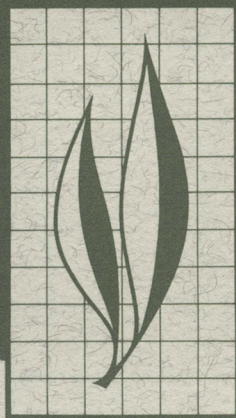


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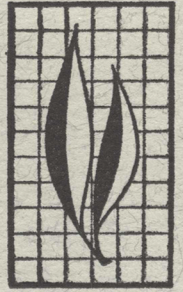
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Natural Enemies of Cabbage Looper on Cotton in the San Joaquin Valley

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ABSTRACT

The roles of predators, parasitoids, and a pathogen in effecting natural biological control of cabbage looper (*Trichoplusia ni* [Hübner]) in San Joaquin Valley cotton were assessed. Life-table analysis indicates that the majority of the generation mortality of cabbage looper occurs during the egg-small larva interval. Observations and experimental evidence strongly indicate that most of this mortality is inflicted by a complex of general predators, primarily adults and nymphs of *Geocoris pallens* Stål, *Nabis americanoferus* Carayon, *Orius tristicolor* (White), and possibly larvae of *Chrysopa carnea* Stephens. These studies, plus evidence from the literature, indicate that the potential for biological control in annual-crop systems is greater than some workers had previously believed, and that the necessity of using only host-specific natural enemies in biological control is a questionable assumption.

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INTRODUCTION

LARVAE OF CABBAGE LOOPER, *Trichoplusia ni* (Hübner), are known to cause damage to at least 119 species, varieties, and cultivars of plants in 29 families (Sutherland, 1966). Cotton grown in the San Joaquin Valley of California is a host for *T. ni* and, at times, serious infestations occur. However, *T. ni* is generally regarded as a secondary pest of cotton in this region. That is because outbreaks of *T. ni* usually occur when its natural enemies are destroyed or suppressed by broad-spectrum, chemical insecticides applied for control of *Lygus hesperus* Knight, *Heliothis zea* (Boddie), or both (van den Bosch *et al.*, 1971; Ehler and van den Bosch, 1974).

Since 1969, I have investigated the dynamics of *T. ni* populations on cotton to better understand the role of natural enemies in effecting control of host density. These enemies include predators, parasites (parasitoids), and

a pathogen, and have been assessed by both experimental and life-table techniques. A major purpose of this paper is to present and analyze the results of these studies.

The evidence presented also has implications for classical biological control. Cabbage looper is presumably a native species (Metcalf *et al.* 1962; Oatman and Platner, 1969) which, as will be shown later, is preyed upon by a predominantly native fauna of natural enemies. As Doutt (1961) suggested, a study of such predator-prey relationships can yield important lessons for classical biological control. In the present paper, the evidence is applied to two questions in such biological control: (1) the utility of general (polyphagous) predators or parasites, and (2) the potential for biological control of insect pests in temporary or annual-crop systems.

ECOLOGY OF CABBAGE LOOPER IN COTTON

The egg is deposited on the underside of the mature cotton leaf. Normally, one egg is found per leaf, although occasionally (especially at high densities) two or more may be present on one leaf. Most of the eggs are in the upper half of the plant (seldom in the terminals). Fye (1972) reported a sim-

ilar spatial relationship for *T. ni* eggs in Arizona cotton.

Upon eclosion, the solitary larva feeds on the underside of the mature leaf, often in the vicinity of the egg. The larva continues to feed, frequently transferring from leaf to leaf, and progresses through five instars. Upon com-

¹ Lepidoptera: Noctuidae.

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pletion of larval development and a brief prepupal period, pupation takes place either on the underside of a leaf or among the plant debris at the soil surface. The adult is an active flier. It can be observed flying about during the day, and is well represented in black-light trap collections.

Personal observations by the author indicate that the incidence and magnitude of *T. ni* populations (using egg density as an index) on cotton during the growing season are generally consistent from year to year. Despite the fact that cotton is planted much earlier (March to late May), the first *T. ni* eggs (and larvae) are usually not

found until late June or early July. At that time, eggs and larvae are sparsely distributed and difficult to detect. However, there often exists a reasonably discrete generation which will be referred to herein as the first generation. The first major or obvious generation (second generation) usually occurs during late July and early August, and the third generation (usually the last) occurs in late August and September. Chemical defoliation of the plants, and possibly lower temperatures, preclude additional development. In the present study, the observations and experimentation were largely conducted during the second and third generations.

NATURAL ENEMIES OF CABBAGE LOOPER

Numerous predaceous and parasitic arthropods occur in California cotton (van den Bosch and Hagen, 1966). In this section, the natural enemies of *T. ni* are considered. Particular emphasis is given to feeding habits, area of indigeneity, and numerical relationships, as these considerations are relevant to later discussions.

Predators

***Chrysopa carnea* Stephens (Neuroptera: Chrysopidae).** According to van den Bosch and Hagen (1966), larvae of this green lacewing are indiscriminate feeders, and prey on spider mites (*Tetranychus* spp.), bollworm larvae (*H. zea*), aphids (*Aphis* spp.), whiteflies (*Trialeurodes* spp.), and various insect eggs. The adult is not predaceous. Additional prey listed by Ehler and van den Bosch (1974) include thrips (*Frankliniella occidentalis* [Pergande]) and eggs and larvae of *T. ni* and beet armyworm, *Spodoptera exigua* (Hübner). The latter authors considered *C. carnea* to be a polyphagous predator in California cotton.

Tjeder (1966) considered *C. carnea* to be the most common and widely distributed species of *Chrysopa* in the

world; also, Tauber and Tauber (1973) reported *C. carnea* to be common and widespread in North America. The latter authors presented empirical evidence which indicates that, in California, two strains of *C. carnea* are in a state of hybridization. Tauber and Tauber (1973) concluded: "It appears likely that the *carnea* strain of *C. carnea* which occurs allopatrically throughout eastern and midwestern North America was introduced secondarily into California where it interbred with the indigenous *mohave* strain. This resulted in genetically variable populations of the *carnea* strain which occur in California's Central Valley and in restricted populations of the *mohave* strain in the foothill and coastal areas." Thus, the actual native home of *C. carnea* populations which occur in California is open to question.

***Orius tristicolor* (White) (Hemiptera: Anthracoridae).** Adults and nymphs of this pirate bug are predaceous on various hosts, including thrips (a favored host), spider mites, eggs and small larvae of various noctuids, aphids, and whiteflies (van den Bosch and Hagen, (1966). Van den

Bosch and Hagen (1966) also indicated that *O. tristicolor* will feed on plant tissue, apparently to obtain moisture. Recent experimental investigations revealed that such phytophagy is of great survival value in this predator (J. Salas, unpublished data). Ehler and van den Bosch (1974) considered *O. tristicolor* to be polyphagous, even though this predator may feed preferentially on thrips or spider mites.

According to Kelton (1963), *Orius* Wolff is a Holarctic genus. In North America, *O. tristicolor* is transcontinental, and has been collected in Canada, Mexico, and Central and South America (Herring, 1966). Presumably, this species is native to North America (J. L. Herring, personal communication).

Geocoris pallens Stål (Hemiptera: Lygaeidae). Van den Bosch and Hagen (1966) stated that adults and nymphs of this big-eyed bug are primary enemies of lygus bugs, leafhoppers (*Empoasca* spp.), spider mites, and small bollworms. Additional prey in California cotton include eggs and small larvae of various noctuids, including beet armyworm, western yellow-striped armyworm (*Spodoptera praefica* [Grote]), and cabbage looper. York (1944) demonstrated that *G. pallens* may feed on plants. In recent studies, Ridgway and Jones (1968) increased longevity of these bugs by allowing them to also feed on cotton plants, whereas Tamaki and Weeks (1972) obtained quickest development, highest egg production, and greatest survival rate when bugs were fed sunflower seeds, insects, and green plant food. *Geocoris pallens* is considered a polyphagous predator in California cotton (Ehler and van den Bosch, 1974), although the above evidence indicates that this species can also be considered omnivorous.

P. D. Ashlock and K. S. Hagen (personal communications) stated that *G. pallens* is a native species. A related

species, *G. punctipes* (Say), occurs in California cotton, although *G. pallens* is the predominant species in the San Joaquin Valley. Since *G. punctipes* was seldom encountered in the present study, it is given no further consideration in this paper.

Nabis americanoferus Carayon (Hemiptera: Nabidae). Both adults and nymphs of this damsel bug are predaceous on a variety of prey, including aphids, leafhoppers, lygus bugs, spider mites, and small caterpillars (van den Bosch and Hagen, 1966). Larvae of cabbage looper, bollworm, and beet armyworm are common prey. Also, Ridgway and Jones (1968) observed plant feeding in *N. americanoferus*, and were able to increase longevity by allowing bugs to feed on cotton plants. This damsel bug is considered to be a polyphagous predator (Ehler and van den Bosch, 1974), and can also be classed as omnivorous.

Carayon (1961) demonstrated that *N. americanoferus* is distinct from the European *N. ferus*. Presumably, *N. americanoferus* is a native species. Personal communications from K. S. Hagen and P. D. Ashlock confirmed this hypothesis. A related species, *N. alternatus* Parsh., occurs in California cotton, but is abundant particularly in the southern desert valleys, not in the San Joaquin (van den Bosch and Hagen, 1966). The latter species is not considered in this paper.

Collops vittatus (Say) (Coleoptera: Malachiidae). Van den Bosch and Hagen (1966) stated that adults of this soft-winged flower beetle feed on such prey as aphids, spider mites, moth eggs, and moth and butterfly larvae. These authors also noted that the larva of *C. vittatus* may be predaceous, although its feeding habits are poorly known. Walker (1957) described "dual feeding" in *C. vittatus*, i.e., adults and larvae are both scavengers and predators. These feeding records indicate that *C.*

vittatus is at least moderately polyphagous, and quite possibly is as polyphagous as the hemipterous predators discussed above.

According to Fall (1912), *C. vittatus* occurs throughout North America. It is likely that this species is also native (K. S. Hagen, personal communication).

***Zelus renardii* Kolenati (Hemiptera: Reduviidae).** Van den Bosch and Hagen (1966) reported that adults and nymphs of this assassin bug are general feeders which are not usually abundant, and apparently are not of major importance in biological control of any cotton pest. My observations generally confirm these beliefs. According to E. R. Hart (personal communication), *Z. renardii* occurs commonly in southwestern U. S., western and southwestern Mexico, and is a native species.

***Sinea diadema* (Fabricius) (Hemiptera: Reduviidae).** Both adults and nymphs of this spined-soldier bug are predaceous and, according to van den Bosch and Hagen (1966), are indiscriminate feeders, probably of no great significance in biological control of cotton pests. This species is widely distributed in North America (Readio, 1924) and is likely a native species (E. R. Hart, personal communication).

Araneida. Many species of spiders occur in California cotton, particularly crab spiders and orb weavers (van den Bosch and Hagen, 1966). Spiders are apparently polyphagous predators, although, in the present case, the species present and their ecological impact have not been studied to any great extent. Unfortunately, these predators must be treated collectively until further work is done.

