



AgEcon SEARCH
RESEARCH IN AGRICULTURAL & APPLIED ECONOMICS

The World's Largest Open Access Agricultural & Applied Economics Digital Library

This document is discoverable and free to researchers across the globe due to the work of AgEcon Search.

Help ensure our sustainability.

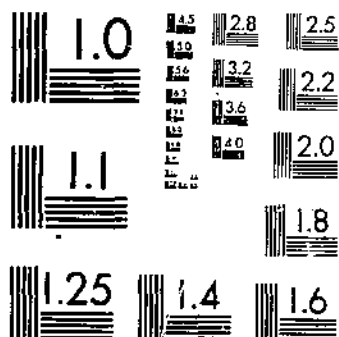
Give to AgEcon Search

AgEcon Search
<http://ageconsearch.umn.edu>
aesearch@umn.edu

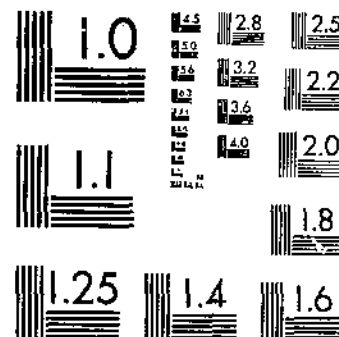
*Papers downloaded from **AgEcon Search** may be used for non-commercial purposes and personal study only. No other use, including posting to another Internet site, is permitted without permission from the copyright owner (not AgEcon Search), or as allowed under the provisions of Fair Use, U.S. Copyright Act, Title 17 U.S.C.*

TB 1434 (1971) USDA TECHNICAL BULLETINS UPDATA
USE OF POPULATION MODELS TO APPRAISE THE ROLE OF LARVAL PARASITES IN
KNEPLING, E. F. 1-OF-1

START



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A

R630
053-1
#1434

**Use of Population Models
to Appraise the Role
of Larval Parasites
in Suppressing
Heliothis Populations**

DEPOSITORY

SUPPLIES

Technical Bulletin No. 1434

Agricultural Research Service

UNITED STATES DEPARTMENT OF AGRICULTURE

Contents

	Page
Establishment of population models	4
Host population model	5
Natural parasite population model	9
Establishing efficiency of parasite in host parasitism	10
Seasonal trend of coexisting parasite and host populations ..	13
Parasite-host population model	15
Testing validity of assumed efficiency of parasite	17
Programed releases of parasites for <i>Heliothis</i> suppression	20
Theoretical effects of low release rates	22
Theoretical effects of moderate release rates	23
Adjustments in host survival rates due to reduced predation	26
Theoretical effects of high and sustained release rates	28
Integration of parasite releases with release of genetically altered males	29
Discussion	30
Summary	34
Literature cited	35

Use of Population Models to Appraise the Role of Larval Parasites in Suppressing *Heliothis* Populations

By E. F. KNIPLING, *Agricultural Research Service*¹

Theoretical studies were undertaken to estimate the role of larval parasites in suppressing *Heliothis* populations. This appraisal was made by employing population models to postulate the parasite-host density relationship and the rate of parasitization to be expected by parasites that are assumed to be completely selective for larvae of *Heliothis zea* (Boddie) and *H. virescens* (F.). Available information on the biology and dynamics of the host and the parasites was utilized to establish parameters. However, it was necessary to postulate a number of relevant parameters, which were tested for validity through theoretical calculations.

The results of these studies provide a sound biomathematical explanation for the inability of native monophagous parasite populations to keep *Heliothis* populations at a low level in a natural environment. Of more practical significance, however, are the results of calculations that indicate the great potential such parasites have for managing host populations when parasites are reared and released on a programed and sustained basis as supplements to natural control agents.

The parasite species that might be employed in population suppression are not identified for this theoretical study. However, several investigators have shown that certain species are highly selective for *Heliothis* larvae. Lewis (1970a, 1970b) discussed the hymenopterous parasite *Microplitis croceipes* (Cresson), which is selective for larvae of *Heliothis* spp.² Jackson et al. (1969) also investigated *Eucelatoria armigera* (Coquillett), a tachinid parasite that seems to be selective for larvae of *Heliothis* spp. In addition, W. J. Lewis and A. N. Sparks (unpublished) studied *Cardichilis nigriceps* (Viereck), a hymenopterous parasite that is selective for *H. virescens*. Other parasite species, not necessarily selective for *Heliothis* spp., have also been shown to be efficient parasites for larvae of *Heliothis* spp. (Noble and Graham 1966, Lingren et al. 1970).

¹ The author acknowledges the assistance of Ronald R. Knipping, graduate student, University of Maryland, who made the calculations for the parasite efficiency index and for most of the population models.

² The year in italic after the author's name is the key to the reference in Literature Cited, p. 35.

The procedure used in these studies was similar to that employed in previous theoretical studies of the numerical interrelationship of certain parasites and their insect hosts. The first of these prior studies entailed *Trichogramma* egg parasites of *Heliothis* spp. on cotton and of the sugarcane borer (*Diatraea saccharalis* (F.)) on sugarcane (Knipling and McGuire 1968). This was followed by studies of the relationship of hymenopterous parasites and their aphid hosts (Knipling and Gilmore 1971). The actions of the parasite are isolated from all other regulatory factors by the use of models, and the effects on the host and parasite populations are calculated.

Heliothis zea (bollworm, corn earworm, tomato fruitworm) and *H. virescens* (tobacco budworm) are among the most destructive insect pests in the United States. They are responsible for much of the use of insecticides required for agricultural production. Biological agents are necessary in the natural suppression of these pests. Without these natural agents the control of *Heliothis* spp. with chemical insecticides or any other means would be extremely difficult. However, the natural agents often do not exert enough suppression to prevent substantial and widespread losses to a variety of crops each year. Such losses have occurred for many years, even before the extensive use of broad-spectrum insecticides, which now often lessen the dependability of natural agents by depleting the numbers available for natural suppression. Moreover, as agriculture becomes intensified, natural plant reservoirs of certain parasites and predators can be expected to be reduced and thus limit the parasites and predators available to move into cultivated crops. The routine release of reared parasites to supplement the natural control agents may therefore prove to be the most ecologically sound and practical way to assure dependable biological control of these pests.

The most efficient use of reared parasites will require sustained releases throughout an agricultural ecosystem irrespective of the type of host plants present. More than one parasite species may be needed since different species may have host plant preferences in their searching behavior. A high degree of population suppression may not be required for effective control of *Heliothis* by biological means if the suppression pressure is applied to the entire population and is sustained each year for several generations. A complete population management procedure as envisioned would be designed to utilize the minimum number of parasites necessary to keep the pest populations suppressed below the economic threshold for most crops grown in the area. The economic threshold may be considered from (1) the threshold density that would require and justify control measures by conventional means and (2) the threshold level that causes

significant crop losses, even though they would not be high enough to justify the expenditure for control measures now available. Obviously the eventual goal will be to eliminate losses completely with the lowest possible investment in control.

Even though emphasis in this study is on estimating the minimum number of parasites required to suppress the host, population models will show that the sustained release of substantial numbers of a selective parasite can so drastically alter the normal parasite-host density relationship and exert sufficient mortality that eradication of an isolated host population would likely be the result.

In view of the general lack of quantitative information on the normal abundance of *Heliothis* insects and their natural enemies, as well as a general lack of information on the behavior of parasites in the field, it must be accepted that any appraisals of the potential role of natural and released parasites by the theoretical procedure cannot be assumed to be accurate in detail. However, in spite of the likelihood of considerable deviation in theoretical values from actual numbers of parasites and hosts that lead to different parasitization rates in a natural environment, the results obtained should portray the general effects to be expected from the presence of various numbers of parasites.

Also, the basic principles governing the population density relationship of a selective parasite and its host, even in the presence of a complex of other interacting forces, can be clearly indicated by appropriate population models. The author is gaining more and more confidence in the validity of conclusions based on using hypothetical insect population models to appraise the feasibility and potential effectiveness of different insect population suppression procedures. Such theoretical appraisals can be particularly useful as a guide for more definitive research, both in the laboratory and field.

There is no substitute, however, for well planned and properly executed practical field experiments on an adequate scale in developing insect population suppression and management systems. By the same token, potentially useful and basically sound suppression methods may often be discarded as ineffective and impractical because of negative results and conclusions drawn from inadequate or faulty field experiments that cannot evaluate or account for all the unknown variables likely to occur. The conduct of field experiments on too small a scale without regard for insect immigration and emigration and a lack of appreciation for the fundamentals of insect population dynamics and suppression are the chief reasons for negative and inconclusive results obtained in many field control experiments in the past.

