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Natural Biological Control of Western Yellow-striped Armyworm, *Spodoptera praefica* (Grote), in Hay Alfalfa in Northern California

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End of Volume

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The effect of natural enemies on populations of western yellowstriped armyworm *(Spodoptera praefica* [Grote]) was assessed in hay alfalfa in the Sacramento Valley of California. Analysis of partial age-specific life tables (i.e., egg to pupa) revealed that most of the generation or real mortality of *S. praefica* occurred during the egg-small-larval age interval. Experimentation revealed that such mortality was largely due to a complex of polyphagous predators. Predators included larvae of *Chrysopa carnea* Stephens; adults and nymphs of *Geocoris pallens* Stål, *G. punctipes* (Say), *G. atricolor* Montandon, *Nabis americoferus* Carayon, *N. alternatus* Parshley, and *Orius tristicolor* (White); adults of *Collops vittatus* (Say); and the notorious ''pest'' species, *Lygus hesperus* Knight. Parasites and disease had a relatively minor impact on populations of *S. praefica.* The results provide further support for biological control of insect pests in temporary agroecosystems and illustrate the importance of polyphagous predators in such biological control.

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Natural Biological Control of Western Yellow-striped Armyworm, *Spodoptera praefica* (Grote), in Hay Alfalfa in Northern California[1]

INTRODUCTION

WESTERN YELLOW-STRIPED ARMYWORM, *Spodoptera praefica* (Grote), is native to the western United States and is an occasional pest of such crops as alfalfa, cotton, sugar beet, and tomato (van den Bosch and Smith, 1955). Periodic outbreaks occur on hay alfalfa in northern California. Several aspects of the biology of this insect were investigated by van den Bosch (1950) in the San Joaquin Valley of California. More recently, Miller (1977), Miller and Ehler (1978) and Miller (1980) studied the ecological relationships among its three major parasitoids in the Sacramento Valley. However, the impact of all natural enemies on populations of this insect has not been thoroughly investigated. The purpose of this study was to evaluate impact of the natural enemies, including parasitoids, predators, and a pathogen, on populations of *S. praefica* on hay alfalfa in northern California. These investigations were conducted during the growing seasons of 1978 and 1979 in the vicinity of Davis, (Yolo County) California.

Results obtained have implications for classical biological control. Alfalfa is a highly disturbed habitat, and *S. praefica* is a native insect preyed upon by native natural enemies, especially generalist predators. Thus, this ecological system is appropriate for assessing (1) feasibility of biological control in temporary or disturbed agroecosystems and (2) utility of general (polyphagous) predators in biological control. Both questions have been debated among practitioners of biological control for a number of years.

BIOLOGY OF *S. PRAEFICA*

Adults of *S. praefica* are nocturnal; both mating and oviposition occur mainly between dusk and midnight. Clusters of about 140 to 1,200 eggs are deposited. A mated female may lay up to 1,500 eggs and live up to 12 days (van den Bosch, 1950). The egg mass is covered by gray scales derived from the tip of the female's abdomen. Eggs are generally laid on the surfaces of alfalfa leaves. Larvae pass through six or seven instars. Pupation is in the soil about 5cm below the surface.

Van den Bosch (1950) listed over 60 species of plants as hosts of *S. praefica.* Among these were such crop plants as alfalfa, cotton, sugar beet, tomato, and bean. However, he considered alfalfa to be the most preferred crop for larvae. He also found that, among the uncultivated plants, filaree *(Erodium)* was preferred over many plants that larvae fed upon. Blanchard and Conger (1932) observed that *S. praefica* preferred rangeland plants (e.g., filaree and foxtail) in early season; later the preference shifted to alfalfa and morning glory. This preference may explain observed trends in seasonal occurrence of the larvae of *S. praefica* on hay alfalfa (see below).

According to van den Bosch (1950) and weekly reports of the *California Plant Pest Report,* the first flight of *S. praefica*

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(in central and northern California) can occur as early as mid-January. However, our observations and those of Miller (1977) and Miller and Ehler (1978) indicate that larvae of *S. praefica* will generally not be collected from hay alfalfa until early May. Thus, the first (and possibly part of the second) generation is probably spent in the foothills or in nonagricultural areas on hosts such as filaree and foxtail. Later, when these plants dry up, *S. praefica* presumably moves into cultivated areas of the valley, and the remaining generations are passed on plants such as hay alfalfa. The insect overwinters as a diapausing pupa in the soil, presumably in both cultivated and uncultivated lands.

Apparently, *S. praefica* has four generations in northern California. The first, which may take three months (from mid-January to mid-April), is apparently restricted to noncultivated areas such as rangeland. The second, which takes 1.5–2 months (from mid-April to early or mid-June), probably occurs in both noncultivated and cultivated zones. The density during this generation on hay alfalfa is not usually sufficient to cause economic damage. The third and fourth generations, which occur from late June to early September, may reach comparably high densities and cause serious damage to hay alfalfa as well as other crops. These generations on hay alfalfa are discrete and thus lend themselves to a life-table analysis. In the present study, age-specific life-tables were constructed and analyzed for these two generations.

NATURAL ENEMIES OF *S. PRAEFICA*

Several species of predators and parasites, plus at least one pathogen, are associated with *S. praefica* in hay alfalfa. Much of the relevant information on the predators was summarized by van den Bosch and Hagen (1966) and Ehler (1977). The latter information is updated here and pertinent biological details of the parasites and pathogen are given.

Predators

Chrysopa carnea **Stephens (Neuroptera: Chrysopidae).** Larvae of *C. carnea* are polyphagous predators in California cotton (Ehler and van den Bosch, 1974). We observed all larval instars feeding upon eggs and larvae of *S. praefica* in the field. Adults of *C. carnea* are not predaceous and rely on substances such as honeydew for maintenance and egg production. In this regard, K. S. Hagen and co-workers have developed a "food spray" containing a yeast product and sucrose which can attract adults and stimulate egg production (Hagen, Sawall, Jr., and Tassan, 1971; Hagen *et al.*, 1976; Tassan, Hagen, and Sawall, Jr., 1979). Research on *C. carnea* in recent years has dealt extensively with systematic and evolutionary biology (e.g., Tauber and Tauber, 1973; 1975; 1977; Tauber, 1974). New (1975) reviewed the use of *Chrysopa* and related species as biological control agents.

Geocoris **spp. (Hemiptera: Lygaeidae).** Three species of *Geocoris* occur in hay alfalfa in northern California: *G. pallens* Stål, *G. punctipes* (Say), and *G. atricolor* Montandon (Benedict and Cothran, 1975). The first is usually most abundant. In this study, these species were not separated and hereafter are referred to as *Geocoris* spp.

Ehler and van den Bosch (1974) considered *G. pallens* to be polyphagous. Ridgway and Jones (1968) and Tamaki and Weeks (1972) demonstrated omnivory in *G. pallens,* and recently, Yokoyama (1980) reared them on a diet of sunflower seeds plus eggs and nymphs of large milk-weed bug, *Oncopeltus fasciatus* (Dallas).