Miscellaneous predators. A number of additional predaceous species occur in California cotton. These may at times feed on *T. ni*, but are apparently of little importance. Included are mantids,

ground beetles (Carabidae), *Anthicus* spp. (Anthicidae), *Polistes* wasps (Vespididae), dragon flies, damselflies, and aphidophagous syrphids and coccinellids (van den Bosch and Hagen, 1966). A notoxus beetle, *Notoxus calcaratus* Horn, is sometimes abundant (van den Bosch and Hagen, 1966). These miscellaneous predators are not further considered in the present study.

Parasitoids

***Microplitis brassicae* Muesebeck (Hymenoptera: Braconidae).** This species is a solitary endoparasite of *T. ni* larvae. The female wasp oviposits in small host larvae (usually 1st and 2nd instars), wherein the larva develops usually in the caudal region of the host. At maturity, the parasite larva exists through the lateral abdominal wall of the host (usually medium-sized larva) and spins a greenish (sometimes grayish) cocoon. Often the host larva is not killed at the time of parasite emergence and may continue living for a few days; however, I have not observed these previously parasitized larvae to feed or survive indefinitely.

In the present paper, *M. brassicae* will be considered a host-specific parasitoid of *T. ni* in California cotton. This is based on previous investigations of Butler (1958), van den Bosch and Hagen (1966), and Ehler and van den Bosch (1974), in which *M. brassicae* was reared only from *T. ni*. At present, the only known additional host of *M. brassicae* is alfalfa looper (*Autographa californica* [Speyer]), which was reported by Krombein (1958). Although *A. californica* occurs in California cotton, it is generally found in early season (prior to *T. ni*), and is relatively rare. Thus, although *M. brassicae* is not totally restricted to *T. ni*, it appears that during periods of *T. ni* abundance, such larvae are the only suitable hosts present. According to Muesebeck *et al.* (1951), *M. brassicae* occurs throughout

the U.S.A. Since this species is relatively host specific to a native insect, and because it is apparently Nearctic in distribution, it is likely that it is a native species.

Hyposoter exiguae (Viereck) (Hymenoptera: Ichneumonidae). This rather common species is a solitary, endoparasite of larvae of *T. ni* and of a number of other species. According to Puttler (1961), the female prefers to oviposit in late 1st or 2nd instar lepidopterous larvae, although Smilowitz and Iwantsch (1973) observed oviposition and complete development of parasite larvae in all five instars of *T. ni*. Observations in the present study indicate that the small larva (1st and 2nd instars) is usually parasitized, and that mortality of the host larva takes place during the 3rd and (or) 4th instars (usually medium-sized hosts).

Analysis of host data reveals that *H. exiguae* is a polyphagous species. Puttler (1961) reared *H. exiguae* from a wide range of Lepidoptera in southern California, including alfalfa looper (*A. californica*) and other noctuid larvae, tomato hornworm larvae (*Manduca quinquemaculata* [Haw.]), and a nymphalid, *Vanessa cardui* (L.). *Hyposoter exiguae* is also known to parasitize larvae of certain pierids and geometrids. In California cotton, *H. exiguae* parasitizes larvae of bollworm (*H. zea*), beet armyworm (*S. exigua*), western yellow-striped armyworm (*S. prae-fica*), and *T. ni* (van den Bosch and Hagen, 1966). Although Ehler and van den Bosch (1974) considered *H. exiguae* to be oligophagous in California cotton, it might best be described as polyphagous. In any event, this species is not host specific.

Distributional data presented by Muesebeck *et al.* (1951) and Puttler (1961) indicate that *H. exiguae* is a Nearctic species and presumably native.

Copidosoma truncatellum (Dalman) (Hymenoptera: Encyrtidae). This tiny

wasp is an egg-larval, polyembryonic parasite of *T. ni*. The female wasp oviposits in the egg of *T. ni*, polyembryonic development occurs in the host larva, and the mature larva or prepupa is killed. Leiby (1926, 1929) reported an average of 1526 individual wasps emerged per parasitized *T. ni*. Leiby also observed that either one or two eggs were inserted in a host egg during each oviposition. When two eggs were inserted, usually (80% of the time) one egg was fertilized and one was not. According to Leiby (1926), this phenomenon accounted for those broods containing both males and females, although such an interpretation had been challenged earlier by Patterson (1917).

According to Peck (1963), *C. truncatellum* has been reared from a number of hosts, including noctuids, geometrids, cossids, and coleophorids. However, van den Bosch and Hagen (1966) reported *C. truncatellum* from only *T. ni* in California cotton, and the results of Ehler and van den Bosch (1974) confirm this finding. The latter authors considered *C. truncatellum* to be host specific to *T. ni* in California cotton. Apparently, *C. truncatellum* is well adapted to *T. ni*, as Stoner and Weeks (1974) reported the synchronization of host and parasite at 25°C to be almost perfect.

Geographic distribution data given by Peck (1963) indicate *C. truncatellum* is Holarctic. The native home of this species is not clear.

Voria ruralis (Fallen) (Diptera: Tachinidae). The larva of this fly is a larval parasite of *T. ni*. Parasitism can be either solitary or gregarious. Oviposition (macrotype egg) occurs on medium-sized or large larva, and the large larva or prepupal host is killed.

Brubaker (1968) surveyed the parasites of a number of noctuid species in Arizona, and reported *V. ruralis* only from *T. ni*, although other hosts have been reported (Butler, 1958; Jackson *et al.*, 1969). Van den Bosch and Hagen

TABLE 1
DENSITIES OF COMMON NATURAL ENEMIES OF *T. NI* DURING THE 1969
GROWING SEASON. HEIMFORTH RANCH, ROSEDALE

Natural Enemy	Mean no./3.7 meters of row/indicated date									\bar{X}	% of Sample
	July			August				Sept.			
	16	23	30	6	13	20	27	3	10		
Predators:											
<i>G. pallens</i> ^a	24	61	50	42	31	39	26	55	30	39.8	31.1
<i>O. tristicolor</i> ^a	36	56	23	14	13	31	17	40	16	27.3	21.4
<i>N. americanoferus</i> ^a	22	29	26	20	9	16	11	23	28	20.4	16.0
<i>O. carnea</i> ^b	10	7.6	1.2	1.2	4.5	14	4.5	14	6.5	7.1	5.6
Araneida ^a	6	2	3	1.8	2	2	2	7.5	8.2	3.8	2.9
<i>Z. renardii</i> ^a	0	0	0	.6	2.5	1.1	3	2.5	1.1	1.2	.9
<i>C. vittatus</i> ^c	0	.3	.5	1.5	.3	.5	.8	.2	.5	.5	.4
<i>S. diadema</i> ^a	0	.3	0	.5	.5	.5	1.3	0	.5	.4	.3
Parasitoids ^c :											
<i>C. truncatellum</i>	0	0	1.3	.3	.3	1	3	129	110	27.2	21.3
<i>M. brassicae</i>	0	0	0	0	0	0	.8	.3	.3	.15	.12
<i>H. exiguae</i>	0	0	0	0	0	0	0	0	0	0	0

^a Adults + immatures.

^b Larvae.

^c Adults.

(1966) reported *V. ruralis* only from *T. ni* on California cotton, although Oatman and Platner (1969) reared this species from beet armyworm (*S. exigua*). Also, Eveleens *et al.* (1973) reported *V. ruralis* as a parasite of *S. exigua* in California cotton, but these authors considered the parasite to be only sporadic. Ehler and van den Bosch (1974) considered *V. ruralis* to be host specific to *T. ni* in California cotton.

According to Elsey and Rabb (1970a), *V. ruralis* is a cosmopolitan species. Whether this species is native is not clear.

Patrocloides montanus (Cresson) (Hymenoptera: Ichneumonidae). This large, shiny-black wasp is a solitary, larval-pupal parasite of *T. ni*. The adult oviposits in a medium-sized larva (or possibly a large larva), and the adult wasp emerges from the *T. ni* pupal case.

There is very little information in the literature on *P. montanus*. Krombein and Burks (1967) indicated the species is Nearctic; presumably, it is also native. The only reported hosts are *T. ni* (Ehler *et al.*, 1973) and *Syngrapha* sp. (Krombein and Burks, 1967). In Cali-

fornia cotton, this species is considered to be host specific to *T. ni* (Ehler and van den Bosch, 1974).

Apanteles spp. (Hymenoptera: Braconidae). Van den Bosch and Hagen (1966) reported two *Apanteles* spp. as parasites of *T. ni* in California cotton. These are *A. glomeratus* (Linnaeus) and *A. marginiventris* (Cresson). In the present study, *A. glomeratus* was not observed, although *A. marginiventris* was reared sporadically from *T. ni* larvae. Distribution data for *A. marginiventris* (Muesebeck *et al.*, 1951) indicate this species is Nearctic. Van den Bosch and Hagen (1966) reared the species from *T. ni*, *S. exigua*, *H. zea*, and *S. praeifica* in California cotton. Ehler and van den Bosch (1974) considered *A. marginiventris* to be oligophagous in California cotton, although polyphagous may be a better description.

Trichogramma spp. (Hymenoptera: Trichogrammatidae). Apparently two species of *Trichogramma* occur in California cotton: *T. semifumatum* (Perkins) and *T. pretiosum* Riley. Both are egg parasites, and probable hosts in-

TABLE 2

DENSITIES OF COMMON NATURAL ENEMIES OF *T. NI* DURING THE 1970 GROWING SEASON. HEIMFORTH RANCH, ROSEDALE

Natural Enemy	Mean no./3.7 meters of row/indicated date												— X	% of Sample
	June		July				August				September			
	23	30	7	14	21	28	4	11	18	25	1	8		
Predators:														
<i>G. pallens</i> ^a	27.2	14.2	28	46.5	33.5	33.2	29.8	35.8	22.2	11.2	5.7	4.2	24.2	40.1
<i>O. tristicolor</i> ^a	46	38.3	16.5	16.9	9.7	16.5	16.5	19.8	13.5	20	15	21.2	20.8	34.5
<i>N. americanoferus</i> ^a	7.2	5.2	5.5	3.2	3.9	7.5	9	11	8.5	6.2	10.5	14.5	7.7	12.7
<i>O. carnea</i> ^b	2	1.5	2	.3	0	0	0	1.5	5	7.5	6.5	8	2.9	4.7
Araneida ^a	3.3	3	2.5	2.7	2.3	1	1.8	2.5	3	3.5	2.2	2.7	2.5	4.2
<i>Z. renardii</i> ^a	0	.5	0	0	0	0	.5	.8	.5	.3	.5	1.3	.4	.6
<i>S. diadema</i> ^a	0	0	0	.5	.5	1.3	0	.8	.3	.5	.5	0	.4	.6
<i>O. vittatus</i> ^c	.3	0	.3	.5	.5	.3	0	.5	.8	.5	0	.7	.4	.6
Parasitoids^c:														
<i>C. truncatellum</i>	0	0	0	0	0	.3	1	0	0	.3	.8	9.8	1	1.7
<i>M. brassicae</i>	0	0	0	0	0	0	0	0	0	0	0	1	.08	.1
<i>H. exiguae</i>	0	0	0	.3	0	0	0	0	0	0	0	0	.03	.04

^a Adults plus immatures.

^b Larvae.

^c Adults.

clude *T. ni*, *S. exigua*, and *H. zea*. These species occur on *T. ni* only sporadically in California cotton, and are considered to be oligophagous to polyphagous.

