvae in the subsequent three generations feed on cotton, other crops, and uncultivated hosts.

METHODS

An intensive sampling program was conducted in a 0.5 ha plot of 'Stoneville 213' cotton during 1978 and 1979. This plot was located in Oktibbeha County, Mississippi, U.S.A. (32° 29′ N, 88° 48′ W). In 1978 sampling began on 14 June and ended 23 August; in 1979 sampling began on 12 June and ended 24 August. The cotton was planted 16 May, 1978 and 17 May, 1979. Stand density was approximately 125,000 plants per ha. or 10 plants per meter row with .91m (30 in.) row spacing for both years. No insecticide was used in the plot during the sampling period of either year. Ambient temperatures were recorded in the plot during 1978 and at a nearby weather station during 1979.

Heliothis spp. eggs and larvae, and cotton fruiting forms—squares, flowers, and bolls—were sampled by visual inspection of plants. A sample unit of 1 meter row of plants was used, except during the latter part of 1978 the unit was changed to 0.5 m. Sampling frequency was three times per week during 1978 and the second half of 1979, and twice per week during the first half of 1979. Sample size was variable, ranging from a low of 8 to a high of 36 units. Sampling effort was held reasonably constant at about 12 person hours, but the time required to inspect one unit increased with increasing plant size and *Heliothis* spp. density (extremely high *Heliothis* spp. density also was why the sample unit was halved for part of 1978). A stratified random sampling pattern with equal allocation was used; the whole plot was divided into 4 equal sized blocks and locations of samples within blocks were chosen from pairs of random numbers. Sampling was always conducted between 0800 hrs. and 1200 hrs. local time.

All *Heliothis* spp. eggs and larvae were collected during sampling, taken to the laboratory, and reared at 25°C (larvae were fed a wheat germ based artificial diet) to record days to eclosion (eggs only), parasitization, disease incidence and *Heliothis* species composition. Field collected larvae were classified to instar by measuring head capsule width (NEUNZIG, 1969) under a stereomicroscope fitted with an ocular micrometer. Larvae that were reared to the fourth instar or beyond but died before pupating were determined to species by the key in NEUNZIG (1969).

Predaceous arthropods were sampled in the plot by shaking plants over a white cloth placed between the rows, a method commonly known as the "drop cloth". Density and composition of the predator complex were recorded in the field. A sample unit of 1 meter row was used, and sample size per sampling occasion was 20 and 24 in 1978 and 1979, respectively. Sample frequency was at least twice weekly in both years, except that no drop cloth samples were taken between 6 and 17 July, 1979, due to unusually wet field conditions. Sampling pattern was similar to but independent of the pattern used in visual sampling. The drop cloth sampling method is practical only after plants have reached approximately 0.5 m in height. Thus predator densities were recorded during visual sampling until plant height was sufficient for drop cloth sampling: 22 June in 1978 and 26 June in 1979.

RESULTS

Estimation of stage recruitment

The *Heliothis* population dynamics recorded during the two years of study are shown in Fig. 1 (1978) and Fig. 2 (1979). There was variation between years in both population density and phenology. Densities were much higher in 1978 than in 1979 (note the different scales in Figs. 1 & 2). Two complete generations of eggs and larvae were observed in cotton during both years, but they were more distinctly separated in 1979 than in 1978. A partial third generation was observed in 1978, but it was not completed due to host plant senescence.

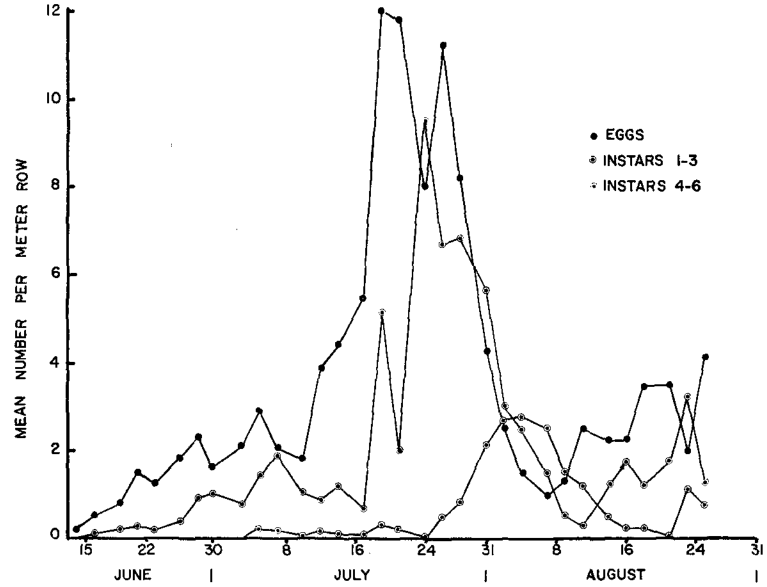

Fig. 1. Population trends of *Heliothis* spp. eggs and larvae during 1978.