Yokoyama (1978) observed adults and nymphs of *G. pallens* maintaining themselves on extrafloral nectar of cotton plants during the period when suitable prey species were not available. Yokoyama (1978) suggested that nectar may have evolved as a defense mechanism by plants for protection against herbivores—i.e., extrafloral nectar would provide the predator with an alternate food in the absence of the suitable prey, whereas the predator in turn would help protect the plant from phytophagous insect attack. Lima (1980) further investigated the importance of nectar feeding on longevity, development, and survival of *G. pallens* on selected cotton genotypes. When *G. pallens* were provided with an abundance of prey, they did not necessarily require nectar for development and survival. However, when deprived of prey, nectar was necessary for survival and development of both adults and nymphs. The rate of prey consumption by adult females was apparently lower on nectaried plants compared to nectar-less plants.

***Nabis* spp. (Hemiptera: Nabidae).** Two species of *Nabis—N. americoferus* Carayon and *N. alternatus* Parshley—occur in alfalfa in northern California. Data of Benedict and Cothran (1975) suggested that *N. americoferus* was always more abundant than *N. alternatus,* but *N. alternatus* appears to be more abundant in the desert valleys of southern California (van den Bosch and Hagen, 1966). Benedict (1975) referred to *N. americoferus* as an opportunistic, polyphagous predator, feeding on the most common, catchable prey species found in alfalfa. Plant feeding by adults and nymphs of *N. americoferus* has also been reported—e.g., Ridgway and Jones (1968) and Stoner (1972) found that plant food (e.g., sap), in conjunction with insect prey, increased longevity of adults.

Two species of parasitoids are reported to parasitize both species of *Nabis* in northern California: A mymarid egg parasite, *Polynema striaticorne boreum* Girault, and a tachinid parasite of adults, *Leucostoma simplex* (Fallen). Benedict and Cothran (1978) believed parasitization by these species could be a regulating factor for *Nabis* populations.

***Orius tristicolor* (White) (Hemiptera: Anthocoridae).** Ehler and van den Bosch (1974) considered *O. tristicolor* a polyphagous predator, even though it may preferentially feed on thrips or spider mites. Also, plant feeding has been demonstrated in this insect. Salas-Aguilar and Ehler (1977) demonstrated that a diet of pollen plus thrips was a suitable diet for development of nymphs, and a diet of green bean plus pollen and thrips was a good diet for increased longevity and fecundity of adults. Yokoyama (1978) observed nymphs and adults feeding on extra-floral nectar of cotton plants. Ryerson and Stone (1979) provided a selected bibliography of both *O. tristicolor* and *O. insidiosus* (Say).

***Collops vittatus* (Say) (Coleoptera: Malachiidae).** Ehler (1977) considered *C. vittatus* to be polyphagous. Nectar feeding by adults of *C. vittatus* was observed by Yokoyama (1978). We observed that this insect can be a voracious predator of eggs and small larvae of *S. praefica,* but its apparent preference for non-prey items—pollen, for example—may reduce its predatory capabilities.

***Lygus hesperus* Knight (Hemiptera: Miridae).** Literature on pest status of *L. hesperus* on several crops is plentiful. In the San Joaquin Valley, *Lygus* populations increase to high levels in hay alfalfa, although they cause no great economic damage. When the hay fields are harvested, *Lygus* adults often migrate to adjacent cotton fields and can cause severe damage (van den Bosch and Stern, 1969). Although *L. hesperus* is predominantly phytophagous, it was frequently observed feeding on *S. praefica* egg masses. Others have reported predatory behavior of lygus bug on a number of prey species. Eveleens *et al.* (1973) observed adults of *L. hesperus* feeding on egg masses of beet armyworm (*Spodoptera exigua* [Hübner]). Therefore, this species is considered part of the predator complex in the present paper.

Miscellaneous predators. Additional species of predatory arthropods occur in hay alfalfa and probably contribute to the overall level of biological control in the system. These include an assasin bug (*Zelus renardii* Kolenati), a soldier bug (*Sinea diadema* [Fabricius]), spiders, dragonflies, and the like. However, densities of these predators were never high, and it is unlikely that they are of any importance with respect to ecology of *S. praefica.*

Parasitoids

Van den Bosch (1950) listed nine species of Hymenoptera and four of Diptera which parasitized *S. praefica.* However, Miller (1977) found that three species of parasitoids accounted for about 95 percent of the apparent mortality of larvae due to parasitization in hay alfalfa in northern California. In this study, the same three parasitoids were the major ones encountered, and only these will be considered.

***Chelonus insularis (= texanus)* Cresson (Hymenoptera: Braconidae).** This is a solitary, egg-larval parasite of *S. praefica,* as well as certain other noctuids (van den Bosch and Hagen, 1966), and was considered polyphagous by Ehler (1977). The female oviposits into the egg of *S. praefica,* and the immature develops within the larva of the host. The parasitoid larva remains within the host until the fourth or fifth host instar. Then the *S. praefica* larva enters the soil prematurely and forms a small earthen cell. The adult parasite emerges from (and kills) its host and spins a white silken cocoon. We observed female wasps several times in the field moving about over the surface of egg masses, dragging the ovipositor and frequently inserting it into an egg. Once a female found the egg mass, she parasitized a large percentage of the eggs.

***Hyposoter exiguae* (Viereck) (Hymenoptera: Ichneumonidae).** This species is a solitary endoparasite of larvae of *S. praefica* as well as many other lepidopteran insects. Ehler (1977) considered it a polyphagous parasitoid. The female oviposits in the early instar host larvae, and all larval stages of the parasitoid are spent within host larvae. The host larva is eventually killed, and the mature parasite larva spins a cocoon attached to the substrate.

***Apanteles marginiventris* (Cresson) (Hymenoptera: Braconidae).** This species is a solitary endoparasite of larvae of *S. praefica.* Ehler (1977) considered it polyphagous. According to van den Bosch (1950), eggs are laid in the body of first or second instar larvae of *S. praefica.* The immature parasitoid develops within the host larva, eventually emerges from it, and spins a white silken cocoon when the host is in the fourth instar. The adult parasitoid later emerges from the cocoon.

Ecological relationships among the three parasitoids in hay alfalfa were discussed by Miller (1977), Miller and Ehler (1978) and Miller (1980). The occurrence of more than one species of parasitoid in a subsample did not reduce total parasitization of larvae of *S. praefica.* Based on reproductive potential and intrinsic competitive ability of these species, Miller (1977) classified them according to the continuum of r- and K-selection (see MacArthur and Wilson, 1967). In this case, *Chelonus insularis* was considered more r-selected and *Hyposoter exiguae* more K-selected, with *A. marginiventris* being intermediate. However, Miller and Ehler (1978) argued that the three species, being more abundant than 10 other species mentioned by van den Bosch (1950), should be considered more r-selected than the others. Miller (1980) suggested that durational stability of the hay-alfalfa agroecosystem—rather than interspecific competition—strongly influenced species composition in this parasitoid guild.

Pathogen

A nuclear polyhedrosis virus (NPV) was the only pathogen found to cause mortality in field populations of *S. praefica.* This virus has been recognized in the western United States since at least 1932 (Blanchard and Conger, 1932) and was first diagnosed by E.A. Steinhaus from a specimen collected at Tracy, California, in 1946. Steinhaus isolated the virus and described it as *Borrelina olethria* Steinhaus in 1949 (Steinhaus, 1951). Van den Bosch (1950) reported epizootics of this virus in populations of *S. praefica* in several alfalfa fields in California.