Chelonus texanus Cresson (Hymenoptera: Braconidae). This species is an egg-larval parasite of such cotton pests as *H. zea*, *S. exigua*, and *S. praefica* (van den Bosch and Hagen, 1966). Ehler *et al.* (1973) presented the first apparent record for *C. texanus* as a parasite of *T. ni*. In general, *C. texanus* is an insignificant parasite of *T. ni*, and has been collected only sporadically. Ehler and van den Bosch (1974) list the species as oligophagous, although it may be best considered polyphagous.

Miscellaneous flies (Diptera: Tachinidae). Van den Bosch and Hagen (1966) listed some additional tachinid flies which are parasitic on *T. ni* in California cotton. These include *Eucelatoria armigera* (Coquillett), *Archytas californiae* Walker, and *Winthemia quadripustulata* (F.). Apparently, none of these species are significant natural enemies of *T. ni* on cotton and are not further considered in this paper.

Pathogen

Nuclear polyhedrosis virus. A nuclear polyhedrosis virus was the only pathogen demonstrated to cause mortality in *T. ni*. Polyhedrosis of *T. ni* is well known, and was described as early as 1915 (Chapman and Glaser, 1915). Mortality of *T. ni* due to polyhedrosis is generally restricted to the larval stage (Vail and Hall, 1969), and usually most of the mortality occurs during the later instars (i.e., 3rd to 5th), depending on environmental conditions (Ignoffo, 1964; Ehler *et al.*, 1973). Ehler and van den Bosch (1974) considered nuclear polyhedrosis virus (NPHV) to be specific to *T. ni* in California cotton.

Numerical relationships

An assessment of the numerical relationships among the predators and parasitoids of *T. ni* is of interest, since density of a natural enemy may be correlated with its ecological impact. Density counts are presented for two cotton-growing areas: (1) Heimforth and Palla Ranches (near Rosedale, Kern County) and (2) Boswell Ranch (near

TABLE 3
DENSITIES OF COMMON NATURAL ENEMIES OF *T. NI* DURING THE 1970
GROWING SEASON. PALLA RANCH, ROSEDALE

Natural Enemy	Mean no./3.7 meters of row/indicated date										\bar{X}	% of Sample
	July				August				September			
	8	15	22	29	5	12	19	26	2	9		
Predators:												
<i>G. pallens</i> ^a	22.5	29.5	31	24.5	33.7	30	23.7	13.5	9.9	9.7	22.8	30.6
<i>O. tristicolor</i> ^a	20.7	23.8	20	14	20.7	11.5	2.3	18	20	21	19.3	25.8
<i>O. carnea</i> ^b	1.2	.8	1.2	1.7	1.7	7.5	25.7	21.7	51.2	55.7	16.8	22.5
<i>N. americanoferus</i> ^a	.8	.3	3.3	2	5.2	10.7	15.8	15.4	24.5	37.4	11.5	15.5
Araneida ^a	3.8	.5	1	1	2.7	2	.5	2.5	1	1.5	1.7	2.2
<i>Z. renardii</i> ^a	.3	0	0	0	1.2	0	0	.3	3.7	.5	.6	.8
<i>C. vittatus</i> ^c	.8	0	1	1.2	1	.5	.3	.7	.3	0	.6	.8
<i>S. diadema</i> ^a	0	0	0	.3	0	2.1	1.3	.7	0	0	.4	.6
Parasitoids ^c :												
<i>C. truncatellum</i>	0	0	0	1.8	2	0	.5	0	.8	2.5	.8	1
<i>M. brassicae</i>	0	0	0	0	0	0	0	.5	.3	0	.08	.01
<i>H. exiguae</i>	0	0	0	0	0	0	0	.3	0	0	.03	.04

^a Adults plus immatures.

^b Larvae.

^c Adults.

Corcoran, Kings County). In the Rose-dale area, data were obtained from whole-plant samples (see Leigh *et al.*, 1970), whereas the D-vac® method was used at the Boswell Ranch (see Ehler *et al.*, 1973). Sample units were 100 suctions or four whole-plant samples per plot. In all instances, the densities given are means of four replications.

Analysis of mean density for the growing season reveals that three predators, *G. pallens*, *O. tristicolor* and *N. americanoferus*, comprised the bulk of the sample fauna and were numerically dominant. At the Heimforth Ranch during 1969, these species comprised 68.5% of the fauna (Table 1); and, at the same ranch in 1970, they made up 87.3% of the sample fauna (Table 2). At the Palla Ranch in 1970 (Table 3), they comprised 78.9% of the sample fauna. At the Boswell Ranch in 1974, these predators comprised 79.5% of the sample fauna (Table 4). In general, densities of other predators and parasitoids were comparatively low. The

dominance of the three hemipterous predators was probably related to their capacity for omnivory.

Among *T. ni* parasitoids, *C. truncatellum* was the numerically dominant species in all instances. In fact, at the Heimforth Ranch in 1969 (Table 1), density of *C. truncatellum* at times was as high or higher than that of many predators, although this trend was not consistent throughout the season. The numerical dominance of *C. truncatellum* over other *T. ni* parasitoids was likely due to its polyembryonic development. Additional parasitoids of *T. ni* which are not listed in the results, were not detected in samples.

These data provide an index of the general level of abundance of the predators and parasitoids of *T. ni* in California cotton. However, it should be noted that most of these enemies are not solely dependent on *T. ni* for energy; thus, underlying explanations for species abundance may vary from one species to the next.

LIFE-TABLE STUDIES

Since the second and third generations of *T. ni* on cotton are relatively

discrete, the age-specific life table was used to describe the timing and inten-

TABLE 4
DENSITIES OF COMMON NATURAL ENEMIES OF *T. NI* DURING THE 1974
GROWING SEASON. BOSWELL RANCH, CORCORAN

Natural Enemy	Mean no./100 D-vac suction/indicated date												
	June				July						August (see Aug. lower left)		
	12	18	24	27	1	11	18	22	25	28	5	8	12
Predators:													
<i>G. pallens</i> ^a	33	36	37.3	31.5	74.5	19	47.7	45.3	46.8	20.5	81.3	82.3	31.3
<i>O. tristicolor</i> ^a	4	.4	9.3	15	22.8	28.3	36.5	34.3	32.5	38.4	98.5	89.3	58.3
<i>N. americanoferus</i> ^a	12.5	13.3	19.3	28.3	58.5	14.5	13	15.3	8.8	15.4	16.5	14.8	5.3
Araneida ^a	2.5	6.3	7.5	6	8.8	3	1.8	1.8	4.3	2.5	5.3	12.8	3.3
<i>C. vittatus</i> ^c	0	.3	0	0	.3	.3	.5	2	1	.5	10.3	14.8	6
<i>C. carnea</i> ^b	0	0	.3	.3	1	.5	.8	2	1	.3	2.3	2.3	1
<i>Z. renardii</i> ^a	0	0	0	0	0	0	0	0	.3	0	.3	0	0
<i>S. diadema</i> ^a	0	0	.8	.3	0	0	0	0	0	.3	.5	0	.3
Parasitoids ^c :													
<i>O. truncatellum</i>	0	.3	0	0	.3	0	0	2	5.5	2.5	.5	0	0
<i>P. montanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>M. brassicae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. exiguae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>V. ruralis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0

Natural Enemy	August (cont. from upper right)					September					— X	% of Sample
	15	19	22	26	29	3	5	9	12	16		
Predators:												
<i>G. pallens</i> ^a	53	26.5	35.5	13.3	14.3	15.5	35	9.3	10.3	14.3	35.3	34.6
<i>O. tristicolor</i> ^a	51.5	12	27.5	37.8	24	27.5	41.5	23.3	19.3	19.5	32.8	32.2
<i>N. americanoferus</i> ^a	9.3	2.5	4.5	.8	2	3.5	11	6.3	4.3	18.3	13.0	12.7
Araneida ^a	3.5	5.5	10.8	7	6.8	7.3	22.8	13.8	20.3	26	8.3	8.1
<i>O. vittatus</i> ^c	6	3.8	2.3	.8	1.8	.5	1.8	.5	.3	.5	2.4	2.4
<i>C. carnea</i> ^b	1.5	2	2.8	2.8	1.5	1.5	4	1.5	3.3	6.8	1.7	1.7
<i>Z. renardii</i> ^a	.5	0	0	.2	0	0	2	.5	.5	2.3	0.3	0.3
<i>S. diadema</i> ^a	.8	.5	.3	.8	0	.3	1	.3	.5	.3	0.3	0.3
Parasitoids ^c :												
<i>O. truncatellum</i>	14.5	4	5.3	12.7	18.5	11.8	42.5	18.3	15.3	14.5	7.4	7.3
<i>P. montanus</i>	0	0	0	0	.3	0	0	0	0	.8	0.05	0.05
<i>M. brassicae</i>	.3	0	0	0	0	0	0	0	0	0	0.01	0.01
<i>H. exiguae</i>	0	.3	0	0	0	0	0	0	0	0	0.01	0.01
<i>V. ruralis</i>	0	0	0	0	0	0	0	0	0	0.3	0.01	0.01

^a Adults + immatures.
^b Larvae.
^c Adults.

sity of intrageneration mortality. In the present study, life-table analysis was used to describe generation survival of *T. ni*, quantify the impacts of parasitization and polyhedrosis, and indicate which mortality factor, if any, can be considered to be the major intragenerational mortality factor.

Materials and methods

Heimforth Ranch (1970). A 4.45-hectare plot of nontreated, Acala SJ-1 cotton on the Heimforth Ranch (near Rosedale in Kern Co.) was sampled

weekly during the 1970 growing season. Eight sampling stations were arranged systematically throughout the field. Eggs and pupae of *T. ni* were determined by visual inspection of 0.5 consecutive row meter of plants, usually at a rate of one sample per station. The litter at the base of the plants was also inspected for pupae. Larvae and adults of *T. ni* were sampled using a whole-plant sampler as described by Leigh *et al.* (1970). In this case, the sample unit was 0.91 consecutive row meter of plants, and usually two samples were

taken per station. An age-specific life table was constructed for the second generation of *T. ni*.

Palla Ranch (1970). On this ranch, also near Rosedale, the plot was ca. 3.2 hectares of Acala SJ-1 cotton. The sampling program was the same as for the Heimforth Ranch. An age-specific life table was constructed for the second generation of *T. ni*.

Boswell Ranch (1970). In this study, four 16.2-hectare plots were randomly selected from a 260-hectare field of Acala SJ-1 cotton located on the Boswell Ranch near Corcoran in Kings Co. These plots (nontreated) were part of a larger experiment reported by Ehler *et al.* (1973) and Eveleens *et al.* (1973). Samples of *T. ni* developmental stages were taken twice weekly at randomly selected sites within the center half of each plot. Eggs and pupae were determined by visual examination of 0.5 consecutive row meter of plants (including plant debris) at four sites per plot. Larvae were sampled at eight locations per plot, using a beating technique described by Eveleens *et al.* (1973). The sample unit for larvae was 1 consecutive row meter of plants. Age-specific life tables were constructed for the second and third generations of *T. ni*.

Boswell Ranch (1971). This study site was located ca. 10 miles northwest of the 1970 site. Four 20-hectare plots were selected at random from a nontreated block of 260 hectares of Acala SJ-1 cotton. Samples of *T. ni* eggs, larvae, and pupae were collected twice weekly (occasionally weekly) in a manner similar to the previous year. Age-specific life tables were derived for the second and third generations of *T. ni*.

