TB 1387 (1968) USDA TECHNICAL BULLETINS UPDATA
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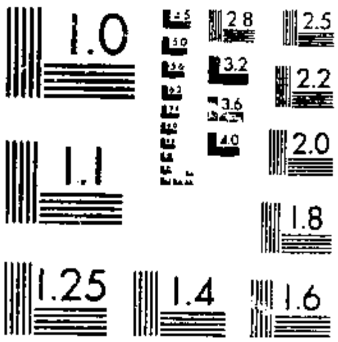
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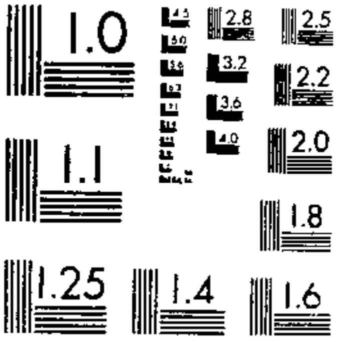
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Population Models to Appraise the Limitations and Potentialities of *Trichogramma* in Managing Host Insect Populations

Technical Bulletin No. 1387

Agricultural Research Service

UNITED STATES DEPARTMENT OF AGRICULTURE

Contents

Population Models to Appraise the Limitations and Potentialities of *Trichogramma* in Managing Host Insect Populations

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In an earlier report, Knipling[2] proposed that biological agents and sterile insects used together in an integrated program could more efficiently suppress insect populations than either method alone. In a later report, Knipling[3] considered the possibility of such a combination in greater depth, following the suggestion of Shipp and Osborn[4] that releasing sterile insects into the environment could add resources that would increase the number of parasites and predators.

Additional theoretical studies have been made to appraise the benefits that might be derived from increasing the resources of host eggs on which the *Trichogramma* parasites can develop. These studies, in turn, led to a detailed consideration of the effect *Trichogramma* parasites have in nature on regulating certain economic lepidopterous populations and the extent to which the release of additional parasites or host egg resources could manage such populations.

In the studies reported here it was necessary first to identify and then to consider in some detail the major factors governing the efficiency of *Trichogramma* and their effect on the relationship between parasite and host density. Parasite-host population models were made to show the importance of these factors and how they affect the trends of both the parasite and host populations. The results might help to explain the variable levels of parasitization observed in nature and could lead to a better understanding of some fundamental

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[1] We acknowledge the assistance of F. R. Lawson of this Division who provided valuable information on predator-prey density relationships as recorded in the literature and who checked the calculations in some of the basic models. We also acknowledge helpful information from other personnel of this Division and of Louisiana State University on the biology, behavior, and population dynamics of the sugarcane borer and *Trichogramma* parasites.

[2] KNIPLING, E. F. SOME BASIC PRINCIPLES IN INSECT POPULATION SUPPRESSION. Ent. Soc. Amer. Bul. 12: 7–15. 1966.

[3] KNIPLING, E. F. FURTHER CONSIDERATION OF THE THEORETICAL ROLE OF PREDATION IN STERILE INSECT RELEASE PROGRAMS. Ent. Soc. Amer. Bul. 12: 361–364. 1966.

[4] SHIPP, E., and OSBORN, A. W. THE THEORETICAL ROLE OF PREDATORS IN STERILE INSECT RELEASE PROGRAMS. Ent. Soc. Amer. Bul. 12: 115–116. 1966.

principles governing both the *limitations* and the *potentialities* of *Trichogramma* as a regulator of insect populations. Such understanding of the underlying factors governing *Trichogramma*-host insect density relationships may lead to a better understanding of predator-prey density relationships in general.

Several eminent authorities on biological control have devoted much effort to a better understanding of predator-prey density relationships. This interest is apparent in the conflicting views of many students of the subject, as discussed in the treatise on Biological Control of Insect Pests and Weeds, edited by Paul DeBach, University of California, Riverside (Reinhold Publishing Corp., New York, 1964). We have not attempted to reconcile the results of our hypothetical study with the extensive literature on predator-prey density in relation to the ecology of insect populations. Instead, our appraisal and procedures are presented and certain conclusions are drawn that may or may not support the views of others.

The procedure followed in these studies was first to establish population models that seemed reasonably representative of the dynamics of some economic lepidopterous hosts whose eggs are often heavily parasitized by species of *Trichogramma*. As with previous similar investigations, the population models are hypothetical and are only indicative of natural populations, since pertinent information is often fragmentary or lacking on the biology, densities, population dynamics, and behavior of the insects these models represent. Nevertheless, we believe enough information is available about many key insects to establish hypothetical population models that are reasonable representations of the densities and trends of natural populations. Such models can then be used as a basis for considering the general magnitude of effects that can be achieved by certain methods of suppressing insect populations.

Specifically we know that the seasonal abundance of our most destructive insects fluctuates widely, though unfortunately little information is available on actual numbers present per acre or per square mile or in the entire population of a given area during different periods in the seasonal cycle. Even less is known about the actual numbers of parasites or predators that prey on the host insects and to what extent the populations fluctuate. We must relate quantitive information on the population densities of both host insect and parasite before we can begin to understand and measure with confidence the quantitive relationships that exist. Moreover, unless we have such understanding, we cannot fully judge the effect that a parasite can have on the host population and, in turn, what effect the host population has on the parasite population.

However, entomologists have obtained substantial information for most of our economically important insect pests on the percentage of host plants or fruit that is damaged. We also have basic information on the egg-laying capability of most insects, and much information on biology and behavior is available. By considering this available information, imperfect as it may be, we were able to construct reasonably representative insect population models.

It may be of interest to discuss the manner in which we arrived at certain population estimates as a guide in establishing the hypothetical host insect and parasite population models. Information is sufficient on host egg densities of such insects as *Heliothis* spp. on tobacco and cotton to conclude that 5,000 host eggs per acre is a realistic estimate of the host egg density for a 10-day period early in the crop-growing season. This should also be reasonably representative of a low density of the sugarcane borer (*Diatraea saccharalis* (F.)) early in the season. From such information we can postulate the general magnitude of the adult population that deposits this number of eggs.

If we assume that each female deposits on an average at least 200 eggs during a 10-day period, the general magnitude of the adult population would be of the order of 50 per acre (25 males and 25 females). If the females deposit on an average 400 eggs each during the 10-day period, the adult population would be 25 per acre. If the estimate of 25-50 adult moths per acre per 10-day period is within the range of a representative natural *Heliothis* population at the beginning of the fruiting period of cotton, we believe that such estimate is sufficiently reliable to undertake meaningful, theoretical population suppression studies. In the absence of precise information on insect population densities, the procedure cited for estimating adult insect densities may be as reliable as any we can employ with current techniques, especially for nonisolated populations.

We also can estimate the general magnitude of *Trichogramma* populations by considering the percent parasitization and the density of the dominant host insect in a given host plant environment. If *Trichogramma* parasitization averages 10 percent when the *Heliothis* host egg density on cotton is estimated to be 5,000 per acre during a 10-day period, this would mean that 500 eggs are parasitized. If two *Trichogramma* parasites emerge from each parasitized egg, the *Trichogramma* population would total 1,000 per acre during the next 10 days. Even if other *Trichogramma* host eggs are present on the cotton and such eggs aggregate half the *Heliothis* egg population, this additional resource would not contribute more than 500 additional *Trichogramma* parasites per acre, making a total of 1,500 per acre. Average density estimates derived by this means are not likely to deviate to a large degree from the true average density in a monoculture environment.

We can in a similar manner estimate the general magnitude of the parasite population when both the host egg density and the parasitization rate are higher. If the *Heliothis* egg population is 15,000 per acre during 10 days and the parasitization is 60 percent (a probable representative condition), we can assume with considerable confidence that the *Trichogramma* population will be about 18,000 per acre for the next parasite generation. Such estimates also give us some idea of the number of *Trichogramma* that must be present during a given period of time to achieve different levels of parasitization.

This is a report of our attempt to determine the limitations and potentialities of *Trichogramma* in regulating the abundance of economically important host insects. The hypothetical host insect, perhaps with only slight modifications, could be taken to represent several lepidopterous species, such as the sugarcane borer, the corn earworm (*Heliothis zea* (Boddie)), the tobacco budworm (*Heliothis virescens* (F.)), the cabbage looper (*Trichoplusia ni* (Hübner)), and certain other important species that are often heavily parasitized by *Trichogramma*. In the hypothetical population models, the interrelationships between three major factors are considered and evaluated: (1) The parasite population density, including searching behavior and efficiency; (2) the host insect egg density; and (3) the area of host plant environment that must be searched by the parasites in seeking host eggs.

Initially in our biomathematical analysis we considered only the quantitive relationships existing between host density and parasite density. Although these two factors are vitally significant, the results did not seem consistent with the natural trends of parasitism that have been observed for such insects as the sugarcane borer. Thus, some other major factor(s) seemed to be involved. By considering the amount of host plant material on which host eggs are distributed as the crop is growing and relating it to the increasing number of parasites that would be required to search for the eggs in the expanding host insect environment, we obtained results that seemed more realistic and meaningful.

To establish the basic population models, we also considered the characteristics of the host insect and the parasite, especially the length of the various stages and the number of generations. Many preliminary population models were "tested" before basic models were selected for detailed analysis. This report therefore presents what we regard as representative population models, even though they are based on incomplete information about the population dynamics of the host insects and their parasites.

We then evaluated the significance of each of the three factors alone and showed how their interrelationship governs both the potentialities and the limitations of *Trichogramma* parasitism. No doubt other factors substantially affect predator-prey relationships, but the three factors alone seemed to explain the variable effects of *Trichogramma* observed in nature or recorded when populations are released for insect control.

It seems academic to again stress that this is a theoretical study and that any conclusions reached will need verification by appropriate experimentation. However, if the study only stimulates further investigations to identify more clearly and to evaluate more fully the importance of the major factors affecting predator-prey density relationships, it will serve the intended purpose. We consider that our results establish the need for much more information before the most efficient use of *Trichogramma*—or any other parasite or predator—can be achieved for insect control. However, even in the absence of more precise information, these biomathematical studies reveal the inherent limitations of *Trichogramma* as a natural population suppressing agent. At the same time, and more significant, the studies reveal that the parasite probably could be effective in controlling insect populations if host resources or parasites could be increased artificially in the manner and to the degree proposed.

The Hypothetical Host Insect Population

The hypothetical host insect chosen is representative of such economically important species as the sugarcane borer, the southwestern corn borer (*Zeadiatraea grandiosella* (Dyar)), the corn earworm, and the tobacco budworm. The host plants are representative of various fast growing field crops such as corn, sugarcane, or cotton. The natural host insect is assumed to increase from a low overwintered or low immigrant population to a high late-season population.

Four adult and four egg-laying generations are assumed, though some of our important lepidopterous species have more or fewer generations. Each host generation from egg to egg is assumed to require 30 days. The adults from overwintered stages or migratory adults are assumed to start from a low of 30 individuals per acre. The male and female ratio is 1:1. It also is assumed that each female deposits 200 eggs that are susceptible to parasitism. The egg-laying capability may exceed this number, but some predation will destroy any eggs exceeding 200 per female. The population is isolated and not exposed to any effect from outside. The increase of the uncontrolled host population is assumed to be fivefold per generation, i.e., all natural environmental hazards, both biological and physical, are assumed to be operating on the natural uncontrolled population.

In the absence of control measures, the natural population is assumed to develop as shown in table 1. For further details in computations, see the appendix.

TABLE 1.—*Assumed natural trend of uncontrolled hypothetical population of lepidopterous insects, showing number of adults and number of eggs deposited per acre during each generation*

Generation	Adults	Eggs
	Number	*Number*
1	30	3,000
2	150	15,000
3	750	75,000
4	3,750	375,000

The first and second generations of the host insect are assumed to be subeconomic, but the third generation is assumed to cause significant crop damage unless controlled. (If corn or sugarcane were the host plants, the host eggs would average about one per plant for the second egg-laying generation and five per plant for the third egg-laying generation.) If effective control of the insect is to be achieved, it is assumed that the suppressive measures must be applied during the second and third generations of the host insects. Since the hypothetical natural population will form the basis for estimating the effects of different control measures, data on the trends of this uncontrolled population are given (table 1).