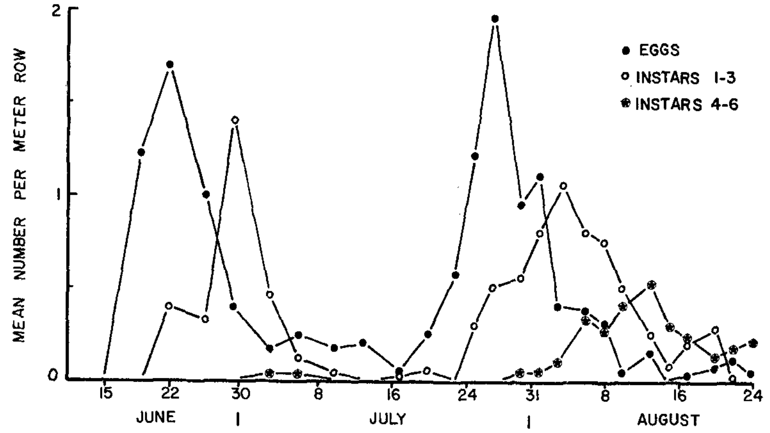

Fig. 2. Population trends of *Heliothis* spp. eggs and larvae during 1979.

Table 1. Mean stage durations in day-degrees above 12.6°C for *Heliothis* spp. eggs and larval instars.

Stage	*H. virescens*	*H. zea*	Pooled
Egg	40.5	40.5	40.5
Instar 1	33.1	37.3	35.2
Instar 2	25.4	29.9	27.7
Instar 3	27.5	29.1	28.7
Instar 4	30.0	33.0	31.5
Instar 5	39.9	44.2	42.1
Instar 6	69.3	65.4	67.3

Recruitment for the eggs and six larval instars for each complete generation were estimated by the graphical method (SOUTHWOOD and JEPSON, 1962). The graphical method estimates stage recruitment by dividing the area under the population curve of the stage by the mean developmental time of the stage. This analysis was conducted for the pooled populations of *H. virescens* and *H. zea.* The developmental times of *Heliothis* eggs and larval instars (Table 1) were measured in day-degrees, rather than days, to neutralize the effects of variable field temperature patterns. The day-degree model assumes a linear relationship between developmental rate and temperature above a "developmental threshold" or base temperature (CAMPBELL et al., 1975). For *Heliothis,* a base temperature of 12.6°C has been found to be realistic (HOGG and CALDERON, 1981) and was used here. Data in Table 1 are presented for each species separately and for the average of the two. Egg developmental times were taken from HARTSTACK et al. (1973); eggs of the two species have virtually identical incubation periods. Instar periods were estimated for larvae reared on cotton squares and bolls at 25°C, and were transformed to the day-degree scale reported by HOGG and CALDERON (1981). Although mean larval developmental times and instar periods of the two species differ slightly, the differences had little effect on recruitment estimates; thus the developmental times averaged for the two species were used to compute recruitment.

Estimates of stage recruitment (number per meter row per generation) for each of the generations are given in Table 2. The variation in population density between years is reflected in the estimates of recruitment; for example, Generation 2 egg recruitment was an order of magnitude larger in 1978 than in 1979. Our efficiency in sampling 1st instar larvae was quite poor due to the small size of these larvae and their tendency to be concealed within small folds of terminal plant tissue; thus estimates of 1st instar recruitment were not included in the analysis of survivorship.

The magnitude and within-stage distribution of mortality can influence the accuracy of the graphical method (SOUTHWOOD, 1978). However, comparison of egg recruitment estimated by the graphical method and by an independent method for 3 of the 4 data sets suggests that the graphical method was reasonably accurate for our data (Table 2). The independent method was based on estimates of egg re-

Table 2. *Heliothis* spp. stage recruitment estimates (no./meter row).

Generation	Stage	Graphical Method	Independent Method
1978-1	Egg	16.38	
	Instar 2	5.68	
	Instar 3	2.99	
	Instar 4	0.40	
	Instar 5	0.64	
	Instar 6	0.05	
1978-2	Egg	61.61	64.66-80.59
	Instar 2	18.01	
	Instar 3	11.48	
	Instar 4	5.76	
	Instar 5	4.11	
	Instar 6	2.21	
1979-1	Egg	4.97	4.12-6.57
	Instar 2	2.22	
	Instar 3	1.13	
	Instar 4	0.14	
	Instar 5	0.00	
	Instar 6	0.00	
1979-2	Egg	6.04	5.73-6.36
	Instar 2	2.20	
	Instar 3	1.49	
	Instar 4	1.22	
	Instar 5	0.65	
	Instar 6	0.29	

cruitment for the evening preceding each sampling occurrence. Eggs deposited the previous evening were separated from older eggs based on incubation time. Since *Heliothis* oviposition is a discrete (nocturnal) activity, incubation time in the laboratory provided an unambiguous criterion for determining the evening on which an egg had been deposited. Recruitment for days falling between samples were estimated by interpolation, and generation recruitment was calculated by summing over all days. However, some of the eggs collected either failed to hatch or were parasitized by *Trichogramma* spp., and therefore could not be aged. Thus two independent recruitment estimates were computed: the lower estimate includes only those eggs that hatched, and the upper estimate includes a proportion of non-hatching or parasitized eggs based on the age structure of hatching eggs. True recruitment probably falls between the two estimates.