Boswell Ranch (1974). These investigations were conducted in a 260-hectare field of Acala SJ-1 cotton in the general vicinity of the 1971 study. In this case, sampling was restricted to the center third (ca. 85 hectares) of the

field. Eggs, larvae, and pupae of *T. ni* were sampled twice weekly as in previous studies at this ranch. However, these samples were obtained at four regularly spaced sampling stations. At each station, five egg and pupal samples were taken, whereas 10 larval samples were collected. In each case, the sample unit was 1 meter of consecutive plants.

Acaricides. As stated previously, these investigations were carried out in nontreated fields, i.e., fields free of chemical insecticides. However, in many cases (e.g., Boswell Ranch) the cotton received up to two applications of dicofol for tetranychid mite control. Since these treatments were applied a few weeks prior to the second *T. ni* generation, and because dicofol has not been shown to have any major toxic effect on the species in question, it is not likely that this practice significantly affected the results presented herein.

Life-table components

In this study, the overall plan for the age-specific life table was modified from that given by Harcourt (1969). The essential entries and their derivations are presented below.

x. In this column, x refers to the age interval (or developmental stage) during which respective samples were taken. The following age intervals were used: (1) egg; (2) small larva (< 0.6 cm), principally 1st and early 2nd instars; (3) medium-sized larva (0.6 to 1.9 cm), mostly late 2nd, 3rd, and early 4th instars; (4) large larva (> 1.9 cm), primarily late 4th and 5th instars; (5) pupa; and (6) adult. The developmental stage of the larva was determined in the field.

1x. This term represents the number of individuals alive at the beginning of a stage, or the number entering a stage. In the present study, 1x values were calculated using the integration method of Southwood and Jepson (1962). Ac-

cording to this method, the mean density of a developmental stage is plotted (ordinate) against time (abscissa), usually one square per individual per day. The area under the curve is determined. Division of the latter by mean developmental time yields the value for $1x$. Southwood (1966) noted that this technique may not give a true value of $1x$, depending on the timing and intensity of mortality. It is likely that the $1x$ values presented here are conservative estimates of actual $1x$ values, since predators (for example) probably destroyed a constant portion of *T. ni* individuals before these could be counted. However, the $1x$ values given should be reliable indices of true $1x$ values.

The $1x$ values for eggs, medium-sized and large larvae, and pupae were determined by the integration technique. The $1x$ for small larvae was not used, as these larvae were difficult to detect. At the Boswell Ranch, the $1x$ for adults was determined from the proportion of laboratory-held pupae which gave rise to adults. In the life tables, all values of $1x$ (and dx) have been converted to a standard sample unit of 1 meter of consecutive plants.

dxF. In this column are listed the mortality factors, demonstrated (or presumed), to be responsible for the number of individuals estimated to have died (dx) during the indicated age interval. For eggs, dxF items included infertility, parasitization, predation, and unknown causes. The former two were determined from field-collected eggs which were held in the laboratory and observed for hatch or parasite emergence. Predation and unknown causes were assigned to residual individuals (i.e., those dying for which no dxF was readily assignable). These latter factors were treated as one mortality factor for eggs and small larvae. The dxF items for medium-sized and large larvae included parasitization, polyhedrosis, predation, and unknown

causes. Parasitization and polyhedrosis were determined from observations of field-collected larvae which were held on an artificial diet in the laboratory (see Ehler *et al.*, 1973). Predation and unknown causes were assigned to the residual. For pupae, dxF included parasitization, which was determined from field-collected pupae allowed to develop in the laboratory, and unknown causes, which represented the residual. Mortality factors for adults were not assessed.

dx. The number of individuals dying during age interval x is denoted by dx . In this case, $dx = (100qx) (1x)$, and is expressed in terms of number per meter of row.

100qx. Apparent mortality, or $100qx$, represents the number of individuals dying during a stage as a percentage of the number alive at the beginning of that stage, i.e., dx as a percentage of $1x$. These mortality rates for parasitoids and nuclear polyhedrosis virus (polyhedrosis) were calculated as an overall average of twice weekly apparent mortality rates during peak density of the respective stage. The $100qx$ values for predation and unknown causes were obtained by deduction.

100rx. Real mortality, or $100rx$, represents the mortality during stage x as a percentage of $1x$ at the beginning of the generation (i.e., egg stage). This figure, also referred to as generation mortality, is used to assess the contributions of various mortality factors to intra-generation mortality. Figures in the $100rx$ column are additive.

Analysis of life-table data

Heimforth Ranch (1970). The life-table data for the second *T. ni* generation are given in Table 5. The bulk of the real or generation mortality (88.8%) occurred during the egg-small larva interval. Presumably, much of this mortality was due to predation, although no experimental evidence was

TABLE 5
AGE-SPECIFIC LIFE TABLE FOR 2ND GENERATION OF *T. NI*.
HEIMFORTH RANCH, ROSEDALE, 1970^a

x	1x	dxF	dx	100qx	100rx
Egg	19.8	<i>T. semifumatum</i>	0.7	3.7	3.7
Small larva	—	Predation + unknown causes	17.6	92.1	88.8
Medium-sized larva	1.5	<i>H. exiguae</i>	0.05	3.0	0.25
		<i>M. brassicae</i>	0.17	11.3	0.75
		Polyhedrosis	0.03	1.7	0.2
Large larva	1.25	<i>C. truncatellum</i>	0.41	33.0	2.0
		<i>V. ruralis</i>	0.1	8.5	0.5
		Polyhedrosis	0.1	8.5	0.5
Pupa	0.43	Unknown causes	0.4	93.0	2.0
Adult	0.03	(S.R. = 53 ♀♀ : 47 ♂♂)	Σ = 19.56	—	Σ = 98.7

^a Key to symbols: x = developmental stage; 1x = number entering stage x; dxF = mortality factor; dx = number dying in stage x; 100qx = percent apparent mortality; 100rx = percent real mortality; S.R. = sex ratio.

TABLE 6
AGE-SPECIFIC LIFE TABLE FOR 2ND GENERATION OF *T. NI*.
PALLA RANCH, ROSEDALE, 1970^a

x	1x	dxF	dx	100qx	100rx
Egg	30.3	Predation +			
Small larva	—	unknown causes	26.9	88.8	88.8
Medium-sized larva	3.4	<i>H. exiguae</i>	0.07	2.0	0.23
		<i>M. brassicae</i>	0.72	21.1	2.3
		<i>A. marginiventris</i>	0.35	1.0	1.2
		Polyhedrosis	0.14	4.0	0.5
Large larva	2.1	<i>C. truncatellum</i>	1.52	72.5	5.0
		<i>V. ruralis</i>	0.2	9.0	0.6
		Polyhedrosis	0.3	13.5	0.9
		Predation + unknown causes	0.08	5.0	0.23
Pupa	0	—	—	—	—
Adult	0	—	—	—	—
			Σ = 30.28	—	Σ = 100

^a Key to symbols: x = developmental stage; 1x = number entering stage x; dxF = mortality factor; dx = number dying during stage x; 100qx = percent apparent mortality; 100rx = percent real mortality.

obtained to test this hypothesis. Total generation mortality was 98.7%. Sex ratio of the surviving adults was approximately 1:1.

A few (3.7%) of the eggs were parasitized by *T. semifumatum*, whereas none were observed to be infertile. A few of the medium-sized larvae succumbed to polyhedrosis and parasitization, *M. brassicae* being the dominant

mortality factor. Mortality of large larvae was effected primarily by *C. truncatellum* (33%), and, to a lesser extent, by *V. ruralis* and polyhedrosis. No mortality of pupae was observed.

Palla Ranch (1970). Data for the second *T. ni* generation are presented in Table 6. As at the Heimforth locality, most (88.8%) of the generation mortality occurred during the egg-small

TABLE 7
AGE-SPECIFIC LIFE TABLE FOR 2ND GENERATION OF *T. NI.*
BOSWELL RANCH, CORCORAN. 1970^a

x	1x	dxF	dx	100qx	100rx
Egg	26.2	Predation +			
Small larva	—	unknown causes	12.1	46.2	46.2
Medium-sized larva	14.1	<i>H. exiguae</i>	1.1	8.1	4.2
		<i>M. brassicae</i>	0.8	5.5	3.1
		<i>C. texanus</i>	0.8	6.0	3.1
		Polyhedrosis	0.3	2.3	1.1
		Predation +			
		unknown causes	2.9	20.6	11.1
Large larva	8.2	<i>C. truncatellum</i>	0.8	10.3	3.1
		Polyhedrosis	0.2	2.2	0.8
		Predation +			
		unknown causes	4.5	54.9	17.2
Pupa	2.7	<i>P. montanus</i>	0.1	3.7	0.4
Adult	2.6	(S.R. = 45 ♀♀:55 ♂♂)	Σ = 23.6	—	Σ = 90.3

^aKey to symbols: x = developmental stage; 1x = number entering stage x; dxF = mortality factor; dx = number dying in stage x; 100qx = percent apparent mortality; 100rx = percent real mortality; S.R. = sex ratio.

TABLE 8
AGE-SPECIFIC LIFE TABLE FOR 3RD GENERATION OF *T. NI.*
BOSWELL RANCH, CORCORAN. 1970^a

x	1x	dxF	dx	100qx	100rx
Egg	91.2	Infertile	7.3	8.0	8.0
Small larva	—	Predation +			
		unknown causes	73.7	87.8	80.8
Medium-sized larva	10.2	<i>H. exiguae</i>	0.4	4.3	0.4
		<i>M. brassicae</i>	0.8	8.1	0.9
		Polyhedrosis	3.2	31.8	3.5
		Predation +			
		unknown causes	1.4	13.7	1.5
Large larva	4.4	<i>C. truncatellum</i>	1.0	22.1	1.1
		<i>V. ruralis</i>	0.1	2.8	0.1
		Polyhedrosis	1.0	22.2	1.1
		Predation +			
		unknown causes	0.3	8.4	0.3
Pupa	2.0	<i>P. montanus</i>	0.6	29.9	0.6
Adult	1.4	(S.R. = 45 ♀♀:55 ♂♂)	Σ = 89.8	—	Σ = 98.3

^aKey to symbols: x = developmental stage; 1x = number entering stage x; dxF = mortality factor; dx = number dying in stage x; 100qx = percent apparent mortality; 100rx = percent real mortality; S.R. = sex ratio.

larva interval. The cause of this mortality was not experimentally determined, although predation was likely a key factor. In samples, neither pupae nor adults were detected; thus, total generation mortality is given as 100%.

Neither parasitization nor infertility of eggs was observed. Among medium-sized larvae, parasitization by *M. brassicae* (21.1%) was the major mortality factor; other parasitoids and polyhedrosis were rather insignificant fac-

TABLE 9
AGE-SPECIFIC LIFE TABLE FOR 3RD GENERATION OF *T. NI*.
BOSWELL RANCH, CORCORAN, 1971^a

x	1x	dxF	dx	100qx	100rx
Egg	8.91	Predation + unknown causes	8.82	99.0	99.0
Small larva	—				
Medium-sized larva	0.09	Predation + unknown causes	0.09	100	1.0
Large larva	0	—	—	—	—
Pupa	0	—	—	—	—
Adult	0	—	$\Sigma = 8.91$	—	$\Sigma = 100.$

^aKey to symbols: x = developmental stage; 1x = number entering stage x; dxF = mortality factor; dx = number dying in stage x; 100qx = percent apparent mortality; 100rx = percent real mortality.

tors. Mortality of large larvae was effected primarily by *C. truncatellum* (72.5%).

