COMBINING EXCLUSION TECHNIQUES AND LARVAL DEATH-RATE ANALYSES TO EVALUATE MORTALITY FACTORS OF *SPODOPTERA EXIGUA* (LEPIDOPTERA: NOCTUIDAE) IN COTTON

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Abstract

By combining pesticide exclusion and cage exclusion techniques, the efficacy of natural enemies in reducing populations of *Spodoptera exigua* (Hübner), the beet armyworm, larvae was effectively demonstrated. Larval collections added information about parasitism and disease, and when combined with data from insecticide treatments, demonstrated that differences in *S. exigua* population densities usually were due to the action of predators. Death-rate analyses demonstrated that much mortality due to parasitism was contemporaneous with death from predation. When predator populations were not reduced by insecticides, most indispensable natural mortality was due to predation. When predators were eliminated, and *S. exigua* populations reached outbreak levels, most larvae died from disease in 1989 and from parasitism in 1990.

Key Words: Contemporaneous mortality, beet armyworm, predation, *Cotesia*

Resumen

Al combinar técnicas de exclusión de pesticida y jaula, la eficacia de enemigos naturales para reducir poblaciones de *Spodoptera exigua* (Hübner) fueron demostradas efectivamente. Colectas de larvas añadieron información sobre parasitismo y enfermedad, y al ser combinadas con datos de tratamientos con insecticida, demostraron que diferencias en densidad de población de *S. exigua* usualmente fueron debidas a la acción de predadores. Analices de índices de muerte demostraron que gran parte de la mortalidad debido a parasitismo fue contemporánea con muerte por predación. Cuando poblaciones de predadores no fueron reducidas por insecticidas, la mortalidad natural más indispensable fue debida a predación. Cuando los predadores fueron eliminados, y poblaciones de *S. exigua* alcanzaron niveles epidémicos, la mayoría de las larvas murieron por enfermedad en 1989 y de parasitismo en 1990.

Evaluating the impact of natural enemies is a critical part of understanding pest population dynamics and of developing IPM systems (Luck et al. 1988; Sterling et al. 1989). One of two major approaches is usually taken to study biological control by indigenous agents in agricultural systems. In the first, exclusion of natural enemies with insecticides, cages, or other techniques is used to free pest populations from the action of the natural enemies. Each exclusion method has biases associated with it, but these biases may be at least partially overcome by combining methods (Luck et al. 1988). Densities of pest populations are then compared to densities of populations that are exposed to biological control agents (Luck et al. 1988). These studies have been used effectively to demonstrate that insecticide applications can disrupt natural enemy populations and lead to secondary pest outbreaks. However, insecticides also may affect insect populations by direct stimulation of fecundity (hormoligosis) or by indirect stimulation of fecundity (trophobiosis) (Risch 1987; Kerns & Gaylor 1993b). Thus, without further evidence, mechanisms of outbreak induction may be unclear.

The second of the common approaches to studying biological control in agroecosystems uses one or more of several techniques (reviewed in Luck et al. 1988) to identify natural enemies that attack a pest. The importance of each natural enemy is then ranked by the proportion of a host population that is parasitized, diseased or preyed upon at various time intervals. Once mortality agents are identified, numerical and functional responses of agents, or groups of agents, to changes in pest densities may be determined. Effects of natural enemies identified by these techniques may then be incorporated into pest models. However, Van Driesche (1983) and Van Driesche et al. (1991) explained why this approach is inadequate for explaining host mortality over a generation. Also, evidence that a particular natural enemy or group of enemies can reduce, or even regulate, a pest population is not adequate evidence that the enemies do reduce the population. Different natural enemies may respond differently to temperature, prey availability or density (Sterling et al. 1989). Thus, any of several agents may be capable of reducing a pest population under specific conditions. Also, the action of one natural enemy may be masked by the actions of contemporaneous mortality factors. Contemporaneous mortality factors are two or more factors that attack a host more or less simultaneously, although death ultimately may be due to a single factor (Royama 1981). For example, an individual insect may be infected by a disease, which would ultimately kill it, but also be parasitized by a parasitoid.

The influences of contemporaneous mortality factors on insect population dynamics may be determined with life-tables (Royama 1981; Gould et al. 1990). Death-rate analysis may be used to estimate mortality rates due to contemporaneous mortality factors as one step in the construction of life tables (Bellows et al. 1992). Marginal attack rates are attack rates by individual mortality agents that would occur in the absence of other mortality agents acting on the same host (Royama 1981). Marginal attack rates, which may be calculated from observed death rates (Royama 1981; Gould et al. 1990), are particularly appropriate in death-rate analysis when the action of one or more mortality agents is difficult to detect (Bellows et al. 1992).

Many of these techniques and concepts, which are commonly used in population and community ecology, are relevant to IPM. However, for reasons that are primarily based on the historical separation between applied and basic research (Levins & Wilson 1980), these techniques have been used little by agricultural scientists.

Life tables alone can not be used to document the efficacy of natural enemies (Luck et al. 1988). However, an effective method of assessing the role of natural enemies in host population dynamics is to contrast life-tables for experimentally manipulated populations, in which one population lacks specific natural enemies and the other population is attacked by the enemies (Bellows et al. 1992).

Spodoptera exigua (Hübner), the beet armyworm, is an induced pest of many crops throughout the world. Historically, *S. exigua* outbreaks in cotton have been common in the western United States, but serious outbreaks also occur in the Southeast. Until recent years, these outbreaks in cotton have been difficult to control with insecticides and may result in complete destruction of some fields (Smith 1989). However, new insecticides such as spinosad (Tracer, Dow Agrosciences, Indianapolis, IN) are relatively effective against *S. exigua* larvae (Halcomb et al. 1998), although somewhat expensive.

S. exigua is attacked by several predators and parasitoids (Eveleens et al. 1973; Pearson 1982; Oatman et al. 1983; Alvarado-Rodriguez 1987) and by protozoan, fungal and viral diseases (Smits 1987). Eveleens et al. (1973) and Hogg & Gutierrez (1980) concluded that in California cotton, *S. exigua* populations are normally held below economic injury levels primarily by predators feeding on eggs and small larvae. Parasitoids and disease apparently were less important as natural mortality agents of non-outbreak populations (Pearson 1982). A nuclear polyhedrosis virus (NPV) was the most important pathogen in *S. exigua* populations attacking tomatoes in Mexico (Alvarado-Rodriguez 1987) or cotton in California (Pearson 1982). In 1988, *S. exigua* outbreaks on cotton in Alabama were eventually controlled primarily by a naturally occurring NPV epizootic (Smith et al. 1989). In fields where the epizootic did not develop, rates of parasitism by a braconid, *Cotesia marginiventris* (Cresson), ranged from 23-43% (M. J. G., unpublished data). In Georgia and northern Florida, *C. marginiventris* parasitized 46% of the *S. exigua* larvae collected from cotton (Ruberson et al. 1993). More recently, Stewart et al. (1996) presented circumstantial evidence that *S. exigua* problem often coincide to areas where intensive insecticide applications are made for other pests, such as during intensive boll weevil eradication, *Anthonomus grandis grandis* Boheman, efforts.

Thus, the importance of biotic mortality factors on *S. exigua* outbreaks has been established. However, for reasons outlined in Van Driesche et al. (1991), none of these studies adequately determined effects of mortality factors on life stages over a *S. exigua* generation or determined effects of contemporaneous mortality factors on population dynamics. In this study, we combined insecticide and cage exclusion techniques with larval collections and death rate analyses to quantify sources of *S. exigua* mortality in cotton.