ESTABLISHMENT OF POPULATION MODELS

The procedure used in this study was first to establish population models that are assumed to depict normal parasite-host density relationships in a typical *Heliothis* environment. This is a prerequisite to subsequent calculations to estimate the effects of supplemental releases of parasites. The establishment of a basic host population model representative of the actual number of *Heliothis* larvae in the population each generation is essential in order to postulate the number of parasites that will develop simultaneously with the host population. The basic hypothetical host population model was designed to account for, but not necessarily to explain the nature of, all natural suppression hazards in an agricultural ecosystem, except for the effects of the selective parasite. The hazards do not include control measures specifically directed against the pests, but they would include all the natural hazards of the usual agricultural practices. The establishment of a representative host population model makes it possible to use such a model to calculate the theoretical effects of a hypothetical selective parasite population on the host population.

In view of the limited information on actual numbers of *Heliothis* larvae per unit area and even less quantitative information on actual numbers of a given parasite coexisting with the *Heliothis* population, attempts to determine the quantitative relationships between the host and parasite might seem futile and meaningless. Flanders and Badgley (1963) described the complex interrelationship of various organisms in a natural environment. They also discussed in detail the difficulty of attempting to assess the role of a given predator in suppressing a host in the presence of almost countless forces that interact in a natural ecological environment. This was why they undertook laboratory studies designed to eliminate interacting factors except for the host and parasites under study.

This is essentially what has been done in this study, except hypothetical models and assumed parameters were used to calculate the effects of a selective parasite that are superimposed on all other natural control factors. A theoretical systems analysis of the numerical relationship, based largely on hypothesis and postulated parameters, may prove to be the only practical way, with current research budget constraints, to make meaningful estimates of the actual numbers of a parasite and its selective host that are present at various density levels, and to appraise the effects of such parasites on the dynamics of the host population.

Field data on host abundance in the past have been largely qualitative. Records are generally made in terms of numbers of eggs or larvae on a given number of plants in a very small fraction of the total ecosystem. Data on the percentage of field-collected host larvae that are parasitized are often regarded as an index of abundance. Such data are generally

recorded without complementary information on the abundance of host insects and host plants. Reasonably accurate information on the actual numerical relationship of a parasite and its hosts in the field throughout a large area, and corresponding information on levels of parasitism at different parasite and host density levels, probably would require intensive studies by a large staff of scientists and support personnel over a period of years. It is questionable whether such appraisals by conventional field data collection methods would assure much more accurate measurements of actual abundance than a careful consideration of theoretical calculations based on assumed or postulated parameters derived from the limited information now available or that can be obtained without extensive studies.

Estimates that would be accurate by either method within a range of 0.5-2 of the true values can be regarded as satisfactory. Whether models are based on limited field data or on theoretical calculations based on hypothetical population models, the results cannot be expected to accurately determine the wide variations in densities and parasitization rates that are likely to occur from month to month, year to year, and from locality to locality. Also, population models cannot be expected to fully account for all the factors that affect the interrelationship of a parasite, the selective insect host, and the plant hosts.

Certain key elements largely govern the role of a selective parasite in managing an insect population. These will be considered in some detail in discussing various aspects of this study. The primary objectives of this study are (1) to estimate the natural numerical relationship of a selective parasite, its host insect, and the plant hosts, (2) to estimate the degree of parasitism occurring naturally and its impact on the host population, and (3) to estimate the impact on the host and the parasite populations when the normal natural parasite-host density relationship is altered by the sustained programed release of different numbers of reared parasites on all the host plants in the ecosystem involved.

Entomologists generally have not utilized theoretical models to any extent to advance entomology (Anonymous 1969). In addition to serving as a guide for developing more acceptable means of control for *Heliothis*, it is hoped that this study will help advance the theoretical systems approach for a better solution to insect pest problems.

Host Population Model

The host population model to be used as a basis for further studies is shown in table 1. It is assumed to be reasonably representative of the actual numbers of host larvae per unit area and in the total population under circumstances and in areas where *Heliothis* populations are generally high and cause substantial losses to crops. The population is

assumed to be in a well isolated area and not subjected to extensive emigration and immigration of moths or parasites from outside the area.

TABLE 1.—*Basic Heliothis larval population model during season without hypothetical parasite*

<i>Heliothis</i> generation	Host plant	<i>Heliothis</i> larvae per acre	Increase (approximate)
	Thousand acres	Number	
1 (overwintered)	500	2,500	4.8-fold.
2	1,500	4,000	3.3-fold.
3	2,500	8,000	1.8-fold.
4	3,000	12,000	1.0-fold.
5 (diapausing)	2,500	14,000

Five generations of the host occur during the season. The first generation represents the larval progeny of adults emerging from overwintered pupae and will require 6 weeks for development from April 15 to May 31. The fifth generation will be regarded as the last and diapausing generation, which developed from September 1 to October 15. The other three generations each require 1 month for development during June, July, and August.

The population model is regarded as reasonably representative of the agricultural area in California. Except for isolation it might also be reasonably representative of certain southern States. If the values in the model were multiplied by a factor of about 7, it might well represent the *Heliothis* complex population in the southern cotton- and tobacco-growing States.

The *Heliothis* population, consisting of one or more species, is assumed to start at the usual low level in the spring but increases steadily during the season. All natural regulating factors are exerting normal suppression of the host population except the hypothetical selective parasite, the effects of which will be studied separately. Thus collectively all density dependent and nondensity dependent suppression factors in an agricultural ecosystem except the parasite are accounted for in the basic hypothetical host population model. These would include such factors as weather, normal agricultural practices except insecticides or other directed control methods, predators, diseases, and parasites other than the hypothetical selective parasite.

No distinction is made between the relative number of host insects developing on different host plants, cultivated or wild. The total host plant

acreage for each *Heliothis* generation is shown and would consist of such crops as corn, cotton, alfalfa, tobacco, vegetables, and a variety of wild host plants.

The establishment of the total acreage of host plants for each generation is regarded as one of the key parameters in this study. A meaningful seasonal population model for the host insect or the parasite could not be constructed without considering the amount of plant host material. An expanding host plant acreage plus considerable growth of most host plants dilute the number of host insects as well as the number of parasites per unit area as the season advances. This expanding host plant environment provides a major escape mechanism and survival factor for the host insect. In fact, this expanding host acreage may be one of the reasons why the endemic *Heliothis* insects can consistently increase to pest levels each year. The host plant acreage was established for this study after considering the data on major agricultural crops in California and various southern States as presented in "Agricultural Statistics," published annually by the U.S. Department of Agriculture.

It can be argued with justification that the construction of a *Heliothis* population model should take into account the preference of these insects for certain host plants, as well as the increased attraction of moths to the same host plants in different stages of growth. It would be desirable to take this factor into account because this no doubt affects the dynamics of the host and its complex of natural enemies. However, this would be difficult to do in view of the lack of quantitative information, and calculations would be much more difficult if variable host and parasite populations were established on various types of host plants.

The primary purpose of this study is to make a reasonable estimate of the density relationship of the total population of *Heliothis* and the total population of the parasite. Average values are regarded as suitable for such a general estimate. Some calculations were made, however, but not included here, which indicate that host suppression by the same number of parasites released would be greater than calculated for the models employed if two-thirds of the host larvae were concentrated on one-third of the host plant acres each generation and provided the released and naturally produced parasites would disperse and concentrate in searching proportional to the concentration of the host insects. Therefore the use of averages, even if somewhat unrealistic, might tend to make the estimates conservative in terms of numbers of parasites required to achieve certain levels of parasitism.

The establishment of a reasonably representative average number of *Heliothis* larvae per host plant acre each generation is another key parameter. The author has studied published data on the abundance of *Heliothis* eggs and larvae for some years, especially in connection with an appraisal of the possibilities of utilizing the genetic approach to *Heliothis*

suppression. Several authorities on *Heliothis* have been consulted to obtain their views on the numbers of *Heliothis* present during the season.³ Estimates by the individuals consulted differed substantially. The host population model (table 1) proposed for this study falls near midway between the extremes in numbers that were judged most representative by those consulted. However, the actual numbers of host larvae per acre and in the total population could deviate substantially from those projected without changing the overall conclusions reached in this study.

The establishment of realistic rates of increase of *Heliothis* each generation as the season progresses is another important parameter that cannot be supported by field data. A fivefold increase per generation has long been used to depict the rate of increase for many of the multiple-generation insect pests starting from a normally low density level. However, it seems logical to assume that the rate of increase will tend to decline as the host population grows and as the total number of natural biotic agents increases.

Accordingly, as may be noted in the model, the rate of increase ranges downward from 4.8-fold for the first generation to 1.0-fold for the fourth when the population is assumed to reach equilibrium in the environment. An analysis of the data in the model shows that the *Heliothis* larval population, in the absence of the hypothetical parasite, would increase from a low of 1.25 billion larvae in generation 1 to a high of 35 billion larvae in generation 5. This represents a twenty-eightfold increase for the season. This seems like a reasonably valid overall increase for one season. If 75 percent of the last-generation larvae that mature are diapausing forms and if about 5 percent of the pupae survived the winter, the starting host population the next year would be similar in size to that for the first year.