The host insect population was purposely established at a level that would represent a low overwintered or low immigrant population capable of increasing readily and steadily to a high level as the season advanced. Precise information is lacking on the host insect density. However, information on the number of tobacco budworm eggs or young larvae or both on tobacco, obtained by F. R. Lawson and associates of the Entomology Research Division, indicates that the density levels assumed for the early generations in these studies are realistic. Adult populations and egg densities assumed for the second host generation are compatible with larval counts of *Heliothis* spp. recorded on cotton early in the growing season by Perry L. Adkisson and associates of Texas A&M University and by H. M. Graham of the Entomology Research Division.

The Hypothetical *Trichogramma* Population

The initial parasites in all population models are assumed to be created artificially by introducing 5,000 per acre into the host environment, except in the final models, for which we constructed a trend of natural increase of parasites. We are not aware of available information on the natural density of *Trichogramma* populations, at least during the early generations. However, based on theoretical considerations (see p. 14), we postulate that the natural *Trichogramma* population is at a very low level during the first host insect generation when the host egg density is low. It is also assumed that each parasitized host egg will produce two parasites. Thus, we have a basis for estimating the parasite density if we have information on the host egg density and the parasitization rate.

Our results indicate that the potential for *Trichogramma* increase is not great enough at low host densities to expect a large parasite population early in the season. In fact, we question whether *Trichogramma* could maintain even a stable population if the potential for increase depended on the generally few host eggs laid by the surviving winter population of a key species. Perhaps the parasite delays its appearance in the spring until the host species has had time to increase. Or it may be essential that some alternate host be sufficiently numerous when the parasites emerge to assure an increasing population, or at least to maintain a fairly stable population, until the primary host is sufficiently numerous to provide the resources needed. Adverse effects on parasite population buildup due to low host egg resources early in the season may be offset in part by the rather limited host plant environment. At that time the host plants are generally small and often less numerous than later in the season.

The life cycle of *Trichogramma* is assumed to be 10 days. Thus, there will be three parasite generations during each host generation, a vitally important element in the population density relationships of the parasite and the host. It is assumed that the parasites find the host eggs by random searching of the plant surfaces where the host eggs occur. *All population models are based on the assumption that 5,000 parasites present during a period of 10 days can search for and parasitize 50 percent of the host eggs on 1 acre of the host insect crop when the plant searching area where host eggs are placed is equal to one unit.* Also, one unit of this searching area is assumed to represent the size of the host plant during the first 10 days of the second host insect generation, which is assumed to coincide with the first parasite generation.

The selection of 5,000 parasites per acre as the starting population was somewhat arbitrary. However, the quantity represents the numbers of parasites per acre that are sometimes sold and released for insect control. The assumption that this number of parasites can find and parasitize 50 percent of the host eggs on 1 acre of host plants with a searching area of one is also somewhat arbitrary though, as will be developed later, it was based on certain quantitive relationships between the host egg and parasite densities.

Relationship of Parasite Density to Parasite Efficiency

If 5,000 parasites search and find 50 percent of the host eggs in a given environment, we postulate that 10,000 parasites could search the same environment twice. However, based on random searching by the parasites, the additional 5,000 parasites would search half the area previously searched and half the unsearched area. Thus, one-fourth the host egg area would still remain unsearched, and 75 percent of the host eggs would be found and parasitized by 10,000 parasites. The efficacy of various numbers of parasites above and below 5,000 per acre is assumed to be governed by the search factor.

The searching capability of *Trichogramma* and its efficiency in parasitizing the host eggs are assumed to be completely independent of the host egg density, i.e., if 5,000 parasites can find and parasitize 50 percent of 5,000 host eggs on one unit of crop surface area on which host eggs occur, they will also find and parasitize 50 percent of 100, 1,000, 10,000, and 20,000 host eggs in the same habitat. Thus, the *number* of host eggs parasitized will vary with the density of the host eggs, but the *percentage* parasitized will be constant for a given number of parasites in a given searching environment regardless of the host egg density.

The assumption of random searching behavior, irrespective of population density of the prey, may be contrary to the views of many authorities on the behavior of parasites and predators. Probably some change in searching behavior does occur among many parasites and predators as the density of the prey changes, but no attempt has been made to place a value on such behavioral changes if they do occur. However, we believe behavioral changes in searching patterns that depend on host density are not among the major factors affecting the efficiency of a parasite like *Trichogramma* operating in the total and prescribed ecological environment set up for this study. Even though a parasite may locate its host partly by direction, i.e., by odor or sound, we believe random searching is still a most vital factor in the behavior, ecology, and dynamics of any parasite population.

If searching behavior changes markedly because of changes in parasite or host density, 95 percent parasitization or above that occurs in nature in some situations would be difficult to explain. Conversely, if the parasites fail to search when host density is extremely low, it would be difficult to imagine how a parasite such as *Trichogramma* could survive in an area where monoculture restricts the amount of alternate host plants present.

The biomathematical analysis of the population models in this report indicates that the parasite population will decline rapidly when the host egg density is low during even one host insect generation, which would be equivalent in time to three parasite generations. Thus, low parasitization within the parameters applied can be expected solely on the basis of biological limitations when the host density is low, even if the searching behavior of the parasite does not change. Conversely, a high host egg density, considered from a biomathematical viewpoint, can be expected to lead quickly to a large parasite population and high parasitization.

The average egg-laying capability of *Trichogramma* females is assumed to offer no limitation to the potential of population increase within the parasite and host density limits of this hypothetical study. However, in actual practice, this capability could be a temporary limitation if the parasite density were very low and the host density were very high. Such a situation might occur if abundant host insects develop naturally or migrate into an environment when the parasite density is extremely low. However, in such circumstances, even a low parasite population would increase rapidly because of the short life cycle of the parasite and the great potential for increase when the host density is high.

Also, *Trichogramma* may parasitize a wide range of host insects. Under some circumstances abundant alternate hosts could change the entire pattern of parasite density in a given environment during different periods of the crop season. However, no attempt was made to consider the effect of alternate host eggs, since the primary purpose of this study was to appraise the interrelationships of *Trichogramma* and a host insect on a given cultivated host crop during two or more generations of the host insect. The trend toward monoculture in agriculture will continue. Also, a given crop is usually severely attacked by only one of a group of related lepidopterous species at any given time; therefore, resources for an increase in *Trichogramma* density on a major crop must come largely from that crop. From a practical viewpoint, we must have a better understanding of the dynamics of a given parasite population under conditions of monoculture, and on the basis of such understanding attempt to find ways of making such parasites more useful under such circumstances. This is the primary objective of this study.

Even though we are concerned with *Trichogramma* only, we recognize that interaction will occur between a complex of parasites and predators and the *Trichogramma* that may be present, and we accounted for such factors by limiting our assumed increase to fivefold for the host insect in its natural unaltered environment, even though its potential is much greater. Thus, for the type of appraisals we are making, we believe that we adequately considered all normal environmental hazards, including the natural biotic agents in the environment, except the effects of the *Trichogramma* parasites that are specifically added to the environment or that result from the manipulation of the environment.

Also, no allowance is made for adjustments in the overall natural predator-prey density relationships that occur as the host insect population fluctuates in response to such manipulation. When the host egg density is high, the population of other parasites or predators should also increase, indicating that fewer host eggs would be available to the *Trichogramma* or that some of the eggs might be destroyed after they are parasitized and before the parasites emerge. Thus, our models may not adequately allow for natural hazards at the higher host and parasite population levels, but in this study we are primarily concerned with parasitization levels that will keep the host from increasing to damaging levels. Also, from a practical standpoint, any such adverse effects on *Trichogramma* that would cause significantly less parasitization than the theoretical projections would be offset by the increased effect of the whole parasite-predator complex. The combination of forces should tend to validate the overall effect on the host that is projected in some models.

The assumed level of 50 percent parasitization for 5,000 parasites per acre on one unit of searching area is based on our judgment. Assumed searching efficiency ranging from 25 to 75 percent for 5,000 parasites per acre per environmental unit was "tested" in various models before the 50 percent level was selected as the most realistic. If the searching and parasitization efficiency of 5,000 parasites on 1 acre consisting of one unit of host-searching environment were substantially below 50 percent, we believe that a *Trichogramma* population would seldom, if ever, increase to levels necessary for 90 percent parasitization in nature. On the other hand, if the searching and parasitizing efficiency of 5,000 *Trichogramma* insects were substantially higher than 50 percent, the records would show *Trichogramma* to be much more efficient in nature than these parasites are. Moreover, it would be difficult to explain the large host insect populations that often occur if a population of 5,000 *Trichogramma* parasites per acre is substantially more efficient than we have judged it to be.

Thus, a capability of searching and finding ranging between 40 and 60 percent for 5,000 parasites on 1 acre having one unit of host plant surface area is probably realistic, and 50 percent was selected as the level of efficiency. Accordingly, the efficiency of increasing and decreasing numbers of parasites from 5,000 in a constant searching environment was calculated to be as follows:

Parasites (number)	*Parasitization (percent)*
1,000	12.95
2,000	24.10
3,000	34.02
4,000	42.57
5,000	50.00
10,000	75.00
15,000	87.50
20,000	93.75
25,000	96.87
30,000	98.44

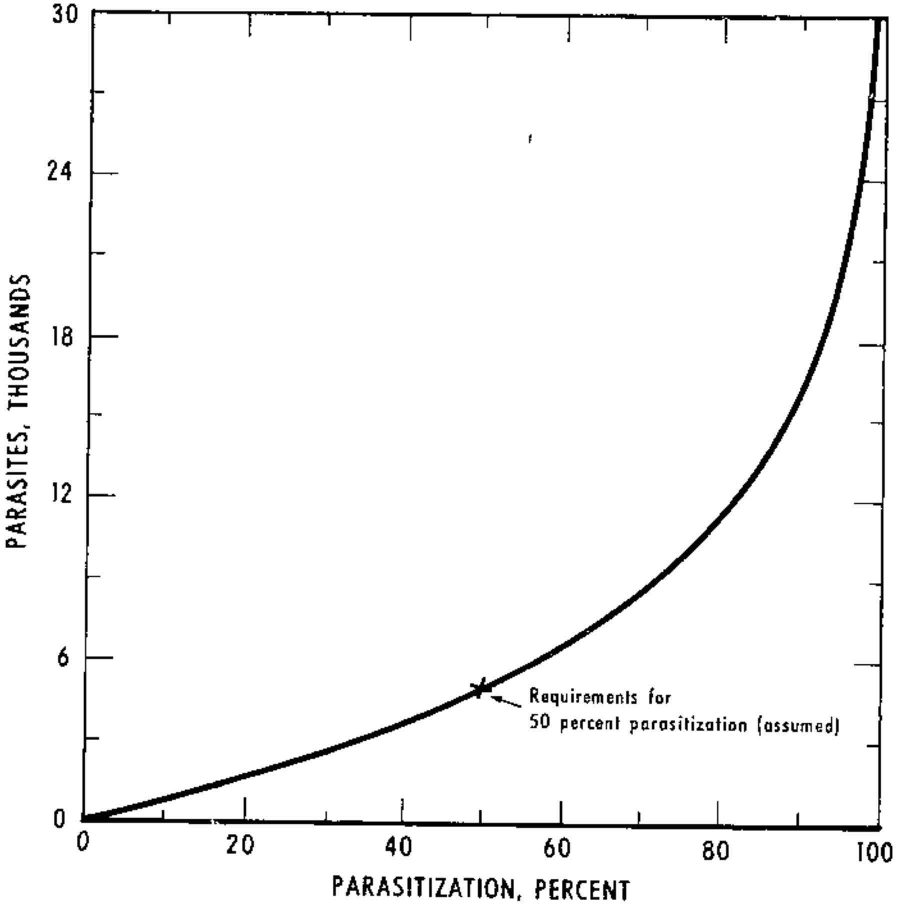

FIGURE 1.—Postulated efficiency of various densities of *Trichogramma* parasites assuming that 5,000 parasites can find and parasitize 50 percent of host eggs when searching environment remains constant at one unit.

The trend of parasitism is also shown in figure 1.