Estimation of recruitment variances

A limitation inherent to the graphical method is that it distills usually highly variable sample data into a single estimate of stage recruitment with no indication of the precision of the estimate. This constitutes loss of information, and it was particularly objectionable in our case since we were ultimately interested in fitting a statistical survivorship model to the data. To overcome this deficiency, we devised a Monte Carlo procedure to estimate recruitment variances. In addition to the estimates of mean stage density per sampling occurrence required by the graphical method, this procedure utilized information on the variability among samples which was contained in estimates of the variance of the mean stage density. Specifically, a computer algorithm was written which, when provided as input the sample mean and its variance for each sampling occurrence for a specific stage within a generation, would stochastically resample the data a specified number of times. Following each iteration, the newly created densities were used to compute stage recruitment by the graphical method; after the final iteration, the mean and variance of the recruitment estimates were computed. The means for each sampling occurrence were assumed to be normally distributed; however, each distribution was truncated at zero to avoid the selection of negative densities. Documentation for the computer algorithm is available from the senior author.

The results of the Monte Carlo simulations are shown in Table 3. Each pair of mean-variance estimates was computed from 1,000 iterations. Simulated means were very similar to the original graphical recruitment estimates (Table 2). More importantly, within each generation recruitment variances were not homogeneous, and in fact the variance tended to increase with the mean. The constraint placed on sampling to avoid negative population densities influenced the simulation results in at least two ways: slight overestimation of recruitment means (in all but two cases simulated means were larger than the graphical estimates), and slight underestimation of recruitment variances. However, it is unlikely that these small biases caused the mean-variance trends evident in Table 3.

Weibull distribution as a survivorship model

The Weibull frequency distribution was chosen as a statistical model to summarize the *Heliothis* survivorship data. PINDER et al. (1978) discussed the use of the Weibull distribution as a survivorship model for natural populations of animals and plants. The form of the Weibull model used by PINDER et al. is given as:

$$S_p(t) = \exp\left[-(t/b)^c\right], \qquad t, b, c > 0 \tag{1}$$

where $S_p(t)$ is the probability at birth of an individual surviving to age t, b is the scale parameter, and c is the shape parameter. This is equal to one minus the Weibull cumulative distribution function. The advantages of using the Weibull distribution as a survivorship model in an ecological context are its great flexibility and the ability to draw statistically and ecologically meaningful inferences from the model parameters. The latter point is particularly important with regard to the shape

Table 3. Simulated *Heliothis* spp. stage recruitment estimates (no./meter row).

Generation	Stage	Mean	Variance
1978-1	Egg	16.40	1.888
	Instar 2	5.76	0.566
	Instar 3	3.06	0.315
	Instar 4	0.43	0.023
	Instar 5	0.65	0.046
	Instar 6	0.06	0.002
1978-2	Egg	61.83	16.933
	Instar 2	18.05	3.966
	Instar 3	11.67	3.424
	Instar 4	5.85	1.046
	Instar 5	4.18	0.598
	Instar 6	2.24	0.157
1979-1	Egg	4.97	0.352
	Instar 2	2.24	0.156
	Instar 3	1.15	0.079
	Instar 4	0.14	0.006
	Instar 5	0.00	—
	Instar 6	0.00	—
1979-2	Egg	6.08	0.565
	Instar 2	2.23	0.161
	Instar 3	1.50	0.110
	Instar 4	1.25	0.063
	Instar 5	0.66	0.018
	Instar 6	0.30	0.007

parameter and the three basic types of survivorship curves defined by PEARL and MINER (1935): $c>1$ implies a Type I survivorship curve, in which mortality rate is an increasing function of age; $c=1$ implies a Type II survivorship curve, in which mortality rate is constant (independent of age); and $c<1$ implies a Type III survivorship curve, in which mortality rate is a decreasing function of age. The main limitation of the Weibull distribution is that it is useful as a survivorship model only if mortality rate is a monotonic function of age; preliminary analysis of the *Heliothis* survivorship data indicated that this condition was met. When mortality rate is not a monotonic function of age, it is preferable to use a model that incorporates a mixture of distributions (SILER, 1979).

In applying the Weibull model to our data, we were confronted with the problem of finding a procedure for estimating parameters and confidence intervals. In examples given by PINDER et al. (1978), survivorship was scaled from 0 to 1, with the implicit assumption that the size of the initial cohort and subsequent numbers surviving were measured without error. This assumption was clearly not tenable for our data (Table 3). We therefore developed the following "modified" Weibull survivorship model:

$$S_n(t) = a \cdot \exp\left[-(t/b)^c\right], \qquad t, a, b, c > 0, \qquad (2)$$

where $S_n(t)$ is the number (rather than proportion) of individuals surviving to age t, a is the initial cohort parameter, and b and c are as in Equation 1. The initial cohort parameter can be interpreted as recruitment into the youngest age class, in this case eggs. Addition of a third parameter does not affect interpretation of the shape and scale parameters, and it allows an appropriate initial density to be selected in the context of the overall model fit. Although an additional parameter must be estimated, one observation (egg recruitment) is added, with no net loss in degrees of freedom.