To the author's knowledge no precise data are available on actual numbers of moths that emerge in the spring in a given area. Based on limited egg and larval records on host plants, especially on tobacco, and on light-trap catch data, the author has regarded 1,000 moths per square mile in typical agricultural areas as a reasonable estimate of overwintered moth abundance. The assumed population of 2,500 larvae per acre on 500,000 acres in the first generation is obviously a rough estimate. However, if both the insect and host plant densities are realistic and if each female *Heliothis* moth survives long enough to deposit 200 eggs, and if in turn half the eggs survive as larvae, 25 females per host plant acre could account for the larvae assumed to be present in the first generation. This would represent a total overwintered population of 25 million moths

³ Information on *Heliothis* populations and levels of parasitism observed in the field was obtained from D. E. Bryan, W. J. Lewis, P. D. Lingren, D. F. Martin, and A. N. Sparks, Entomology Research Division, Agricultural Research Service, and Charles Lincoln, University of Arkansas.

(both sexes) for the ecosystem established, which is assumed to be representative of the State of California. This estimate of the overwintered moth population agrees with the estimate used in appraising the possibilities of the genetic approach to *Heliothis* population suppression (Knippling 1970).

It must be obvious to the reader that the risk of inaccuracies in each of the established parameters is substantial because many of the assumptions are based on little or no valid data. However, if the host population model is a good approximation of a typical *Heliothis* population for a large ecological area, it would still serve the purpose of this study.

Natural Parasite Population Model

The development of a hypothetical parasite population model was even more difficult than the development of a host population model. There is no way of knowing on the basis of available field density data how accurate the basic parasite population model will prove to be. However, it is the author's view that it is not an unrealistic projection of the number of parasites of a selective species that could be expected to coexist with the proposed *Heliothis* population. The reasons for this confidence will become evident as results of the study are projected and discussed.

The hypothetical parasite is assumed to be completely selective for *Heliothis* larvae for survival and development. This assumption of complete selectivity eliminates a number of variables one could expect if a polyphagous parasite were used as a model species. A species dependent on *Heliothis* larvae must continue to search at all host density levels or its survival would be in jeopardy. Also, such a parasite can be assumed to be sufficiently mobile to concentrate where host larvae occur. The population models will clearly show that the density of the parasite population is governed by the density of the host population. This is in accord with accepted views regarding parasite-host density relationships, but the author has attempted to quantify this relationship in terms of the total population in an ecosystem.

The development of the natural population model for the parasite required the establishment of numerical values for two important parameters: (1) An estimate of the efficiency of various numbers of parasites in achieving host parasitism and (2) an estimate of the average number of adult parasites present per acre of host plants in the total area during the first generation. If these two parameters are reasonably realistic, it is possible to postulate the seasonal growth of the parasite population as the host population grows. However, survival values for parasitized hosts as the season advances also become a key parameter in making the estimates.

A tentative efficiency value for a hymenopterous larval parasite was originally postulated on the basis of field observations (unpublished) made by P. D. Lingren of the Entomology Research Division. Lingren reported 5-percent parasitization of *Heliothis* larvae collected on cotton during midseason. After testing various hypotheses by theoretical calculations, the writer (unpublished) postulated that approximately 280 parasites per acre per host generation could be expected to parasitize 50 percent of *Heliothis* larvae present.

W. J. Lewis and A. N. Sparks (unpublished) obtained field data on the abundance of *C. nigriceps* attacking *H. virescens* larvae on cotton. They counted the adult females and the rate of parasitization. From these field data, calculations were made to estimate the searching efficiency of the parasite, which is selective for *H. virescens*. Their estimates are about the same as the author's initial estimates.

In the more detailed studies reported here and after considering and testing in hypothetical models several assumed efficiency values, it was decided to base all projections on an assumed parasitism efficiency value of 50 percent for a total of 300 parasites of both sexes searching on 1 acre of *Heliothis* host plants during one host and parasite generation.

Some specialists in biological control propose that the searching behavior of a parasite changes greatly depending on the host density. Low rates of host parasitization when the host density is low is assumed to occur because searching for the host largely ceases at low host densities. This may be an important factor applicable to a polyphagous predator or parasite. However, for a completely selective species, such an explanation seems entirely inadequate.

In this study continued searching is assumed at all levels of host and parasite densities. It is doubtful that a selective species could survive unless it continued unrelenting searching at all host density levels. The only alternative for survival would be some escape mechanism such as diapause until a more favorable host density occurs. This would also be a risk to parasite survival. There seems to be an entirely valid explanation for wide fluctuations in the percent parasitization on the basis of the assumed host-finding ability of the parasite and the parasite-host density relationships established for this study. This will become more evident as we consider the trends of the parasite and host populations and the levels of parasitism in the various hypothetical population models.

Establishing Efficiency of Parasite in Host Parasitism

If the percent efficiency of any given number of a selective parasite can be established for a given period of time in a given area, it is possible to calculate the percent efficiency to be expected for any other number of parasites under the same conditions. The amount of searching and

researching in the host insect environment at various parasite density levels determines the efficiency of a given number of the parasite. This is the hypothesis previously advanced in studies of parasite-host density relationships. It will also be the basis for studies on the relationship of parasites of *Heliothis* larvae and their hosts.

Thus the following efficiency values are based on the assumption that a total of 300 parasites per acre during a host and parasite generation will parasitize 50 percent of the total host larvae during that period. An additional increment of 300 parasites is assumed to parasitize 50 percent of the remaining unparasitized larvae, totaling 75-percent parasitization. Thus we can establish examples of the efficiency values as follows:

<i>Parasites per acre</i>	<i>Percent parasitization</i>
0	0
123
5	1.15
10	2.3
25	5.6
50	10.9
75	15.9
100	20.6
150	29.3
200	37.0
300	50.0
600	75.0
900	87.5
1,200	93.75
1,500	96.87

These values conform to the following formula:

$$P = 1 - \left(1/2\right)^{\frac{N}{300}}$$

where P = parasitization rate (where 1.0 = 100-percent parasitization)

N = number of parasites per acre per generation

This formula is derived from the original assumption of 50-percent parasitization from 300 parasites per acre. One-half is the fractional equivalent of 50 percent. The exponent $\frac{N}{300}$ denotes the geometric rate at

which parasitization increases. P is expressed as a rate from 0 to 1, where 1 is 100-percent parasitization.

For example, for 600 parasites per acre, we replace N with 600 to get

$$P = 1 - \left(1/2\right)^{\frac{600}{300}}$$

Reducing the exponent, we get

$$P = 1 - \left(1/2\right)^2$$

$$\left(1/2\right)^2 = 1/4$$

Thus $P = 1 - 1/4$

$$P = 3/4 = 75 \text{ percent}$$

For most values of N , the arithmetic is more complicated.

Where $N = 25$, for example, we get

$$P = 1 - \left(1/2\right)^{\frac{25}{300}}$$

$$P = 1 - \left(1/2\right)^{1/12}$$

In order to find the value of $\left(1/2\right)^{1/12}$ we must use logarithms. After consulting a logarithmic table and making appropriate calculations, we find that $\left(1/2\right)^{1/12} = 0.944$.

Thus $P = 1 - 0.944$

$$P = 0.056 = 5.6 \text{ percent}$$

Most of the values, particularly for the lower values of N in the tabular data were calculated by using logarithms. In this manner we can calculate P for any value of N .

A generation of the parasite is assumed to coincide with each host generation. The parasite is also assumed to be highly mobile and will concentrate in accordance with the host population on the various host plants. The number of host larvae present on the host plants will not change the percentage of larvae found by a given number of parasites but does affect the number of larvae found and parasitized. The egg-laying capability of the parasite population is regarded as adequate to parasitize all host larvae that the parasites can find, even at the highest host density levels. This is in accord with assumptions in studies on *Trichogramma* egg density relationships (Knipling and McGuire 1968), but it is not in accord with studies on parasite-aphid host relationships (Knipling and Gilmore 1971).

Seasonal Trend of Coexisting Parasite and Host Populations

Table 2 shows the seasonal development of the parasite population, parasitization rates, and growth of the host population. The calculations are based on the host population model (table 1). After testing several population models, 40 parasites per acre was established as a representative starting population in the first generation. Based on the efficiency values (p. 11), 40 parasites would be capable of parasitizing 8.8 percent of the host larvae present.

Another essential basic parameter is now required. To estimate the number of adult parasite progeny in the next generation, it is necessary to assign a mortality factor for the parasite from the egg to the adult stage. The parasite survival rate for each generation, based on the number of parasitized host larvae, is shown in table 2. The highest survival of parasites after parasitizing the host larvae is assumed to be 20 percent, which occurs during the first generation. The survival rate declines in subsequent generations by increments of 2.5 percent. These are also the assumed survival rates of the *Heliothis* larvae for each generation.

Any hazard that destroys the host larvae before the parasites mature and leave the host to pupate will also destroy the egg and larval stages of the parasite. Complete correlation between host and parasite mortality will not occur because some host mortality can be expected before and after parasitism normally takes place. However, this difference is assumed to be offset by substantial mortality of the parasites during the pupal stage, which would be independent of the larval host mortality. Therefore the same mortality factor that is representative for host larvae would seem to be a reasonably valid factor for the parasite.