The postulated efficiency of different numbers of *Trichogramma*, based on the 50 percent efficiency level, is the key element in this study. If a 50 percent efficiency can be established for any parasite population, particularly for species that tend to be host specific, we believe that the efficiency of increasing or decreasing numbers will follow the same trend as that shown for *Trichogramma*, except perhaps for extremely low or extremely high parasite populations.

The assumed efficiency of different parasite densities in a stable environment, if reasonably realistic, provides a biomathematical basis for estimating the efficiency of different *Trichogramma* densities in any given situation. However, once again these calculations are based on two important assumptions. One is that 5,000 parasites have the capability of searching and finding 50 percent of the host eggs in a given prescribed environment. The second is that the random searching behavior of the total population of parasites is constant in a prescribed environment, regardless of host density. Thus, the parasitization in a given environment is wholly determined by the number of parasites present. But the search factor becomes an important limitation on the number and percentage of eggs actually parasitized and alone can explain why 100 percent parasitization is difficult to achieve. The increasing size of the searching environment as the crop-growing season advances will further tend to decrease the efficiency of parasite populations in the environment.

According to the parameters established, the higher parasite populations (p. 10) cannot occur when the host density is low if the primary host is the only resource for the parasites. However, we are attempting to establish basic values of efficiency for a given number of parasites that may occur naturally or that may be added to the environment. If the only resource for parasite progeny in the environment were a single host insect species present at the assumed economic density threshold of 5,000 eggs per acre per parasite generation, the absolute maximum parasite density that could develop naturally, according to our basic parameters, would be 10,000. But if 10,000 parasites developed when the host density is 5,000 eggs, the parasite would have parasitized all the eggs of the host during that period. We know this does not happen at host density levels as low as 5,000 per acre per parasite generation. For the effect of the host egg density on the parasite density, see table 6.

However, it seems desirable in considering the basic efficiency data (p. 10) to mention the limitations that host egg densities impose on parasite densities in a natural situation. If only 2,500 or as many as 10,000 parasites were required to achieve 50 percent parasitization, it is our view that the relative efficiency of increasing or decreasing numbers should still be as postulated, and the percent efficiency would not change from that shown (p. 10).

The economic density threshold of the primary host insect (5,000 eggs per acre per parasite generation) cannot furnish the natural biological resources necessary to allow enough parasites to develop to produce the high parasitization shown (p. 10). Also, we think it unlikely that parasite densities of 10,000 to 20,000 per acre per parasite generation in a rapidly growing field crop would achieve consistent levels of parasitization ranging as high as 75–93 percent. If this density occurred when the host population is relatively low, we would have an automatic barrier to the development of large populations of such host insects as *Heliothis* spp. and the sugarcane borer that often occur. By the parameters we have established, when the level of induced parasitization reaches 80 percent above all other natural environmental hazards, no further increase in the host insect population would occur because of the basic assumption that a fivefold increase is representative of the normal increase of an uncontrolled population.

In actual field situations, however, we know that host egg densities of such insects as *Heliothis* spp. on cotton and corn and the sugarcane borer on sugarcane often continue to increase above the number that would permit the development of the maximum number of parasites tabulated (p. 10). Therefore, some other major factor or factors must limit the efficiency of *Trichogramma*. We reached this conclusion to reconcile theoretical mathematical values with observed effects in nature. The logic led us to introduce and consider the effect of the plant growth factor, i.e., the expanding environment where host eggs can be placed and where parasites must search for them.

Effect of Plant Growth Factor on Limiting *Trichogramma* Efficiency

We believe that the plant growth factor, which affects the amount of plant surface area where host eggs are likely to be found, can largely explain the apparent discrepancies between the theoretical values of parasitization (p. 10) and actual parasitization observed in the field. When parasites are present during midseason on rapidly growing field crops like corn, sugarcane, cotton, and tobacco, the number of parasites would have to increase progressively each 10 days (one generation) to search the same percentage of the plant surface occupied by the host eggs.

However, the growth rate factor in terms of plant surface area may not coincide precisely with the size of the specific areas where host eggs are placed, because the host insect is often selective in the placement of eggs, for example the silks of corn or the terminals of cotton plants. Moreover, the parasites, too, may be selective in their searching. Nevertheless, it still seems reasonable to assume that the egg-laying environment for the host insect (leaf surfaces, terminals) will expand to a degree that is reasonably comparable to the expanding surface area of a growing crop. The growth rate factor of a given crop is thus assumed to reflect the expanding searching environment of the parasite as the crop-growing season advances.

According to data published by Kiesselbach,[5] the leaf surface of growing corn increases at a rapid rate during the early stages of growth. On the basis of his data, we estimate that if corn has a leaf surface area equal to one unit when the plants are about 2 feet high, an additional surface area unit will be formed each 10 days for about 50 days; then growth stops rather abruptly. Thus, each successive parasite generation must search for eggs of specific hosts in an environment that virtually increases by a factor of one each 10 days until the crop has matured.

B. M. Waddle of Crops Research Division, Agricultural Research Service, provided growth data for cotton (personal communication). On the basis of his data, the leaf surface area of cotton increases about one-half unit each 10 days, if we regard the beginning of squaring as representing one unit of surface area. James E. Irvine of Crops Research Division furnished data on the growth rate of sugarcane (personal communication). His data indicate that the surface area of this crop will increase by a factor of about 1.2 each 10 days after the sugarcane is about 2 feet high.

If the plant surface area on which host eggs are deposited increases one unit during each parasite generation, the effect on parasitization, according to the basic parameters, can be marked, as shown in table 2. The percent parasitization achieved by adding an increasing number of *Trichogramma* when the plant surface area remains constant at one unit is the same as that shown previously (p. 10), but the figures are repeated in table 2 for comparison with the assumed parasitization rate of the same number of parasites in an expanding host

TABLE 2.—*Estimated effect of host plant growth factor on parasitization with various* Trichogramma *populations per acre when host egg searching area remains constant at 1 unit and when it increases by 1 unit per parasite generation*[1]

Parasite generation	Parasites per acre	Parasitization when host egg searching area— Remains constant at 1 unit	Parasitization when host egg searching area— Increases 1 unit per parasite generation
	Number	*Percent*	*Percent*
1	5,000	50.00	50
2	10,000	75.00	50
3	15,000	87.50	50
4	20,000	93.75	50
5	25,000	96.87	50

[1] Model assumes 50 percent searching efficiency and parasitization by 5,000 *Trichogramma* parasites on 1 unit of host egg searching area.

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[5] KIESSELBACH, T. A. PROGRESSIVE DEVELOPMENT AND SEASONAL VARIATIONS OF THE CORN CROP. Nebr. Agr. Expt. Sta. Res. Bul. 166, 49 pp. 1950.

egg environment. If the basic assumptions are correct, we would expect the parasitization rate to remain virtually constant in an expanding environment when the host density is low even though the numbers of parasites added were increased substantially as the crop grew.

If we accept the premise that a population of parasites such as *Trichogramma* searches at random for the host eggs, the expanding searching environment must be a major factor affecting the parasitization that will occur during the crop-growing season. Thus, this factor is probably one of the most significant limitations to the parasitization achieved by *Trichogramma*. It provides an escape mechanism for a host insect, permitting the insect to increase in density, even though the total parasites and predators throughout an environment may also increase. In such circumstances, the parasite eventually may begin to gain a marked advantage when the mass of host plants and the searching environment stabilize, or especially if they diminish when some of the host plants are destroyed after harvest.

Based on the estimates in table 2, we concluded that if 5,000 parasites per acre on a rapidly growing crop initially produce 50 percent parasitization, 5,000 additional parasites would be required each 10 days just to maintain 50 percent parasitization until the crop stops growing. If the number of parasites released plus the natural progeny remains constant at 5,000, but the searching area expands as indicated, we could expect a marked reduction in parasite effectiveness as the crop grows.

In table 3, we assume that if 5,000 parasites will search and parasitize 50 percent of the host eggs in one unit of searching area, 2,500 parasites will be provided for each unit area when the total surface area increases to two. On the same basis, 1,667 parasites would be available for each searching unit area when the host plant surface area increases to three. Again note that the efficiency of different numbers of parasites per unit area is determined on the basis of the data previously shown (p. 10).

TABLE 3.—*Estimated parasitization of host eggs by constant population of 5,000* Trichogramma *per acre per parasite generation in expanding host egg searching area*

Parasite generation	Searching area	Estimated parasitization
	Units	*Percent*
1	1	[1]50.00
2	2	29.29
3	3	20.63
4	4	15.91
5	5	12.95

[1] Assumed.

If the population of host insects starts at 5,000 eggs per acre and if the normal increase is fivefold per generation, 80 percent parasitization (above all other natural hazards throughout the growing period) would be required to prevent an increase in the population. Also, according to the basic efficiency values for different numbers of parasites per unit of searching area (p. 10), the initial parasite population would have to number about 11,610 to achieve 80 percent parasitization when the plant surface area had a unit of one. Then on the basis of the assumed effect of the growth factor, 11,610 additional parasites would have to be present each 10 days to maintain 80 percent parasitization (table 4).

TABLE 4.—*Estimated parasites per acre necessary to prevent buildup of hypothetical host insects in expanding host egg searching area*

Parasite generation	Searching area	Parasites required for 80 percent parasitization
	Units	*Number*
1	1	11,610
2	2	23,219
3	3	34,829
4	4	46,438
5	5	58,048
6	5	58,058

The model in table 4 does not indicate the source of the parasites. Obviously if the host egg density is constant at the economic threshold of 5,000 and if these eggs are the only resource for a natural buildup of parasites, we would have to rear and release most of the parasites or develop some other means of increasing the density to the levels needed to maintain 80 percent parasitization and thus keep a host population at or below 5,000 eggs per acre per parasite generation. When the host density remains constant at 5,000 eggs per acre and parasitization remains constant at 80 percent, only 8,000 parasites would be produced naturally for each parasite generation. The additional parasites necessary will have to come from another source.

Effect of Host Egg Density on Number and Effectiveness of *Trichogramma* Populations

We have appraised the efficiency of different numbers of parasites in relation to the searching area involved, but largely without regard to the source of the parasite. To evaluate the potential efficiency of the parasites when they are produced in nature, we must consider the vitally important factor of host egg density.

If *Trichogramma* parasites find the host eggs by chance encounter, as we have assumed, we can estimate the population trends and determine their efficiency in nature provided we know (1) the basic searching efficiency of various numbers of *Trichogramma* in a total population in a given size host egg environment, (2) the effect of the searching area on the ability of a given number of parasites to locate host eggs, and (3) the number of parasite progeny produced by a given number of parasitized eggs. By considering the interrelationship of these three major factors in relation to the biology of the parasite and its potential of biotic increase, we can construct hypothetical population models that depict more clearly than has been possible with earlier models both the limitations and the potentialities of the parasite for controlling a host insect.

Theoretically we should be in a position to achieve a high degree of control of a host insect in a given environment by the direct effect of reared and released parasites. However, as noted, if the projections in table 4 are reasonably realistic, many more parasites would have to be released than in past efforts to control insects directly by this means. Generally *Trichogramma* has been used for seeding or inoculation, with the expectation that it would subsequently increase naturally to levels that would provide effective control. However, our theoretical study indicates that such releases alone cannot assure a large parasite population when the host density is at a subeconomic level or even much higher than the economic density level that we have established. We can develop hypothetical models that support this statement. If the host egg density is below a certain level, a natural population of *Trichogramma* will decline rapidly, regardless of the number of parasites released for seeding, because of the limitations imposed by the number of progeny produced from the parasitized eggs.

The hypothetical model in table 5 shows why such decline is inevitable when host density is low if we accept the parameters established for this study. Again we assume that 5,000 *Trichogramma* will parasitize 50 percent of the host eggs on 1 acre of crop having one unit of searching area. The calculations show the inherent limitations imposed by low host egg densities on the increase potential of a *Trichogramma* population and, in turn, on the parasitization rate that can be expected. Even if the searching efficiency were 100 percent for the 5,000 parasites, the parasite population would still decline, because, according to the parameters, 1,000 host eggs could produce only 2,000 parasite progeny, which is less than the 5,000 released. However, we can safely conclude that 5,000 parasites per acre would never achieve even close to 100 percent parasitization. As noted, the assumed 50 percent parasitization efficiency for 5,000 parasites for one unit of searching area seems a more valid level to use as a basis for calculations. Then with 50 percent parasitization, the parasite population would decline rapidly after the initial release, and the decline would continue until extinction if the host density remained at 1,000 per acre.