Materials and Methods

In 1989 and 1990, 'DPL90' cotton was planted in ≈ 0.3 ha plots at the Wiregrass Substation of the Alabama Agricultural Experiment Station in Henry County, AL. In 1989, untreated plots were not possible because the area was within an active boll weevil eradication program. Our treatments were applications of malathion (Cythion 46.2% RTU, American Cyanamid Company, Princeton, NJ; applied at 1.4 kg [AI]/ha) or methyl parathion 6 EC (formerly marketed by Cheminova, Wayne, NJ; applied at 0.6 kg [AI]/ha), each applied to four main plots in a randomized complete block design. Both insecticides are effective against boll weevil and most predators and parasitoids but not against *S. exigua*. Insecticides were applied with ground equipment every four to eight days.

Boll weevils were less numerous in 1990, and malathion applications were mandated by the eradication program only on 3 and 6 July. In 1990, main plots were four insecticide treatments: (1) λ-cyhalothrin (Karate 1E, Zeneca Ag Products, Wilmington, DE) applied alone at 0.028 kg (AI)/ha, (2) diflubenzuron (Dimilin 25 W [wettable], Uniroyal Chemical Company, Middlebury, CT) + a crop oil (Super Savol, Leffingwell, Brea, CA) (0.036 kg [AI] + 0.16 kg/ha), (3) a combination treatment of λ-cyhalothrin + diflubenzuron + crop oil (0.028 kg [AI] + 0.036 kg [AI] + 0.16 kg/ha) and (4) no insecticide. Four replicates of each insecticide treatment were used.

Diflubenzuron was applied to treatments 2 and 3 on 29 June, 20 and 27 July and 17 August. λ-cyhalothrin was applied to treatment 1 at 3- to 10-d intervals from 29 June to 24 August and to treatment 3 from 3 to 24 August. λ-cyhalothrin was tank mixed with the diflubenzuron on 29 June, 20 July and 17 August in treatment 3. λ-cyhalothrin is not effective against *S. exigua*, but it reduces populations of most predatory arthropods (Smith et al. 1993). Diflubenzuron may be effective against some *S. exigua* populations (Coudriet & Seay 1979; Ruberson et al. 1993; Smith et al. 1993) and is relatively non-damaging to populations of beneficial arthropods (Keever et al. 1977; Deakle & Bradley 1982).

Larval *S. exigua* and predator populations were estimated during both years with 1 to 3 drop-cloth samples, each sampling 1.8 row-m, per plot taken one or two times weekly. In 1989, weekly mean numbers of *S. exigua* were estimated. Larvae were not separated by size. In 1990, mean numbers were estimated for *S. exigua* in each of three size classes: small (first and second stadia), medium (third stadium) and large (fourth and fifth stadia). Effects of insecticide treatments on weekly mean numbers of predators and *S. exigua* larvae were compared by analysis of variance and, when significant main effects were found, means were separated with Fisher's LSD using the PROC GLM procedure (SAS Institute 1988) at $\alpha = 0.05$.

The combined effect of predators and parasitoids on *S. exigua* survival was determined using exclusion cages similar to those of Rice & Wilde (1988) and Kerns & Gaylor (1993a). Cages were 2 liter plastic bottles with two ≈ 13 × 9 cm windows covered with cloth mesh. A Velcro closure was used on one window for access to the interior of the cage. In 1989, cages were of three mesh sizes: large (6.4 mm diam. opening), medium (1.5 mm diam. opening), and small (NoSeeum netting, Balson Hercules, Providence, RI). The small mesh excluded all predators and parasitoids. The medium mesh excluded large predators and parasitoids but allowed small predators and parasitoids access to the *S. exigua* larvae. The large mesh allowed access by most invertebrate predators and parasitoids. Only small and medium mesh cages were used in 1990. Because methods of disease spread in *S. exigua* populations are unknown, proportions dying from disease were assumed to be equal in all cages and in the field.

Each week, one cage with each of the mesh sizes was placed on individual leaves on the periphery of separate plants in a subplot of each main plot. Subplots were 3-m sections of one row of cotton. Subplots were isolated from surrounding cotton by removing all plants from the ends of the subplots for a distance of ≈ 2 m on each end and all cotton from the 3-m sections of adjacent rows. An egg mass (≈ 25 eggs) within one day of hatching or ≈ 25 newly eclosed larvae were placed into each cage. All eggs or larvae were from a laboratory colony, reared on a meridic diet, established in 1988 from *S. exigua* collected from cotton and periodically infused with wild males. Cages were moved to other leaves within the same subplot when the larvae had consumed most of the original leaf.

In 1990 *S. exigua* populations were established outside cages in separate subplots instead of in large mesh cages. A *S. exigua* egg mass from the laboratory colony or from a natural infestation in the same main plot was placed on the ventral side of a leaf to simulate a natural infestation. It was difficult to find all larvae on large plants in late-season, and large plants provided more food for developing larvae. Therefore, subplots were thinned to 10 contiguous plants in midseason. For late-season releases, subplots were thinned to 3 contiguous plants per subplot. During both years, caged and uncaged larvae were counted 3 to 5 times weekly until all had died or pupated.

Because stadia could not be accurately determined in the field, a developmental rate model (Ali & Gaylor 1992) was used to estimate *S. exigua* stadia on each sample date. Daily maximum and minimum temperatures were measured at a weather station that was within 1 km of the plots. Kerns & Gaylor (1993a) found no differences in temperatures inside or outside cages placed within the cotton canopy.

Larval mortality was estimated for each cohort and each mesh size. Totals, instead of means, were used because of initial differences in numbers of first instar larvae in individual cages. Initial population size for small larvae was arbitrarily set at 1,000. Mortality was estimated by multiplying the proportion of larvae surviving from one stadium to the next by 1,000. Because survivorship curves included only four data points, regression analyses were not performed. Instead, survivorship within cohorts for larvae in cages with different mesh sizes were compared with 3 × 4 contingency tables using the PROC FREQ/CHISQ procedure (SAS Institute 1988) at df = 6, $\alpha = 0.05$. When cage effects were found, differences in survivorship between cages were compared with 2 × 4 contingency tables (df = 3, $\alpha = 0.05$). Differences between cages in survivorship for each stadium (first and second stadia were combined) were compared with 2 × 2 contingency tables (df = 1, $\alpha = 0.05$).

To determine the incidence of disease and parasitism, larvae were collected from each main plot 2-4 times weekly, placed into individual plastic cups containing velvetbean caterpillar diet (Greene et al. 1976) chilled and returned to the laboratory. When available, larvae were collected from drop cloth samples and by visually searching plants in appropriate plots. However, each week 50 to 100 eggs or neonate larvae also were placed on cotton in a third subplot. Larvae were collected from these artificial infestations when natural infestations were low. When sufficient numbers were present, at least five larvae of each of the three size classes (small, medium and large) were collected from each plot on each collection date. Collected larvae were examined daily in the laboratory to determine their fate.

Immature parasitoids attacking *S. exigua* are difficult to identify. Thus, rates of parasitism were based on emergence of adult parasitoids. Pathogens were not isolated and cultured. Instead, estimates of disease incidence were based on visual symptoms. Larvae in which internal organs and integument remained intact, with minimal darkening of the integument after ≈ 24 h, were classed as dying of unknown causes. Cadavers classed as "fungal infected" collapsed and were covered with mycelia within a few hours of death. Larvae were judged to have died of "other diseases" if the internal organs liquefied or the integument became fragile within ≈ 24 h of the death of the larva. These are symptoms of acute infection by pathogens such as nuclear polythedrosis virus (NPV) or by *Bacillus thuringiensis* Berliner (Bt).

The head capsule from the first molt after collection was measured with an ocular micrometer to determine the instar of each larva at the time of collection. Using the developmental rate model for *S. exigua* on cotton (Ali & Gaylor 1992), larval eclosion dates were estimated.

S. exigua generations occur at about one-month intervals (Trumble & Baker 1984). The first *S. exigua* infestations normally occur in southern Alabama cotton in July. Hence, the developmental rate model (Ali & Gaylor 1992) was used to place all larvae into July or August cohorts' equivalent to field generations of *S. exigua*. Contingency table analyses were used ($\alpha = 0.05$) to compare effects of insecticide treatments, larval size classes, and cohorts within years on mortality caused by parasitism, disease or unknown causes. When contingency tables were significant, differences between causes were separated with 2 × 2 contingency tables ($\alpha = 0.05$).