Baculoviruses of Lepidoptera, including NPV of *S. praefica,* have been shown to be less host-specific than originally thought (Tinsley, 1979). Thus, this virus may be cross-infective to closely related species such as *S. ornithogalli* (Guenee) and *S. exigua* (Hbn.) and even other noctuids which occur in hay alfalfa. However, the necessary host-specificity and cross-infectivity tests have not been conducted.

THERMAL REQUIREMENTS

Phenology and development of insects are temperature dependent. The relationship between temperature and rate of development has been studied for many insects (Campbell *et al.,* 1974; Morris and Fulton, 1970). In such studies, developmental velocity (the inverse of developmental time) is regressed against temperature. Developmental velocity/temperature relationships for insects are seldom linear especially at high and low temperatures; however, they are usually linear at intermediate temperatures. The latter phenomenon has often been used to establish a theoretical threshold temperature for development (Arnold, 1960). For a given species or developmental stage, the temperature below which no measurable development occurs is the threshold of development. The amount of heat units required over time for an insect to complete some aspect of its development is a thermal constant (Campbell *et al.,* 1974).

The heat unit or degree-day accumulation system has implications for pest management as well as other areas of applied entomology. The degree-day system is a fundamental basis for temperature-dependent population models which have been widely used for prediction of population events in the past decade (e.g., Gilbert and Gutierrez, 1973; Guppy and Harcourt, 1978; Whalon and Smilowitz, 1979). Also, using the degree-day system, indices have been developed for predicting the need for and timing of pesticide applications for many pest species (e.g., Sevacherian, 1977; Reid and Laing, 1978; Johnson *et al.,* 1979).

In this section, the developmental threshold and degree-day requirements for all developmental stages of *S. praefica* are reported. Results of these studies are used in construction of age-specific life-tables for generations of *S. praefica* in later sections. Developmental threshold and degree-day requirements may also be of value to future investigators in developing pest-management programs for *S. praefica.*

Materials and methods

Larvae of *S. praefica* were field collected and colonized in the laboratory under the following environmental conditions: 16 hr photoperiod, 30 ± 1 °C and 40 ± 5% R.H. To maintain genetic quality of the colony, moths reared from field-collected larvae were added at every possible opportunity. Egg masses were collected from cages in the rearing room daily and transferred to 1 oz (30 cc) capped plastic cups. Cups were placed in growth chambers (16 hr photoperiod) until the eggs hatched. When eggs were near hatching, they were examined every 2 hours, and hatching times were recorded. Upon hatching, first-instar larvae were transferred to and held individually in 2 oz (60 cc) capped plastic cups. Each cup contained a small bouquet of fresh alfalfa, placed in a small vial filled with distilled water. Fresh alfalfa was supplied as needed. Larval development was observed every 8–12 hr, depending on the speed of development. Instar determination was accomplished by painting a small spot on the dorsum of the larva with "Catalina Tempera 105 Red Orange" (Ray Color Co., Inc., Los Angeles). The paint apparently did not cause any abnormality or change in the development of larvae. When a larva was ready to pupate, the alfalfa bouquet was removed and the cup was half filled with sterilized sand to provide a pupation site. The pupae were kept in a growth chamber until adult emergence.

Five temperatures were chosen: 15, 20, 25, 30, and 35 °C, with 16 hr photoperiod in all regimes. Sample size for eggs varied from 46 to 141 egg masses at each temperature, and that for larvae varied from 56 to 80 newly hatched first instar larvae for each temperature. Larvae that died before completing a stage were discarded and not included in the attendant analysis. Therefore, the number of individuals under consideration decreased from first to last instar larval, especially at low and high temperatures.

Results and discussion

Hatching of eggs and larval development occurred in all five temperature regimes. However, no larvae in the 15 °C regime pupated. Pupal mortality at 35 °C was also high and only 26 percent of the attendant sixth instar larvae developed into adults. High mortality in these two regimes was probably due to the adverse effects of extreme temperatures, as mortality in other regimes was not especially high.

Mean developmental times, standard deviations and sample sizes for individuals in these regimes are presented in table 1. Duration of developmental stages decreased with increase in temperature, up to 30 °C. At 35 °C, duration of most developmental stages was essentially the same as that obtained at 30 °C. However, duration of the pupal stage was longer at 35 °C than 30 °C. It would thus appear that 35 °C is not in the linear portion of the developmental velocity/temperature curve; thus the data obtained at 35 °C were not used in regressing the developmental velocity against temperature. Developmental times obtained at 15, 20, 25, and 30 °C, which were in the linear portion of the curve, were used in calculating heat units.

Recriprocals of days needed for development of eggs, larva, prepupa, pupa, egg-to-prepupa, and egg-to-adult were regressed against temperature to estimate respective developmental thresholds. Regression equations and sample coefficients of determination are shown in table 2. The coefficient of determination for most stages was higher than 0.95, which indicates temperature explains virtually all of the variation in developmental rate. The X-intercepts for the regression lines were used to estimate the developmental thresholds. Thresholds varied from 11.43 to 13.46 °C. The estimated developmental threshold for the prepupal stage (15 °C) was consistent with results of developmental studies at 15 °C. That is, no measurable development occurred beyond sixth instar among larvae reared at 15 °C. Hence, regression equations for prepupal and pupal stages were determined from results obtained at 20, 25, and 30 °C.

The thermal constant is the number of day-degrees above the developmental threshold required for completion of a developmental stage. Mathematically, it is the reciprocal of the slope (b) of the regression line (Campbell *et al.*, 1974). The day degrees required for completion of each stage and combination of stages were calculated using this technique. These are shown in the fifth column of table 2. Development of egg, larval, pupal stages, and from egg-to-adult required 49.02, 185.19, 169.49, and 392.16 day degrees, respectively.

TABLE 1
DEVELOPMENTAL TIMES OF *S. PRAEFICA* IN RELATION TO TEMPERATURE

Developmental stage	Sample size and mean developmental time (days) at indicated temperatures									
	15 °C		20 °C		25 °C		30 °C		35 °C	
	N	$\bar{X}$ ± SD	N	$\bar{X}$ ± SD	N	$\bar{X}$ ± SD	N	$\bar{X}$ ± SD	N	$\bar{X}$ ± SD
Egg	141	12.11 ± 1.12	75	7.40 ± .82	128	3.90 ± .86	46	2.61 ± .10	47	2.49 ± .36
1st instar	80	7.52 ± .18	56	4.75 ± 0	56	2.75 ± 0	56	1.79 ± 0	56	1.83 ± 0
2nd instar	80	7.00 ± .21	56	3.72 ± .27	56	2.50 ± .21	56	1.14 ± .17	56	1.20 ± .32
3rd instar	76	8.20 ± .58	56	3.24 ± .27	56	1.88 ± .27	55	1.36 ± .22	56	1.33 ± .14
4th instar	42	12.00 ± 1.94	54	3.82 ± .32	56	2.13 ± .26	54	1.31 ± .24	55	1.31 ± .23
5th instar	30	16.20 ± 3.20	54	4.59 ± .59	56	2.66 ± .36	52	1.95 ± .24	55	1.92 ± .32
6th instar	16	26.20 ± 5.60	51	7.63 ± 1.03	56	3.88 ± .42	52	3.04 ± .54	50	3.44 ± .38
1st–6th instar	—	77.12 ± 11.71	—	27.48 ± 2.48	—	15.8 ± 1.52	—	10.59 ± 1.41	—	11.03 ± 1.39
Prepupa	—	—	47	4.22 ± .34	53	2.29 ± .31	52	1.46 ± .24	36	1.40 ± .19
Pupa	—	—	33	21.23 ± 3.65	51	12.24 ± .93	50	8.59 ± .67	13	10.96 ± .92