The establishment of an 80-percent mortality level for the first-generation larvae of *Heliothis* was based on various hypothetical life tables. If the average *Heliothis* female is capable of depositing 500 eggs and if natural hazards result in 50-percent mortality of the adult female population before all eggs are deposited, the average net egg production potential is reduced to 250. Then if we assign a 60-percent mortality in the egg stage, the average number of larvae produced by each *Heliothis* female would be 100. If each female *Heliothis* produces 100 larvae, we might reasonably expect only 20 to survive to maturity. Finally if 50 percent of the pupae survive, the adult progeny would number 10 from one pair of moths. This is close to the assumed 4.8-fold increase established for the host during the first generation. As previously noted, the rate of increase of the *Heliothis* population is assumed to decline each generation because of the expected increase in general predation and other density dependent hazards until the fourth generation, when the mortality and survival rates reach equilibrium.

TABLE 2.—*Estimated normal trend of Heliothis and parasite populations and parasitization rates for each Heliothis generation during season*

<i>Heliothis</i> generation	Host plant	Host larvae per acre	Normal increase ¹	Adult parasites per acre	Parasiti- zation	Parasitized host larvae per acre	Parasite survival	Parasites emerging per acre	Total parasites for next generation
	<i>Thousand acres</i>	<i>Number</i>		<i>Number</i>	<i>Percent</i>	<i>Number</i>	<i>Percent</i>	<i>Number</i>	<i>Millions</i>
1	500	2,500	4.8-fold	40	8.8	220	20	44	22
2	1,500	3,648	3.3-fold	15	3.4	124	17.5	22	33
3	2,500	6,978	1.8-fold	13	2.9	202	15	30	75
4	3,000	10,164	1.0-fold	25	5.6	569	12.5	71	213
5	2,500	11,514		85	17.8	2,049	10.0	205	512

¹ Actual increase of host larvae for each generation is reduced by percent parasitization shown.

If a population of *Heliothis* is greatly reduced below the usual level for a number of generations or over several years, we could expect a considerable readjustment in the survival rate of both the host insect and its selective parasites. Perhaps the host population will increase substantially because of a decrease in density dependent suppression forces. However, in such an event the survival rate of a selective parasite might also increase. This possibility will be considered and discussed later.

Parasite-Host Population Model

Even though the parameters established for the parasite population are for the most part based on hypothesis, they are logical and should be sufficiently accurate to serve as a basis for calculating the numerical relationship of a parasite population and its host population and to project the rate of parasitization to be expected as the host and parasite populations grow during the season. The hypothetical parasite-host population model is shown in table 2.

In the first generation the host plant acreage in the total ecosystem is 500,000 (table 2). The host larvae per acre total 2,500. By multiplying these values we obtain 1.25 billion host larvae for the total population. The starting parasite population is assumed to average 40 per acre during the first generation. This would mean 20 million in the total population. According to the efficiency values (p. 11), 40 parasites per acre would achieve 8.8-percent parasitization as shown in table 2. Thus 220 of the 2,500 host larvae per acre will be parasitized. If 20 percent of the parasitized larvae survive to produce parasites, this would result in parasite emergence at the rate of 44 per acre or a total population of 22 million that will be present for the next generation. Thus the parasite population increased very slightly in the first generation.

A total of 22 million adult parasites distributed on 1.5 million assumed host plant acres in the second generation will mean an average of about 15 parasites per host plant acre. Simultaneously, however, the *Heliothis* population, according to the basic model (table 1), would be expected to increase 4.8-fold in the absence of the selective parasite. Since 8.8-percent of the hosts were parasitized, the actual host population will be reduced by 8.8 percent, making a total larval population of 3,648 per acre on 1.5 million acres. The parasite population of 15 per acre, according to the efficiency values, would result in 3.4-percent parasitization in the second generation. This represents a substantial drop in percent parasitization even though the number of parasites in the total population is slightly higher than in the first generation. All other calculations for subsequent generations were made in the same manner.

The hypothetical parasite-host population model serves to explain several fundamental principles of parasite-host relationships that may not

have been adequately considered by ecologists in the past. If one considers the rates of parasitization only, the model clearly shows how misleading these data can be as a basis for understanding the dynamics of a parasite population. Based on the rates of parasitization, one might conclude that a parasite population normally declines in midseason. However, when the number of host larvae and the number of host plant acres are taken into account, the total parasite population increases progressively. The lag in growth rate of the parasite population in relation to that of the host population is also clearly depicted in the hypothetical model, a generally recognized phenomenon. The model shows a slow rate of growth of the parasite population when the host population is lowest and an accelerated growth as the host population increases. The host population shows the highest rate of growth when it is low and a decelerated growth rate as it increases. The rate of growth of the host population can best be noted by multiplying the number of host plant acres by the number of host larvae per acre (table 2).

The percent parasitization remains generally low and actually declines during the early part of the season in spite of a steady growth in the total parasite population. This is due to the increase in host plant acreage and perhaps also due in part to an increase in size of host plants that must be searched. However, near the end of the season the parasite population has grown manyfold and the percent parasitization begins to take a sharp upturn as the acreage of host plants declines (table 2).

Field data on rates of parasitization throughout a crop season are limited. No doubt the parasitization of *Heliothis* larvae has also been reduced in recent years by the general use of insecticides in the agroenvironment. Although the theoretical data cannot be fully confirmed by field observations, the theoretical results do not seem to conflict with observations made by several members of the Entomology Research Division that host larval parasitism is higher in the early and late parts of the season than during midseason.

It is apparent from the data in table 2 that the parasite alone is not a major factor in the suppression of a *Heliothis* population, especially early in the season and during the midseason. Field data from Mississippi do not show a high rate of parasitization in *Heliothis* larvae. Nevertheless the seemingly low rate of parasitization superimposed on all other hazards, as indicated in the parasite-host population model, does significantly affect the total population of *Heliothis* by the season's end.

According to this model, the *Heliothis* larval population increases by a factor of about twenty-threefold. This compares with twenty-eightfold for the basic host population model in the absence of the selective parasite. At the same time, the parasite population would increase from an assumed starting minimum population of 20 million to a maximum population of 512 million in the fifth and last generation. This represents an increase of

about twenty-fivefold. Thus the host and parasite populations would increase at a similar degree by the season's end. Therefore the parasite-host population model may be a realistic projection of the dynamics of a parasite population in relation to the dynamics of the host population coexisting in a natural environment.

An insect population such as *Heliothis* is subject to attack by dozens of predators and parasites. Although two or three predaceous species might predominate, probably most species alone do not account for more than a few percent of the total suppression. The interaction between predators and parasites is probably profound and limits the effect of any one species. Any other relationship would result in the destruction of both the host and eventually the parasite and predator.

TESTING VALIDITY OF ASSUMED EFFICIENCY OF PARASITE

Perhaps the most important parameter established in this study is the assumed efficiency of the parasite. The validity of this parameter is not only of academic importance in understanding parasite-host relationships but also a critical factor in appraising the feasibility of suppressing *Heliothis* populations by the programed release of mass-produced parasites. Although the results of studies thus far should contribute to a better understanding of the interrelationship of a parasite, host insect, and the host plants, the primary purpose of the study is to appraise the feasibility of controlling *Heliothis* and other similar pests by altering the normal parasite-host density relationship through supplemental releases of parasites.

In order to test the hypothesis that 300 parasites per acre is a reasonably valid index of efficiency, special models were established and calculations made on the basis of higher and lower efficiency indexes. For a lower efficiency index, the assumption is made that 600 parasites per acre would be required to parasitize 50 percent of the host larvae. For the higher efficiency index, 150 parasites per acre are assumed to parasitize 50 percent of the host larvae. All other parameters remained constant.

In other words, calculations were made to compare the dynamics of parasite and host populations and the rates of parasitization if the hypothetical parasite is only half as efficient as postulated or inherently two times as efficient. The results are shown in table 3.

It seems clear from the results that the postulated efficiency of 300 parasites per acre for 50-percent parasitization must be close to reality if all other relevant parameters are reasonably valid. If the parasite is only half as efficient as assumed (600 parasites = 50-percent parasitization), it is questionable whether it could survive (table 3). The number of

TABLE 3.—*Relative trends of Heliiothis and parasite populations and parasitization rates when hypothetical parasite has a basic searching efficiency potential of 600 and 150 parasites per acre for 50-percent parasitization¹*

<i>Heliiothis</i> generation	Host plant	600 parasites per acre for 50-percent parasitization			
		Host larvae per acre	Adult parasites per acre	Parasitization	Parasites emerging per acre during next generation
	<i>Thousand acres</i>	<i>Number</i>	<i>Number</i>	<i>Percent</i>	<i>Number</i>
1	500	2,500	40	4.50	22
2	1,500	3,821	7	.75	5
3	2,500	7,506	3	.35	4
4	3,000	11,220	3	.35	5
5	2,500	13,510	6	.66	9

<i>Heliiothis</i> generation	Host plant	150 parasites per acre for 50-percent parasitization			
		Host larvae per acre	Adult parasites per acre	Parasitization	Parasites emerging per acre during next generation
	<i>Thousand acres</i>	<i>Number</i>	<i>Number</i>	<i>Percent</i>	<i>Number</i>
1	500	2,500	40	16.9	85
2	1,500	3,323	28	12.2	71
3	2,500	5,778	43	18.1	157
4	3,000	7,098	131	45.4	403
5	2,500	4,651	484	89.2	415

¹ Values are to be compared with those in table 2, which show trends when parasite is assumed to have assigned searching potential of 300 parasites per acre for 50-percent parasitization. Not all values and calculations are shown in table 3, but those shown were derived by following the procedure described for the population model in table 2.

parasites starting from a level of 40 per acre (20 million in the total population) would quickly drop to a low level and the population would barely hold its own by the season's end. Assuming normal winter mortality and the inability of the parasite population to increase substantially at usual host densities the next season, the species probably could not exist for more than a few years.