Death-rate tables were developed for each cohort each year. Because of the broad-spectrum effects of both insecticide treatments used in 1989, death-rate tables were developed from both treatments combined. Data from untreated and diflubenzuron plots were combined in 1990 because diflubenzuron has little effect on predator populations (Keever et al. 1977; Deakle & Bradley 1982). Separate tables also were constructed for combination (λ-cyhalothrin + diflubenzuron) plots and for λ-cyhalothrin plots.

To construct death-rate tables, the initial population size (l_x) for small larvae was set arbitrarily at 1,000 because separate populations were used to determine mortality rates. The numbers of larvae in each size class dying (d_x) of parasitism, disease or "unknown" were estimated for each cohort by multiplying the proportion of field-collected larvae dying of each factor by l_x for the cohort and size class.

Marginal attack rates (m) for disease, parasitism and unknown mortality factors were calculated by the formulae of Gould et al. (1990):

$$m_A = v_A/(1\text{-}cm_B)$$

and

$$m_B = \{(c\text{-}1)v_A + cv_B + 1 - [(v_A - cv_A - cv_B - 1)^2 - 4cv_B]^{1/2}/2c\}$$

where v_A = proportion of hosts dying of factor A: v_B = proportion of hosts dying of factor B; c = proportion of hosts dying of factor B, when A and B attack the same individual. In this case, c was assumed to be 0.5 because outcomes of competition between parasitoids and disease and "unknown" mortality factors are unknown. Marginal attack rates were calculated for each factor by letting v_A = the proportion of larvae dying of one factor and v_B = the proportion dying of all other factors except predation.

Estimating mortality due to predation is difficult because hosts that are preyed upon usually disappear from the system. In many life tables, mortality due to diseases and parasitoids is calculated, and predation is assumed to be the residual mortality that is unaccounted for by other factors (Bellows et al. 1992). This technique may underestimate the importance of predation because predation may be contemporaneous with other factors. Alternatively, predation effects may be overestimated if mortality rates due to abiotic, physiological, or unknown factors are high. Thus, an independent measure of deaths due to predation is needed.

In 1989, the boll weevil eradication program made an untreated control impossible. Thus, marginal attack rates for predators were estimated from the cage experiment using the formula from Royama (1981):

$$m_B = (m_{A+B} - m_A)/(1 - m_A)$$

where m_B = marginal attack rate of predators; m_A = marginal attack rate by parasitoids, estimated from collected larvae; m_{A+B} = total mortality due to A and B. However, m_B in this formula is not independent of m_A.

Because mortality was estimated from different host populations, marginal attack rates were used to estimate the proportion of larvae of each size class that should have died of each factor if all factors were acting on the same population (v). This was done by solving the formula of Gould et al. (1990) for v_A. Thus,

$$v_A = m_A (1 - cm_B)$$

where c was assumed to be 0 when factor A was predation because larvae killed by predators would not produce parasitoids or disease symptoms. Values of l_{x+1} were obtained by subtracting total v_x from l_x.

In 1990, predation rates for each *S. exigua* cohort were estimated from differences in population densities in insecticide treatments. Based on larval collections, the most dense *S. exigua* population was assumed to have been reduced by the action of all agents except predators. Less dense populations were attacked by all natural enemies. Because success rates of most predators are unknown, we assumed that attacks by predators were always successful. Contemporaneous attacks that included predation were assumed to always be won by predators because there was no evidence that predators were less successful in attacking diseased or parasitized *S. exigua* than in attacking larvae that were not affected by other mortality factors. Thus, marginal attack rates for predation were equal to observed mortality (v) due to predation. To estimate the marginal attack rate for predators, the area under the potential population density curve for a *S. exigua* population unaffected by natural enemies was first estimated by:

$$PP_{i,j} = PO_{i,j}/(1-v_{tot})$$

where $PP_{i,j}$ = area under the potential population density curve for the i^{th} size class in the j^{th} cohort, PO = the area under the curve for the most dense *S. exigua* population, v_{tot} = proportion of the population that was calculated to have died of all causes except predation. In all cases, except for large *S. exigua* in the second cohort, the most dense *S. exigua* populations were in the λ-cyhalothrin treatment. In the second cohort, more large larvae were in the λ-cyhalothrin + diflubenzuron treatment than in the other treatments. The marginal attack rate for predation (m_{pred}) was estimated by:

$$m_{pred} = (PO_{i,j} - PL_{i,j})/PP_{i,j}$$

where PL = the area under the curve for the least dense *S. exigua* population. Competition among mortality factors in a single population includes predation. Therefore, a modified proportion (v') of larvae of each size class that would have died of each factor if all factors were acting on a single population was calculated by incorporating m_{pred} into the formula of Gould et al. (1990) for m_A and solving for v'. Thus,

$$v'_A = (1 - m_{pred}) (m_A (1 - (0.5 (m_B + m_C))))$$

The total of all v' for a *S. exigua* size class in a cohort was subtracted from l_x for the class to get l_x for the subsequent size class.

Indispensable mortality (IM) is mortality that would not be replaced in the host population by the subsequent action of other mortality factors if the factor under consideration were removed (Bellows et al. 1992). Within each size class and cohort for each year, IM was estimated for each mortality factor by subtracting the number of larvae surviving for the cohort from the number surviving when the effect of the factor was removed.

RESULTS

Insecticide Exclusion

In 1989 there were few differences in predator or *S. exigua* population densities due to insecticide treatments (Fig. 1). The first "wild" *S. exigua* egg mass was found on 17 July 1989. Larval *S. exigua* were first counted in beat sheet samples on 9 August, but populations remained sparse until 30 August, when 3.2 ± 0.95 and 5.5 ± 0.23 larvae per 0.9 row-m were found in malathion and methyl parathion-treated plots, respectively. Weekly mean *S. exigua* population densities were not significantly different between treatments (F = 0.74, 1.83, 2.57, 0.47; df = 1,36, 1,26, 1,3, 1,3; for 9, 16, and 30 August and 6 September, respectively; $P > 0.05$).

Total predator densities declined after 5 July 1989 in plots treated with either insecticide. Predator populations then increased in mid- and late-August in both treatments, but densities were higher in the malathion-treated plots than in the methyl parathion-treated plots on 23 (F = 3.72, df = 1,34, $P < 0.05$) and 30 August (F = 1.94, df = 1,35, $P < 0.05$).

The imported fire ant, *Solenopsis invicta* Buren, was especially abundant in early season, comprising ≈ 90% of the predators in malathion plots on 5 and 12 July and ≈ 80% in the methyl parathion plots on 5 July. When total predator populations were least dense (2 August), ants were only ≈ 20% of the predator populations in both treatments. When the total predator population peaked again (23 August in the malathion plots) fire ants were ≈ 70% of the population.

Medium sized *S. exigua* were found in the first 1990 samples, during the week of 4 July (Fig. 2). These larvae were from the first of three *S. exigua*

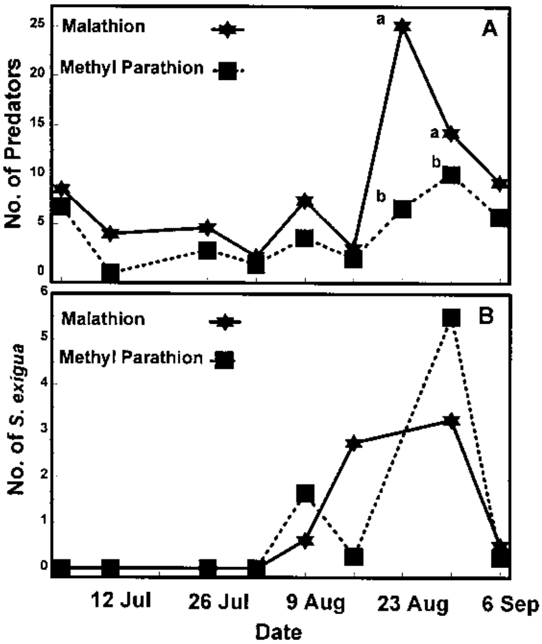

Fig. 1. Mean number of *S. exigua* larvae and predators per 1.8 row-m during 1989. Means on the same date not accompanied by the same letter are significantly different ($P < 0.05$) according to Fisher's LSD (SAS Institute 1988).