TABLE 2
THERMAL REQUIREMENTS FOR DEVELOPMENT OF *S. PRAEFICA*

Developmental stage	Regression equation	r^2	Developmental threshold	Thermal constant
Egg	Y = −.2447 + .0204 X	.97	12.00	49.02
1st instar	Y = −.3270 + .0286 X	.97	11.43	34.97
2nd instar	Y = −.6287 + .0467 X	.90	13.46	21.41
3rd instar	Y = −.4988 + .0410 X	.99	12.17	24.39
4th instar	Y = −.6202 + .0451 X	.99	13.75	22.17
5th instar	Y = −.3875 + .0302 X	.99	12.83	33.11
6th instar	Y = −.2610 + .0200 X	.99	13.03	50.00
Prepupa	Y = −.6780 + .0452 X	.99	15.00	22.12
Pupa	Y = −.0780 + .0064 X	.95	12.19	156.25
1st—6th	Y = −.0700 + .0054 X	.99	12.96	185.19
Egg—6th	Y = −.0530 + .0044 X	.99	12.05	227.27
Egg—adult	Y = −.0340 + .0025 X	.98	13.35	392.16
Prepupa + pupa	Y = −.0781 + .0059 X	.99	13.24	169.49

LIFE-TABLE STUDIES

In 1978, field populations of *S. praefica* did not become large enough for life-table analysis until late July. Therefore, an age-specific life-table was constructed for only the fourth (August) generation. In 1979, however, age-specific life-tables were constructed for the third and fourth generations. Life-table analysis was used to quantify different mortality factors and to indicate which could be considered the major intrageneration mortality factor.

Materials and methods

A 22-acre (8.91 hectares) alfalfa field near Davis, California, planted in 1977 to Moapa 69 variety, was the study site. This field was surrounded by older alfalfa fields on three sides and an interstate highway on the fourth. One application of insecticide was applied for control of alfalfa weevil in February in both 1978 and 1979. During the growing season, the field was harvested and flood irrigated at 32 ± 3 day intervals. It was sampled at 4–5 day intervals from early July to late September in 1978 and from early June to early October in 1979. Three sampling methods were utilized; these are explained below.

Egg samples. Eggs of *S. praefica* are in clusters and show a patchy distribution in the field. Optimum sample size for estimating number of eggs was determined by the formula given by Karandinos (1976) for the negative binomial distribution. A circular area (34 cm diam.) was the sample unit; optimum sample size was 400 samples. On each sampling date, a 34-cm diameter wood frame was randomly thrown 400 times in different areas of the field. Leaves of alfalfa plants surrounded by the frame were inspected for egg masses. Egg masses were collected and taken to the laboratory where their gross weight was determined to the nearest 0.01 mg. Egg masses were then kept at 30 ± 1 °C and 16-hour photoperiod until hatching.

A regression equation was established to relate weight of egg masses to number of eggs per mass. Forty egg masses were weighed and number of eggs in each mass determined. The resultant regression equation was $Y = 16.9X + 19.42$, where X represents weight of eggs (mg) and Y the number of individual eggs per egg mass. The difference between predicted number of eggs (from the regression equation) and number of first instar larvae hatching from a given egg mass was used to measure inviability (or infertility) of eggs.

D-Vac samples. Dietrick, Schlinger, and van den Bosch used a vacuum collection machine to measure populations of arthropods associated with alfalfa. We used the back-pack unit, modified by Dietrick (1961), in combination with whole plant samples. A sample unit contained two 34-cm diam. circular areas. In each subsample, plants were sampled with the D-Vac and then clipped near the soil surface. The latter area was sampled again with the D-Vac. Plants were taken to the laboratory and inspected for any arthropods. Arthropods collected by the D-Vac were separated from debris using a Berlese funnel apparatus. On each sampling date, 20 samples (2 subsamples/sample) were taken randomly to estimate absolute density of *S. praefica* larvae and associated natural enemies. Optimum number of samples (20) was determined utilizing the formula given by Karandinos (1976) for a normal distribution.

Sweep-net samples. To assess percent parasitization and incidence of disease, 400 sweep-net samples were taken on each sampling date. A standard (38 cm diam.) sweep net was used. Larvae collected were taken to the laboratory and reared individually on artificial bean diet in capped 30 cc transluscent plastic cups at 30 ± 1 °C. Larvae were inspected daily. Larvae infected with nuclear polyhedrosis virus and parasitized were recorded.

Life-table components

The age-specific life table is a convenient method for measuring mortality occurring in each generation of an insect population. Our format for life tables was modified from that given by Morris and Miller (1954). Emphasis is on intrageneration mortality—specifically, the mortality occurring in early stages of development of *S. praefica*. The column headings for the life-tables are discussed below.

x. This term refers to the age-interval (or developmental stage) of *S. praefica*. The following were used: (1) egg; (2) small larva: first and second instars; (3) medium-sized larva: third and fourth instars; and (4) large larva: fifth and sixth instars. Adult and pupal stages were not included due to sampling limitations. Thus, these life tables are partial ones in which the survival of *S. praefica* is tabulated from egg to last instar larva.

lx. This term denotes the number of individuals alive at the beginning of age class x, or the number entering that stage. Our lx values were calculated using the integration technique of Southwood and Jepson (1962), with some modification.

Mean density of a developmental stage was plotted (ordinate) against time expressed in day-degrees (abcissa), allowing one square/individual/day-degree. Area under the curve was determined; division of the area under the curve by mean developmental time (in day-degrees) yielded the appropriate estimate for lx.

According to Southwood (1978), the technique described above is the crudest and simplest of the methods of integration. However, the method is robust and gives results comparable to many more complicated methods. The lx values given here, however, may be conservative estimates of actual lx values, as some mortality factors (e.g., predators) probably destroyed a portion of the hosts before these could be sampled. The lx values are expressed as number of individuals in 3.6 m^2 (40 ft^2).

dxF. Mortality factors responsible for the number estimated to have died (dx) during the indicated stage are given in this column. For eggs, dxF included failure to hatch, predation and residual (or unknown); for small larvae, it included predation, polyhedrosis, mowing and residual; for medium-sized larvae, it included parasitization (by *C. insularis, H. exiguae,* and *A. marginiventris*), polyhedrosis, mowing, and residual; and for large larvae, polyhedrosis was the only detectable mortality factor.

dx. Number of individuals dying during age interval x is denoted by dx and is expressed in terms of number per 3.6 m^2. Hatch failure for eggs was determined from the field collected eggs held in the laboratory and observed for hatch or nonhatch. Failure to hatch was determined as outlined earlier. Predation on eggs and small larvae was quantified through cage exclusion experiments performed in the field concurrently (see later section). Number of individuals dying from polyhedrosis and parasitization was determined by rearing field-collected larvae on artificial bean diet in the laboratory. The parasitoid species oviposit in different developmental stages of the host; however, in all three species, the adult parasitoids emerge from the third or fourth instar larvae. Therefore, in analysis of life tables, parasitization was considered as mortality of medium-sized (third and fourth instars) larvae. Mortality due to mowing was calculated by assuming that, at time of harvest, all larvae smaller than fifth instar died due to starvation, movement of harvesting machines, and irrigation of the field. Unknown causes (or residual) presumably represent abiotic mortality, sampling error, and undetected predation.