Nonlinear least squares (HELWIG and COUNCIL, 1979) using the Marquardt method was used to estimate the parameters of the modified Weibull model (Equation 2). A square root transformation was applied to the graphical recruitment estimates and to the model prior to parameter estimation to stabilize heterogeneous recruitment variances (Table 3). The Weibull parameter estimates for the survivorship curves from the four generations are given in Table 4. Standard errors shown are asymptotic estimates. For each generation the initial cohort parameter estimated for this unconstrained model was very similar to the graphical estimate of egg recruitment (Table 2). For both Generation 1 data sets the shape parameter was greater than one ($P < .05$), suggesting for these populations that mortality rate increased with age. For both Generation 2 data sets the shape parameter was essentially equal to one, suggesting for these populations that mortality rate was constant. Survivorship curves with recruitment plotted on a logarithmic scale (Figs. 3 and 4) illustrate the inferences made from the shape parameter. The Generation 1 data sets (Fig. 3) show the concave downward response typical of a Type I survivorship pattern, whereas the Generation 2 data sets (Fig. 4) show the log-linear response typical of a Type II survivorship pattern.

Table 4. Modified Weibull model parameter estimates (± standard errors) for *Heliothis* spp. survivorship curves.

Generation	$\hat{a}$	$\hat{b}$	$\hat{c}$
1978-1	16.47±2.29	71.98±5.45	1.71±0.22
1978-2	61.70±2.25	60.57±3.93	1.02±0.07
1979-1	4.86±0.43	86.86±4.43	2.97±0.42
1979-2	6.02±0.30	78.13±5.66	1.09±0.11

Heliothis species composition

In addition to analyzing pooled populations of *H. virescens* and *H. zea*, the proportion of each species sampled was determined for each life stage from each of the four generations (Table 5). A larger proportion of the population was composed

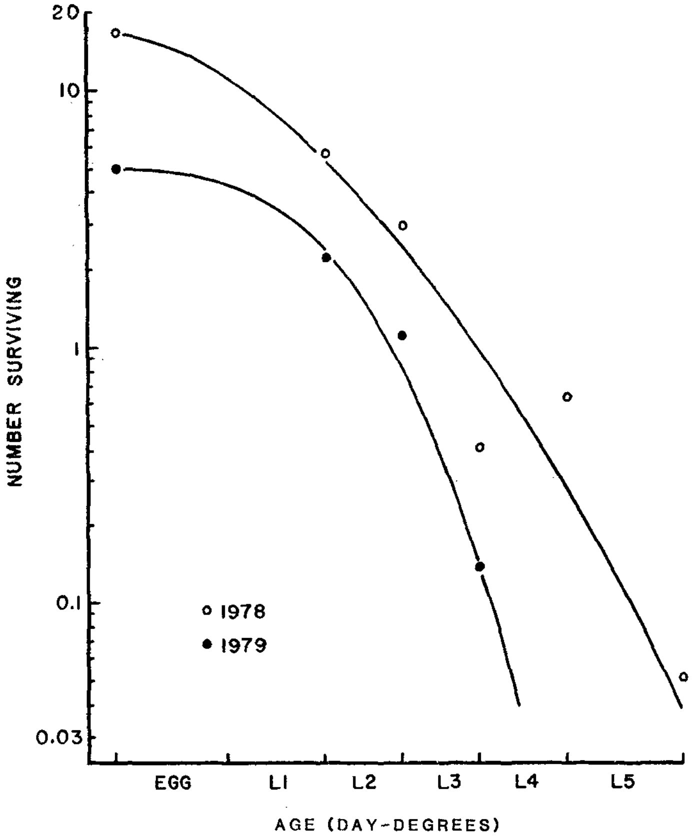

Fig. 3. Survivorship curves for *Heliothis* spp. eggs and larvae, Generation 1 data sets.

of *H. virescens* in 1978 than in 1979. During 1978 and Generation 1 of 1979, species composition was reasonably constant among stages within each generation; thus, the survivorship curves for the individual speces would be expected to be similar to those of the pooled populations. However, in Generation 2 of 1979 the proportion of *H. virescens* in the population dropped rather abruptly between larval instars 2 and 3. The mechanism responsible for this apparent shift in species composition is unknown.

We analyzed the *H. virescens* and *H. zea* populations separately for Generation 2, 1979, to determine what effect the change in species composition had on survivorship patterns. Species-specific developmental periods (Table 1) were used to estimate the respective stage recruitment values, and the modified Weibull model (Equation 2) parameters were estimated as previously described. The results (Table 6) indicate that the shape parameter was essentially equal to one for both species. This inference is identical to that made from the analysis of the pooled population (Table 4). However, the instantaneous mortality rate (which can be estimated as the reciprocal of the scale parameter when mortality rate is constant) was quite different for the