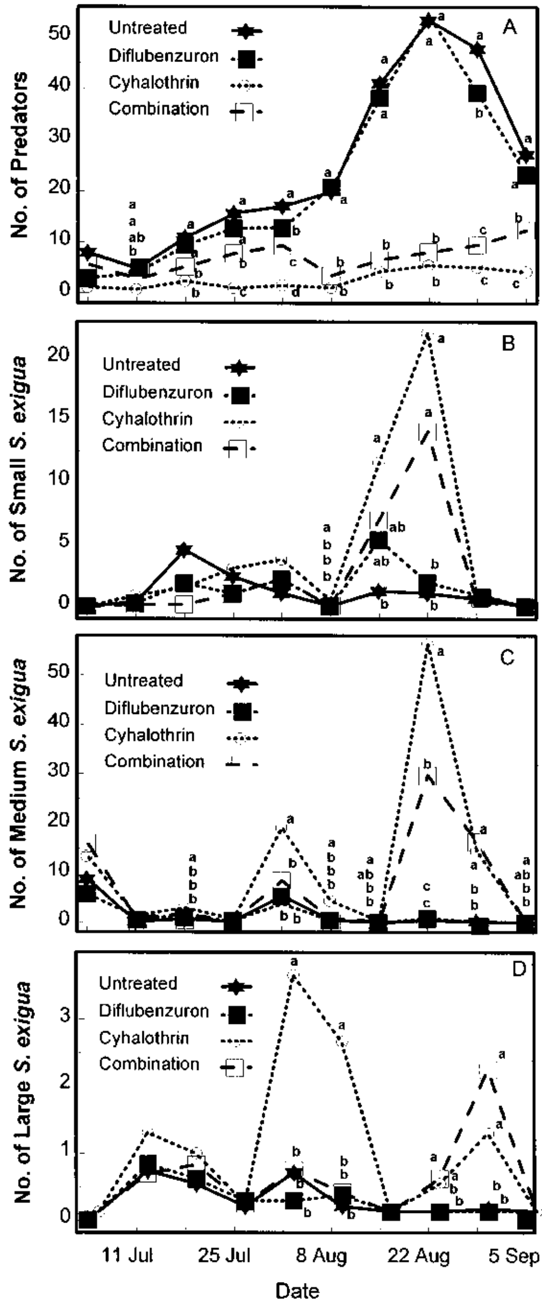

Fig. 2. Mean number of (A) small, (B) medium, and (C) large *S. exigua* larvae and (D) predators per 1.8 row-m during 1990. Means on the same date not accompanied by the same letter are significantly different ($P < 0.05$) according to Fisher's LSD (SAS Institute 1988).

generations in 1990. Populations of small larvae of the second generation peaked in mid-July and small larvae of the third generation peaked in mid-August (Fig. 2). Thus, the assignment of larvae to July and August cohorts represented the occurrence of second and third generations in 1990.

λ-cyhalothrin treatments affected *S. exigua* and predator population densities in 1990 (Fig. 2). Mean numbers of small *S. exigua* in the July cohort were not different among insecticide treatments ($F = 2.46, 0.56, 1.81$; df = 3,108, 3,89, 3,89; for 11, 18, and 25 July, respectively; $P > 0.05$). Although more medium larvae were in the λ-cyhalothrin treatment than in the other plots on 18 July and 8 August ($F = 4.02$, and 2.8, respectively; df = 3,89; $P < 0.05$), populations in all treatments were small. Beginning on 18 July, total predator populations were lower in the λ-cyhalothrin and combination plots than in untreated and diflubenzuron plots ($F = 7.60$, df = 3,89, $P < 0.05$). On 25 July, fewer predators were in plots that had been treated regularly with λ-cyhalothrin (treatment 1) than in any other treatments ($F = 13.05$, df = 3,89, $P < 0.05$). Predator population densities in combination plots were intermediate between those in λ-cyhalothrin-treated plots and those in plots that were not treated with λ-cyhalothrin. When λ-cyhalothrin was applied to combination plots at frequent intervals beginning on 3 August, predator populations were quickly reduced. From 8 August until the end of August, predator populations were not different in the λ-cyhalothrin and combination plots, and they were lower than in plots that were not treated with λ-cyhalothrin

(F = 27.75, 19.15, 67.64 and 34.58 for 8, 15, 22 and 29 August, respectively; df = 3,89; $P < 0.05$). When *S. exigua* populations peaked (22, 22 and 29 August for small, medium and large larvae, respectively), population densities for each size class were lower in plots with dense predator populations (not treated with λ-cyhalothrin) than in λ-cyhalothrin treated plots (F = 6.23, 14.51, and 34.58 for small, medium and large, respectively; df = 3,89; $P > 0.05$). *S. exigua* population densities were not different between control and in diflubenzuron plots. Thus, in plots with dense predator populations, diflubenzuron did not further reduce *S. exigua* populations. Densities of medium *S. exigua* in combination plots were intermediate between those in λ-cyhalothrin-treated and untreated plots on 22 August. Thus, diflubenzuron reduced these population densities when predator populations were lower.

Ants made up 48-93% of the predator populations during the first week of sampling (4 July 1990). Subsequently, ants were virtually eliminated in plots treated with λ-cyhalothrin at 3- to 10-d intervals. Big-eyed bugs, *Geocoris* spp., were the most abundant predators in these plots. Both ant and big-eyed bug populations increased rapidly in August in all plots, but big-eyed bugs were the most abundant predators by 15 August. λ-cyhalothrin did not reduce big-eyed bug population densities below those in untreated plots, but ants remained less abundant in the λ-cyhalothrin-treated plots (F = 8.15, 14.30, 12.78 and 7.72 for 8, 15, 22 and 29 August, respectively; df = 3,89; $P < 0.05$).

Results of the insecticide exclusion experiment provided anecdotal evidence that, at least in 1990, predators controlled *S. exigua* populations. *S. exigua* populations increased dramatically when predator populations were eliminated by frequent applications of λ-cyhalothrin. However, effects of contemporaneous mortality factors (disease and parasitism) were not assessable by this experiment.

Cage Exclusion

Results of the cage exclusion experiment were similar to the results of the insecticide exclusion experiment. In both 1989 cohorts, more *S. exigua* survived to the fifth stadium in the total exclusion cages than in the cages that allowed access by predators and parasitoids (χ^2 = 19.642 and 58.293 for July and August, respectively; df = 6; $P < 0.05$) (Fig. 3). However, in July, there were no differences in survival for individual stadia. In August, survival was greater in total exclusion cages only during the third stadium, indicating that most of the differences in survival were due to mortality to medium larvae. There were no differences in survival in no exclusion and partial exclusion cages. In the July cohort, survival to the fifth stadium was 38.6 and 13.2% in total and no exclusion cages, respectively, and survival was 54.2 and 12.2% in total and partial exclusion cages in the August cohort. Thus, larval survival differed most in the total exclusion cages versus the other cages when predator populations were most dense.