If a host egg density of 1,000 is inadequate to furnish the biotic resource necessary to maintain a parasite population, the logical question is: What level of host density is necessary to maintain a stable parasite population and what levels of host density are

TABLE 5.—*Estimated* Trichogramma *population trend and parasitization when host egg density remains at 1,000 per acre and host egg searching area is constant at 1 unit*

Parasite generation	Parasites[1]	Parasitization	Eggs parasitized	Parasite progeny
	Number	*Percent*	*Number*	*Number*
1	5,000	50.0	500	1,000
2	1,000	12.9	129	258
3	258	3.5	35	70

[1] Natural populations per acre, except 5,000 added during first parasite generation.

needed to assure an increased parasite population and, hence, an increased rate of parasitization? Reasonably accurate answers to these questions are among the most important that we hoped to obtain in the study. Therefore, various levels of host egg density were established and tested to determine their effect on the parasite population and hence on the parasitization expected.

According to the established parameters, host egg density must reach a level of 5,000 for the parasites to maintain a constant population in a constant searching environment of one unit. However, a progressive increase in density above the 5,000 level would lead to progressively larger parasite populations and consequently to progressively higher parasitization rates if the host egg environment area remained at one unit.

Theoretically each increasing increment in host egg density above 5,000 will permit the development of a larger parasite population and consequently a higher maximum parasitization in a constant searching environment, but the parasite population and the parasitization levels will quickly stabilize at the particular level that the host egg resource will permit. Such leveling off is shown in the hypothetical models in table 6.

A stable host density of 5,000, according to the parameters used, will result in a stable population of 5,000 parasites and a stable parasitization level of 50 percent. A stable host density of 10,000 will result in a stable population of about 18,000 parasites and a stable parasitization of about 91 percent. At a host density of 20,000, the parasite population could increase to about 40,000 and

TABLE 6.—*Models showing effect of different host egg densities per acre on* Trichogramma *population trend and parasitization when host egg searching area is constant at 1 unit*

Parasite generation	Parasites[1]	Parasitization	Eggs parasitized	Parasite progeny
MODEL 1—HOST EGG DENSITY CONSTANT AT 5,000 PER PARASITE GENERATION				
	Number	*Percent*	*Number*	*Number*
1	5,000	50.00	2,500	5,000
2	5,000	50.00	2,500	5,000
MODEL 2—HOST EGG DENSITY CONSTANT AT 10,000 PER PARASITE GENERATION				
1	5,000	50.00	5,000	10,000
2	10,000	75.00	7,500	15,000
3	15,000	87.50	8,750	17,500
4	17,500	91.20	9,120	18,240
5	18,240	92.02	9,202	18,404
MODEL 3—HOST EGG DENSITY CONSTANT AT 20,000 PER PARASITE GENERATION				
1	5,000	50.00	10,000	20,000
2	20,000	93.75	18,750	37,500
3	37,500	99.45	19,890	39,780
4	39,780	99.59	19,918	39,836

[1] Natural populations per acre, except 5,000 added during first generation in each model.

achieve a constant parasitization approaching 100 percent. These data indicate that *Trichogramma* has an unusual potential for increase when the host egg density is high and constant, provided the searching area in which the host eggs occur is relatively restricted and also remains constant.

However, in nature such conditions could not exist for any substantial time in the total natural environment occupied by the parasite and the host. According to the parameters established and based on the calculations made for the various models (table 6), a constant population of about 7,500 host eggs and a constant host egg searching environment of one unit will lead to a parasite population capable of producing about 80 percent parasitization. The result would be a host population stabilized at 7,500 eggs per acre per parasite generation. This host egg density theoretically could not increase naturally above 7,500. We know that a maximum density of 7,500 host eggs per acre per 10 days in nature is not realistic. Thus, we again must assume the existence of some vitally important factor such as the plant growth factor to explain the observed limitations in parasite efficiency in nature as opposed to the theoretical efficiency (table 6).

Since the number of parasites necessary to achieve and maintain 80 percent parasitization in an expanding environment cannot occur naturally when the host density is low or even moderately high, *we postulate that it is impossible for* Trichogramma *to develop naturally to levels that will maintain a host population below economic levels*, if we accept the suggestion that the subeconomic level of density is 5,000 eggs per acre per parasite generation. As shown by additional hypothetical models (table 9), the host density would have to be substantially higher than 5,000 in an expanding host environment for parasites to develop naturally to the numbers necessary to reach 80 percent parasitization and hence to control the host population.

Thus, we again conclude that *the only way that a host population could be stabilized by* Trichogramma *at or below the assumed economic threshold (a density level of 5,000 eggs per acre per parasite generation) would be to rear and release enough parasites to maintain 80 percent parasitization or to create an artificial host egg resource that would permit the required natural increase in the parasite population to achieve this parasitization level.*

We know that parasitization in natural populations of such insects as the sugarcane borer and the corn earworm does exceed 80 percent. *Thus, we must assume that such high rates of parasitization (80 percent or above) throughout the host insect environment can occur only after the host density has already reached a high and damaging level.* This statement, based on theoretical calculations, does not conflict with field observations. Normally high host densities and crop damage occur late in the season, and at this time high parasitization rates are most commonly observed. The population models show that a combination of high host egg density and a stabilized searching environment can quickly lead to a large parasite population and, hence, to a high parasitization level. But if the number of host eggs necessary in such models reasonably represents natural situations, the crop would be severely damaged before a high parasitization could be expected.

Postulated Effects of Inoculative Releases of *Trichogramma* to Control a Hypothetical Host Insect Population

Hypothetical Models to Appraise Extent of *Trichogramma* Releases Necessary to Achieve Effective Control

We will first appraise the natural parasitization rates and the effect we might expect with an inoculative release of 5,000 *Trichogramma* parasites made to control a representative natural host insect population. As a reminder, the natural population of the host insect, in the absence of such control, is assumed to follow the trend shown in table 1.

We have already postulated that a seeding population of *Trichogramma* cannot be effective in controlling a host insect population when its egg density remains low. However, we will now consider more precisely the results to be expected in nature from a single release of 5,000 *Trichogramma* parasites per acre during the first 10 days of the second host insect generation. Again we assume that the host egg density will total 5,000 per acre per parasite generation or 15,000 eggs during the 30 days of the second host generation (table 1). We have also postulated that when the host plant searching area is one unit, the release of 5,000 parasites will lead to 50 percent parasitization. A growth factor increase of one unit of host plant surface area each 10 days for 50 days will be assumed; then the growth stabilizes. On the basis of these and the other assumptions previously stated, we estimated the trend of the parasite population, the parasitization rate, and the trend of a natural host insect population during the second, third, and fourth host generations. The results are shown in table 7 (model 1).

This study is primarily concerned with the dynamics of a hypothetical host insect and a hypothetical *Trichogramma* population during the second and third host generations. We elected to follow through into a fourth generation and a partial fifth to show how the gradually increasing host egg density will eventually tip the balance in favor of the parasite and lead to a parasitization rate that would prevent any further increase in the host insect population. Four or five generations of host insects per season would be representative of an insect like the sugarcane borer or *Heliothis* spp. on a succession of host plants in a long warm season.

In estimating the effects of parasitism on a host insect population, the natural uncontrolled population is still assumed to in-

TABLE 7.—*Models showing estimated trend of natural* Trichogramma *population per acre, parasitization, and trend of natural host insect population*[1] *when host egg searching area expands 1 unit and 1/2 unit*

Parasite generation	Parasites[2]	Assumed natural host egg density	Searching area	Parasitization	Parasite progeny	Adult host insects
MODEL 1—EXPANSION OF SEARCHING AREA BY 1 UNIT						
	Number	*Number*	*Units*	*Percent*	*Number*	*Number*
1	5,000	5,000	1	50.00	5,000	50
2	5,000	5,000	2	29.30	2,930	50
3	2,930	5,000	3	12.66	1,266	50
4	1,266	12,500	4	4.30	1,076	125
5	1,076	17,700	5	2.94	1,040	177
6	1,040	21,800	5	2.84	1,238	218
7	1,238	59,800	5	3.37	4,030	598
8	4,030	85,900	5	10.57	18,160	859
9	18,160	105,900	5	39.56	83,788	1,058
10	83,788	288,900	5	90.20	521,176	2,889
MODEL 2—EXPANSION OF SEARCHING AREA BY ½ UNIT						
1	5,000	5,000	1	50.0	5,000	50
2	5,000	5,000	1½	37.0	3,700	50
3	3,700	5,000	2	22.6	2,262	50
4	2,262	12,500	2½	11.8	2,946	125
5	2,946	15,800	3	12.7	4,023	158
6	4,023	19,300	3	16.9	6,547	193
7	6,547	55,100	3	26.1	28,773	551
8	28,773	68,900	3	73.5	101,338	689
9	101,338	80,100	3	99.1	158,710	801

[1] Uncontrolled host insect population is assumed to increase fivefold during each generation.

[2] Natural populations per acre, except 5,000 added during first parasite generation.

crease fivefold per generation. Any parasitism resulting from the released parasites will, therefore, cause a corresponding reduction in the population of treated host insects compared with the untreated population. For example, the assumed parasitization of 50 percent for the first 10 days of the second host insect generation would leave 50 percent fewer adults in the corresponding period in the third generation compared with the uncontrolled population. Also, any decline in the number of adult host insects would lead to a corresponding decline in the host egg density.

Based on the results in table 7 (model 1), the inoculative release of 5,000 *Trichogramma* per acre during a 10-day period when the host egg density is subeconomic (5,000 per acre per parasite generation) cannot increase the natural *Trichogramma* population or cause a high parasitization rate during at least the first two host generations because of (1) the low host egg resource and (2) the reduced efficiency of *Trichogramma* resulting from the progressive increase in searching environment caused by the rapidly growing crop.

A substantial decline in the parasite population and an even greater decline in the parasitization rate will occur before the end of the second host generation after the initial release of parasites. Even though the host egg density will increase substantially and exceed the economic density threshold in the third generation in this hypothetical situation, the increase in host eggs will not be adequate for several parasite generations to permit the development of enough parasites to cause high parasitization in the growing crop.

The release of the 5,000 parasites will have some deterrent effect on the normal trend of the host insect population during its second and third generations, but a high degree of control cannot be expected. The third host insect generation (second generation after the parasite releases) would develop a total adult reproducing population of 520 compared with 750 for the natural untreated population, that is, about 30 percent fewer adults would comprise the third generation largely because of the direct effect of the inoculative release of 5,000 parasites at the beginning of the second host generation. Also, the few parasites present during the egg-laying period of the third generation would further reduce development of larvae by about 3.3 percent. Thus, overall control in the third generation would aggregate about 33.3 percent. For the relatively small investment made in the single release of *Trichogramma*, such an effect could produce a significantly adverse effect on the host population.

In marginal situations when the overall parasite-predator complex limits the increase potential to less than we have assumed in our models, the extra parasitism could be of great value. However, based on the calculations, this level of control would offer little hope of protection from crop damage when the increase potential is fivefold or higher. The host insect population would steadily increase beyond the economic levels.

Since some of our lepidopterous insects have four to five generations per season, the trends of the parasite population, parasitization rates, and the host insect population, as previously noted, are projected into a fourth and partial fifth generation (third and fourth generations after the release of parasites). The increase in host eggs and the assumed stabilization of plant growth during this time will eventually permit the parasites to increase considerably and will produce about 40 percent parasitization by the end of the fourth host insect generation and 90 percent by the beginning of the fifth. However, as stated, when this increase occurs, the crop will have suffered severe attack by the high host population.