In sharp contrast to this situation, if the parasite is two times as efficient as postulated (150 parasites = 50-percent parasitization) (table 3), the number of parasites would increase rapidly from the beginning of the season. The rate of parasitization would be fairly high during the early part of the season and reach a very high level by the season's end. The moderate rates of parasitization for each generation when considered alone might not be regarded as a serious hazard to the host. However, the accumulative impact of moderate parasitism early in the season and at midseason *superimposed on all other natural hazards* plus the high level of parasitism at the season's end would pose a serious threat to survival of the host population.

In terms of diapausing larvae, the host population would be reduced by about 87 percent as compared with the population subjected to a parasite of the assumed normal efficiency (table 2). In the second year the starting parasite population would be about two times normal size and the host population would be only about one-eighth normal size. This would further aggravate the density relationship. Such a drastic decrease in the host population would no doubt result in some upward readjustment in the survival rate of all stages of the host due to less effect of all other density dependent factors. This would tend to offset the impact of a parasite of such high efficiency. A state of equilibrium between the parasite and host would no doubt be reached. But this level of equilibrium could be expected to be much lower than projected for the representative population. It is questionable whether *Heliothis* would be abundant enough to be a significant pest if a selective parasite of such high efficiency coexisted with the host. It is even questionable if *Heliothis* could exist under the suppression pressure of such an efficient parasite.

In view of the results of calculations involving higher and lower efficiency values in table 3, the assumed efficiency of 50 percent for 300 parasites should be reasonably accurate. The results of the appraisal of the efficiency of the hypothetical *Heliothis* larval parasite as depicted by the various models clearly show that an extremely delicate balance exists between a selective parasite and its host in a natural environment. No conflict can be seen in the results with the classical concepts of parasite-host relationships. Rather, the results should help to develop a greater appreciation for nature's balance and the coevolutionary process involved in parasite-host relationships.

The numerical relationship of a parasite and host population as depicted by the models should be of considerable value in developing a better understanding of parasite-host relationships. However, an important practical question follows—will it be feasible and practical to release enough parasites to drastically upset the normal relationship between a selective parasite and the host? This question will be explored fully in the next section, in which the theoretical effects of programed releases of various numbers of reared parasites will be calculated.

PROGRAMED RELEASES OF PARASITES FOR HELIOTHIS SUPPRESSION

If a selective parasite for *Heliothis* larvae has a finding efficiency reasonably close to the values postulated, and if the parasite density is as delicately balanced with the host density as indicated earlier in this bulletin, it should be possible through supplemental releases of parasites to drastically suppress *Heliothis* populations. An appraisal of this possibility is the primary purpose of this study.

Effective alternative and selective methods of suppressing these insects are urgently needed. *Heliothis* species on most crops seem to be highly vulnerable to natural biological agents in spite of the widespread damage they cause. Sustained releases of a parasite or a complex of several species if necessary in appropriate numbers could prove to be the most effective, the most dependable, as well as the most economical and safest way to control these pests throughout an ecological area. Such an approach used throughout an agroecosystem might manage an insect population at almost any level required.

Programed releases could also have an important role when integrated with genetic methods for the continuous suppression and management of *Heliothis* populations in large areas. Thus two highly complementary systems of suppression, both completely selective for the target pests, could be employed. Integrating two or more complementary suppression methods takes advantage of the inherent benefits to be gained by combining them.

All basic parameters previously established remain constant except the number of parasites produced naturally is supplemented by programed releases of additional parasites. Such releases would achieve two significant results. By increasing the number of parasites above natural levels, the percentage of parasitization can be immediately increased as the direct result of the released parasites. This in turn produces more parasite progeny and even higher levels of parasitism.

This method of insect control, as well as using predators and pathogens, is the only system of insect population suppression that potentially has a greater efficiency when the insect population is high than when it is low.

This is the reverse of the efficiency potential of the genetic technique and the use of pheromone traps. The efficiency of insecticides, cultural measures, other attractant techniques, and physical methods are not affected by the density of the insect to be controlled. The increased efficiency of the biological method at high host densities is due to the potential increase in progeny resulting from adding biological agents to the environment rather than the direct effect of the parasites released.

According to the basic parameter established for this study, the efficiency of a given population of biological agents remains constant at high or low host levels in terms of the percentage of available hosts attacked. However, the number of hosts attacked increases in proportion to the density of the hosts available. Exceptions may occur if the number of hosts a parasite population can encounter exceeds the egg-laying capability of the parasite population. This is likely at relatively low parasite densities and high host densities for some species like aphid populations (Knippling and Gilmore 1971). However, this is not regarded as a limiting factor for hymenopterous or dipterous parasites of *Heliothis* larvae or for *Trichogramma* parasites of *Heliothis* eggs.

As research progresses toward the concept of total insect population suppression and continuous management to keep populations reduced, we need to apply the most efficient suppression procedures available, either alone or in combination with other suppression methods. Full understanding and recognition of the effect of density on the efficiency of different insect suppression procedures will be essential in determining the strategy to use in managing insect populations in the future.

The sustained programed release of a selective parasite is theoretically capable of drastically altering a normal parasite-host density relationship. This will be shown by population models. A substantial increase in the number of parasites in relation to the number of host insects can have a dramatic impact on the population trends of the host. In the extreme it should have an equally dramatic impact on the number of parasites developing naturally. The artificial manipulation of numbers of selective parasites can reverse the normal numerical relationship of a parasite and host that may have evolved over thousands of years of coexistence.

The type and degree of change in the numerical relationship of a parasite and host population that can occur from adding reared parasites to the environment could never happen in a normal ecological environment because of inherent biomathematical limitations. Therefore it seems safe to assume that an insect host population has never encountered a situation when a selective parasite population remained at a constant high or even a moderate level for a period spanning several host generations or for many generations over several years. Yet this in effect is what is contemplated in the proposed approach to *Heliothis* suppression throughout an agroecosystem.

There is every reason to believe that such a disruption of a natural delicate balance that has evolved through natural laws and natural regulating mechanisms will have a drastic impact on a host population. This logic is amply supported by the results of theoretical calculations to be presented. Calculations will be made to appraise the effect of parasite releases at levels of 100 or 200 per acre during each of three generations and also at a high level of 500 parasites per acre during each of five generations.

Theoretical Effects of Low Release Rates

Table 4 shows the calculated results of releasing 100 parasites per acre during each of the first three host generations. This will be regarded as a low release rate and is proposed as the minimum required to assure a substantial reduction of a *Heliothis* population during one season. Such a release rate would require 450 million parasites for 4.5 million accumulative acres of host plants. This could be reasonably representative of requirements for *Heliothis* suppression in California, Mississippi, Georgia, and perhaps other States.

A study of the host population trend with a low rate of supplemental releases (table 4) as compared with the assumed population trend under conditions of natural parasitism (table 2) shows the theoretical impact of the supplemental releases. The parasitism would be only moderately high during the first three generations but would remain at a moderate level through the fourth and fifth host generations, even though parasite releases are discontinued. The accumulative impact of a seemingly moderate level of parasitism superimposed on all other natural hazards would theoretically keep the host population at a substantially lower level than a normal population. Suppression by the end of the fifth generation would be about 79 percent as compared with the normal population. Thus the number of diapausing larvae compared with the normal population could be expected to be reduced to this extent.

As already noted, the suppression impact is due to two factors. The parasites released greatly exceed the numbers that can develop in a normal population when the host density is low to moderate. This increases the rate of parasitization, which in turn increases the number of parasite progeny available to attack the next host generations. The combined effect of the two sources of parasites results in much greater suppression than could ever occur naturally when the host density is still low.

A general suppression of the *Heliothis* population to the extent indicated without direct interference with other natural suppression factors should greatly reduce potential damage to most of the crops throughout an agricultural area. The suppression of the population to less than one-fourth of the usual population would probably obviate the need

for insecticides or other means of control on most crops. Highly sensitive crops such as sweet corn no doubt would require additional protection even with a substantially reduced population.

Continued releases of parasites at 100 per acre of host plants for about three generations in subsequent years should keep *Heliothis* populations suppressed at least 80 percent below the usual level.