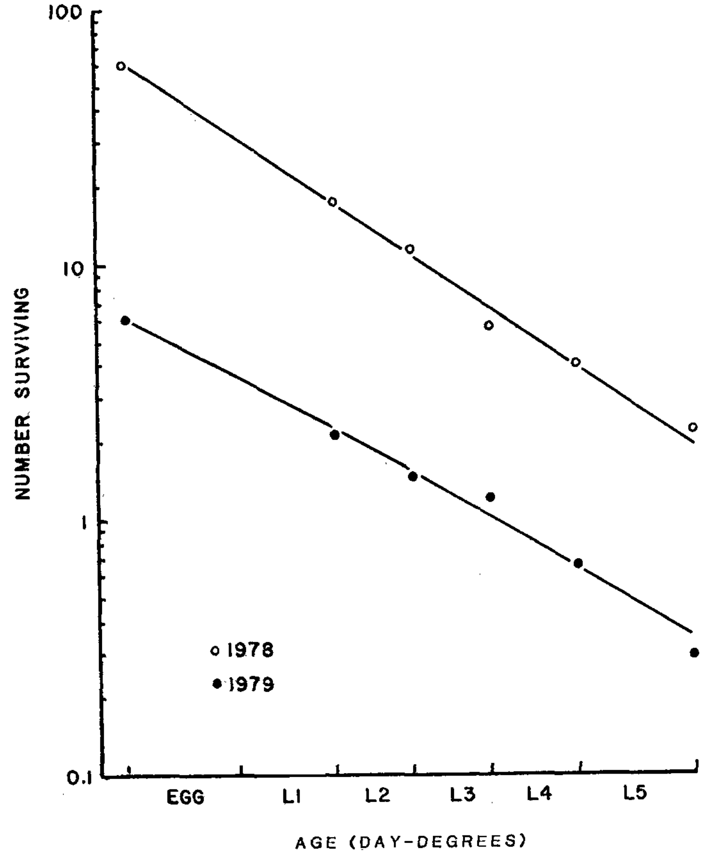

Fig. 4. Survivorhip curves for *Heliothis* spp. eggs and larvae, Generation 2 data sets.

Table 5. *Heliothis* species compositions for each life stage from each generation.

	% *H. virescens*			
Stage	1978-1	1978-2	1979-1	1979-2
Egg	99.6	89.3	88.5	61.2
Instar 1	100	94.5	78.6	53.4
Instar 2	100	91.6	81.6	54.5
Instar 3	97.7	98.2	66.4	33.1
Instar 4	100	92.0	78.6	29.8
Instar 5	100	96.8	—	37.1
Instar 6	100	92.6	—	35.3

two species: .017 for *H. virescens* and .009 for *H. zea*. Thus, only alteration of the magnitude of the mortality rate, and not alteration of the shape of the survivorship curve, was associated with the shift in *Heliothis* species composition.

Heliothis natural enemies

Populations of natural enemies of *Heliothis* eggs and larvae were monitored

Table 6. Modified Weibull model parameter estimates (± standard errors) for *H. virescens* and *H. zea* survivorship curves, Generation 2, 1979.

Species	$\hat{a}$	$\hat{b}$	$\hat{c}$
H. virescens	3.72±0.36	57.17± 9.64	1.05±0.20
H. zea	2.32±0.25	108.14±14.03	1.16±0.25

during the two years of study. These natural enemies included parasites (i. e. parasitoids) and predators; no diseased larvae (pathogens) were observed.

Parasites, all belonging to the Hymenoptera, were reared from *Heliothis* eggs and larvae; thus, parasitization was estimated directly. Egg parasites included two trichogrammatids, *Trichogramma exiguum* Pinto and Platner and *T. pretiosum* Riley. Larval parasites included two braconids, *Cardiochiles nigriceps* Viereck and *Microplitis croceipes* (Cresson), and an ichneumonid, *Pristomerus spinator* (F.).

Trichogramma spp. oviposit in and eventually kill eggs of both *H. virescens* and *H. zea*. *C. nigriceps* oviposits in larvae of both *H. virescens* and *H. zea*, but the eggs of this parasite are encapsulated by *H. zea* (Lewis and Brazzel, 1966); thus, *C. nigriceps* is effective only against *H. virescens*. *C. nigriceps* attacks 1st through 5th instar *Heliothis* larvae (Lewis et al., 1972), and parasitized larvae are killed in the 4th or 5th instar (Lewis and Brazzel, 1966). *M. croceipes* is a parasite of both *H. virescens* and *H. zea*. *M. croceipes* attacks larvae as small as 1st instar (Lewis, 1970), and we observed that parasitized larvae died in the 4th or 5th instar. *P. spinator* also is a parasite of both *H. virescens* and *H. zea*. We observed that *P. spinator* could parasitize larvae as small as 1st instar, and that parasitized larvae died in the 4th or 5th instar.

The species compositions of the larval parasites reared during each year are given in Table 7. *C. nigriceps* was the most abundant species taken during 1978, whereas *P. spinator* was the most abundant during 1979. *M. croceipes* was not taken in 1979. The decline from 1978 to 1979 in relative abundance of *C. nigriceps* may have been related to the *Heliothis* species composition (Table 5).

Table 7. Compositions of *Heliothis* spp. larval parasite complexes (percent of total for each year).