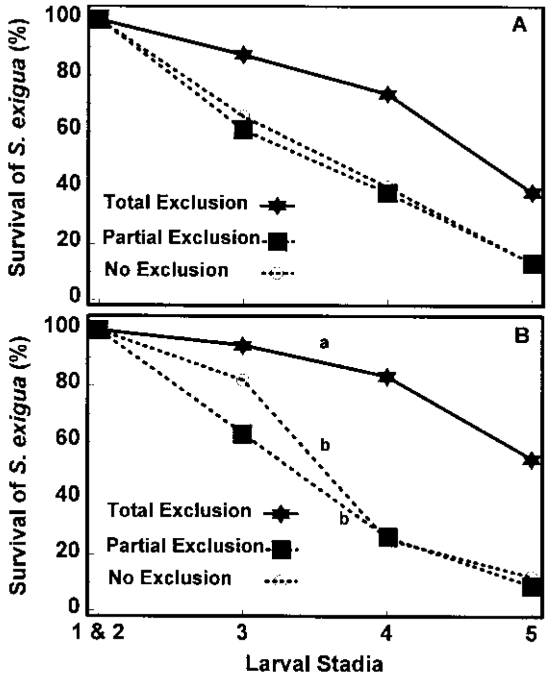

Fig. 3. *S. exigua* larval survival in 1989 inside total, partial and no exclusion cages. (A) July cohort. (B) August cohort. Survival within stadia not accompanied by the same letter are significantly different ($P < 0.05$) according to 2 × 2 χ^2 tests (SAS Institute 1988).

In 1990, in plots with relatively few predators, *S. exigua* survival inside total exclusion cages (Fig. 4) was not different from survival outside cages (χ^2 = 3.313, 6.019 and 0.801 for July cohorts treated and not treated with λ-cyhalothrin and for the treated August cohort, respectively; df = 3; $P > 0.05$). In July, survival outside cages in plots not treated regularly with λ-cyhalothrin (Fig. 4A) was intermediate between that inside partial and total exclusion cages. In λ-cyhalothrin-treated plots (i.e., few natural enemies) in July (Fig. 4B) and August (Fig. 4D), there were no differences in *S. exigua* survival inside total exclusion cages versus outside cages, but survival was lower in partial exclusion cages.

More larvae survived in total exclusion cages than outside cages in plots with dense predator populations (Fig. 4C). Thus, exclusion of predators by cages increased *S. exigua* survival when predator populations were dense, but not when predator populations were sparse. Data from the combination plots were included with data from untreated plots in July but were combined with

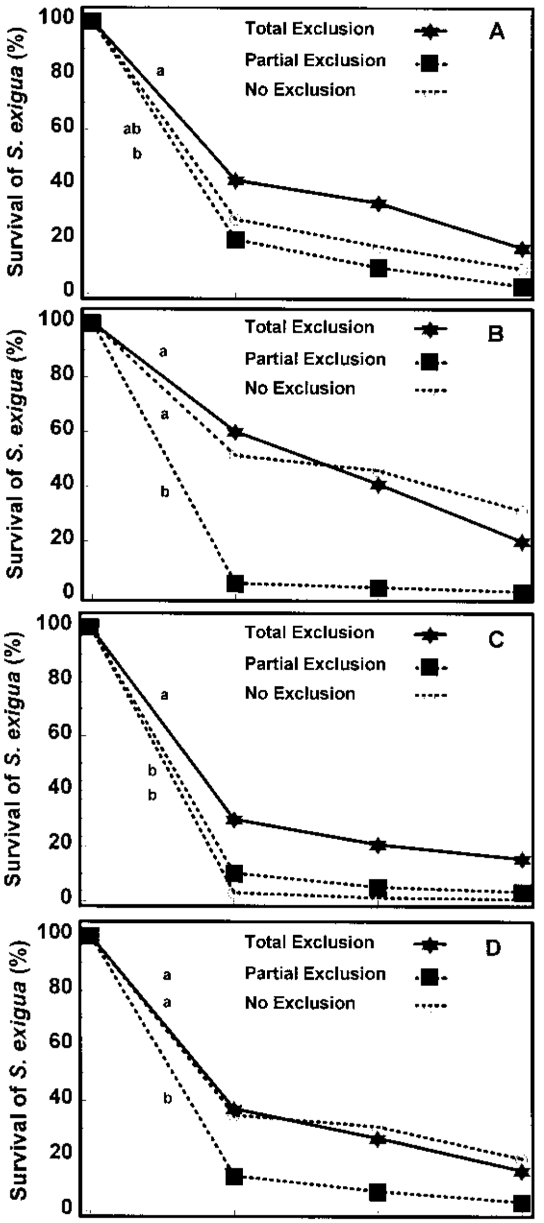

Fig. 4. *S. exigua* larval survival in 1990 outside exclusion cages and inside total and partial exclusion cages. (A) July cohort in cotton not treated with λ-cyhalothrin at 3- to 10-d intervals. (B) July cohort in cotton treated with λ-cyhalothrin. (C) August cohort in cotton not treated with λ-cyhalothrin. (D) August cohort in cotton treated with λ-cyhalothrin. Survival within stadia not accompanied by the same letter are significantly different ($P < 0.05$) according to 2×2 χ^2 tests (SAS Institute 1988).

data from cyhalothrin-treated plots in August because λ-cyhalothrin dramatically reduced natural enemy populations in August but not in July. In all cohorts in 1990, most *S. exigua* mortality occurred while larvae were small.

Insecticide and cage exclusion methods provided supporting evidence that *S. exigua* populations were controlled by natural enemies acting primarily on small and medium sized larvae. The λ-cyhalothrin-induced outbreak apparently was due to destruction of natural enemy populations. However, neither exclusion method provided information about contemporaneous mortality or the individual impact of different mortality agents attacking incipient versus outbreak populations.

Larval Collection

Prior to 4 August 1989, few *S. exigua* could be collected to determine parasitism or disease incidence. Because survival of laboratory-reared and released larvae was low, only 161 larvae were collected from the July 1989 cohort; 1273 larvae were collected from the August cohort (Table 1).

There were no differences in sources of mortality for different sizes of *S. exigua* larvae in July 1989 (χ^2 = 2.418, df = 2, $P > 0.05$). The most common mortality factor affecting larvae in this cohort was "unknown" (16.2%), that may have been partially attributable to handling and to the collected larvae originating from a laboratory colony. The first parasitoids emerged from larvae collected as 3rd instars on 20 July 1989, but little parasitism and no disease were found in this cohort.

Disease was a more important mortality factor in August. The first larva to die from disease was collected during the week of 9 August 1989. It was infected with a fungal pathogen. Rates of disease infection increased as larvae matured. In this cohort, more medium than small larvae (χ^2 = 27.395, df = 1, $P < 0.05$) and more large than medium larvae (χ^2 = 14.622, df = 1, $P < 0.05$) were diseased. Most diseases were fungal diseases; 3.4, 18.9, and 35.0% of small, medium, and large larvae were infected by fungi, respectively. However, within a single week the infection rate was even greater. On 6 September, 46 and 88% of the medium and large larvae, respectively, produced mycelia. Other diseases killed only 2.1% of the larvae collected from the August cohort.

In August 1989, most parasites emerged from medium larvae (Table 1). Effects on parasitism rates of the area-wide insecticide applications applied in 1989 for the boll weevil are unknown.

In 1990, 860 and 414 larvae were collected for the July and August cohorts, respectively. In both cohorts, insecticide treatments had no statistically significant effect on the incidence of disease (χ^2 = 5.67 and χ^2 = 4.09 for July and August, respectively; df = 2; $P > 0.05$), parasitism (χ^2 = 2.46 and χ^2 = 0.24 for July and August, respectively; df = 2; $P > 0.05$), or unknown factors (χ^2 = 3.27 and χ^2 = 1.27 for July and August, respectively; df = 2;

TABLE 1. SOURCES OF MORTALITY TO THREE SIZES OF *S. EXIGUA* LARVAE COLLECTED FROM COTTON.