100qx. Apparent mortality, or 100qx, represents the number dying during a given stage as a percentage of the number which entered that stage—i.e., dx as a percentage of lx for a given stage.

100rx. Real mortality, or 100rx, represents mortality during a given stage as a percentage of lx at the beginning of the generation—i.e., egg stage. Thus, 100rx represents total or generation mortality and is used to assess the contribution of mortality factors to intrageneration mortality. Percent mortality in this column is additive.

Analysis of life-table data

Life table data for the fourth (August) generation of *S. praefica* in 1979 are presented in table 3. Most of the generation mortality (96.93%) occurred during the egg-small larval interval; 63.8% of this mortality occurred during the egg stage. Concurrent experimentation (next section) revealed that predation was largely responsible for mortality of eggs. Also, 15.1 percent of the generation mortality occurring during the egg stage is indicated as residual in the life table. This mortality was due to infertility, and other biotic or abiotic factors. In contrast 33.13 percent of the generation mortality occurred during the small-larval stage. Although it was not experimentally verified, a considerable amount of this was presumably caused by predators. Parasitization, polyhedrosis and mowing accounted for 1.44, 2.44, and 1.43 percent of the generation mortality, respectively. A significant finding is that, although parasitoids caused an apparent mortality of 46.96 percent, their contribution to real mortality was only 1.44 percent. Total generation mortality (through last-instar larva) was 99.71 percent.

Life-table data for the third (July) generation of *S. praefica* in 1979 are presented in table 4. Again, most of the generation mortality (97.83%) occurred during the egg-small larval interval. Experimentation (see next section) revealed that most of this was caused by predators. Also 11 percent of the generation mortality was apparently due to the failure of eggs to hatch. Parasitization, polyhedrosis and mowing were minor factors and accounted for 0.73, 1.27 and 1.98 percent of the generation mortality, respectively. Total generation mortality —99.74 percent through last instar— was again high.

Life table data for the fourth (August) generation of *S. praefica* during 1979 are presented in table 5. As before, most of the generation mortality (96.24%) occurred during the egg-small-larval interval. Experimentation (see next section) revealed that most of this was caused by predators. Failure of eggs to hatch accounted for 11 percent of the generation mortality. Parasitization, polyhedrosis, and mowing were again minor factors and caused 1.37, 2.07, and 1.54 percent of the generation mortality, respectively. Total generation mortality (through last-instar larva) was 99.61 percent.

TABLE 3
AGE-SPECIFIC LIFE TABLE FOR FOURTH GENERATION OF *S. PRAEFICA*
DAVIS, CALIFORNIA 1978*

x	lx	dxF	dx	100qx	100rx
Egg	900.92	Predation	438.72	48.7	48.7
		Residual	136.00	15.1	15.1
Small larva	326.20	Predation and unknown causes	268.66	82.36	29.82
		Polyhedrosis	20.28	6.22	2.25
		Mowing	9.54	2.92	1.06
Medium-sized larva	27.72	*C. insularis*	7.20	26.01	.80
		H. exiguae	5.24	18.92	.58
		A. marginiventris	.56	2.03	.06
		Polyhedrosis	1.60	5.74	.18
		Mowing	3.34	12.05	.37
		Residual	7.02	25.32	.78
Large larva	2.76	Polyhedrosis	.12	4.29	.01
Total	—	—	898.28	—	99.71

*Key to symbols: x = developmental stage; lx = number entering stage x; dxF = mortality factor; dx = number dying during stage x; 100qx = percent apparent mortality; 100rx = percent real mortality.

TABLE 4

AGE-SPECIFIC LIFE TABLE FOR THIRD GENERATION OF *S. PRAEFICA* DAVIS, CALIFORNIA 1979*

x	lx	dxF	dx	100qx	100rx
Egg	339.35	Predation	177.82	52.4	52.4
		Hatch failure	37.33	11	11
		Residual	22.62	6.67	6.67
Small larva	101.58	Predation	82.28	81	24.24
		Polyhedrosis	3.33	3.28	.98
		Mowing	5.84	5.75	1.72
		Residual	2.78	2.74	.82
Medium-sized larva	7.35	*C. insularis*	.36	4.92	.11
		H. exiguae	1.63	22.13	.48
		A. marginiventris	.48	6.56	.14
		Polyhedrosis	.98	13.33	.29
		Mowing	.87	11.84	.26
		Residual	2.3	31.29	.68
Large larva	.73	Polyhedrosis	0	0	0
Total	—	—	338.62	—	99.74

*Key to symbols: x = developmental stage; lx = number entering stage x; dxF = mortality factor; dx = number dying during stage x; 100qx = percent apparent mortality; 100rx = percent real mortality.

TABLE 5

AGE-SPECIFIC LIFE TABLE FOR FOURTH GENERATION OF *S. PRAEFICA* DAVIS, CALIFORNIA 1979*

x	lx	dxF	dx	100qx	100rx
Egg	541.81	Predation	291.49	53.8	53.8
		Hatch failure	59.60	11	11
		Residual	13.51	2.49	2.49
Small larva	177.21	Predation	138.22	78	25.51
		Polyhedrosis	7.98	4.5	1.47
		Mowing	6.13	3.46	1.13
		Residual	4.54	2.56	.84
Medium-sized larva	20.34	*C. insularis*	0.92	4.5	.17
		H. exiguae	6.10	30	1.13
		A. marginiventris	0.37	1.8	0.07
		Polyhedrosis	3.25	16	0.60
		Mowing	2.22	10.91	0.41
		Residual	4.7	23.11	.86
Large larva	2.78	Polyhedrosis	0.70	25	0.13
Total	—	—	539.73	—	99.61

*Key to symbols: x = developmental stage; lx = number entering stage x; dxF = mortality factor; dx = number dying during stage x; 100qx = percent apparent mortality; 100rx = percent real mortality.

EXPERIMENTAL STUDIES

Analysis of life-table data for three generations of *S. praefica* revealed that the bulk of the intrageneration mortality occurred during the egg-small-larval interval. Experimentation was used to test the hypothesis that this mortality was largely due to predation. A modified "mechanical (cage) exclusion method" (cf. Smith and DeBach, 1942) was used. These cage-exclusion studies were performed on three occasions.