If the increase in parasitization is, in fact, so dependent on a high host density, as indicated in table 7, we can readily understand why it has been difficult to demonstrate an increase in *Trichogramma* parasitization with such insects as the sugarcane borer on sugarcane and *Heliothis* spp. on cotton after "seeding" releases of

Trichogramma early in the season to build up natural parasitism. The calculations clearly indicate that such releases cannot be expected to lead to high parasitization during the regular growing season. The parasites would deter but not prevent a steady increase in the natural host population until the host population reaches a high and damaging level of density. By the time the host density reaches a sufficiently high level to permit a large parasite population to develop naturally, and hence to produce a high parasitization, excessive crop damage can be expected.

The trend of parasitization in table 7 (model 1) assumes that the environment where host eggs are placed will expand one unit each 10 days, which is equivalent to a generation of parasites. Obviously the expanding environment will vary greatly depending on the type of crop and growing conditions. Moreover, the area where host eggs are placed and where parasites will search may be more restricted than is indicated by the actual growth rate of the plant. Therefore, another model was established to calculate the trend of parasitization after an inoculative release of 5,000 parasites per acre at the beginning of the second host generation on the assumption that the host egg environment is expanding at only one-half unit each 10 days until crop growth stabilizes. The resulting trend is also shown in table 7 (model 2). All other assumptions are the same as for the first model in table 7.

The analysis for both the parasite and the host insect is shown through three host generations and nine parasite generations. In this second model, the parasite population and the parasitization rate are substantially higher than in the first model. However, the trends are still similar. The higher parasitization rates tend to delay the buildup of the host insect, but parasitization is still far below the level required to prevent a steady rise in the host population based on a fivefold increase factor. The host insect would exceed the threshold of economic density, according to the established parameters, and would severely damage the crop long before the parasite population and the parasitization rate increased to effective levels. However, by the end of the third host insect generation after the initial release, the parasites would definitely gain the upper hand. The result would be the earlier collapse of the host insects.

The second model (table 7) shows that the parasite population does not decline much through the first six parasite generations, even though the parasitization level declines markedly. The advantage is in favor of the host until the host increases to the level of critical density. Then the advantage swings to the parasite, and its population and parasitization increase rapidly. The models of hypothetical parasite-host insect populations shown in table 7 emphasize the significance of host egg density and expanding host egg environment as the host plants grow.

The calculations suggest that certain changes in agricultural practices could affect considerably the predator-prey density relationships. For example, a fast and rank growing crop produced on fertile irrigated lands will grow much faster and the growing period may be more prolonged than on nonirrigated lands. Such circumstances could so favor host insects that an insect pest could increase to substantially higher than normal levels before parasites and predators could begin to suppress it. We might speculate that irrigation plus fertilization has given the host insect a significant advantage over its parasites. This situation would not occur to the same degree in a more natural environment.

Trichogramma parasites have been and are still being used for repeated inoculative releases to control sugarcane borers on sugarcane and bollworms (*Heliothis* spp.) on cotton, and the 5,000 parasites per acre per release period are reasonably representative of the numbers thus released. A model was therefore established to estimate the effect such practice would have on a natural insect population developing in a typical growing season, during which the searching environment expands one unit per parasite generation for the first five generations. The theoretical results are shown in table 8. All parameters and calculation methods were as previously stated.

Obviously the addition of 5,000 parasites each parasite generation during the developmental period for three host generations would have a substantially greater effect than the release of only one seeding population of 5,000 parasites (table 7). However, according to the parameters established, this type of program would not produce a large parasite population and a high parasitization so long as the host density remained low to moderately low, and it would not prevent the host insect from increasing to a high and damaging level.

Theoretically the parasitization would average about 46 percent in the first host generation exposed to parasite releases. This control would result almost equally from the direct effect of the released parasites and the progeny from the parasitized eggs. However, the parasites from both sources would not be adequate to

TABLE 8.—*Postulated effect on host insect population and parasitization of adding 5,000* Trichogramma *parasites per acre per parasite generation under circumstances of fivefold increase for uncontrolled population*

Parasite generation	Total parasites	Natural host egg density	Searching area	Parasitization	Naturally produced parasites	Adult host insects
	Number	*Number*	*Units*	*Percent*	*Number*	*Number*
1	5,000	5,000	1	50.0	5,000	50
2	10,000	5,000	2	50.0	5,000	50
3	10,000	5,000	3	37.0	3,700	50
4	8,700	12,500	4	26.0	6,508	125
5	11,508	12,500	5	27.0	6,830	125
6	11,830	15,800	5	28.0	8,836	158
7	13,836	46,200	5	31.9	29,438	462
8	34,438	45,400	5	61.5	55,852	454
9	60,852	56,900	5	79.4	90,300	569

assure a high parasitization. The rate of parasitization would decline in the next host generation to an average of about 27 percent. However, the overall impact on the host insect population in an area would be substantial, even though adequate control might not be achieved.

In comparison with an uncontrolled population, the adult population in the third generation would be reduced by 45.7 percent. This reduction, plus the calculated 27 percent parasitization of eggs deposited by the third generation of adults (second generation exposed to parasitization), would aggregate 60.4 percent control compared with the untreated population. For the effort involved, this degree of control might be regarded as highly significant, especially if the host insect does not increase to the extent assumed. However, since the increase of the uncontrolled host insect is assumed to be fivefold per generation, 60.4 percent control would not prevent a steady increase in the population.

If a total of 15,000 host eggs per acre during the 30 days of the second host insect generation represents the economic threshold of density, the crop damage would occur during the third host insect generation, because the total host eggs would be about 42,300. However, about 27 percent would become parasitized, and approximately 30,880 eggs would be left to produce larvae to attack the crop. At the same time, the uncontrolled population would produce 75,000 eggs per acre during the 30 days. In both the treated and untreated populations, the eggs and larvae would be subjected to the normal environmental hazards according to the original parameters established for this hypothetical study. Continued releases of parasites into the fourth or last host generation (third generation exposed to releases of parasites) would result in a steadily increased parasitization, primarily because the natural host egg density would by then reach a level that permits a sufficient increase in parasite progeny to achieve a high level of control.

Practical Significance of Theoretical Calculations on Releasing Parasites

This theoretical study indicates the results to be expected from adding relatively low numbers of *Trichogramma* to a natural insect population. However, until experimental evidence supports the reliability of these methods in determining the limitations and potentialities of *Trichogramma*, we do not propose to take a position for or against the practice of adding small numbers of *Trichogramma* to crops to control such insects as the sugarcane borer and *Heliothis* spp. However, based on published information, there is relatively little conclusive evidence that the release of *Trichogramma* in numbers commonly used against such insects as *Heliothis* spp. and the sugarcane borer has provided practical control. When the effects of these releases have been appraised, they generally have been minimal, inconclusive, or negative compared with the effects of natural parasitism on untreated areas. Thus, our appraisal seems to fully support practical experience.

We are sufficiently confident of the validity of our results, however, to advance the following views on the efficiency of *Trichogramma* in maintaining subeconomic host populations in a natural host environment: *Because of biological and physical limitations,* Trichogramma *species in nature are incapable of developing sufficiently large populations on such insects as* Heliothis *spp. and the sugarcane borer to achieve a high parasitization of the host insect when its population ranges from low to substantially above the economic threshold during rapid growth of such crops as corn, cotton, or sugarcane. Because of these limitations, natural parasitization by* Trichogramma *cannot become effective and reliable in achieving natural control of the insect until the host insect population has substantially exceeded the economic threshold.*

The addition of an inoculative population of Trichogramma *at the right time may deter host insect populations, but only temporarily and to a rather low degree. A subeconomic host population will not provide sufficient host egg resources to permit the released* Trichogramma *to maintain even its original population level, and the parasites and parasitization will decline so long as the natural host density remains below the economic threshold. Repeatedly introducing* Trichogramma *into the environment at 5,000 per acre per parasite generation would theoretically have a considerable impact on the overall host insect population, and measurable control could be expected. However, even such a program would provide little assurance that the host insect would remain at subeconomic levels.*

The limitations in the value of inoculative and sustained low releases of *Trichogramma* do not rule out the practical use of larger numbers of reared and released *Trichogramma* parasites for controlling insect populations. The release of adequate numbers of parasites on a sustained basis could provide an effective and practical method of keeping an insect population at subeconomic levels. Based on our appraisals, the number released should be much higher than that generally used in the past. *The parasite releases would have to be sustained and would have to be much higher than 5,000 per acre for each parasite generation to achieve and maintain a stabilized host insect population at a subeconomic level.*

This discussion strongly suggests that *Trichogramma* parasites in nature are inherently limited in preventing host insects from increasing to damaging levels, even when low to moderate numbers of this parasite are regularly added to the environment. At the same time, the hypothetical models indicate that *Trichogramma* parasites are capable of quickly developing high population levels and high parasitization rates if the host density reaches a sufficiently high level. Thus, we should not consider *Trichogramma* parasites of minor importance as natural agents for regulating insect populations. Even though the calculations projected in this study indicate that the parasite may not be a major natural factor in protecting a given crop, its ability to increase and to produce high parasitization rates when host densities are high could be a most vital natural factor in preventing enormous populations of certain economically important host insects.

The parasites are probably most valuable in a natural environment by preventing high overwintering populations and by limiting the insects that could develop on one crop and spread to subsequent susceptible crops in areas with a diversified cropping system and a long crop-growing season. Perhaps of greater practical importance, these studies indicate that through manipulation the natural density relationships between the parasite and its host insects could be completely reversed, and in this way the parasite could be used to maintain an insect population at a subeconomic level.

Manipulation of Parasite and Host Egg Densities to Regulate Host Insect Populations

The various hypothetical models discussed indicate that if it were practical to rear enough *Trichogramma* parasites to make sustained releases and thus to maintain a high population, the direct effect on the host should be substantial, even though the host egg density were low (see especially p. 10 and table 4). The models also suggest that if it were feasible and practical to maintain a high host egg density that would not endanger the crop, the natural *Trichogramma* population would increase naturally and quickly to high and effective levels.

The first possibility of mass rearing and releasing *Trichogramma* at a high and sustained level needs further consideration as a practical way to control the insect (see table 4). Mass production and release would provide a practical way to control some of the economically harmful lepidopterous insects. However, the hypothetical population models indicate that the number of parasites now used in routine releases is far below the level needed for high control. We will have to think in terms of rearing and releasing as many as 50,000 or more per acre per parasite generation, depending on the crop and the crop-growing conditions. Also, the number required for effective control will vary substantially, depending on the stage of plant growth, which reflects the amount of host egg environment to be searched by the parasites.

When we consider the high cost and the sometimes objectionable features of chemical control and the great advances made in mass rearing large numbers of insects at low cost, the large numbers of parasites needed for effective control should not discourage researchers from fully exploring this approach to controlling some of our more important lepidopterous insects. However, for such measures to be successful, it is our view that *the method must be applied against the total population or against large segments of the total host population in well-coordinated community-wide or re-*

gional programs. Moreover, we believe that the total host plants in the area should be considered and not just the crop to be protected.

Although the rearing and sustained release of *Trichogramma* may be a practical and dependable way to control certain important insects, we are intrigued by a second possibility. This would involve the sustained addition of sufficient host egg resources to the environment to permit the development and maintenance of large natural populations of parasites, irrespective of the natural density of the insect host. This approach to environmental manipulation of insect populations could be more successful than direct and sustained releases of large numbers of parasites, particularly if a high host egg density is necessary in the environment for the parasites to continue normal and vigorous searching. Also, a given number of *Trichogramma* parasites developing in the natural environment may be more vigorous and more efficient in host seeking and finding than the same number reared in a controlled environment and then released.

The host egg resource on which *Trichogramma* could develop naturally might be supplied in one of several ways:

(1) Mass produce a natural host insect, obtain large numbers of host eggs, sterilize the eggs or otherwise render them incapable of hatching, and begin the sustained addition of sufficient numbers to the natural environment before the insect to be controlled has reached the economic threshold level. These host insect eggs would then provide the resources needed for the parasites to develop naturally to high levels in nature.

(2) Mass produce and begin the sustained addition of sufficient eggs of a suitable alternate host that will not attack the crop but that will provide resources on which *Trichogramma* could develop in nature.