Although the release of 100 parasites per acre is projected as the lowest rate, the possibility of achieving sufficient suppression to virtually eliminate damage to certain major crops, such as cotton, tobacco, and soybeans, by releasing fewer than 100 parasites per host plant acre should not be ruled out.

Theoretical Effects of Moderate Release Rates

Table 4 shows the calculated trend of *Heliothis* and parasite populations and the parasitization rates from releasing 200 parasites per acre during each of the first three host generations. This rate of release to supplement natural production of the hypothetical parasite would greatly alter the normal parasite-host density relationship. Consequently, this would result in a very high degree of host suppression throughout the season. By the season's end the number of diapausing pupae per acre of host plants theoretically would be suppressed by about 87 percent compared with the uncontrolled population. Such a high degree of suppression should have a marked impact on the host population in the first year, and if releases are continued, the suppression should be even greater in subsequent years. Management of the population should be assured at a level that could virtually eliminate all crop losses. Population suppression the second and subsequent years would be due principally to the direct effect of parasite releases, since the host resources would be so low that relatively little added effect would result from parasite progeny produced naturally.

A careful study of the actual numbers of parasites produced naturally during each generation, as shown in table 4, will reveal that host density is a governing factor in the number of parasites produced and the rate of parasitization to expect. If the total number of parasites for each generation is compared with the normal parasite population (table 2) and the population is subjected to releases of 200 parasites per acre for each of the three generations (table 4), it will be noted that the parasite-host density relationship tends to become reversed. For the normal relationship, the natural parasite population starts at a low level and reaches a peak in the fifth generation. However, the peak of parasite abundance for the treated population (table 4) occurs in the third generation. By the fifth generation the parasite population, in spite of substantial numbers

TABLE 4.—Trends of *Heliothis* and parasite populations and parasitization rates when natural parasite population is supplemented by release of different numbers of parasites at different times

<i>Heliothis</i> generation	Host plant	Host larvae per acre	Normal increase	Adult parasites per acre	Parasit- ization	Parasitized host larvae per acre	Parasite survival	Parasites emerging per acre	Total parasites
	Thousand acres	Number		Number	Percent	Number	Percent	Number	Millions
100 PARASITES PER ACRE DURING EACH OF 1ST 3 HELIOTHIS GENERATIONS									
1	500	2,500	4.8-fold	140	28.1	702	20.0	140	70
2	1,500	2,876	3.3-fold	147	29.1	837	17.5	146	438
3	2,500	4,037	1.8-fold	188	35.2	1,421	15.0	213	532
4	3,000	3,924	1.0-fold	177	33.6	1,318	12.5	165	495
5	2,500	3,127	198	36.7	1,148	10.0	115	287
200 PARASITES PER ACRE DURING EACH OF 1ST 3 HELIOTHIS GENERATIONS									
1	500	2,500	4.8-fold	240	42.6	1,065	20.0	213	106
2	1,500	2,296	3.3-fold	271	46.5	1,067	17.5	187	280
3	2,500	2,433	1.8-fold	312	51.3	1,248	15.0	187	467
4	3,000	1,777	1.0-fold	156	30.3	538	12.5	67	201
5	2,500	1,487	80	16.9	251	10.0	25	62

500 PARASITES PER ACRE DURING EACH OF 5 HELIOTHIS GENERATIONS

1	500	2,500	4.8-fold	540	71.0	1,775	20.0	355	178
2	1,500	1,152	3.3-fold	619	75.8	873	17.5	151	226
3	2,500	622	1.8-fold	589	74.3	462	15.0	69	173
4	3,000	240	1.0-fold	557	71.4	171	12.5	21	63
5	2,500	85		525	70.0	60	10.0	6	15

100 PARASITES PER ACRE DURING 3D HELIOTHIS GENERATION

1	500	2,500	4.8-fold	40	8.8	220	20.0	44	22
2	1,500	3,648	3.3-fold	15	3.4	124	17.5	22	33
3	2,500	6,978	1.8-fold	113	23.0	1,605	15.0	241	602
4	3,000	8,060	1.0-fold	201	37.1	2,990	12.5	374	1,122
5	2,500	6,084		449	64.5	3,924	10.0	392	980

released during the first three generations, would theoretically be about 88 percent lower than for the population assumed to develop naturally. This is due to the greatly reduced host resources in generations 4 and 5.

Although we must recognize the probability that projections based on theoretical appraisal cannot be precise, the models clearly depict the overriding effect of host density on the number of parasites that can develop naturally. The models in quantitative terms clearly show that the welfare of a selective parasite population is dependent on the welfare of the host population. As emphasized before, a parasite-host density relationship that theoretically will develop under conditions of programed releases of substantial numbers of selective parasites can never occur naturally throughout an ecosystem because of biomathematical limitations. This is a point that must be kept in mind in weighing the limitations and merits of dependence on natural parasitism versus the merits and limitations of sustained supplemental releases.

A parasite release rate of 200 per host plant acre for three generations, according to the total acreage of host plants, would require the rearing and release of 900 million parasites on 4.5 million accumulative acres of crops and wild host plants.

Adjustments in Host Survival Rates Due to Reduced Predation

An important factor in appraising the continuing impact of sustained parasite releases on the management of a given host population is possible adjustments in the host survival rate due to the decreasing effect of other density dependent mortality factors. The host population trends in the two models subjected to the release of 100 and 200 parasites per acre do not provide for adjustments in the survival rate due to these factors. It seems inevitable that with a greatly reduced host population some decrease or slowdown in overall density dependent predation will occur in comparison with a normally developing host population. This would seem to occur especially for the population subjected to releases of 200 parasites per acre.

Accordingly an effort was made to estimate the degree of adjustment in survival that might be reasonable to expect. A presentation of the results involving various population models and different adjustments in the survival rates of both the host and parasite would require considerable discussion and will not be included in this bulletin. However, under conditions of supplemental releases of a completely selective parasite at low rates, any adjustments in host survival rates due to a reduction in general predation would be minor and would not materially change the general trend of the host and parasite populations and the parasitization

rates. The reasons for this opinion will be discussed in some depth because it seems important to speculate on the ecological consequences of a substantial and sustained suppression by selective means of an insect complex like the *Heliothis* spp. throughout an ecosystem.

The basic parameter provides for the release of a completely selective parasite for *Heliothis*. Therefore the parasite releases would have no direct suppression effect on any other organisms in the ecosystem. This method of *Heliothis* suppression would be in strong contrast to the ecological effect of broad-spectrum insecticides or perhaps even the adverse ecological effect of rigid cultural practices such as host plant destruction. Either method could be expected to drastically reduce food resources for parasites and predators as well as to destroy many parasites and predators in the environment when the control measures are applied.

Any effort to estimate the ecological impact of a high degree of suppression or complete elimination of *Heliothis* populations can be expected to be extremely difficult, whether this be by field observations or by hypothesis. Based on theoretical grounds, it is the author's opinion that the effect would be nil with low parasite releases as shown in table 4. In all probability the food and reproductive resources for polyphagous predators and parasites that *Heliothis* insects provide in an agroecological system would not exceed 10 to 15 percent of the total resources for all insects that serve as prey for such parasites and predators.

In the first generation the release of parasites should have no measurable effect on general predation of *Heliothis* eggs or larvae because suppression of the host would not begin until late in the last larval and pupal stages. In subsequent generations the host population is suppressed gradually and not completely. Any effect this would have in reducing the abundance of polyphagous predators and parasites would permit other species of host insects to increase. This would tend to fill the partial vacuum of food and reproductive resources for polyphagous species. Therefore near normal abundance of the complex of predators and parasites should be maintained. However, even if a significant increase in the survival rate of *Heliothis* should occur, this should be nullified in large measure by a simultaneous increase in the survival rate of the parasites within the larval hosts.

The selective parasite release method has a built-in regulating factor that no other suppression method possesses. If there is a significantly higher rate of *Heliothis* survival due to decreased general predation and parasitism, this automatically increases the number of *Heliothis* larvae available for parasitism, which in turn leads to a higher number of parasite progeny and a higher level of parasitism. This, together with a higher survival rate for the selective parasite, would tend to maintain a high level of parasitism. This is the basis for the belief that relatively low releases of a selective parasite for a single host species or a complex of two

host species in the case of *Heliothis* would have relatively little impact on general insect predation in an agroecosystem.

Results will not be presented, but a hypothetical population model was established in which the assumption was made that the host survival rate would increase by 10 percent in each generation from the second to the fourth because of reduced general predation and parasitism. Simultaneously, however, a 5-percent increase in the survival rate of the parasite is assumed because of decreased predation of parasitized larvae. In the light of the prior discussion, a higher survival rate of *Heliothis* would hardly seem likely. However, a 10-percent increase in survival of *Heliothis* would mean that the relative increase rates, respectively, for generations 2 to 4 would be 3.6 versus 3.3, 2 versus 1.8, and 1.1 versus 1.0. Such adjustment in survival rate if it occurred when parasitism did not increase above normal would be highly significant because by the season's end the total increase for *Heliothis* would be thirty-eightfold instead of twenty-threefold for the normal population. However, under the system of releases of the selective parasite, the effect would be quite different.