Boswell Ranch (1970). Life-table data for the second generation of *T. ni* are presented in Table 7. Approximately half of the generation mortality (46.2%) occurred during the egg-small larva interval. Most of this mortality was due to predation (see later section). Total generation mortality was 90.3%, and the adult sex ratio was approximately 1:1.

Neither infertility nor parasitization of eggs was detected. The major mortality affecting medium-sized larvae was unaccountable, and is termed predation plus unknown causes. Rates of parasitization and polyhedrosis of medium-sized larvae were generally rather low. Among large larvae, predation and unknown causes accounted for 54.9% mortality, whereas *C. truncatellum* (10.3%) and polyhedrosis (2.2%) were less significant. For pupae, parasitization by *P. montanus* (3.7%) was the only mortality factor detected.

Life-table data for the third *T. ni* generation at the same site are presented in Table 8. Again, the majority of the generation mortality (80.8%) occurred during the egg-small larva interval. The components of this mortality were not experimentally determined.

Total generation mortality was 98.3%, and the sex ratio of surviving adults was again approximately 1:1.

A few eggs (8%) failed to hatch, but no egg parasitization was observed. Polyhedrosis was the major mortality factor affecting medium-sized larvae, whereas polyhedrosis and parasitization by *C. truncatellum* were the major mortality agents affecting large larvae. Larval parasitization by *H. exiguae*, *M. brassicae*, and *V. ruralis* was comparatively low. Approximately one-third of the pupae were parasitized by *P. montanus*. Rates of polyhedrosis, and parasitization by *C. truncatellum* and *P. montanus*, were considerably higher than in the previous generation.

Boswell Ranch (1971). The *T. ni* density for the second generation was extremely low. No life table was constructed; however, some observations were made. Infertility and parasitization of eggs were not detected. Interestingly, parasitization by *H. exiguae* and *V. ruralis* was detected despite paucity of *T. ni* larvae. No pupae or adults were detected in samples. Total generation mortality was apparently 100%.

Life-table data for the third *T. ni* generation are shown in Table 9. Virtually all (99%) of the generation mortality occurred during the egg-small larva interval. Neither infertility nor

TABLE 10
AGE-SPECIFIC LIFE TABLE FOR 2ND GENERATION OF *T. NI*.
BOSWELL RANCH, CORCORAN. 1974^a

x	1x	dxF	dx	100qx	100rx
Egg	35.8	Infertile	2.0	5.6	5.6
Small larva	—	Predation + unknown causes	20.2	59.8	56.4
Medium-sized larva	13.6	<i>H. exiguae</i>	0.5	3.9	1.4
		<i>M. brassicae</i>	0.6	4.1	1.7
		Polyhedrosis	0.7	5.4	2.0
		Predation + unknown causes	6.6	48.5	18.4
Large larva	5.2	<i>C. truncatellum</i>	1.4	27.3	3.9
		Polyhedrosis	0.3	5.4	0.8
		Predation + unknown causes	2.8	53.8	7.8
Pupa	0.7	<i>P. montanus</i>	0.2	22.4	0.6
Adult	0.5	(S.R. = 58 ♀ : 42 ♂)	Σ = 35.3	—	Σ = 98.6

^a Key to symbols: x = developmental stage; 1x = number entering stage x; dxF = mortality factor; dx = number dying in stage x; 100qx = percent apparent mortality; 100rx = percent real mortality; S.R. = sex ratio.

parasitization of eggs was detected. No large larvae, pupae, or adults were observed; thus total generation mortality is given as 100%. Experimentation during this generation (see next section) revealed much of this mortality was probably due to predation.

Boswell Ranch (1974). A final life-table analysis was made for the second generation of *T. ni* (Table 10). As in earlier studies, much of the generation mortality (56.4%) occurred during the egg-small larva interval, and as shown in the next section, much of this mortality was due to predation. Total generation mortality was 98.6%, and the sex ratio of surviving adults was slightly in favor of females.

A few eggs (5.6%) were infertile, although no evidence of egg parasitization was obtained. Among medium-sized larvae, predation and unknown causes

(residual) accounted for 48.5% of the mortality. Parasitization by *H. exiguae* and *M. brassicae* was comparatively insignificant, as was also polyhedrosis. Among large larvae, parasitization by *C. truncatellum*, and predation plus unknown causes, were the major mortality factors. Some pupae (22.4%) were parasitized by *P. montanus*.

Discussion. From analysis of life-table data for the second and third *T. ni* generations, a major theme emerges; namely, that regardless of date or location, the majority of the intrageneration mortality of *T. ni* occurs during the egg-small larva interval. Previous evidence (Falcon *et al.*, 1968; Ehler *et al.*, 1973) and observations indicate that a complex of predators is largely responsible for this mortality. This hypothesis is subjected to experimental validation in the next section.

EXPERIMENTAL STUDIES

Experimentation was used to test the hypothesis that the mortality during the egg-small larva interval is due largely to predation. The method of

chemical exclusion (DeBach, 1946) was used. In this method, a chemical insecticide which does not adversely affect the host insect is used to suppress or

TABLE 11
PREDATOR ABUNDANCE IN DIMETHOATE TREATED AND NONTREATED
PLOTS. CORCORAN, 1970

Predator ^b	Mean number of predators ^a		"t" value ^c
	Treated	Nontreated	
<i>O. tristicolor</i> (A)	203.8	359.8	*
<i>O. tristicolor</i> (N)	60.3	127.8	**
<i>G. pallens</i> (A)	32.3	135.3	**
<i>G. pallens</i> (N)	30.3	96.5	**
<i>N. americanoferus</i> (A)	14.8	36.3	NS
<i>N. americanoferus</i> (N)	16.0	46.8	NS
<i>C. vittatus</i> (A)	4.8	16.0	NS
<i>C. carnea</i> (L)	41.5	33.0	NS
<i>Z. renardii</i> (A + N)	0.2	0.3	NS
Araneida (All Stages)	22.0	48.0	NS

^a Cumulative totals for July 21 to August 11; mean of 4 replications.

^b A = adult, N = nymph, L = larva.

^c * = significant at 5% level; ** = significant at 1% level; NS = no significance.

exclude natural enemies of the host. Differences in host density between such treated and nontreated plots can be considered causally related to the natural enemies which were manipulated.

Boswell Ranch (1970)

Materials and methods. In this study, conducted during the second *T. ni* generation, a treated and a nontreated plot were compared. In the treated plot, dimethoate insecticide was applied prior to full moon phase at rates of ca. 0.03 kg and 0.08 kg/hectare on July 11 and 18, respectively. These applications were timed to cause destruction of natural enemies just prior to the beginning of the second *T. ni* generation (i.e., late July). All plots were 16 hectares; treated and nontreated plots were each replicated four times.

Predator populations were monitored twice weekly, using a D-vac® mechanical suction machine (Dietrick *et al.*, 1959; Dietrick, 1961). In each plot, 100 suction samples were taken from the terminal portion (usually upper half) of the plants. Predator abundance was expressed as a cumulative total for each species. Densities of *T. ni* developmental stages were determined in the same manner as in the life-table studies.

Results and discussion. The dimethoate sprays reduced the densities of most predators (Table 11). Significant reductions occurred in the adults and nymphs of *O. tristicolor* and *G. pallens*. Also, populations of *N. americanoferus*, *C. vittatus*, and spiders were greatly reduced, although the differences were not statistically significant. These trends in predator populations represent cumulative totals for the period July 21 to August 11—the period of peak abundance for *T. ni* eggs and small larvae.

Survival of *T. ni* larvae in these plots (Table 12) was directly correlated with predator abundance (Table 11). In both instances, the generation started with virtually the same number of eggs; however, larval survival during the generation was consistently and significantly greater in plots where predators were suppressed, compared to plots with a normal complement of predators. Although no significant differences in egg densities were detected, it cannot be assumed there was no egg predation. Larvae of *C. carnea*, a potential egg predator, were not adversely affected in the treated plots; thus, any egg predation by this predator would have gone undetected. The bulk of the mortality seemed to occur in the small-larva in-

TABLE 12
SURVIVAL OF *T. NI* DEVELOPMENT STAGES IN PLOTS WITH DIFFERENT
PREDATOR DENSITIES. CORCORAN, 1970

Stage	Mean number entering stage ^a		“t” value
	Normal complement of predators	Predators suppressed	
Egg	25.1	28.7	NS
Medium-sized larva	14.1	34.5	**
Large larva	8.2	22.4	*
Pupa	2.7	7.1	**
Adult	2.5	7.0	**

^a Age-specific life table data for 2nd generation; mean of 4 replications.

terval. In the nontreated plot, 25.1 eggs yielded 14.1 medium-sized larvae; in the treated plot, 28.7 eggs yielded 34.5 medium-sized larvae. The discrepancy in the latter plot (i.e., more larvae than eggs) is likely due to the fact that the larvae were much larger and easier to observe than the eggs.

It is concluded that the differences in survival of small larvae (and possibly larger larvae) were due primarily to differences in predator abundance. This conclusion becomes particularly tenable in view of the fact that no evidence of egg parasitization or infertility was obtained, and because those parasites which oviposit in small larvae (e.g., *H. exiguae* and *M. brassicae*) do not produce mortality until the host is medium-sized. The predators especially responsible for the mortality most likely were *O. tristicolor*, *G. pallens*, and *N. americanus*, as these species were most abundant and most affected by chemical treatments. During the third generation at this site, predator populations resurged in the previously treated plot, to a level equal to that of the nontreated control. In this setting, larval survival did not differ significantly between plots (Ehler *et al.*, 1973).

Boswell Ranch (1971, 1974)

Materials and methods. These studies were conducted in the plots used for 2nd generation life-table studies in

the respective fields. In this case, survival of small larvae was determined in plots with a normal complement of predators, and in cages from which predators were chemically excluded. The nontreated plots each consisted of 0.5 meter of consecutive plants which were inoculated with small *T. ni* larvae, principally late 1st and early 2nd instars. Usually, 10 larvae were placed in each plot, and the experiment was replicated 4 or 5 times. In the chemical treatment, field cages (described by van den Bosch *et al.*, 1969) were placed over the plants (2 rows × 3.7 meters), sealed, and treated with a liberal dose of dimethoate insecticide which destroyed virtually all insects within the cage. After 1 week, the cages were inoculated with *T. ni* larvae (late 1st and early 2nd instars), concurrent with inoculations in the nontreated plots. Only 3 replications of the cage treatment were available. Survival of *T. ni* larvae in both chemically treated and in nontreated plots was determined after 24 hours. Sampling was accomplished with the beating technique discussed by Eveleens *et al.* (1973).

Results and discussion. The results of these experiments are presented in Table 13. In all three, survival of small *T. ni* larvae was significantly lower in plots with a normal complement of predators, compared to plots (in cages) from which predators were chemically excluded. The most abundant preda-

tors, and probably those responsible for most of the mortality of *T. ni* larvae, were *O. tristicolor*, *G. pallens*, and *N. americoferus*. These results are consistent with earlier observations and experimentation, and indicate a prompt response of predators to sudden increases in prey density.