Materials and methods

In August 1978, four 1-m^3 cages covered with nylon organdy (78-mesh) were randomly placed in the field shortly after mowing. Areas under the cages were vacuumed with a D-Vac machine and then sprayed with fenvalerate. Vacuuming and spraying presumably excluded all parasitoids and predators. Seven days later, egg masses previously laid on paper towel in the laboratory, were stapled onto the leaves of alfalfa plants under the cages (i.e., 1 egg mass/cage). Four egg masses were stapled onto leaves in uncaged areas and thus served as controls. The latter were checked twice daily for predator activity. Shortly before hatch, eggs were collected and the number of surviving eggs determined.

In both July and August 1979, ten 30 × 30 × 45-cm wood cages covered with nylon organdy (78-mesh) were randomly placed in the field shortly after moving. The area under the cages was again sprayed with fenvalerate. Seven days later, egg masses attached to paper towels were stapled onto the leaves (1 mass/cage). Other egg masses (10 in July and 20 in August) were stapled onto leaves in uncaged areas to serve as controls. Egg masses were checked three times daily. All egg masses were removed shortly before they hatched.

Exclusion studies utilizing small larvae of *S. praefica* were conducted in both July and August, 1979. Ten organdy covered cages (predators excluded) and 10 open cages (predators present) were used. Organdy cages were similar to those in the previous test and were sprayed in the same manner. Open cages made of galvanized tin were painted inside with "Fluon T.F.E." (I.C.I. United, Inc., Wilmington, Delaware) to prevent movement of larvae out of the cages. Open cages covered the same amount of area as closed cages.

Seven days after the closed cages were sprayed, 10 newly hatched, first instar larvae of *S. praefica* were introduced into each of the closed and open cages. Four days later (when the larvae were third instars) the areas under each cage were vacuumed and inspected to determine the number of surviving larvae.

A "Student's t-test" was used to test differences in survival in all exclusion experiments. Values of percent survival were transformed to a logarithmic scale, in order to satisfy assumptions of the t-test.

Results and discussion

Survival of eggs of *S. praefica* in areas containing predators vs. without predators is shown in table 6. Approximately 90 percent of the eggs in areas without predators survived to the first instar. Where predators were present, only 44.9 percent of the eggs in 1978 and about 30 percent in 1979 survived to first instar. The differences were all highly significant.

Survival of first instar larvae of *S. praefica* in areas with and without predators is summarized in table 7. Here, 92–93 percent of the larvae in predator-excluded areas survived to the third instar, while only 12 to 14 percent of those exposed to predators survived to third instar. These differences in survival rates were highly significant in both experiments.

Results of the exclusion experiments provide strong empirical support for the hypothesis that generalist predators are responsible for most of the intrageneration mortality of *S. praefica* in hay alfalfa in northern California. Furthermore, it is reasonable to assume that application of broad-spectrum insecticides in hay alfalfa which destroy these predators can lead to outbreaks of *S. praefica* and other pests.

TABLE 6
SURVIVAL OF EGGS OF *S. PRAEFICA* IN CAGES. DAVIS, CALIFORNIA

		Mean % survival		
Experiment	**N**	**Predators absent**	**Predators present**	**t value**
August 1978	4	93.60 ± 2.47	44.90 ± 8.29	5.63**
July 1979	10	88.70 ± 1.75	31.60 ± 10.78	5.24**
August 1979	10, 20	86.94 ± 1.04	30.17 ± 7.98	7.98**

TABLE 7
SURVIVAL OF FIRST INSTAR LARVAE OF *S. PRAEFICA* IN CAGES. DAVIS, CALIFORNIA

		Mean % survival		
Experiment	**N**	**Predators absent**	**Predators present**	**t value**
July 1979	10	93 ± 2.47	12 ± 2.78	21.77**
August 1979	10	92 ± 3.10	14 ± 3.52	16.62**

ANALYSIS OF MORTALITY FACTORS

Predation

About 76 to 79 percent of the generation or real mortality of *S. praefica* was apparently due to predators. Most of this involved predation of eggs and small larvae. The predators observed feeding upon the eggs and small larvae included: adults and nymphs of *O. tristicolor, Geocoris* spp. and *Nabis* spp.; larvae of *C. carnea;* adults of *C. vittatus;* and adults and nymphs of the otherwise phytophagous species, *L. hesperus.*

Seasonal abundances of the major predators in 1978 and 1979 growing seasons are presented in tables 8 and 9, respectively. Analysis of variance was used to estimate differences in mean densities of these predators. Duncan's multiple range test was then utilized to group predators according to mean densities. Results indicated three statistical groups of species in both years. For 1978, *O. tristicolor* was most abundant, whereas *Geocoris* spp., *Nabis* spp., and *L. hesperus* comprised the second group, and *C. carnea* and *C. vittatus* the third. During 1979, the first group included *O. tristicolor* and *Geocoris* spp.; the second included *Nabis* spp. and *L. hesperus;* and the third included *C. carnea* and *C. vittatus.* Differences among mean densities of different groups in both years were highly significant ($P < 0.01$).

Adults and nymphs of *O. tristicolor* comprised 43.5 and 33.6 percent of the predators in 1978 and 1979, respectively. These predators are relatively small compared to other predators and consequently may consume fewer *S. praefica* eggs and small larvae per predator. Also adults and nymphs may preferentially feed upon thrips and spider mites (Ehler and van den Bosch, 1974; Salas-Aguilar and Ehler, 1977). These two factors may impair the efficacy of *O. tristicolor* as a predator of *S. praefica.* However, when populations of thrips and spider mites

TABLE 8

DENSITIES OF COMMON PREDATORS OF *S. PRAEFICA* DURING THE 1978 GROWING SEASON. DAVIS, CALIFORNIA

Predator	Mean no./3.6m² on (date): July*						August*					September*				$\bar{X}$	% of sample
	2	8	12	17	24	28	7	11	17	23	28	8	13	19	25		
O. tristicolor																	
Adult	62	62	148	194	70	160	42	178	96	126	164	52	116	126	72	111.2	21.5
Nymph	96	20	26	48	256	546	84	40	12	46	32	140	124	162	78	114	22.0
Geocoris spp.																	
Adult	24	30	12	42	28	28	16	30	22	20	18	54	30	42	10	27	5.2
Nymph	52	30	98	160	116	150	26	58	50	104	72	114	38	72	70	80.6	15.6
Nabis spp.																	
Adult	28	22	30	22	38	70	32	78	100	22	40	30	32	36	14	39.6	7.7
Nymph	52	20	78	136	82	94	0	6	0	4	0	40	54	68	24	43.8	8.5
L. hesperus																	
Adult	20	2	16	8	64	76	10	16	16	12	28	20	10	20	2	21.4	4.1
Nymph	40	28	136	140	94	92	8	6	18	54	80	48	62	146	106	70.6	13.6
C. carnea																	
Adult	0	0	0	4	2	0	0	0	0	2	2	2	0	0	2	1	.2
Larva	10	0	0	14	18	38	0	6	0	4	0	18	2	2	4	7.8	1.5
C. vittatus																	
Adult	0	0	2	0	0	2	0	0	2	0	0	0	0	4	0	.6	0.1

*Dates coincide with one cutting cycle of alfalfa (ca. 32 days).