	Percent mortality					
	July			August		
Source	Small	Medium	Large	Small	Medium	Large
			1989			
Unknown	34.8 Aa	5.7 Aa	10.0 Aa	22.4 Aa	11.0 Bb	3.5 Cb
Parasitism	4.4 Aa	2.9 Aa	5.0 Aa	3.7 Bb	24.2 Aa	4.5 Bb
Disease	0.0 Aa	0.0 Aa	0.0 Aa	6.0 Cb	21.1 Ba	36.7 Aa
Total	39.2 Aa	8.6 Aa	15.0 Aa	32.1 B	56.3 A	44.7 AB
N	80	35	46	512	408	353
			1990			
Unknown	47.1 Aa	25.4 Ba	8.1 Cb	26.1 Aa	12.3 Ab	17.7 Aa
Parasitism	27.1 Aab	29.4 Aa	14.8 Ba	23.1 Aa	28.1 Aa	22.4 Aa
Disease	12.9 Ab	9.1 Bb	4.0 Cc	6.0 Bb	15.8 Aab	17.7 Aa
Total	87.1 A	63.9 B	26.9 C	55.2 A	56.2 A	57.8 A
N	85	330	420	134	114	147

Means within months and rows followed by the same capital letter are not significantly different according to $2 \times 2\, X^2$ analysis, df = 1, $P < 0.05$. Means within years and columns followed by the same lower case letter are not significantly different according to $2 \times 2\, X^2$ analysis, df = 1, $P < 0.05$ (SAS Institute 1988).

$P > 0.05$). Rates of disease were low throughout 1990, and in July, disease incidence decreased as larvae matured (Table 1). In August, rates of disease increased as larvae matured. "Unknown" causes killed ≈ 20% of the larvae from both 1990 cohorts. The highest rate of fungal infection (8.8%) was in large larvae from the August cohort.

Parasitism was one of the most common causes of mortality in both cohorts in 1990. In July, higher rates of parasitism were found in small and medium larvae than in large larvae. In August, however, there was no significant difference associated with host size.

Over both seasons, parasitoids emerged from 15% of collected *S. exigua*; 10, 26 and 11% of the large, medium and small larvae, respectively, were parasitized. The most common parasitoid found in both years was *Cotesia marginiventris* (Cresson) (det. P. M. Marsh). This species, which attacks the larvae of at least 21 lepidopteran species (Krombein et al. 1979), emerged from 95% of parasitized *S. exigua* collected as small or medium-sized larvae. *Meteorus rubens* (Nees) (det. P. M. Marsh) emerged from 3% of parasitized medium larvae. The tachinid *Lespesia aletiae* (Riley) (det. N. E. Woodley) emerged from 86% of the parasitized *S. exigua* collected as large larvae. In 1990, the gregarious, external parasitoid, *Euplectrus pathypenae* Howard emerged from three fourth instar *S. exigua*. *E. comstockii* Howard (det. M. E. Schauff), emerged from one fourth instar. The hyperparasitoids *Mesochorus discitergus* (Say) (det. R. W. Carlson) and *Spilochalcis hirtifemora* (Ashmead) (det. E. E. Grissell) also emerged from *S. exigua* collected in 1989.

Because larvae were not dissected to determine rates of parasitism, attack rates could not be estimated directly. However, 98% of *C. marginiventris* emerged from larvae collected as small or medium larvae in 1989 and 1990 combined. Ruberson et al. (1993) also found that *C. marginiventris* oviposited primarily in small and medium sized larvae. In contrast, only 3 of the 103 *L. aletiae* that emerged were from *S. exigua* collected as small or medium larvae. Thus, there was little contemporaneous mortality caused by the two most abundant parasitoids in this study.

Results of this experiment alone might lead to the conclusion that in August 1989, fungal disease of large larvae was the most important *S. exigua* mortality factor. *C. marginiventris* was the most abundant parasitoid both years, but its effects on *S. exigua* population densities is unclear from these data. Contemporaneous mortality, even for parasitism and disease, is not addressed by these results.

Mortality Tables

In 1989, different natural enemies were responsible for most mortality in the two *S. exigua* cohorts (Table 2). In July, marginal attack rates (m) and indispensable mortality (IM) from all causes combined were higher for small *S. exigua* than for the other size classes. Thus, death of small larvae appeared to be most important in the decline of this nonoutbreak larval population. However, much of the "unknown" mortality could be removed from the analysis if the high mortality rates for small larvae due to unknown causes were artifacts of

TABLE 2. DEATH RATE ANALYSES FOR *S. EXIGUA* LARVAE IN 1989.

Mortality factor	Stage	July					August				
		l_x	d_x	m	v[1]	IM	l_x	d_x	m	v[1]	IM
Unknown	Small larvae	1,000	342.8	0.357	0.287	0.148	1,000	223.8	0.237	0.204	0.027
Parasitism			43.5	0.053	0.036	0.004		36.8	0.043	0.033	0.000
Disease			0.0	0.000	0.000	0.000		59.5	0.069	0.054	0.007
Predation			(219.0)[1]	0.175	0.175	0.057		(124.6)	0.085	0.085	0.008
Total			610.3	0.586	0.498	0.263		444.7	0.434	0.377	0.051
Unknown	Medium larvae	502	28.7	0.058	0.046	0.016	623	68.7	0.146	0.064	0.014
Parasitism			14.4	0.029	0.023	0.000		151.1	0.299	0.146	0.004
Disease			0.0	0.000	0.000	0.000		131.3	0.265	0.126	0.030
Predation			(110.5)	0.197	0.197	0.065		(355.2)	0.387	0.387	0.112
Total			153.6	0.284	0.265	0.096		706.3	1.097	0.723	0.219
Unknown	Large larvae	369	36.9	0.103	0.085	0.031	172	6.1	0.045	0.030	0.005
Parasitism			18.4	0.053	0.042	0.000		7.7	0.057	0.039	0.001
Disease			0.0	0.000	0.000	0.000		63.3	0.386	0.322	0.054
Predation			(73.2)	0.154	0.154	0.048		(29.8)	0.123	0.123	0.012
Total			128.5	0.309	0.281	0.104		106.9	0.611	0.514	0.088
	Pupae	265					84				

[1]Observed mortality (d_x) due to predation was from caged data and includes predation and parasitism.

their being from a laboratory colony and of handling. Marginal probabilities for total mortality of each size class would then be nearly equal. Alternatively, if much "unknown" mortality was due to insecticides, it should be included in the analysis.

Marginal attack rates and IM for predation were similar for all *S. exigua* size classes, indicating that predators attacked different sizes equally. Indispensable mortality due to predation on all size classes combined and "unknown" mortality to all sizes were similar (Table 3). Parasitism and disease were of little importance to the July cohort, and 26.5% of larvae hatching in July survived to pupation (Table 2).

When *S. exigua* reached outbreak levels in August 1989, larval mortality for the generation increased dramatically (Table 2). Only 8.4% of the August cohort pupated. The highest levels of m and IM were for medium larvae. The parasitoid *C. marginiventris* parasitized ≈ 30% of the medium larvae in the August cohort. However, because much of the parasitism was contemporaneous with other mortality factors, only 15% of medium larvae from a single population would have produced parasitoids (v' = 0.146). Indispensable mortality due to predation on medium larvae was much higher than IM for any other mortality factor affecting this size class (Table 2). Thus, predation was most responsible for reducing the proportion of this cohort that reached the most damaging developmental stage. Marginal probabilities of attack on medium larvae due to predation and of large larvae due to disease were about equal. However, disease of large larvae affected a smaller portion of the cohort than did predation on medium larvae. Thus, IM for predation on medium larvae was higher than IM for disease of large larvae. Parasitism caused little indispensable mortality to this generation. When all sizes were combined, IM for disease was higher than for any other factor (Table 3).

Because levels of disease, parasitism and unknown mortality were not different across insecticide treatments, mean percentages of mortality due to these factors were used to construct deathrate analyses in 1990 (Table 4). In July, in plots that had not been treated regularly with λ-cyhalothrin (untreated, diflubenzuron and combination), *S. exigua* suffered relatively high rates of predation on medium and large larvae. About one-third of the large *S. exigua* in these plots were attacked by predators (m = 0.343 and 0.313 in control and combination plots, respectively). Predation caused more indispensable mortality than any other factor attacking large larvae.