Conclusion

The experimental evidence strongly supports the hypothesis that predators

are largely responsible for the majority of the intrageneration mortality of *T. ni* on cotton in the San Joaquin Valley. Thus, it is not surprising that secondary outbreaks of *T. ni* occur so often after use of broad-spectrum insecticides (for control of other pests) which decimate these predators. Among the predators, the most important are probably adults and nymphs of *O. tristicolor*, *G. pallens*, *N. americoferus*, and possibly larvae of *C. carnea*.

TABLE 13
SURVIVORSHIP OF SMALL *T. NI* LARVAE IN PREDATOR VERSUS
PREDATOR-FREE PLOTS

Experiment	Percent Survival		“t” value
	Predators present	Predators excluded	
1. Corcoran 1971	12.5	95.0	**
2. Corcoran 1974	22.0	67.0	*
3. Corcoran 1974	32.0	93.3	**

ANALYSIS OF BIOTIC MORTALITY OF CABBAGE LOOPER

Mortality of eggs

Parasitization. Parasitization of *T. ni* eggs by either *T. semifumatum* or *T. pretiosum* was insignificant, with only a few eggs being parasitized by *T. semifumatum* at the Heimforth Ranch in 1970 (Table 5). No parasitized eggs were detected in the Corcoran studies despite the rather intensive surveys which were made. In both areas, host eggs were continuously available throughout the latter part of July, all of August, and the first part of September. Yet the egg parasites were seemingly unable to exploit this resource. The reasons for this lack of parasitization are in need of investigation.

Predation. Although a number of species are considered to be predators of *T. ni* eggs, the potential impact of these agents was not clearly revealed in the present work. That is, the experi-

mental studies at the Boswell Ranch in 1970 clearly showed that the survival of *T. ni* larvae was inversely related to predator abundance, but the same was not demonstrated for eggs. In fact, there was no significant difference in egg densities between plots with the normal complement of predators and plots where predators were chemically suppressed. However, as noted earlier, larvae of *C. carnea*, a potential egg predator, were not significantly affected by the chemical treatments; thus, any egg mortality due to this species would have gone undetected in the experiment.

Infertility. In most instances, all the eggs collected in the field and held in the laboratory were viable and hatched in a few days. A few infertile eggs were detected at the Boswell Ranch in 1970 (Table 8) and 1974 (Table 10), although aspects of the sampling technique could also have caused this.

Mortality of small larvae

The evidence presented herein strongly supports the hypothesis that most of the biotic mortality of small *T. ni* larvae is inflicted by a complex of predators, particularly adults and nymphs of *O. tristicolor*, *G. pallens*, and *N. americoferus*. Also, it appears that these predators are largely responsible for the major portion of the total generation or real mortality of *T. ni* populations on cotton in the San Joaquin Valley. In each of four experiments, survival of small *T. ni* larvae in the general absence of predators was significantly greater than in plots with a normal complement of predators.

The impact of predators on *T. ni* larvae in California cotton has also been demonstrated by previous workers. Utilizing the insecticidal-check method, Falcon *et al.* (1968) calculated that during one period of time, 3.5 *T. ni* eggs in the nontreated control yielded 1 larva, whereas in Bidrin®-treated plots, 1.9 eggs resulted in 1 larva. During a second period, 6.9 eggs in the nontreated control yielded 1 larva, while in Bidrin® plots, 1.2 eggs resulted in 1 larva. Similarly, egg:larva ratios for a third period were 6:1 in the nontreated control and 4.4:1 in the Bidrin® plot. These authors concluded that predators, chiefly *O. tristicolor*, *G. pallens*, *N. americoferus*, *C. carnea*, and *C. vittatus*, were largely responsible for this differential survival. Finally, in more recent studies, secondary outbreaks of *T. ni* larvae have followed applications of Toxaphene-DDT (Falcon *et al.*, 1971) and dimethoate (Gutierrez *et al.*, 1975).

Parasitization and polyhedrosis apparently have little or no impact on small larvae. Larval parasitoids such as *H. exiguae* and *M. brassicae*, which oviposit in small larvae, kill the host during later instars (i.e., medium-sized larvae). Previous studies have shown that death from polyhedrosis is generally restricted to medium-sized and

large larvae (Ignoffo, 1964; Ehler *et al.*, 1973), although it is conceivable that small larvae infected with a massive dose of polyhedra could succumb to polyhedrosis prior to becoming medium-sized.

Mortality of medium-sized larvae

M. brassicae. This species appears to be the major parasitoid associated with medium-sized *T. ni* larvae. However, in life-table studies, parasitization seldom exceeded 20% apparent mortality; and, compared to the action of predators, *M. brassicae* contributed little to total generation mortality. Additional surveys of parasitization of *T. ni* larvae (apparent mortality) in cotton fields in Kern Co. revealed a similar trend. The results at five sites in 1969 were: 36.4% (N=22), 2.2% (N=45), 4.2% (N=48), 0% (N=5), and 0% (N=11). During 1974, the results were 30.8% (N=13) and 7.1% (N=14). Ehler and van den Bosch (1974) noted that for three successive generations in 1970, parasitization by *M. brassicae* was generally highest at lowest host density, and appeared to be inversely related to host density. Thus, it is somewhat surprising that parasitization by *M. brassicae*, a relatively host-specific parasitoid, is not directly density-related, and does not appear to be a major biotic mortality factor in *T. ni* in cotton.

H. exiguae. Parasitization by this species seldom exceeded 10% apparent mortality and, in general, *H. exiguae* contributed comparatively little to total generation mortality. Surveys in additional cotton fields in Kern Co. revealed a similar trend. During 1969, apparent mortality of *T. ni* larvae (at peak density) due to *H. exiguae* parasitization at five sample sites was as follows: 4.5% (N=22), 0% (N=45), 0% (N=48), 0% (N=5), and 0% (N=11). At two sample sites in 1974, no evidence of parasitization was detected in samples of 13 and 14 larvae. Ehler and van den Bosch

(1974) suggested that parasitization by *H. exiguae*, as with *M. brassicae*, was inversely related to host density. The reasons for this poor performance by *H. exiguae* are not clear, although partial host immunity, as shown for this species in *S. exigua* (Puttler and van den Bosch, 1959), is a possible explanation.

Other parasitoids. Parasitization by *C. texanus* and *A. marginiventris* was detected sporadically, and never exceeded 6% apparent mortality. These species likely have little, if any, impact in natural control of *T. ni* populations on cotton.

Polyhedrosis. The proportion of medium-sized larvae which succumbed to nuclear polyhedrosis virus was comparatively low, and seldom exceeded 5% apparent mortality. However, during the third *T. ni* generation at Corcoran in 1970 (Table 8), 31.8% of the larvae died of polyhedrosis. Also, surveys in additional Kern Co. cotton fields revealed epizootic levels in some instances. During 1969, samples of *T. ni* larvae taken during time of peak density at five sites, yielded the following rates of polyhedrosis: 0% (N=22), 57.8% (N=45), 37.5% (N=48), 40% (N=5), and 90.9% (N=11). Thus, virus epizootics do occur, although these are not always consistent in time and space. Polyhedrosis should not be considered a consistent, major mortality factor for medium-sized larvae.

This conclusion contrasts markedly with previous studies of *T. ni* on cole crops. In southern California, Oatman and Platner (1969) considered polyhedrosis to be the major mortality factor for *T. ni* on cabbage during the summer and fall. Hofmaster (1961) considered polyhedrosis to be the most important factor influencing abundance of cabbage looper on broccoli in Virginia.

Residual. In some instances, a portion of the mortality of medium-sized

larvae was unaccounted for, and thus was labeled as "predation + unknown causes." The precise components of this residual have not been deduced, although predation by larger predators (e.g., *N. americanoferus*, *C. carnea* larvae, *Z. renardii*), abiotic factors, and sampling error are likely explanations. This mortality of medium-sized larvae was substantial (20.6%) in one case (Table 7).

Mortality of large larvae

C. trunctellum. This species was the dominant parasitoid of large *T. ni* larvae, and was often the major mortality factor associated with large larvae. In fact, *C. trunctellum* appears to be the dominant parasitoid of *T. ni* larvae in the San Joaquin Valley cotton. Apart from life-table studies, additional surveys in Kern Co. cotton revealed generally high levels of parasitization (apparent mortality) of *T. ni* by *C. trunctellum*. During 1969, the figures for five sampling sites were 40.9% (N=22), 37.8% (N=45), 50% (N=48), 40% (N=5), and 0% (N=11). During 1974, apparent mortality at two sites was 46.2% (N=13) and 78.6% (N=14).

Ehler and van den Bosch (1974) considered parasitization by *C. trunctellum* to be density related. This was logical, since polyembryonic development gives the species the potential to promptly exploit the *T. ni* egg population during periods of egg abundance. In addition, the ratio of females to males in *C. trunctellum* is usually much greater than one. For example, analysis of the adult parasitoids which emerged from parasitized hosts from two cotton fields near Rosedale in 1969, revealed that 89 of 107 (81.8%) and 116 of 144 (79.8%) of the mummified hosts contained predominantly females. At the Boswell Ranch in 1974, 72.4% of all *C. trunctellum* taken in D-vac samples were female. Thus, *C. trunctellum* possesses two important attributes

which increase its potential as a biological control agent in California cotton: polyembryony and a comparatively greater number of females available for searching and parasitization of *T. ni* eggs.

Previous studies indicated that *C. truncatellum* is a major enemy of *T. ni* in other areas and crops. Oatman (1966) stated that *C. truncatellum* was the dominant hymenopterous parasite of *T. ni* on southern California cabbage, and Clancy (1969) considered this species to be the most common hymenopterous parasite of *T. ni* from wild hosts in southern California. Harcourt (1963) considered *C. truncatellum* to be the most important parasite of *T. ni* on cabbage in eastern Ontario. Also, Burleigh (1971) rated *C. truncatellum* as the predominant parasite on soybean looper (*Pseudoplusia includens* [Walker]) in Louisiana.

V. ruralis. Parasitization of large larvae by *V. ruralis* was usually less than 10%, and, in some cases, was not detected. Presumably, *V. ruralis* contributes little to natural control of *T. ni* on cotton; and, as Ehler and van den Bosch (1974) noted, parasitization by this species is somewhat erratic and apparently not density related.

However, these results on cotton are in striking contrast to those in previous studies of the impact of *V. ruralis* on *T. ni* populations on other crops. Oatman and Platner (1969) found *V. ruralis* to be the dominant parasite of *T. ni* in southern California cabbage plantings, and suggested that it was the principal mortality factor affecting *T. ni* populations during the winter months. According to Clancy (1969), *V. ruralis* was the most common parasitoid of *T. ni* larvae collected during fall and winter from annual weeds, tree tobacco, and alfalfa in southern California. In Arizona, McKinney (1944), Butler (1958), and Brubaker (1968) showed *V. ruralis*

to be the most common parasitoid of *T. ni* larvae from weeds and various crops. Elsey and Rabb (1970b) considered *V. ruralis* to be the most important parasitoid of large *T. ni* larvae on collards in North Carolina.