	1978	1979
Cardiochiles nigriceps	68.4	28.6
Microplitis croceipes	21.1	0.0
Pristomerus spinator	10.5	71.4

Naturally occurring populations of predaceous arthropods have been shown to play an important role in suppressing populations of *Heliothis* eggs and larvae (Fletcher and Thomas, 1943; Whitcomb and Bell, 1964; and van den Bosch et al., 1969). Unlike parasites, the mortality caused by predators usually is not amenable to direct estimation. The predator groups or species we commonly encountered included: *Geocoris* spp. (Hemiptera: Lygaeidae) nymphs and adults, primarily *G. punctipes* (SAY); *Orius insidiosus* (SAY) (Hemiptera: Anthocoridae) nymphs and adults; nabid (Hemiptera: Nabidae) nymphs and adults, a complex probably composed of six species (HORMCHAN et al., 1976); *Chrysopa* spp. (Neuroptera: Chrysopidae) larvae; coccinellid (Coleoptera: Coccinellidae) larvae and adults, which included *Coleomegilla maculata* (DEGEER) and *Hippodamia convergens* (GUERIN-MENESVILLE); and spiders (Araneida), which included at least four families (Argiopidae, Oxyopidae, Salticidae, and Thomisidae) and numerous species.

Geocoris spp., *O. insidiosus*, and coccinellids primarily prey on *Heliothis* eggs and 1st and 2nd instar larvae, and *Chrysopa* spp. primarily prey on *Heliothis* eggs and 1st through 3rd instar larvae (RIDGWAY and LINGREN, 1972). Spiders can prey on *Heliothis* eggs and 1st through 5th instar larvae, though there is variability among spider species regarding size or stage of prey attacked (RIDGWAY and LINGREN, 1972).

The trends in abundance of the predator complex during the two years of study are shown in Fig. 5. Densities were greater in 1978 than in 1979 until August, and predators colonized the field approximately one week earlier in 1978 than in 1979. The compositions of the predator complexes for the two years are given in Table 8. Spiders comprised almost half of the complex during both years. *Geocoris* spp. and coccinellids were the most abundant predatory insects during 1978 and 1979, respectively. Of all predators, *O. insidiosus* was the only one that increased substantially in density from 1978 to 1979.

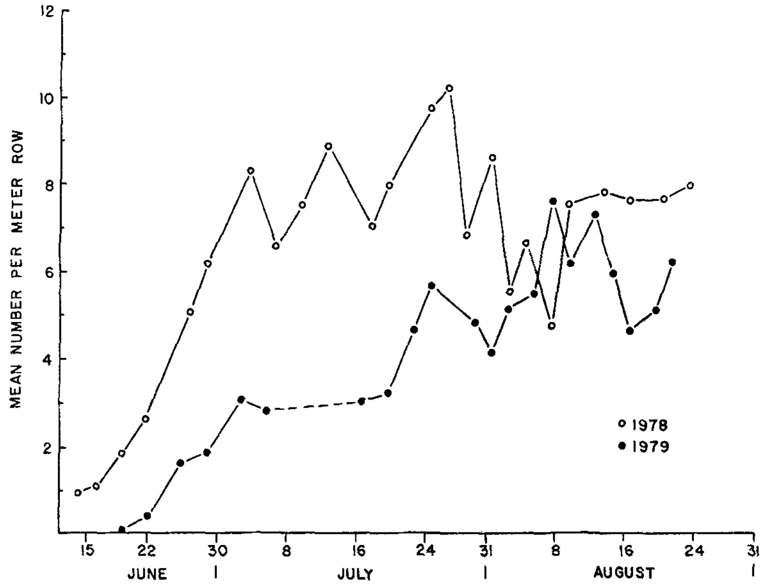

Fig. 5. Trends in the density of the complex of predaceous arthropods during 1978 and 1979.

Table 8. Compositions of predator complexes (overall mean density and percent of total for each year).

	1978		1979	
	$\bar{x}/m$	%	$\bar{x}/m$	%
Geocoris spp.	1.57	24.4	0.29	7.5
Orius insidiosus	0.28	4.3	0.58	14.9
Nabids	0.64	9.9	0.36	9.3
Chrysopa spp.	0.03	0.5	0.04	1.0
Coccinellids	0.92	14.3	0.83	21.3
Spiders	3.00	46.6	1.79	46.0
Total	6.44		3.89	

Life tables

To assess the relative contributions of various factors to stage-specific mortality, partial life tables were constructed for the pooled *Heliothis* populations (Tables 9 and 10). Numbers entering each stage (l_x) were obtained from the Weibull model. In addition to parasites and predators, mortality was attributed to failure of eggs to hatch and to unknown causes (larvae only). Of the eggs that failed to hatch, some apparently were unfertilized (no sign of embryonic development), whereas others showed signs of partial development. Mortality remaining after larval parasitization was inferred to have resulted from predation plus unknown causes.

Data in Tables 9 and 10 suggest that there was considerable variation among generations in the contributions of specific mortality factors. However, much of the variability can be attributed to differences between generations within years. The following discussion provides important details.

Table 9. Partial life tables for *Heliothis* spp. eggs and larvae, 1978.