Nevertheless, because of high rates of parasitism of small and medium larvae (Table 4), parasitism was most responsible for reducing the density of this population before it reached the large larvae stage. When mortality to all sizes was combined (Table 5), parasitism caused more indispensable mortality to the July 1990 cohort than did predation or disease. In all insecticide treatments in both 1990 cohorts, m values for parasitoids were greater for small and medium larvae than for large larvae (Table 4). Thus, *C. marginiventris*, which caused almost all parasitism in small and medium larvae, appeared to be the most important parasitoid.

In August 1990, contemporaneous mortality was high in plots where predators were abundant (untreated and diflubenzuron). For example, when predation was precluded by collecting larvae, 28% of medium larvae were parasitized (Table 1). Thus, marginal attack rates for parasitism were high (Table 4). However, predation rates also were high in these plots. Predators attacked ≈ 45% of the medium larvae (Table 4). Because of contemporaneous mortality, only 15% of larvae in these plots would have died from parasitism (*v*' = 0.152). In these plots, predation caused more indispensable mortality than any other factor in August (Table 5). Rates of predation were low (Table 4) where predator populations were virtually eliminated (λ-cyhalothrin treatment and in the combination plots in August), and parasitism was the most important mortality factor.

Natural mortality was greater for each cohort of *S. exigua* larvae when predators were present than when they were eliminated. Pupal l_x values were less in plots with dense predator populations than in plots with reduced predator populations. However, even in the 1990 plots with few predators (combination plots in August and both cohorts of λ-cyhalothrin-treated), larval mortality was greater than in 1989 (Table 2). These differences apparently were due to higher marginal attack rates by "unknown" factors and by parasitoids.

TABLE 3. TOTAL INDISPENSABLE MORTALITY[1] TO LARVAE IN 1989.

Mortality factor	July	August
Unknown	0.223	0.053
Parasitism	0.005	0.006
Disease	0.000	0.118
Predation	0.208	0.086

[1]Indispensable mortality was calculated from larval death rates by subtracting the number entering the pupal stage when the mortality factor was included from the number entering the pupal stage when the factor was not included.

TABLE 4. DEATH-RATE ANALYSIS FOR *S. EXIGUA* LARVAE IN COTTON UNDER THREE INSECTICIDE REGIMES IN 1990.

		July					August				
Stage	Mortality factor	l_x	d_x	m	v'	IM	l_x	d_x	m	v'	IM
					Untreated and diflubenzuron alone						
Small larvae	Unknown	1,000	471.0	0.675	0.434	0.037	1,000	261.0	0.316	0.175	0.011
	Parasitism		271.0	0.440	0.234	0.018		231.0	0.284	0.155	0.009
	Disease		129.0	0.221	0.094	0.005		60.0	0.081	0.038	0.002
	Predation		38.0	0.038	0.038	0.001		321.0	0.321	0.032	0.009
	Total		909.0	1.374	0.800	0.077		873.0	1.001	0.689	0.053
Medium larvae	Unknown	200	50.7	0.330	0.130	0.012	311	38.2	0.162	0.065	0.005
	Parasitism		58.7	0.373	0.151	0.014		87.3	0.338	0.152	0.011
	Disease		18.2	0.129	0.044	0.004		49.1	0.204	0.084	0.006
	Predation		95.0	0.476	0.476	0.018		140.2	0.451	0.451	0.016
	Total		222.6	1.308	0.800	0.077		314.8	1.155	0.751	0.058
Large larvae	Unknown	40	3.2	0.090	0.053	0.002	77	13.7	0.229	0.096	0.007
	Parasitism		5.9	0.158	0.097	0.004		17.3	0.282	0.122	0.009
	Disease		1.6	0.045	0.026	0.001		13.7	0.229	0.096	0.007
	Predation		13.7	0.343	0.343	0.010		33.8	0.438	0.438	0.015
	Total		24.4	0.637	0.519	0.021		78.5	1.178	0.752	0.058
Pupae		19					19				
					λ-cyhalothrin + diflubenzuron						
Small larvae	Unknown	1,000	471.0	0.675	0.405	0.052	1,000	261.0	0.316	0.220	0.036
	Parasitism		271.0	0.440	0.218	0.026		231.0	0.284	0.194	0.032
	Disease		129.0	0.221	0.080	0.007		60.0	0.081	0.048	0.007
	Predation		102.0	0.102	0.102	0.003		147.0	0.147	0.147	0.011
	Total		973.0	1.438	0.814	0.120		699.0	0.827	0.610	0.102
Medium larvae	Unknown	186	47.3	0.330	0.189	0.017	390	48.0	0.162	0.098	0.016
	Parasitism		54.8	0.373	0.220	0.020		109.7	0.338	0.231	0.038
	Disease		17.0	0.129	0.064	0.005		61.7	0.204	0.128	0.021
	Predation		44.0	0.236	0.236	0.009		64.8	0.166	0.166	0.013
	Total		163.1	1.068	0.708	0.067		284.2	0.870	0.622	0.107
Large larvae	Unknown	54	4.4	0.090	0.055	0.003	147	26.1	0.229	0.170	0.023
	Parasitism		8.0	0.158	0.101	0.006		33.0	0.282	0.218	0.030
	Disease		2.2	0.045	0.027	0.002		26.1	0.229	0.170	0.023

Table 4. (Continued) Death-rate analysis for *S. exigua* larvae in cotton under three insecticide regimes in 1990.

Stage	Mortality factor	July l_x	d_x	m	v’	IM	August l_x	d_x	m	v’	IM
	Predation		17.0	0.313	0.313	0.013		0.0	0.000	0.000	0.000
	Total		31.6	0.607	0.497	0.027		85.2	0.740	0.558	0.082
Pupae		27					65				
						λ-cyhalothrin alone					
Small larvae	Unknown	1,000	471.0	0.675	0.451	0.110	1,000	261.0	0.316	0.258	0.033
	Parasitism		271.0	0.440	0.243	0.054		231.0	0.284	0.228	0.029
	Disease		129.0	0.221	0.098	0.014		60.0	0.081	0.056	0.007
	Predation		0.0	0.000	0.000	0.000		0.0	0.000	0.000	0.000
	Total		871.0	1.336	0.792	0.221		552.0	0.680	0.542	0.071
Medium larvae	Unknown	208	52.8	0.330	0.247	0.035	458	56.3	0.162	0.118	0.015
	Parasitism		61.0	0.373	0.288	0.042		128.6	0.338	0.276	0.035
	Disease		18.9	0.129	0.083	0.011		72.3	0.204	0.153	0.019
	Predation		0.0	0.000	0.000	0.000		0.0	0.000	0.000	0.000
	Total		132.6	0.832	0.618	0.094		257.2	0.704	0.547	0.073
Large larvae	Unknown	79	6.4	0.090	0.081	0.006	207	36.7	0.229	0.112	0.022
	Parasitism		11.7	0.158	0.148	0.012		46.4	0.282	0.143	0.028
	Disease		3.2	0.045	0.040	0.003		36.7	0.229	0.112	0.022
	Predation		0.0	0.000	0.000	0.000		71.1	0.343	0.343	0.032
	Total		21.3	0.294	0.268	0.021		190.9	1.083	0.710	0.147
Pupae		58					60				

TABLE 5. TOTAL INDISPENSABLE MORTALITY[1] TO *S. EXIGUA* LARVAE DUE TO FOUR MORTALITY FACTORS UNDER THREE INSECTICIDE REGIMES IN 1990.