Thus, it is somewhat surprising that *V. ruralis*, a relatively host-specific parasite of *T. ni* in San Joaquin Valley cotton, is a rather poor performer based on its performance in other areas and crops. The underlying reason(s) for this are in need of investigation.

Polyhedrosis. Incidence of nuclear polyhedrosis of large larvae followed a trend similar to that of polyhedrosis of medium-sized larvae. Polyhedrosis was seldom the major mortality factor affecting large larvae, although, as Ehler and van den Bosch (1974) indicated, the incidence of disease can be density related, and epizootics often occur during late season or during *T. ni* outbreaks.

As in the cases of polyhedrosis of medium-sized larvae and of parasitization by *V. ruralis*, the incidence of polyhedrosis of large *T. ni* larvae on cotton differed markedly from that of previous investigations. Oatman and Platner (1969), Clancy (1969), and Brubaker (1968) reported high polyhedrosis rates for *T. ni* larvae. Indeed, Oatman and Platner (1969) considered polyhedrosis to be the major mortality factor affecting *T. ni* during the summer and fall in southern California cabbage plantings. Similarly, Hofmaster (1961) stated that polyhedrosis was the most important factor influencing abundance of cabbage looper on broccoli in Virginia. Also, Elsey and Rabb (1970b) considered polyhedrosis to be the principal agent affecting large larvae during late season generations on North Carolina collards.

The discrepancies between polyhedrosis of *T. ni* larvae in cotton and in cole crops is as yet unexplained.

However, the fact that cole crops are often planted in succession, thus providing temporal continuity, whereas cotton is not, may allow nuclear polyhedrosis virus to accumulate and eventually reach epizootic levels. This may also enhance the efficiency of *V. ruralis* in similar situations.

Residual. Some mortality of large larvae which was not assigned to any specific factor(s) was often significant. The components of this residual are probably similar to those for medium-

sized larvae, which include predation, abiotic factors, and sampling error.

Mortality of pupae

The only demonstrated cause of *T. ni* pupal mortality was parasitization by *P. montanus*. Such parasitization was detected only in the Corcoran area, and *P. montanus* was often a major factor affecting pupal mortality. Ehler and van den Bosch (1974) suggest parasitization by *P. montanus* can be density related, although the response is not a strong one.

IMPLICATIONS FOR BIOLOGICAL CONTROL

Previous analyses of successful, classical biological control programs revealed that most successes involved pests of perennial plants. However, I have shown how naturally occurring biological control agents greatly affect the natural control of *T. ni* on cotton in the San Joaquin Valley (an annual crop), and that when predators responsible for this control are removed, secondary-pest outbreaks can occur. I suggest these findings have implications for classical biological control, particularly in annual crops.

Biological control in annual crops

Literature review. Various authors have assessed the potential for biological control in annual crops. Lloyd (1960) speculated that certain temporal dimensions of the annual-crop habitat (e.g., frequent habitat disruption) were causally related to the inadequacy of classical biological control in such crop ecosystems. Hansberry (1968) considered the record of successes in biological control given by DeBach (1964), and concluded that "Therefore, it seems very unlikely that we can ever expect biological methods to control field and truck-crop pests." Newsom (1970) analyzed the same record and concluded that few cases of biological control (none complete) were

reported for pests of crops that "feed the world," meaning cereals, oil seeds, and vegetable crops. Ridgway (1972) analyzed the record given by DeBach (1964) from a slightly different point of view. He concluded that every case of successful, classical biological control in the continental United States involved a pest of a perennial crop; and that less than 15% of the major crop losses in the United States, according to U.S.D.A. statistics for 1965, were associated with perennial crops. More recently, van den Bosch *et al.* (1976) analyzed those biological-control successes given by DeBach (1964), which occurred in row crops (i.e., 13 of 110 cases). They concluded that, "The poor record probably relates largely to the instability of the row-crop environment, which presumably does not permit establishment of the effective host-natural enemy relationships which often characterize more stable environments."

Theoretical considerations. From the available empirical evidence, it is clear that successful cases of classical biological control have occurred predominantly in perennial crops. Also, the apparent lack of success in annual or short-cycle crops can be correlated with the instability, or lack of temporal con-

tinuity, in these agroecosystems. Practical application of biological control in the latter setting could be accomplished in three major ways: (1) manipulation of enemies to improve their efficiency (see DeBach and Hagen, 1964); (2) modification of the environment to enhance natural enemies (see van den Bosch and Telford, 1964); and (3) importation and colonization of exotic natural enemies (classical biological control). The technical feasibility of manipulation and environmental modification has been demonstrated. However, the potential for classical biological control is in question.

Organisms adapt to the environment in which they live. Since perennial and nonperennial crop environments differ in temporal and spatial dimensions, it follows that natural enemies adapted (or preadapted) to temporary and/or disturbed environments may be suitable agents for biological control in annual crop systems. Thus, the necessary properties of a successful biological control agent for a pest in a perennial crop may not coincide with those of such an agent for a pest of an annual crop.

Current ecological theory suggests that some organisms are adapted to stable, predictable environments, whereas others are adapted to unpredictable, disturbed environments. For example, Baker (1965, 1974) considers a plant to be a weed if, in a particular region, its populations occur predominantly or entirely in situations markedly disturbed by man (i.e., exclusive of deliberately cultivated species). Erdtman (1963) noted that some species live in stable environments (i.e., statocrats), while others do not (i.e., apocrats). Hutchison (1951) wrote of "fugitive species," meaning those which specialize in the occupation of transient habitats, and disappear as habitat stability returns and competition becomes keen. Wilson (1965) noted that fugitive species are able to survive by the rela-

tively quick and temporary occupancy of suitable new habitats, and that these species are characterized by superior dispersal and reproductive powers. Indeed, there are numerous terms in the literature which describe, in whole or in part, species which exist in temporary and/or disturbed habitats (see Margalef, 1968). Recent entomological investigations have revealed how such ecological theory may be relevant to biological control.

Force (1972, 1974) investigated an endemic host-parasitoid community in California consisting of a midge (*Rhopalomyia californica* Felt) which forms galls on the endemic coyote brush (*Baccharis pilularis* DeCandolle), and is parasitized by at least 10 species of parasitic Hymenoptera. Force (1972) observed that, in undisturbed sites, the parasite with the highest reproductive rate (r_m) and poorest competitive ability (*Tetrastichus* sp.), was least dominant numerically and rarely responsible for more than 1% mortality. However, at a disturbed site (i.e., many plants removed, others cut low to the ground), parasitization by *Tetrastichus* increased rapidly from 1% to 46%, and remained at that level for several months. Parasitization by *Tetrastichus* then declined as the habitat returned to normal.

Using the classification of MacArthur and Wilson (1967), Force (1972) labeled *Tetrastichus* an r-strategist (i.e., high r_m , poor competitor) as opposed to a K-strategist (i.e., comparatively low r_m , good competitor). Force (1972) predicted that "What would appear to be needed to control pests in situations where they have invaded new, often disturbed (agricultural, etc.) environments are natural enemies that are r-strategists." Force also postulated that r-strategists are good colonizers. He suggested that these agents could be defined operationally as those species that are least dominant numeri-

cally in undisturbed situations, are found consistently over a wide geographical or ecological range, and are relatively more abundant in newly disturbed habitats.

In a recent study of the parasitoid complex of Swaine jack pine sawfly (*Neodiprion swaini* Middleton), Price (1973) endorsed Force's predictions and gave empirical evidence in support. Price showed that early colonizers have high fecundity and low competitive ability (i.e., r-strategists), and later colonizers have low fecundity and high competitive ability (i.e., K-strategists). Price also noted that his data supported Force's (1972) prediction that r-strategists will be found as numerically dominant species in newly available situations.

Evidence presented in the present paper supports Force's predictions concerning the impact of numerically dominant natural enemies in disturbed habitats. That is, certain predators, particularly *O. tristicolor*, *G. pallens*, and *N. americanoferus*, are clearly the numerically dominant species. As life-table and experimental studies indicate, these predators are largely responsible for much of the total generation mortality of *T. ni* on cotton. Also, when these predators are eliminated or reduced, secondary-pest outbreaks of *T. ni* can occur. Among parasitoids, *C. truncatellum* was numerically dominant, and usually produced a greater amount of real mortality than did any of the other species (see Tables 5, 6, 10). Life-table analysis revealed that *C. truncatellum* was the dominant parasitoid associated with mortality of large *T. ni* larvae.

To summarize, the theory of r- and K-selection provides a major theme for considering ecology of insects in stable versus unstable or disturbed habitats. That is, r-strategists generally occupy unpredictable or disturbed environments, possess a comparatively high ca-

capacity for increase (r_m), and are comparatively poor competitors. K-strategists generally exist in more constant or stable environments, have a comparatively lower capacity for increase, and are relatively good competitors (Pianka, 1970; Force, 1975). It follows that certain natural enemies (e.g., r-strategists) may be comparatively better adapted to such habitats as annual or short-cycle crops. Thus, these agents may be especially suitable for biological control in these environments (Force, 1972; Ehler and van den Bosch, 1974). Regarding such natural enemies, it should be expedient to consider their essential attributes which predispose them for use in biological control.

Natural enemies in annual crops

Ehler and van den Bosch (1974) predicted that natural enemies capable of effective colonization of the habitat and rapid exploitation of the prey population should be suitable agents for biological control of pests in temporary or annual-crop agroecosystems. These natural enemies probably represent an extreme of r-selection. I suggest that the natural enemies most responsible for control of *T. ni* on California cotton (i.e., predators) possess these two important attributes.

Colonization. According to Johnson (1969), it is generally accepted that migratory behavior has evolved in those species which exist in habitats which periodically become adverse for breeding, or disappear completely. For example, Brown (1951) studied migration rates of certain aquatic Heteroptera, particularly corixids, and concluded that migration rates were related to the degree of impermanence of the habitat. Similarly, Southwood (1960) noted that species of Heteroptera trapped most abundantly in light traps and in suction traps, were those which bred predominantly on annual

plants, or on plants which grew in temporary habitats. Later, Southwood (1962) validated the hypothesis for the major taxa of terrestrial arthropods. He concluded that the evolutionary advantage of migratory movement lies in enabling a species to keep pace with changes in habitat location, and that the degree of migratory movement is positively correlated with impermanence of habitat.

In the case of the major predators of *T. ni* in cotton, there is substantial indirect evidence for such migratory movement or colonizing ability. First, cotton is an annual crop which is planted, cultured, and harvested in a matter of months. At the end of the season, the plant remains are plowed down and destroyed. The following season the same events occur, often in another location. It follows that those species capable of keeping pace with this relatively frequent habitat destruction are competent colonizers. This seems to be the case for the common predators of *T. ni*, as those species are usually relatively abundant in early season (Tables 1-4).

Second, several of the predator species suggested to be competent colonizers have been shown to be rather vagile species. For example, Rakickas and Watson (1974) demonstrated that when fully-grown hay alfalfa was cut, certain adult predators migrated to half-grown alfalfa hay, up to 67 meters away. These predators included *O. tristicolor*, *C. vittatus*, and *N. americanoferus*. The authors were unable to assess *C. carnea* and *G. pallens*, as these species were not abundant. In similar studies conducted in California, van den Bosch and Stern (1969) reported that most of the same predators moved to alternate strips of alfalfa (up to 122 meters) when existing strips were harvested.