		Generation 1			Generation 2		
x	d_xF	l_x	d_x	$100q_x$(%)	l_x	d_x	$100q_x$(%)
Egg		16.47			61.70		
	Failure to hatch		0.30	1.8		2.10	3.4
	Parasites		2.45	14.9		7.22	11.7
	Predators		2.39	14.5		20.59	33.4
			5.14	31.2		29.91	48.5
Instars 1-3		11.33			31.79		
	Predators & unknown		10.34	91.3		25.01	78.7
Instars 4 & 5		0.99			6.78		
	Parasites		0.71	71.7		2.73	40.2
	Spiders & unknown		0.24	24.2		2.14	31.6
			0.95	95.9		4.87	71.8
Instar 6		0.04			1.91		
				Total=99.8			Total=96.9

Table 10. Partial life tables for *Heliothis* spp. eggs and larvae, 1979.

		Generation 1			Generation 2		
x	d_xF	l_x	d_x	$100q_x$(%)	l_x	d_x	$100q_x$(%)
Egg		4.86			6.02		
	Failure to hatch		0.04	0.8		0.22	3.7
	Parasites		0.44	9.1		0.46	7.6
	Predators		0.00	0.00		1.65	27.4
			0.48	9.9		2.33	38.7
Instars 1-3		4.38			3.69		
	Predators & unknown		4.22	96.3		2.66	72.1
Instars 4 & 5		0.16			1.03		
	Parasites		0.16	100		0.04	3.9
	Spiders & unknown		0.00	0.00		0.65	63.1
			0.16	100		0.69	67.0
Instar 6		0			0.34		
			Total=100			Total=94.4	

Eggs. Apparent mortality ($100q_x$) due to failure to hatch and parasitization was reasonably constant between generations within each year. The remaining mortality, which was inferred to have been caused by predators, was much greater in Generation 2 than in Generation 1 for both years. Data in Figs. 1, 2, and 5 suggest why a difference in egg predation should have occurred. For both years, predators were abundant at the time Generation 2 eggs were present. In 1979, predators were absent or just starting to build up in numbers when Generation 1 eggs were present, and no mortality was inferred to have been due to egg predation. In 1978, predator numbers initially were low but then increased substantially during the period Generation 1 eggs were present, and 14.5% mortality was attributed to predators.

Instars 1-3. No parasites recovered kill their larval hosts during these stages. Therefore, all mortality was caused by predators and unknown factors. For both years, mortality from these sources was greater during Generation 1 than Generation 2. This is the opposite of what occurred with the eggs, though the relationships between *Heliothis* density (Figs. 1 and 2) and predator density (Fig. 5) were similar to those discussed for the eggs.

Instars 4 & 5. Parasites destroyed a much greater proportion of these larvae in Generation 1 than in Generation 2. In 1978, the impact of predators (spiders) plus unknown factors was similar for the two generations, whereas in 1979 these factors had virtually no impact during Generation 1 (all larvae were parasitized) but had a large impact during Generation 2 (parasitization was quite low).

DISCUSSION

A substantial amount of variation in the densities and compositions of *Heliothis* and the natural enemy complex was observed in the two years of study. Nevertheless, *Heliothis* survivorship curves conformed to Type I for both Generation 1 data sets and Type II for both Generation 2 data sets. The Weibull model proved to be quite useful for characterizing these survivorship curves. PINDER et al. (1978) suggested that the Weibull distribution would have limited utility as a survivorship model in the case of short-lived species, due to the influence of three factors on mortality rates: (1) season, (2) stages in the life cycle, and (3) environmental stochasticity. Although *Heliothis* spp. would be considered short-lived species, "seasonality" (i. e., Generation 1 vs. Generation 2) was actually a component of our analysis, and the life stages we studied were exposed to similar hazards (i. e., the natural enemy complex). Stochastic changes in the physical environment (i. e., weather) were not analyzed, but apparently this source of variability did not have a significant impact on survivorship.

Our analysis of the factors contributing to stage-specific mortality indicated that for eggs and larval instars 4 and 5, the action of natural enemies was responsible for between-generation differences in survivorship. However, this inference could not be made for larval instars 1-3, suggesting that a factor other than predators was responsible for between-generation differences in survivorship. But if not predators, then what caused the differences ? We think the answer can be found by considering the dynamics of the food resource utilized by the *Heliothis* larvae. The changes in the fruit load (squares, flowers and bolls) of the cotton plant population for the two years are shown in Fig. 6. It is clear that the availability of fruit for *Heliothis* larvae changed substantially during each season. There also were large between-year differences in the overall abundance of fruit, though the fruiting patterns were similar for the two years. SLOSSER et al. (1978) found that *Heliothis* larval sur-

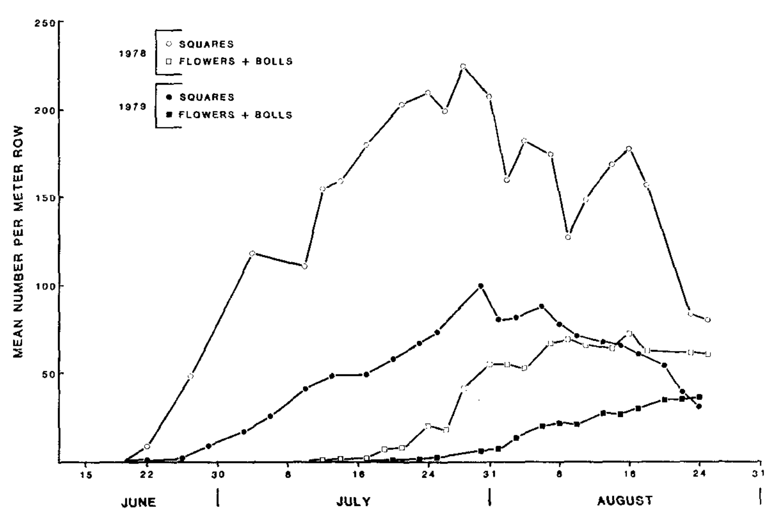

Fig. 6. Trends in the densities of cotton fruiting structures during 1978 and 1979.