	Untreated and diflubenzuron		λ-cyhalothrin + diflubenzuron		λ-cyhalothrin only	
Mortality factor	July	August	July	August	July	August
Unknown	0.080	0.031	0.114	0.104	0.242	0.097
Parasitism	0.057	0.047	0.082	0.159	0.172	0.147
Disease	0.011	0.019	0.015	0.064	0.032	0.059
Predation	0.039	0.073	0.031	0.027	0.000	0.032

[1]Indispensable mortality was calculated from larval death rates by subtracting the number entering the pupal stage when the mortality factor was included from the number entering the pupal stage when the factor was not included.

DISCUSSION

This study demonstrated that, as Luck et al. (1988) suggested, biases associated with the use of a single natural enemy exclusion method can be at least partially overcome by combining methods. For example, if our experiment had included only exclusion cages (no λ-cyhalothrin treatments), effects of natural enemies would have been apparent in August because of higher survival when *S. exigua* were protected from natural enemies by the cages (Fig 4C). In July, however, cage effects also reduced *S. exigua* survival. Evidence included greater mortality in partial exclusion cages than in total exclusion cages, coupled with similar survival in total exclusion cages and with no predator exclusion (Fig. 4A). The insecticide exclusion experiment showed that λ-cyhalothrin reduced predator populations and that *S. exigua* was abundant in treated plots. However, this experiment did not eliminate reduced parasitism or disease incidence, trophobiosis or hormoligosis as mechanisms of outbreak induction. Combining cage exclusion with insecticide exclusion demonstrated that, in plots treated with insecticides, the increase in *S. exigua* populations resulted from fewer natural enemies. Because rates of disease, parasitism and "unknown" mortality of collected larvae were not different across insecticide treatments, differences in *S. exigua* population densities (Fig. 2) between insecticide treatments could be attributed to differences in predation.

The death rate analyses for experimentally manipulated populations effectively demonstrated which mortality factors were important in both insecticide-treated and untreated cotton. This analysis also showed that different factors were important for mortality in outbreak and nonoutbreak populations.

Estimating predation rates based on exclusion cages with the formula of Royama (1981), which subtracts effects of parasitism from combined effects of parasitism and predation, suffers some of the shortcomings of the common practice of assigning unexplained mortality to predation. If rates of parasitism are low, as in 1989, estimates of predation should be relatively accurate. In 1990, observed mortality due to parasitism of collected larvae usually was at least equal to estimates of mortality due to a combination of parasitism and predation in exclusion cages. Thus, if estimates of mortality due to combined factors are accurate and parasitism is common, predation may be seriously underestimated.

As in California cotton (Eveleens et al. 1973; Hogg & Gutierrez 1980), when predator populations were not disrupted with insecticides, *S. exigua* populations were held below outbreak densities primarily by polyphagous predators. In California, adult and immature *Geocoris pallens* Stalh, *Orius tristicolor* (White), *Nabis americoferus* Carayon and immature *Chrysopa carnea* Stephens were important predators of *S. exigua* eggs and newly eclosed larvae (Eveleens et al. 1973). Many of the same, or closely related species, are common in Alabama cotton (Gaylor & Gilliland 1976; Fleischer et al. 1985). Fire ants also have been reported to be effective *S. exigua* predators in Alabama (Cobb 1973). All of these polyphagous predators, except adult *Nabis* spp., are capable of entering cages covered by the medium mesh, and may have contributed to natural control of *S. exigua*. However, only fire ants were more abundant in plots with few *S. exigua* larvae than in plots with dense larval populations. Thus, circumstantial evidence indicates that fire ants were key *S. exigua* predators in plots that were not treated with λ-cyhalothrin.

When populations of predators were not reduced by insecticides, as in 1990, the parasitoid, *C. marginiventris*, was relatively unimportant as a larval mortality agent. The species was important in reducing populations of small and medium *S. exigua* in both insecticide-treated and untreated plots in July 1990. Despite high levels of parasitism by *C. marginiventris* in August 1990, the parasitoid was not responsible for the sparse *S. exigua* populations in cotton that had dense predator populations. When predators were present, they attacked both parasitized and unparasitized *S. exigua*, and little damage to cotton occurred. Parasitism was insufficient to prevent an economically damaging *S. exigua* population from occurring in plots with few predators. Despite the presence of the parasitoid, defoliation of cotton treated with λ-cyhalothrin was severe in August. Thus, the presence of a sufficient predator population was necessary to prevent an outbreak of *S. exigua*. This does not imply that parasitoids were unimportant in regulating populations of *S. exigua*. Our treatments did not affect parasitoid attack rates. If parasitism had been reduced by insecticide applications, we would have expected to observe even more dramatic increases in beet armyworm larval populations.

In California, egg predation (39%) also was important to *S. exigua* population regulation (Hogg & Gutierrez 1980). We did not estimate egg mortality, but it probably was not important in λ-cyhalothrin-treated plots in 1990 because predator populations were sparse. If 39% egg predation were added to our death-rate analyses for plots with predators, l_x for small larvae would be reduced to 610. However, indispensable mortality for egg predation in plots with predators would be only 0.007 for each cohort in control plots and 0.010 in combination plots in July 1990. In 1989, IM for eggs would have been 0.103 and 0.003 for July and August, respectively. Thus, 39% egg predation would have been important only in July 1989. Instead of determining which factors regulate densities of an entire host generation, pest managers may want to know which mortality agents in an agroecosystem reduce the pest population density before it reaches a damaging stage or before it enters sites where it is protected from natural mortality agents or pesticides. Small and medium size *S. exigua* cause less damage to cotton than do large larvae. Therefore, a primary objective of some cotton IPM programs is to establish conditions that favor mortality by natural enemies to *S. exigua* eggs and small and medium size larvae, so that economically damaging numbers do not survive to the large size class.

Survival past the larval stage is important only if survivors contribute to a subsequent generation that causes economic injury. Thus, mortality to large larvae of the July *S. exigua* generation is important only if survivors contribute substantially to outbreaks in August. Mortality to pupae could be important, but pupal mortality apparently is negligible (Hogg & Gutierrez 1980). The occurrence of each *S. exigua* generation is associated with peaks in adult flight activity (Trumble & Baker 1984). The role of immigration in *S. exigua* outbreaks in August is unknown but may be important. Thus, the relative importance of the July *S. exigua* generation and of immigration in August to outbreaks in August is unclear.

The August *S. exigua* generation does not contribute to subsequent damage to cotton. Most cotton in Alabama is not susceptible to *S. exigua* damage after August, and *S. exigua* apparently does not readily overwinter in the state. Thus, natural mortality to early developmental stages of the August generation should be more important to the pest manager than is mortality to the entire generation. Diseases of large larvae were most important in the decline of the *S. exigua* outbreak in August 1989. However, natural mortality due to predation on early developmental stages may have been more important than mortality to later stages if the goal was to avoid a damaging outbreak.

Unlike most population ecologists, pest managers often are confronted with identifying natural control agents in an agroecosystem that has been modified by insecticides. Despite the risks of insecticide-induced outbreaks of *S. exigua*, pyrethroids usually are applied in southern Alabama cotton for control of *Helicoverpa zea* (Boddie) and *Heliothis virescens* (F.). Consequently, the pest manager also may want to know which mortality factors might be manipulated to reduce the density of a pest population that has reached damaging levels as a result of insecticide applications. Adult and pupal *C. marginiventris* are susceptible to pyrethroids (Ruberson et al. 1993), but during 1990, rates of parasitism by this species were not different in treated and untreated cotton. When a broad-spectrum insecticide must be applied to control other pests, parasitism and disease may be the most important natural mortality factors remaining. If techniques can be developed for augmenting populations of *C. marginiventris* or diseases, these natural enemies might have potential in applied biological control programs.

Levins & Wilson (1980) listed several reasons for the lack of application of ecological theory to agroecosystems. A primary reason for this situation is the different perspectives of the basic ecologist and the pest manager. However, questions of interest to both the ecologist and the pest manager can be addressed by combining experimental methods that are commonly used in studying natural control in agroecosystems with death-rate analyses or with life tables.

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