Calculations indicate that by the fifth generation the host population would be only about 12 percent higher than that shown without the readjustment in survival rates. As noted earlier, the increase in host larvae would provide more parasitized larvae. Moreover, if the survival rate of parasites is increased by 5 percent in generations 2 to 5, inclusive, the combined effect of a significant increase in both the number of parasitized larvae and the survival of the parasitized hosts would virtually offset the potential increase in hosts due to an assumed 10-percent increase in host survival because of a decline in general predation. For these reasons the host population trends as calculated under a regime of parasite releases at 100 per acre per host generation probably would not be altered enough by reduced general predation to materially change the trend of the *Heliothis* populations as depicted in table 4.

It seems more probable that a higher degree of *Heliothis* suppression, especially if sustained over a period of years, would lead to substantial readjustment in the survival rate of the host insect. The increase potential of the species at very low densities might well reach tenfold early in the season if selective species were absent or at a very low level and when general predation is usually at a low level. However, under the regime of high level releases of an efficient and selective parasite, the impact on the host population should still approach that projected in table 4.

Theoretical Effects of High and Sustained Release Rates

The theoretical impact of sustained releases of a selective parasite at a level of 500 per host plant acre offers an interesting lesson in selective parasite-host density relationships. The results are shown in table 4.

The theoretical model depicts the complete dependence for survival of a selective parasite on its host. It shows that a strong reversal in the normal parasite-host density relationship will lead to virtual elimination of the host population within five generations and in turn will lead to virtual elimination of the natural parasite population. In comparison with the normal population, the *Heliothis* larval population available for diapausing in the last generation would be reduced by about 99.8 percent. The parasite progeny would also be greatly reduced. Continued releases for 2 or 3 years probably would lead to extinction of the host population. Simultaneously the selective parasite would also become extinct. The release of 500 parasites per acre in each of the five generations would necessitate the rearing of 5 billion parasites for release on 10 million accumulative host plant acres during the first year.

If the effects projected were realistic, a critical analysis of the cost and benefits of such a suppression program would have to be made, including the ecological consequences of such a control measure.

INTEGRATION OF PARASITE RELEASES WITH RELEASE OF GENETICALLY ALTERED MALES

The concept of integrating the release of mass-produced parasites with the release of sterile insects as a means of insect control has been advanced (Knipling 1966). More recently a theoretical appraisal was made of the feasibility of managing *Heliothis* populations in an agricultural area like California by releasing partially sterilized males (Knipling 1970). Suppression of *Heliothis* larval populations with parasites as projected in this study followed by using sterile or genetically altered insects could provide a highly compatible and efficient integrated suppression system.

As already proposed, the selective parasite release method should possess the greatest suppression efficiency when host populations are high, whereas the genetic method possesses the greatest suppression efficiency when the host populations are low. Both methods would be completely selective against the target pest and would not be expected to adversely affect any organisms except the host itself and those completely dependent on the host.

An integrated program involving the two methods could be more effective and practical than either method employed alone. The parasite release procedure projected in the models already discussed would not necessarily be the most efficient to follow in an integrated parasite-genetic system. The theoretical effect of releasing 100 parasites for generation 3 only is shown in table 4. The impact by the season's end would be almost as great as if the same level of releases per plant host acre was made

during each of the first three generations. Approximately 78-percent suppression of the overwintered population would result from parasite releases during the third generation only as compared with a theoretical suppression of 79 percent when releases are made during the first three generations.

This result theoretically would reduce the requirements for sterilized insects the following season by more than 75 percent. If the projections in this bulletin and in the report on genetic control (Knipling 1970) are realistic, the integrated system would require the rearing and release of 250 million parasites followed by the rearing and release of 125 million partially sterile moths instead of 500 million sterile moths as calculated for the genetic method alone. The cost of such an integrated system should be reduced by almost one-half that of each method used alone. Continued suppression by the release of even fewer genetically deficient insects each season might then be possible as a continuing procedure in an area subjected to infiltration of very few of the insects under control.

DISCUSSION

It must be acknowledged that there are serious gaps in our knowledge of the interrelationships of parasites, their insect hosts, and the host plants. This makes it difficult to estimate the accuracy of the projected requirements for achieving effective control of *Heliothis* populations by the sustained release of parasites. However, the chances seem good that a well planned practical field experiment using one or perhaps a complex of two or more selective parasites will show that the projected requirements and effects are reasonably accurate.

This is the third in a series of in-depth theoretical studies undertaken to appraise the potential role of highly selective parasites in suppressing insect populations under natural conditions and under conditions of timely and programed releases of parasites to supplement natural parasite populations. Results of such studies on *Trichogramma* parasites of certain Lepidoptera and aphid parasites have been mentioned. Although each appraisal required the establishment of different parameters based on the nature and behavior of the parasites and host insects involved, the basic principles governing the density relationship of the parasites and the host were essentially the same. In each study the results of theoretical calculations clearly indicated that a single selective parasite is incapable of exerting a high degree of suppression on the host until the host population has already exceeded the economic density threshold.

Although this is the conclusion for all the pests studied, the same conclusion will not apply to all parasites and host insects. Whether a parasite is capable of suppressing a host population in a natural environment before significant damage is done will depend on the nature of the damage caused

by the pest, the susceptibility of the plant, and the amount of damage that can be tolerated from an economic viewpoint. However, for the host insects considered, they are often damaging and there is no indication that any naturally occurring parasite for the pests studied will produce high levels of parasitism, at least until high host densities occur.

The models developed in this study strongly support the hypothesis that the welfare of a selective parasite is dependent on the welfare of the host. Enough natural suppression pressure by any selective parasite (or predator) to jeopardize the survival of the host would be contrary to natural laws governing the relationship of a selective parasite and its host, because a parasite and host could not coexist under such circumstances. In stressing the inherent limitations of a parasite under natural conditions, there is no intent to discount the importance of natural parasitism by a selective species. Even a low and consistent degree of parasitism by a given species superimposed on the total suppression pressure of a wide range of predators, parasites, and diseases, plus nondensity dependent hazards to survival, becomes significant in the overall regulating mechanisms applicable to an insect population. The development of progressively higher numbers of a parasite as its host population grows adds to the assurance that host populations will not get out of hand.

In considering the role of the complex of natural biological agents, we may tend to regard all of them as a natural force working for our benefit in suppressing a pest. This would be a gross misconception. It seems clear from this study that competition between biological agents is very great indeed. Although predators of *Heliothis* larvae as a group are perhaps the most important of the natural population-regulating forces, they are at the same time probably by far the most damaging of the natural hazards to survival of larval as well as egg parasites. The rearing and release of adult parasites to supplement those produced naturally provides a means of largely bypassing the hazards to parasites that predators normally cause.

The values assigned to various parameters in this study may deviate substantially from true values without nullifying the overall conclusions reached in this study. Possibly the assumption that the natural and released parasites will search for and be equally efficient in parasitizing host larvae on all host plants is subject to the greatest error. Larvae of *Heliothis zea* in ears of corn may be largely immune to attack by even the most efficient of the selective parasite in our ecosystem. Corn is largely a manmade host plant and it is likely that none of the *Heliothis* larval parasites have evolved to be efficient in host attack when the hosts are present in ears of this plant. Thus the efficiency values assigned may not apply to the parasite on corn. Such limitation would not be expected for *H. virescens*. However, if the overall efficiency projections are reasonably valid for all hosts except corn, other methods of selective control may be

developed and employed to deal with *H. zea* on corn during the period when corn is a major host plant in the seasonal development of *H. zea* populations.

If we accept the premise that the estimated number of parasites required to achieve different degrees of suppression of a host population, as herein projected, is reasonably correct, the question naturally arises as to the feasibility and practicability of managing insect populations in this way. What are the chances of developing reliable and low cost methods for rearing parasites in terms of hundreds of millions each year? A consideration of this question is of obvious importance in reaching decisions on research priorities under circumstances of limited research resources for investigating various alternative and more acceptable ways of meeting insect problems. Therefore we might venture to make an appraisal of the possibilities of developing this approach to *Heliothis* control in an agricultural area like California.

According to the 1968 Crop Loss Estimate Report for California, issued by the California Department of Agriculture, *Heliothis zea* caused yield losses valued at \$9,818,203. The cost of control, largely with insecticides, was estimated at \$10,408,825. Losses and costs of control reported by the Department have been higher in other years. In relation to the usual costs of control plus the losses in spite of the current investment in control, we might consider the potential cost-benefit factor of a control procedure based on the programmed release of parasites throughout the agricultural area in California.