(3) Develop a method of sterilizing both males and females of the insect to be controlled so the sterilized males can reduce the reproductive potential of the females in the natural population and the sterilized females when released on a sustained basis can deposit large numbers of sterile eggs that will serve as the host egg resource on which *Trichogramma* can build up and remain at a highly effective level in nature. Such sterile eggs deposited by the released sterile females would have to be comparable to the natural fertile eggs in attractiveness to the parasites and also provide adequate resources for developing parasite progeny.

This use of sterile natural host insects to furnish host egg resources would also place the preferred host eggs in the precise parts of the environment where the parasite would be most likely to search. In addition, a given strain of parasites might be more efficient if it develops on the host to be controlled rather than on some alternate host. Ways of sterilizing female insects without adversely affecting their ability to deposit eggs are being investigated at the Metabolism and Radiation Research Laboratory, Agricultural Research Service, Fargo, N. Dak.

For our biomathematical study of this approach to achieving increased parasitism, we will assume that the host insect eggs added to the environment will be comparable to the natural wild host insect eggs as a reproductive resource for *Trichogramma* and that no selective behavioral changes will occur in the *Trichogramma* parasites that develop on the artificially added host eggs.

Five models in table 9 show the effect of various levels of artificially created host egg densities on the *Trichogramma* population trend and parasitization rate. The parameters will be those used previously. The crop will be growing rapidly, starting when the searching area unit is one. The plant surface area is presumed to increase by one unit during each 10 days, coinciding with successive parasite generations, until crop growth stabilizes. The seeding population of 5,000 *Trichogramma* added only during the first parasite generation, which corresponds to the beginning of the second insect host generation, is assumed to result in 50 percent parasitization. Higher and lower numbers of parasites developing naturally will have the basic searching efficiency that was projected previously (p. 10). The area consists of 1 acre of host crop.

TABLE 9.—*Models showing effect of different levels of artificially created host egg densities per acre on* Trichogramma *population trend and parasitization in expanding searching area*

Parasite generation	Parasites[1]	Searching area	Parasitization	Parasite progeny
MODEL 1—HOST EGG DENSITY CONSTANT AT 5,000 PER PARASITE GENERATION				
	Number	*Units*	*Percent*	*Number*
1	5,000	1	50.00	5,000
2	5,000	2	29.30	2,930
3	2,930	3	12.66	1,266
4	1,266	4	4.30	430
5	430	5	1.18	118
6	118	5	.33	33
7	33	5	.09	9
8	9	5	.03	3
9	3	5	.01	1
MODEL 2—HOST EGG DENSITY CONSTANT AT 10,000 PER PARASITE GENERATION				
1	5,000	1	50.00	10,000
2	10,000	2	50.00	10,000
3	10,000	3	37.00	7,400
4	7,400	4	22.62	4,524
5	4,524	5	11.79	2,358
6	2,358	5	6.33	1,266
7	1,266	5	3.45	690
8	690	5	1.89	378
9	378	5	1.05	210
MODEL 3—HOST EGG DENSITY CONSTANT AT 20,000 PER PARASITE GENERATION				
1	5,000	1	50.00	20,000
2	20,000	2	75.00	30,000
3	30,000	3	75.00	30,000
4	30,000	4	64.64	25,856

Model 3—Continued

Parasite generation	Parasites[1]	Searching area	Parasitization	Parasite progeny
5	25,856	5	51.20	20,480
6	20,480	5	43.32	17,328
7	17,328	5	38.15	15,260
8	15,260	5	34.50	13,800
9	13,800	5	31.79	12,716
MODEL 4—HOST EGG DENSITY CONSTANT AT 30,000 PER PARASITE GENERATION				
1	5,000	1	50.00	30,000
2	30,000	2	87.50	52,500
3	52,500	3	91.16	54,696
4	54,696	4	84.98	50,988
5	50,988	5	75.68	45,408
6	45,408	5	71.61	42,966
7	42,966	5	69.59	41,754
8	41,754	5	68.58	41,148
9	41,148	5	68.05	40,830
MODEL 5—HOST EGG DENSITY CONSTANT AT 40,000 PER PARASITE GENERATION				
1	5,000	1	50.00	40,000
2	40,000	2	93.75	75,000
3	75,000	3	96.87	77,496
4	77,496	4	93.18	74,544
5	74,544	5	87.34	69,872
6	69,872	5	85.59	68,478
7	68,478	5	85.02	68,016
8	68,016	5	84.83	67,864
9	67,864	5	84.77	67,816

[1] Natural populations, except 5,000 added only during first parasite generation in each model.

The host egg density of 5,000 (table 9, model 1) would lead to a rapid decline in both the parasite population and the parasitization rate. Also, the chance of host egg encounter will progressively diminish because of limited host egg resources for parasite production and because of the expanding searching area. The combined effect of these two adverse factors would cause a steadily declining *Trichogramma* population and consequently a low and declining parasitization rate. We conclude that the parasite would not exist long with such a sustained low host density.

When the host egg density is constant at 10,000 (model 2), the parasite population will increase temporarily for three generations and then decline. The percent parasitization will remain constant for two parasite generations and then decline because of the expanding host egg environment that must be searched. We conclude that a constant artificially created host density of 10,000 per acre per parasite generation is inadequate to develop and maintain high parasitization during the crop-growing season.

The artificially created host egg density of 20,000 (model 3) will cause a rapid increase in the *Trichogramma* population after inoculation and will result in a moderately high parasitization rate. However, the expanding host insect environment will gradually cause a decline in both the parasite population and the parasitization. With the fivefold increase potential of an uncontrolled insect population, this artificially created host egg density will fall short of producing enough parasites to maintain a stable host insect population, but a high level of control would result. A substantially diminished adult host population compared with an uncontrolled host population, plus the added effect of parasitism above normal hazards, should provide a high degree of crop protection. If about 15,000 parasites were released initially, a substantially higher degree of control would be achieved and virtually assure adequate protection of the crop, based on a fivefold increase potential for the host insect.

When the artificial host egg density remains constant at 30,000 (model 4), the parasite population will increase to a high level and parasitization will reach a maximum of about 91 percent, which, temporarily at least, will depress the natural host insect population in the environment. The parasite population will eventually decline slightly and parasitization will decrease more sharply to less than 70 percent, largely because of the expanding environment. However, the parasitization achieved because of the high host egg resource should prevent or greatly slow down an increase in a natural host population in such an environment. This effect, plus a moderately high parasitization in the third host generation, should assure adequate protection of the crop.

A much greater impact would be achieved if the initial inoculative parasite releases were higher. In actual practice this would seem advantageous.

The artificially created 40,000 host egg density per acre per parasite generation will theoretically permit a maximum of almost 97 percent parasitization. Also, in spite of the plant growth factor, parasitization will remain high. According to the parameters established, a natural host insect in such an environment could not maintain its population level, and it would steadily decline so long as the artificial host egg resource remained at 40,000.

The models in table 9 indicate the significance of host egg density in determining the parasite density and, hence, the parasitization rate. At the lower host egg densities, the parasite could not maintain itself; at the highest density, the parasite would eventually eliminate the host. The models indicate further that the interrelated factors profoundly affect the limitations and the potentialities of *Trichogramma* parasitism. More important, they suggest ways we might manipulate the environment to permit *Trichogramma* to achieve high control when the natural host is below economic levels. The models support the general premise stated earlier *that the parasites can have relatively little impact on the host insect until the natural host egg density substantially exceeds the economic threshold level.* However, the models also clearly suggest that artificially created and sustained high host egg densities would so build up the parasite populations that high parasitization would occur, even when the natural host population is low and the host plant is growing rapidly.

The information obtained from these models does not conflict with any observations in nature on the limitations and potentialities of *Trichogramma.* It does indicate that a delicate but favorable balance exists between *Trichogramma* and its host insect and that this relationship is essential for the survival of each. Since the parasite in nature cannot exert a strong adverse effect on the host when the host density is low, the host has greater opportunities to increase. However, when the host density is high, a population of *Trichogramma* has an amazing reproductive potential, and a high parasite density as well as a high parasitization will soon follow. These increases will lead, in turn, to a decline in the host insect population.

We believe that the data in the various hypothetical population models are not incompatible with but actually lend strong support to the classical concepts of predator-prey density relationships. However, we are particularly intrigued by the possibilities of drastically changing this relationship by creating an artificial reproductive resource for the parasite so the number of parasites and the parasitization rate will remain high and virtually constant, even when the natural host density is low. Control of a natural host insect thereby will be achieved and maintained irrespective of its density.

Control of a Hypothetical Host Insect Population by Adding Host Eggs for *Trichogramma* to Environment

From the information in table 9, the host egg density would have to be maintained at about 30,000 per acre per parasite generation for *Trichogramma* to attain a high enough parasitization to offset the normal increase of the host insect. If such a rate could be achieved when the natural host population is at a subeconomic level and if this level is sustained by maintaining an artificial host egg resource, the natural host insect could not increase to damaging numbers.

We therefore established a hypothetical control program to determine what effect an artificially created and constant resource of 30,000 host eggs per acre per parasite generation would have on a natural host insect population that, in the absence of control, would develop as shown in table 1. During the first 10 days of the second host insect generation, when the natural host egg density is 5,000 per acre, suitable alternate host eggs for *Trichogramma* are assumed to be added to the environment at the rate of 30,000 per acre each 10 days for a total period corresponding to five parasite generations. The natural and artificially added host eggs will total 35,000 each for the first three parasite generations. An inoculative population of 5,000 *Trichogramma* parasites per acre then will be added during the first 10 days to assure an adequate parasite population. The effect of such manipulation on the environment will be determined on the basis of the various assumptions already made and on an expanding searching environment of one unit for each parasite generation except the sixth. The results are shown in table 10.

TABLE 10.—*Hypothetical trend of host insect population,* Trichogramma *population, and parasitization rate when 30,000 host eggs are added per acre per parasite generation*

Parasite generation	Parasites[1]	Host egg density	Searching area	Parasitization	Parasite progeny	Host insect population
	Number	*Number*	*Units*	*Percent*	*Number*	*Number*
1	5,000	5,000 natural; 30,000 added.	1	50.00	35,000	50
2	35,000	5,000 natural; 30,000 added.	2	91.16	63,812	50
3	63,812	5,000 natural; 30,000 added.	3	94.76	66,332	50
4	66,332	12,500 natural; 30,000 added.	4	89.96	76,466	125
5	76,466	2,200 natural; 30,000 added.	5	88.00	56,672	22
6	56,672	1,300 natural; none added.	5	79.22	2,060	13

[1] Natural populations, except 5,000 added during first parasite generation.

The natural population of host insects is assumed to consist of 150 adults per acre during its second generation (table 1), and this natural population will contribute the 5,000 natural host eggs in the environment each 10 days during the first three parasite generations as noted. Then the host egg resource in the third host generation will amount to 30,000 added each 10 days for the fourth and fifth parasite generations. The added eggs, plus eggs deposited by the natural population of host insects present during each parasite generation, will constitute the total host egg resources for *Trichogramma*. No host eggs will be added during the sixth parasite generation, because in this simulated practical test we are assuming that the crop will mature and not be subject to attack after 60 days.

The total natural population of 15,000 eggs in the beginning (5,000 eggs per acre each 10 days) is regarded as the economic threshold for crop damage. The addition of the 5,000 inoculative population of *Trichogramma* during the first 10 days provides only 50 percent parasitization of the natural and the added host eggs. This rate above all other natural hazards will eliminate any crop damage during the 10 days. However, the addition of the 30,000 alternate host eggs will provide the extra host egg resources required for *Trichogramma* to build up quickly to high levels.

Theoretically the parasite population will increase rapidly enough to produce 91.16 and 94.76 percent parasitization, respectively, during the second and third parasite generations. The overall control of the second host insect generation will average 78.64 percent. If the 15,000 natural host eggs for one host generation in an uncontrolled population represent a marginal economic population so far as crop damage is concerned, this parasitization rate should prevent crop damage. Also, the 78.64 percent parasitization in the second host insect generation will reduce the adult population in the third host insect generation by this degree in comparison with the uncontrolled population.

Since the increase potential is fivefold, and 80 percent parasitization would be required to stabilize the host insect population, the number of adults will show a slight overall increase in the third host insect generation (total of 160 in the third generation versus 150 in the second generation). However, parasitization during the egg laying period of the third host generation will average 85.73 percent. Thus, the number of host eggs available to produce larvae will fall far below the economic level.