vivorship on cotton was dependent on the availability of fruit; of particular importance to larval population success was the density of squares $\geq$ 6 mm in size. Comparison of Figs. 1 and 2 with Fig. 6 indicates for both years of our study that much less fruit was available to larvae during Generation 1 than was available during Generation 2. We did not record sizes of squares, but a square requires approximately 12 days to attain a size of 6 mm (SLOSSER et al., 1978); thus, in our plot 6 mm squares were probably not present until after 1 July in either year (Fig. 6). We propose that fruit availability was the factor primarily responsible for the relatively poor survivorship of larval instars 1-3 during Generation 1. Since both fruit and predators were abundant when Generation 2 larvae were present, in this case predation probably was the primary cause of mortality to larval instars 1-3.

Fruit availability could influence larval survivorship in at least two ways. SLOSSER et al. (1978) implied that mortality occurs simply because larvae are unable to find sufficient food. Another possibility is that increased mortality results from the interaction of fruit availability and natural enemies. While feeding on squares, larvae are concealed by the bracts that envelop the bud. Lower fruit density would require larvae to spend more time exposed while searching for food, which would increase the probability of encountering a predator. Thus, the impact of a relatively small population of natural enemies could be magnified due to increased encounters with prey. Evidence consistent with this hypothesis can be found in the case of *Heliothis* larval parasites; e. g., LEWIS and BRAZZEL (1968) reported a lower parasitization rate for larvae feeding on hosts that afforded concealment. In addition, this hypothesis might explain why we observed greater parasitization of Generation 1 larvae than of Generation 2 larvae. However, elucidation of the mechanism or mechanisms whereby larval survivorship is influenced would require further experimentation.

As noted earlier, the results of the *Heliothis* survivorship analysis were remarkably similar for the two years. It should be pointed out, however, that certain types of hazards that could figure prominently in survivorship in other situations were absent from our study. For example, no diseased *Heliothis* larvae were encountered; SEARS and SMITH (1975) found that under certain circumstances epizootics of a nuclear polyhedrosis virus could have profound effects on survivorship of *H. zea* larvae. With this qualification, our results suggest that natural enemies and fruit availability play important and predictable roles in determining the shape of the survivorship curve for *Heliothis* eggs and larvae on cotton.

SUMMARY

Population dynamics of *Heliothis virescens* (F.) and *Heliothis zea* (BODDIE) (Lepidoptera: Noctuidae) eggs and larvae were studied for two years in a small plot of cotton, *Gossypium hirsutum* (L.). Due to morphological and ecological similarities, the pooled *Heliothis* population was considered for most of the analyses. Two generations of *Heliothis* eggs and larvae were completed during each year. Stage recruitment was estimated for the eggs and larval instars 2-6, and recruitment variances were estimated by a Monte Carlo method. A modified form of the Weibull distribution was developed and used as a model to characterize survivorship curves for each of the four *Heliothis* generations. A Type I survivorship curve (mortality rate increasing with age) was inferred for both Generation 1 (early season) data sets, whereas a Type II survivorship curve (mortality rate constant and thus independent of age) was inferred for both Generation 2 (late season) data sets. The shapes of the survivorship curves for the individual *H. virescens* and *H. zea* populations were inferred to be the same as those for the pooled populations. Analysis of the contributions of various factors to *Heliothis* stage-specific mortality indicated that natural enemies (predators and parasites) and the availability of food for larvae were responsible for between-generation differences in survivorship patterns.

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ワタミムシ個体群の令別生存数の解析

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ワタミムシ（*Heliothis virescens* と *H. zea* の2種混合）の卵および幼虫個体群の動態を2年にわたって調べた。両種は形態的にも生態的にも極めて良く似ていてワタ畑では共に2世代を経過するので，両種の個体数をプールして取り扱った。令別加入数を卵および幼虫の各令について求め，バリアンスをモンテカルロ法により推定し，少し修正を加えたワイブル分布を用いて生存曲線の特徴を分析したところ，第1世代の生存曲線は死亡率が令につれて増加していくタイプであり，第2世代のそれは死亡率が令にかかわらず一定であるタイプであると考えられた。またこの傾向は*H. virescens* と *H. zea* を別々に取り扱っても変らないと考えられた。これらの結果にもとづき，令別死亡率に対する各種要因の働き方を分析したところ，世代間の生存様相の違いにはその時の天敵（捕食者および寄生者）および幼虫期間における食物の多少が大きく関与していることが示された。