Theoretical calculations suggest that about 79-percent suppression of *Heliothis* populations can be achieved by rearing and releasing 450 million parasites during the season. We might assume that suppression would actually amount to 75 percent because of readjustments in host survival due to reduced predation. If it is within the realm of feasibility to rear and release one or more selective parasites at a cost of \$5 per 1,000, the total cost would be \$2.25 million annually. A 75-percent suppression of the normal *Heliothis* population each year cannot be expected to reduce all losses. However, there is reason to believe that for these insects, which are normally suppressed by a wide range of predaceous organisms, such an added level of suppression of the total population by a selective method that would not significantly disrupt the effect of natural agents would in turn reduce crop losses by 75 percent.

If this is a valid assumption, an investment of \$2.25 million annually would represent a gain of more than \$8 million over present control methods plus a yield loss reduction of about \$15 million. Moreover, the proposed technique could be expected to greatly reduce the need for insecticides and thereby contribute to a reduction in environmental pollution.

The population models also suggest that a parasite release rate at two times the above rate, or 200 parasites per acre on all host plant acres during each of the first three generations, would suppress *Heliothis* populations by more than 85 percent. A suppression program at this high level maintained over several years should virtually eliminate all losses, except possibly for the most sensitive crops such as sweet corn. If this could be achieved at a projected cost of \$4.5 million each year, this would be less than half of current control costs and should reduce losses to virtually nothing.

If the cost projections for rearing and releasing parasites on a programed basis were low, by a factor of 2-3, but the benefits were realistic, the use of natural parasites would still be a much more economical system of suppression than the use of insecticides and should provide an ecologically acceptable solution to a major insect problem.

It must be stressed that the effectiveness and cost-benefit projections cited should not be regarded as anything more than a goal for the future. Even though several laboratories of the Entomology Research Division and several land-grant institutions have made a great deal of progress in the mass production of *Heliothis* larvae, pupae, and adults, mass-rearing methods for parasites of these pests have not been developed. However, Lingren et al. (1970), Lewis and Burton (1970), and Jackson et al. (1969) have shown that parasites of *Heliothis* larvae can be reared in the laboratory. There seems to be no reason why low-cost mass-production methods for parasites cannot be developed.

The theoretical calculations are based on the potential role of a completely selective parasite for controlling *Heliothis* larvae. However, in practical control of these pests, as pointed out by P. D. Lingren (personal communication), a species highly attracted to *Heliothis* larvae when released in *Heliothis* environments, even though not completely selective, might be equally or more effective than a completely selective species. The costs of rearing such parasites may also be lower.

A polyphagous parasite would have a more abundant host resource on which to develop and thereby a higher parasite population might be maintained under a regular release regime even though the population of *Heliothis* was greatly suppressed. Moreover, the use of a polyphagous parasite or a complex of two or more species might lead to additional benefits by suppressing other lepidopterous species attacking crops in the released area. However, a polyphagous species released in large numbers that would suppress a wide range of species, both destructive and nondestructive, is more likely to cause significant imbalances in the predator-prey complexes in an ecological area, especially if such releases are sustained over a period of years. However, by carefully selecting the

types of parasites to release, it would be difficult to conceive that such parasites could be more damaging to the environment than the extensive use of nonselective insecticides.

Although emphasis in this bulletin has been on the suppression of the total *Heliothis* population developing on all host plants, the possibility of releasing an appropriate parasite to control *Heliothis* on specific crops should not be ruled out. Knipling (1971) has considered this possibility and proposed a procedure that might be followed.

It is apparent that extensive and intensive research on insect rearing methods and on parasite, insect host, and plant host relationships will be required to determine the feasibility and effectiveness of the methods of insect suppression proposed. The costs for such research can be expected to be high. However, there is an urgent need for scientists to concentrate investigations on various systems of insect management that offer reasonable chances of being more effective, economical, and ecologically acceptable than currently used methods.

The present methods of control, based largely on the use of insecticides in an uncoordinated manner against small segments of the total population in an area, cannot truly manage populations of wide ranging insects, such as the *Heliothis* species, which attack a diversity of crops some of which have a low economic threshold. Such limited attack on populations of any major insect pest will mean continued losses year after year with a continuing high investment in control. On the other hand, the proposed biological approach, which would take full advantage of the high degree of suppression that nature already provides, could virtually eliminate losses throughout a large agroecosystem at much less cost and without significant adverse effects to the environment.

SUMMARY

By using hypothetical parasite and *Heliothis* population models, results of calculations are given to show the close interrelationship of a selective parasite and *Heliothis* larval hosts. As concluded from similar studies of other parasites and pest hosts, the theoretical results indicate that under natural conditions a single selective parasite for *Heliothis* larvae produces a minor natural suppression factor for the host until the host population reaches a high level. Results of the study lead to the conclusion that such parasites alone cannot be a major natural factor in the management of *Heliothis* populations. On the other hand, theoretical calculations show that the sustained supplemental releases of parasites at levels ranging from 100 to 200 per host plant acre for each of the first three host generations are capable of achieving a high degree of suppression of *Heliothis* populations. When release rates are sustained at 500 parasites per host plant acre, eventual elimination of the host population seems inevitable.

The need for much additional research is acknowledged before the proposed system of *Heliothis* population management can be regarded as effective and practical. However, the author cites reasons for investigating the possibilities of employing mass-produced and regular releases of parasites as a means of suppressing *Heliothis* populations throughout an agricultural ecosystem. The potential benefits and costs of the total population suppression system in relation to benefits and costs of current methods seem highly favorable.

The theoretical parasite-host density relationship at various parasite and host density levels is depicted in a series of hypothetical population models. The results of the theoretical studies generally support the concepts of parasite-host relationships and should lead to a better understanding of such relationships in a natural environment. The hypothetical parasite and host population models clearly depict the complete dependence of a selective parasite on the host for population growth and survival. The merits of using released parasites when the host density is high integrated with the release of genetically deficient insects after the host population has been reduced are considered.

LITERATURE CITED

ANONYMOUS.

1969. INSECT-PEST MANAGEMENT AND CONTROL. V. 3 of Principles of Plant and Animal Pest Control. Natl. Acad. Sci. Pub. 1695, 508 pp.

FLANDERS, S. E., and BADGLEY, M. E.

1963. PREY-PREDATOR INTERACTIONS IN SELF-BALANCED LABORATORY POPULATIONS. *Hilgardia* 35, No. 8, pp. 145-183.

JACKSON, C. G., BRYAN, D. E., and PATANA, R.

1969. LABORATORY STUDIES OF EUCELATORIA ARMIGERA, A TACHINID PARASITE OF HELIOTHIS SPP. *Jour. Econ. Ent.* 62: 907-910.

KNIPLING, E. F.

1966. SOME BASIC PRINCIPLES OF INSECT POPULATION SUPPRESSION. *Amer. Ent. Soc. Bul.* 12: 7-15.

-
1970. SUPPRESSION OF PEST LEPIDOPTERA BY RELEASING PARTIALLY STERILE MALES—A THEORETICAL APPRAISAL. *BioScience* 20, No. 8, pp. 465-470.

-
1971. INFLUENCE OF HOST DENSITY ON THE ABILITY OF SELECTIVE PARASITES TO MANAGE INSECT POPULATIONS. Tall Timbers Conference on Ecological Control of Animals by Habitat Management, Tallahassee, Fla., Proc. 1970 (Feb. 26), pp. 3-21.

and GILMORE, J. E.

1971. POPULATION DENSITY RELATIONSHIPS BETWEEN HYMENOPTEROUS PARASITES AND THEIR APHID HOSTS—A THEORETICAL STUDY. U.S. Dept. Agr. Tech. Bul. 1428, 34 pp.

KNIPLING, E. F., and MCGUIRE, J. U.

1968. POPULATION MODELS TO APPRAISE THE LIMITATIONS AND POTENTIALITIES OF TRICHOGRAMMA IN MANAGING HOST INSECT POPULATIONS. U.S. Dept. Agr. Tech. Bul. 1387, 44 pp.

LEWIS, W. J.

- 1970a. LIFE HISTORY AND ANATOMY OF MICROPLITIS CROCEIPES (HYMENOPT.: BRACONIDAE), A PARASITE OF HELIOTHIS SPP. (LEPIDOPT.: NOCTUIDAE). Amer. Ent. Soc. Ann. 63: 67-70.

- 1970b. STUDY OF SPECIES AND INSTARS OF LARVAL HELIOTHIS PARASITIZED BY MICROPLITIS CROCEIPES. Jour. Econ. Ent. 63: 363-365.

_____ and BURTON, R. L.

1970. REARING MICROPLITIS CROCEIPES IN THE LABORATORY WITH HELIOTHIS ZEA AS HOSTS. Jour. Econ. Ent. 63: 656-658.

LJNGREN, P. D., GUERRA, R. J., MICKELSEN, J. W., and WHITE, C.

1970. HOST AND HOST-AGE PREFERENCE OF CAMPOLETIS PERDISTINCTUS. Jour. Econ. Ent. 63: 518-522.

NOBLE, L. W., and GRAHAM, H. M.

1966. BEHAVIOR OF CAMPOLETIS PERDISTINCTUS (VIERECK) AS A PARASITE OF THE TOBACCO BUDWORM. Jour. Econ. Ent. 59: 1118-1120.

END