The combined effect of the 78.64 percent reduction in the adult populations and the 85.73 percent parasitization will aggregate 97 percent control of the third host generation in comparison with the uncontrolled population. Therefore, 75,000 eggs would be deposited per acre by the uncontrolled population subjected to normal environmental hazards only. In contrast, the controlled population would deposit only about 16,000 eggs, and only about 2,300 would escape parasitization, a number far below the assumed economic threshold of 15,000 established originally. Thus, host eggs added at 30,000 per acre per parasite generation should be more than adequate to assure crop protection.

In actual practice, as previously indicated, it would seem more efficient to increase the inoculative dose so that it would immediately provide a high level of control and also permit the parasite to quickly reach the maximum density that the egg resources would permit. However, we have again elected to start with a theoretical 5,000 inoculative rate to further stress the significance of a high host egg density in the development of a high parasitization.

If the host insect egg environment expands by one-half unit, as we might expect for cotton, instead of one unit, the host egg resource required to maintain a stable host insect population would be substantially lower.

If the estimate of the potential effect of the projected addition of host eggs is reasonably valid, the question is how practical would it be to develop and use this approach to insect control. We might speculate. Let us assume that the principal host crops of *Heliothis* spp. (e.g., corn, soybeans, and cotton) in a given agricultural area aggregate 1 million acres. *Heliothis* spp. may cause an average annual loss of $10 per acre in spite of an average annual expenditure of $5 per acre for control. Thus, the losses would total $15 million.

If host eggs were added at the rate of 150,000 per acre per season, which seems more than adequate, the total requirement for 1 million acres would be 150 billion host eggs. No accurate estimate of production costs of host eggs can be made, but it should be possible to produce large numbers at a cost of $10 per million or $10,000 per billion. (Entomologists have developed mass rearing methods for tropical fruit flies that average about $30 per million.) Then the cost of producing 150 billion host eggs would be $10,000 × 150 or $1,500,000. If the cost of applying eggs in the environment equaled the cost of egg production, the total cost of keeping the insect population below economic levels would amount to $3 million, which would compare favorably with the assumed cost of $5 million for current methods of control. In addition, if the entire population of *Heliothis* were held to subeconomic numbers, the $10 million in losses caused by the insects would be saved.

In actual practice one could expect wide latitude in the number of host eggs needed from month to month and season to season, depending on surveys and circumstances. An adequate level of population suppression might be achieved at a cost substantially below the estimate, because natural factors would help suppress the population more effectively than is now possible when insecticides are used.

The use of eggs of an alternate host presupposes that the searching behavior of *Trichogramma* will not change and that the parasites will not discriminate between eggs of the host insect to be controlled and eggs of the alternate host. The use of such supplemental host eggs also presupposes that behavioral changes will not occur in the selection of the two types of eggs for parasitism. Should changes in behavior occur when parasites are reared on an alternate unnatural host, it should be feasible and practical to rear the natural host and apply the required number of these eggs. Such eggs would be added to the environment after being rendered incapable of hatching, perhaps by irradiation.[6]

Possibly the most effective and practical way to add host eggs to the environment would be to develop a suitable way to sterilize female moths of the species to be controlled so they will deposit infertile eggs. Such eggs would not create a hazard to the crop, but hopefully they would provide the host egg density required for the natural development of a large parasite population. Such a procedure could have the advantage of placing eggs in the environment where they will be most readily found by the parasites. Also, aside from possible improved efficiency of parasitism, the use of sterile egg-laying females as the host egg resource would permit the integration of the effects of releasing sterile males and the increased parasitism, as suggested by Knipling.[7]

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[6] The use of irradiated eggs may have an advantage over normal eggs. Neal Spencer of Biological Control of Insects Research Laboratory, Columbia, Mo., has reported (unpublished data) that sterile eggs of the cabbage looper and imported cabbage worm will remain susceptible to parasitism longer than normal eggs that hatch in 3–4 days. If eggs added to the environment were available for two times as long as normal eggs, this could produce a bonus effect of great significance in the buildup of egg parasites by artificial means.

[7] See footnotes 2 and 3.

Validity of Assumptions and Calculations

The many assumptions established for the hypothetical studies logically raise questions about the validity of the assumptions and, hence, about the validity of the conclusions. Perhaps the basic searching and finding efficiency curve postulated for *Trichogramma* is the most important element, and this assumption may also provide the greatest possibility of error. Another key issue is the expanding host egg environment and the values given this factor. The assumed population densities of the hypothetical host insect and of the hypothetical parasite and their rates of increase are also critical factors, the accuracy of which is subject to great variation.

Notwithstanding the possibilities of considerable deviations from true values in our assumptions and in our methods of calculating the results, we gained increasing confidence in the soundness of the established parameters as the hypothetical studies progressed. However, to estimate the magnitude of any deviations from the relationship that actually exists between *Trichogramma* and its primary host in nature, we put the methods and results of our theoretical appraisals to the "test" by selecting the sugarcane borer in Louisiana and *Trichogramma* as test insects.

After many years of research in Louisiana by scientists with the University of Louisiana and the Entomology Research Division, a wealth of information exists on the dynamics of the sugarcane borer and of *Trichogramma*. Unfortunately much of the data on the host insect are qualitative. Thus, we found it necessary again to establish logical values but not confirmed by quantitive field data. However, the information on the population of overwintering sugarcane borers in sugarcane fields, the percentage of stalks bored during different times of the growing season, the egg-laying habits of the adult moths, and other aspects of the biology and ecology of this major insect pest were used to construct a representative seasonal population model for sugarcane borer adults and the eggs deposited by them.

The sugarcane borer has about four generations each season in Louisiana. We deviated from the fivefold increase per generation assigned to the basic hypothetical host models in the establishment of the hypothetical sugarcane borer population model, because this increase applied to each of the first three generations would produce a density level by the fourth generation that seemed much too high. In addition, we allowed a longer growth period for sugarcane than we assumed for the hypothetical host plants in the basic models. The host egg environment is assumed to increase by a factor of one for each 10 days for six generations of *Trichogramma* instead of five for all previous models. Also, our hypothetical population of sugarcane borers is assumed to start with 100 overwintered moths per acre, instead of 30 for the basic models, and then to increase, respectively, by fivefold, threefold, and twofold in the next three generations.

Ralph Mathes, Leader of Sugarcane Borer Investigations with the Entomology Research Division at Houma, La., provided field data on natural *Trichogramma* parasitism of the sugarcane borer so that we could relate our basic parameters to natural parasitism. We requested that the estimated trends of natural parasitism be based on a moderately high population of sugarcane borers in situations where chemical control had not been used. On the basis of available data, he submitted a model that was judged to be representative of the natural trend of *Trichogramma* parasitism through four generations of sugarcane borers (table 11).

We then determined whether our parameters governing parasitism by *Trichogramma* could be applied to a hypothetical sugarcane borer population as already described and show a trend of parasitism that would approximate the natural trend. The results of this projection are given in table 12. In order that the relative trends of the *Trichogramma* populations and the parasitization rates can be more clearly noted for the hypothetical and the natural populations, the data in tables 11 and 12 are also depicted in figure 2.

TABLE 11.—*Proposed representative seasonal trend of natural parasitization of sugarcane borer eggs by* Trichogramma *in Louisiana sugarcane fields not treated with insecticides* [1]

Host insect generation (30 days)	Parasite generation	Parasitization	Average parasitization per host generation
		Percent	*Percent*
1		0	0
2	1	Trace	2
	2	2	
	3	4	
3	4	8	20
	5	17	
	6	34	
4	7	65	80
	8	85	
	9	90	

[1] Estimate based on composite field data obtained on sugarcane borer by Ralph Mathes and various investigators.

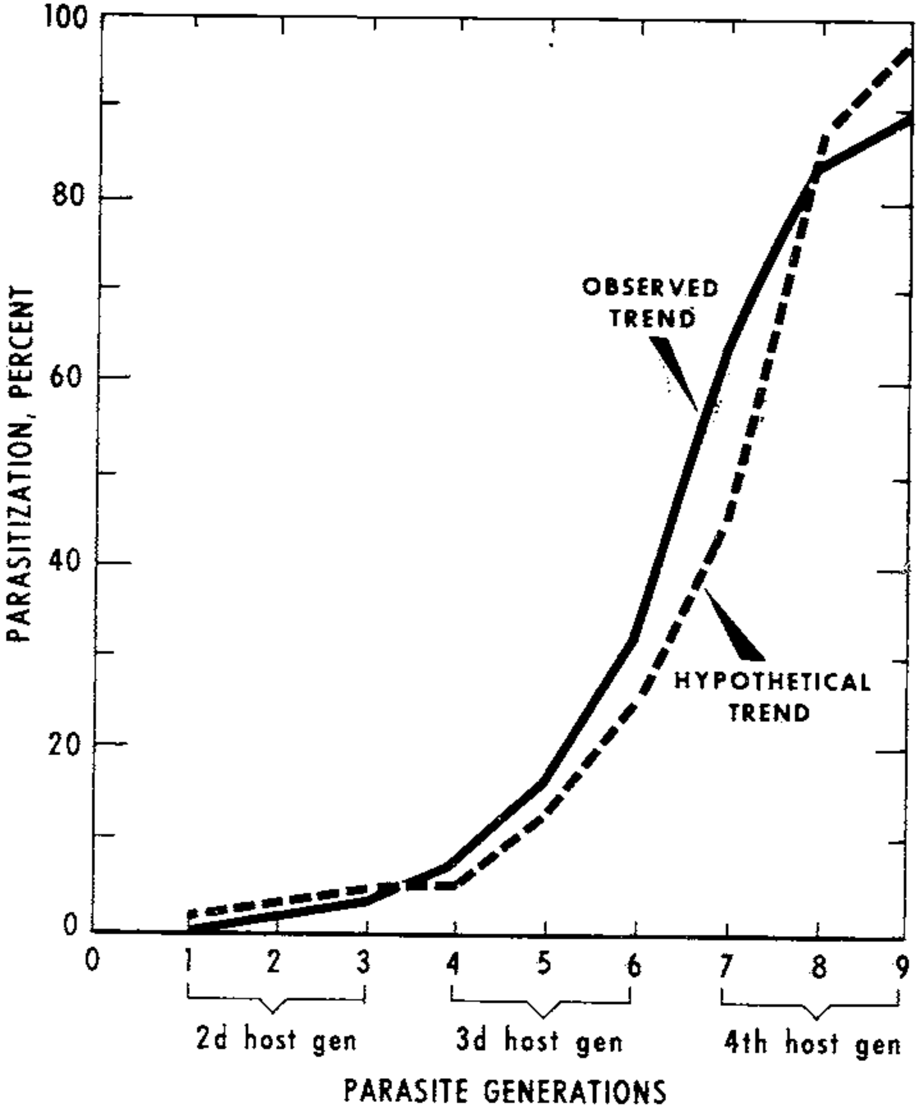

FIGURE 2.—Postulated trend of *Trichogramma* parasitism of hypothetical sugarcane borer egg population, based on established parameters, compared with observed natural trend of parasitism in Louisiana sugarcane fields.

TABLE 12.—*Calculated hypothetical population trends of sugercane borer and of* Trichogramma *and parasitism trends*

Host generation	Sugarcane borer adults per acre	Parasite generation	Parasites	Host egg density	Searching area	Parasitization	Parasite progeny	Average parasitization per host generation
	Number		*Number*	*Number*	*Units*	*Percent*	*Number*	*Percent*
1	100			10,000		0	0	0
2	500	1	100	16,666	1	1.4	466	3.2
		2	466	16,666	2	3.2	1,066	
		3	1,066	16,666	3	4.9	1,636	
3	1,500	4	1,636	50,000	4	5.5	5,500	15.0
		5	5,500	50,000	5	14.0	14,000	
		6	14,000	50,000	6	26.0	26,000	
4	3,000	7	26,000	100,000	6	45.0	90,000	77.0
		8	90,000	100,000	6	87.5	175,000	
		9	175,000	100,000	6	98.4	197,000	

In line with our basic assumption, we did not expect *Trichogramma* populations to be significant during the first host generation. A host density of 3,333 eggs per 10 days (10,000 eggs for the first host generation) would not, according to our parameters, permit the parasite to maintain its population. If a *Trichogramma* population restricted to sugarcane normally attempted its seasonal development during the first host generation, it would be suicidal. Field data showed no significant parasitism of sugarcane borer eggs in nature during the first generation of sugarcane borers. Thus, our basic assumption about the absence of parasitism by *Trichogramma* during the first host generation is not incompatible with field observations.