TABLE 9

DENSITIES OF COMMON PREDATORS OF *S. PRAEFICA* DURING THE 1979 GROWING SEASON. DAVIS CALIFORNIA

	Mean no/3.6m² indicated date																				
	June-July*					July*				August-September*					September-October*						% of
Predator	13	18	23	29	5	15	20	25	31	12	18	23	28	3	11	15	20	26	2	$\bar{X}$	sample
O. tristicolor																					
Adult	102	87	159	101	60	163	189	158	151	102	91	108	96	124	10	49	74	77	109	105.8	21.4
Nymph	10	9	17	78	295	97	61	6	97	71	40	15	2	15	53	172	54	25	27	60.2	12.2
Geocoris spp.																					
Adult	9	2	32	54	59	35	34	51	74	62	39	64	98	36	6	21	34	44	62	43	8.7
Nymph	41	17	82	79	109	107	221	196	190	257	142	188	104	104	110	178	125	157	179	136.1	27.5
Nabis spp.																					
Adult	8	1	20	32	42	27	23	20	48	25	23	17	12	9	9	29	30	13	33	22.2	4.5
Nymph	49	4	60	59	77	18	54	23	43	86	67	53	71	104	11	27	40	31	23	47.4	9.6
L. hesperus																					
Adult	0	0	41	44	53	8	6	16	29	9	14	14	17	26	5	20	20	9	40	30.1	6.1
Nymph	0	0	50	51	56	27	63	32	89	16	38	27	28	42	14	17	23	19	179	40.9	8.3
C. carnea																					
Adult	1	2	4	3	0	1	0	4	1	1	1	0	0	2	0	0	0	3	16	2.1	.4
Larva	3	2	2	19	18	1	0	11	7	4	0	0	3	9	6	12	2	0	1	5.3	1.1
C. vittatus																					
Adult	0	0	1	0	0	2	1	2	6	6	4	3	4	2	1	1	0	1	1	1.8	.4

*Indicated dates coincide with one cutting cycle of alfalfa (i.e., ca. 32 days).

are low, *Orius* may obtain a large portion of its nutritional requirements from eggs and small larvae of *S. praefica* and related prey species.

Adults and nymphs of *Geocoris* spp. comprised 20.8 and 36.2 percent of the predators in 1978 and 1979, respectively. These predators are very active and were observed voraciously feeding upon the eggs and small larvae of *S. praefica* in the field. Thus, because of their high population densities and voracious feeding habits, *Geocoris* spp. probably destroyed a considerable portion of the eggs and small larvae of *S. praefica.*

Adults and nymphs of *Nabis* spp, comprised 16.3 and 14 percent of the predators in 1978 and 1979 growing seasons, respectively. The two species of parasitoids attacking *Nabis* spp. in northern California may be responsible for the relatively low populations of the predator in hav alfalfa (Benedict and Cothran, 1978). In a laboratory feeding experiment (unpublished data of B.B.-E.), when offered only eggs of *S. praefica,* an average adult *Nabis* consumed more eggs than the other predators ($\bar{X}$ = 118 eggs/adult/24 hr). An adult *Nabis* can consume 24 first-instar lepidopteran larvae during a 24-hour period (Benedict and Cothran, 1980). We observed that a *Nabis* adult would feed upon an egg mass of *S. praefica* for up to 90 minutes and destroy up to 180 eggs.

We suggest that *O. tristicolor, Geocoris* spp., and *Nabis* spp. be considered major predators of *S. praefica* in hay alfalfa in northern California. This is not suprising as these predators play an important role in controlling populations of a number of pest insects in many crops. Also, application of insecticides in cotton can reduce numbers of these predators and cause secondary outbreaks later in the season (Ehler, Eveleens, and van den Bosch, 1973; Eveleens, van den Bosch, and Ehler, 1973; Stoltz and Stern, 1978).

Adults and nymphs of *L. hesperus* occurred in numbers comparable to *Nabis* spp. and comprised 17.7 and 14.4 percent of the predators in 1978 and 1979 growing seasons, respectively. In the laboratory, an adult *Lygus,* when offered only *S. praefica* eggs, consumed as many eggs as an adult *Nabis* (i.e., $\bar{X}$ = 104 eggs/adult lygus/24 hr). However, this does not necessarily mean that *L. hesperus* may be as important as *Nabis* in destroying the eggs and small larvae of *S. praefica* in the field. That is, *L. hesperus* is primarily an herbivorous insect and feeds on plant juices for the most part. The value of this insect as a predator and the extent of its preference for plant vs. animal food is yet to be fully determined.

Larvae and adults of *Chrysopa carnea* did not occur in large numbers in the field and comprised only 1.7 and 1.5 percent of the predators in 1978 and 1979, respectively. This could be due to the lack of dense aphid populations, and consequently lack of honeydew, which is a necessary part of the adult nutrition. Providing proper nutrition for adults could augment this species in the field when this predator is needed for controlling *S. praefica* and other lepidopteran pests. This goal presumably can be achieved by spraying the alfalfa fields with a "food spray" described earlier.

Adults of *C. vittatus* comprised 0.1 and 0.4 percent of the predators in 1978 and 1979 growing seasons, respectively. Observations indicated that adults of this predator can be voracious predators of eggs and small larvae of *S. praefica.* In one case, an adult fed upon a *S. praefica* egg mass for 135 minutes and destroyed the entire mass (235 eggs).

Parasitization

Three species of parasitoids—*C. insularis, H. exiguae* and *A. marginiventris* —accounted for no more than 2 percent of the generation mortality of *S. praefica.* An important fact become clear from the analysis of life-tables: the difference between apparent (100qx) and real (100rx) mortality for these parasitoids. Total parasitization amounted to an apparent mortality of 46.96, 33.61, and 36.30 percent of the medium-sized larvae of *S. praefica* in August 1978, July 1979, and August 1979, respectively. However, corresponding real mortality was only 1.44, 0.73 and 1.37 percent respectively. These results are consistent with those of Miller and Ehler (1978). Thus, assessing impact of natural enemies (especially parasitoids) based on sweepnet samples alone (i.e., apparent mortality) could give misleading results. Finally, our results and those of Miller (1977) and Miller and Ehler (1978) indicate that neither a single parasitoid species nor a combination of them should be considered highly important in controlling populations of *S. praefica* in hay alfalfa. However, as they are generalists (Ehler, 1977; Miller, 1977), and have an impact on populations of other pest species in the alfalfa agroecosystem, their importance as natural enemies in such a context should not be totally overlooked.

Polyhedrosis

Infection with NPV never accounted for more than 3 percent of the generation mortality. Epizootics may occur in populations of *S. praeifca,* particularly late in the growing season. Van den Bosch (1950) reported epizootics of this virus in several fields. He considered NPV one of the major mortality factors of *S. praefica* larvae, especially late in the season. Also, NPV may cause a considerable amount of apparent mortality (e.g., 41% in August 1979) in the medium-sized and large larvae. However, as this mortality usually occurs in older larvae, its contribution to the generation mortality is relatively low (e.g., 0.73% in August 1979).