Third, as Southwood (1960) showed, migratory species which exist in temporary habitats are relatively abundant

in the air, compared to species found in more permanent habitats. In the present case, most adults of common *T. ni* predators have been taken at relatively high altitudes. For example, *O. tristicolor* was taken at altitudes of up to 915 meters over Central Texas (Glick and Noble, 1961), and up to 152 meters over South Texas (Glick, 1957). Glick (1939) collected *C. carnea* at 915 to 1524 meters over Tallulah, Louisiana. Glick and Noble (1961) collected *G. pallens* at 61 meters over Central Texas and Glick (1939) collected the related *G. punctipes* at 1524 meters in Louisiana. Other relevant species collected in these studies were *C. vittatus* at up to 305 meters over Central Texas (Glick and Noble, 1961), and *Z. renardii* at 61 meters over South Texas (Glick, 1957). Of the major parasitoids of *T. ni* in California cotton, only *C. truncatellum* was represented in these surveys, having been collected at 610 meters over Louisiana (Glick, 1939).

Thus, the available evidence strongly indicates that the major predators of *T. ni* (i.e., *O. tristicolor*, *G. pallens*, *N. americanoferus*) are competent dispersers, and can be considered colonizing species. Also, this seems to be the case for *C. truncatellum*, which is often the dominant parasitoid of *T. ni* on cotton. Unfortunately, more definitive studies (e.g., mark-recapture) have not been made.

Exploitation. Although a natural enemy may be capable of effective colonization of new habitats, for it to be an effective agent in biological control it must also be capable of exploiting, and presumably controlling, the prey or pest population density. Since prey populations in such temporary agroecosystems are often transient, an effective biological-control agent should be capable of prompt or rapid exploitation of the prey. Indeed, adaptations which allow such exploitation of *T. ni* in cotton exist among the natural enemies largely re-

sponsible for biological control of this pest.

Among the important predators, lack of prey specificity (i.e., polyphagy) is an attribute which preadapts these natural enemies to exist in cotton, and appears directly correlated with their ability to exploit *T. ni* populations. Since these predators are polyphagous, their populations can be maintained at comparatively high levels because various food items are available. When *T. ni* density increases, these predators are presumably able to exploit this new resource. Apparently, in these species there exists a "switching" mechanism (Murdoch, 1969) whereby such general predators are able to stabilize, or control, prey populations by switching between or among prey, as the relative abundance of the prey species changes.

Empirical evidence presented earlier supports this hypothesis. That is, when sudden increases in density of small *T. ni* larvae were experimentally induced, predators apparently destroyed the bulk of these larvae in a matter of 24 hours; but most larvae protected from predators (in cages) survived (Table 13). Also, it has been shown that these predators respond in a similar fashion with respect to other prey (see next section).

Plant feeding by *O. tristicolor*, *G. pallens*, and *N. americoferus* may also account for their abundance and presence in cotton when various prey species are not abundant. For example, Sweet (1960) hypothesized that such omnivorousness may account for the high abundance of many geocorines. He suggested that certain species may feed on plants when prey density is low, and thus continue to survive. Indeed, Ridgway and Jones (1968) were able to increase longevity of *N. americoferus* and *G. pallens* when adult bugs were allowed to feed on cotton plants. Similarly, Tamaki and Weeks (1972) found that, for *G. pallens*, a combination of

sunflower seeds, insects, and green plant food was the best diet for quickest development, highest egg production, and highest survival rate.

Among parasitoids of *T. ni*, polyembryony particularly preadapts *C. truncatellum* for exploitation of a temporary resource, and, presumably, enables this parasitoid to be an effective natural enemy of *T. ni*. In this case, reproductive output (\bar{X} of 1526 individuals/host) is substantially greater than reproductive input (1 or 2 eggs/host). Also, the sex ratio of *C. truncatellum* is predominantly in favor of females; thus, comparatively more individuals are available for parasitization of hosts. It is not surprising then, that *C. truncatellum* is the numerically dominant parasitoid, the major parasitoid associated with mortality of large larvae, and, in many cases, the dominant parasitoid associated with *T. ni* on cotton in the San Joaquin Valley.

The evidence indicates that host specificity is not an essential attribute of the effective natural enemies of *T. ni* on cotton. The case for general predators has been documented. Among the host-specific parasitoids (i.e., *M. brassicae*, *V. ruralis*, *C. truncatellum*, and *P. montanus*), only *C. truncatellum* can be considered to be a major mortality factor. However, in this case, polyembryonic development and a sex ratio in favor of females, presumably allow this host-specific parasitoid to exert a greater degree of control of *T. ni*.

Discussion. I have emphasized that natural enemies capable of colonization of the habitat and prompt exploitation of the prey population are potentially suitable agents for biological control of pests in annual crops. Certain general predators of *T. ni* are good examples of this. However, it must not be assumed, *a priori*, that natural enemies lacking any of the attributes discussed (e.g., host-specific species) would be unsuitable. Also, these attributes do not guar-

antee a natural enemy can be successfully used in biological control.

But the notion that a natural enemy in successful biological control must have a high degree of host specificity is questioned. The data relative to natural biological control of *T. ni* in San Joaquin Valley cotton provide a clear exception to this belief, and indicate that, at least in some instances, the opposite may be true. Therefore, in the following section, particular attention is given to the use of general or polyphagous predators in biological control.

General predators in biological control

Literature review. It appears to be conventional wisdom in biological control that the natural enemies used should be host specific (see Mesnil, 1958). However, Douthett and DeBach (1964) concluded that this belief may not be entirely tenable, and should not lead to exclusion of general or polyphagous feeders. Other workers have emphasized the need for host-specific enemies. This is implicit in the work of Flanders (1962), Hassell and May (1973), and Hassell and Rogers (1972).

More recently, DeBach (1971) and Huffaker *et al.* (1971) considered attributes of an effective enemy in biological control. The latter authors stated that "An effective natural enemy has the following characteristics: (a) high searching ability, (b) high degree of host specificity or preference, (c) good reproductive capacity relative to the host, and (d) good adaptation to a wide range of environmental conditions." However, Huffaker *et al.* (1969) cautioned that "... If their numbers are consistently maintained at a good level from feeding on alternative foods, they (meaning generalists) could exert a degree of control both consistent and more complete than that achieved by the specialist. ... Such a form could be

said to be a poorer *regulator* but a better control factor."

The belief that the most effective biological-control agent will be host specific has been challenged on both empirical and theoretical grounds. Liu (1958) analyzed the record of successful biological control and found that in 30 cases involving 32 species of natural enemies, only 6 species of natural enemies were known from only one host. According to Mesnil (1958), several pests were brought under successful biological control by natural enemies with a number of alternative hosts. Also, Beirne (1962), Watt (1965), Connell (1971), Ehler and van den Bosch (1974), and Hughes *et al.* (1974) considered the attributes of a natural enemy which suit it to environments where the prey population is ephemeral (or unstable) and suggested that lack of prey specificity may be of advantage in biological control of such pests.

In view of these latter arguments and the evidence presented in this paper, it appears that the belief that host-specific natural enemies are highly desirable in all biological control programs is a questionable assumption. Indeed, additional empirical evidence presented below tends to support the hypothesis that general feeders (e.g., polyphagous predators) can be important biological-control agents in certain cases.

Empirical evidence. The evidence presented earlier clearly indicates that polyphagous predators are responsible for most of the biological control of *T. ni* on San Joaquin Valley cotton. Additional studies in cotton have also revealed the same group of predators to be important in biological control of beet armyworm (*S. exigua*), bollworm (*H. zea*), and lygus bug (*L. hesperus*).

In the Corcoran area, Falcon *et al.* (1971) recorded secondary outbreaks of *S. exigua* following Toxaphene-DDT applications for control of *L. hesperus*. Eveleens *et al.* (1973) and Gutierrez *et*

al. (1975) noted similar secondary outbreaks following applications of dimethoate for lygus control. Eveleens (1972) and Eveleens *et al.* (1973) thoroughly investigated such outbreaks. They concluded that predators were largely responsible for maintaining *S. exigua* at low levels; and when the predators were experimentally excluded, secondary outbreaks occurred. Also, Eveleens (1972) placed egg clusters of *S. exigua* in nontreated cotton and observed predator activity. Where predators were observed feeding on *S. exigua* egg masses, the predominant species were *G. pallens*, *O. tristicolor*, *N. americanoferus*, and larvae of *C. carnea*.

In the Rosedale area, van den Bosch *et al.* (1969) reported that naturally occurring predators destroyed from $\frac{2}{3}$ to $\frac{9}{10}$ of *H. zea* larvae in one experiment. In cage studies, these authors found that *G. pallens* reduced *H. zea* density 50%, and that *N. americanoferus* and *C. carnea* gave even greater mortality. In the Dos Palos area, van den Bosch *et al.* (1971) reported resurgences of *H. zea* following monocrotophos applications which significantly reduced predators (primarily *O. tristicolor*, *G. pallens*, and *C. carnea*).

Investigations of the impact of these predators on *L. hesperus* by J. T. Shimizu (personal communication) have given similar results. For example, in nontreated cotton near Corcoran in 1970, Shimizu exposed string beans containing lygus eggs to naturally occurring predators. After 24 hours, 55% of the eggs had been destroyed by predators. In 1971, 20 to 60% were destroyed

in 24 hours and 38 to 82% after 48 hours. In both experiments, *G. pallens*, *O. tristicolor*, and *N. americanoferus* were the most frequent visitors, respectively.

Discussion. These studies clearly indicate that a complex of general predators, primarily *G. pallens*, *O. tristicolor*, *N. americanoferus*, and larvae of *C. carnea*, is an important biotic mortality factor for the four major insect pests of cotton in the San Joaquin Valley of California. Hence, it can be argued that such polyphagous natural enemies might be effective agents for classical biological control in similar situations.

However, as Ehler and van den Bosch (1974) pointed out, introduction and establishment of such natural enemies should be attempted when sufficient evidence exists to assure that the enemy, despite its feeding habits, will not cause serious disruption of existing biological control. Interestingly, a number of the polyphagous predators discussed in this paper have been imported elsewhere, apparently causing no significant disruption. These include importation into Hawaii of *G. pallens* and *G. punctipes* (Usinger, 1936), *O. tristicolor* and the related *O. insidiosus* (Weber, 1953; Davis and Krauss, 1963), and *Z. renardii* Swezey, 1936; Nishida, 1955). Furthermore, if Tauber and Tauber (1973) have correctly interpreted the origin of the California strain of *C. carnea*, it can be concluded that the introduction of this predator has had a significant impact on biological control of a number of important agricultural pests, and has caused no apparent disruption of existing biological control.

CONCLUSION

I have shown how a predominantly native fauna of natural enemies effect biological control of cabbage looper on cotton in the San Joaquin Valley of California. In addition, these natural enemies are capable of controlling other

pests of cotton, such as beet armyworm, bollworm, and lygus bug. The attributes of these enemies which preadapt them for use in biological control in annual or short-cycle crops are given. I suggest that the deliberate importation and es-

tablishment of such natural enemies, coupled with the feasibility of manipulation of naturally occurring species,

will lead to a greater understanding and appreciation of the potential for biological control of pests in annual crops.

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