The first parasite generation is assumed to occur during the first 10 days of the second generation of sugarcane borers. The 10-day duration of each parasite generation and the 30-day duration of each host generation are the same values used for other models. Thus, we expected three parasite generations for each host insect generation. Also, we assumed that during the first parasite generation, the host egg searching area would consist of one unit per acre and that the searching area would increase by one unit each 10 days for 60 days and then stabilize at six units as the sugarcane matured.

Our hypothetical population model starts with 100 *Trichogramma* parasites per acre during the first parasite generation. A starting population of 100 *Trichogramma* per acre when the host egg searching area is equal to one unit would, according to the basic efficiency curve (fig. 1), result in 1.4 percent parasitization, which compares with the "trace" natural parasitization in table 11. With this low starting parasite population and the conditions of our hypothetical host population model, the parasite population and parasitism trend would develop as shown in table 12. The calculated parasitism trend in the hypothetical model, based on the parasite-host density relationships we have developed, proved to be basically similar to the natural parasitism trend of sugarcane borer eggs proposed by Mathes and his coworkers (table 11).

The parasitization rates for the third host generation in our hypothetical model are slightly lower than those recorded for the third host generation in the natural field populations, but the trend is remarkably similar. The trends in the fourth host generation are also remarkably similar in both models, even though the parasitization in our hypothetical model is higher in the ninth parasite generation than the observed natural level.

A logical explanation is that in nature when the host insect population and the parasite population reach the high levels of the fourth host generation in the hypothetical model, certain density dependent factors unaccounted for in our parameters prevent the development of the maximum number of parasites that could theoretically be produced. It is reasonable to suppose that predation of both the host eggs and the parasite would increase substantially when the host density reaches the level shown in the fourth generation of the hypothetical model. This would tend to quickly reduce the number of *Trichogramma* progeny and, hence, would prevent parasitization approaching 100 percent throughout a total host population environment. It should be mentioned, however, that natural parasitization does approach 100 percent in some sugarcane fields. However, disregarding the rather marked difference in the two models in the last parasite generation, the similarity of the parasitization rates during the first, second, third, and most of the fourth host generations in both the hypothetical and the natural populations further increased our confidence in our hypotheses.

Moreover, we believe that the biomathematical approach based on the establishment of hypothetical insect population models for both the host and the parasite, even in the absence of precise quantitive data, can be of great value in developing a better understanding of predator-prey density relationships. This understanding can, in turn, suggest how *Trichogramma* and perhaps other parasites might be used more effectively in the management of insect populations.

Summary and Conclusions

This report advances certain hypotheses regarding the interrelationships of *Trichogramma* parasites, host insects, and host plants and then appraises the validity of these hypotheses. In conducting the study we took into account available information to establish certain assumptions regarding the biology, behavior, and population dynamics of the parasite and host insect and the growth characteristics of the host plant. Hypothetical population models representing the total insect populations in a prescribed area were established, based perhaps equally on judgment and on available information obtained by many investigators. The quantitive interrelationships of the hypothetical parasite and host insect populations then were postulated.

The procedure followed in making the calculations is indicated in the tables and explained in more detail in the appendix. Before arriving at the parameters that form the basis of the hypothetical study, different assumed values were tested, and the results were considered in relation to reported seasonal trends of *Trichogramma* parasitism for certain host insects and to results that seemed realistic and logical. Adjustments were made in assumed values (e.g., the number of parasites assumed to achieve 50 percent parasitization) until the results appeared logical and agreed with available information on natural parasitism reported for specific host insects on various cultivated host plants.

On the basis of the established procedures, this report presents the results of extensive theoretical calculations, in which hypothetical insect population models were used to identify and appraise the importance of major factors governing the density relationships between an egg parasite, *Trichogramma,* and its lepidopterous hosts. The three major interacting factors proposed as the chief elements governing the number of parasites produced and the parasitization rates by *Trichogramma* for such host insects as the sugarcane borer (*Diatraea saccharalis* (F.)) and the *Heliothis* spp. are (1) the parasite population density, (2) the host insect egg density, and (3) the amount of host plant environment that must be searched by the parasites in seeking host eggs. Limitations imposed by the searching factor resulting from an assumed random searching behavior represent an additional element in the overall efficiency of the parasites.

After postulating the basic efficiency of a given number of *Trichogramma* parasites in finding and parasitizing the host eggs present in one unit of host egg searching area, hypothetical population models were developed to study the interaction of parasite density, host egg density, and expanding plant environment and, in turn, the effect of such interaction on the parasitization rate. From the findings an evaluation is made of the *limitations* and *potentialities* of *Trichogramma* in suppressing hypothetical insect populations. The rates of parasitization to be expected by adding various numbers of reared *Trichogramma* or host eggs to the environment are shown in the insect population models.

We advance the hypothesis, supported by the hypothetical models, that when the population of the primary host insect is below the economic threshold during normal crop-growing conditions, the *Trichogramma* parasites in a total environment are incapable, because of biological limitations, of increasing naturally to density levels that will control the host insect. We conclude that the addition of one-shot inoculative populations of 5,000 *Trichogramma* parasites per acre to this environment cannot lead to a high and sustained parasite population. The parasitization level will continue to decline so long as the host population remains subeconomic. *Trichogramma* can increase to effective levels only when the number of host eggs reaches a level substantially above the economic threshold. By the time the natural host insect reaches such densities, the crop will be severely damaged.

We also postulate that the parasitization level, beyond other natural hazards, which would be required to stabilize a host population at an uneconomic level, must reach 80 percent or more. Hypothetical models are established to show that such high parasitization by *Trichogramma* can occur in nature only when host densities have already exceeded the economic threshold.

In spite of the limitations of *Trichogramma* as a regulator of host insect abundance in nature when the host egg density is low, theoretical calculations show that these parasites have remarkable potentialities for increase and for high parasitization rates when the host egg density is high. Even though natural parasitism, according to theoretical calculations, cannot develop to a high level until host egg densities are well above the economic threshold, *Trichogramma* is a major regulating mechanism for host insect populations. High parasitization rates late in the season are vitally important in limiting the host insects that can survive to the next season or that can move to alternate host crops grown successively in areas with long growing seasons.

Low host egg densities, low parasite densities, searching behavioral characteristics of parasites, and the expanding host egg environment limit the population buildup of *Trichogramma* and its parasitism in nature. Consequently, we suggest two procedures for overcoming these inherent obstacles to efficient and practical use of *Trichogramma* in managing insect populations so they will remain below the economic density level: (1) Mass rear and inundate the total host insect environment with enough sustained releases of *Trichogramma* to achieve direct control; or (2) maintain, by sustained releases, a high artificial alternate host egg population on which the parasites can develop naturally to the levels necessary for effective control.

Hypothetical population models are presented to support the theory that if a host insect population is to be held below the economic threshold by *Trichogramma* parasitism, a major source of parasites must be provided other than those produced on the natural wild host population. Results obtained with hypothetical population models suggest that the release of parasites at 5,000 per acre per parasite generation is inadequate to achieve a high parasitization on rapidly growing field crops. Calculations are made to show that for reasonably effective control of the host insect, the parasites required per acre for each parasite generation should range between 12,000 and 50,000, depending on the type and growth stage of the crop.

The maintenance in nature of a high and constant artificial egg host density is suggested as another method of reversing the normal parasite-host insect density relationship. In other words, we propose that a high artificial host egg density be created in early host generations when the natural host egg density is usually still low. Various hypothetical population models are established to show that high parasite populations and high parasitization levels could be achieved and maintained by creating a high and constant host egg resource of about 30,000 eggs per acre per parasite generation. If such density is achieved before the natural host exceeds the economic threshold, enough parasites should develop naturally to assure high enough parasitization to maintain the host insect populations at subeconomic levels.

An integrated program is suggested that would use reared sterilized males to suppress reproduction in the natural female population while appropriately sterilized females deposited sterile eggs. Thus, the necessary artificial host egg resource would be provided for a natural buildup of *Trichogramma* to high population levels and, hence, to high levels of parasitization. Such a program would theoretically achieve population suppression by two noninteracting methods, thereby taking advantage of this integrated method of insect population suppression.

A test of the validity of the parameters established to appraise the relationship of *Tricho-*

gramma and its host insect was made by comparing theoretical parasitism in a hypothetical population of sugarcane borers versus the natural parasitism in a representative natural population observed by authorities working with the sugarcane borer and *Trichogramma*. The calculated trend of parasitism in the hypothetical population model closely agreed with the observed natural trend of parasitism. This close correlation further supports our conclusion that the factors governing the limitations and potentialities of *Trichogramma* as parasites of certain economically important lepidopterous insects, as postulated in this theoretical study, are valid in principle.

Appendix

For those interested in how the values for the tables were obtained, we include the following biomathematical formulas:

The mathematics of an uncontrolled population has been described many times in the literature.[1] [2] [3] The rate at which a population changes with respect to time is denoted mathematically by the derivative

$$\frac{dN}{dt}$$

where N stands for any number whatever and t stands for time. We are safe in assuming that this rate of change will depend on the number, N, already present in the area. Therefore

$$\frac{dN}{dt} = k\,N \qquad (1)$$

where k is simply a proportionality factor. Since k must depend on the number of births or eggs laid (b) and the number of deaths (d) in the population, k is a function of $(b - d)$. By integrating (1) over all time, we get the solution

$$N_t = N_0\,e^{kt} \qquad (2)$$

where N_t stands for the number in the population at time, t, and N_0 for the number in the population when $t = 0$.

Since we have specified that there is a fivefold increase from one generation to the next, then $N_t = (5)\ N_0$. Therefore from equation (2) we see that $5 = e^k$, since $t = 1$. Solving for k, we have

$$k = ln\ 5 = 0.693147181$$

and equation (2) can be written as

$$N_t = N_0\,e^{0.693t} \qquad (3)$$

The remaining computations are based on the following equation:

$$(\text{Parasite progeny})_{g+1} = 2E\,(1 - (0.5)^n) \qquad (4)$$

where E = number of eggs not found by parasites and $n = \frac{P_g}{5{,}000\ u}$ = searching factor; where P_g = number of searching parasites in generation g and u = searching units in environment.

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[1] ANDREWARTHA, H. G., and BIRCH, L. G. THE DISTRIBUTION AND ABUNDANCE OF ANIMALS. 782 pp. Univ. Chicago Press, Chicago, Ill. 1954.

[2] CHAPMAN, R. N. ANIMAL ECOLOGY. 464 pp. McGraw-Hill Book Co., Inc., New York. 1931.

[3] LOTKA, J. J. ELEMENTS OF MATHEMATICAL BIOLOGY. 460 pp. Dover Publications, Inc., New York. 1957.

The exponent n indicates that when the searching parasites number 5,000 and they search one unit of the environment, exactly 50 percent of the eggs will be missed. All the computations then depend on the solution of

$$q = (0.5)^n \qquad (5)$$

where q is the proportion of eggs not parasitized and n is as previously defined. We can solve equation (5) using logarithms:

$$ln\ q = \frac{P_g}{5{,}000\,u}\ ln\ (0.5) \qquad (6)$$

Once we have computed q, we get p, the proportion of eggs parasitized, from $p = (1 - q)$. This method of computation was used for all tables except table 4, where the solution of equation (6) for P_g was required for a given value of q.

Since we required $p = 0.8$, then $q = 0.2$. Therefore for any given value of u, P_g can be computed from the following equation:

$$\begin{aligned} P_g &= 5{,}000\ u\ \frac{ln\ (0.2)}{ln\ (0.5)} \\ &= u\,\frac{(5{,}000)\ (-1.60944)}{(-0.69315)} \\ &= u\ (11{,}609.6083) \end{aligned}$$

This calculation when rounded gives the results shown in table 4.

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