Mowing

Harvesting hay alfalfa at 32 ± 2 day intervals generates discrete generations of *S. praefica* from June to September, with one generation occurring per cutting cycle. At harvest, most young larvae are presumably killed due to movement of the harvesting machine, subsequent irrigation, and lack of suitable foliage. In construction of life tables, we assumed that individuals younger than fifth instar died as a result of these factors. However, such mortality never exceeded 2 percent of the generation mortality and therefore may not be very important.

Residual

Residual mortality included factors not measured with the sampling techniques utilized. This presumably includes sampling error, other predators, and abiotic mortality. However, residual mortality never exceeded 7 percent of the generation mortality.

IMPLICATIONS FOR BIOLOGICAL CONTROL

Analysis of age-specific life tables and cage exclusion experiments indicated that a complex of general predators was responsible for most of the mortality of *S. praefica* in hay alfalfa. These findings have implications for classical biological control, particularly the feasibility of biological control in temporary habitats and the utility of general predators in biological control.

Feasibility of biological control in temporary agroecosystems has been debated by ecologists and biological-control practitioners over the last two decades. Lloyd (1960) argued that, because most of the successful cases of biological control occurred with pests of perennial plants, such as olive, citrus, and the like, the method may be limited to such crops. Newsom (1970) and Ridgway (1972) came to similar conclusions based on review of records of successful cases of biological control given by DeBach (1964). However, Ehler (1977) and Ehler and Miller

(1978) challenged these views. Their arguments were based largely on the fact that certain noctuid pests of cotton in the San Joaquin Valley of California were under good natural biological control; this control was due largely to a complex of polyphagous predators, as in the case of *S. praefica* in hay alfalfa. However, despite these developments, there are still those who argue that biological control is less promising for pests of annual crops compared to pests of orchard crops, and the like (Simmonds and Bennett, 1977).

Conway (1976) suggested a classification of pests based on their position on the hypothetical r-K continuum. According to his model, there are "r-pests," "intermediate pests," and "K-pests". Conway predicted that natural enemies could not be expected to control r-pests —that chemical control would be the dominant tactic for such pests. Conway's model and its predictions were generally endorsed by Southwood (1977*a, b*). However, Ehler and Miller (1978) challenged the prediction concerning natural enemies of "r-pests" and suggested that such pests may well be controlled by "r-selected" natural enemies. The argument was supported with empirical evidence involving three noctuid pests of cotton in San Joaquin Valley of California.

Our results give further empirical support to the latter argument and add another example to the list of "r-pests" controlled by what could be called "r-strategist natural enemies." The present system for production of hay alfalfa in northern California (harvesting at 32 ± 2 day intervals) creates a highly disturbed habitat. Also, *S. praefica* conforms to Conway's description of an "r-pest;" it has high reproductive potential, short generation time, good dispersal ability, and catholic food preferences. Females of *S. praefica* can deposit an average of 626 eggs/female (van den Bosch, 1950), whereas generation time (egg to egg) in a typical summer month (daily $\overline{X}$ of 25 °C) is about 33 days (see table 5). Van den Bosch (1950) listed over 60 species of plants as hosts of *S. praefica,* which clearly attests to its polyphagous nature. Adult *S. praefica* are also capable fliers. Flight from rangelands to the cultivated areas is an indication of strong dispersal ability of the moth (Blanchard and Conger, 1932; van den Bosch, 1950). These characteristics are of particular value in enabling this insect to keep pace with the disruptions of harvesting that occur in the alfalfa agroecosystem and the summer drought that occurs in rangeland areas.

Our analysis indicated that populations of *S. praefica* were primarily controlled by a complex of generalist predators. As documented by Ehler (1977), these predators are polyphagous, colonizing species and show an extreme r-strategy. (Here, we use the term r-strategist as a shorthand notation for opportunistic species as opposed to more operational definitions of the term.) Among the predators, *O. tristicolor, Geocoris* spp. *Nabis* spp., and *L. hesperus* are also omnivorous. Predators were present in alfalfa even before *S. praefica* were detected. They presumably maintained relatively high population levels by feeding upon available prey species and/or plant juices (except *C. carnea* and *C. vittatus*). When *S. praefica* arrived, predators apparently destroyed most of the eggs and small larvae and thus prevented any significant crop damage.

Host-specific natural enemies, such as parasitoids, if they were to control populations of *S. praefica,* would require certain characteristics to enable them to keep pace with the unstable habitat and the long-range dispersal of their host. Also, at each harvest the agroecosystem is so highly disturbed that an extreme r-strategy (e.g., polyphagy) may be required in order to enable the enemy to cope with the prey population. It is thus not surprising that host-specific parasitoids of *S. praefica* seldom occur in hay alfalfa in northern California (Miller, 1977; Miller and Ehler, 1978).

Evidence in the literature supports our contentions regarding biological control in temporary agroecosystems. Sears and Smith (1975) constructed age-specific life tables for *Heliothis zea* (Boddie) in peanut agroecosystems of Texas and convincingly showed that most of the real or generation mortality occurred during the egg stage of *H. zea.* The authors concluded that natural control of *H. zea* was "excellent" and that misuse of insecticides could easily upset this balance. Ignoffo *et al.* (1976) discussed the roles of predators, parasites, and pathogens in effecting biological control of insect pests in soybean agroecosystems of Missouri. These authors concluded that predators were a "major factor" in limiting populations of caterpillars. Experiments with *Trichoplusia ni* (Hübner) revealed that general predators could inflict mortality on eggs of this pest which was comparable to that observed in California cotton (cf. Ehler, 1977). Collins and Washino (in press) showed survival of pasture mosquito (*Aedes nigromaculis* [Ludlow]) in northern California irrigated pastures was greatly reduced ($\overline{X}$ = 18%) in plots where general predators were allowed access compared to enclosed areas ($\overline{X}$ = 87%).

Similar evidence comes from nonagricultural settings. Randolph (1973) noted that species of land snails which occupied variable physical environments had more general food requirements compared to species in less fluctuating environments. Sciarappa *et al.* (1977) demonstrated that *Typhlodromips sessar* DeLeon was the dominant phytoseiid mite in immature and unstable habitats throughout areas of secondary succession in New Jersey; *T. sessar* is also a general predator. In New York, Eickwort (1977) concluded that general predators were the most important mortality factors associated with milkweed leaf beetle *(Labidomera clivicollis)* under field conditions. Finally, Post and Riechert (1977) detected a decrease in the number of specialist species of spiders as habitat heterogeneity decreased.

Hall and Ehler (1979) analyzed rates of establishment of natural enemies in classical biological control. They found the rate of establishment increased as degree of habitat stability increased. However, analysis of attendant rates of success given by Hall, Ehler, and Bisabri-Ershadi (1980) showed that rate of all successes for habitats of intermediate levels of stability was significantly higher than the rate for either disturbed or stable habitats. Therefore, it seems that no general prediction can be made about outcome of natural-enemy introductions into systems of varying degrees of habitat stability. Consequently, it would be misleading to limit practice of biological control to any specific habitat. Instead, as suggested by Ehler and van den Bosch (1974), each kind of system should be considered separately and theories developed based on the ecological properties of the system (see also Hassell, 1978). With respect to temporary agroecosystems, it is clear that good biological control can be obtained and that certain natural enemies, such as general predators, can be well suited as biological-control agents in these settings.

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